The role of communication in the foraging process of social bees

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Summary

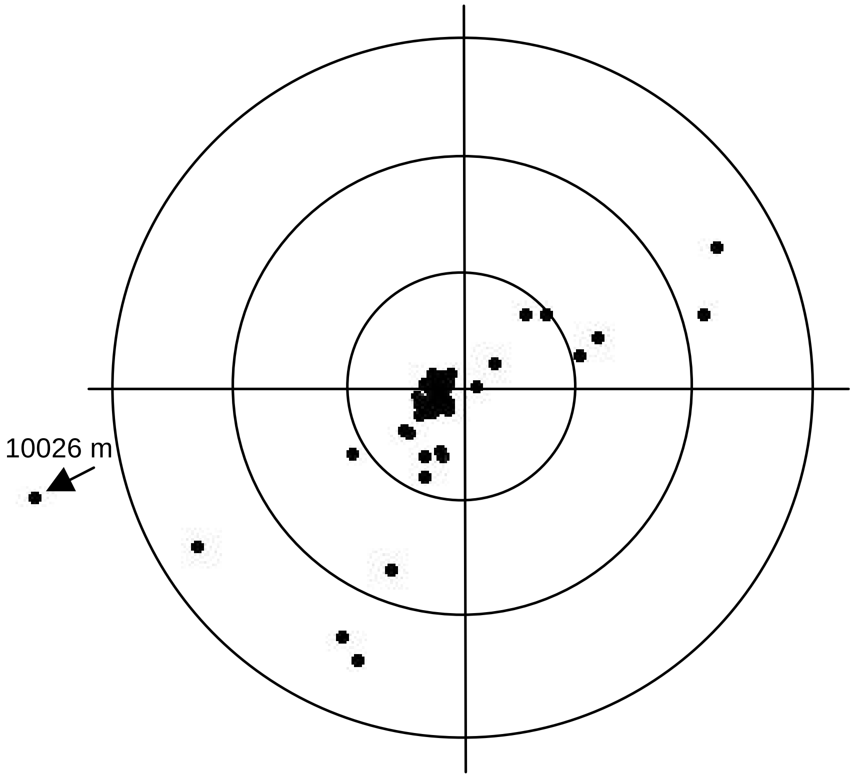


Fig. 0.1: Honey bees are able to tell their nestmates about food sources over 10 km from the hive (shown is a map constructed from analysis of waggle dances of an Apis mellifera hive in the Nilgiris, India; circles are at 1 km intervals). By communicating distance and direction to nestmates, honey bees probably transfer more information at the nest than any other social bee. This is one way of comparing communication systems in social bees: to look at information content of the signals.

0.1 english

In the various groups of social bees, different systems of communication about food sources occur. These communication systems are different solutions to a common problem of social insects: efficiently allocating the necessary number of workers first to the task of foraging and second to the most profitable food sources. The solution chosen by each species depends on the particular ecological circumstances as well as the evolutionary history of that species. For example, the outstanding difference between the bumble bee and the honey bee system is that honey bees can communicate the location of profitable food sources to nestmates, which bumble bees cannot. To identify possible selection pressures that could explain this difference, I have quantified the benefits of communicating location in honey bees. I show that these strongly depend on the habitat, and that communicating location might not benefit bees in temperate habitats. This could be due to the differing spatial distributions of resources in different habitats, in particular between temperate and tropical regions. These distributions may be the reason why the mostly temperate-living bumble bees have never evolved a communication system that allows them to transfer information on location of food sources, whereas most tropical social bees (all honey bees and many stingless bees) are able to recruit nestmates to specific points in their foraging range.

Nevertheless, I show that in bumble bees the allocation of workers to foraging is also regulated by communication. Successful foragers distribute in the nest a pheromone which alerts other bees to the presence of food. This pheromone stems from a tergite gland, the function of which had not been identified previously. Usage of a pheromone in the nest to alert other individuals to forage has not been described in other social insects, and might constitute a new mode of communicating about food sources. The signal might be modulated depending on the quality of the food source. Bees in the nest sample the nectar that has been brought into the nest. Their decision whether to go out and forage depends not only on the pheromone signal, but also on the quality of the nectar they have sampled. In this way, foraging activity of a bumble bee colony is adjusted to foraging conditions, which means most bees are allocated to foraging only if high-quality food sources are available. In addition, foraging activity is adjusted to the amount of food already stored. In a colony with full honeypots, no new bees are allocated to foraging. These results help us understand how the allocation of workers to the task of food collection is regulated according to external and internal nest conditions in bumble bees.

0.2 german

Innerhalb der sozialen Bienen tritt eine Vielzahl verschiedender Systeme zur Kommunikation über Futterquellen auf. Diese Kommunikationssysteme sind verschiedene Lösungen eines Problems, mit dem alle sozialen Insekten konfrontiert sind: wie lässt sich regulieren, daß die benötigte Anzahl an Arbeiterinnen der Aufgabe des Futtersammelns, und dazu möglichst den besten vorhandenen Futterquellen, zugeteilt wird? Die von einer Art gewählte Lösung hängt von den speziellen ökologischen Rahmenbedingungen, aber auch von der evolutionären Vorgeschichte dieser Art ab. Ein herausragender Unterschied zwischen Honigbienen und Hummeln beispielsweise ist, daß Honigbienen den Ort einer profitablen Futterquelle ihren Nestgenossinnen mitteilen können, was Hummeln nicht tun. Um Selektionsdrücke zu identifizieren, die diesen Unterschied bewirken könnten, habe ich den Nutzen einer solchen Kommunikation quantifiziert. Es zeigt sich, daß dieser Nutzen stark vom Habitat der Bienen abhängt, und daß Kommunikation über den Ort von Futterquellen in temperaten Habitaten unter Umständen keine Vorteile für Bienen bedeutet. Das könnte daran liegen, daß sich die räumliche Verteilung der Ressourcen zwischen Habitaten, und besonders zwischen temperaten Gebieten und den Tropen, unterscheidet. Dieser Umstand könnte der Grund dafür sein, daß die hauptsächlich in temperaten Regionen lebenden Hummeln nie eine Methode zur Kommunikation von Information über den Ort von Futterquellen evolviert haben, während die meisten tropischen sozialen Bienenarten (alle Honigbienen und viele stachellose Bienen) Nestgenossinnen zu bestimmten Orten rekrutieren können.

Jedoch stellte sich in meinen Experimenten heraus, daß auch bei Hummeln die Zuordnung von Arbeiterinnen zur Aufgabe des Futtersammelns über Kommunikation reguliert wird. Erfolgreiche Sammlerinnen produzieren ein Pheromon, welches andere Hummeln auf die Präsenz einer Futterquelle aufmerksam macht. Dieses Pheromon stammt aus einer Tergaldrüse am Abdomen, deren Funktion bisher nicht bekannt war. Die Benutzung eines Pheromons zur

Kommunikation über Futterquellen im Nest ist von anderen sozialen Insekten bisher nicht bekannt. Das Pheromonsignal wird vermutlich abhängig von der Qualität der Futterquelle moduliert. Hummeln im Nest kosten außerdem den neu eingetragenen Nektar. Ihre Entscheidung auszufliegen und zu sammeln ist sowohl vom Pheromonsignal als auch von der Qualität des von ihnen gekosteten Nektars abhängig. Die Sammelaktivität der Hummelkolonie wird damit an die Sammelbedingungen angepasst – nur wenn profitable Futterquellen vorhanden sind, werden viele Sammlerinnen aktiviert. Zusätzlich hängt die Sammelaktivität von der Vorratssituation im Stock ab. Sind die Honigtöpfe gefüllt, werden keine neuen Arbeiterinnen zum Sammeln aktiviert. Diese Ergebnisse helfen uns zu verstehen, wie bei Hummeln die Anzahl der aktiven Sammlerinnen je nach den Bedingungen innerhalb und außerhalb der Kolonie reguliert wird.

Introduction

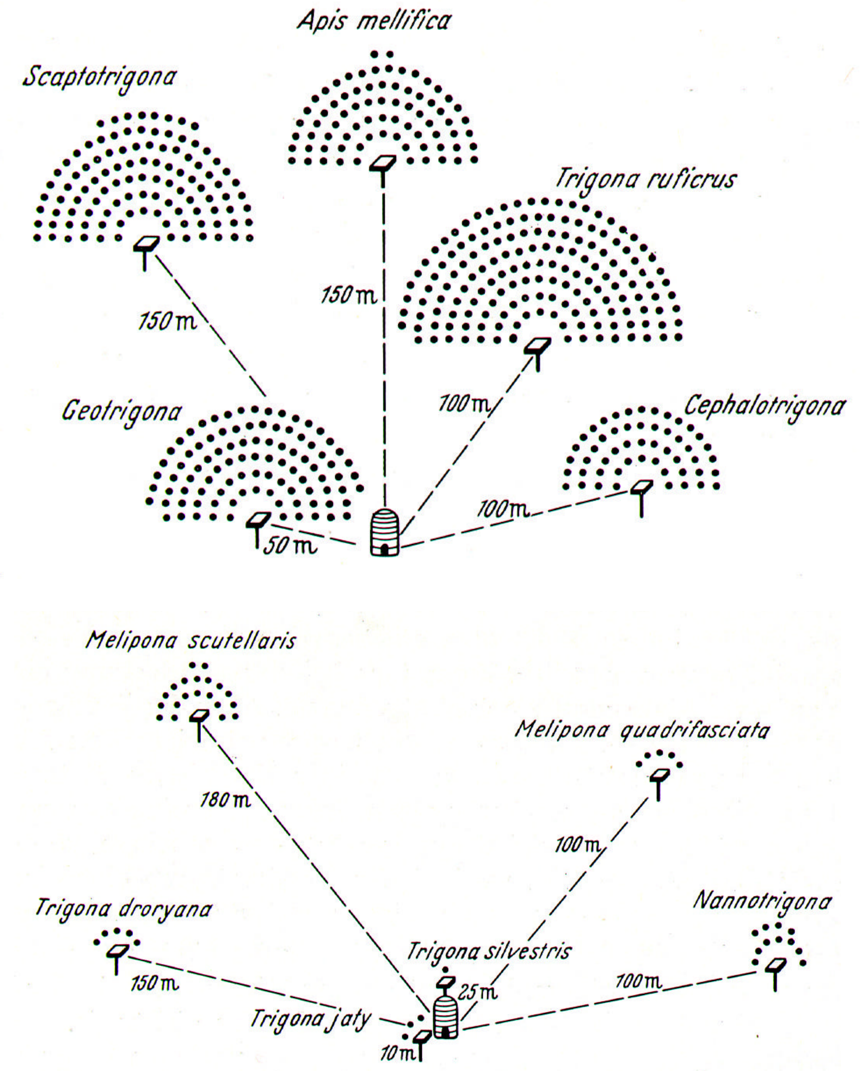


Fig. 1.1: Another way of comparing recruitment systems is the measurement of recruitment success, by counting the number of individuals arriving at an artificial food source that a few foragers have been trained to visit. However, one should keep in mind that the colony size differs between species from a few hundred, like in some Melipona, to 200 000 in Trigona ruficrus. The Apis mellifera colony in this experiment contained about 8000 bees. Shown here is the number of recruits (black circles) arriving at a feeder within 1 hour, while five foragers of the respective species were visiting the feeders (figure from Lindauer and Kerr 1960).

1 Introduction

When he wrote his book on the origin of species, Charles Darwin was worried that his theory, which was to alter the science of biology, would not be applicable to social insects (Darwin 1859). The social insects display such a high degree of cooperativeness, complexity and organization, that he considered them a serious threat to the theory of evolution by natural selection. General truisms about behavior in animals often seemed to be not so true for ants, bees, wasps, and termites. Instead of incessant competition between individuals, here apparently individuals sacrifice their labor and life for a common good. Instead of communicating to manipulate or mind-read others, which are often the functions of information transfer in other systems (Dawkins and Krebs 1978), social insect workers communicate lots of valuable information to others, investing time and energy apparently without direct benefit to themselves. Darwin was finally convinced that even the extraordinary cooperativeness in social insects could be explained by his theory of evolution through natural selection (Darwin 1859) by the argument that not only an individual's own offspring, but also its other relatives, such as brothers and sisters, can carry its inherited characters to the next generation. This argument was further elaborated in William

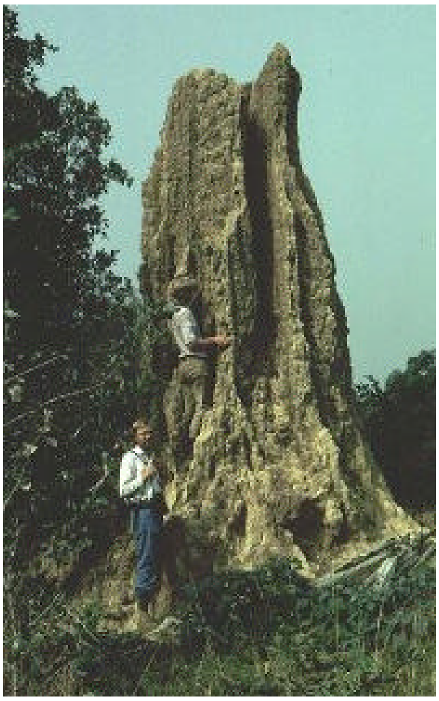


Fig. 1.2: This picture of a termite nest was taken from a website that intended to prove that such structures could not be created by evolution but must be the result of divine creation (http://www.exchangedlife.com/Creation/african_macroterm.htm).

Hamilton's kin selection theory (Hamilton 1970), which allows the dynamics of social groups to be analysed in the same evolutionary terms that apply to all other species. Nevertheless, social insects remain a fascinating example of complexity emerging from the actions and interactions of many individuals. Collectively, they achieve some of the most impressive feats, such as building huge elaborate nests (like, for example, the nests of termites, which can rise up to 5 m above ground, Fig. 1.2, Lüscher 1961). Social insects as groups also seem to be able to find the solution to complex geometrical problems, as in the construction of honey bee combs (Fig. 1.3). The hexagonal pattern of the honey cells is the mathematically perfect solution for the storage of a maximum amount of honey while using as little wax as possible (Aristotle 1868, Darwin 1859). Social insect colonies also often have foraging ranges the diameter of which is over a million times the body size of the individuals (as is known from honey bees; Seeley 1995). And in addition to this, social insects are remarkably successful ecologically: the biomass of ants and termites in a tropical forest can contribute up to a third to the total animal biomass, and worldwide the social insects might constitute half of the total insect biomass, although they only account for two percent of the insect species (Hölldobler and Wilson 1994).

Because of this success, social insect colonies have become models for groups of our own species which try to optimize collective performance, be they companies, societies, or traffic flow (Möhring 1996, Nagel and Rasmussen 1992, Prietula et al. 1998). Even in technical applications, social insects and the organizational principles they use serve as model systems, because if a task can be achieved using multiple

Fig. 1.3: The arrangement of hexagonal cells in a honey bee comb is the best pattern of equal tiles completely filling a surface with the shortest total wall-length, i.e. the least wax material needed (figure from Bellmann, 1995).

independent but interacting units, this is often more flexible, more robust and more efficient than using one central control structure (Brooks and Flynn 1989, Parunak 1997). Examples for the usage of organizational principles of social insects in practical applications are plans for building structures using multiple small robots (Brooks et al. 1990), the allocation of tasks to machines in a car factory (Parunak 1996), and, in computer programming, multiple "software agents" which perform their own subtasks, are now often used (Parunak 1997, Weiss 1999).

One of the organizational principles common in social insects is the usage of the shared nest environment as a collective information pool. Individuals are able to collect only very limited, local information if on their own. But a social insect colony works as an information center (Brown 1988, Seeley 1985), where each individual can base its decisions on the information collected by many nestmates. This sometimes relies on sophisticated communication systems; but it can also rely on the fact that the actions of individuals in some way modify the nest environment, and other individuals can perceive these changes and react accordingly. Such changes, if they are by-products of other behaviors, are called cues, as opposed to signals that have specifically evolved for the purpose of communication (Seeley 1998). An example for a cue is the change in nectar stores caused by a foraging bumble bee (see Chapter 2.2). Unloading nectar into a honeypot is part of the foraging task, not primarily a signal to nestmates. Nevertheless, bees in the nest recognize that new nectar has been added to the stores and react by

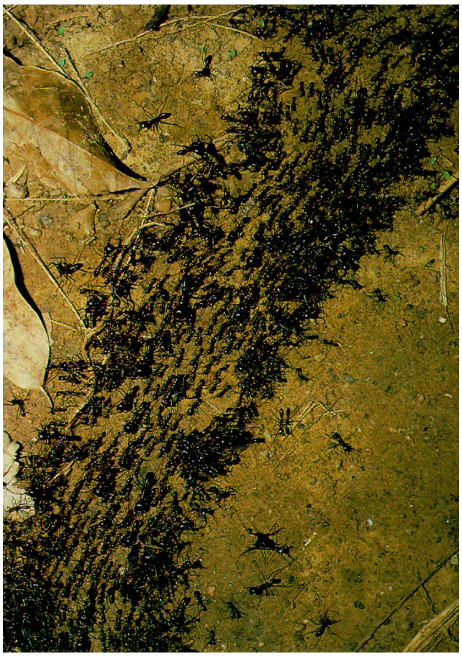


Fig. 1.4: A driver ant foraging raid (photograph from Gotwald 1995). Ants often use pheromone trails to organize their foraging activity.

starting to forage themselves. However, in the context of foraging often multiple kinds of signals and cues are important. Foraging is one of the most complex tasks faced by a social insect colony. A fraction of the colony's inhabitants have to collect food for all the others. A special difficulty, when comparing social to solitary insects, is that often a large area has to be covered in foraging to provide enough food for the large number of individuals living at the immobile colony, where solitary insects would just move to new foraging grounds once an area is depleted. Social insects in addition often have to collect enough food that it can be stored and is sufficient to take the whole society through periods of dearth, which further increases the necessary foraging range.

It is no wonder then that the different modes of communication about food sources are one of the most explored areas of social insect research. The mass communication occurring in ants at war (Hölldobler and Wilson 1990), the ant highways on pheromone trails observable in many a garden and kitchen, and the "dance-language" of honey bees (Frisch 1967) are well-known examples even to the non-biologist (Fig. 1.4). These are, however, only the examples which stand out. Even among closely related groups, a large amount of variation can occur in the modes of communication. For instance, the three major social bee groups within the Apinae, the honey bees, stingless bees, and bumble bees, show very different systems of organizing foraging activity and of communicating information about food sources to nestmates.

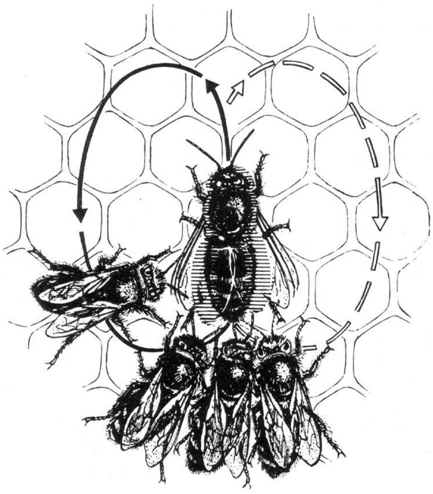


Fig. 1.5: The honey bee waggle dance. The "dancer", a successful forager who has returned to the hive, moves in a figure-eight-shaped pattern, wagging her abdomen while moving on a straight line in the middle. The dances are attended by often several other bees (figure from Frisch 1967).

The communication system of honey bees (tribe Apini), the waggle dance, is certainly the one most studied. All species of honey bees perform waggle dances (Frisch 1967, Dyer and Seeley 1989). These “dances” are stereotyped, repetitive motor patterns (Fig. 1.5). In the movements the distance as well as the direction of a food source is coded (Gould 1975, Polakoff 1998, Esch et al. 2001). In addition, foragers dance longer for better food sources, thus attracting more recruits (Seeley and Towne 1992). Potential recruits also get food samples from the foragers, and learn the scent of the food. They use this in addition to the dance information to localize the food source in the field (Frisch 1967, Wenner et al. 1969).

