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# 11 Mobilizing the Foraging Force

## *Mechanical Signals in Stingless Bee Recruitment*

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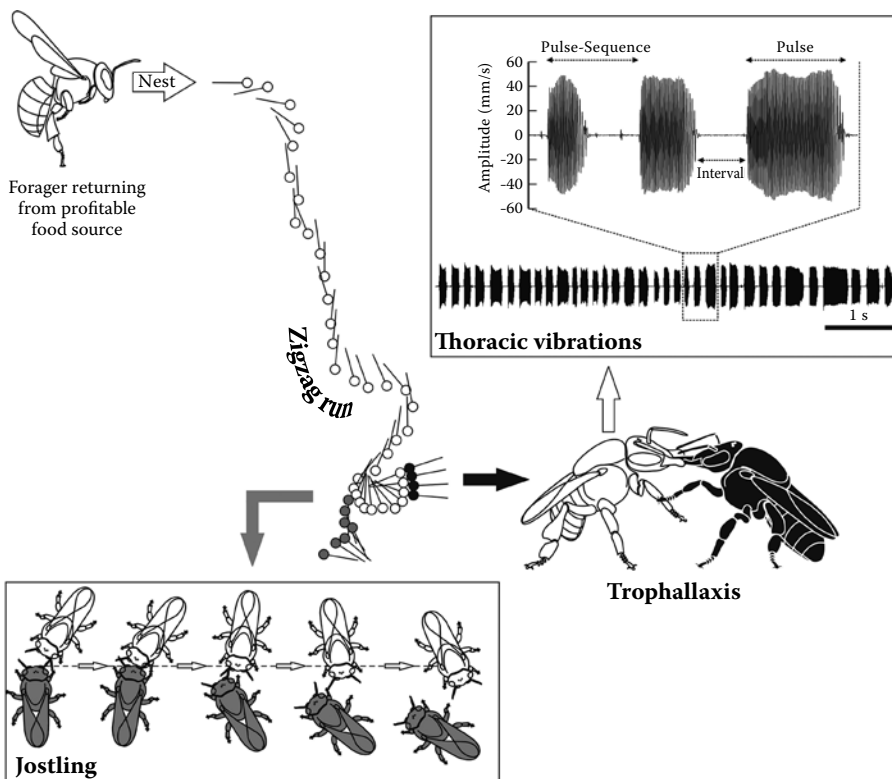
### INTRODUCTION

Already at school, probably all of us have learned that bees perform dances that map the position of a food source. This is certainly true—but only for the honey bees (*Apini*; about ten species), which merely constitute a meager 1% of all eusocial bee species within the *Apidae* family. So far, we do not have the least evidence for dances encoding either the direction or the distance of a food source among the remaining 99%, comprising the stingless bees (*Meliponini*; more than 400 species) and

the bumble bees (*Bombini*; about 250 species)—not to mention the primitively eusocial colony stages found in several species within the tribes *Allodapini* and *Ceratini*, or within the family *Halictidae* (Michener 2000).

Among the stingless bees, we encounter a broad spectrum of signals involved in foraging and recruitment processes (Lindauer and Kerr 1958, 1960; Nieh 2004; Barth et al. 2008). In this bee group, both the search for and the choice of a specific food patch are strongly biased by signals and cues in the field (field-based information). In some *Meliponini*, for instance, collecting foragers deposit pheromone marks at and near the food source to guide newcomers to the goal. Consequently, the foraging processes in colonies of these species are extremely directed toward one particular target area (see Chapter 12). Apart from such genuine signals, field-based social cues have been shown to affect the foraging decisions of searching individuals. Within a food patch, a bee's choice of where to collect is influenced by scent marks left on flowers (see Chapter 12), and by the physical presence of con- or heterospecific foragers (Slaa et al. 2003a, 2003b; Biesmeijer and Slaa 2004; see also Chapter 8).

Yet, the use of field-based information is not the entire story of success in the *Meliponini*. Foragers that return from an extremely profitable food source run agitatedly through the nest, thereby jostling their nestmates (Lindauer and Kerr, 1958, 1960; Nieh 1998; Hrncir et al. 2000) (Figure 11.1). In addition to these excited movements, the foragers generate thoracic vibrations (“sounds”) in the course of their stay in the hive, predominantly during trophallactic interactions with hive bees (Lindauer and Kerr 1958, 1960; Hrncir et al. 2006a, 2006b) (Figure 11.1). The agitated jostling run



**FIGURE 11.1** Nest-internal behaviors displayed by stingless bee foragers. When a forager (white bees and symbols) returns from a high-profit food source, she excitedly runs through the colony (zigzag run), thereby jostling her nestmates (grey bees and symbols). While running, but predominantly during trophallaxis with hive bees (black bee and symbols), the forager generates pulsed thoracic vibrations.

as well as the sound production attracted the attention of scientists because both behaviors were considered potential meliponine equivalents to the dance “language” of the honey bees (Esch et al. 1965; Nieh 1998; Dyer 2002). The present chapter gives an overview of what is currently known about the potential message(s) and meaning(s) of these putative signals.

## ECOLOGICAL CONSIDERATIONS

Similar to honey bees, stingless bees live in perennial colonies, which typically comprise a few dozen to several thousand individuals (Schwarz 1948; Michener 1974, 2000; Roubik 1989). As in other social insects, the survival of a colony greatly depends on the success of foraging individuals in finding and collecting carbohydrates (usually nectar) and proteins (usually pollen). Both are stored within the nest to guarantee a permanent food supply and, consequently, to ensure the survival of the colony during possible events of resource scarcity. Since stingless bees are mainly found in the tropical regions around the globe, where periods without a considerable number of plant species in bloom are insignificant (Bawa 1983), the acquisition of food occurs all year round. Nevertheless, meliponine colonies adjust their collecting activity to the availability of resources in the environment by increasing both the individual foraging activity and the foraging force as soon as a surplus of food is available (Roubik et al. 1986; Eltz et al. 2001; Nagamitsu and Inoue 2002; Hofstede 2006; Hofstede and Sommeijer 2006).

### RESOURCE AVAILABILITY

In the tropics, we encounter two distinct patterns of flowering: one in which the individual plant produces small numbers of flowers over an extended period of time (“steady state”), and the second in which an individual produces a large amount of new flowers each day over a short period of time, often less than a week (“big bang” or “mass flowering”) (Gentry 1974; Augspurger 1980, 1983). Within a plant population, mass-flowering individuals of one species bloom synchronously in most cases (Figure 11.2a). Asynchronous blooming, which also occurs, results in an extended blooming period on the population level (Bawa 1983).

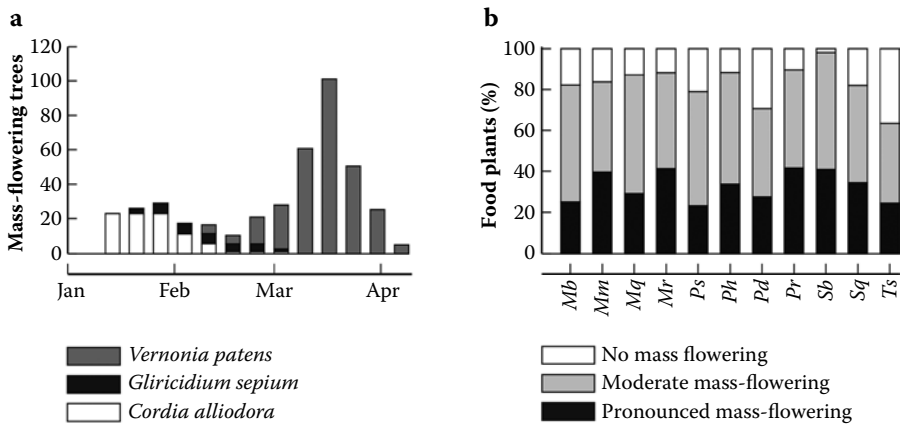
These two modes of flowering constitute two distinct resource types for tropical bees:

1. *Low profitability—long-lived resources.* Since steady-state plants offer only a small number of flowers, bees occasionally have to move long distances between conspecific specimens to encounter an open flower (increased search costs and risk of predation). However, as soon as a bee knows all (or many) individuals of a steady-state species within her flight range, these plants represent a reliable food source due to a flowering period that often exceeds her foraging lifetime.
2. *High profitability—short-lived resources.* Since mass-flowering plants produce an excess of flowers,\* bees foraging on this kind of resource have low search costs and can rapidly fill their crop, or load pollen, during a single foraging trip.†

The two flowering patterns, steady state and mass flowering, should result in different foraging strategies of eusocial bee colonies exploiting these food sources. Steady-state resources provide a continuous but low food influx into the colony. Due to the small number of available flowers within the foraging range of a colony, such resources can be exploited by solitary foraging. And since the value (profitability) of the resource is low, recruitment to these plants should be low or inexistent. By contrast, in order to efficiently exploit mass-flowering plants that offer a great opportunity to hoard

\* Mori and Piploy (1984) estimated up to five hundred thousand open flowers per day and individual for the tropical tree *Miconia minutiflora*, Melastomaceae.

