Chapter 12
Stingless Bee Food Location Communication: From the Flowers to the Honey Pots

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12.1 Introduction

Colonies of social insects lack a central control yet they function as a coherent whole, adjusting their activities in response to a changing environment (Seeley 1995; Visscher 1998; Wilson 2000). How such biological systems are organized has been one of the biggest questions raised by researchers in this field. Honey bees have been studied since ancient times. Aristotle noted that honey bees may recruit nestmates to rich food sources (Nieh 1999). It was the Austrian scientist, Karl von Frisch, at the end of World War I, who described a series of behavioral patterns in the honeybee *Apis mellifera* (Hymenoptera: Apidae, Apini) that seemed related to the organization of the colonies of this species (von Frisch 1967). To observe their behaviors inside the colony, he designed a glass-walled hive, which allowed him to notice that some bees were performing particular behaviors which he called dances. These dances apparently had information about where the dancing forager had found pollen or nectar. Von Frisch discovered what it is now known as the honeybee dance language. Later, with his book "The dance language and orientation of bees" published in 1967, von Frisch described in detail the communication behaviors observed in *A. mellifera* and briefly discussed similar behaviors in other insects. Subsequently, other researchers raised the possibility that recruits may orient only to the smells of the food brought back by the explorer. They hypothesized that the dance behavior was actually an experimental artifact, or a behavior that did not convey location information to nestmates (Wenner et al. 1969; Gould and Gould 1988; Wenner 2002). However, subsequent studies provided detailed, convincing evidence that bees can use the spatial information encoded in the dance language

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and that a correct interpretation of this information is beneficial for colony fitness (Robinson 1986; Dyer 2002b; Dornhaus et al. 2006).

Parallel to the research on the honeybee language, a rising interest in unveiling the ultimate and the proximal mechanisms involved in its evolution led researchers to investigate other species, like the stingless bees (Hymenoptera, Apidae, Meliponini). Stingless bees have proven to have mechanisms of communication as remarkable as the honeybee's, although behaviors identical to the honeybee waggle dance have not been observed in studied species. However, stingless bees consist of hundreds of species that display a diversity of behaviors and ecological adaptations. Thus, they deserve to be studied in their own right, given their importance in their respective ecological niches.

In the following pages, the reader is acquainted with elementary knowledge about stingless bee food location communication. First, we give a general view of the topic. Then, several communication mechanisms are described. External and internal factors that affect the communication system in stingless bees are detailed. Finally, as a result of integration of these elements, the food communication systems and their influence on the foods collected become evident. The characteristics of the pot-honey and pot-pollen are of course affected by the food matter thus collected.

12.2 Food Location Communication Systems in Highly Social Bees (Apidae)

After the initial discovery of the honeybee dance, von Frisch turned his attention to the evolutionary origins of this behavior. Because the meliponines (stingless bees) are similar to honeybees, Martin Lindauer, one of von Frisch's students, began to study stingless bee recruitment communication (Lindauer and Kerr 1960; Lindauer 1967). Together with the Brazilian scientist, Warwick Kerr, Lindauer found a wide range of potential recruitment and communication behaviors in the several meliponine species that they studied, including behaviors that were not observed in honeybees: random searching (no location communication) and odor trails, to name two. They hoped to help elucidate the evolution of the *A. mellifera* waggle dance. Whether stingless bee and honey bee recruitment communication derived from a common ancestor or evolved independently is unclear, although molecular evidence suggests that the two groups are not as closely related as once thought (Cameron and Mardulyn 2001). Nonetheless, even if their recruitment communication systems have evolved convergently, they exhibit certain similarities that suggest common pathways, perhaps deriving from traits shared by both groups of bees and similarities in the ecological niches that they occupy.

More recently, it has been demonstrated that the meliponine bees have communication systems as complex, in their own ways, as those described by von Frisch for *A. mellifera* (Dyer 2002a; Nieh 2004). In general, social insects use communication for various purposes, such as to ensure the cohesion of the colony, to warn the presence of danger, to find mates, and to communicate the spatial location of resources, to name a few (Wille 1983; Gould and Gould 1988; Collins et al. 1989; Wilson 2000). With respect to foraging communication systems, the focus of von Frisch's work, it has been observed that highly social bees such as *A. mellifera* and stingless bees have developed sophisticated mechanisms to recruit nestmates to resources such as pollen, nectar, water, resins, and places to establish new colonies (von Frisch 1967; Nieh 2004; Seeley 2010). With these mechanisms, scouts can send recruits to specific sites that offer profitable resources, a process often referred to as "food recruitment". In fact, the arrival of recruits to an advertised food source is the conclusion of a series of processes that occur at various levels of the colony and the individual (Biesmeijer and Slaa 2004). Meliponines are a good model to study the evolution of recruitment because they are a highly diverse taxon and display correspondingly diverse strategies to reach the same goal: recruit nestmates to rich food sources.