Such “waggle dances” do not occur in stingless bees (tribe Meliponini). Nevertheless, in some species of stingless bees, recruitment can be as efficient as in honey bees (Fig. 1.1 on p.10). In these cases, probably scent marks or even scent trails are used by foragers to guide recruits to the food source (Lindauer and Kerr 1960). Other stingless bee species seem to communicate

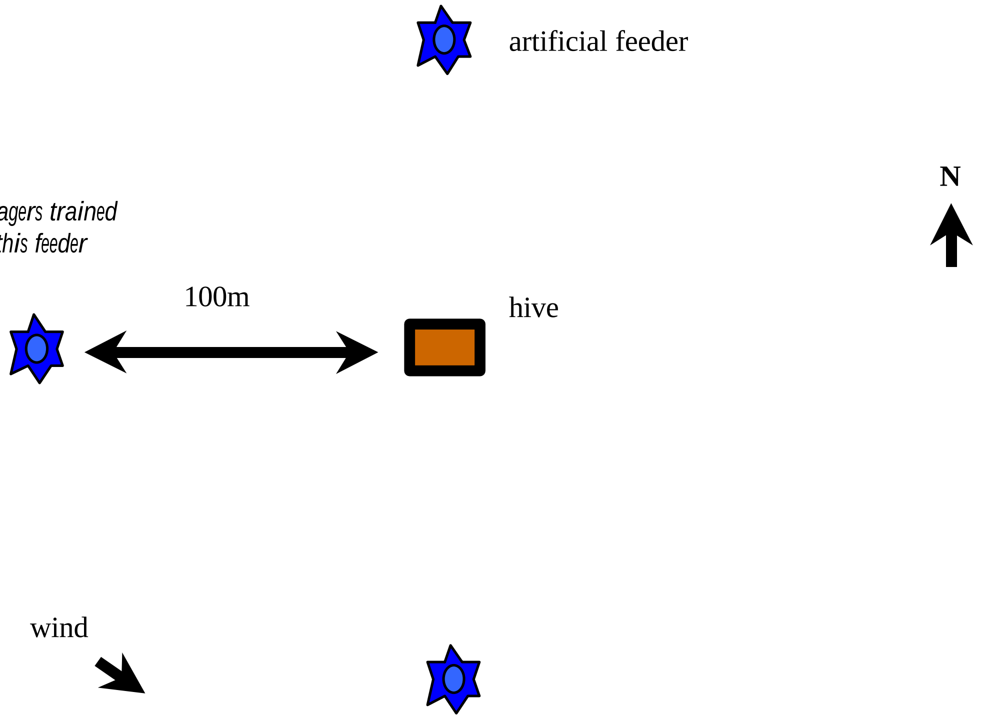


Fig. 1.6: To test for recruitment in bumble bees, two foragers were trained to visit a feeder 100 m west of the nest. Two identical feeders were set up at the same distance, but in other directions (north and south). The arrival of recruits was monitored at all feeders and all recruits were captured. The number of bees arriving was the same at all feeding stations - that means foragers were not able to selectively recruit nestmates to the feeder they are foraging from (experiment and figure from Dornhaus 1999b).

distance of food sources using acoustic signals in the nest (Nieh and Roubik 1995). In some species, however, the location of food sources is not communicated to recruits at all. Instead, foragers merely alert nestmates to the presence of food; these then search for the food source in all directions from the hive (Lindauer and Kerr 1960).

The third major group of eusocial bees, the bumble bees (tribe Bombini), have been studied very little in regard to their regulation of foraging activity in general, and in particular their methods of exchanging information about food sources (Dornhaus 1999b). It has been demonstrated that at least alerting by successful foragers, similar to stingless bees, is present in bumble bees (Dornhaus 1999). Information on the location of food sources is, however, not exchanged (Dornhaus and Chittka 1999; Fig. 1.6).

The communication systems used by different bee species thus differ in modalities, as well as in information content. Why is this so? Would bumble bee recruits, for example, not profit from getting information on location of food sources, just like honey bee recruits do? These questions point in a direction unexplored in the field of social insect research. Since it is easy to be impressed by the marvelous feats of insect societies, most studies

Fig. 1.7: Social carrying is a form of recruitment where a forager recruits only a single other individual: by carrying it. (from Hölldobler and Wilson 1994)

have been concerned with proximate questions, i.e. explaining how these feats are achieved. It is often stated how well adapted and successful the social insects are, although adaptivity of traits, in the sense of increased fitness in a particular environment (Reeve and Sherman 1993), is usually not measured. Variation in traits is often explained with plausible, but untested arguments, not the least because the characters in question are often hard to manipulate. For example, differing modes of communication in different ant species have been explained by referring to the resources used by the respective species (reviewed by Hölldobler and Wilson 1990). Some resources seem to make recruitment less worthwhile than others: ants using resources that are easily depleted or mobile, like insect prey, tend to use only tandem running or social carrying (where a forager recruits a single additional individual, Fig 1.7) or no communication at all. In contrast, ants using rich resource patches, like harvester ants collecting seeds, are more likely to employ mass communication. To test such an argument, one would have to compare foraging success on these different resources with various communication systems. This is what I have done in honey bees: measured foraging success in different environments with two different modes of communication.

The differences between communication systems used by social bees cannot be explained by the kind of food collected by them. All social bees forage for nectar and pollen, and although different species have slightly different preferences, the highly social species are usually generalists foraging on many different kinds of flowers (Waser et al. 1996). In chapter 2.1, I have explored one factor that might nevertheless create different selection pressures on communication systems in different species: spatial resource distribution. A simple technique allowed the manipulation of the communicated information and the measurement of foraging success under different conditions (see chapter 2.1). I found that bees living in different habitats benefit differently from communicating locations of food sources to nestmates. Selection may have favored location communication more in the originally tropical honey bees than in temperate bumble bees. The study however also shows that communication systems are not perfectly flexible, since honey bees today living in temperate habitats still do, and tropical bumble bees do not seem to use location communication (Esch 1967). If a species colonizes new habitats, adaptation to the new situation is not immediate, there might be evolutionary lag or other constraints influencing whether a theoretical fitness optimum is reached. This is important to consider when investigating variability in a behavioral character, such as a communication system.

Bumble bees do not communicate locations of food sources to nestmates. But this does not mean that they do not communicate in a foraging context at all or that they behave like solitary bees foraging solely by individual initiative (Heinrich 1979). Information about the presence and scent of food sources is transferred from foragers to nestmates, resulting in these bees becoming alerted and leaving the nest to search for food (Dornhaus and Chittka 1999).

In this study, I have investigated the mechanisms of this alerting signal. I discovered that both a direct signal, namely a pheromone from a tergite gland (chapter 2.3), and cues in the nest, namely changes in the nectar stores (chapter 2.2), play a role in this information transfer between successful foragers and other bees in the nest. The function of the tergite glands involved was so far undescribed in bumble bees. Usage of a pheromone in the nest to alert other individuals to forage has not been described in other social insects, and might constitute yet another mode of communicating about food sources. The distribution of an alerting signal in the bumble bee group and implications for the evolution of bee communication systems are discussed in chapter 2.2 and 2.6.

I was also able to show that information on the quality of food sources is passed from foragers to recruits (chapter 2.4). This means that bumble bees can base their decision to forage on the presence of high quality food sources, indicated to them both via cues in the nest and information they receive directly from foragers (chapter 2.4). In social insect communication systems, this kind of redundant information is not unusual. For example, the quality of food sources is expressed in the honey bee system in speed and vigor of the dance (Waddington 1982), temperature of the dancer (Stabentheiner and Hagmüller 1991), and recruits can also judge from food samples given to them (Seeley 1995). However, we do not know which of these information channels available are actually attended to by the recruits. Potentially recruits in honey bees do not judge dances based on any of these criteria but follow a randomly selected dance (Seeley and Towne 1992). Since foragers are more likely to dance and dance longer for better food sources, this is sufficient to enable the colony to choose the best food sources (Seeley and Towne 1992).

The decision to forage is, however, not only based on food availability. Bumble bees, unlike honey bees, do not accumulate large honey stores. They do not survive over the winter in temperate regions, and usually do not collect stores for more than a few days of unfavorable weather (Heinrich 1979 and pers. observ.). I show that if the colony's nectar stores are already well filled, no alerting takes place (chapter 2.5). This is different from nectar collection in honey bees, for example. Honey bees adjust their nectar foraging activity primarily to food availability, since the amount of honey they can collect before the winter is one of their main fitness limitations (Seeley 1985). Thus they do not stop foraging when they have accumulated a certain amount of honey. If there is no storage room left, they build new cells, and if more nectar is coming in than can be processed by nectar-receiver bees, more receiver bees are recruited by the tremble dance (Seeley 1995). Thus the way foraging activity is regulated, like mechanism and information content of recruitment signals, depends on the ecology and selection pressures acting on the respective species.

2 Projects

Why do honey bees dance?

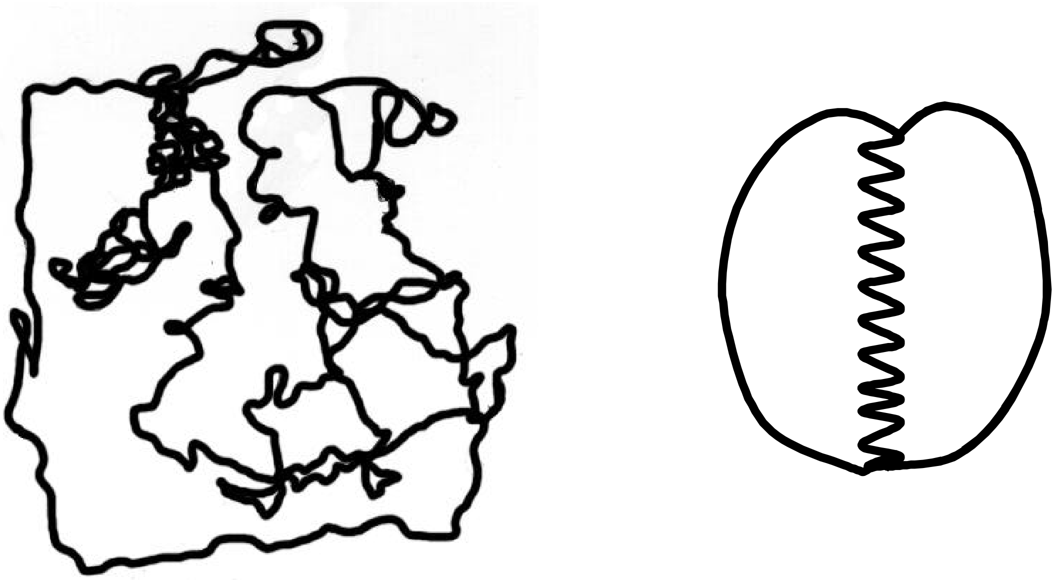


Fig. 2.1.1: Bumble bees also "dance": but their movements in the nest after discovering a rewarding food source (left) are not like the stereotyped, orderly dances of honey bees (right). The proximate explanation for this is that in honey bees, the movements themselves actually code information on location of food sources, whereas in bumble bees they do not, although they might serve to distribute a pheromone in the nest. But what is the ultimate reason for this difference? Why have bumble bees not invented a dance for transmitting information? Data from honey bees suggest that in fact bumble bee foragers, living in temperate habitats, might not profit from communicating locations of food sources.

2.1 Why do honey bees dance?

2.1.1 Abstract

Honey bees communicate the location of a rich food source using the waggle dance, which is regarded as one of the most intriguing communication systems in non-human animals. To examine the question which ecological circumstances would have favored its evolution, I quantified the benefits of this communication system under different conditions. Surprisingly, the waggle dance does not seem to provide any benefits to bees in temperate habitats - foraging success of colonies in which information transfer in the dances was prevented proved not to be different from that in unmanipulated colonies in two European locations. Then why do honey bees dance? In contrast to temperate locations, foraging success was substantially impaired in an Asian tropical forest if dance communication was disabled. A possible reason for this difference is a more patchy distribution of resources in the tropical forest. Combining published data and our own, I assessed the clustering of bee forage sites in a variety of habitats by evaluating the bees' dances. I found that indeed the sites indicated in the dances are more clustered in tropical than in temperate habitats. These findings support the hypothesis that the dance language is an adaptation to the tropical conditions under which the honey bees evolved. It also indicates that to understand the ecology and evolution of a behavioral trait, the species history as well as its current ecological conditions have to be considered.

2.1.2 Introduction

A honey bee forager, returning to the colony from a successful foraging trip, often performs a curious behavior: the waggle dance. During a waggle dance the bee walks in circles, periodically “wagging” her abdomen. This

Fig. 2.1.2: Artificial feeder on an empty field (at the Gieshügel near Würzburg) - the only food source available to bees in this area at close range in late summer.

behavior had already been observed in the 18th century and even then it was suspected that it might be related to communication (Spitzner, 1788). However, not until Karl von Frisch started investigating bee behavior was its meaning deciphered. Frisch showed that the waggle dance was a means of recruiting nestmates to rich food sources, and that the distance and direction of these food sources was coded in the pattern of the dance (Frisch 1967). Since then, a considerable body of literature has developed, partly concerned with details of how the communication takes place (e.g. Esch 1961, Tautz 1996, Rohrseitz and Tautz 1999) and partly with what became to be known as the “dance language controversy”. Mainly stimulated by Wenner and colleagues (e.g., Wenner 1967), Frisch’s original experiments were repeated in many variations to ascertain that bees were indeed able to use the abstract location information coded in their nestmates’ dances (e.g. Lindauer 1975, Gould 1976, Wenner et al. 1991, Polakoff 1998, Esch et al. 2001). It is now well established that information on the location of food sources is coded in the waggle dances, and that bees in the nest are able to use this information to find the food sources indicated.

Fig. 2.1.3: A floral distribution as can be found in Mediterranean habitats. Typically there are many flowers containing small nectar amounts (figure from Schönfelder and Schönfelder 1997).

All of the above studies were aimed at the understanding mechanisms of this unusual communication system. This was done under extremely artificial conditions; usually ad lib feeders with sugar solution were used (Fig. 2.1.2), which are extremely good, point-shaped resources, very unlike the scattered flowers of which bee foragers often visit hundreds before returning to the hive (Fig. 2.1.3). Only very few studies have been concerned with what bees do in their natural environment (Visscher and Seeley 1982, Seeley and Visscher 1988, Schneider 1989, Waddington et al. 1994, Beekman and Ratnieks 2000). We know that bees can use dance information, but how often do they use it? How important is the dance information for finding food sources? Why is it important? The plausible assumption that recruits find food sources faster if they know beforehand where these are was shown to be wrong in the only study that investigated this question (Seeley and Visscher 1988). The same study showed that recruits, who had used waggle dance information, carried larger loads back to the nest than

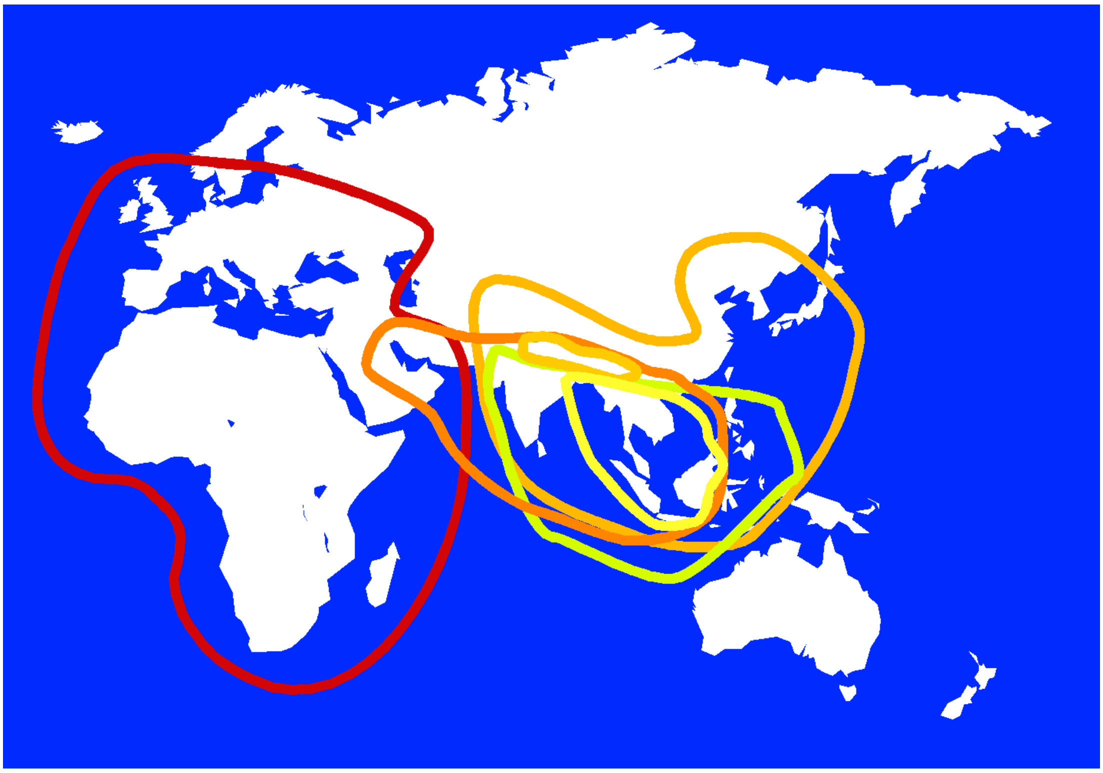


Fig. 2.1.4: Distribution of different honey bee species before the spread of A. mellifera *by man. (*A. mellifera*: red, other Apis species: yellow-orange colors)*

scouts, who had not used this information. However, this is bound to depend to a large degree on the ecological circumstances, specifically the spatial distribution and the temporal variability of resources available to the bees. If resources are homogenously distributed in space, there is no advantage in informing nestmates of the location of a profitable food source. The answers to the above questions might thus depend much on the honey bees' environment. The spatial distribution of resources is explored here by evaluating the locations indicated in the dances of bees, since such dances provide a map of forage sites which are of sufficient interest for the bees (Seeley and Visscher 1988).

I especially focus on the comparison between tropical and temperate habitats, because is is assumed that the waggle dance evolved in a tropical habitat. There are several species of honey bees (tribe Apini), all of which use the dance for recruitment (Frisch 1967). Most of these species are exclusively tropical (Fig. 2.1.4), indicating that their last common ancestor lived in the Asian tropics and already used a waggle dance for communication not much different from the dances seen today (Dyer and Seeley 1989). Even though the dance evolved in a tropical environment, it was studied mostly in a species native to temperate habitats: *Apis mellifera*. *A. mellifera*, the European honey bee, is the species most often used in honey production. It is today cosmopolitan due to the activities of man, and occurs in a wide spectrum of habitats (Ruttner 1988). However, it is native to Europe (and secondarily has colonized Africa).

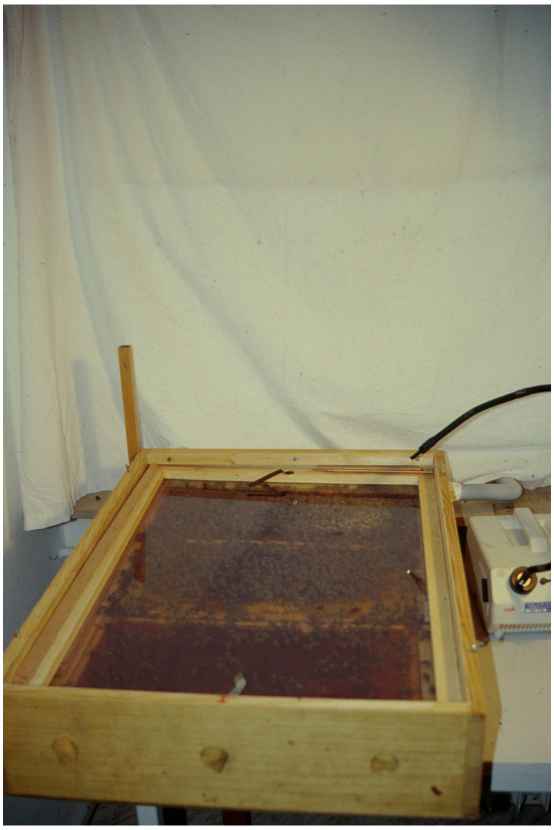
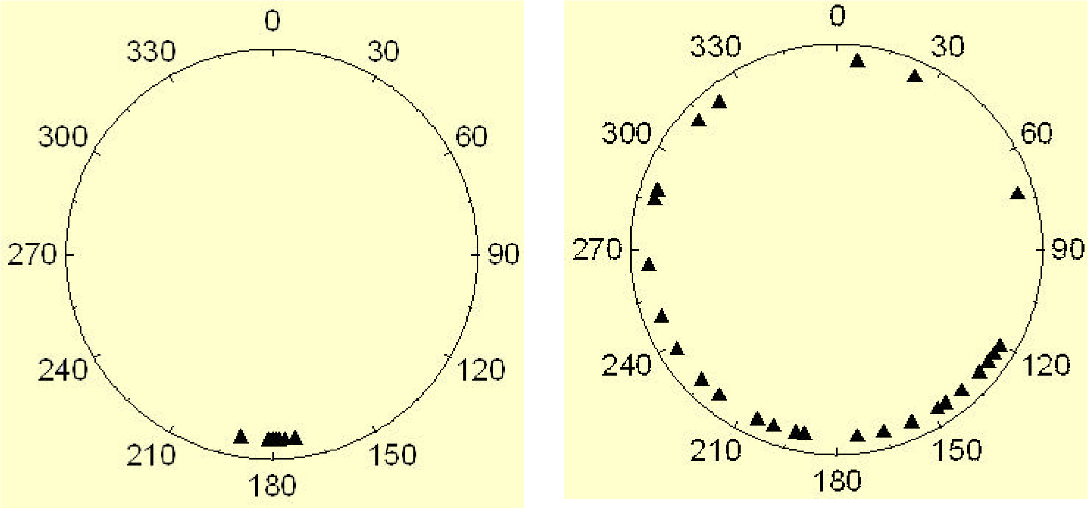


Fig. 2.1.5: A 3-frame observation hive in horizontal position. A cool light source illuminates the dance floor, such that bees can orient to the light instead to gravity. Apart from the artificial light source, there is only diffuse lighting. This is ensured by placing a screen over the window.



oriented dance **disoriented dance**

Fig. 2.1.6: In a normal waggle dance (left), waggle runs point in the same direction relative to gravity with little scatter (although scatter does vary, depending on the distance of the indicated food source). In a disoriented dance on a horizontal surface however, waggle runs point in random directions (right).