† An example for three *Melipona* species collecting nectar on the mass-flowering shrub *Hybanthus prunifolius*, Violaceae, is given by Roubik and Buchmann (1984).



**FIGURE 11.2** Availability of mass-flowering plants and their significance for stingless bees. (a) Synchronous blooming of mass-flowering trees. Given is the number of individuals of three tree species in bloom between January and April 2004, within a circumference of 500 m around stingless bee hives (*Melipona beecheii*) in a Neotropical forest in El Salvador (data from Hofstede 2006). (b) Food plants used by stingless bees in the Brazilian Atlantic rainforest. Given is the proportion of plants with pronounced (black bars) or moderate (grey bars) mass flowering, or without mass flowering (white bars), on which bees of the respective species foraged. *Mb*, *Melipona bicolor*; *Mm*, *M. marginata*; *Mq*, *M. quadrifasciata*; *Mr*, *M. rufiventris*; *Ps*, *Paratrigona subnuda*; *Ph*, *Partamona helleri*; *Pd*, *Plebeia droryana*; *Pr*, *Plebeia remota*; *Sb*, *Scaptotrigona bipunctata*; *Sq*, *Schwarziana quadripunctata*; *Ts*, *Trigona spinipes*. (Data from Wilms et al. 1996.)

large amounts of nectar or pollen for bee colonies, the entire potentially available foraging force should be quickly activated to visit the respective food source.

In fact, mass-flowering plants are the predominant source of nectar and pollen for stingless bees (Absy et al. 1980, 1984; Wilms et al. 1996; Wilms and Wiechers 1997; Ramalho 2004) (Figure 11.2b). In a detailed survey of the floral resources used by native stingless bees in the Brazilian Atlantic rainforest, Wolfgang Wilms and co-workers (Wilms et al. 1996; Wilms and Wiechers 1997) and Mauro Ramalho (2004) found that mass-flowering plants contributed by up to 90% to the annual nutritional input into the colonies. The peaks in collecting activity during mass-flowering events found in meliponine colonies (Roubik et al. 1986; Hofstede 2006) are a result of both an increased activity of the individuals and a boost in the total foraging force (Hofstede 2006).

## COMPETITION OVER FOOD SOURCES

Stingless bees are opportunistic generalists (Biesmeijer and Slaa 2004; Nagamitsu and Inoue 2005). Therefore, since the foraging ranges of different meliponine colonies in a community highly overlap (Hubbell and Johnson 1977, 1978; Ramalho 2004), a particular resource will not be in private hands of a single colony. Instead, it will be shared by both conspecific non-nestmates and heterospecifics (Biesmeijer and Slaa 2004). This generalized utilization of a common resource will inevitably result in exploitive competition over valuable food sources, such as mass-flowering plants (Nagamitsu and Inoue 2005).

Among the stingless bees we encounter different strategies to deal with the competition over food sources. *Competition winners* are those species that are able to quickly guide large groups of individuals to a specific location and, in addition, aggressively chase away conspecific non-nestmates or heterospecifics from the food sources. This kind of foraging strategy, referred to as “extirpation” by Leslie K. Johnson (1983), has been described for some species of the genera *Trigona* and *Oxytrigona* (Kerr and Cruz 1961; Kerr 1969; Johnson and Hubbell 1974, 1975; Hubbell and Johnson

1978; Roubik 1980; Johnson 1983; Nagamitsu and Inoue 1997; Slaa 2003; Biesmeijer and Slaa 2004; Nieh et al. 2004). Through aggressive group foraging, foragers from a single colony manage to monopolize clumped resources. The trade-off for this elevated competitive ability, however, is a reduced capacity to independently discover new food sources or even neighboring food patches (Hubbell and Johnson 1978; Biesmeijer and Slaa 2004).

*Competition avoiders*, by contrast, should be able to quickly switch to a new food patch as soon as they are dislodged by the aggressive species. Here, recruitment mechanisms with little or no location specificity, relying, however, on the simultaneous discovery of various patches of the same food source, would be an advantage. A colony whose foraging force leaves the nest only with information on the odor of a food source is capable of discovering most or all of the existent food patches within its foraging area (Hubbell and Johnson 1978). Certainly, field-based information, such as olfactory or visual cues, biases the distribution of the foragers toward those patches that have not been discovered—or are not yet dominated—by aggressive species (Slaa et al. 2003b; Nieh et al. 2004). In cases where recruitment occurs, the activation of new foragers is sustained as long as the food source remains profitable, or as long as potential recruits are available within the nest. The important advantages of competition avoiders over competition winners are their ability to discover new food patches independently and their capacity to switch the colony's foraging focus to another food patch. Due to this increased agility in their foraging, in contrast to the aggressive group foraging species, the competition avoiders are able to capitalize on highly valuable food sources, but only as long as they keep one step ahead of the extirpators.

A third strategy to benefit from rich food sources is *competition indifference*. Here, solitary foragers, or foraging groups, collect food at the same patches as other species, yet without physical interference with other bees (Johnson 1983; Biesmeijer and Slaa 2004).

These three strategies of how to deal with resource competition are not species specific (Biesmeijer and Slaa 2004), but rather depend on the composition of the foraging community present at the food patch. Some species, for instance, which act in a competition-indifferent manner when other not-aggressive species are present, can switch to competition avoidance and abandon the patch as soon as an aggressive species shows up.

## INFERENCES ON RECRUITMENT MECHANISMS

Which conclusions can now be drawn regarding the nest-internal recruitment mechanisms employed by stingless bees? In nature, recruitment of foragers occurs predominantly during “big bang” events (Hofstede 2006). Since all individuals of a mass-flowering species bloom in synchrony, we often encounter a high spatial density and abundance of a single type of food source (Augspurger 1980; Bawa 1983; Mori and Piploy 1984; Wilms and Wiechers 1997; Hofstede 2006) (Figure 11.2a). Hence, a rapid activation of foragers, informed solely about the scent of the resource prior to leaving the nest, would be adequate for a colony to quickly discover many or all patches within its foraging area. The conspicuous odor emitted by the multitude of flowers, which can be detected even by human noses over long distances (Mori and Piploy 1984; da Silva and Pinheiro 2007), is certainly sufficient to guide the foragers toward a patch. For colonies of not-aggressive Meliponini, chiefly for competition avoiders, a quick detection of many food patches and a quick activation of all available foragers are necessary to get a head start before being dislodged from some of the patches. Aggressive species, on the other hand, need to rapidly mobilize huge numbers of foragers in order to chase other species away from a food patch, and to subsequently defend this patch against other aggressive colonies. In these species, as far as is known, the guidance of the group toward a specific location is accomplished by pheromone marks at and near the food patch itself (see Chapter 12). Although competition winners and competition avoiders employ fundamentally different foraging strategies, a quick activation of unemployed foragers is required in both cases. Consequently, nest-internal recruitment mechanisms in stingless bees should predominantly aim at mobilizing the foraging force.

