Review article

Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini)

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Abstract – The stingless bees (Hymenoptera, Apidae, Meliponini) have evolved sophisticated communication systems that allow foragers to recruit nestmates to good resources. Over the past 50 years, a growing body of research has shown that foragers can communicate three-dimensional resource location, uncovered several potential communication mechanisms, and demonstrated new information transfer mechanisms. Some of these mechanisms are unique to stingless bees and some may provide insight into how the ability to encode location information, a form of functionally referential communication, has evolved in the highly social bees. The goal of this review is to examine meliponine recruitment communication, focusing on evidence for contact-based, visual, olfactory, and acoustic communication and what these mechanisms can tell us about the evolution of recruitment communication in stingless bees.

1. INTRODUCTION

Insect societies have evolved information transfer systems of remarkable complexity (Wilson, 1971). Highly social bees (honeybees and stingless bees) use sophisticated methods to exploit resources such as pollen, nectar, water, resin, and nest sites (Kerr, 1969). Social bees can recruit, increase the number of nestmates searching for a particular resource, to specific or non-specific locations. Mechanisms that allow highly social bees to communicate resource location have been the subject of intensive study, particularly in honeybees, which can communicate the polar coordinates (distance and direction) of a resource through a waggle dance (von Frisch, 1967; Dyer, 2002). Researchers have sought to understand how such complex recruitment communication systems have evolved, and some studies have therefore focused on stingless bees, exploring possible homologies between the

recruitment communication of the Meliponini and the Apini (Kerr, 1969).

Stingless bees are a monophyletic group principally found in tropical and subtropical areas of America, Africa, Australia, and parts of Asia (Roubik, 1989). Unlike honeybees, which consist of approximately 11 species in one genus, stingless bees consist of several hundred species distributed through more than 36 genera (Michener, 2000). Honeybees and stingless bees are the only highly social bees, but stingless bees lead more diverse lifestyles, including obligate necrophagy (Roubik, 1982a; Camargo and Roubik, 1991), and can recruit for resources such as dead animals, pollen, nectar, mud, resin, water, and nests (Roubik, 1989). Stingless bees also use a greater diversity of recruitment communication systems (ranging from odor trails to the potential referential encoding of food location) than honeybees, in which all studied species use the waggle dance

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(Kerr, 1969; Roubik, 1989; Dyer, 2002). Research on stingless bees (Lindauer and Kerr, 1958; Kerr and Esch, 1965; Esch, 1967; Nieh et al., 2003c) has uncovered intriguing similarities and important differences between recruitment communication in the Meliponini and the Apini (honeybees). However, stingless bees have not been as intensively studied as honeybees, and thus our understanding of their biology is at an early stage relative to what is known of the Apini.

Within the last decade, interest in stingless bee recruitment communication has renewed. The goal of this review is to provide an overview of the field while focusing on these new findings, and examining their implications for understanding the evolution of recruitment communication in the Apidae. It has been argued that olfaction is the sole source of orientation information for honeybee recruits (Wenner, 2002), and this controversy may also play out in the stingless bees (Dyer, 2002). Thus one objective of this review is to examine the evidence for olfactory and non-olfactory communication. I will begin by discussing experimental methods and review the literature on recruitment to a specific spatial location. I will then examine several potential communication mechanisms, ranking them in their classically hypothesized order of evolutionary complexity: contact and visually-based communication, followed by olfactory communication, and finishing with a discussion of acoustic communication (von Frisch, 1967; Kerr, 1969; Wille, 1983). Although the phylogeny of the Meliponini remains largely unresolved, the classic ordering gives us a starting point to pursue evolutionary questions.

In the literature, multiple synonyms often exist for each species name and there can be disagreement on the appropriate synonym (Roubik, 1989; Michener, 1990; Inoue et al., 1999; Michener, 2000). I have therefore followed the assignments of Michener (2000) and refer the reader to the original source literature for more detailed information to determine the appropriate nomenclature.

2. METHODOLOGY

First, it is useful to review the methods generally used. These methods can be deceptively simple, as von Frisch (1967) noted, because although they are conceptually straightforward, there are several key details that should not be overlooked.

2.1. Intranidal observations

Lindauer and Kerr (1958) and Esch (1967) pioneered the description of motions and sounds produced inside the nest by foragers returning from a food source. In addition, they performed intriguing preliminary experiments testing the function of recruitment sounds. The general method is to train bees to a feeder at a specific location and record the behavior of these foragers when they return inside the nest (Esch, 1967). It is also possible to mark individually the entire colony and thus examine the role of intranidal contacts and the eventual success of nestmates in reaching the advertised food source (Seeley, 1995; Hrncir et al., 2000).

2.2. Feeder arrays

Karl von Frisch (1967) developed the general methods for investigating bee location communication. These methods involve training bees to an artificial feeder filled with sucrose solution (the experimental feeder) at a particular location. Once trained, these bees are known as experienced foragers (Biesmeijer and de Vries, 2001). The investigator then individually marks a fixed number of trained foragers that are regularly censused to insure that a constant number of bees visit the feeder. All newcomers (unmarked bees) are then counted and captured or immediately marked. These newcomers are presumptive recruits that must be shown (1) to come from the colony under study (generally by verifying their return to the colony) and (2) to have had a high probability of arriving based upon information provided in the nest by the experienced foragers. Both points can be demonstrated if newcomers from the colony under study arrive only when trained foragers feed and do not arrive when these trained foragers are captured. If these criteria are fulfilled, then newcomer recruitment has occurred.

In order to test whether bees can recruit to a specific location, at least two identical feeders, one control and one experimental, are placed

in an array in which only one spatial dimension is altered at a time. Foragers are trained to the experimental feeder, but not to the control feeder. For example, to test directional communication, the experimental and control feeders are placed at different directions equidistant from the nest and at the same height above the ground. If foragers can communicate the tested dimension, then significantly more recruits should arrive at the experimental feeder than at the control feeder. In order to control for potential site bias, it is important to conduct trials with the training feeder at different locations.

These methods are elegant, yet not necessarily simple to execute. Highly social bees will only recruit under the right conditions of colony need and generally only to an artificial feeder if it provides a resource that is more difficult to obtain in the natural environment (von Frisch, 1967; Roubik, 1989; Seeley, 1995). Thus researchers usually work during periods of natural food dearth in order to train bees to artificial feeders (Lindauer and Kerr, 1960; Esch, 1967; Nieh and Roubik, 1995; Jarau et al., 2000).

2.3. Experimental challenges

In general, the feeder array experiments testing meliponine location communication have used feeders placed less than 200 m from the nest (Tab. I), whereas the Meliponini probably forage at much greater distances for natural food sources. Roubik and Aluja (1983), reported flight ranges of approximately 1.7–2.1 km from capture and release studies of stingless bees (*Cephalotrigona capitata* and *Melipona panamica*) living in a tropical forest. Van Nieuwstadt and Ruano (1996) discovered a positive correlation between bee size (head width) and foraging distance: 600–900 m for *Trigona corvina*, *Partamona* aff *cupira* Smith[i], *Trigona* (*Tetragonisca*) *angustula*, and *Nannotrigona testaceicornis*, as estimated from capture and release studies. Thus it is desirable to test location communication at greater distances. However, such relatively short feeder-array distances are often the result of working in environments where, even in times of dearth, there are sufficient natural food sources such that foragers cannot be trained to greater distances and still recruit. It is also possible that foragers do not usually recruit for natural food sources beyond a certain distance. This remains to be determined.

With stingless bees, small colony sizes also limit the sample size per experiment and the number of experiments that can be conducted. A typical *M. quadrifasciata* colony contains 300–400 total bees, of which only a fraction are foragers (Lindauer and Kerr, 1960). Location experiments with such small colonies rapidly use up newcomers, turning them into experienced foragers. This occurs because a newcomer is defined as a forager that has never previously visited any feeder (von Frisch, 1967). Such a rigorous definition is necessary because bees are highly flower constant (Seeley, 1995; Slaa and Biesmeijer, in press) and can search on their own for food sources, particularly if they possess a search image acquired through prior experience and search as reactivated foragers (von Frisch, 1967; Biesmeijer and de Vries, 2001). In location experiments, counting foragers that have previously experienced the feeder at a different place or time as newcomers can lead to misleading results, such as finding no or weak communication of food location when experienced foragers search on their own for displaced food sources (Nieh et al., 2003b). If significantly more reactivated foragers continue to arrive at the experimental feeder, even after the feeder positions are changed, it is possible to conclude that location information is being transferred to reactivated foragers. However, if reactivated foragers arrive in equal numbers at experimental and control feeders, one cannot conclude that there is no communication of location because such information may be present and used by newcomers, but not by reactivated foragers. The effect of meliponine location communication on reactivated foragers has yet to be explicitly studied. Typically, honeybee researchers distinguish between newcomers and reactivated foragers by capturing and killing all newcomers once they become experienced foragers (von Frisch, 1967; Seeley, 1995). However, this solution would rapidly destroy a small colony of stingless bees, and thus the usual practice is to mark

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[i] *P. cupira* does not occur in Costa Rica, and thus the species may be either *P. bilineata* or *P. orizabaensis* (Roubik, personal communication).