We have investigated the benefits gained by bees through the waggle dance under relatively natural conditions. This was done by quantifying foraging success while bees were prevented from communicating resource locations. Specifically, we could show that the foraging success on the colony level in one habitat (tropical forest) depended on whether bees were able to communicate location of food sources to nestmates, whereas in two other habitats it did not.

2.1.3 Materials and Methods

To prevent bees from exchanging information on food location, I used a simple trick. In the dark hive, the angle of the dance relative to the direction of gravity on the vertical comb indicates the direction of food relative to the azimuth of the sun (Frisch 1967). Tilting the combs into a horizontal position eliminates the possibility to use gravity as a reference (Fig. 2.1.5). Bees then perform dances in random directions, so that the dances lose their spatial information (Frisch 1967). Recruits then have to rely on cues outside the hive, such as scent marks, to find food sources (Kirchner and Grasser 1998). However, if bees are offered direct view of the sun or polarized skylight, oriented and functional dances are again performed even on a horizontal surface (Frisch 1967). I nevertheless performed a control experiment, in which the dance directions were measured in horizontal hives (Fig. 2.1.6), and differences in recruitment success for artificial food sources were demonstrated (chapter 2.7).

I compared the foraging success of colonies with and without location communication in two temperate locations representative of the present distribution of European honey bees, (*Apis mellifera*) and one tropical location representative of the habitats where the honey bees' dance evolved. The habitats tested were a Mediterranean shrubland habitat in the Sierra Espadán Nature Reserve, Spain, a Central European site near Würzburg, Germany, where agricultural land is mixed with natural meadows, and a dry deciduous forest in Bandipur Biosphere Reserve, India. I placed two *Apis mellifera* hives with 10 horizontal combs and approx. 5000 workers in each of these locations. Hives had a window above the comb on which dances were performed; by covering or uncovering the window I controlled whether bees were able to perform oriented dances. The colonies were switched from oriented to disoriented dancing every two days. Foraging success was assessed by using the daily weight changes of hives, which mostly reflect nectar intake (Seeley 1995). As a control for disturbing effects of the horizontal position of the combs *per se*, foraging success was also measured in the hives while they were undisturbed (with vertical combs) for the colonies used in the experiment in India.

Experiments were performed in spring in the temperate habitats and in the dry season in the tropical habitat. To test for seasonal effects, I repeated the same experiment with two 3-comb hives monitored over the entire foraging season from May to September in the central European location.

If no differences in foraging success are found between days on which bees were able to use the waggle dance to communicate location and days on which they were not, this could potentially be due to the fact that bees compensate lower per-trip intake rates by making more trips per bee or dispatching more bees as foragers. To control for such effects of total number of foraging trips, I measured the number of bees leaving the hive per time interval (the colony's ”activity”) on different days. Activity was measured for 5 minutes at 11 am, 2 pm and 5 pm for the hives in the experiment run in Spain; in the experiment run in India, activity was measured for 5 min every hour from 6 am to 6 pm for each hive.

One explanation for differential effects of preventing bees from communicating in different habitats is different spatial distribution of resources (see Discussion). Since mapping the actual resource distribution in the bees' foraging range (approx. 100 km^2) was impossible, I used the information that the bees themselves give us on the locations where they forage, by analyzing their waggle dances. In the Indian location all dances occurring on the first frame of an undisturbed beehive were videotaped for 5 min every hour from 6 am to 6 pm on 10 days during the experimental period. The direction of the waggle runs was measured for each dance and translated into the corresponding compass direction using a table of the sun's position calibrated to the location and time of year (provided by A. Wittman of the Observatory of Göttingen University). The time per dance circuit was calculated by measuring the time needed to perform at least 5 waggle runs. The average number of dances recorded and analyzed in this way was 31 per day. Time per dance circuit (T) was transformed into a distance from the hive (D) using the formula

$$D=89.695-345.256*T+228.224*T^2-10.951*T^3$$

(Waddington et al. 1994). This method has been used previously to create forage maps of honey bees (Beekman and Ratnieks 2000, Schneider 1989, Visscher and Seeley 1982, Waddington et al. 1994). To see if the degree of patchiness varied between different habitats, our maps and the maps previously published were used to calculate the patchiness coefficient R (Clark and Evans 1954). A value of 1 for R indicates random distribution, lower values indicate clumping and higher values hyperdispersion (non-random distribution with maximized distances between neighbors). R is calculated as the relation of observed mean nearest neighbor distances to expected nearest neighbor distances under conditions of random dispersion (for details on the calculation of R see Clark and Evans 1954). I calculated R for each day, using all dances analyzed in our data and all dances shown on the maps for published data, for the area around the hive within the radius of the farthest location danced for on that day.

2.1.4 Results

As in previous studies (Seeley 1995), there was high variation in daily weight changes of hives (from -630 g to +710 g). There was no significant difference in weight change, and thus foraging success, between days with or without oriented dancing in the temperate habitats (median weight changes of all hives were 0 g vs. -40 g in the central European and -60 g vs. -75 g in the Mediterranean habitat; p>0.1 in both cases, Kolmogorov-Smirnov-Test, n=44 and n=42). Neither was an effect of eliminating dance information found in the 3-comb hives monitored over the entire foraging season (p>0.1, n=187). Thus, foraging success in the temperate habitats was not significantly lower even if bees were not able to communicate information on the location of profitable food sources via the waggle dance. It cannot be fully excluded that the waggle dance does provide benefits

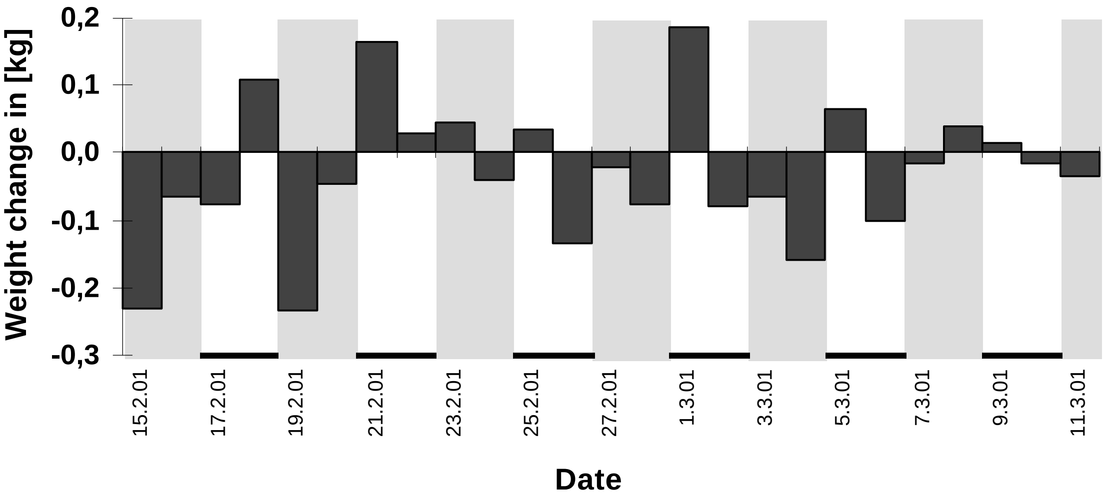


Fig. 2.1.7: Example of weight changes of one hive in the tropical forest (shaded areas mark periods with disoriented dances). There is high day-to-day variability in nectar intake of the colony. The most successful foraging days are always within periods with oriented dances, which probably means that high-quality food sources could only be exploited efficiently if location communication was possible.

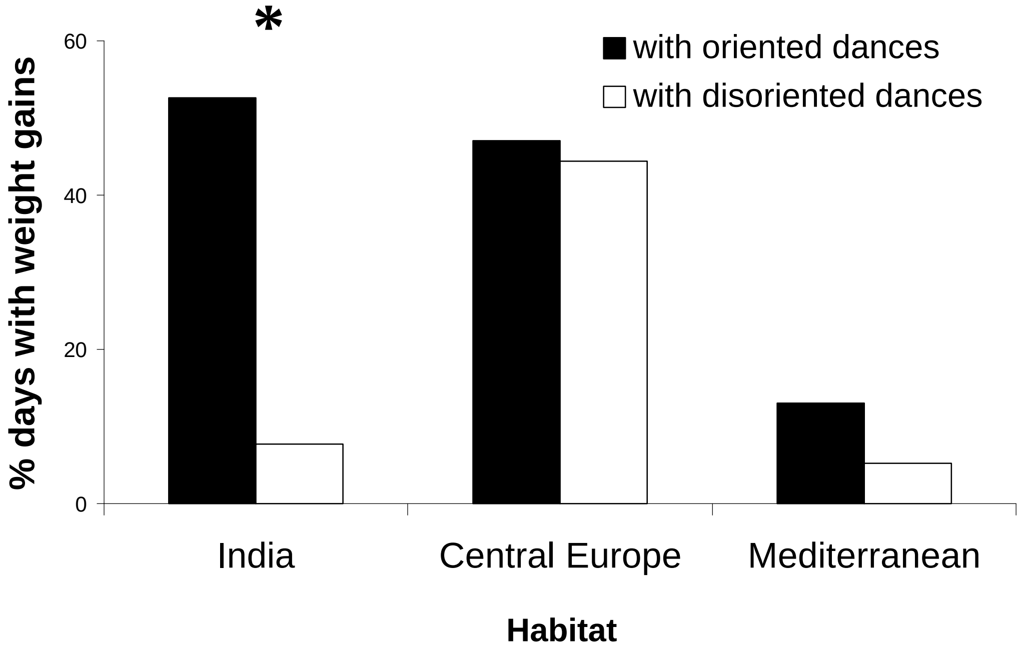


Fig. 2.1.8: Relative frequency of weight gain days in colonies with and without ability to communicate location of food sources in waggle dances. A significant effect of dance manipulation was found in the tropical habitat, where without dance communication, colonies rarely ever gained weight. No so 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).

to the bees, but either only very rarely or such small increases in foraging success, that these were not detectable with our sample size.

This was not the case in the tropical habitat. Foraging success there was significantly increased with functioning communication: median weight change was +5 g on days with oriented dances compared to -65 g on days when location communication was disrupted ($p<0.025$, $n=45$, Fig. 2.1.7). This means that eliminating the information content of the dance reduced the number of successful foraging days (with weight gains) to one seventh (Fig. 2.1.8). I found no significant difference in foraging success between days with oriented dances on horizontal combs and days when combs were in their natural vertical position ($p>0.1$, $n=28$).

The flight activity of the colonies did not depend on the manipulation performed. In the experiment in Spain the median number of bees leaving the hive in the 15 min measured was 161 on days with, and 119 on days without oriented dancing ($p=0.92$, $n=42$, Mann-Whitney-U-Test). For the experiment in India, the median number of bees leaving the hive in the 60 min of measurement per day was also not significantly different between days with and without oriented dancing (medians were 759 and 699, p=0.89, n=24, Mann-Whitney-U-Test). So the colonies did not react to the dance manipulation by making more or fewer foraging trips.

In the temperate habitat in Spain, there was no correlation between flight activity and weight change (p=0.20 and p=0.37 on days of disoriented and oriented dancing, respectively, n=17 and 21, Spearman R=-0.3 and -0.2). In the tropical habitat, where foraging success was influenced by the bees' ability to communicate, the colony's activity significantly correlated with the change in hive weight if bees were able to communicate location (p<0.005, n=13, Spearman R=0.74), indicating that in more trips, more

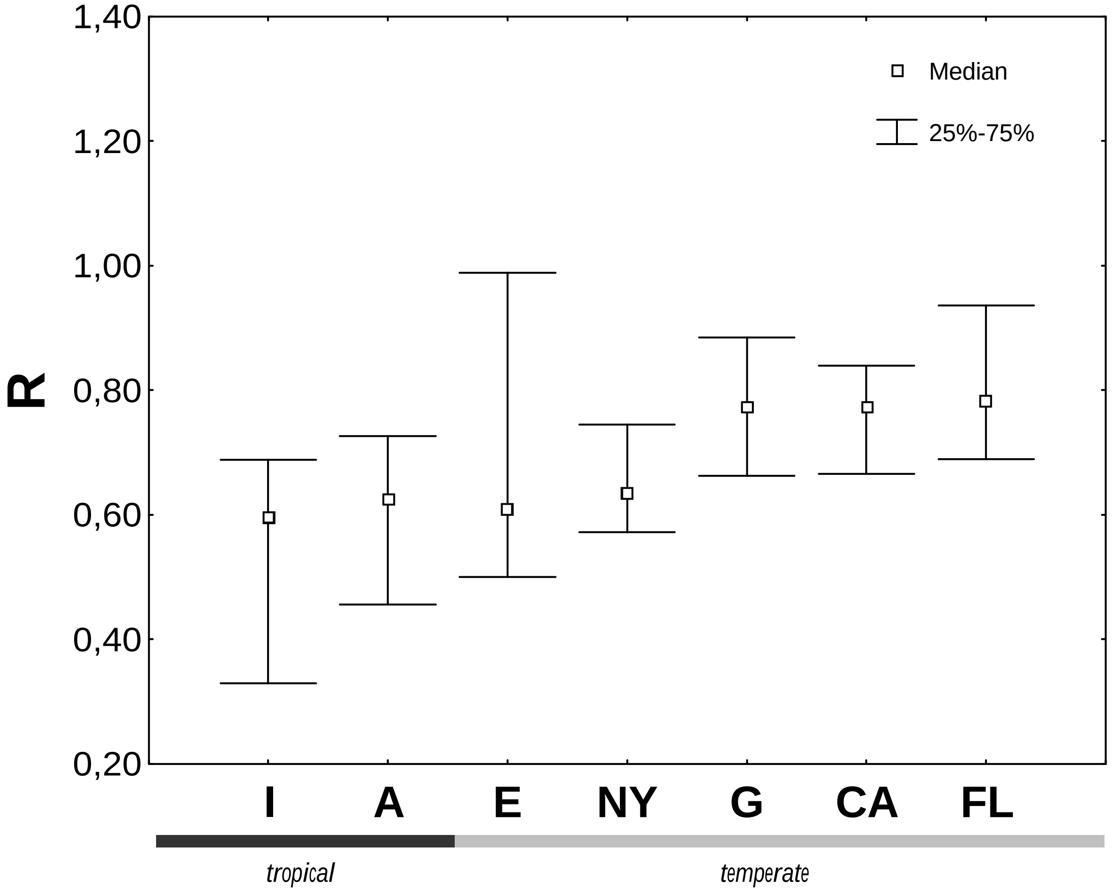


Fig. 2.1.9: In different habitats, the resources indicated by bees in their dances show different degrees of clustering. Temperate habitats tend to show more randomly distributed dances, reflected in values of R closer to 1. (Shown are I: India; A: Africa; E: England; NY, FL, CA: USA; G: Germany.)

food is collected. However, if bees were prevented from communicating location, there is no such correlation between activity and the colony's harvest ($p=0.44$, $n=11$, Spearman $R=0.26$). This may reflect that individual nectar loads in the tropical habitat vary less with functioning communication, because most foragers are allocated to good food sources, whereas without such communication, nectar loads vary widely, depending on the quality of the resources discovered by each individual. Only in the former case could a close connection between number of trips made and total nectar intake of the colony be expected.

The video analysis of waggle dances showed that bees in the tropical habitat were foraging up to 10 km from the hive, but most of the dances indicated sources much closer to the colony (Fig. 0.1, p. 5). The median distance indicated was 462 m. The average patchiness coefficient R was 0.53 (s.d. 0.22), indicating a high deviation from a random distribution. Patchiness is significantly higher (indicated by lower values of R) in the tropical (Africa, Schneider 1989, and India, this study) compared to the temperate (Beekman and Ratnieks 2000, Visscher and Seeley 1982, Waddington et al. 1994) habitats ($p<0.01$, $n=58$, Mann-Whitney-U-Test; Fig. 2.1.9).

2.1.5 Discussion

The spatial arrangement of floral food has a significant influence on the importance of the dance language for colony foraging success. I showed that under some conditions, foraging success is independent of the ability to communicate locations of food sources. To understand why communicating these locations benefits bees only in some situations, one may have to look at the spatial and temporal distribution of resources used by them. It should be expected that foragers profit most from location information if there are few but rich resource patches which are widely spaced. The analysis of maps constructed from the bees' waggle dances indicated that temperate habitats might tend to provide bees with more randomly dispersed food sources than tropical habitats. This is supported by what we know about the nature of food sources used by bees. In tropical forests, trees are the main source of food for bees (Whitehead 1968). These often offer millions of flowers (Fig. 2.1.10, Kress and Beach 1994) with large nectar amounts (Appanah 1990), but densities of trees in flower are often low (Clark 1994, Frankie et al. 1974, Janzen 1971), which creates an extremely patchy environment. In addition, tropical trees often flower only for a few days (Primack 1985). In such a situation, knowing where these few, quickly changing resource patches are, might be essential for efficient foraging by a bee colony. In temperate habitats, on the other hand, the bees' diet consists mainly of widely distributed herbs and shrubs (Heinrich 1979), since most trees are wind-pollinated (Whitehead 1968). Plant individuals have only small numbers of flowers with often minute nectar amounts (Heinrich 1976) and longer flowering times (Primack 1985). These factors may make location communication less worthwhile, if not unnecessary, in temperate habitats.

The results of this study support the hypothesis that the honey bee dance language is an adaptation to the tropical conditions under which the genus *Apis* diversified, and is no longer essential for efficient foraging in temperate habitats. When

Fig. 2.1.10: A tropical flowering tree at the experimental site in India ("Flame of the Forest").

food is less aggregated in space than in tropical forest, foraging by individual initiative, or communication only through floral scent and location-unspecific alerting signals (Dornhaus and Chittka 1999) may be as efficient as communication of location. In temperate habitats, the waggle dance may have been maintained because of such an alerting function or simply because it may not confer a selective disadvantage. This hypothesis is supported by the fact that there is a higher scatter in the direction indication in dances of temperate honey bees than in dances of tropical species (Towne and Gould 1988) or even dances of the same bees communicating locations of nest sites instead of food sources (Weidenmüller and Seeley 1999). Although previously interpreted as an adaptive character of the waggle dance (Towne and Gould 1988, Weidenmüller and Seeley 1999), this increased imprecision might also indicate reduced selection pressure. On the other hand, dances might be important only in extreme, but rare, situations in temperate habitats. For example, the resource that would conform most to the attributes "rich" and "rare" are other bee colonies which can be robbed of honey. Communicating the location of those might provide bees with an edge over competitors who are not able to recruit very many foragers to a point-shaped and rare resource. However, this would not explain the difference between temperate and tropical locations. We have only started to get answers to the question of why honey bees dance.

Food alert in *Bombus terrestris*: mechanisms and evolutionary implications

Fig. 2.2.1: Inside a nest of Bombus terrestris.

2.2 Food alert in *Bombus terrestris*: mechanisms and evolutionary implications

2.2.1 Abstract

It was recently shown that the return of a successful bumble bee forager stimulates nestmates to leave the nest and search for food. Here I 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 bumble bee recruitment behavior for the evolution of communication in bees are discussed.

2.2.2 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 honey bees, stingless bees and bumble bees - diverse communication systems have evolved, differing both in information transmitted and in mechanisms. In some species, such as in bumble bees (*Bombus terrestris*; Dornhaus and Chittka 1999) and some species of stingless bees, for example *Trigona angustula*, *T. iridipennis*; (Lindauer and Kerr 1960; Esch et al. 1965; Kerr 1969), communication involves just an alerting signal, which only conveys that food is now 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 honey bees (Lindauer 1956; Frisch 1967) there are sophisticated recruitment systems, enabling foragers to communicate not only odor and quality, but also the precise location of profitable food sources (Frisch 1967). These more advanced systems of information exchange make use of repetitive motor patterns, sounds, and substrate vibrations (Esch et al. 1965; Frisch 1967; Dreller and Kirchner 1993; Tautz 1996; Nieh 1998).

Bumble bees 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 get information on the quality of food sources through pheromone signals in the field. At the nest, bumble bees also get information on food availability and floral odor (Dornhaus and Chittka 1999). If one bee forages successfully, other bumble bees in the nest are induced to forage and search for food sources with the same odor as the food collected by the successful bee. The mechanism by which this happens has not been investigated until now. Here I present evidence that recruits get information on foraging conditions using at least two sources of information. The colony's nectar stores function as a cue by which bees can get information 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.

2.2.3 Materials and Methods

2.2.3.1 *General setup*

The experiments were conducted with laboratory colonies of *Bombus terrestris*. They contained a queen and 50 to 150 workers. The nest was contained in a wooden box (15 cm x 13 cm x 10 cm), which was connected to a foraging arena (50 cm x 70 cm x 30 cm) with a transparent plexiglas tube (15 cm; Fig. 2.2.2). The bees were fed by placing a feeding dish filled with 1:1 (volume) sucrose/water solution in the arena. For individual recognition, bumble bees were marked with numbered plastic tags glued to the thorax.