## OF JOSTLING AND BUZZING: THE EARLY FINDINGS BY LINDAUER AND KERR

In the first experimental analyses of the recruitment abilities of stingless bees, Martin Lindauer and Warwick Estevam Kerr investigated the nest-internal behaviors of foragers in eleven species of Meliponini that showed evident differences in their success to activate nestmates to food sources (Lindauer 1956; Lindauer and Kerr 1958, 1960). In some species, for instance, five collecting bees recruited only one or a few additional nestmates to a feeding dish during 1 h (e.g., *Frieseomelitta silvestrii*, one recruit, food source 25 m from the nest). Other species, by contrast, were even more successful than honey bees (e.g., *Scaptotrigona postica*, 107 recruits; *Apis mellifera*, 77 recruits; both food sources 150 m from the nests) (Lindauer and Kerr 1958, 1960). Inside the nest, the authors observed two conspicuous behaviors performed by the foragers upon their return from “a good source of food” (von Frisch 1993, p. 307): *jostling in zigzag runs* and *buzzing sounds*. Both were postulated to occur in all stingless bee species, in some more accentuated than in others (Lindauer and Kerr 1958, 1960; Kerr 1969): “To Lindauer’s surprise, the behavior of the foragers on the combs did not reveal any significant differences, whether he was dealing with species that had little success in arousing their comrades or with others that had much” (von Frisch 1993, p. 309).

### WHY HAD FORAGER SOUNDS NOT BEEN NOTICED BEFORE 1953?

That stingless bee foragers emit sounds on their return from a profitable food source was first noticed by Warwick E. Kerr: “Some idea of the intensity of this buzzing is given by the fact that it was heard for the first time by Kerr in 1953, produced in a colony of *M. quadrifasciata* in an observation hive 1½ m away; even at this distance the sound was strong enough to attract attention” (Lindauer and Kerr 1960, p. 34).

By the time Lindauer and Kerr published their findings on the recruitment abilities of stingless bees, and on the communication mechanisms that are potentially involved in that process (Lindauer and Kerr 1958, 1960), several detailed accounts on the biology of the Meliponini existed (e.g., von Buttel-Reepen 1903; von Ihering 1904; Schwarz 1948). Interestingly, none of these studies ever mentioned sounds or buzzing within the nests during food gathering processes, although nest-internal behaviors as well as foraging had been surveyed in some detail. How could something as conspicuous as sounds, which are audible from a distance of more than a meter away, have escaped the attention of the biologists before 1953?

A possible answer to this puzzle is the use of artificial food sources (feeding dishes) for the systematic study of recruitment behavior in bees, which was a novelty in stingless bee research in the mid-twentieth century. The method was introduced in 1919 by the Austrian Karl von Frisch for the study of honey bees (see von Frisch 1993, p. 18), and finally adopted with success\* in the late 1940s by the Brazilians Warwick E. Kerr and Paulo Nogueira-Neto for their research on stingless bees. In fact, when the sounds of *Melipona quadrifasciata* were registered for the first time, the foragers were indeed collecting sugar solution at a feeding dish (Kerr and Esch 1965). Compared to natural food sources, the time and energy spent by the foragers to find the food and fill their crop is extremely reduced when collecting at artificial food sources that offer sugar or honey solutions *ad libitum*. Consequently, feeding dishes constitute “nectar sources” of unnaturally high profitability. Since in stingless bees the temporal pattern of the pulsed forager sounds as well as the foragers’ disposition to produce them depend to a high degree on the profitability of a food source (see below), it stands to reason that both the sounds and their occurrence during foraging processes differ between natural food sources (observations before 1950) and artificial food sources (Lindauer and Kerr 1958, 1960, and subsequent studies until today). Yet, it would be wrong to assume that the generation of sounds by stingless bee foragers is a behavioral artifact induced by the use of feeding dishes. Sounds are, *de facto*, also produced by foragers that collect at natural nectar and pollen sources. In these

\* Lutz (1933) reported an unsuccessful attempt to train *Trigona cressoni parastigma* (= *Frieseomelitta paupera*) to several kinds of syrup during a stay in Panama.

cases, however, if sounds occur at all, these are generated at a lower rate (Kerr et al. 1963) and with lower amplitude (Hrncir, unpublished data) than sounds produced by foragers collecting at artificial food sources.

### THE ALERTING HYPOTHESIS

Lindauer and Kerr (1958, 1960) considered both the excited zigzag runs and the buzzing of stingless bee foragers “methods of alerting” nestmates about the existence of a valuable food source—comparable, actually, to the round dance in *Apis mellifera* (Lindauer and Kerr 1960, p. 68). The authors observed that the behavior of the returning foragers caused a general agitation within the colony, which was followed by an increasing number of newcomers arriving at the feeding dishes. In those species, however, that showed a less vigorous nest-internal forager behavior (*Frieseomelitta silvestrii*, *Plebeia droryana*) the number of collecting bees hardly increased at all (Lindauer and Kerr 1958, 1960).

The publications by Lindauer and Kerr (1958, 1960), unfortunately, do not provide any details to what extent a correlation between the nest-internal behavior of foragers and spatial parameters of the food source was systematically analyzed. But given the extraordinary observation experience of these two scientists, it was certainly not without cause when they declared: “Neither the ‘buzzes’ nor the zigzag runs gave any support of the idea that the alerting system included an indication of distance or direction” (Lindauer and Kerr 1960, p. 36; see also Lindauer 1956).

### THE RECRUITER’S EXCITEMENT

From the pioneering studies on the recruitment behavior in stingless bees by Lindauer and Kerr (Lindauer 1956; Lindauer and Kerr 1958, 1960), we learn the following about the nest-internal recruitment signals in Meliponini: (1) Both their occurrence and their vigor depend on the profitability of a food source. (2) The signaling behavior of the foragers goes along with both an elevated excitement within the colony and an increased number of nestmates arriving at the food source. (3) Neither zigzag runs nor buzzing seem to depend on spatial parameters (distance, direction) of the food source.

Techniques and tools to observe, record and analyze the behavior of bees have considerably advanced during the last 50 years. How much progress, however, has our knowledge about the message(s) and the meaning(s) of the nest-internal recruitment signals in stingless bees really made since these early findings by Lindauer and Kerr?

### THE FOOD SOURCE’S VALUE AND THE RECRUITER’S EXCITEMENT

Foraging eusocial bees evaluate the current value of a food source for their decision whether to continue or stop collecting (Biesmeijer et al. 1998). In the case of nectar foraging, important parameters that indicate the profitability of a food patch are the sugar concentration of the collected nectar and the availability of exploitable flowers. Both are subject to sometimes striking variations in the course of a collecting period. The availability of exploitable flowers within a specific food patch, in addition to the plant-specific alterations in the number of open flowers throughout the day, is strongly affected by the density of collecting con- and heterospecific foragers. Here, the quick usurpation of a patch by aggressive competition winners can result in a rapid and unpredicted decline of available flowers for competition avoiders.

The food sources’ profitability not only affects a bee’s foraging decision, but also influences both the thoracic temperature of foragers (honey bees, Stabentheiner and Haggmüller 1991; Stabentheiner et al. 1995; Stabentheiner 2001; Farina and Wainseboim 2001; stingless bees, Nieh and Sánchez 2005) and their “excitement” when returning to the colony (honey bees, Waddington 1982, 2001; Waddington and Kirchner 1992; Seeley et al. 2000; stingless bees, Hrncir et al. 2004a, 2004b).

These measurable forager qualities can be scientifically exploited to investigate which parameters of a collecting trip are used by the bees to evaluate the profitability of a food source (Chittka 2004). In stingless bees, so far, the following parameters have experimentally been determined: the sugar concentration of the collected food (Aguilar and Briceño 2002, Hrncir et al. 2002, 2004b; Nieh et al. 2003; Nieh and Sánchez 2005; Schmidt et al. 2008), the energetic costs during foraging (Hrncir et al. 2002, 2004a), the distance of a food patch from the nest (Nieh and Sánchez 2005), and the past foraging experience of the foragers (Schmidt et al. 2006b).