Table I. Summary of location communication experiments in stingless bees. Results are pooled for all distance, direction, and height experiments with each respective species. P-values are obtained from a 2-tailed Chi-square test (*P = 0.001, **P = 0.0001). The maximum distance to which bees were trained is given for each type of experiment in order to provide a sense of scale. Multiple control values indicate that more than one control feeder was used. Dashes indicate no data available.

Location communication	Species	DISTANCE Training specific?	Training feeder	Training #control	#exp	DIRECTION Training specific?	Training feeder	Training #control	#exp	HEIGHT Training specific?	Training feeder	Training #control	#exp	Paper(s)
Non-specific	*Plebeia droryana*	no	200 m	79	17	no	150 m	21	25	?	—	—	—	Lindauer & Kerr 1958, Lindauer & Kerr 1960
Some specificity	*Partamona helleri*	?	—	—	—	yes**	36 m	14	53	?	—	—	—	Kerr 1969
	T. carbonaria	no	150 m	11, 211	125	yes**	150 m	31, 40	144	?	—	—	—	Nieh et al. 2000
	M. scutellaris	no	100 m	55	27	no	160 m	20	27	?	—	—	—	Lindauer & Kerr 1958, Lindauer & Kerr 1960
		yes**	≤30 m	33	107	yes**	140 m	60	203		—	—		Jarau et al. 2000[†]
		no	50–70 m	133	120						—	—		Jarau et al. 2000[†]
	M. quadrifasciata	yes**	≤40 m	63	118	yes**	≤30 m	33	94	?	—	—		Jarau et al. 2000[†]
		no	50 m	78	45	no	50–140 m	73	65		—	—		Jarau et al. 2000[†]
	T. spinpes	yes*	300 m	0, 2	19	yes*	300 m	3, 3	78	?	—	—	—	Lindauer & Kerr 1958, Lindauer & Kerr 1960
	S. depilis[††]	yes**	50 m	0–2.5%	97.5–100%	yes**	50 m	0–1.1%	98.9–100%	?	—	—	—	Schmidt et al. 2003
	T. hyalinata	yes**	146 m	14	61	yes**	146 m	26	92	?	—	—	—	Nieh et al. 2003a
	M. mandacaia	yes**	100 m	0	22	yes**	100 m	0	34	no	12 m high	44	41	Nieh et al. 2003b
3-D specificity	*S. postica*	yes**	150 m	6	117	yes**	150 m	2	42	yes**	20 m high	0	80	Lindauer & Kerr 1958, Lindauer & Kerr 1960
	M. panamica	yes**	175 m	12	103	yes**	175 m	14	180	yes**	40 m high	26	252	Nieh & Roubik 1995, 1998
	M. bicolor	yes**	100 m	3	45	yes**	100 m	3	49	no	0 m high	7	9	Nieh et al. 2003b
										yes*	12 m high	0	15	Nieh et al. 2003b

[†] See text. [††] Sample sizes not given.

and release the newcomers and to not count marked bees as newcomers (Nieh and Roubik, 1995).

Thus a limited time window coupled with small available sample sizes creates challenges for studying recruitment communication in some stingless bee species. In addition, some species are difficult to work with, being so aggressive that they resist resettlement and generally die in observation nests (*T. spinipes*, Almeida and Laroca, 1988); are difficult to train, preferring to attack feeders placed near the nest rather than feed at them (personal observations); are highly sensitive to disturbances (Sakagami, 1966; Roubik, 1989; Kolmes and Sommeijer, 1992); or are susceptible to stress caused by artificial manipulations (Nogueira-Neto, 1997, 1999).

3. RECRUITMENT TO NON-SPECIFIC LOCATIONS

The classic hypothesis, in keeping with the theory of ritualization (Tinbergen, 1952; Zahavi, 1980; Krebs and Dawkins, 1984; Bradbury and Vehrencamp, 1988), posits that bee recruitment communication evolved from excitatory behaviors that do not communicate resource location into communicatory behaviors that indicate resource location (Kerr, 1960; Esch et al., 1965; von Frisch, 1967; Kerr, 1969; Michener, 1974).

Although the communication of resource location can be beneficial, allowing social insects to rapidly exploit food sources (Hölldobler and Wilson, 1990; Seeley, 1995), these benefits depend upon several factors such as colony need, the spatial and temporal distribution of resources, and whether the resource is amenable to exploitation through mass recruitment (Roubik, 1982b; Seeley, 1995; Breed et al., 2002; Dornhaus, 2002, 2004; Sherman and Visscher, 2002; Jarau et al., 2003; Slaa, 2003; Biesmeijer and Slaa, 2004). Thus location communication may not always be advantageous (von Frisch, 1967; Dyer, 2002; Dornhaus and Chittka, 2004), and searching for advertised resources at non-specific locations appears to exist in all social bee groups (Kerr, 1969), including the primitively eusocial bumblebees (Dornhaus and Chittka, 2001). Such searching is not location-specific, but is not necessarily random, because foragers may use a specific search pattern (Wehner, 1992) and because the searches likely involve some level of olfactory orientation (Dyer, 2002; Wenner, 2002).

In honeybees, returning foragers perform a round dance for food sources close to the nest, and this round dance leads recruited nestmates to search in all directions (von Frisch, 1967). Only the waggle dance, performed for food sources at greater distances (typically >100 m for *Apis mellifera carnica*), leads foragers to search at a particular distance and direction (von Frisch, 1967; Gould, 1976; Dyer, 2002). In bumblebees, it was known that foragers of some species produce excitatory movements upon returning from a rich nectar source (Wagner, 1907; Brian, 1954; Jacobs-Jessen, 1959), and recent studies show that this behavior results in an increase in foraging activity at non-specific locations (Chittka and Dornhaus, 1999; Dornhaus and Chittka, 1999, 2001, 2004; Dornhaus and Cameron, 2003).

In comparison to the number of meliponine species cited as communicating resource location, there are surprisingly few species for which even preliminary feeder array data are published (Tab. I). I therefore focus on species for which published data are available. Recruitment to non-specific locations has been reported in *Nannotrigona testaceicornis*, *Meliponula* (*Axestotrigona*) *ferruginea tescorum*, *Frieseomelitta silvestrii, F. flavicornis*, and *F. freiremaiai* (Kerr, 1969) and shown through recruitment experiments with *Plebeia droryana* (Lindauer and Kerr, 1958). Lindauer and Kerr (1958) performed preliminary experiments with *M. scutellaris* and their data also suggest no communication of distance or direction in this species (Tab. I). Such non-specific location recruitment may be an ancestral state in the evolution of recruitment location communication (Lindauer and Kerr, 1958; Kerr, 1969). Overall, data on species demonstrating a complete inability to communicate distance and direction are quite limited (Tab. I). It is unclear if this paucity of data reflects a rare strategy or if researchers have selectively focused on species with some ability to communicate distance or direction.

4. SPECIFIC LOCATION COMMUNICATION

The communication of resource location may represent a more derived state in the evolution of bee recruitment communication systems (Kerr, 1960; Esch et al., 1965; von Frisch, 1967; Kerr, 1969; Michener, 1974). Table I shows that the communication of resource location is widespread among the stingless bees, but can occur to different degrees of specificity, even to the extent of indicating height (which honeybees do not communicate, Dyer, 2002). It is unclear whether increasing levels of location specificity or accuracy reflect an evolutionary trend, because location specificity may also be tailored to the habitat and niche occupied by different species over evolutionary time (Nagamitsu and Inoue, 1997; Eltz et al., 2001, 2002).

For example, *T. carbonaria* is thought to be a relatively basal species (on the basis of behavioral traits), and foragers can guide nestmates to the correct direction, but not the correct distance (Nieh et al., 2000). In contrast, *Scaptotrigona postica* has a good ability to communicate three-dimensional location and can recruit nestmates to a feeder placed 20 m above the ground (Lindauer and Kerr, 1958). Within the *Melipona*, there is evidently variation in the ability of different species to communicate three-dimensional food location (Tab. I). However the phylogenetic relationship between these three groups remains unclear (Wille, 1979, 1983; Michener, 1990; Camargo and Pedro, 1992; Fernandes-Salomao et al., 2002; Costa et al., 2003).