2.2.3.2 Forager behavior

To examine behavior of forager bees and thus the means by which successful foragers induce other bees to search for food, I 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. I quantified the duration of in-nest stays of foragers as a

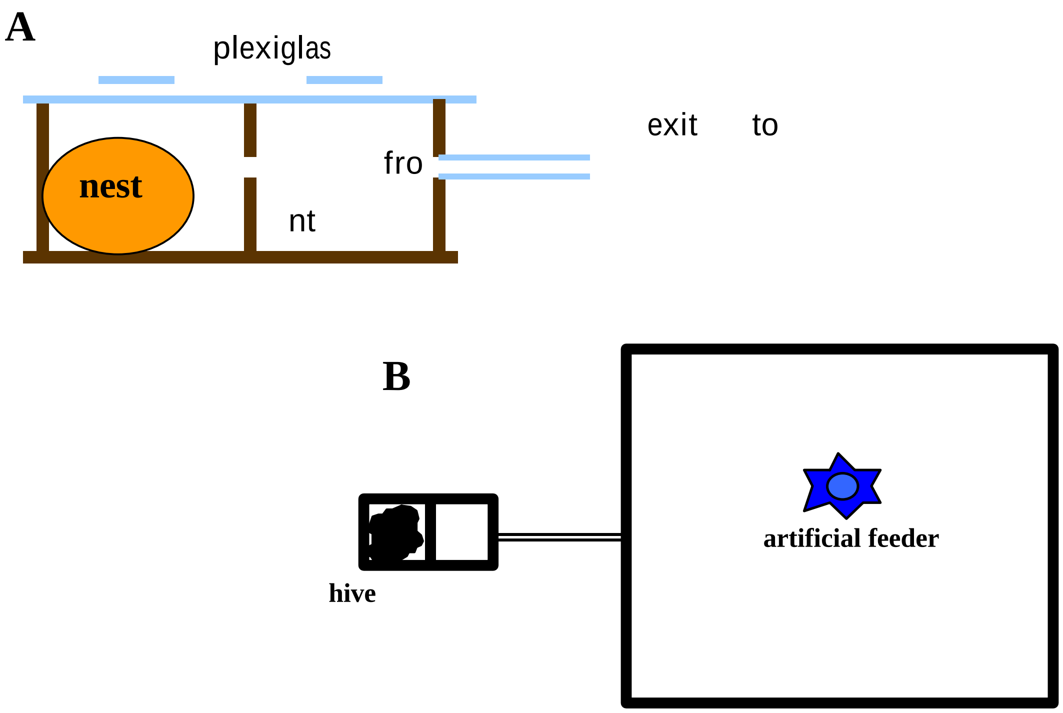


Fig. 2.2.2: Basic setup of bumble bee experiments. A nest box (A, viewed from the side), consisting of two chambers and with transparent plexiglas covers is connected to a foraging arena via a plexiglas tube (B, from top). Access to the arena can be regulated with paper shutters inserted into the tube.

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 its nestmates, I analyzed the nestmates' behavior, including their movement speed. I videotaped the bees' behavior in the nest when no food was being collected (resting colony) and after 30 minutes of food collection by a single forager (alerted colony). In both of these 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.

2.2.3.3 Possible signals

I was interested in the question of whether a forager's motor behavior (and the food she brings home) are necessary to alert nestmates, or whether other signals,

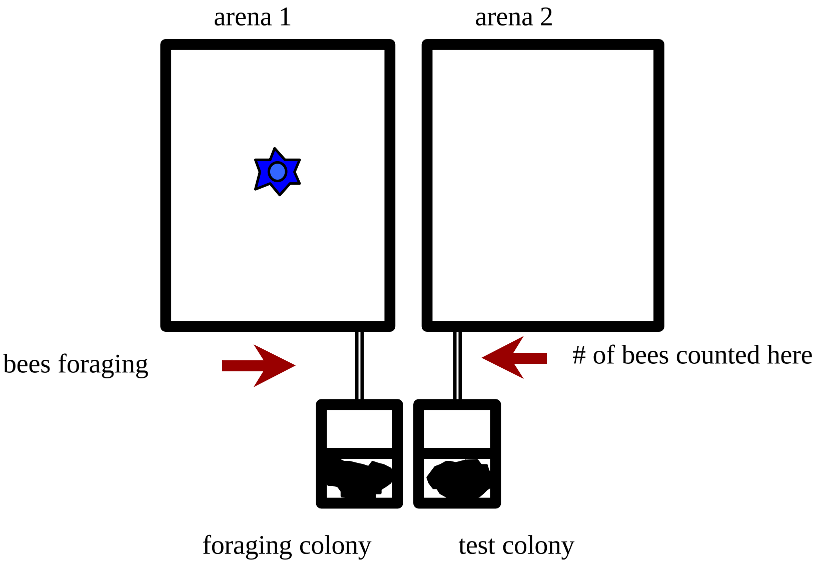


Fig. 2.2.3: To investigate possible signals transmitted between bees, two bumble bee colonies were set up next to each other. One colony was allowed to forage on an artificial feeder (foraging colony), and the activity of the other colony was monitored (test colony). Between the two nests was a double screen of wire mesh, so that air could pass from one nest box to the other.

such as substrate vibrations or pheromones might be essential. To this end, I 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 cm x 5 cm in the sides, covered with wire mesh. These windows faced each other so that the wire meshes were approximately 1 cm apart. Each of the nest boxes was connected to its own foraging arena to which bees had free access (Fig. 2.2.3). One colony was designated "test colony", the other "foraging colony". I tested whether successfully foraging bees in the latter had an effect on the activity of the test colony. Our measure for the number of bumble bees motivated to forage was the number of bees leaving the nest per unit time, in the following termed "activity level". It 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 constantly monitored.

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 would then collect food, and if they produced signals that could be transmitted through a wire mesh, the test colony would be expected to react by increased activity as well. To further investigate the modality of the potential signal, the experiment was repeated in another 10 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 - should not be substantially impaired compared to the condition without the plastic wrap.

2.2.3.4 Nectar stores

If nest bees react to successful foraging by other bees, this need not necessarily be related to signals emitted by these foragers. I 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. I 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 the increase of the colony's activity level takes approximately 30 min to develop, 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

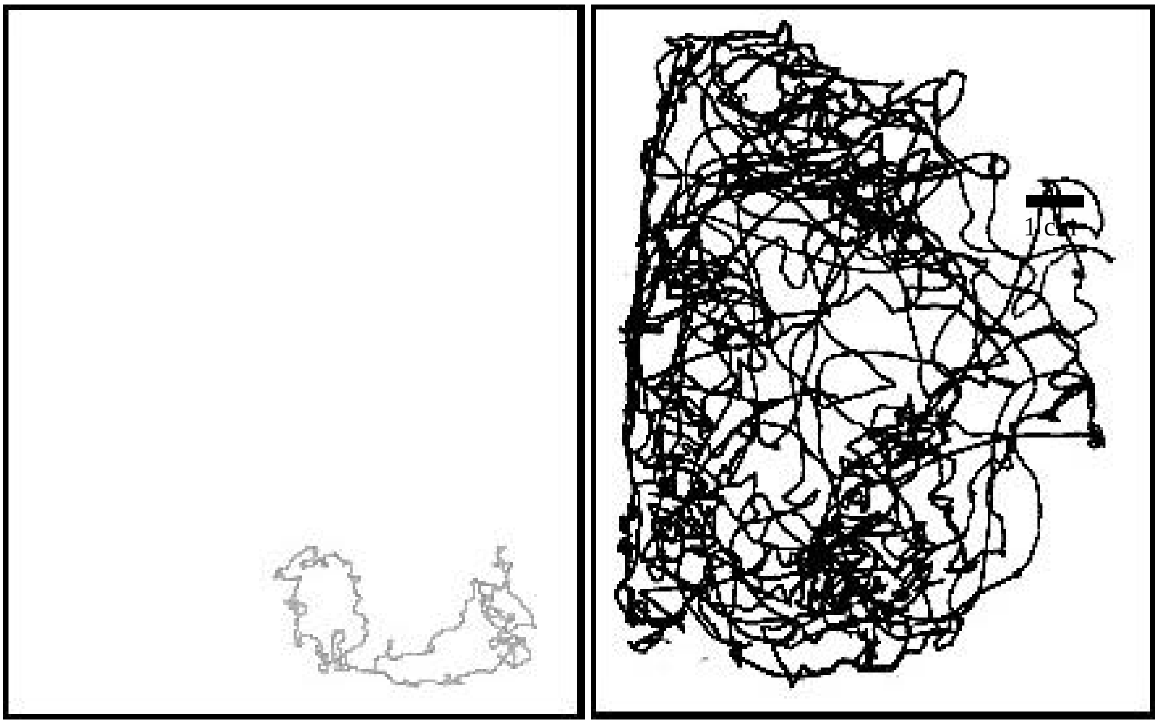


Fig. 2.2.4: Path of a forager in the nest box during an in-nest stay of 5 min (black line) and of a non-forager in the same time interval (gray line). The black frame indicates the size of the nest box. The nest itself covers most of this area, honeypots and brood cells being scattered across its surface. The entrance to the box is in the middle of the wall to the right.

pipette into the nest every 5 min, I conducted 10 test runs of a control experiment during which a pipette was inserted into the nest every 5 min but no sucrose solution was injected.

2.2.4 Results

2.2.4.1 Forager behavior

Successful bumble bee 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. 2.2.4), bumping into and climbing over other workers, and 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 honey bees. During these activities, bumble bee 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 ($p=0.001$, Wilcoxon-Test; $n=40$). 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 6th trip ($p=0.046$, Wilcoxon-Test; $n=6$). Probing might serve to find a suitable pot for unloading, but could also have the function of surveying nectar

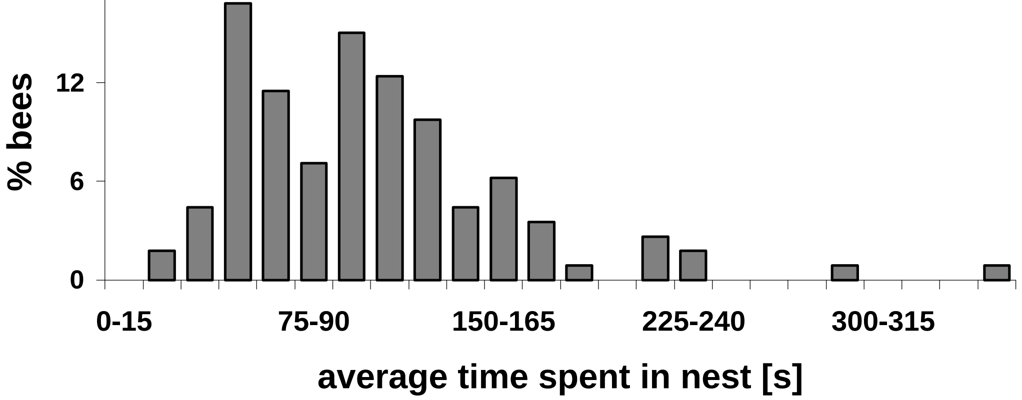


Fig. 2.2.5: Frequency distribution of average time spent in the nest among bees (n=114 bees).

stores. After unloading, a bee might spend several more minutes running around before she leaves for another trip to the food source. I 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 time spent in the nest was 105 ± 5.4 s (standard error), with large differences between individuals (Fig. 2.2.5). The time spent running in the nest between foraging bouts depended on how many bouts had already been completed (Fig. 2.2.6). 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 6th trip of the same foragers it was only 80 ± 5.4 s (p<0.00001, paired T-Test; n=104; data were normally distributed with p<0.01, Lilliefors-Test). Bees spent significantly more time after unloading than before, median time is 15 s (IQR=23 s) before versus 35 s (IQR=19 s) after unloading (p<0.001, Wilcoxon-Test; n=33 bees). The relation did not change with trip number (p=0.82, Wilcoxon-Test; n=32) but varies

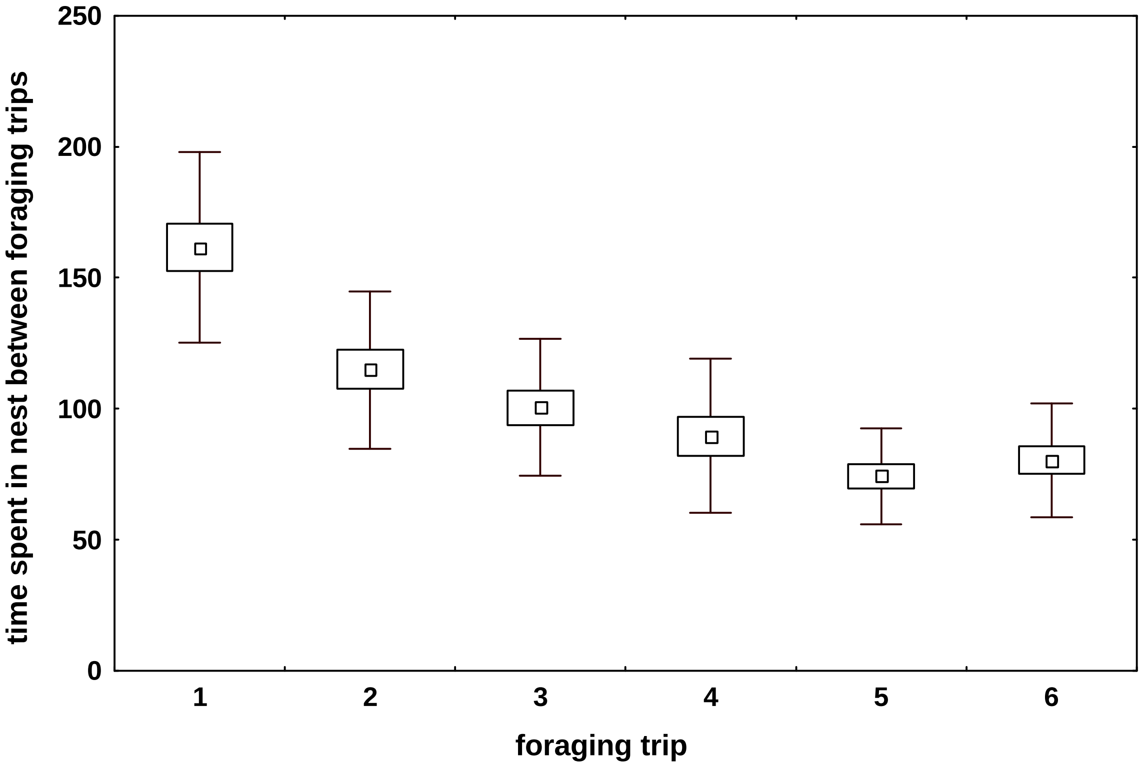


Fig. 2.2.6: Duration of in-nest stays of foragers depends on number of foraging trips completed (mean, standard error, range without extremes shown, time in [s]).

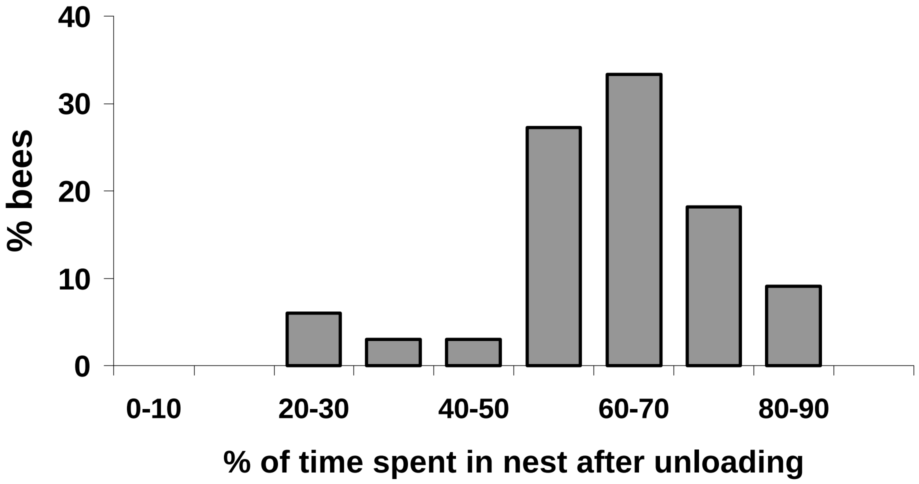


Fig. 2.2.7: Frequency distribution of time spent in the nest after unloading in % among bees (n=33 bees).

between bees (Fig. 2.2.7). The fact that foragers spend more time in the nest after than before unloading, while probing into pots takes 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 into communication. Often the bees could be seen fanning

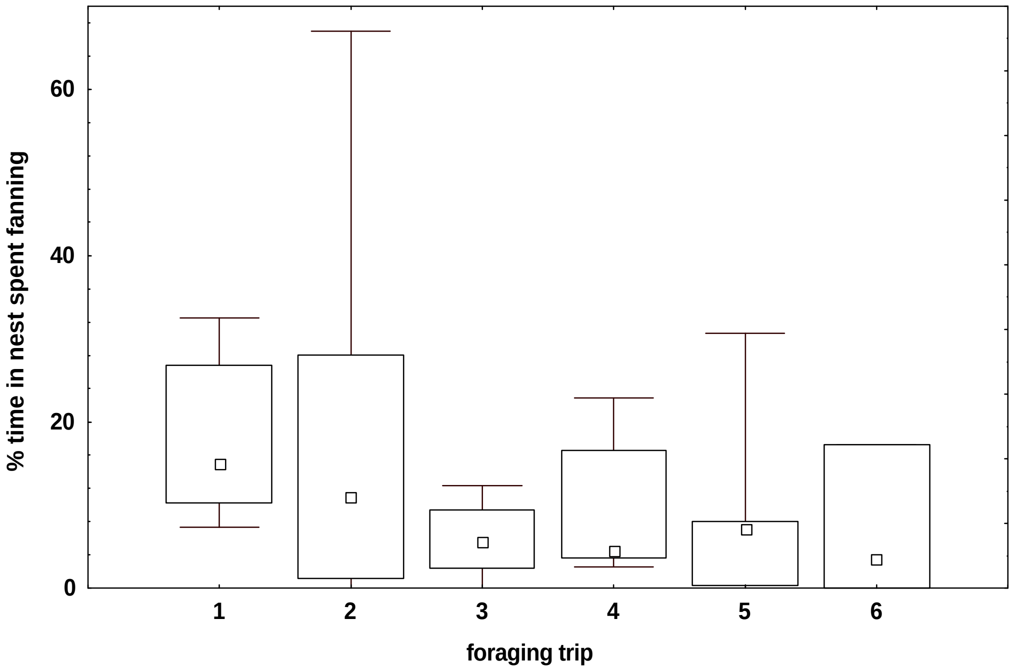


Fig. 2.2.8: Duration of fanning, in % of time spent in the nest, is dependent on number of foraging trips completed (median, IQR and range shown).

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 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 (p=0.021, Wilcoxon-Test; n=38). The fanning duration per time in nest also declined with trip number (p=0.028 for a comparison of 1st and 6th trip, Wilcoxon-Test; n=6; Fig. 2.2.8). Fanning behavior thus occurs when the forager spends more time in the nest.

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, other 4%). Since it was not directed mostly to one body part, it probably did not serve to deposit pheromone from a particular gland on the combs, at least it did not only serve this purpose. Grooming always took place after unloading (in a total of 42 filmed trips I never observed grooming before unloading). The function of grooming might be to remove wax accidentally picked up while bees probe honeypots.

I never observed extended interactions of the forager bee with other bees of the colony. Most contacts that occur appear to be accidental quick touching or pushing by the forager forcing its way around the nest. Other bees do not show immediate reactions to contacts. Median number of such contacts per time in the nest is 0.89 per s (IQR=0.30 per s), and does not change after unloading (p=0.77, Wilcoxon-Test; n=35). It declines slightly with trip number, from a median of 1.04 per s on the first to 0.86 per s on the 6th trip (p=0.015 for a comparison of the 1st and 2nd with the 5th and 6th trips, U-Test; n=13). Because there seem to be no deliberate or specific interactions between the forager and other bees, I suppose that no signal dependent on physical contact is involved in alerting 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 towards the hive exit. After a forager had collected food for 30 min (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 for them nothing outside the nest had 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 speed of bees in the nest after one bee had been foraging for 30 min (alerted colony) was 1.18 cm/s (p<0.00001, Mann-Whitney-U-Test; n=30). The forager's speed when in the nest after 30 min of foraging was 2.83 cm/s.

2.2.4.2 Possible signals

Active foragers had a positive influence on the foraging activity of others, 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. 2.2.9a; 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. 2.2.9b; 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 transmittable 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 impaired by the plastic wrap any more than by the wire meshes separating the two colonies.

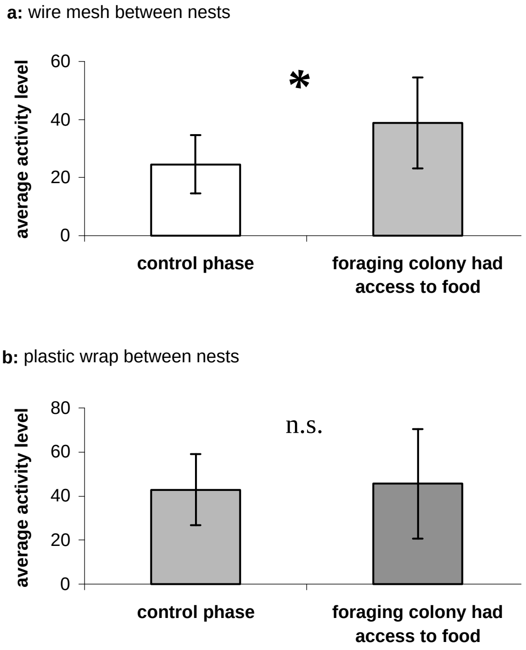


Fig. 2.2.9: Comparison of the average activity levels of the test colony during the control phases and the second half of the 60 min period in which the foraging colony was fed (: p<0.05; n.s.: not significant)..*

2.2.4.3 Nectar stores

By manipulating nectar stores, a higher activity level could be induced in the bumble bee colonies. The activity levels during periods in which sucrose solution was added to the colony's nectar stores were significantly higher than during control phases (Fig. 2.2.10a; 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. 2.2.10b; 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.