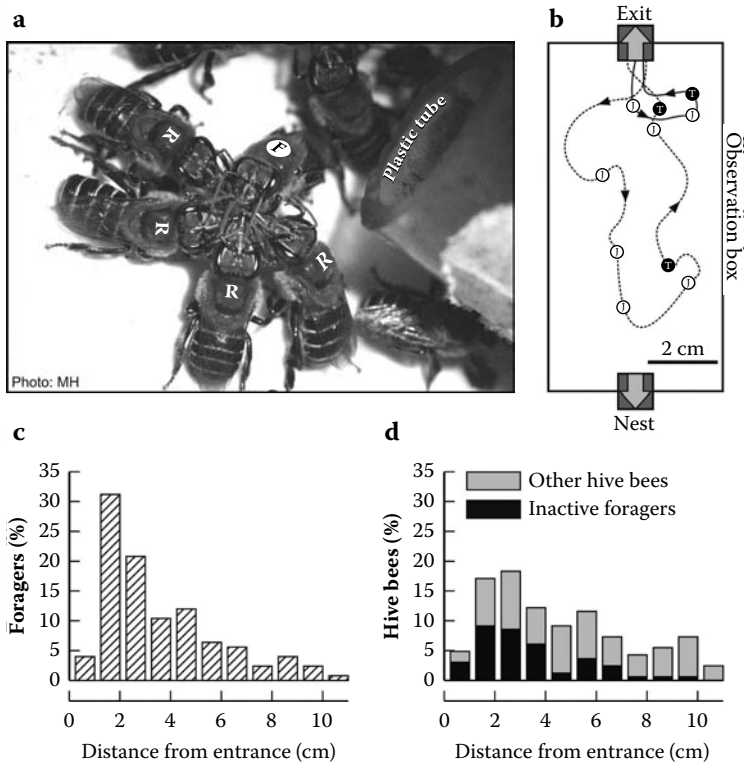
## THE AGITATION THRESHOLD

Agitated movements and thoracic vibrations of foragers can only be observed when the profitability of a food source is above a certain threshold. The profitability value necessary to elicit the bees' excitement is certainly not identical for all foragers, and it also changes—at the colony level—in the course of a year. Thus, researchers are sometimes confronted with the fact that meliponine foragers do not show any form of nest-internal agitation, even if collecting highly concentrated sugar solutions. In an analogous manner, Lindauer (1948) described for the dances of the honey bee: “Es gab Tage, an denen ich mit einer  $\frac{1}{8}$  mol Zuckerlösung Tänze auslösen konnte, während zu anderer Zeit, wo eine 2 mol Lösung am Futterplatz aufgestellt war, kaum noch Tänze zu verzeichnen waren” [On some days, I could trigger dances with a  $\frac{1}{8}$  mol sugar solution, whereas on others, even when a 2 mol solution was offered at the feeding place, almost no dances could be registered] (Lindauer 1948, p. 352). Lindauer (1948) found that the dance threshold in honey bees greatly depends on the season (high threshold in spring, low threshold in late summer and autumn), but also, to a minor extent, on the weather situation and the colony's food reserves (see also Michener 1974). In stingless bees, the season might play a similarly important role for the foragers' excitement, since on several occasions—and in different species—no obvious nest-internal recruitment activity by bees that collected at highly rewarding artificial food sources occurred during the spring and early summer months in Brazil (September–November/December) (for *Melipona quadrifasciata*, *M. scutellaris*, *M. seminigra*, MH, unpublished observations; for *Nannotrigona testaceicornis*, Allerstorfer 2004; for *Scaptotrigona* aff. *depilis*, Veronika M. Schmidt, personal communication). So far, however, potential factors that influence and determine these periods of stagnation in the foragers' excitement have not been systematically studied in the Meliponini.

## EXCITEMENT AND MOTION

Probably the most eye-catching behavior by returning foragers is their excited running through the nest, or at least through parts of it, which can be observed in bees collecting sugar solution from feeding dishes as well as in bees gathering nectar or pollen at natural sources (Sommeijer et al. 1983). So far, however, all detailed investigations of these excited movements have been performed with foragers trained to artificial food sources, and their movement patterns have been studied on “unloading platforms” (Nieh 1998; Nieh et al. 2003) or in “observation boxes” (Hrncir et al. 2000; Samwald 2000; Schmidt et al. 2006b, 2008) placed between the entrance/exit and the actual hive (Figure 11.3). Although such platforms and boxes are no ideal copy of the natural nest entrance, which is usually a batumen-lined tube, funnel, or similarly spatially restricted structure (Wille and Michener 1973; Nieh 1998; Morawetz 2007), they prove to be essential for the observation of the nest-internal forager behavior. For the interpretation of the results it should be kept in mind, however, that the foragers' movements in natural nests are strongly influenced and determined by the complex, narrow, and curved environment, and that they certainly differ from the motion patterns exhibited by the bees on the flat and spacious entrance substitutes.

In recent years, the “zigzag runs,” as the foragers' excited movements had been denominated by Lindauer and Kerr (1960), were meticulously dissected into the following subunits: running path, turning behavior, and spinning behavior. Typically, a bee that returns from a collecting trip enters



**FIGURE 11.3** Foragers entering the hive after a foraging trip. (a) Foragers (F) distribute the collected food to receivers (R) predominantly close to the nest entrance (shown is the entrance tube of an observation box). (b) Running path of a forager in an observation box (positioned between the entrance/exit and the nest) on two subsequent returns to the colony (*Melipona seminigra*, recorded in March 2005). Arrowheads indicate the running direction. Open circles, J, locations of jostling contacts; filled circles, T, locations of trophallaxis. (c) Unloading position (distance from the nest entrance) of ten active *M. panamica* foragers during multiple visits back to the nest. (Data from Nieh 1998.) (d) Position of inactive *M. panamica* foragers (black bars) and other hive bees (grey bars) in relation to the nest entrance. (Data from Nieh 1998.)

the nest and runs around until she finds a hive bee to unload the food (Figure 11.3). After unloading her crop, the forager performs excited spinning movements on the spot (observed in *M. favosa*, Pereboom and Sommeijer 1993; *M. panamica*, Nieh 1998; *M. quadrifasciata*, *M. scutellaris*, Hrncir et al. 2000; *M. beecheii*, Hart and Ratnieks 2002). While running to the nest exit to leave for the next foraging bout, “the zigzag run was interrupted by a sharp turn in a semicircle; then the bee gave up another portion of syrup and immediately continued the zigzag movement” (Lindauer and Kerr 1960, p. 33).

### Running Path

The movement pattern of foragers varies considerably. A bee collecting at a feeder might unload her food directly at the entrance without even properly entering the nest, but run excitedly through the colony the next time she returns from the feeding site (Hrncir et al. 2000; Samwald 2000) (Figure 11.3). Already from this simple observation, it can be concluded that the actual length of a forager’s running path is not influenced by features of the food source, like its position or its quality. Most probably it is the presence and availability of food-unloading bees around the entrance that determines how far a forager enters into the nest (Nieh 1998) (Figure 11.3).

## Turning and Spinning

Although the sudden turnings during the zigzag runs of stingless bee foragers vaguely remind one of the honey bee's waggle movements, neither the number nor the angles of the turnings correlate with either the distance or the direction of the food source (*M. quadrifasciata*, Hrncir et al. 2000). Similarly, the forager's spinning movements after food unloading are independent of the position of the feeding site (*M. panamica*, Nieh 1998; *M. quadrifasciata*, *M. scutellaris*, Hrncir et al. 2000). In *Melipona panamica*, James C. Nieh (1998) observed an interesting feature of the spinning: although the foragers started their spinning at random orientation with respect to the nest exit, they stopped their movement, on average, facing it (Nieh 1998). A similar, yet more narrative description had already been given by Martin Lindauer in 1956 for *T. iridipennis*:

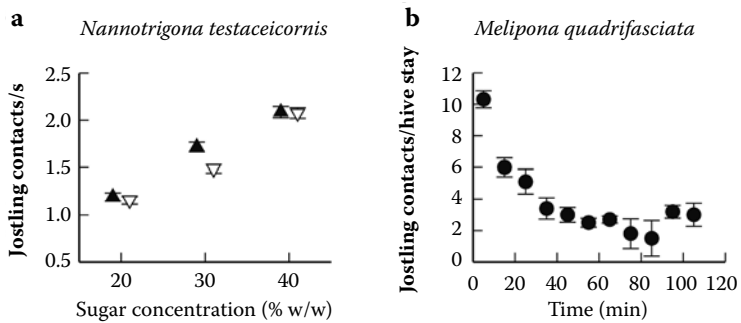
Gleichzeitig macht die Trachtbiene deutliche Schüttelbewegungen mit dem ganzen Körper, was die umstehenden Bienen veranlaßt, sich ihr zuzuwenden, sie mit den Antennen zu betasten und ihr ein Stück zu folgen. Besonders auffallend ist, daß die Sammlerin, wenn sie auf solche Weise ein Gefolge von 3-4 Bienen hinter sich hat, sich plötzlich umdreht und mit betonten Schüttelbewegungen zum Flugloch weist. [At the same time, the forager performs conspicuous shaking movements with her entire body, which causes the surrounding bees to turn towards her, to touch her with the antennae, and to follow her part of the way. It is particularly eye-catching that, as soon as the collecting bee has 3-4 followers behind her, she suddenly turns around and points towards the exit with pronounced shaking movements]. (Lindauer 1956, pp. 553-54)

Although it is tempting to interpret this feature of the foragers' spinning as a signal for the nest-mates to leave the nest, it remains to be investigated whether and how the hive bees perceive that the forager is facing toward the exit.