Detailed studies of habitat-specific variations in location communication have only been conducted with the *Melipona*. *Melipona panamica* lives in tropical forests with high canopies (up to 40 m high, Croat, 1978), whereas *M. bicolor* lives in an Atlantic Rainforest habitat with intermediate canopy heights (approximately 15 m, Wilms et al., 1997), and *M. mandacaia* (not to be confused with *M. mandaçaia*, Nogueira-Neto, personal communication) lives in an arid Caatinga habitat where food sources are seldom more than a 5–6 meters above the ground (Martins and Aguilar, 1992; Rizzini, 1997). These species possess a correspondingly graded ability to communicate

height. In paired feeder experiments, *M. panamica* shows an excellent ability to communicate height, recruiting nestmates to the correct height, even for height differences as small as 10 m (Nieh and Roubik, 1995). *Melipona bicolor* only recruited nestmates to the correct height when the feeder was at canopy height (12 m high); and *M. mandacaia* could not recruit to the correct height, regardless of whether the feeder was 12 m high or on the ground (Nieh et al., 2003b). Food resources can be dispersed at different canopy levels, and thus the ability to specify height could be advantageous, particularly in competitive environments with tall canopies (Roubik, 1993; Nagamitsu and Inoue, 1997; Roubik et al., 1999; Eltz et al., 2001).

It is unclear whether there is variation in the ability to communicate distance and direction among the *Melipona*. Jarau et al. (2000) reported that *M. quadrifasciata* communicated direction and distance only when the food source was respectively ≤30 m and ≤40 m from the nest (Tab. I). *Melipona scutellaris* communicated direction up to 140 m from the nest (the maximum distance tested), but communicated distance only up to 30 m from nest. In these experiments, both species appeared to search initially at random locations before showing some ability to communicate specific location (Jarau et al., 2000). These results are surprising given that precise distance communication should be more important for more distant food sources than for nearby food sources (Weidenmuller and Seeley, 1999; Dyer, 2002). Because experienced foragers may have been counted as newcomers (sample sizes exceeded the total number of foragers in the colonies used, Jarau et al., 2000), the interpretation of these results is unclear (Nieh et al., 2003b).

5. MECHANISMS OF INFORMATION TRANSFER

5.1. Contact and visual communication

5.1.1. Contact

Trophallactic contact (food exchange) may be the most primitive form of meliponine communication (Hart and Ratnieks, 2002) and

could provide information about food quality and odor, as it does in honeybees (De Marco and Farina, 2003). For example, Hrncir et al. (2000) showed that the number of trophallactic (food exchange) contacts between *M. quadrifasciata* and *M. scutellaris* recruiters and potential recruits increases before the recruit successfully reaches the feeder. More such experiments should be conducted to determine the amount and type of information that foragers need to receive before they arrive at the advertised resource.

Studies of meliponine nest recruitment behavior report jostling (bees appearing to purposefully run and bump into nestmates), zigzag running (changing direction several times while running), and spinning (clockwise and counterclockwise body rotations) by recruiting foragers (Lindauer and Kerr, 1958; Kerr, 1960; de Bruijn and Sommeijer, 1997; Nieh, 1998a; Hrncir et al., 2000). In honeybees, physical contact, particularly antennal contact, may be important in the transmission of waggle dance information (Rohrseitz and Tautz, 1999). In stingless bees, body contacts may help to transfer relevant odors and communicate excitement about the relative quality of the food source. Hrncir et al. (2000) showed that the number of bees visiting a feeder is highly correlated with the mean number of jostles performed by recruiting *M. quadrifasciata* and *M. scutellaris* foragers inside the nest. In addition, antennal contacts may help transfer acoustic information to recruits (Nieh, 1998a; Nieh and Roubik, 1998). *Melipona panamica* nestmates hold their antennae closely around and sometimes touching the vibrating wings and body of a recruiting forager (Nieh, 1998a).

5.1.2. Visual

Visual communication plays a role in recruitment orientation outside the nest. Slaa et al. (2003) have shown that foragers of *Trigona amalthea*, *Tetragonisca angustula, Partamona cupira*[ii], and *Oxytrigona mellicolor* display local enhancement and orient towards the visual presence of nestmates on a food source. Foragers of several species may also guide experienced foragers for at least part of the distance to the food source, and visual tracking

of the leader is hypothesized to be the primary orientation mechanism (Esch, 1967; Kerr, 1969). Esch et al. (1965) reported observing *M. quadrifasciata* foragers perform a zigzag piloting flight that pointed in the direction of the feeder, but which the nestmates did not follow beyond 30–50 m (Esch, 1967). Kerr (1969, 1997) proposed that the whitish reflective abdominal hairs of some species may facilitate orientation to experienced foragers as they leave the nest. *Melipona panamica* foragers appear to communicate direction outside the nest because separating experienced foragers from potential recruits as they exit the nest resulted in equal numbers of newcomers arriving at the control and experimental feeders, located in opposite direction from the nest (Nieh and Roubik, 1998). However zigzag piloting flights have not been observed in *M. panamica* (Nieh and Roubik, 1998), *M. scutellaris* (Hrncir et al., 2000), or of *M. quadrifasciata* (Hrncir et al., 2000).

5.2. Olfactory communication

Several odor sources can influence forager orientation in social bees: food odor, olfactory signals, cues deposited by foragers, and locale odors—odors of the environment surrounding the food source (von Frisch, 1967; Goulson et al., 2000; Goulson et al., 2001; Dyer, 2002; Nieh et al., 2003b). To date, no studies have specifically isolated and examined the effect of locale odors on stingless bee foraging.

Whenever evidence for attractive odor marking of food sources has been sought, it has been found in the highly social bees (Kerr et al., 1963; von Frisch, 1967; Kerr, 1972; Nieh, 1998b; Aguilar and Sommeijer, 2001; Stout and Goulson, 2001; Jarau et al., 2002; Nieh et al., 2003d; Schmidt et al., 2003; Hrncir et al., 2004). However, stingless bees are the only bees known to produce long odor trails beginning near the nest and extending to the food source (reaching a reported 900 m in *T. amalthea,* Kerr, 1960). Although odor trails usually lead to nectar or pollen resources, obligate necrophages such as *T. necrophaga* reportedly use odor trails to indicate their food sources (Roubik, 1982a). Bumblebees also produce odor trails, but these are limited to the close vicinity of the nest (Cameron and Whitfield, 1996; Cameron et al., 1999). Within

[ii] Ibid.

the stingless bees, there is a gradation of strategies, ranging from complete odor trails that begin in the vicinity of the nest and extend to the food source, short odor trails that only extend a short distance away from the food source in the direction of the nest (Nieh et al., 2003a), and odor-marking of the food source alone (Nieh, 1998b; Hrncir et al., 2004). Odor trail marking is reported in many meliponine species (Lindauer and Kerr, 1958, 1960; Kerr and Cruz, 1961; Kerr et al., 1963; Kerr and Esch, 1965; Kerr, 1960, 1969, 1972, 1973, 1994; Blum et al., 1970; Kerr et al., 1981; Kerr and Rocha, 1988), but I will focus on those species for which there are data showing that the putative odor marks attract nestmates.

5.2.1. Complete odor trails

Lindauer and Kerr (1958) discovered that stingless bees could produce an odor trail consisting of odor droplets deposited periodically on vegetation between a food source and the nest. The distance between odor marks ranges from 1 m to 8 m in different species (Kerr, 1969). In all described cases, such odor marking occurs after the forager has finished feeding and as she returns back to the nest (Lindauer and Kerr, 1958; Kerr, 1969, 1972, 1973; Kerr et al., 1981; Nieh et al., 2003a). Foragers prefer to land on prominent vegetation, and thus odor trails can be studied on ropes or wires hung with leaves and elevated above the ground (Lindauer and Kerr, 1958; Kerr et al., 1963). The literature on odor trails has focused on complete odor trails that begin 7.5 m (Lindauer and Kerr, 1958) to 35 m (Kerr et al., 1981) from the nest and extend to the food source. However, little is known about the detailed spatial structure of these trails (Lindauer and Kerr, 1958, 1960).

Lindauer and Kerr (1958) provide the only detailed descriptions of complete odor trails. They followed and recorded the spatial pattern of odor marks left by *S. postica*, recording a fairly even spacing of odor marks with increasing distance from the feeder (see Figs. 10–12 in Lindauer and Kerr, 1958). They also performed a series of ingenious experiments showing that these odor marks were necessary for recruitment. Foragers were trained to the opposite side of a pond, but did not recruit over the open water until a rope

with leaves was stretched across the pond. Foragers began to odor-mark the leaves and recruited. Kerr et al. (1963) performed a similar set of experiments on a grass field with *S. bipunctata* and *T. spinipes*, using wires attached to the tops of bamboo poles.