2.2.5 Discussion

In *Bombus terrestris*, the foraging activity at the colony level is adjusted via the activity of successful foragers and changes in the nectar stores. It is likely that the extensive movements of the active foragers cause at least some of the effect, but it is difficult to obtain conclusive evidence for this hypothesis: it is hard to mimic the

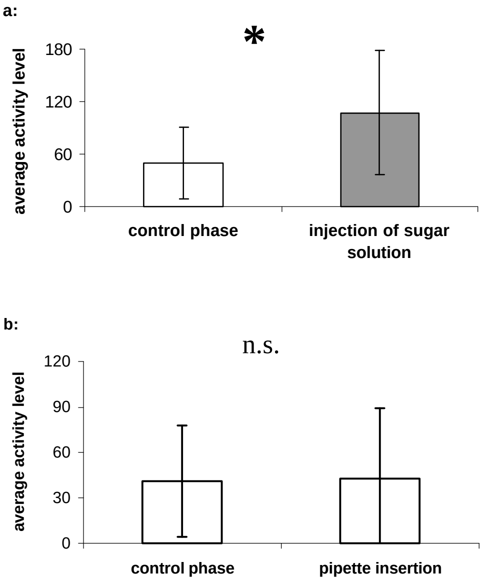


Fig. 2.2.10: Activity levels during the 30 min before (control phase) and the second half of the 60 min period in which sucrose solution was injected into the nest's honeypots.

movements of a bumble bee forager running across the nest, while eliminating other signals that it might emit during its runs within the nest. 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 unloaded. Often foragers groomed and fanned their wings after unloading. Fanning and fast running might directly or indirectly serve a communicative function, while grooming has probably only the function of cleaning the bee. My experiments provide evidence that recruits are activated even when direct mechanical contact between foragers and recruits is eliminated, as in our two-nest setup. Even though returning bumble bee foragers sometimes buzz their wings in characteristic short pulses (Heidelbach 1998), the mode of information transmission is unlikely to be airborne sound: such sounds are heard by bees only at extremely close distance (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 *Bombus terrestris* are, however, subterranean, so that within-nest activities take place in near-perfect darkness. Thus it is unlikely that visual cues 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 honey bees and stingless bees (Esch et al. 1965; Tautz 1996). Again, I 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, most likely a volatile pheromone, is released while foragers run around the nest, and running and fanning might serve in the efficient distribution of such a pheromone. 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 (chapter 2.3). 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 bumble bees used to pollinate crops in greenhouses.

The running activity of successful foragers declines with the number of completed foraging bouts. This coincides with an increase of foraging activity of recruits, which clearly makes sense: once the forager force of a colony has been activated, there is no longer any necessity to devote time to recruitment. It is unknown what feedback mechanism causes the foragers to spend less time recruiting. They 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 honey pots, its foragers reacted by leaving the nest to search for food. It is not known 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.

Before departing on a foraging trip, a bee can get 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, as shown in experiments performed previously (Fig. 1.6 on p. 15). Bumble bees of several subgenera (and from habitats temperate to tropical) have been shown to not recruit nestmates to particular places [*Bombus (s. str.) terrestris*; *B. (Megabombus) agrorum* (now *pascuorum*), *B. (Pyrobombus) hypnorum,* and *B. (Fervidobombus) atratus;* Dornhaus and Chittka 1999; Jacobs-Jessen 1959; Esch 1967; Kerr 1969]. Jacobs-Jessen (1959) had already noted the extended, but irregular, runs of returning foragers 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 Dornhaus and Chittka (1999), are needed for more species of bumble bees to confirm that the behavior patterns observed here for *B. terrestris* are generally valid among the bumble bees (see chapter 2.6).

What do bumble bees tell us about the evolution of recruitment in the social bees? Can we deduce from bumble bee behavior the origins of one of the most intriguing systems of animal communication, the honey bee's waggle dance? This question requires a comparison of the honey bee recruitment system with those of their close relatives, the stingless bees and bumble bees (which presumably are sister groups; Cameron 1993). Bumble bees 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 honey bees. Therefore, we might conclude that the common ancestor of the social bees possessed irregular runs which predated the more sophisticated, location-coding, dances of honey bees, assuming that the last common ancestor of honey bees and bumble bees 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 have been shown to be 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). It is possible that the common ancestor of the stingless bees and bumble bees possessed an excitatory motor display, but unfortunately the motor activities of stingless bees and bumble bees 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 honey bees; Dyer 1991).

There is a second argument that suggests independent origins of the honey bee dances and the irregular runs of the bumble bees and stingless bees. Honey bees do have a recruitment behavior with similar information content as the runs of bumble bees, but the behavior displayed by honey bees is wholly unlike that of bumble bees. In their “round dances”, honey bees 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 (Frisch 1967). Thus, the information transmitted is the same as in bumble bees, but the path of the honey bees' round dance is highly regular. There is no conceivable selection pressure for honey bees to evolve a round dance if their ancestors already had behavioral means which, albeit seemingly more primitive, conveyed the same information. Thus, the honey bee waggle dance is more likely to have evolved from ritualized intention movements (aborted flights towards the target), as supposed by Haldane (1954) and 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 bumble bee foragers has any excitatory function itself, or if it simply serves to distribute a pheromone with low volatility around the nest. If that is the case, are bumble bees unique in terms of pheromone recruitment? Or do other social bees have similar pheromones? It has been suggested that honey bee dancers might use a pheromone to attract other bees in the hive (Tautz and Rohrseitz 1998), but direct evidence has yet to be gained. It is also well known to scientists working with honey bees that they (like bumble bees) can be stimulated to start foraging by injecting sugar solution into the hive. Information about similar phenomena in stingless bees is not available to our knowledge, and unfortunately we also lack knowledge of 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. Bumble bees remain a key group in solving these riddles.

Bumble bees alert with pheromone from tergite glands

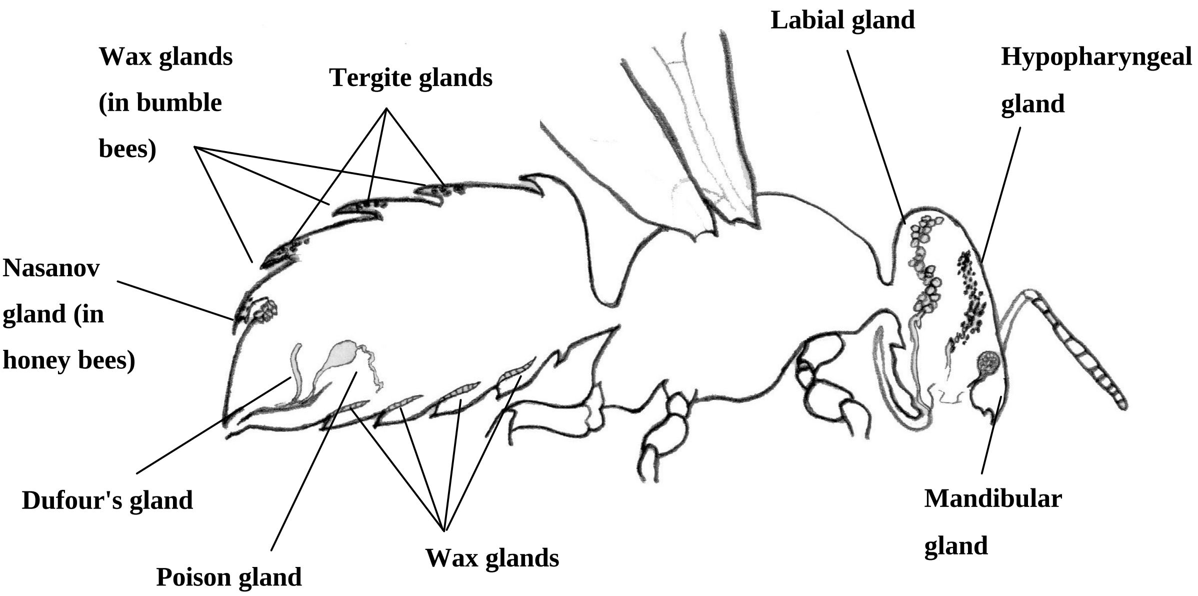


Fig. 2.3.1: Pheromone-producing glands in an Apine bee (after Free, 1987).

2.3 Bumble bees alert with pheromone from tergite glands

2.3.1 Abstract

Foragers of *Bombus terrestris* are able to alert their nestmates to the presence of food sources. It has been proposed that this happens at least partially through the distribution of a pheromone inside the nest. I substantiate this claim using a behavioral test in which an alerting signal is transmitted from one colony to another by long distance air transport, so excluding all other modalities of information exchange. I then investigated the source of the pheromone and was able to show that a hexane extract from tergites V to VII of bumble bee workers elicits higher activity, like a successful forager does. Extracts from other glands, such as the mandibular, labial, hypopharyngeal, and Dufour's gland as well as from other parts of the abdominal cuticle had no effect. This suggests that bumble bees possess a pheromone-producing gland, similar to the Nasanov gland in honey bees. Indeed, an extract from the honey bee Nasanov gland also proved to alert bumble bee workers, suggesting a possible homology of the glands.

2.3.2 Introduction

Bumble bees are eusocial insects and live in colonies of up to a few hundred individuals. Nevertheless, they were long thought to be foraging by „individual initiative“ (Heinrich 1979). This would mean that each bee essentially behaves like a solitary forager, making all decisions on the basis of information collected by itself. However, recent research has revealed a more complex picture. Bumble bees do not communicate spatial co-ordinates of food sources as honey bees do with the waggle dance.

But successful bumble bee foragers do inform nestmates about the general availability and the scent of rewarding food sources (chapter 2.2, (Dornhaus and Chittka 1999, 2001). This helps recruits to avoid searching for food when foraging conditions are unfavorable, as well as aiding in the discovery of rewarding flowers which bees can recognize by the scent they have learned while in the nest.

How is this information about food availability communicated in the nest? Successful bumble bee foragers, when returning to the colony, often show a curious behavior, consisting of excited runs with bouts of wing-fanning. The reaction shown by previously passive bees in the nest is to become active and leave the nest in search of food. This increase in activity is transmitted from one colony to an adjacent one when air exchange is possible, but a single sheet of transparent plastic wrap disrupted transmission. This procedure would not disable visual communication or substrate vibrations, and I therefore concluded that a pheromone is the most likely means of alerting recruits to food (chapter 2.2 and Dornhaus and Chittka 2001). But the procedure in the previous experiments could not fully exclude other possibilities, such as air flow or airborne sound (Oeynhausen and Kirchner 2001). I therefore conducted a new experiment to conclusively demonstrate the involvement of a pheromone in bumble bee recruitment.

I then move on to identify the production site of this putative pheromone by testing extracts from several potentially pheromone-producing glands known from bumble bees (Fig. 2.3.1, p. 53). I used a bioassay to test for the alerting function of various glandular extracts as well as different parts of the abdominal cuticle, where several small glands are located. Interestingly, an extract from the last three abdominal tergites elicited increased activity, like a successful forager does. In honey bees, this is the site of the Nasanov gland (Snodgrass 1956), but the function of such a gland in bumble bees has not been described previously.

2.3.3 Materials and Methods

2.3.3.1 Bumble bees

All experiments were performed with lab-reared colonies of *Bombus terrestris* (obtained from Koppert, Netherlands). Each nest was contained in a wooden box (26 cm x 14 cm x 10 cm), which was connected to a foraging arena (40 cm x 60 cm x 30 cm) with a plexiglas tube. Nest box and foraging arena had transparent plexiglas covers, so that the behavior of the bees could be observed. Bees were fed by placing a dish with 2 M sucrose solution (feeder) into the arena. Pollen was given directly into the nest box.

2.3.3.2 Experiment 1

As a confirmation that the alerting signal produced by foragers is indeed chemical and volatile, I tested whether the signal would pass from one colony to another if direct contact of bees was prevented, as a more rigorous version of the two-colony experiment in (Dornhaus and Chittka 2001). Here the setup was modified such that the signal between colonies had to pass through a 1.7 m long glass tube (inner diameter 5 mm), rather than just through a double mesh (Fig. 2.3.2). Glass funnels on both sides of the tube were placed approx. 3 cm over the nest structure. In the middle of the glass tube, a pump was mounted, which created a flow of air from the "sender" colony to the "receiver" colony (strength of flow was 0.4 l per min).

Activity of both colonies was measured by counting the number of bees leaving the nest in each 5 min interval through a control phase of 30 min and an experimental phase of 60 min. During the control phase, no

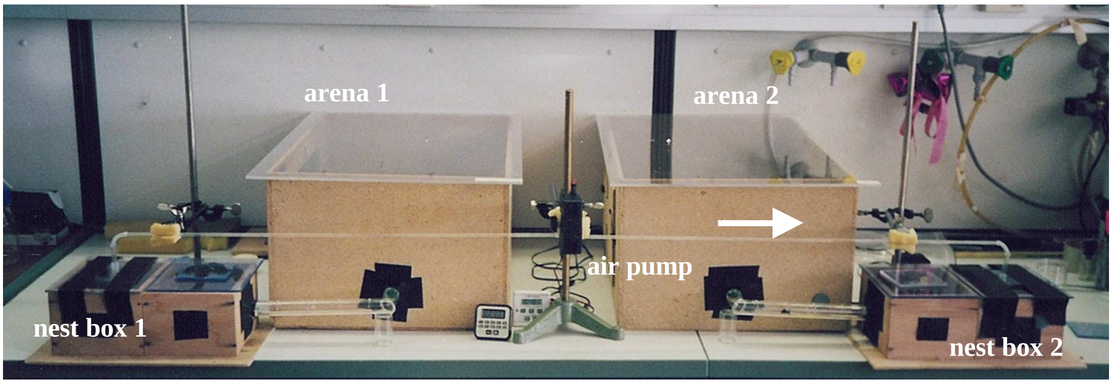


Fig. 2.3.2: Setup in Experiment 1. The two bumble bee nest boxes are connected by a glass tube; air is pumped from the sender to the receiver colony.

food was available to any of the colonies. At the beginning of the experimental phase, a feeder was set up in the foraging arena of the "sender" colony. Bees from that colony were allowed to forage freely, whereas bees from the "receiver" colony had no food available throughout the experiment. Changes in activity of the "receiver" colony which depend on activity of the "sender" colony during the experimental phase, but not the control phase, would then indicate that some information passed through the glass tube.

2.3.3.3 *Experiment 2*

To identify the glands which are involved in the production of the alerting pheromone, I used a bioassay in which the effect of various gland extracts on the activity of a bumble bee colony was measured. Each experiment consisted of a 30 min control phase and a 60 min experimental phase for each extract tested. Activity of the colony was measured continuously as before. During the experimental phase, 10 µl extract was injected every 5 min onto a piece of filter paper placed in a little metal cage in the bumble bee nest. In some experiments, instead of a control phase entirely without manipulation, the solvent (hexane) was injected onto the filter paper in the nest, to control for effects of the manipulation and the solvent.

In a first set of experiments, Dufour's gland, mandibular, labial, and hypopharyngeal glands were tested using extracts made from glands of 10 bees in 300 µl hexane. Also tested was an extract made from tergites VI and VII, which would include various glands on the cuticle of the bumble bees. All extracts were always kept on ice and never used more than 24 h after preparation. Since the cuticular extract proved to be the most interesting, a second set of experiments was performed, in which various parts of the cuticle were extracted. This was done to further localize the involved gland, which could be one of the various small cuticular glands described in the literature (Altenkirch 1961, Cruz-Landim 1963, Hesselhaus 1922, Jacobs 1925) or the effect might be due to some component from the wax glands, which are located on all tergites and sternites in bumble bees (Cruz-Landim 1963, Hesselhaus 1922). I used extracts from sternites, anterior tergites, and posterior tergites. For the sternite extract, sternites V-VII were cut out, clipping off the joints to both tergites and the adjoining sternites. Likewise, the tergites III-V (anterior tergites) and V-VII (posterior tergites) were cut out. In all cases, tracheae and inner organs were thoroughly removed. Sternites or tergites from 10 bees were placed into 300 µl hexane.

2.3.3.4 Experiment 3

In honey bees, a gland used in the context of foraging is located between tergites VI and VII: the Nasanov gland. To investigate possible similarities between the Nasanov gland and potential glands in the same location in bumble bees, an extract of tergites V to VII of *Apis mellifera* bees was prepared in the same way as in experiment 2 with *Bombus terrestris*. The honey bees were taken from a large colony which was foraging outside. The effect of the extract on activity of a bumble bee colony was tested in the same manner as in experiment 2.

I also tested geraniol, the main component of the honey bee Nasanov pheromone, and citral, one of its most active components (Free 1987). These substances were diluted

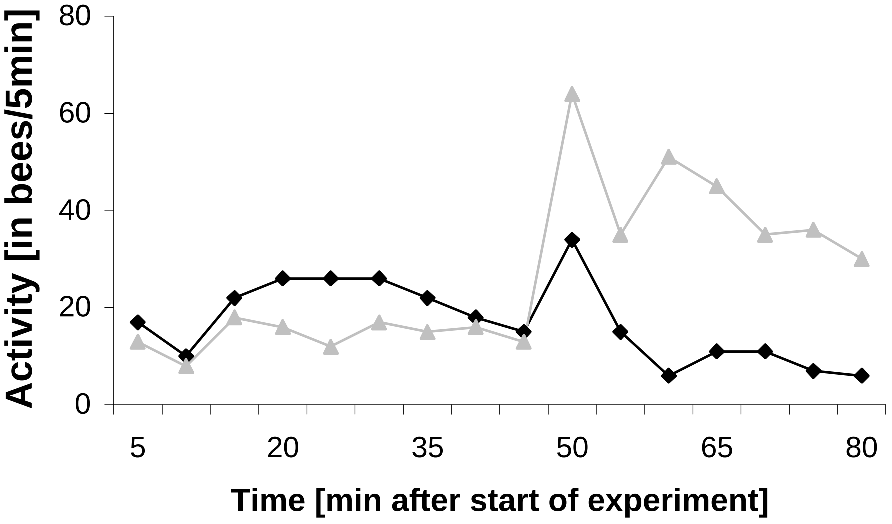


Fig. 2.3.3: Activity of the sender and receiver colonies during the control phase (from 0 to 30 min) and after the sender colony has started foraging (35 to 80 min, shaded area). Shown is one run of the experiment. The activity of the sender colony rises as more bees start foraging (grey triangles). A peak in receiver colony activity can be seen at 50 min (black diamonds).

with hexane (1:1000) and, as in experiment 2, 10 µl per 5 min was injected into a bumble bee colony for 60 min, after a control phase of 30 min and a phase of hexane injection of 60 min (the solvent control).

2.3.4 Results

2.3.4.1 Experiment 1

An alerting signal passed through a 1.7 m glass tube: when the foragers of the "sender" colony started foraging, and presumably comm-unicated to their nestmates the new availability of food, the "receiver" colony also showed a brief activity peak, usually lasting about 5 min (Fig. 2.3.3). The activity in the "receiver" colony correlated significantly with the change in "sender" colony activity (correlation significant with p<0.01, r=0.24, n=120 5 min intervals). This means that an increase in activity in the "sender" colony, presumably because of foragers alerting their nestmates, resulted in higher activity in the "receiver" colony. There was no such correlation in the control phase (p=0.50, r=0.09, n=60).

2.3.4.2 Experiment 2

The only extract that seemed to have any effect in the first set of experiments was the cuticular extract made from tergites VI and VII, which induced a significantly higher activity of bumble bee colonies. The median number of bees leaving the nest per 5 min interval increased from 10.4 during the control phase to 24.3 (p<0.01, n=10, Wilcoxon-Test). When Dufour's gland was used, the activity also increased, from 9.8 (bees/5 min) during the control to 14.2 during the following experimental phase, but this was not significant (p=0.42, n=11, Wilcoxon-Test).