12.3 Food Recruitment in Stingless Bees

Stingless bees are a monophyletic group found in tropical and subtropical areas of the world, in America, Asia, Africa, and Australia (Roubik 1989). Unlike honeybees, which consist of approximately 11 species in one genus (*Apis*), stingless bees consist of hundreds of species distributed in 36 genera (Michener 2000). In addition, stingless bees have multiple lifestyles, including necrophagy, and can recruit to resources such as dead animals, nectar sources, and even the food reserves of other bee species (Roubik 1989). Also, stingless bees exhibit a great diversity of behaviors for transferring information about the location of a resource. These range from pheromone trails to the referential coding through sounds (Nieh 2004). Unfortunately, no studies on stingless bees have been conducted as intensively as in *A. mellifera*, so the understanding of their biology is in an early stage compared to what is known in the Apini. Fortunately, the meliponines have recently drawn the attention of researchers in animal communication, since their study could have implications for understanding the evolution of communication within the Apidae.

It is useful at this point to define some key terms for understanding the processes that arise during food recruitment in social bees. An individual is considered a forager if it is collecting resources for the colony. A scout is a forager that leaves the colony to find resources on its own. A forager is considered to be a recruit if it receives information from the scout about the location of a rich food source (von Frisch 1967). Food recruitment is a communication system that refers to a set of behaviors involved in the transfer of information between scouts and recruits; these behaviors are known as mechanisms for information transfer or simply communication mechanisms. The latter explanation is more specific because communication generally occurs through signals whereas information transfer involves both signals and cues. In general, we can classify communication according to where it occurs: inside the colony (recruitment movements, trophallaxis, and sounds) and outside the colony (social facilitation, pheromones). This, however, is not sufficient to understand the complexity that occurs in the communication systems. Biesmeijer and de Vries (2001) proposed the following classification of the individuals involved in food recruitment in order to better understand the phenomenon of communication:

1. Naïve forager: forager without any previous experience in collecting resources.
2. Explorer (also known as a scout): forager using only internal information to search for resources not previously known to it.
3. Recruit: forager using external information, generally from scouts, to find resources not previously known by her.
4. Engaged recruit (also called employed recruit): forager collecting resources in a known location; it does not usually follow external information while collecting resources.
5. Unemployed experienced foragers: individuals that are temporarily idle because the resource they were visiting was depleted.
6. Inspector: individual temporarily idle that periodically revisits depleted food sources expecting to find them profitable again.
7. Reactivated forager: individual that resumes its foraging activities after having received external information on the availability of resources it previously collected.

The information delivered by communication about resources outside the nest along with other information such as weather and the external experiences of foraging outside the nest are jointly referred to as external information (Biesmeijer and Slaa 2004). Thus there are two types of external information according to its source: information from other bees and information from the environment.

The other source of information used by foragers, which has not received sufficient attention yet, is internal information, which can be more precisely defined as the physiological and genetic status of the individual. A bee's experience, genetic variation, age, and hormone levels are examples of internal information (Biesmeijer and Slaa 2004). Although it is not a communication mechanism, internal information has a significant influence on the decision of recruits and experienced bees (Biesmeijer et al. 1998).

The overall strategy that colonies use to gather resources is thus the result of the interaction between the communication system, the conditions inside and outside the colony, and forager internal information. In the end, this results in either the recruitment or non-recruitment of foragers to a specific location.

12.4 External Sources of Information: Mechanisms of Communication and Recruitment

Insects search for and gather food in unpredictable environments (Goulson 1999). This makes it difficult to exploit efficiently those resources. To keep foragers from wasting time and energy in the tasks of resource gathering, highly social bee species have developed organization systems that allow them to make continuous adjustments in the number of individuals performing certain tasks inside or outside the colony. This is achieved through behaviors that enable bees to communicate with each other, establishing the conditions for the colony to survive in cohesion, in addition to providing a competitive advantage, in some cases, over other species that do not communicate or coordinate to the same degree (Dornhaus et al. 2006). Thus, by understanding the mechanisms of foraging communication we will be able to understand more in general about communication systems in social insects.