5.2.2. Short odor trails

Kerr and Rocha (1988) hypothesized that *M. rufiventris* and *M. compressipes* could deposit a short odor trail consisting of one to three putative "urine" marks (anal droplets) extending up to 8 m from the food source (Kerr, 1994). However, no experiments were conducted to test the attractiveness of these putative marks. Recently, Nieh et al. (2003a) reported that *T. hyalinata* foragers produced short odor trails, that extended up to 27 m from the food source towards a nest 146 m away. Displacing a rope odor-marked by *T. hyalinata* foragers resulted in a significant increase in the number of newcomers visiting a control feeder, as did displacing the odor-marked feeder alone.

5.2.3. Odor trail polarization

Lindauer and Kerr (1958) first hypothesized that stingless bee odor trails might increase in concentration at the food source to indicate the exact food location. Kerr et al. (1963) introduced the term "polarity" to describe this effect, and experiments show that *Scaptotrigona postica* (Kerr et al., 1963) and *T. hyalinata* (Nieh et al., 2003a) newcomers will ignore a feeder placed within the odor trail, between the nest and the training feeder (Tab. I). Thus the newcomers have some means of determining the correct endpoint. Recently, Schmidt et al. (2003), showed that *Scaptotrigona depilis* is able to find the odor-marked feeder, even when it is displaced away from the putative odor trail or into the putative odor trail. The ability of newcomers to reach the correct endpoint may be due to differences in the concentration of odor marks deposited on the target (Lindauer and Kerr, 1960).

5.2.4. Target-only odor marking

Target-only odor marking, defined as odor-marking of the food source alone, is widespread among the social bees (Kerr et al.,

1963; Stout and Goulson, 2001). However, because some meliponine species also use odor trails, one must show that meliponine foragers mark the target, but do not deposit an odor trail, to demonstrate target-only odor marking. To do this, one may observe that foragers do not land to deposit a putative odor trail or show that foragers do not need or use an odor trail to recruit across a water gap, because odors cannot be effectively deposited or retain their spatial structure on water (Lindauer and Kerr, 1958; Nieh and Roubik, 1995). The latter form of evidence is more conclusive.

Although target-only odor marking may be widespread among stingless bees, good evidence has only been obtained for *M. panamica*. In this species, foragers odor-mark the food source (Nieh, 1998b), but do not deposit odor trails because they could recruit to the correct direction across a large water gap that prevented odor trail deposition (Nieh and Roubik, 1995). On the basis of visual observations, *Frieseomelitta silvestrii, F. flavicornis, F. freiremaiai* (Kerr, 1969), *M. panamica* (Nieh and Roubik, 1995), *M. scutellaris, M. quadrifasciata* (Hrncir et al., 2000), *M. mandacaia*, and *M. bicolor* (Nieh et al., 2003b) foragers have not been observed to land and deposit odor trails. It is unclear whether *M. rufiventris* and *M. compressipes* deposit short odor trails, because the attractiveness of the putative marks was not tested (Kerr and Rocha, 1988; Kerr, 1994).

Target-only odor marking may account for the ability of *M. bicolor* foragers to specifically recruit nestmates to the top of a 12 m high tower, but not to its base, because of differences in the active space of odor marks caused by increased wind or other microclimate differences (Bradbury and Vehrencamp, 1988) between the base and the top of the tower (Roubik, 1989; Nieh et al., 2003b).

5.2.5. Aerial odor trails

Kerr (1969, 1994) hypothesized that foragers of some species such as *Partamona helleri* deposit aerial odor trails, creating an "odor tunnel" as they fly to the food source. Kerr (1994) proposed that this mechanism could function during windless conditions

under a dense forest canopy. To date, no studies have examined this hypothesis.

5.2.6. Odor mark sources

Meliponine odor marks have several glandular sources (Cruz-Landim et al., 1998) and may also consist of cues such as anal droplets. Using feeder choice experiments, Jarau et al. (2002) and Hrncir et al. (2004) have shown that tarsal gland extracts from *M. seminigra* are attractive to foragers. Nieh et al. (2003d) reported that *M. mandacaia* foragers produce an attractive ventro-abdominal odor in addition to other attractive odor sources, including an odor cue, anal droplets.

Anal droplets are clear droplets of fluid excreted from the anus of foragers, usually after foragers have finished feeding. They have been described in several species: *M. rufiventris* and *M. compressipes* (Kerr and Rocha, 1988), *M. favosa* (Aguilar and Sommeijer, 1996, 2001), *M. panamica* (Nieh, 1998b), and *M. mandacaia* (Nieh et al., 2003d) and are generally produced in greater number at more dilute food sources for which foragers do not recruit (*M. mandacaia*) or which lead foragers to greatly reduce their rate of recruitment (*M. panamica*). However, anal droplets can attract nestmates in paired feeder assays (Aguilar and Sommeijer, 2001; Nieh et al., 2003d). These droplets may therefore be excreta (Nieh, 1998b) and serve as cues, not signals (Nieh et al., 2003d). Further work may reveal that meliponine food-marking odors generally consist of multiple odor sources, as has been shown in honeybees (Free et al., 1982; Free and Williams, 1983).

Lindauer and Kerr (1958) reported that mandibular glands extracts could attract *S. postica* foragers to a food source and were used in depositing odor trails as well as marking the feeder. Subsequent studies found a similar attractive role for mandibular gland secretions in *T. spinipes* (Kerr et al., 1981) and *T. hyalinata* (Nieh et al., 2003a) odor trails. However, a recent study by Jarau et al. (2004) found attraction to labial gland excretions deposited at food sources, not to mandibular gland excretions. Thus the role of mandibular gland secretions in odor marking should be more rigorously evaluated. The composition of mandibular gland secretions has been examined in species such

as *T. silvestriana* (Johnson et al., 1985), *Scaptotrigona tubiba* and *S. postica*, and is complex, consisting of over 25 compounds that exert different behavioral effects (Kerr, 1969) and increase in diversity with worker age in *Meliplebeia denoiti* (de Korte et al., 1998) and *S. postica* (Cruz-Landim and Ferreira, 1968). A major component is 2-heptanol (Smith and Roubik, 1983), which, in a synthetic preparation, attracted *T. spinipes* foragers to a feeder (Kerr et al., 1981). Citral is also present in the mandibular gland secretions of many species (Kerr, 1969), and a synthetic preparation of citral can attract *T. subterranea* foragers to feed (Blum et al., 1970). In the robber stingless bee, *Lestrimelitta*, high concentrations of citral released during attacks may assist in the orientation of *Lestrimelitta* recruits towards the victimized nest (Wittman et al., 1990; Sakagami et al., 1993).

5.2.7. Odor-mark deposition

Stingless bees can deposit odors in several ways. Mandibular gland secretions may be deposited by rubbing the substrate with the mandibles (Kerr, 1969), and tarsal gland secretions by walking on the substrate (Jarau et al., 2002). When depositing odor marks on surrounding foliage, foragers generally land briefly (average of 1.4 ± 0.7 s for *T. hyalinata*, Nieh et al., 2003a) and rub their mandibles (Lindauer and Kerr, 1958; Kerr, 1972; Kerr and Rocha, 1988) and tongue (*T. hyalinata*, Nieh et al., 2003a) against the substrate. Foragers can also groom when depositing odor marks, but it is unclear if grooming deposits odors (Kerr, 1994; Nieh et al., 2003d).

5.3. Acoustic recruitment behavior

Sound production is an intriguing aspect of meliponine recruitment behavior. Although studies document the existence of recruitment sounds in several species, these sounds have been quantitatively studied in relatively few. Bees do not possess tympana, and thus do not hear the pressure component of sound (Michelsen et al., 1986b). However, the Meliponini may share the ability of honeybees to detect the particle-velocity component of sound (Kirchner, 1994; Michelsen, 2003) and sound vibrations transmitted through the substrate (Michelsen et al., 1986a; Sandeman et al., 1996; Visscher et al., 1999; Nieh and Tautz, 2000).

There is evidence from preliminary playback experiments that meliponine recruitment sounds play a role in activating nestmates that have previously experienced the feeder (reactivated foragers) to go out and forage (Lindauer and Kerr, 1958; Esch, 1967). In addition, correlations have been found between recruitment sounds and the quality and location of the food source (Esch et al., 1965; Nieh and Roubik, 1998; Aguilar and Briceño, 2002; Hrncir et al., 2002; Nieh et al., 2003c).