The glands from the head did not seem to cause any change in activity (Fig. 2.3.4A). Median activity when only the solvent was injected into the nest was 4.8 (bees/5 min), which is not significantly different from the control phase without manipulation (median activity 3.9, n=10, p=0.31). Activity during the phase when mandibular gland extract was injected (median activity 2.4) was also not different from the solvent control (n=10, p=0.72, Wilcoxon-Test), the same is true using labial glands (median activity was 5.5, n=13, p=0.20) and using

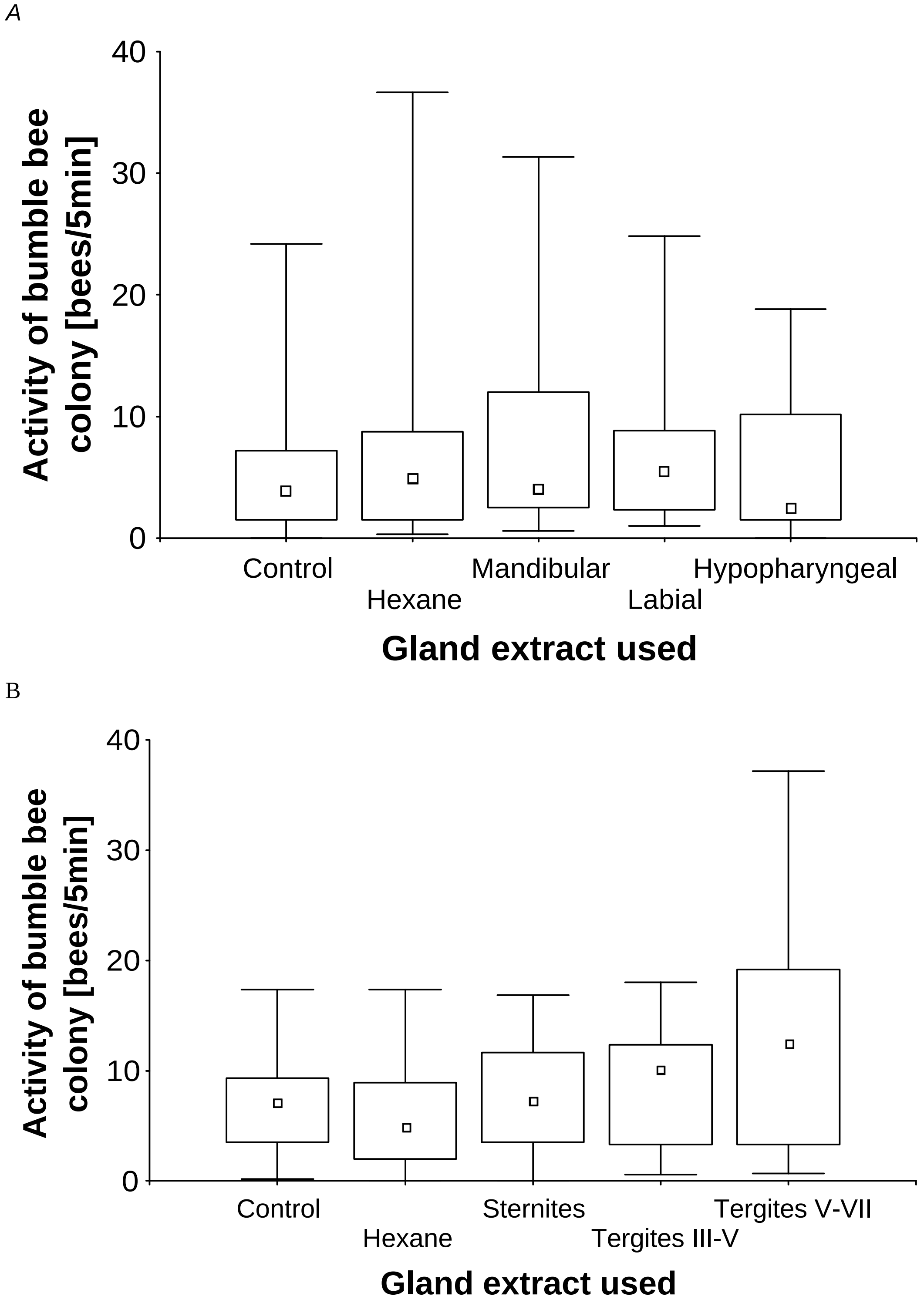


Fig. 2.3.4: Injecting the solvent or extract from different glands or parts of the cuticle has no effect on the activity of the bumble bee colony. Only an extract from tergites V-VII elicits higher activity. Shown are medians, 1st and 3rd quartiles (boxes) and ranges (error bars), all experiments pooled (for statistical analysis data were not pooled but tested pairwise).

hypopharyngeal glands (median activity 4.0, n=13, p=0.83). Thus the first set of experiments already indicated that the alerting pheromone might be produced by a gland associated with the cuticle.

The second set of experiments, comparing different parts of the cuticle, showed that only the extracts from the posterior tergites (V-VII) motivated bumble bees to leave the nest, the solvent or other cuticular extracts had no effect (Fig. 2.3.4B). The activity during the experimental phases when the posterior tergite extract was injected into the nest was again significantly higher than the activity during the control phase ($p<0.05$, $n=14$, Wilcoxon-Test). Activity after injection of extract from sternites or anterior tergites did not differ from activity during control phases ($p=0.21$ and 0.07, $n=15$ and 13 respectively). I conclude that the gland effecting the “food alert” in bumble bees is present only in the posterior tergites.

2.3.4.3 Experiment 3

The extract from *Apis mellifera* tergites results in an increase in activity of a bumble bee colony: from 2.1 bees per 5 min interval during control (and 2.7 during injection of hexane) to 5.7 when the extract was injected ($p<0.05$, $n=10$, Wilcoxon-Test). It is thus likely that the extract made from honey bee tergites, and thus probably the honey bee Nasanov gland, contained substances that are also present in the bumble bee alerting pheromone. Geraniol and citral did not result in an increase in activity ($p=0.21$ and $p=0.29$, $n=9$ and $n=12$, respectively, Wilcoxon-Test); this in turn means that the active substances were neither geraniol nor citral, at least not in their pure form. It is possible that bumble bees are only alerted by a mixture of these or other substances which are contained in the honey bee Nasanov gland.

2.3.5 Discussion

A volatile chemical is used by successful bumble bee foragers as a signal to alert nestmates to the availability of food. While our experiments do not exclude that signals of other modalities, like acoustical signals (Oeynhausen and Kirchner 2001), can also be employed, the passage of the signal through a 1.7 m glass tube and a vibrating and noisy pump demonstrates that at least part of the alerting effect is due to a pheromone. Furthermore, a chemical was sufficient to elicit the reaction of passive bumble bees that a successful forager also induces – increased mobility and bees leaving the nest, presumably to search for food. Only an extract from the cuticle of the posterior tergites (V to VII) of the bumble bees' abdomen had this effect.

In honey bees, the anterior part of tergite VII is where the Nasanov gland is located. This gland consists of a high number of Leydig cells which open into a groove between tergites VI and VII (Jacobs 1925, Renner 1960). Honey bees expose the Nasanov gland, thereby releasing the secretion, to attract nestmates; they do so when swarming, at the nest entrance, and sometimes at very rewarding food sources (Renner 1960). The behavior of exposing the gland by stretching the abdomen (called "sterzeln" in German, Fig. 2.3.5) is not known in bumble bees. Bumble bees also do not possess the morphological structures associated with the Nasanov gland in honey bees, which vary even within the genus Apis (Jacobs 1925). However, clusters of secretory gland cells have also been described in bumble bees (Hesselhaus 1922, Jacobs 1925). These occur on all tergites and also on sternites (Altenkirch 1961, Jacobs 1925). Some of the more dispersed gland cells have been speculated to serve to lubricate the joints between the tergites ("Schmierdrüsen"; Hesselhaus 1922), but to our knowledge there is no evidence for this function, and most authors classify their function as "unknown" (Altenkirch 1961, Duffield et al. 1984, Jacobs 1925). In *Bombus terrestris*, Jacobs (Jacobs 1925) finds structures on the intersegmental membrane which he interprets as adapted to facilitate evaporation of glandular secretion; because of this, he supposes that these bumble bees have scent glands on the anterior and posterior sides of tergite VI (Jacobs 1925). Another study (Cruz-Landim 1963) also claims that bumble bees possess a "scent gland" in the same location, and in a more recent review

Fig. 2.3.5: Honey bees fanning and exposing their Nasanov glands at a hive entrance.

bumble bees are even said to possess a Nasanov gland (Duffield et al. 1984).

I have demonstrated that an extract from the tergites VI and VII induces higher activity in a bumble bee colony, whereas an extract from other tergites or from sternites does not; this indicates that glands on the posterior tergites contain a pheromone which is not, or to a lesser extent, produced in the other segments. These gland cells might be then homologous to the Nasanov gland in honey bees. Our experiments show that bumble bees are even alerted by an extract from honey bee tergites, containing the Nasanov gland. Thus the gland used by bumble bees in alerting produces at least partly the same or similar components as the Nasanov gland in honey bees. Bumble bees are however not alerted by geraniol or citral. This could either mean that only a mixture of substances is recognized by bumble bees as alerting pheromone, or that one of the other components of the Nasanov pheromone is the alerting substance.

Although the similarity between the bumble bee tergite gland and the honey bee Nasanov gland could be a matter of convergent evolution, it could also mean that these glands have a common origin. If that is the case, bumble bees use their “Nasanov gland” to produce a pheromone, not for attraction or recruitment, but, in a similar context, for alerting nestmates to the presence of rewarding food sources. Bumble bees do not show the behavior of exposing their gland by stretching the abdomen like honey bees. However, like honey bees, they show fanning behavior when they are presumably giving the pheromone signal (i.e. in the nest between foraging trips; Dornhaus and Chittka 2001). Whether the glands of bumble bees used in alerting and the honey bee Nasanov gland are homologous can only be shown by a phylogenetic analysis including the stingless bees (for which such a gland is not yet known). Investigation of the fine structure of the gland and chemical analysis of its components would give further information on characters that could potentially show whether these glands are homologous.

Alerting signals are common in social insects. Motor signals, such as excited running or waggle displays are often used by foragers inside the nest to activate nestmates. This has been described in ants (for a review see Hölldobler and Wilson 1990), wasps (Richter 2000), and stingless bees (Lindauer and Kerr 1960, Nieh 1998). Bumble bees might be unusual, because they use a pheromone inside the nest for the purpose of motivating nestmates. On the other hand, similar pheromones in ants or stingless bees might be unknown because they have not been looked for, and therfore still await discovery.

How information on food source quality is transferred from foragers to nestmates

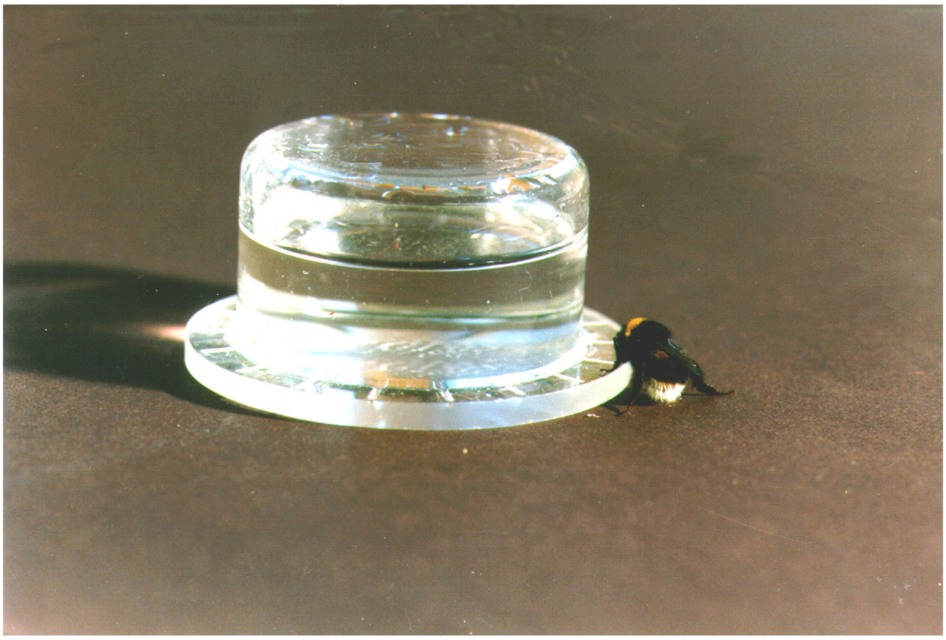


Fig. 2.4.1: Bumble bee forager drinking from an artificial food source.

2.4 How information on food source quality is transferred from foragers to nestmates

2.4.1 Abstract

Information distribution can work in two ways. Senders can broadcast it to receivers (“push”-distribution), who then select the information relevant to them; or receivers can request it from sources which are likely to have the necessary information (“pull”-distribution). In bumble bee communication, both of these methods might be employed at the same time. Inactive forager bees in the nest collect information on the quality of available food sources before deciding whether to start foraging. They might get this information from the forager that has discovered the food source, who gives an alerting signal that is modulated according to food source quality ("push"). But they can also collect information on quality on their own initiative, presumably by sampling the new nectar in the honeypots ("pull"). As a result, the colony-level foraging activity is adjusted to the current availability of high-quality food sources.

2.4.2 Introduction

In bumble bees, the information whether or not conditions are favorable for nectar foraging is available to bees in the nest through two channels. Nest-bees monitor honeypots and notice any influx of nectar, such as when other bees are successfully foraging; and secondly, when a forager has discovered a good food source, she distributes a pheromonal signal in the nest (Dornhaus and Chittka 2001 and chapter 2.3). In response to nectar influx or such pheromonal signals, soon more bees start searching for food. When no other bee is currently successful, on the other hand, bees profit by being less motivated to start foraging; thereby unsuccessful trips during periods with unfavorable conditions for foraging are avoided. On a colony level, most of the foraging force is thus only activated when food is available; at other times, workers and energy are spared for other tasks.

Here I investigate whether bumble bees (of the species *Bombus terrestris*) with this system also exchange information about the quality of the resources they are collecting from inside the nest. I show that this is the case, and that this information could be transmitted both through the forager's alerting signal and through the monitoring of the honeypots (and sampling of their contents) done by inactive foragers in the nest. Thus the same two channels that nest-bees use to get information on food presence are also used to distribute information on food quality. With this communication of presence and quality of food sources, and in addition scent (Dornhaus and Chittka 1999), the information content of the bumble bee alerting signal is equivalent to that of honey bee round-dances.

2.4.3 Materials and Methods

In all experiments, laboratory-reared bumble bee colonies (obtained from Bunting Brinkman and Koppert, Netherlands) were used. The wooden nest boxes (26 cm x 14 cm x 10 cm) were connected to two foraging arenas (40 cm x 60 cm x 30 cm) with a Y-shaped, transparent plexiglas tube. Access to each arena could be controlled by the experimenter with shutters inserted into the tube. Nest box and foraging arenas had transparent plexiglas covers, so that the bees' behavior could be observed. Bees were fed outside of the experiments by placing a dish with 0.5 M sucrose solution (feeder) into an arena. Pollen was given directly into the nest box.

2.4.3.1 Experiment 1

First I tested whether food of differing quality would elicit different alerting responses. As high-quality food I used 2 M sucrose in water solution, as low-quality food I used 0.5 M sucrose solution. The alerting response was quantified as in

Dornhaus and Chittka (1999), by counting the number of bees leaving the nest per 5 min interval (this is hereafter termed the “activity” of the colony) before and after a forager had started collecting sugar solution. The activity of the colony was measured constantly during a control phase of 30 min and an experimental phase of 60 min. In the control phase no food was offered to the bees. 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. The marked forager was offered either high- or low-quality food. The experiment was run 22 times with a total of 7 different colonies. In 13 of these runs, high-quality food was offered for 60 min and low-quality food for another 60 min; the order in which these two were offered was balanced between runs.

2.4.3.2 Experiment 2

When the marked foragers used in experiment 1 were in the nest between their foraging trips, they were observed for the occurrence of bouts of fanning, a behavior which might be connected to their investment into communicating food availability to nestmates either because it serves to distribute a pheromone (Dornhaus and Chittka 2001) or possibly because it produces a buzzing sound attended to by other bees (Oeynhausen and Kirchner 2001). The number of bouts per trip as well as the total number of fanning bouts occurring in 60 min of experimental phase were counted and compared between phases during which sugar solution of different quality was collected.

2.4.3.3 Experiment 3

To test whether only the differing behavior of the forager can cause different reactions of the colony to high- or low-quality food, I made use of the fact that even if sugar solution is merely injected into the nest, some bees become motivated to start foraging (Dornhaus and Chittka 2001). In a similar setup as in experiment 1, I measured the activity of a bumble bee colony during a 30 min control phase and a 60 min experimental phase. During the experimental phase, 100 µl of

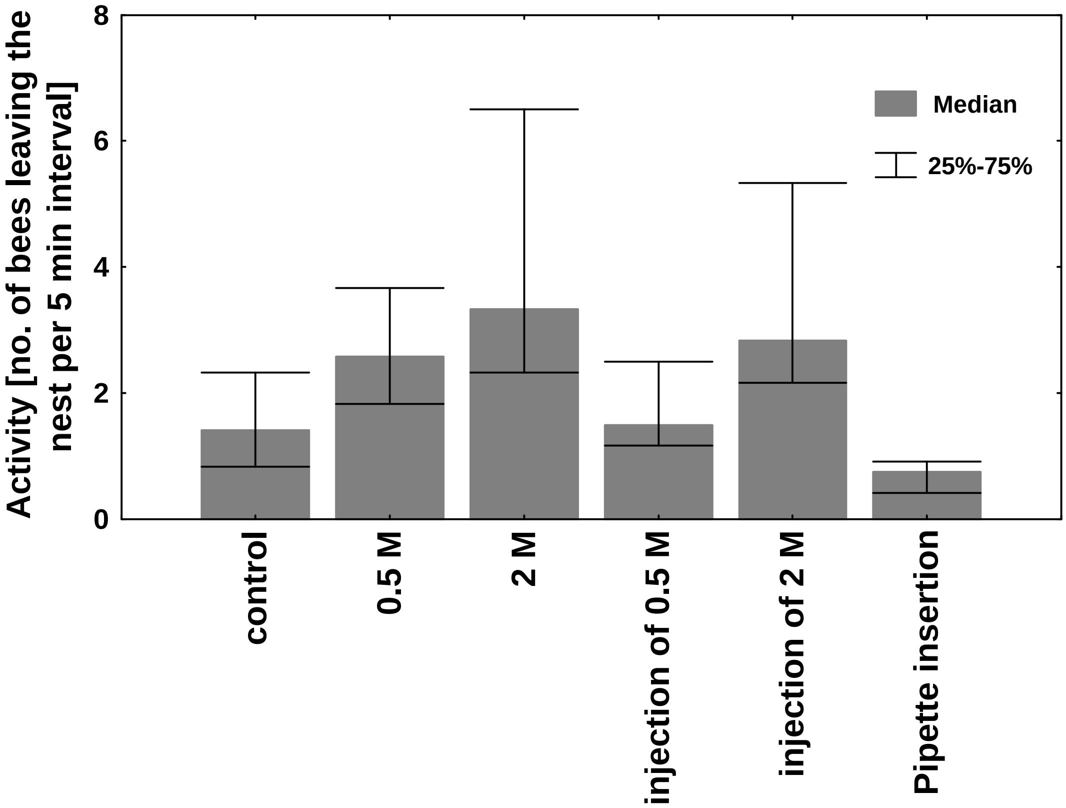


Fig. 2.4.2: Activity of bumble bee colonies when a forager was collecting 0.5 M or 2 M sugar solution or when these sugar solutions were injected into a honeypot in the nest. The statistical tests follow a paired design, where each value is paired with the respective control, but in this graph all control values are pooled.

sugar solution were injected into a honeypot in the nest every 5 min. No food was made available in the arena. This was repeated 15 times each with the high- and the low-quality sugar solution.

2.4.4 Results

2.4.4.1 Experiment 1

The activity of a bumble bee colony is modulated according to the quality of the food sources discovered by its foragers. During the experimental phase, where a forager was allowed to collect concentrated (high-quality) or diluted (low-quality) sugar solution, the activity 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 (in experiments with high-quality solution: $p<0.001$, n=21 runs; for the low-quality solution, $p<0.01$, n=22). 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 (Fig. 2.4.2). For the experiments in which high- and low-quality food were offered for one hour each immediately adjacent to one another, the high-quality food source resulted in significantly stronger alerting than the low-quality food source ($p<0.05$, n=13 experimental runs, Wilcoxon-Test).

2.4.4.2 Experiment 2

When returning from the food source, foragers showed “excited runs” (chapter 2.2) in the nest, and while running, they often fanned their wings in short fanning bouts. When they were foraging from a food source of higher quality, foragers showed more fanning inside the nest. They performed more fanning bouts in the nest both per foraging trip (medians are 8 vs. 2; $p<0.0001$, n=65 foraging trips, Mann-Whitney-U-Test) and in total in 60 min (74 vs. 22; $p<0.05$, n=4 runs, Fig. 2.4.3) in the experimental runs with the 2 M sucrose solution compared to the 0.5 M sucrose solution.

Fanning might serve the purpose of distributing an alerting pheromone in the nest. If this is the case, the foragers distributed the pheromone more, and they might have discharged more pheromone when coming from high-quality food sources. This could be one explanation for the more pronounced increase in activity with high-quality sugar solution in experiment 1: more bees might have been alerted due to a stronger alerting signal from the forager.

2.4.4.3 Experiment 3

Injection of better quality sugar solution into the honeypots results in a higher increase in activity of the bumble bee colony than injection of low-quality sugar solution ($p<0.01$, n=10, Wilcoxon-Test, Fig. 2.4.2). Thus, even without a foraging bee present, bees in the nest did not only notice the influx of sugar solution, they also reacted more strongly to food of higher quality. This means that the quality-dependent effect in experiment 1 could also be due to differential reaction of nest-bees, not necessarily depending on a modulated signal by the forager.

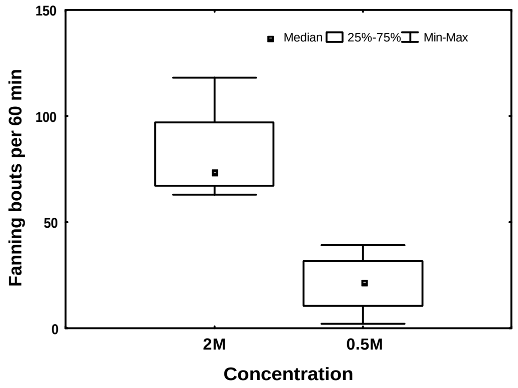


Fig. 2.4.3: The number of fanning bouts displayed depends on the sugar concentration of the solution the forager was feeding from.