## EXCITEMENT AND JOSTLING RUNS

An important parameter, which often appears to be ignored when nest-internal behaviors of bees are analyzed and interpreted, is the complete darkness inside a bee hive (with exception of the open-nesting *Apis* species), which impedes the use of visual information. Therefore, all intranidal recruitment signals by foragers—like the waggle movement of the honey bees or the agitated running of the stingless bees—require unequivocal mechanical or chemical components to be perceptible for hive bees.

In stingless bees, one possible way for prospective recruits to perceive the presence of excited foragers within the nest is the amount of contacts with this forager during a certain time interval. As had already been pointed out by Lindauer and Kerr (1958, 1960), agitated foragers jostle their nestmates while running through the colony. Recent studies indicate that this jostling activity of the foragers depends on the value of the visited food source. In *Nannotrigona testaceicornis*, for instance, the number of jostling contacts by the foragers correlated directly with the sugar concentration of the collected food (Schmidt et al. 2008) (Figure 11.4a). Interestingly, in *M. quadrifasciata* (Hrncir 1998; Hrncir et al. 2000), the jostling activity of foragers was found to be highest immediately after they started collecting at a food source (Figure 11.4b). In light of the fact that *Melipona* bees are competition avoiders (Biesmeijer and Slaa 2004), and that the risk of a sudden detection and usurpation of the food patch by competition winners increases with time, the value of a food patch for these bees is certainly highest right after its discovery. Therefore, it may be assumed that in *Melipona*, too, the individually experienced value of a food source influences the jostling activity of the foragers. In line with the findings for *Nannotrigona* and *Melipona*—although appearing contradictory at first sight—are the findings for *Scaptotrigona* aff. *depilis* (Schmidt et al. 2006b). In this species, the foragers' jostling activity remained constant when they collected at a food source of steadily increasing quality. It significantly decreased, however, when the bees experienced a successive decline in food profitability in the course of an experiment (Schmidt et al. 2006b). Apparently, the foragers of *Scaptotrigona* aff. *depilis* include their past foraging experience when evaluating a food source. As long as the exploitation of the food source seems



**FIGURE 11.4** Jostling contacts of returning foragers. (a) In *Nannotrigona testaceicornis*, the number of jostling contacts directly correlated with the sugar concentration of the collected food. Given are mean values  $\pm 1$  SE of the foragers' jostling contacts when the sugar concentration at the food source steadily increased (filled triangles;  $N = 8$  bees) or decreased (open triangles;  $N = 8$  bees). (Data from Schmidt et al. 2008; raw data kindly provided by Veronika M. Schmidt.) (b) In *Melipona quadrifasciata*, the amount of jostling contacts by the foragers decreased with time (mean values  $\pm 1$  SE;  $N = 10$  bees). (Taken from Hrnčir 1998.)

“worthwhile” (constant or increasing sugar concentration at the food patch), the foragers' nest-internal recruitment behavior remains more or less the same. The foragers “lose interest”, however, when experiencing a gradually decreasing sugar concentration at a food patch. In consequence of such a successive depletion, or a decline in profitability, the foragers show a reduced excitement inside the nest.

For an unemployed hive bee, a high amount of contacts with foragers potentially indicates the existence and availability of a valuable food patch. In addition, the amount of jostling contacts could as well provide important information to active foragers. One prerequisite for an efficient exploitation of nectar sources in eusocial bees is a balance between food gatherers and food processors (Seeley 1992; Anderson and Ratnieks 1999). Therefore, if during periods of high resource abundance the nectar influx exceeds the food processing capacity of the colony, nectar receiving should be reinforced or, as an alternative, the colony's foraging activity should be reduced. Yet, the premise for any form of control mechanism to be actuated is the detection of the imbalance between the food intake rate and the nectar processing capacity. In honey bees, nectar foragers perceive a shortage of food receivers through long search times inside the nest when trying to unload their crop (Seeley 1992; Seeley and Tovey 1994; Kirchner and Lindauer 1994). In stingless bees, additionally, nectar foragers could perceive the presence and abundance of hive bees close to the nest entrance by the amount of contacts experienced in the course of their jostling runs. Thus, food collectors could assess both the colony's current nectar processing capacity and the availability of inactive recruitable foragers—which predominantly cluster around the nest entrance (Nieh 1998) (Figure 11.3)—during their stay in the nest.

## EXCITEMENT AND THORACIC VIBRATIONS

Without doubt, the best-studied nest-internal recruitment behavior in stingless bees is the generation of thoracic vibrations (“sounds”) by foragers that collect at high-profit nectar sources—or rather at nectar source substitutes. “Immediately after feeding had started, and the returning foragers began to enter the hive, a persistent high-pitched buzz could be heard, consisting of long and short components, for instance: · · — — · — · · · · — · — — —” (Lindauer and Kerr 1960, p. 34). The pulsed structure of these vibrations, which reminds one of a Morse code, gave birth to the idea that information about the food source could be encoded within the temporal pattern of the sounds. From what we know today, however, the assumption that stingless bees use a symbolic “language” similar to that of the honey bee (Esch et al. 1965; Esch 1967), or even a more sophisticated one (Nieh and Roubik 1998), has to be reconsidered.

The key to decoding the message of a putative signal is the unequivocal identification of the factors that influence and shape this communication behavior (Seeley 1992). From this point of view, the first attempts to decipher the message of the thoracic vibrations in stingless bees (Esch et al. 1965; Esch 1967; Nieh and Roubik 1998) had drawn overhasty conclusions about the existence of a referential location communication. These studies solely focused on a correlation analysis between the sounds and the spatial parameters of a food source relative to the nest, but did not consider at all numerous additional criteria that could potentially influence the temporal pattern of the sounds. In fact, the foragers' thoracic vibrations have now been shown to correlate with a variety of factors. Thus, their actual message is not easily detected. Yet, with every new finding it becomes more and more evident that the thoracic vibrations reflect the excitement of a collecting bee rather than actually encode spatial information about the visited food patch.

### Threshold

In accordance with their agitated movements, foragers do not generate thoracic vibrations as long as the value of a food source is below a certain threshold. Since in all available studies the bees had been trained to feeding dishes that offered sugar solution *ad libitum*, the threshold was governed by the energetic gains in terms of the sugar concentration of the collected solution (Esch 1967; Hrncir et al. 2000; Schmidt et al. 2006b, 2008). Yet, another important determinant for the excitement of a forager is the individually experienced profitability of the visited food patch. Consequently, alterations in sugar concentration-independent parameters of profitability, like search and collecting times, lead to changes in the bee's disposition to generate thoracic vibrations inside the nest.\*