5.3.1. Sound production

To date, successful foragers of 18 meliponine species have been observed to produce pulsed sounds upon returning to the nest: *Frieseomelitta silvestrii*, *F. flavicornis*, *F. freiremaiai*, *Leurotrigona muelleri*, *M. bicolor*, *M. costaricensis*, *M. mandacaia*, *M. seminigra merrillae*, *M. panamica*, *M. scutellaris*, *M. seminigra*, *Nannotrigona testaceicornis*, *Plebeia droryana*, *Cephalotrigona capitata*, *S. postica*, *Tetragonisca angustula*, *Trigona (Hetetrotrigona) carbonaria,* and *Meliponula (Axestotrigona) ferruginea tescorum* (Lindauer and Kerr, 1958; Esch, 1967; Kerr, 1969, 1994; Nieh and Roubik, 1998; Hrncir et al., 2000; Aguilar and Briceño, 2002; Hrncir et al., 2002; Nieh et al., 2003c). These sounds have air- and substrate-borne components (Esch, 1967) and may be produced as foragers vibrate their wings and thoracic muscles, much as honeybees produce sound during the waggle dance (Michelsen, 2003). No detailed physiological investigations of sound production mechanisms have yet been conducted with stingless bees.

In *Meliponula* (*Axestotrigona) ferruginea tescorum* and *Nannotrigona testaceicornis*, Kerr (1969, p. 141) reported a form of acoustic chorusing, "in these species, when a worker, having discovered a source of food, enters the hive, it produces a characteristic sound. Immediately thereafter the bees closest to it begin to produce the same sounds, and then others join in, and within less than 1 min all the hive will be buzzing, and all available bees leave the hive looking for food". This behavior has not been investigated in greater detail.

Kerr et al. (1963) also reported that *M. quadrifasciata* foragers produce sounds on food sources. In *M. panamica,* foragers produce sounds upon departing from a feeder, and the rate of sound production is positively correlated with sucrose concentration, suggesting that feeder sounds may be related to forager perceptions of food quality (Nieh, 1998b). However, the significance of feeder sounds remains a mystery.

5.3.2. Effect of food location

Recently, Hrncir et al. (2003) have shown that *M. seminigra* foragers, like honeybees (Srinivasan et al., 2000; Esch et al., 2001), can use optic flow to measure the distance to a food source. Esch et al. (1965) discovered that some stingless bees (*M. seminigra merrillae* and *M. quadrifasciata*) may encode the distance to the food source in the duration of recruitment sound pulses. Foragers of both species increased the duration of sound pulses as distance to a food source increased. This discovery created great excitement because honeybees were the only animals previously known to referentially encode food distance (von Frisch, 1967). The discovery of a meliponine distance-encoding communication system would provide a new animal model of functionally referential communication and perhaps yield insights into the evolution of the waggle dance in the closely related honeybees (Esch et al., 1965; Esch, 1967). Some 80 years after von Frisch's (1923) discovery of the waggle dance, the ability of honeybee foragers to communicate distance and direction with the waggle dance has largely been accepted, following numerous tests (Gould, 1976; Michelsen et al., 1989; Esch et al., 2001; Sherman and Visscher, 2002; Dornhaus and Chittka, 2004). However, the ability of any *Melipona* species to communicate distance through sounds has not been conclusively demonstrated.

The evidence for the acoustic communication of distance is primarily based upon correlations between sound pulse duration and food distance in different species: *M. seminigra merrillae*, *M. quadrifasciata* (Esch, 1967), *M. panamica* (Nieh and Roubik, 1998), *M. costaricensis* (Aguilar and Briceño, 2002), *M. mandacaia*, and *M. bicolor* (Nieh et al.,

2003c). In *M. panamica*, Nieh and Roubik, (1998) found correlations between the height above ground and the distance to a rich (2.5 M) food source and the duration of sound pulses during two phases of the recruitment performance: respectively, the food-unloading phase and the dance phase. During the food-unloading phase, when returning foragers transfer their gathered nectar to nestmates, sound pulses were significantly longer if the food source was on the ground than when it was 40 m above the ground in the forest canopy. During the dance phase, when recruiting foragers run rapidly and can spin clockwise and counterclockwise inside the nest, the sound pulses increased in duration with increasing distance to the food source.

Hrncir et al. (2003) state that the term "dance" is inappropriate as applied to these spinning motions because they do not communicate distance or direction. However, the term "dance" is also applied to forms of honeybee behavior related to foraging that do not communicate distance or direction, such as the tremble dance (Seeley, 1992; Nieh, 1993; Seeley et al., 1996) and round dance (von Frisch, 1967; Waddington, 1982; Waddington and Kirchner, 1992; Kirchner et al., 1998). Moreover, correlations are found between distance and sounds produced during this spinning phase in *M. panamica* (Nieh and Roubik, 1998). Thus the communication of distance may occur during the dance phase of *M. panamica*, as it does in the honeybee waggle dance (von Frisch, 1967).

Nieh and Roubik (1998) also performed experiments testing the ability of newcomers to find the food source at the correct direction, distance, and height based upon information transmitted inside the nest (see above). These experiments prevented newcomers from following recruiters, even for a short distance, to the food source and, in the distance and height experiments, removed odor-marks deposited by foragers on the food sources. When such potential sources of information were excluded, *M. panamica* newcomers did not arrive at the correct direction (equal numbers arrived in opposite directions), but significantly more did arrive at the correct distance and height. These experiments did not disturb locale odors or putative odor trails. Aguilar and Sommeijer (2001) argued that these separation experiments

did not exclude the possibility of newcomers using odor trails or locale odors, because such odors cannot be removed. However, if newcomers can use odor trails or locale odors alone, they should have arrived in the correct direction during the separation treatment. They did not.

One could object that the separation treatment was disruptive and prevented newcomers from using odor trail and locale odor information. However, significantly more newcomers arrived at the correct distance and height in separate experiments during the separation treatment, even when forager-deposited odors on the feeder were removed (Nieh and Roubik, 1998). Thus the existence of forager-deposited odor trails does not consistently account for the results of the direction, distance, and height separation experiments with *M. panamica* (Nieh, 1998a, b; Nieh and Roubik, 1998).

Furthermore, there is no evidence in *M. panamica* for forager orientation over long distances to forager-deposited odors (Nieh and Roubik, 1998). Forager-deposited odor marks on the feeder are only able to influence forager orientation within 12 m of the feeder (Nieh, 1998b). Thus distance and height information are evidently transmitted inside the nest, whereas direction information is evidently transmitted outside the nest.

It remains unclear if the information content of *M. panamica* recruitment sounds is sufficient to account for the specificity of location communication. There are high variances in the sound pulse durations, particularly in the food unloading pulses whose durations may be correlated with resource height (Nieh and Roubik, 1998). Correlations between distance and other temporal parameters such as pulse duration also exist in *M. costaricensis*, although the variances of the putative distance-encoding sounds are again quite high at each distance (Aguilar and Briceño, 2002).

Such high variances may be due to the analysis of weak and strong performances by foragers with varying degrees of motivation. In honeybees, variances in the strength of recruitment performances have long been noted (von Frisch, 1967) and detailed investigations have shown that forager motivation affects parameters such as the return phase of the waggle dance (Seeley et al., 2000) and the reversal rate in the round dance (Waddington, 1982;

Waddington and Kirchner, 1992). There is evidence that nestmates are sensitive to variations in recruiter motivation in honeybees (von Frisch, 1967) and stingless bees (Nieh, 1998a, b). In *M. panamica*, recruitment performances for food of different qualities attract different numbers of potential recruits (Nieh, 1998a). More potential recruits cluster with their antennae held closely around the vibrating wings of sound-producing recruiters returning from a rich 2.5 M food source than from a poorer 1.0 M food source (Nieh, 1998a) and recruitment rates are significantly higher for richer food sources (Nieh, 1998b).

There are also questions concerning the ability of some *Melipona* species to encode distance in recruitment sounds. Hrncir et al. (2000) performed a detailed analysis of recruitment sounds and found no evidence for distance encoding in *M. quadrifasciata* or in *M. scutellaris*. It is quite possible that different species possess different communication mechanisms. However, they were unable to replicate the results of Esch et al. (1967) with *M. quadrifasciata*. The smaller sample sizes used by Hrncir et al. (2000) may partly account for differences between their results and those of Esch et al. (1967). It is also unclear if *M. quadrifasciata* foragers successfully recruited while Hrncir et al. (2000) recorded sounds, and thus it is uncertain if recruitment communication was associated with the measured sounds (Nieh et al., 2003c).