12.4.1 Mechanisms of Communication Inside the Nest

Successful foragers of most stingless bee species produce sounds and execute particular behaviors inside the nest or hive after returning from a good food source. In some species, these sounds may indicate the distance from the colony to the food source. Lindauer and Kerr (1960), Esch et al. (1965), and Esch (1967) were the first researchers to describe in detail the patterns of dances, the sound pulses, and the trophallactic interactions in colonies of stingless bees, with special attention paid to explorers returning from profitable resources. The general method is based on training bees to a feeder placed at a known distance and direction from the colony and recording the behavior (trophallaxis, dances, and sounds) of the foragers returning to the colony. In fact, this is the same method currently used to investigate possible correlations between a particular behavior and spatial parameters such as distance, direction, and height of stingless bees (Nieh 2004).

12.4.1.1 Behavioral Rituals (Dances) in Meliponini

In several species of recruiting bees, including *Apis* spp. and meliponines, successful foragers display specific behaviors inside the colony to draw the attention of their fellow foragers in order to transfer information related to the site where they discovered resources (Lindauer and Kerr 1960; von Frisch 1967). The dances in *Melipona scutellaris* and *M. quadrifasciata* consist of agitated running and jostling, without any discernible pattern that can be associated with the location of resources found by the scouts (Hrncir et al. 2000). In other species, like *M. panamica* (Nieh 1998a) and *M. beecheii* (Sánchez and Vandame, unpublished data) the returning foragers display both clockwise and counterclockwise turns while emitting sounds. But so far, no dance similar to the honeybee waggle dance has been described in stingless bees. It has been shown that variations in the intensity of the dance of *Apis* and some meliponine species are related to the quality of the resource (Aguilar and Briceño 2002; Dyer 2002a; Nieh et al. 2003b). However, the recruitment "dance" movements of meliponines apparently do not communicate the polar coordinates of resources (distance and direction) as the dance of *Apis* does (Nieh 2004). In studies with *M. panamica*, Nieh (1998a) found no effects of food distance, direction, or height on forager movement patterns inside the nest. In the species *M. scutellaris* and *M. quadrifasciata*, Hrncir et al. (2000) also found no clear correlation between the dances observed in these species and any parameter of the resource's location. This suggests that meliponines are unable to encode direction, distance, or height in recruitment dance movements. Similarly, bumble bee foragers evidently do not communicate resource location and instead forage individually after being activated by the return of a successful forager (Dornhaus and Chittka 2004). Thus, the recruitment dance of meliponines appears to work as a mechanism to alert potential recruits about the presence of a highly profitable resource.

12.4.1.2 Sounds

The pioneering work of Esch et al. (1965) and Esch (1967) suggested that the stingless bee species *M. quadrifasciata* and *M. seminigra* were able to communicate the distance at which the resource was located through sound pulses inside the colony, produced by the flight muscles of successful scouts. Other work has shown similar results, describing in *M. panamica* the production of sound pulses by successful explorers; for instance, the duration of individual pulses correlated well with the distance at which the resource is found (Nieh and Roubik 1998). Moreover, they distinguished sound pulses produced during unloading food (trophallaxis) and pulses produced after unloading food (during the dance) in *M. panamica*. While the duration of the first type of pulses correlated negatively with food quality, the duration of the second type of sound correlated positively with the distance of the resource from the hive. That is, *M. panamica* may be able to communicate through sound pulses both the quality of the resource and its distance. However, the pulse durations were highly variable and thus it is unclear if they could provide the level of precise information observed in how recruits find the indicated food sources. Thus, this area requires further investigation. In a different species, *M. quadrifasciata*, no clear correlation has been found between the recruitment sound pulses and any parameter of the resource's location (Hrncir et al. 2000), although they were correlated with the quality of the food source (Hrncir et al. 2004). Thus, there are many aspects of recruitment communication in the genus *Melipona* that require further study, including the possibility of significant interspecific variation in communication mechanisms. In addition, it is necessary to conduct experiments where the sounds recorded in the colony are played back with high fidelity in order to see whether there is any effect of recruitment to a specific distance.