In fact, it is not clear whether bees in the nest reacted to an influx of low-quality sugar solution at all, since the activity does not increase significantly compared to control phases (p=0.10, n=15, Wilcoxon-Test). If 2 M solution is injected, activity does increase significantly compared to controls (p<0.001, n=15, Wilcoxon-Test).

2.4.5 Discussion

Bumble bees can get information on the sugar concentration of available nectar sources before leaving the nest. Without taking the risks associated with sampling foraging conditions and food sources outside, they can thus decide whether it would be profitable to start foraging.

If a food source is close to the nest, honey bees communicate exactly the same information. For these close food sources, honey bee foragers perform round dances and give food samples to nestmates. The recruits are so able to learn about the scent and quality of the food by sampling it, after they have been alerted to the presence of food sources by the movements of the forager in the round dance. In bumble bees, the foragers also alert nestmates by performing excited runs, and in addition use a pheromone for alerting (chapter 2.2 and 2.3). Nest bees sample the nectar brought into the nest, even if they do not get it directly from the forager (chapter 2.2), and thus learn about the scent of food sources (Dornhaus and Chittka 1999). And, as this study shows, by sampling or through modulated signals by the forager, the nest bees can learn about the quality of the food source. The bumble bee communication system is thus in information content equivalent to the round dances of honey bees.

Also like in honey bees, there is more than one way for bumble bees in the nest to collect information on food source quality. Nest bees can either sample the new nectar in the honeypots, or they can extract the relevant information from the forager's behavior. The former would require initiative from the receiver of the signal, the nest bee, who has to find the honeypot that the foragers are unloading into to sample the nectar. Such a process, where a receiver actively searches for information, is called "pull" information distribution in information technology. On the other hand, the foragers distribute information on food source quality to nestmates by a modulated pheromonal signal. This can be called "push" information distribution, because the initiative to communicate comes from the sender. The receivers can then decide whether to attend to the signal or ignore it. The results of this study show that in bumble bees, both of these ways of information distribution could be used to communicate food source quality. However, although the information on quality is available from the behavior of the forager, we do not know whether nest bees attend to it; it is also possible that they rely only on the information collected by themselves by sampling the contents of the honeypots.

Nectar stores determine a bumble bee colony’s reaction to new food sources

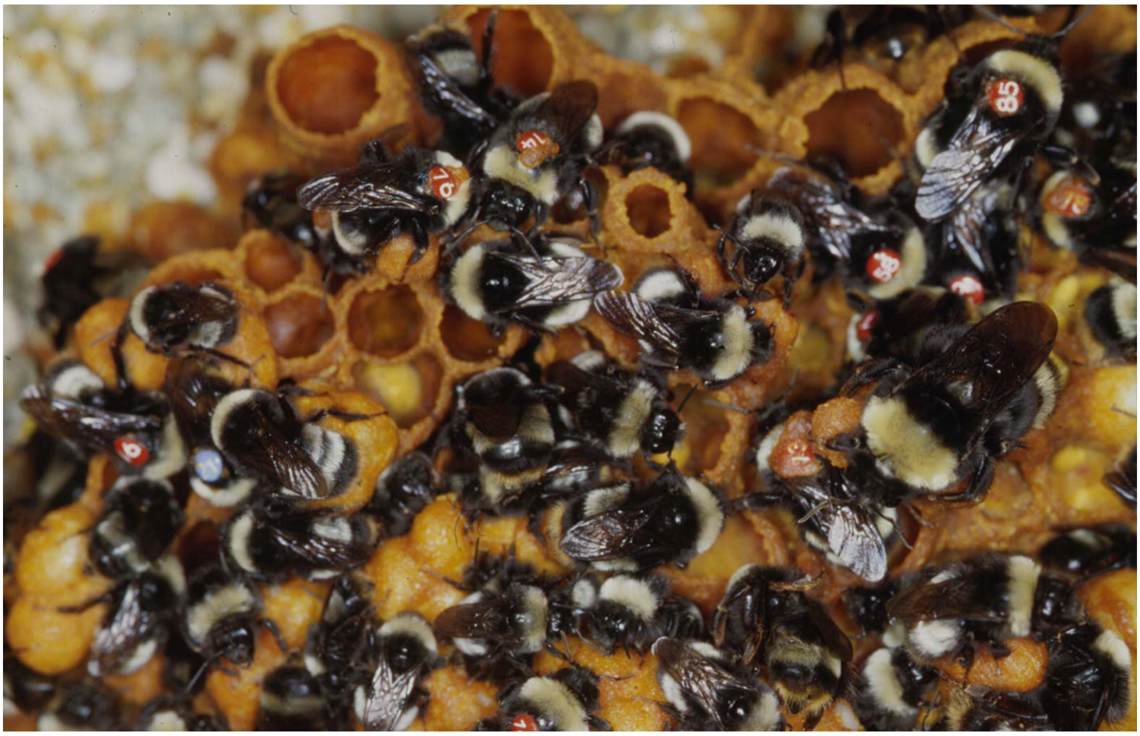


Fig. 2.5.1: A colony of B. occidentalis; the queen is the larger individual to the right. Several empty food storage pots can be seen. Colored number-tags enable individual identification of bees.

2.5 Nectar stores determine a bumble bee colony's reaction to new food sources

2.5.1 Abstract

Foraging activity in social insects is often regulated not only according to food availability but also depends on demand. While the mechanism of this regulation is well studied in honey bees, it is not known whether and how colony food demand influences foraging activity in bumble bees. To investigate this question, I kept bumble bee colonies under conditions of high and low food availability to manipulate their food demand. The activity of these colonies did not differ when there was no food source present. However, when a food source was discovered by one forager, this resulted in an activation of colonies with low nectar stores (and high food demand). If a colony had high amounts of nectar already stored, reflecting low demand for nectar, no activation took place, even though the forager who discovered the food source continued collecting nectar. This means that colonies do not stop foraging when food demand is low, but cease to allocate more foragers even to good food sources. If food demand is high on the other hand, a large number of workers are allocated to foraging as soon as a profitable food source is discovered.

2.5.2 Introduction

One of the characters of social insect colonies that has fascinated researchers most is their ability to flexibly allocate workers to different tasks (Oster and Wilson 1978, Hölldobler and Wilson 1990, Gordon 1996). Depending on what needs to be done, the sizes of worker groups occupied with each task are

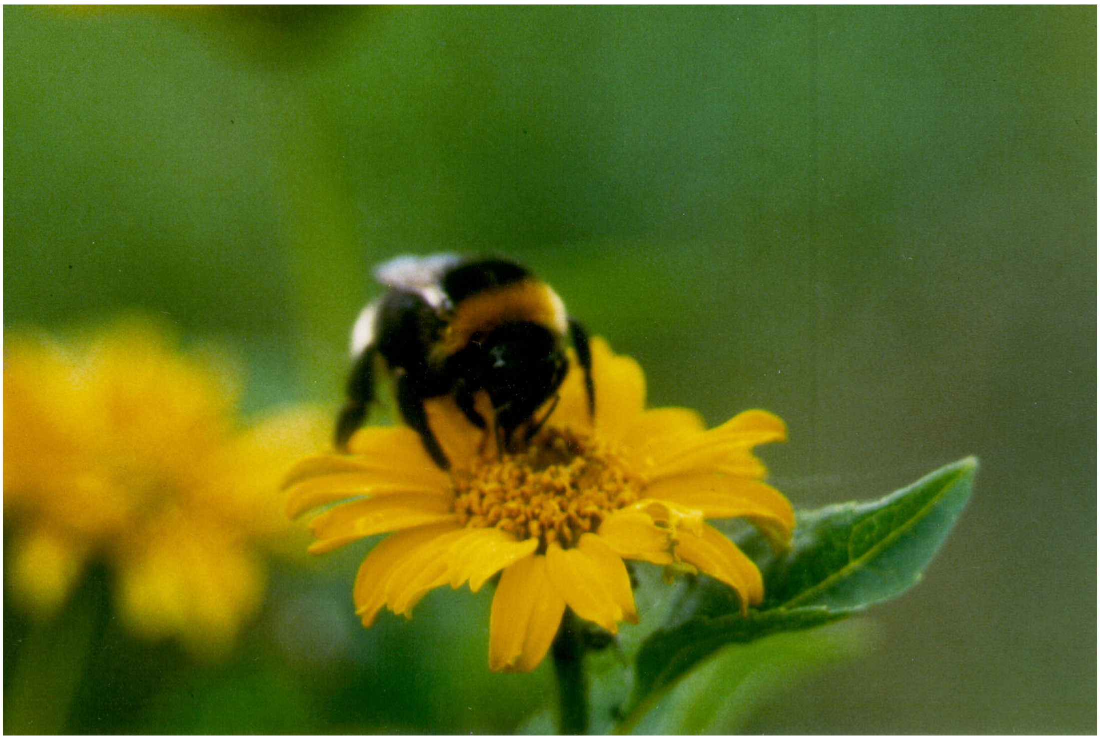


Fig. 2.5.2: Foraging bumble bee. Foraging is associated with many risks compared to the relatively safe nest environment.

increased or decreased (Robinson 1992, Gordon 1996). This can happen by switching of workers within a group from an active into a passive state (or vice versa), and often, workers are also able to switch between task groups (Wilson 1971, Gordon 1996). Not only is it important that enough workers are available for tasks that urgently need completion; if a sufficiently high number of workers is already performing a task, it is also in the colony's interest to save energy by not dispatching more workers to this task.

Foraging in bees (Fig. 2.5.2) is a task which can be both risky and energy-demanding (Seeley 1985). A bee colony thus should regulate the number of bees searching for food depending on the expected benefits and costs in a given situation. Benefits and costs of foraging or searching depend on the availability of food. For example, if there is little food available, search costs are likely to be high. However, the benefits of foraging not only depend on the net caloric value of food collected, but also on the demand for food in the colony. Food demand is determined by the amount of food already stored and by the number of workers and brood in the colony. Changing food demands change the relative benefits of a certain amount of food collected. In a period of dearth, the food gathered might directly influence the number of colony members surviving; if a colony already has enough food stored, the benefits of additional foraging on the other hand might not outweigh the risks of losing foragers.

Fig. 2.5.3: A trophallactic contact between two honey bees in the hive.

In honey bee colonies, the number of workers foraging is therefore adjusted to food availability and demand. This regulation is achieved through interactions of foragers and nest-bees. Only the foragers already active have access to information on food availability; if foraging conditions are good and profitable food sources available, these foragers stimulate others to start foraging by performing waggle dances in the hive (Frisch 1967, Seeley 1995). On the other hand, the interactions between foragers unloading the nectar they have brought and the nectar-receiver bees give the former cues on the capacity of the colony to process the incoming food (Seeley 1995, Ratnieks and Anderson 1999). There is, however, no limit to the “demand” of a honey bee colony to gather nectar; a large amount of honey is needed to safely survive the extended period during the winter months where no foraging is possible. This might even be the main fitness limitation for temperate-living honey bees (Seeley 1995).

For pollen foraging this is not so. Honey bee colonies keep only a small pollen storage, and therefore pollen foraging is tightly coupled to demand. Pollen foragers however do not 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. If protein content is already high, they stop foraging for pollen; if it is very low, they recruit additional pollen foragers by means of waggle dances (Seeley 1995, Weidenmüller 2002).

Fig. 2.5.4: A bumble bee colony usually contains several honeypots scattered aound the brood areas, often towards the borders of the nest structure. Here some pots filled with honey can be seen.

The system by which foraging in a honey bee colony is regulated according to food availability and demand is thus quite well understood. But what about bumble bees? How do passive bees in a bumble bee nest decide when to start foraging? Some major differences between bumble bees and honey bees suggest that bumble bees might use a different system than honey bees. Bumble bee colonies are smaller, containing at most a few hundred workers (but early in the season much fewer), compared to the several thousand in a honey bee colony. The nest structure itself is also smaller, suggesting that it might be easier for an individual forager to monitor the food stores by itself. Also, bumble bees do not perform trophallaxis (the direct feeding of one individual by another, Fig. 2.5.3), which makes them unable to give direct food samples to nestmates. It also means that foragers store their harvest themselves, there is no group of “receiver bees”. And finally, bumble bee colonies do not survive over the winter, which means that they do not amass large nectar stores. By contrast, foraging activity seems to be adjusted quite well to demand, because one can usually find stores for at most a few days in a bumble bee colony (Heinrich 1979, Fig. 2.5.4). How is this achieved?

We already know how foraging activity is regulated depending on food availability. If high-quality food stores are available, the foragers that have discovered them stimulate more bees to start foraging by distributing a pheromone in the nest (chapters 2.2 to 2.4). However, it is not known whether, and how, this alerting signal is coupled to food demand in the colony, or whether foragers monitor nectar stores. Here I explore this relationship by testing whether alerting is dependent on nectar stores, and thus on food demand, in the nest.

2.5.3 Materials and Methods

Methods for keeping bumble bees and testing for an alerting effect were the same as in (Dornhaus and Chittka 1999, 2001).

Alerting was tested in the same colonies with full and empty nectar stores. To guarantee that a colony had full nectar stores, they were fed *ad libitum* for one day and tested on the next day. By then, the bees would still have several full honeypots in the nest. If colonies were tested with empty nectar stores, they were, on at least two days before the experiment, only fed as much as they actually used per day (approx. 5 ml of 2 M sugar solution, depending on the size of the colony) Prior to the start of the experiment no honey was visible in any of the honeypots. The alerting response was quantified as the difference between activity during the control phase and activity during the experimental phase, when the marked forager was foraging from the feeder. Activity of the colony was defined as the average number of bees leaving the nest per 5 min, calculated for the 30 min control and the second half of the experimental phase (also 30 min), respectively.

2.5.4 Results

The median difference between activity during the control and experimental phases was 1.3 if bees had been fed and 6.3 if they had no stores of honey (p<0.01, n=41 experiments, Mann-Whitney-U-Test, Fig. 2.5.5 and Fig. 2.5.6). Honey stores thus had a significant influence on the occurrence of an alerting effect. The activity of the bumble bee colony did not increase from control to experimental phase if it had full honeypots (p=0.41, n=17, Wilcoxon-Test), but it did increase significantly when honeypots were empty (p<0.0005, n=24). The forager's discovery of a food source thus did not lead to activation of more bees. This means that either the forager did not give an alerting signal (which would imply that the foragers knew about the situation in the honey stores) or that bees in the nest did not react to alerting signals from foragers if stores were full.

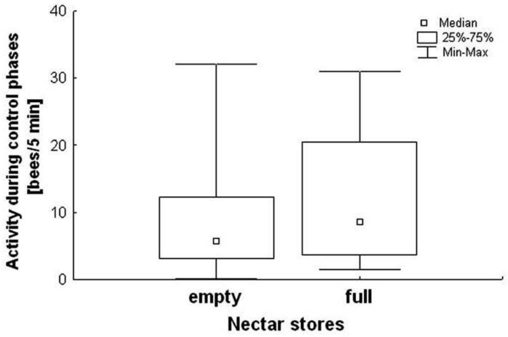


Fig. 2.5.7: Activity during control phases does not differ significantly between conditions of empty or full honeypots.

The activity of colonies with

Fig. 2.5.5: When nectar stores were low (black bars), a single forager who discovered a new food source is able to stimulate many inactive bees to start looking for food. This is reflected by an elevated activity in the experimental phase (measured in bumble bees leaving the nest per 5 min). If the colony still had full honeypots, activity remained unchanged (white bars). (n gives the number of experiments)

low or high nectar stores does not differ significantly if there is currently no food source available, i.e. during control phases ($p=0.45$; $n=41$; Mann-Whitney-U-Test; Fig. 2.5.7). This means, although colonies with low nectar stores are more sensitive to newly discovered food sources, they do not generally send out more bees to search for food. On the contrary, there is a trend to higher activity when stores are already full. One possible reason for this is that colonies with low nectar stores try to economize their foraging effort more, i.e. only investing energy in food searching activity if there is some certainty that this would lead to successful foraging.

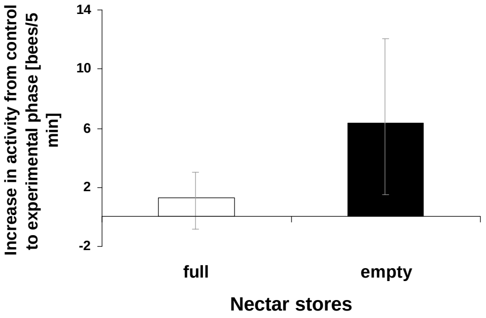


Fig. 2.5.6: Median change in activity across all colonies. Only if nectar stores are empty a significant activation of the colony takes place when a forager has discovered a food source.

2.5.5 Discussion

The food alert in bumble bees (Dornhaus and Chittka 2001) only occurs if nectar stores in the colony are low. If that is not the case, no new bees are activated when a forager discovers a food source. As long as no food is discovered, searching activity is not higher in colonies with low nectar stores. In fact, there is a trend towards lower activity when honeypots are empty. The reason for this might be that searching activity is costly (in terms of energy costs and predation risk), and therefore in particular colonies without resources to spare do not allocate many bees to searching. As soon as food is available however, food demand in the colony determines how many bees become active and try to start foraging. Foraging activity in bumble bees is therefore adjusted to food availability and demand.

However, these experiments do not yet show exactly *what* is adjusted and *who* monitors the nectar stores. Do foragers, when searching for a cell to unload, judge how much honey is already in the nest and then modulate or omit distributing their alerting pheromone? Or do nest-bees, before reacting to such a pheromone, check nectar stores and then decide whether to start foraging? Further experiments will have to show which is the case or if both contribute to the regulation of foraging activity according to demand in the nest.

Food alert in Bombus transversalis

Fig. 2.6.1: B. transversalis occurs in lowland tropical rainforest in South America. My experiments were performed in a field station in the Tampopata area of South-East Peru at the start of the rainy season.

2.6 Food alert in *Bombus transversalis*

2.6.1 Abstract

After a forager of *Bombus transversalis* discovers a new food source and starts foraging from it, her nestmates are alerted and motivated to start foraging. This kind of "food alert" effect was shown previously in *Bombus terrestris* (subgenus Bombus s. str.). Its presence in *B. transversalis* (belonging to the distantly related Fervidobombus) and in some groups of stingless bees suggests that it may have been present in the common ancestor of these two eusocial bee groups. If the invention of an alerting system predates the diversification of the bumble bees and stingless bees, it might have been the starting point in the evolution of the many recruitment systems found in the eusocial bees.

2.6.2 Introduction

Bumble bees, stingless bees, and honey bees, the three major groups of eusocial bees, have very different systems of organizing colony foraging activity, sometimes involving sophisticated mechanisms of recruitment. Honey bees, as the most well known example, perform "waggle dances", highly stereotyped motor patterns, which contain various bits of information about co-ordinates and properties of newly discovered food sources (Frisch 1967). In the stingless bees (Meliponini), mechanisms and information content of communication about food sources vary among species from mere alerting systems (no communication of location, only of presence of food sources) to, at the other extreme, communication about location and distance of a food source via scent marks and acoustic signals, respectively (Lindauer and Kerr 1960, Nieh 1998). In bumble bees, an alerting system which involves communicating presence and odour, but not location of food sources was found in *B. terrestris* (Dornhaus and Chittka 1999, 2001, and chapter 2.2). However, before concluding that this alerting system is a character of all bumble bees and not solely an invention of *B. terrestris*, its presence in other bumble bees should be demonstrated. This is what I report here.

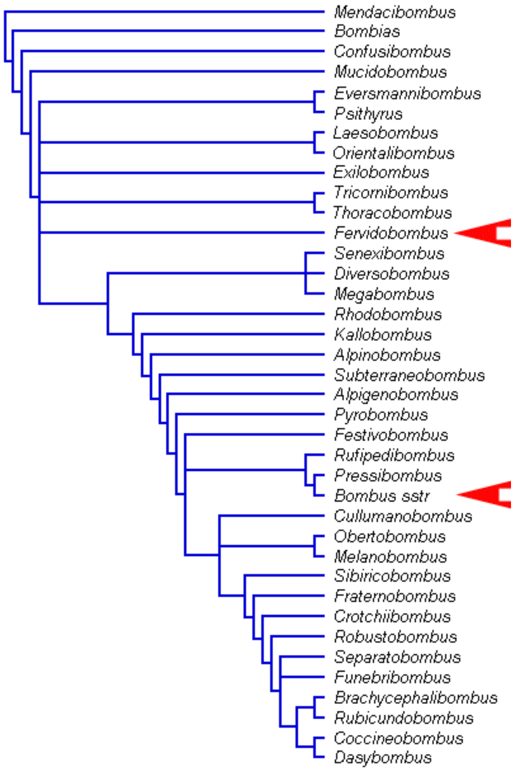


Fig. 2.6.2: Cladogram of Bombus subgenera

I examined recruitment behavior of the Amazonian bumble bee, *B. transversalis*. This is one of the few bumble bee species adapted to living in the wet tropics (Cameron et al. 1999). As *B. transversalis* is in the subgenus *Fervidobombus,* it is relatively distantly related to *B. terrestris* (Fig. 2.6.2; Williams 1994). If the same alerting effect were found in *B. transversalis* as in *B. terrestris*, it would suggest that an alerting mechanism might be broadly distributed across bumble bees.