5.3.3. Effect of forager motivation

Recently, Hrncir et al. (2002) have shown that stingless bee recruitment sounds can vary with forager motivation. *Melipona seminigra* foragers reduced the amount of recruitment sound produced as food quality decreased by decreasing the pulse duration and increasing the interpulse interval (the time between two sound pulses). Limited sucrose solution flow also led to shorter pulses and longer interpulses than unlimited flow, and pulse duration increased with increasing foraging duration (Hrncir et al., 2002). Nieh et al. (2003c) reported that food quality (sucrose concentration) has a similar effect on *M. mandacaia* and *M. bicolor* recruitment sounds, decreasing the pulse duration and increasing the interpulse duration as sucrose concentration decreases.

This raises the question of whether pulse duration is a reliable measure of distance, given that it varies with both distance and food quality. However, Nieh et al. (2003c) reported that *M. mandacaia* and *M. bicolor* foragers did not successfully recruit newcomers to sucrose concentrations sufficiently low to affect the recruitment sounds. Thus potential recruits are evidently able to discriminate between recruitment performances for low and high quality food sources, and may use the interpulse interval to discriminate between sound pulses that reliably encode distance and those that do not (Nieh et al., 2003c).

6. CONCLUSION

Thus stingless bee foragers may use multiple sensory modalities (touch, vision, olfaction, and audition) to transfer information concerning the existence of a resource and, in some cases, to communicate its specific 3-dimensional location (Tab. I). These mechanisms of information transfer allow the colony to collectively and appropriately allocate foraging resources (Roubik, 1989; Biesmeijer et al., 1998, 1999a; Biesmeijer and Ermers, 1999; Biesmeijer and Slaa, 2004). Stingless bees, like honeybees, act as a superorganism with decentralized control of foraging based upon the decisions of individual foragers (Seeley, 1983, 1985, 1989a, b; Biesmeijer and de Vries, 2001; Biesmeijer and Slaa, 2004). Thus the transfer of recruitment information should be reliable and, inside the often noisy and crowded nest (Nieh, 1999), multimodal communication may provide information redundancy (Hölldobler and Wilson, 1978, 1990) enabling foragers to reliably alert nestmates to the existence of a good resource.

In those species with specific location communication, multimodal information transfer may also enhance the ability of nestmates to find a resource when noise degrades information sources (Nieh, 1999). Different sensory channels are affected by noise to different degrees and also have different characteristics of temporal persistence, coherence, and information content (Bradbury and Vehrencamp, 1988). These can be exploited in attracting potential recruits to recruitment performances

inside the nest (Tautz and Rohrseitz, 1998) or to odors or the putative piloting flights of foragers outside the nest. Thus greater study of the different communication channels will likely reveal more about the processes that guide colony foraging.

6.1. Communication channels

6.1.1. Contact and vision

Inside the nest, the function of recruiter motions and contacts between recruiters and potential recruits remains little understood. However, the experiments of Hrncir et al. (2000) show that jostling behavior and contacts between the recruiter abdomen and the antennae of potential recruits are associated with successful recruitment. Thus further examination of intranidal contact behavior may be quite revealing.

The existence of visual following (piloting) in the communication of resource location remains unclear. Such piloting is thought to be the ancestral state in the evolution of recruitment communication, and may be used by some extant species (Esch et al., 1965; Esch, 1967; Kerr, 1969). The difficulty of following at high flight speeds or of maintaining visual contact while bypassing obstructions or flying through dense vegetation may have contributed to evolution of other strategies (Nieh, 1999), but the advantages and disadvantages of following have not been experimentally evaluated.

6.1.2. Olfaction

Little is known about the behavior and sensory physiology of how stingless bees detect odors in the field (Stort and Moraes, 1997, 1998). In some meliponine species, experienced foragers may guide recruits who then use the odor trail as a backup source of information (Lindauer and Kerr, 1958; Kerr et al., 1981). *Trigona hyalinata* recruits arrive in large groups that may be guided by experienced foragers, with final orientation assisted by a short odor trail (Nieh et al., 2003a). A similar grouping effect has been observed in stingless bee (*T. corvina*: Roubik, personal

communication) and honeybee foraging (Tautz and Sandeman, 2003). Odor trails are particularly interesting because, unlike worker ants, bees fly to the resource and must detect the odor droplets from some distance away. Thus far, studies have shown that some odor marks are attractive and some are repellant (Villa and Weiss, 1990; Goulson et al., 2001), that they are deposited in such a way (i.e. mouthpart rubbing to deposit secretions of cephalic glands and walking to deposit tarsal gland secretions) that is suggestive of their source, and that extracts of cephalic glands can attract foragers. It would be desirable to chemically assay these odor marks to demonstrate that they actually contain compounds produced by cephalic glands and to study olfactory sensilla (Stort and Moraes, 1997, 1998) in greater detail. The active space and effective duration of the odor plumes created by odor marks (both in odor trails and also in target-only odor-marks) should also be described. In this respect, a modification of lab techniques (Vázquez et al., 2003) to produce field electroantennograms may be informative.

6.1.3. Audition

One of the most important questions to be answered is whether some stingless bee species use functionally referential communication, the ability to abstractly encode environmental information in signals understood by receivers (Marler et al., 1992; Blumstein, 1999). This debate focuses on the ability of certain *Melipona* species to transfer location information inside the nest (Esch et al., 1965; Esch, 1967; Nieh and Roubik, 1998; Hrncir et al., 2000, 2002; Nieh et al., 2003c). In *M. panamica*, intranidal information is evidently necessary for recruits to find the indicated food source at the correct distance and height (Nieh, 1998b; Nieh and Roubik, 1998). Locale odors were not sufficient to guide recruits to the correct direction (Nieh, 1998b; Nieh and Roubik, 1998). Thus locale odor alone does not account for the ability of *M. panamica* recruits to orient to the correct three-dimensional resource location.

In some species, the temporal structure of pulsed recruitment sounds is correlated with distance and (in *M. panamica*) height informa-

tion. However, in some species, recruitment sounds have high temporal variances and appear to encode both food quality (motivation) and food location (referential information). It is therefore unclear whether nestmates can reliably obtain location information from such sounds. Some of this variance may be due to the inclusion of less motivated performances (that are ignored by potential recruits) into the acoustic analysis (Nieh and Roubik, 1998; Hrncir et al., 2000, 2002, 2003; Nieh et al., 2003c). However, high variances may also be an inherent property of recruitment sounds produced by highly motivated foragers. Given that the evolution of functionally referential communication is hypothesized to have occurred through the ritualization of motivationally related behaviors, such signals can possess both motivational and referential components and be classified within a motivational to referential continuum (Marler et al., 1992). Current debate on the information content of *Melipona* recruitment sounds (Hrncir et al., 2002, 2003; Nieh et al., 2003c) can be explored with this continuum concept, particularly with respect to how the variance in temporal structure is affected by motivation and whether this variance prevents receivers from obtaining reliable information. For example, if *Melipona* foragers only communicate motivation, yet encode location information that is not used by receivers, researchers will have uncovered a presumptive intermediate stage in the evolution of functionally referential communication. Detailed studies of motivational behaviors may thus reveal potential early stages in the evolution of functionally referential communication.

It also is unclear whether and how stingless bees hear air-borne sounds and vibrations, although the preliminary experiments of Lindauer and Kerr (1958) and Esch (1967) suggest that recruitment sounds may play a role, and the experimental methods used to study honeybee audition provide guidance (Kirchner, 1994; Michelsen, 2003). The development of a sound playback system based upon the work of Esch (1967) would enable us to systematically investigate acoustic communication. Such experiments have proven difficult in honeybees (Michelsen et al., 1989; Michelsen, 2003), but they may be somewhat simpler with stingless bees, given that the

motion of the recruiter does not appear to contain any location information (Nieh, 1998a; Hrncir et al., 2000), and because sound alone is evidently sufficient to excite experienced foragers to go to a feeder (Lindauer and Kerr, 1958; Esch et al., 1965; Esch, 1967).