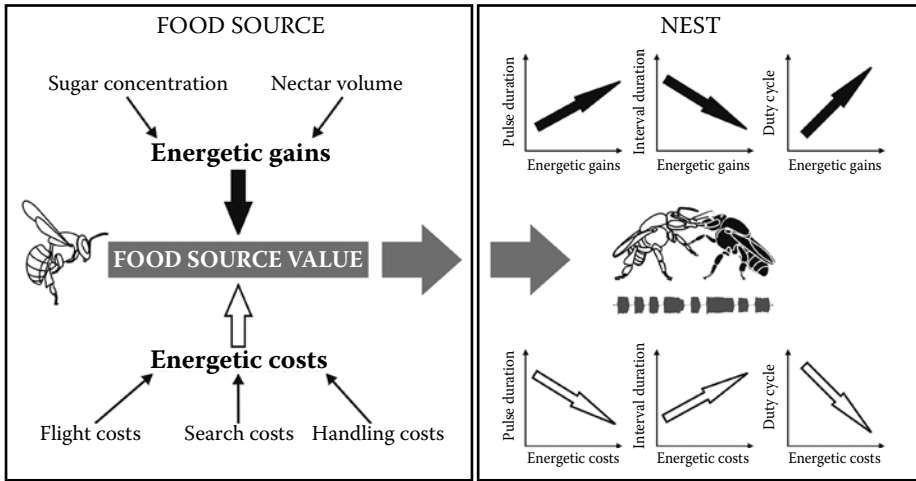
### Energetic Gains

The energetic gains during a foraging trip, which, in bees, are strongly influenced by the sugar concentration of the collected food (Roubik and Buchmann 1984; Roubik et al. 1995; Hrncir et al. 2004b; Schmidt et al. 2006b, 2008), are probably one of the principal factors used by foragers to determine the profitability of a food patch. In honey bees, the liveliness of the waggle and round dances, as well as the temporal pattern of the concomitant sounds generated by the foragers, strongly depends on the imbibed sugar concentration (Esch 1963; Waddington 1982, 2001; Waddington and Kirchner 1992; Seeley et al. 2000; De Marco and Farina 2001). Although the importance of food quality for the honey bee's communication has been known for more than 80 years (von Frisch 1923), the possible relation between nest-internal recruitment signals and the food profitability in stingless bees has only recently been investigated (*Melipona costaricensis*, Aguilar and Briceño 2002; *M. bicolor*, *M. mandacaia*, Nieh et al. 2003; *M. seminigra*, Hrncir et al. 2002, 2004a, 2004b; *M. rufiventris*, Hrncir et al. 2006a; *Nannotrigona testaceicornis*, Allerstorfer 2004; Schmidt et al. 2008; *Scaptotrigona* aff. *depilis*, Schmidt et al. 2006b).

In all studied *Melipona* species, as well as in *N. testaceicornis*, the temporal pattern of the foragers' pulsed thoracic vibrations is significantly related to the energetic gains at the food patch. As soon as the value of the food exceeds the agitation threshold, the duration of the pulses increases and the interval between the pulses decreases with increasing sugar concentration (*M. costaricensis*, Aguilar and Briceño 2002; *M. bicolor*, *M. mandacaia*, Nieh et al. 2003; *M. rufiventris*, Hrncir et al. 2006a; *M. seminigra*, Hrncir et al. 2002, 2004a, 2004b; *N. testaceicornis*, Allerstorfer 2004; Schmidt et al.

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\* During an experiment in which three *M. seminigra* foragers collected a 40% w/w ( $\approx 1.4$  mol/l) sugar solution at a feeding dish, the bees suddenly stopped to produce sounds when returning to the colony. The fact that the foragers continued to deliver food to their nestmates indicated that the artificial food patch still provided food. Yet, several dozen *Trigona recursa* foragers had usurped the feeder. Due to this mass occupation by another species, the foragers of *M. seminigra* only occasionally managed to land on the feeding dish and collect sugar solution (MH, unpublished observation). In this case, apparently, the cessation of the foragers' recruitment activity was not related to a decrease in sugar concentration below the agitation threshold, but to a sudden decay in the overall profitability of the food patch due to an increase in search and collecting times.



**FIGURE 11.5** The value of a food source influences the thoracic vibrations of stingless bee foragers. Several energetic parameters determine the value of a food source for collecting bees and, consequently, influence the temporal pattern of the foragers' thoracic vibrations: Increasing energetic gains at the food patch result in longer pulses, shorter intervals, and consequently, an increasing duty cycle (duty cycle = pulse duration/[pulse duration + interval duration]). Increasing energetic costs, by contrast, result in shorter pulses, longer intervals, and a decreasing duty cycle.

2008) (Figure 11.5). In *Scaptotrigona* aff. *depilis*, by contrast, the collected sugar concentration had only a small effect on the bees' thoracic vibrations (Schmidt et al. 2006b). Similarly to what has been found for the jostling activity in this bee species (see above), the past foraging experience strongly influenced the temporal pattern of the foragers' thoracic vibrations. The sound pattern remained more or less the same when the foragers collected a constant or an increasing sugar concentration at the food patch. Yet, their excitement decreased (decreasing pulse duration, increasing interval duration) when experiencing a gradual reduction of the food's profitability (Schmidt et al. 2006b).

### Flight Costs

Energetic costs during foraging might be another important factor for the foragers' evaluation of the food source's profitability. Consequently, and in accordance with the findings for energetic gains, increased energetic expenses during a collecting trip should reduce the agitation of a forager. And indeed, in *Melipona seminigra* the effect that elevated flight costs had on the temporal pattern of the foragers' thoracic vibrations was exactly the opposite of that of increased energetic gains\* (Hrncir et al. 2004a, 2004b) (Figure 11.5).

\* Foragers had been trained to collect sugar solution first at the entrance, and then at the far end of flight tunnels that varied in their width and in the visual pattern of their lateral walls (black-and-white stripes either perpendicularly or parallel to the flight direction of the bees). In fact, these experiments had been designed to study the possible influence of the visual flow (lateral image motion)—which foragers of *M. seminigra* use to estimate their flight distances (Hrncir et al. 2003)—on potential recruitment signals of these bees. It turned out that the thoracic vibrations were not at all affected by differences in the visual flow (induced through different tunnel widths) experienced by the bees. Even so, the temporal pattern of the foragers' vibrations differed between the feeding situations at the tunnel entrance and at the far end of the tunnel, respectively. As soon as the bees had to pass through a tunnel to get to the food source, the duration of the pulses decreased significantly, and the interval between the pulses increased (Hrncir et al. 2004a). A possible explanation for the observed reduction in the foragers' excitement is an increase in energetic costs as soon as the bees collected at the far end of the tunnels. The foragers' flight speed inside all tunnels was about 0.3 m/s, and therefore considerably reduced compared to their flight velocity in a natural environment (ca. 4.25 m/s) (Hrncir et al. 2004a). Since the energetic expenditures of flying bees are substantially higher at low flight velocities (<1 m/s) than at velocities of about 4 m/s (measured in honey bees, Nachtigall et al. 1995), the foragers of *M. seminigra* quite possibly spent more energy when collecting at the far end of the tunnel than when collecting at the tunnel entrance.

## Natural Nectar Sources

When stingless bee foragers collect at natural food sources, their foraging trips are considerably longer than when they collect at feeding dishes (Allerstorfer 2004). Since sugar solution foragers do not have to search for a rewarding flower, the round-trip times mainly depend on the distance of the feeding dish from the nest. Foraging times of bees that collect at natural nectar sources, by contrast, are composed of the time to reach a food patch plus the time to find and exploit rewarding flowers.\* In addition to increased collecting times, bees that collect at natural resources often return with only a partly filled crop (Roubik and Buchmann 1984). Therefore, due to elevated energetic expenses and reduced energetic gains, the profitability of natural nectar sources is certainly lower than that of sugar solution feeders—even if both sources provided food of the same sugar concentration. Consequently, we should expect less excitement when foragers collect at natural nectar sources than when they collect at feeding dishes.

To this day, the thoracic vibrations of stingless bee foragers that collect at natural food sources have not been studied (or at least results have not been published). In *M. seminigra*, however, two studies tentatively simulated a natural feeding situation in order to investigate the possible influence of a reduced nectar intake together with increased search times on the foragers' vibrations (Hrncir et al. 2002; Hrncir, unpublished data). The bees collected sugar solution at feeder arrays consisting of either six (Hrncir et al. 2002) or nine (MH, unpublished data; Figure 11.6) small cups, of which only three contained a small reward. This collecting situation, which caused elevated search times and reduced energetic gains for the bees, indeed resulted, as predicted, in a reduced excitement of the foragers inside the nest (Figure 11.6). Although the foragers' collecting times were almost two times longer at the cup feeder arrays than at common feeding dishes (collecting time: 62 s at cup feeder, 30 s at feeding dish; MH unpublished data), they still were considerably shorter than foraging times at natural food sources.\* We can, consequently, venture the prognosis that bees foraging at natural nectar sources show even less nest-internal excitement than those collecting at the artificial “mass flowers.”