2.6.3 Material and Methods

Two colonies of *B. transversalis* were located in tropical lowland rain forest in the Tambopata river area in southern Peru (12° 49' S, 69° 24' W, Fig. 2.6.3) during late dry season (Oct. 2001). Colonies were excavated and transferred to wooden nest boxes (30 cm x 30 cm x 15 cm, with transparent plexiglas cover). Both colonies had begun to produce young queens and males; one was queenless. The queenless colony contained approximately 60 workers, the queenright colony approximately 200 workers, both contained brood.

Experimental methods for

Fig. 2.6.3: The experiments were performed in a field station in the Tambopata area, south of Puerto Maldonado in Peru, South America.

testing for alerting were taken from (Dornhaus and Chittka 1999). The nest box was connected to two flight arenas (30 cm x 30 cm x 30 cm) using a Y-shaped plexiglas tube. All bees had access to one of the arenas, whereas into the other arena only one, individually marked forager bee was allowed to enter. The experiment was run 12 times with different bees as marked foragers. Each experimental run consisted of a control and an experimental phase. During the control phase, no food was available to the bees. Their activity was measured by counting the number of bees leaving the nest box per 5-min interval. At the start of the experimental phase, a feeder filled with 2 M unscented sugar solution was set up in the arena to which only the marked forager had access. The forager collected sugar solution on several trips during the experimental phase. It thus had information that a food source was present, but the other bees did not. The except if they got information directly or indirectly from the forager. Any change in activity between the control and experimental phases would show a transfer of information.

2.6.4 Results

Indeed a change in activity takes place between the control and

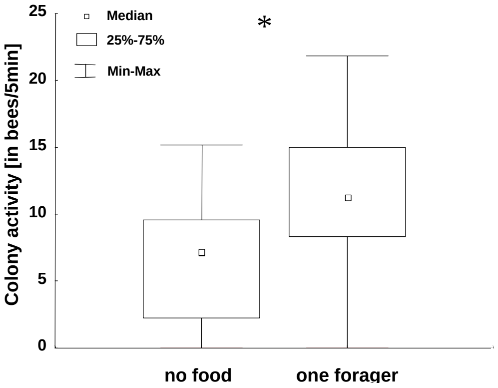


Fig. 2.6.4: Colony activity, measured as number of bees leaving the nest per 5-min interval not including the trips by the marked forager, increased significantly when the marked forager was allowed to start foraging (n=12 experimental runs).

experimental phases: the activity during the second half of the experimental phase was significantly higher than during the control phase in *B. transversalis* (p<0,01, n=12, Wilcoxon-Test; Fig. 2.6.4). This is the same reaction as that shown in *B. terrestris* colonies (Dornhaus and Chittka 1999).

2.6.5 Discussion

Since both *B. transversalis* and *B. terrestris* thus possess an alerting mechanism, it is possible that this is a widespread trait in the bumble bee group, although more data from other species are needed to verify this conclusion. Indeed alerting signals, in the form of conspicuous running and often sound production, as means of regulating colony foraging activity, may have existed very early on in the evolution of the eusocial bees, since they are not only present in bumble bees (Oeynhausen and Kirchner 2001, Dornhaus and Chittka 2001), but also in all studied species of stingless bees (Lindauer and Kerr 1960, Wille 1983). Thus simple alerting as found in the bumble bees might have given rise to the more sophisitcated communication systems present in some stingless bees and in the honey bees today (Chittka and Dornhaus 1999).

Significance of honey bee recruitment strategies depends on foraging distance

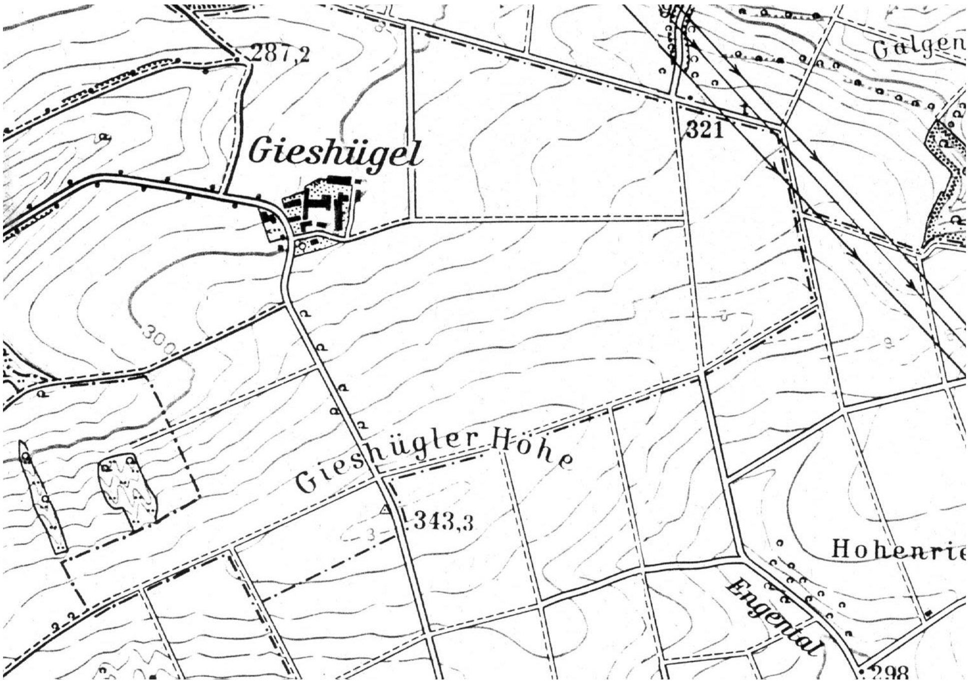


Fig. 2.7.1: Map of the area where the field experiments were carried out.

2.7 Significance of honey bee recruitment strategies depends on foraging distance

2.7.1 Abstract

The importance of the spatial information which is communicated in the honey bee (*Apis mellifera*) waggle dance relative to other cues used by bees in finding food sources was investigated. The effect of recruitment with and without transmission of direction information in the waggle dance was quantified using artificial, plentiful unscented food sources. Hives were turned to a horizontal position to disrupt orientation of dancing bees and thereby eliminate the spatial information from dances. In these experiments transmission of location information improves recruitment substantially only at distances greater than 400m. Recruitment declines rapidly with distance if dances are disoriented, while with normal dances recruitment is as effective at 1000m as at 300m. However, even without dance information, foragers manage to recruit some bees to their food source. But this process is so slow that by the time a group of recruits has reached the food source, it may not be worth exploiting any more. Transmission of spatial information thus is especially important if distant food sources which often change in nectar availability are exploited.

2.7.2 Introduction

Honey bees (*Apis mellifera*) recruit nestmates to rewarding food sources. They do this using a multitude of communication channels. The most remarkable of these is the waggle dance, because of its unique ability to convey information on location of food sources inside the nest. In the waggle dance, direction and distance of a food patch from the hive are communicated. Direction is indicated by the angle of the wagging run in relation to gravity, and distance by the length of the wagging run (Fig. 1.5 on p. 14; Frisch 1967). Besides communicating location in this abstract fashion, foragers also provide recruits with information on scent of the food itself (Frisch 1967) as well as potentially environment-associated odor cues (Wenner 1967). Outside the hive, recruits might follow experienced foragers or search for pheromones deposited directly on the food source (Free 1987).

Several studies have shown that even without these additional cues, the spatial information provided in the waggle dance is sufficient to direct recruits to a food source (Esch et al. 2001, Gould 1975, Polakoff 1998). Information on the relative significance of the waggle dance in a natural foraging situation however is still lacking, because most studies have tried to eliminate other communication channels. Here I investigate how important the waggle dance information is in a situation where no other cues potentially used by the bees are excluded. To quantify the improvement in recruitment effect achieved by the waggle dance, recruitment with and without functioning waggle dances was measured and compared. Recruitment success was measured by counting the number of trips made by bees of the experimental colony to the food source in a certain time period (2 h). The number of trips ultimately determines nectar intake and thus foraging success of the colony. To quantify recruitment without spatial waggle dance information, waggle dances were deprived of their location information by turning the hive such that the combs were in a horizontal position. On horizontal combs, waggle dances lose their spatial information, because bees cannot use gravity as a reference to indicate direction: they perform disoriented dances (Fig. 2.1.6) with interrupted wagging runs, thus direction as well as distance information is lost from the dances (Frisch 1967, Kirchner and Grasser 1998). Thus by comparing success of recruitment to a food source of a hive in horizontal with the same hive in the normal vertical orientation, the importance of the communication of spatial information with the waggle dance system can be elucidated.

2.7.3 Material and Methods

All experiments were conducted with two queenright Apis mellifera carnica colonies, housed in regular 10 frame hives. The frames were fastened such that the hives could be turned on the side, with the combs coming into a horizontal instead of a vertical position. The experiments were conducted in an agricultural area which was poor in forage for bees at the time (June and August 2000). No other beehives were present in a radius of >800m around the site of the experimental hives.

Feeders were glass dishes filled with 2M saccharose solution placed in wooden boxes; around the entrance to the box an orange star on a blue background was fitted (Fig. 2.1.2). Bees were allowed to feed on an artificial feeder which was of the same design as in the experiments close to the hive for 2 weeks, so that many foragers of the colony had learned to associate feeders of this design with reward.

After this pre-training, a feeder was placed in a location not used previously and monitored until the first forager arrived. The number of bees arriving per 5-minute interval was then counted for two hours. All arriving bees were allowed to freely forage from the feeder to allow buildup of a forager group through positive feedback as would happen on a natural food source. The experiment was repeated 2 to 4 times with oriented and disoriented dances for each of the following distances: 125m, 300m, 500m, 600m, 800m, and 1000m.

2.7.4 Results

For close distances, preventing bees from communicating location of feeders to nestmates via the waggle dance does not impair recruitment to novel feeder locations. When the feeder was less than 400m from the hive, the number of bees arriving at the feeder within 2 hours of its first discovery was not significantly different with or without functioning waggle dances (p=0.38, n=8, Mann-Whitney-U-Test). In the experiments where the feeder was farther away

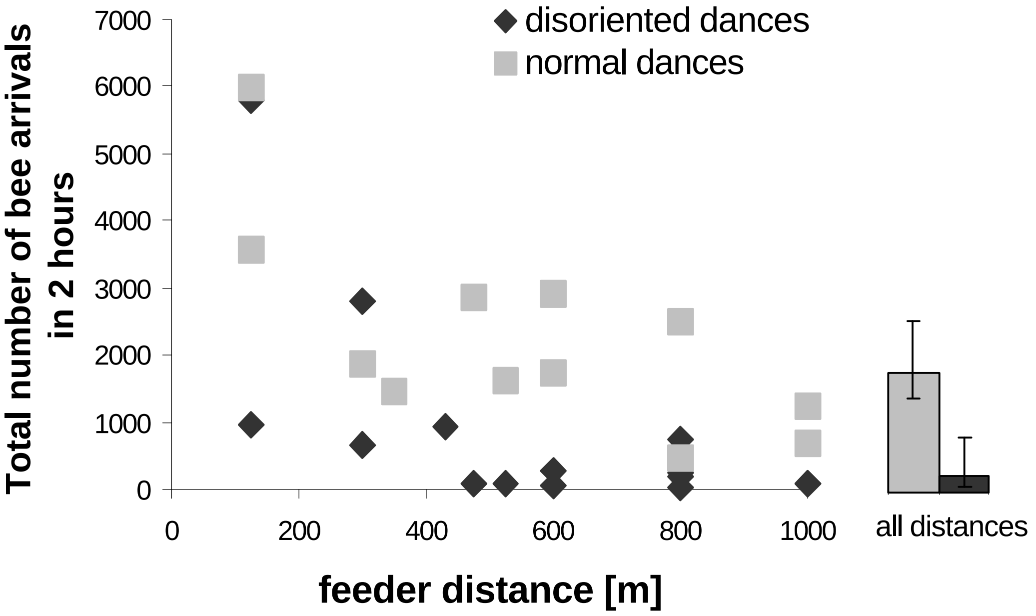


Fig. 2.7.2: The number of bees arriving at the feeder depends strongly on distance only if dances are disoriented and thus no location information communicated.

from the hive however, recruitment was substantially impaired when bees could not use waggle dance information to locate the food source: there were both fewer bee arrivals at the feeder within the first 2 hours (p<0.001, n=19, Mann-Whitney-U-Test) and recruitment took longer (a median 2.5 hours until 50ml of sugar solution were collected without, but only 1.25 hours with oriented waggle dances, p<0.05, n=12, Mann-Whitney-U-Test). Recruitment success is practically independent of distance when bees were allowed to communicate location information through the dance (number of trips does not correlate with distance; p=0.06, n=23, Fig. 2.7.2), excluding the closest distance (125m), where a very high number of bees reaches the feeder. Without dance information, the number of bee visits declines sharply with feeder distances (r=-0.56, p<0.05, n=13, 125m distance also excluded).

In all experiments, bees arriving at unrewarded control feeders at the same distance as the rewarded feeder were also counted. When the rewarding feeder is discovered by a scout, the number of bees arriving at the control feeder increases as well: the number of arrivals at the control feeder in the first half hour is significantly lower than in the 2nd, 3rd, or 4th half hour after the first visit to the rewarded feeder (all p<0.05, n=27, Wilcoxon-Test). However, only very few bees ever arrive at control feeders compared to rewarded feeders (Fig. 2.7.3). This means that some bees, albeit few, are alerted to the presence of food, but do not receive enough location information to find the rewarded feeder before encountering the control feeder. This is true both for oriented and disoriented dances.

2.7.5 Discussion

The spatial information that is communicated in the honey bees' waggle dance only improves foraging success at food sources which are more than 400m from the hive. At closer distances, either other cues or communication signals are sufficient to direct recruits to the food, or recruits find the food source on the base of their own search effort after being alerted to the presence of food. Since without information on location of the goal, the area that has to be searched increases rapidly with distance from the hive. This searching is bound to take much longer if the

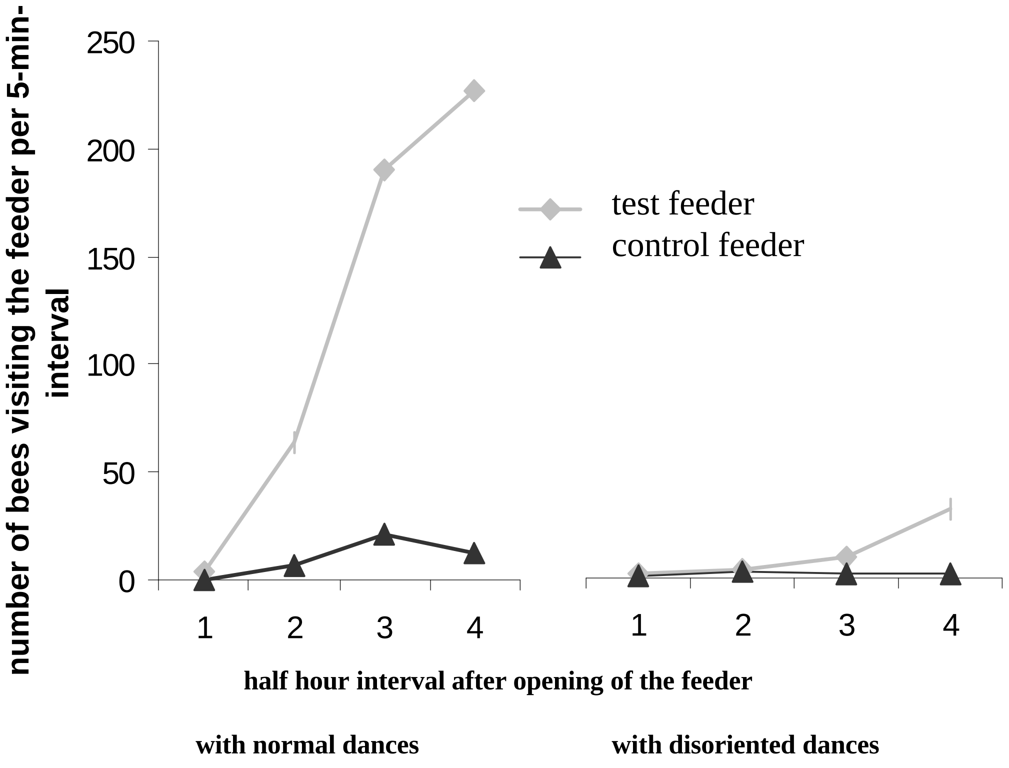


Fig. 2.7.3: For a feeder at 600m distance from the hive, there is strong recruitment only if dances are oriented and thus convey information on location of the feeder. Nevertheless, some recruits arrive at a control feeder in a different direction (same distance) from the hive.

food source is farther away. Thus the farther a food source is located from the hive, the more important dance information becomes. This distance dependence is in agreement with a previous study (Kirchner and Grasser 1998) in which the significance of dance information was quantified; however, the distance at which they found dance information to become unnecessary was much smaller, between 10 and 100m. This difference is probably due to differences in the amout of information available to recruits in the two studies. In Kirchner and Grasser (1998) the dancers did not forage from the food station where recruits were captured; this means that pheromone marks on the food source made by foragers were probably not perceived by recruits, and also visual cues (foragers at the food source) could not be used by them. Another difference is the fact that in In Kirchner and Grasser's study, recruits were captured at several monitor stations. This means that recruits which searched in a wrong direction first were prevented from finding the food later. However, in a natural situation these recruits would be able to search and find the advertised food patch even if they did not depart in the correct direction right away.

A further interesting result is that recruitment success varies considerably between trials even at the same distance. One possible explanation for this are differences in dance motivation between the first foragers to discover the food source. Since recruit arrivals were counted 2 hours from the first food collection trip of the first forager bee discovering the food source, recruitment success might depend to a large degree on the motivation of that first bee to dance. Therefore, to more exactly quantify recruitment success at different distances, a higher number of trials would be necessary. In Kirchner and Grasser (1998), only one trial per distance was reported. However, in their study a number of foragers were trained - variation in dance motivation between bees therefore should have had less effect. In this study, at least two trials were performed per distance, but to have an exact estimate of how much recruitment success can be increased by waggle dances, more experimental trials would be needed.

The results from this study show that even at large distances from the hive some recruitment is still possible without dance information. But this recruitment is so slow that the quality of the food source might have degraded by the time a group of recruits arrives there, since high nectar availability is limited in many plants to a couple of hours per day (Kleber 1935). The spatial information communicated in the waggle dance is thus especially important if food sources are distant from the hive and have fast changing nectar availability. This means that the significance of waggle dance information depends on the spatial and temporal resource distribution and can vary with the bees' environment.

Conclusion

3 Conclusion

The honey bee to many people is “the bee”: the bee whose honey we eat, whose hives our uncle has in his backyard, and the bee that we have studied most - thanks to its economic importance, its long association with men and its unique communication system. What I hope to have contributed to with this thesis is the understanding that it is not sufficient to look at the honey bee as a model for all systems of social insect foraging. Within the social bees, the honey bees’ waggle dance is not the only recruitment system. The bumble bees have their own system of regulating foraging activity. Bumble bees transfer information on presence, odor and quality of available food sources at the nest. Foragers use a pheromone from a tergite gland to stimulate nestmates to forage, a mechanism not known from honey bees. And nectar foraging activity is adjusted to food demand in the colony. The bumble bee communication system thus differs in information content as well as in modalities used from that of honey bees. The reason for this could be that the different bee species are exposed to different selection pressures, for example if they live in different habitats, and consequently evolve differing communication systems. But even if this is not the case, constraints, evolutionary lag or chance effects can determine the outcome of communication system evolution, and therefore produce variable solutions to the same problems. If we want to use social insects as model systems for other processes, it might be necessary to consider the different organizational principles employed by different species, instead of concentrating too much on a one model organism.

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5 List of figures

6 Curriculum Vitae

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1996 - 1997 University of Massachusetts Amherst, USA
Organismal and Evolutionary Biology Graduate Program (as exchange student)
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1980 - 1993 School education Germany
Montessori-Schule, Aachen
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Teaching+other

Animal Physiology Exercises – fall semester 95
Advanced course in Animal behavior - 12/98, 12/99, 12/00, 5/01, 12/01
Introductory Neurobiology class (lab course with lecture) - 10/00, 3/00, 10/99, 3/99
Field excursion (to Spain, with advanced students) - 3-4/00
Course on Multi-Agent-Simulations in Animal Behavior research (in cooperation with Artificial Intelligence Department) – fall semester 00, 01
refereed for Apidologie and Journal of Comparative Physiology A

7 Publication list

Papers

Anna Dornhaus, "When do dances make a difference? Significance of honey bee recruitment depends on foraging distance", 2002, *in press*

Anna Dornhaus, Lars Chittka, "Why do honeybees dance?", 2002, *in press*

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8 Erklärung

Ich erkläre,

daß ich außer meines Diploms in Biologie an der Universität Würzburg keine akademischen Grade erworben oder zu erwerben versucht habe;

daß diese Dissertation weder in gleicher noch ähnlicher Form in einem anderen Prüfungsverfahren vorgelegen hat;

daß ich keine anderen als die angegebenen Quellen oder Hilfsmittel verwendet habe.

9 Acknowledgements

Social insect researchers like to start their acknowledgements with profound sentences like „Science is a social enterprise ...“ etc. Sounds grand, doesn’t it? Nevertheless, I found that the right social environment can contribute a lot to success and fun. I won't name everybody who has contributed to the fun part, but whoever has been to my parties, gave me chocolate when I was still in the lab late, played badminton with us, or simply cheered me up when I was crampy because everything seemed to go wrong: thanks!

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