6.2. Phylogeny and evolution

The goal of understanding the evolution of recruitment communication in the Apidae depends upon a good phylogeny of this group. Unfortunately, there is disagreement concerning the evolutionary relationships between groups in the Apidae, and eusociality and recruitment communication may have evolved independently in honeybees and stingless bees (Winston and Michener, 1977; Chavarria and Carpenter, 1994; Cameron and Mardulyn, 2001; Cameron, 2003). However, even if advanced eusociality has evolved twice, primitive sociality (that was lost in the communal Euglossini) may still have been the plesiomorphic state for all four groups in the Apidae (Bombini, Euglossini, Meliponini, and Apini, Michener, 2000). Recent work on the Bombini suggests that the Apidae may have shared a primitively social ancestor that excited nestmates after discovering food (Dornhaus and Chittka, 2004). Upon returning from a rich food source, bumblebees can motivate nestmates to forage through food-alert runs, bouts of running through the nest and interacting with other bees (Dornhaus and Chittka, 1999, 2001; Dornhaus and Cameron, 2003). This food-alert behavior is similar to the excitatory zigzag and jostling behaviors performed by foragers of several meliponine species, including species that do not communicate food location (Lindauer and Kerr, 1958; Nieh, 1998a; Hrncir et al., 2000). Thus the communication of food quality through a graded series of excitatory behaviors (movements and sounds) may be plesiomorphic to the four tribes in the Apidae but was lost in the solitary Euglossini. Nieh et al. (2003c) have termed this the "excitable ancestor" hypothesis and predict that decreasing food quality will increase the duration between food-alert runs in bumblebees and stingless bees, even in stingless bee species that do not communicate food location.

Within the stingless bees, a well-resolved phylogeny remains an elusive goal, although

molecular data are providing new information and alternative topologies (Fernandes-Salomao et al., 2002; Costa et al., 2003). It is not within the scope of this review to consider all of these topologies in detail, but I hope to give a sense of the issues. On the basis of morphological and behavioral characters, Wille (1979, 1983) proposed that the *Melipona*, in which some species encode food distance in pulsed sounds (Tab. I), were fairly derived within the Meliponini, although the relationship of this genus with other groups such as *Scaptotrigona* and *Trigona* (that mainly appear to use odor trails) is unresolved. Michener (1990) proposed a topology with *Melipona* as a basal group and *Scaptotrigona* and *Trigona* as more derived. Subsequently, Camargo and Pedro (1992) placed the *Melipona* as a more derived group but basal to the *Nannotrigona* (which reportedly does not communicate food location, Kerr, 1969) and *Scaptotrigona*.

Recently, Costa et al. (2003) have published topologies based upon mitochondrial 16s rDNA sequences (550 bp fragment). In the maximum likelihood analysis, *Scaptotrigona* is more derived than *Melipona* which is more derived than *Nannotrigona* (Costa et al., 2003). However, a parsimony analysis of the same molecular data provides yet another topology for these groups (Costa et al., 2003). The addition of more genes to such analyses may increase our resolution, and groups are currently working on molecular phylogenies of the Meliponini (Roubik, personal communication; Cameron, personal communication).

Given the topological uncertainties, we are not currently able to make detailed statements about the mappings of communication characters. Nonetheless, the data continue to support the hypotheses of Lindauer and Kerr (1958), von Frisch (1967), Kerr (1969), Esch (1967), and Wille (1983) that the ancestor to the stingless bees (and possibly of the Apidae) made excitatory movements at the nest after returning from a good food source, and possessed some form of odor marking (Kerr and Esch, 1965; Kerr, 1969). Meliponine species that deposit mandibular gland secretions as food-marking odors also use the same secretions as alarm pheromones (Kerr, 1969; Smith and Roubik, 1983; Johnson et al., 1985). Mandibular gland pheromones are involved in alarm

and defense in a wide range of bee groups, including honeybees (Collins et al., 1989; Brockmann et al., 1998; Winston and Slessor, 1998) and the solitary Colletidae and Halictidae (Duffield et al., 1984), and thus mandibular gland odor-marking to indicate food resources may be apomorphic, evolving from a plesiomorphic alarm or defensive pheromone widely found in bees. However, the recent work of Jarau et al. (2004) suggests that rigorous verification of the attractive properties of mandibular gland pheromone are necessary before this scenario can be further explored.

Within the Meliponini, excitatory sound production that does not encode food location may be a plesiomorphic trait (Lindauer and Kerr, 1958; Esch, 1967; von Frisch, 1967; Kerr, 1969; Wille, 1983). Whether such sound production is plesiomorphic to Meliponini and Apini is unclear. It may have evolved separately in both groups (Dyer, 2002). To further explore these evolutionary issues, it would be good to understand more about the precise mechanisms of communication and the detailed phylogeny of genera such as the *Melipona*, in which species form a clear taxonomic group but also display a range of recruitment communication strategies (Pisani et al., 1977; Correa-Rego, 1990; Nieh and Roubik, 1995; Nieh et al., 2003b, in press).

6.3. Selective pressures

The selective pressures that have shaped recruitment communication and given rise to functionally referential communication in honeybees and, potentially, in stingless bees are poorly understood. Thus questions of why such communication systems have evolved and how functionally referential communication systems are advantageous remain fertile areas for new hypotheses. Potential selective pressures include resource spatial distribution (habitat), and competition (Kerr, 1951; Johnson and Hubbell, 1974; Hubbell and Johnson, 1977, 1978; Johnson, 1980, 1981; Roubik and Buchmann, 1984; Nagamitsu and Inoue, 1997; Wilms and Wiechers, 1997; Biesmeijer et al., 1999b; Steffan-Dewenter and Tscharntke, 2000; Eltz et al., 2001, 2002; Liow et al., 2001).

The ability to communicate different dimensions of food location may be influenced by habitat. The height of food sources above the ground (Nagamitsu and Inoue, 1997) or the spatial distribution and clumping of food (Johnson, 1981) in different distances and directions could play a role in the ability of different species to recruit nestmates to a set of dimensions, either through shaping communication mechanisms or the search behavior of recruits (see work on honeybees, Roubik et al., 1999; Dornhaus and Chittka, in press). The role of habitat has yet to be considered in detail, but the diversity of meliponine species and habitats suggests that this may be a promising line of inquiry.

Competition for resources may also have imposed an important selective pressure on stingless bee recruitment (Johnson, 1974; Johnson and Hubbell, 1974; Johnson and Hubbell, 1987; Nagamitsu and Inoue, 1997; Slaa et al., 1997; Biesmeijer et al., 1999b). Given that foragers orient towards and are highly attuned to odor marks, there is an intriguing possibility that some species may use olfactory eavesdropping to exploit good resources visited by other colonies. Lindauer and Kerr (1958) trained a colony of *S. postica* and a colony of *S. xanthotricha* to feeders placed such that the odor trails of both colonies crossed. In this experiment, two *S. postica* foragers arrived at the *S. xanthotricha* feeder and 28 *S. xanthotricha* foragers arrived at the *S. postica* feeder. It is unclear how many of each species would have arrived at the feeder of the opposite species in the absence of odor marks, but this experiment suggests that interspecific odor-mark recognition may exist.

Nieh (1999) proposed that competition and olfactory eavesdropping of odor trails may have contributed to the evolution of concealed intranidal communication, and thus to the evolution of functionally referential communication as referential information replaced odor trail information. To date, no studies show that less conspicuous odor trails decrease competition at the indicated resource. However, the short odor trail of *T. hyalinata* may represent an intermediate communication strategy between full trail marking and target-only odor marking (Nieh et al., 2003a). Whether this strategy is less conspicuous than full-trail marking, and therefore advantageous, remains to be tested.

The role of competition in the evolution of honeybee referential communication has not been considered, but given the recent finding

that waggle dancing is more important in tropical than in temperate habitats, it would be interesting to explore the effects of competition for the tropical resources that were found to be more spatially clumped than the temperate resources (Dornhaus and Chittka, 2004).

In general, the behavioral ecology of meliponine foraging is now being studied in greater detail (Biesmeijer and Slaa, in review), and the relative benefits and roles of different recruitment strategies are beginning to be elucidated (Jarau et al., 2003). There are promising signs that the field of stingless bee research is growing. With more detailed studies on the sensory physiology and mechanisms of recruitment information transfer, we may reach firmer ground and begin to understand the evolution of the amazing recruitment communication systems used by social bees.

Résumé – Communication du recrutement chez les abeilles sans aiguillon (Hymenoptera, Apidae, Meliponini). Les mécanismes qui permettent aux abeilles sociales supérieures de communiquer le lieu d'une bonne source de nourriture ont fait l'objet d'intenses études et peuvent donner un aperçu de la façon dont la capacité à encoder l'information d'un lieu, forme de communication fonctionnellement référentielle (Marker et al., 1992 ; Blumstein, 1999), a évolué chez les abeilles sociales supérieures (Esch, 1967). Ainsi le but de cette revue est d'examiner la communication du recrutement chez les abeilles sans aiguillon, en se concentrant sur les divers types de communication.