## MOBILIZING THE FORAGING FORCE

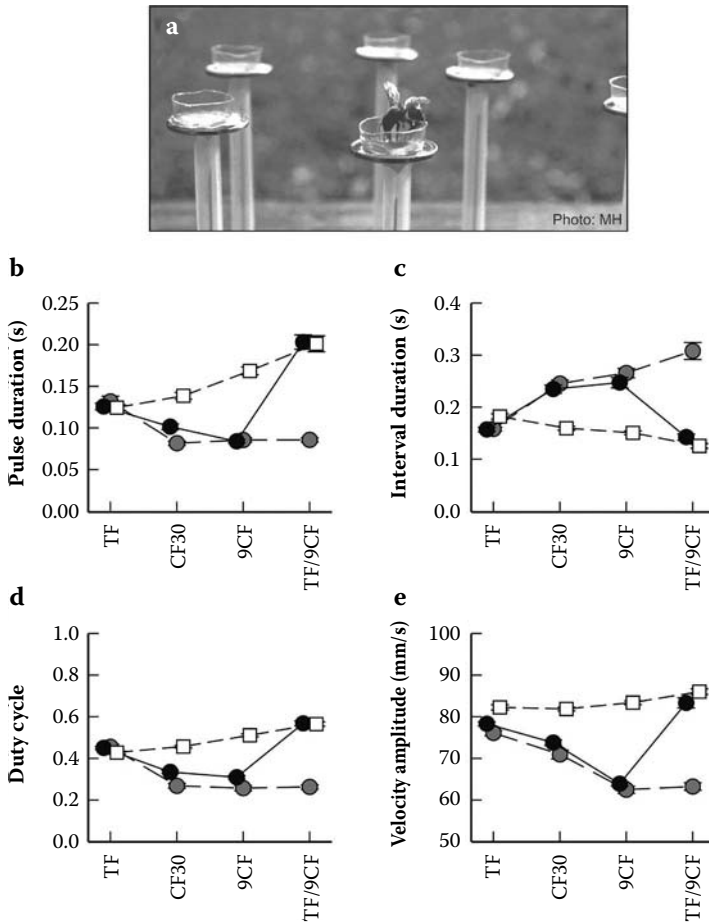
Due to the high competition over food sources, a quick activation of the colonies' foraging force to a profitable resource would be advantageous for several meliponine species. For unemployed but food source-experienced foragers, scent/taste information provided by returning foragers that matches their own experience is sufficient to make them return to the food patch they previously visited (Biesmeijer et al. 1998; see also Chapters 9 and 10). On the other hand, those bees that have no previous experience with the resource in question start their collecting activity only when their foraging motivation is above a certain threshold (Biesmeijer et al. 1998). Therefore, any recruitment signal that aims at activating new foragers should primarily modulate the foraging readiness of inexperienced nestmates by increasing their foraging motivation.

## THE EXCITEMENT OF POTENTIAL NEWCOMERS

Research on the nest-internal recruitment communication in stingless bees, so far, has focused on the behavior of the recruiters. In order to understand a communication system in-depth, however, both the sender and the receiver of a signal have to be considered. In most cases, the sender—in the present case the employed forager—is easily identified. By contrast, it often proves difficult to pinpoint the receivers, due to sometimes very subtle changes of their behavior in response to the signal.

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\* Roubik and Buchmann (1984) calculated foraging times between 7 and 12 min for three *Melipona* species collecting nectar at a mass-flowering shrub. In compliance with these calculations, de Bruijn and Sommeijer (1997) observed that nectar foragers of *M. costaricensis* spent up to 10 min on a foraging trip, and Allerstorfer (2004) described natural foraging times of even up to 50 min in *N. testaceicornis*.



**FIGURE 11.6** Thoracic vibrations of foragers collecting at an artificial “mass flower”. Foragers of *Melipona seminigra* were trained to collect sugar solution (50% w/w) from a feeding dish with unlimited solution flow (TF). In the subsequent experimental step, the feeding dish was replaced by a small plastic cup containing 30  $\mu$ l of sugar solution (CF30), which is less than the average full crop load of the foragers (about 40  $\mu$ l; Hrncir et al. 2004b). Thereafter, 30  $\mu$ l of sugar solution was distributed among three randomly chosen cups in a nine-cup feeder array (9CF), which resulted in elongated search times for the foragers. In the last experimental step, half of the foragers (grey-filled circles; N = 6 bees) continued foraging at the cup feeder array, whereas the other half (black-filled circles; N = 6 bees) returned to collecting at the training feeder. Each experimental step lasted 30 min. A third group (open squares; N = 6 bees) collected at TF for 120 min to control for eventual changes in the thoracic vibrations along with the duration of an experiment. The thoracic vibrations of all foragers were recorded during trophallaxis inside an observation box placed between the entrance/exit tube and the nest. (a) *M. seminigra* forager collecting at a cup feeder array. (b–e) There were significant changes in the temporal pattern of the thoracic vibrations in the course of an experiment (given are mean values  $\pm$  1 SE): the duration of the pulses (b), the duty cycle (d), and the velocity amplitude (e) decreased, and the duration of the intervals (c) increased when the collected reward decreased below the full crop load of the foragers (TF  $\rightarrow$  CF30). The thoracic vibrations changed even more as soon as the foragers’ search times increased (CF30  $\rightarrow$  9CF). The comparison with the control group demonstrates that the observed decrease in the foragers’ excitement was a consequence of reduced energetic gains and increased search costs at the food patch (Hrncir, unpublished data).

In the case of recruitment communication, the only receivers that can unequivocally be determined are those recruits that reach an advertised food patch during an ongoing foraging process.

Studies on the nest-internal case history of individually marked recruits demonstrated that, before hive bees initiated their foraging activity, their interactions with active foragers steadily increased (*Melipona quadrifasciata*, Hrncir 1998; Hrncir et al. 2000; *M. seminigra*, Kronberger 2000). Prospective newcomers to a food source had trophallactic interactions with the foragers, but also attended trophallactic food transfers without receiving food samples, staying close to the forager's thorax-abdominal region (Hrncir 1998; Hrncir et al. 2000; Samwald 2000). In both these situations the forager's thoracic vibrations are putatively transmitted to the recruits (Hrncir et al. 2006b, 2008). During such interactions, therefore, hive bees are potentially informed about the agitation level of a forager—expressed in the temporal pattern of its thoracic vibrations—and consequently, about the profitability of the food source. This information is important for the hive bees' decision whether or not to forage (Biesmeijer et al. 1998). Some bees, apparently, require only little input (interactions with active foragers) to initiate their collecting activity (low foraging threshold), whereas others need repeated information from the active foragers (high foraging threshold). In *M. quadrifasciata* and *M. seminigra*, for example, the studied prospective newcomers received between one and fifteen food samples, and attended between two and thirteen trophallaxes, respectively, before leaving the nest for the food source (Figure 11.7).

Considering that communication is characterized as “the process in which actors use specially designed signals or displays to modify the behaviour of reactors” (Krebs and Davies 1993, p. 349), we have to ask whether and to which degree prospective newcomers change their behavior after their interactions with active foragers. One behavioral parameter that can be used for these investigations is the agitation level of inactive foragers. Lindauer and Kerr (1960) observed: “Until the first bees reached the feeding table, the bees in the hive were quiet, inactive and scattered about. But they started running about excitedly when the first bees returned from the feeder” (Lindauer and Kerr 1960, p. 33). This agitation inside the hive immediately after the onset of a collecting process is certainly, in parts, due to the raised activity of nectar unloaders and food processors. Yet, an elevated agitation can also be observed in inactive foragers. In *Melipona seminigra*, for instance, prospective newcomers significantly increased their jostling activity after their first contacts with active foragers (Kronberger 2000; Figure 11.7c). This sudden excitement of inactive foragers can be taken as an indicator for their elevated foraging motivation in response to the interactions with the food collectors, and it supports the idea that the nest-internal behaviors of active foragers are indeed communication signals.