12.4.1.3 Trophallaxis

When a successful honey bee forager enters the colony, it can produce recruitment dances to attract potential recruits, some of which extend their proboscis to make contact with the mandible of the explorer. When the forager stops dancing it begins to share the collected nectar with her nestmates, resulting in a trophallactic interaction. Trophallaxis thus refers to the exchange of liquid food between individuals of the same colony (Wilson 1971). Trophallactic contact is a primary form of information transfer. It can give information about the quality and odor of food resources. Trophallaxis is believed to have evolved with the need to communicate. However, not all the bees that receive nectar follow the dancer, and vice versa. The bees that both follow the dance and get nectar, on the other hand, receive more information about the resource the explorer just visited. Many of these bees follow to receive the forager's dance information and may decide to visit the resource (Farina and Nunez 1995; Stabentheiner 1996; Wainselboim and Farina 2000; De Marco and Farina 2003).

12.5 Mechanisms of Communication Outside the Nest

Foragers have to make decisions about where and when to explore new places in search of resources. They can make decisions based on innate behavior, their experience, or their interactions with other bees through communication mechanisms. These interactions can occur, as previously stated, inside the nest or outside the nest. Social facilitation and pheromone deposition are mechanisms of communication outside the nest that have been observed in several species of meliponines.

12.5.1 Social Facilitation

In stingless bees, the phenomenon of social facilitation occurs when the behavior of executers influences the behavior of observers (Slaa and Hughes 2009). Social facilitation has also been studied in vertebrates, in which it seems to be one of the most important mechanisms to learn how to gather food, how to build nests, etc. (Wilson 2000). In social vertebrates, social facilitation provides further advantages: it makes it easier to find and handle resources and improves both the recruitment of nestmates and the collection of food, which may additionally reduce the individual probability of being preyed upon (Galef 1976; Burger and Gochfeld 1992; Galef and Giraldeau 2001). Social insects other than stingless bees also exhibit social facilitation, which has been shown to influence decisions about where to gather resources. In social bees, there are two types of social facilitation: local inhibition (foragers avoid places already occupied by other individuals) and local promotion (foragers are attracted to and learn about rewarding resources based upon the presence of other individuals already performing a task). Both have been described in meliponine species (Slaa 2003). Experience and learning also play an important role in the development of these two types of social facilitation. For example, the selection of patches of resources, or even the selection of individual flowers within a patch, can be guided by the physical presence of other bees on the basis of prior learning, modulating the final decision.

12.5.2 Pheromonal Signaling

Several sources of olfactory information can influence bees' orientation: the smell of the resource itself, pheromones and potentially locale odors (Aguilar and Sommeijer 2001; Nieh 2004; Arenas et al. 2007; Barth et al. 2008). Even though resource odors, such as floral scents, have proven to be very important in guiding foragers little has been studied regarding the importance of locale odors (the odors of the environment immediately surrounding the rewarding food source).

Pheromones are mixtures of chemical compounds secreted externally by bees. They convey critical information about many aspects of the status of the individual or of the colony. Pheromones used in recruitment are mainly secreted in glands located in the abdomen, head, and in the legs. In addition to the diversity in the chemical composition of pheromones in stingless bees, there is also a great variation among species in the way they are deposited. These behavioral differences in the ways of depositing pheromones may, in part, be adaptations to the different ecological needs of each species.

12.5.2.1 Complete Pheromone Routes

Some meliponine species can deposit an odor trail extending from the nest to the food source. Successful foragers lay a pheromone trail upon their return from the food source to the nest by depositing pheromone droplets on vegetation (Lindauer and Kerr 1960; Kerr et al. 1981). In some species, the distance between the marks ranges 1–8 m (Nieh 2004). In this way direction and distance to the food source are communicated.

12.5.2.2 Incomplete Pheromonal Routes

Some species leave incomplete pheromone trails that extend from the food source to part of the distance towards the nest. In this case, successful foragers deposit pheromone droplets nearby the advertised resource, but not all the way back to the nest, up to 8 m from the target in *M. rufiventris* and *M. compressipes* and up to 27 m in *Trigona spinipes* (Nieh 2004). By doing this, foragers signal the direction where the resource is located, but not the distance. Such partial odor trails appear to provide partial guidance for a swarm of foragers that is recruited at the nest and guided towards the food source.

12.5.2.3 Polarization of Pheromone Trails

This is an interesting behavior observed in *T. spinipes* and *T. hyalinata* and that may occur in other species (Nieh et al. 2003a, 2004). Basically, foragers deposit larger amounts of pheromones as they reach the resource, thus decreasing towards the nest. In this way recruits can determine with high precision where the food is located, because this is indicated with the highest concentration of pheromones.