Pour étudier la communication du recrutement, les chercheurs dressent des abeilles à butiner sur un nourrisseur placé dans un lieu donné et à enregistrer le comportement de ces butineuses à l'intérieur du nid (Esch, 1967). Afin de tester si les abeilles peuvent recruter pour un lieu donné, on place au moins deux nourrisseurs identiques, l'un témoin et l'autre expérimental, de façon à ce qu'une seule dimension spatiale soit modifiée à la fois (von Frisch, 1967). Il est important de ne compter comme recrues que les abeilles qui n'ont jamais expérimenté auparavant un nourrisseur. Mais on rencontre plusieurs défis lorsqu'on travaille avec des abeilles sans aiguillon. Certaines espèces d'abeilles sans aiguillon recrutent des membres du nid pour un lieu donné, alors que d'autres ne le font pas et le nombre de dimensions qui peuvent être communiquées varie (peut-être en liaison avec l'habitat) (Tab. I). Les mécanismes de communication du recrutement incluent le contact, la vision, l'olfaction et peut-être l'audition (Lindauer et Kerr, 1958 ; Esch, 1967 ; Kerr, 1969). Les butineuses peuvent contacter leurs consœurs à l'intérieur du nid pour les alerter de l'existence de bonnes sources de nourriture (Hrncir et al., 2000) ou les orienter vers la présence visuelle d'autres butineuses sur une source de nourriture (Slaa et al., 2003). Les butineuses de certaines espèces peuvent déposer des odeurs qui marquent les bonnes sources de nourriture et constituer un chemin odorant complet entre le nid et la source de nourriture (Lindauer et Kerr, 1958) ou un chemin odorant court qui part de la source en direction du nid (Nieh et al., 2003a) ou ne marquer que la source de nourriture comme cible (Nieh et Roubik, 1995 ; Nieh, 1998b). Enfin les butineuses de nombreuses espèces produisent à l'intérieur du nid des sons de recrutement intenses et pulsés. Chez certaines espèces, les sons sont corrélés à la distance et à la hauteur de la source de nourriture (Aesch et al., 1965 ; Nieh et Roubik, 1998 ; Aguilar et Briceño, 2002 ; Nieh et al., 2003c). On n'est pas certain que ces sons communiquent le lieu de la source. Des questions restent en suspens concernant le contenu de l'information et la fiabilité de ces sons. Pourtant des expériences antérieures en play-back suggèrent que les sons de recrutement peuvent faire retourner à une source de nourriture des butineuses expérimentées (Lindauer et Kerr, 1958 ; Esch, 1967).

Les butineuses des abeilles sans aiguillon peuvent ainsi utiliser des modalités sensorielles multiples pour indiquer de façon appropriée les sources de nourriture. Puisque la phylogénie des abeilles sans aiguillon n'est pas encore claire (Michener, 1990 ; Camargo et Pedro, 1992 ; Costa et al., 2003), il est difficile de faire des déclarations précises sur l'évolution de la communication du recrutement. Néanmoins, il se peut que l'ancêtre des abeilles sans aiguillon (et peut-être des Apidae) ait fait des mouvements d'excitation une fois rentrée au nid après avoir trouvé une bonne source de nourriture, qu'elle ait possédé une forme de marquage odorant (Kerr et Esch, 1965 ; Kerr, 1969), par des éléments qui ont pu évoluer vers les phéromones d'alarme (Kerr, 1969). Les pressions de sélection sur la communication du recrutement peuvent inclure la distribution spatiale des sources de nourriture et la compétition, issue de l'utilisation potentielle de marques odorantes étrangères, qui a pu contribuer à l'évolution de la communication cachée interne au nid. Ainsi, au cours de l'évolution, l'information sur les chemins odorants aurait pu être remplacée par une communication fonctionnellement référentielle.

Meliponini / transfert d'information / recrutement / communication référentielle / multimodalité

Zusammenfassung – **Rekrutierungskommunikation bei Stachellosen Bienen (Hymenoptera, Apidae, Meliponini).** Die Mechanismen der Kommunikation über den Ort einer guten Nahrungsquelle bei hoch sozialen Bienen sind intensiv untersucht worden. Diese Kenntnis kann uns einen Einblick geben, wie sich eine funktionale, ortsweisende Kommunikation und die Fähigkeit zur Entschlüsselung der Information über den Ort (Blumstein, 1999; Marler et al., 1992) in hoch sozialen Bienen entwickelt (Esch, 1967) hat. Dementsprechend wird hier ein Überblick über die Untersuchungen der Rekrutierungskommunikation bei Stachellosen Bienen mit einer Ausrichtung auf die verschiedenen Mechanismen der Kommunikation gegeben.

Zur Untersuchung von Rekrutierungskommunikation dressieren Forscher Bienen auf eine Futterstelle und notieren das Verhalten der Sammlerinnen im Nest (Esch, 1967). Um zu testen, ob Bienen andere Nestgenossinnen zu einer spezifischen Stelle rekrutieren können, werden mindestens zwei identische Futternäpfe, ein Kontroll- und ein Versuchsnapf, so plaziert, dass jedesmal nur eine der räumlichen Dimensionen verändert wird (von Frisch, 1967). Es ist wichtig, nur Bienen als Neulinge zu werten, die niemals zuvor Erfahrungen an einem Futternapf gemacht haben.

Bei Stachellose Bienen stellen sich bei dieser Arbeit mehrere Herausforderungen. Einige Arten der Stachellose Bienen können Nestmitglieder zu einem bestimmten Ort rekrutieren, andere dagegen nicht. Zusätzlich variiert (wahrscheinlich abhängig vom Lebensraum) die Zahl der Dimensionen, die vermittelt werden können (Tab. I). Mechanismen der Rekrutierungskommunikation beinhalten Kontakt, Sehen, Riechen und vielleicht auch Hören (Esch, 1967; Kerr, 1969; Lindauer und Kerr, 1958). Sammelbienen können mit ihren Nestgenossinnen im Nest Kontakt aufnehmen, um sie auf die Existenz einer guten Nahrungsquelle aufmerksam zu machen (Hrncir et al., 2000) oder sie können sehen, dass sich andere Sammelbienen an der Nahrungsquelle aufhalten (Slaa et al., 2003). Sammlerinnen einiger Arten können gute Futterstellen auf unterschiedliche Weise mit Duftstoffen markieren: es kann eine vollständige Duftspur von der Futterstelle zum Nest (Lindauer und Kerr, 1958), eine kurze Duftspur nur ein kleines Stück in Richtung zum Nest gelegt werden (Nieh et al., 2003a), oder es erfolgt nur eine Zielmarkierung an der Nahrungsquelle (Nieh, 1998b; Nieh und Roubik, 1995). Schließlich können Sammelbienen vieler Arten laute, pulsierende Rekrutierungstöne im Nest erzeugen. In einigen Arten sind diese Töne mit der Entfernung und der Höhe der Futterstelle korreliert (Aguilar und Briceño, 2002; Esch et al., 1965; Nieh et al., 2003c; Nieh und Roubik,

1998). Es ist noch nicht klar, ob diese Töne den Ort des Futters angeben. Auch bleiben Fragen in Bezug auf den Inhalt der Information und der Zuverlässigkeit dieser Töne bestehen. Frühere Versuche mit Rückspielungen dieser Töne weisen darauf hin, dass diese Rekrutierungstöne erfahrene Sammelbienen veranlassen, zur Futterstelle zurückzukehren (Esch, 1967; Lindauer und Kerr, 1958).

Demnach können Stachellose Bienen mehrere sensorische Modalitäten nutzen, um Nahrungsquellen ausreichend anzuzeigen. Da die Phylogenie der Stachellose Bienen noch ungeklärt ist (Camargo und Pedro, 1992; Costa et al., 2003; Michener, 1990), ist es schwierig detaillierte Feststellungen über die Entwicklung der Rekrutierungskommunikation zu machen. Ursprüngliche scheinen die Vorfahren der Stachellose Bienen (und wahrscheinlich der Apidae) anregende Bewegungen im Nest gemacht zu haben, wenn sie von einer guten Futterstelle zurückkehrten, und sie hatten eine Art der Duftmarkierung (Kerr, 1969; Kerr und Esch, 1965) mit Elementen, die sich aus den Alarmpheromonen entwickelt haben könnten (Kerr, 1969). Selektionsdruck auf die Rekrutierungskommunikation könnte durch die räumliche Verteilung der Nahrungsquellen und durch die aus der Möglichkeit der Fremdnutzung der Duftspuren entstehende Konkurrenz geformt worden sein, diese könnte zur Evolution von verborgener Kommunikation innerhalb des Nestes beigetragen haben. So könnte während der Evolution die Information über Duftwege von einer auf funktionell hinweisenden Kommunikation ersetzt worden sein (Nieh, 1999).

Meliponini / Informationstransfer / referentielle Kommunikation / Rekrutierung / Multimodalität

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