12.5.2.4 Odor-Marking the Resource

This strategy refers to the deposition of pheromones on the resource itself. This behavior is frequently found together with pheromone trails, either complete or incomplete. *Melipona panamica* and *M. favosa*, however, only odor-mark the resource, without laying any pheromone trail (Nieh 1998b; Aguilar and Sommeijer 2001).

12.5.2.5 Aerial Pheromones

This is a hypothesis not tested rigorously to date (Kerr 1994). It refers to the releasing of pheromones during the flight back to the resource from the nest, creating a sort of tunnel filled with pheromones that recruits follow as they fly to the food.

12.6 Effect of Internal Information on Communication Systems

The decision to continue or to stop visiting a resource depends on a balance between external and internal information. However, the food recruitment process, as studied until recently, only considered the information from the scout bees and the nutritional needs of the colony to describe the phenomenon, without considering the internal status of recruits. In fact, the influence of internal factors, such as age and experience, has been little studied in meliponines. However, we do know that there are several behavioral stages that scouts and recruits go through, depending upon their experience with resources previously visited. These experiences in turn largely determine the effect that recruitment information will exert upon foragers (Biesmeijer and de Vries 2001). More detailed investigations revealed that naïve bees follow most of the information conveyed by scouts, contrary to experienced bees, which only need an indication that the resource is available once again (Biesmeijer et al. 1998). Other internal sources of information, such as individual's hormone levels, genetic load and experience, affect decisions about what foragers do and where and when to collect resources (Biesmeijer et al. 1998; Robinson 1998; Johnson et al. 2002). The genetic variability among individuals within a colony may give rise to different preferences: some honey bees have a tendency to collect pollen while others prefer nectar (Robinson and Page 1989; Page et al. 1995). Thus food recruitment information may have different influences on the recipients.

12.7 Efficiency and Accuracy of Communication Systems

The purpose of the recruitment systems is to concentrate foragers into a profitable resource trying to bring the majority of recruits to the exact site, preventing their spread in areas where there may be no resources to exploit (Sánchez et al. 2004). To achieve this goal, communication between individuals must be efficient. Efficiency in the context of communication may be defined as the amount of time and energy that explorers use to be "understood" by recruits. The cost of communication should therefore be much less than the energy gained by retrieving the resource, i.e., it must be profitable to communicate. The accuracy of the communication systems is part of their efficiency, and can be defined as the ability of recruits to choose the resource over other non-communicated alternatives (Sánchez et al. 2004). Choosing only one option is therefore the end result of the transfer of information made through the communication systems. Evaluating the accuracy is thus a practical way to measure the adaptation of communication systems in evolutionary time (Towne and Gould 1988).

12.8 Concluding Remarks

Previous studies on the accuracy of the communication system of *A. mellifera* focused on the waggle dance, in an attempt to find an adaptive explanation of this behavior in relation to the size of resource patches that *A. mellifera* foragers visit and their distribution in time and space (Towne and Gould 1988; Weidenmuller and Seeley 1999). However, we now know that additional factors, such as social facilitation, are an essential part of bee foraging communication systems. In fact, more recent studies with stingless bees have revealed high accuracy, even greater than that observed in *A. mellifera*, where bees are allowed to use all means and modalities of communication (Schmidt et al. 2003; Sánchez et al. 2004). However, communication mechanisms are not the only factors that affect accuracy. There is evidence that experience changes the decision making in bees (Sánchez et al. 2007) inexperienced bees being more accurate than experienced ones. Thus, it seems to be more appropriate to study recruitment systems from a multimodal perspective that incorporates information about individual forager experiences to understand the evolution of communication in highly social bee species.

The characteristics of the pot-honey, the pot pollen, and the cerumen the colonies generate are the result of decisions made by the foragers and the resources within the flight range of foragers. For some species that are highly efficient at recruiting nestmates, like *S. mexicana* (Sánchez et al. 2004), it is expected that the pot-honey they produce is less nectar-diverse than that produced by a less efficient bee, like *Tetragonisca angustula* (Aguilar et al. 2005), provided they occur in the same spot. Pot-honey characteristics may thus be inherently different between stingless bee species depending upon the specific recruitment mechanisms used by each bee species.

In this chapter, we briefly explained some of the processes involved in the organization of the foragers, which are the responsible for bringing resources to the colony. Those resources become the goods that beekeepers obtain from their colonies and that make stingless bees so appreciated by rural farmers, their families and until recently considered a delicacy in many international *cuisines*.

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