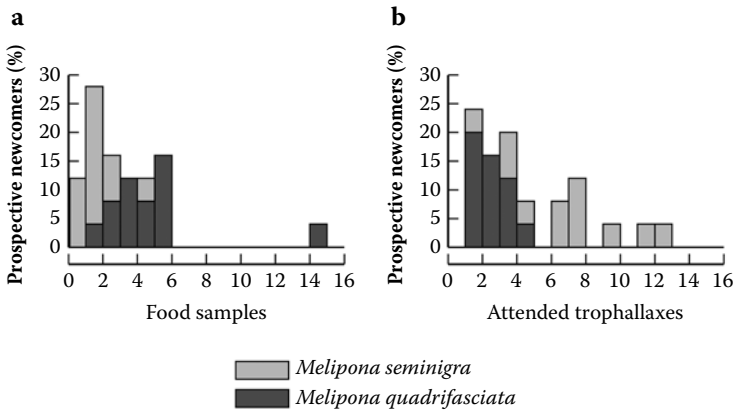
### RECRUITER'S EXCITEMENT AND RECRUITMENT SUCCESS

A fact that corroborates the alerting hypothesis of Lindauer and Kerr (1958, 1960) is the correlation between the profitability of a food source and the recruitment success (amount of newcomers per unit time) of the bees collecting there.

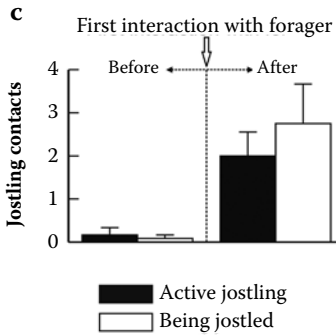
As long as the value of the food is below the agitation threshold of a forager (neither excited movements nor sounds inside the nest), no newcomers arrive at the food source (Jarau et al. 2000).<sup>\*</sup> If, however, the food source's profitability exceeds the agitation threshold, the foragers' recruitment success correlates with the sugar concentration of the collected food. This fact has been demonstrated for several *Melipona* species (*M. bicolor*, *M. mandacaia*, Nieh et al. 2003; *M. panamica*, Nieh and Sánchez 2005) and for *N. testaceicornis* (Schmidt et al. 2008) (Figure 11.8). Since in these species, however, the recruiters' excitement directly correlates with the energetic gains at the food source (see above), it is difficult to ascertain whether the recruitment success depends on the sugar

<sup>\*</sup> Researchers have made use of this circumstance when trying to avoid the initiation of recruitment processes while training foragers to a specific feeding site (e.g., Jarau et al. 2000, 2003; Schmidt et al. 2006a, 2008).

### Interactions with foragers

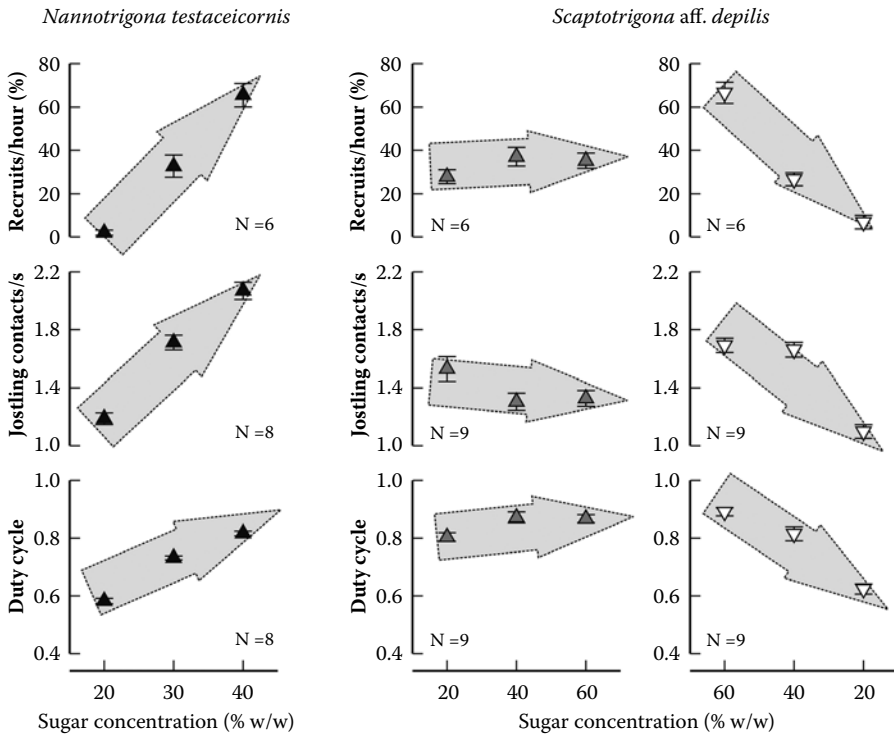


### Jostling activity



**FIGURE 11.7** Behavior of prospective newcomers inside the nest prior to reaching a food source. Prospective newcomers of *Melipona quadrifasciata* (dark grey; N = 13 bees) and *M. seminigra* (light grey; N = 12 bees) received between one and fifteen food samples (a) or attended between two and thirteen trophallaxes without receiving food (b) before initiating their collecting activity. (c) The jostling activity of prospective newcomers (means + 1 SE for twelve individuals of *M. seminigra*) increased significantly after their first interactions with active foragers. (Data for *M. quadrifasciata* from Hrnčir 1998; data for *M. seminigra* from Kronberger 2000.)

concentration of the collected and distributed food per se, or whether it is related to the foragers' nest-internal agitation. Here, the possible solution is provided by experiments with *Scaptotrigona* aff. *depilis*, in which the recruiter's excitement (jostling activity as well as thoracic vibrations) was shown to depend on the past foraging experience rather than on the current food profitability (see above). When offering a steadily increasing sugar concentration at the food source, the foragers' nest-internal excitement did not change, and neither did the recruitment success (Schmidt et al. 2006b) (Figure 11.8). Hence, the quality of the received food samples did not influence the foraging motivation of the hive bees. Yet, when the profitability of the food source continuously decreased, both the recruiters' excitement and their recruitment success diminished (Schmidt et al. 2006b) (Figure 11.8). From these findings, it can be concluded that—at least in this bee species—the foraging motivation of inexperienced bees does not depend on the quality of the food brought in by the foragers but, indeed, on the excitement of the recruiters.



**FIGURE 11.8** Recruitment success compared to the excitement of the recruiters. In *Nannotrigona testaceicornis*, both the amount of recruited bees (100% = total number of recruits per experiment) and the excitement of the foragers—expressed in their jostling activity and the temporal pattern of their thoracic vibrations (duty cycle given as example; duty cycle = pulse duration/[pulse duration + interval duration])—correlated with the sugar concentration of the collected food. In *Scaptotrigona aff. depilis*, by contrast, the amount of recruited bees and the recruiters’ excitement did not change much when the foragers experienced a steadily increasing food quality (dark-grey-filled triangles). Only when the food quality decreased in the course of time (open triangles) did the recruitment success and the bees’ nest-internal excitement diminish. These findings suggest that the recruitment success depends on the foragers’ excitement rather than on the actual sugar concentration of the food brought into the colony. Graphs represent mean values  $\pm$  1 SE; numbers of experiments (recruitment success) and foragers (jostling contacts and duty cycle) are indicated in the respective plots. (Data from Schmidt et al. 2006b, 2008; raw data kindly provided by Veronika M. Schmidt.)

### CONCLUDING REMARKS

The scientific interest in stingless bees has steadily increased during the past decades, since from this ecologically and biologically highly diverse group of eusocial bees much can be learned about the organization of insect societies. Nevertheless, we are still a far way behind what is known about honey bees, which is probably due to the fact that in the Meliponini we have to cope with more than four hundred species. Yet, it becomes more and more evident that stingless bees are far from simply being a group of “more primitively organized” honey bees (von Frisch 1993, p. 306).

Regarding the foraging and recruitment strategies of stingless bees, we encounter a fascinating variety and diversity among the different species (Lindauer and Kerr 1958, 1960; Nieh 2004; Barth et al. 2008). So far, however, we have only managed to grasp a small fragment of this meliponine world of scents and sounds.

To this day, the significance of the behaviors displayed by employed foragers inside the nest is not entirely unscrambled. In addition to the alerting hypothesis introduced by Lindauer and Kerr

(1958, 1960; see also Hrnčir et al. 2000, 2004a, 2004b; Jarau et al. 2000), several studies claimed a meliponine equivalent to the honey bee's dance language, postulating that *Melipona* foragers encode the distance of a food source from the nest—and even its height above ground level—within the temporal pattern of their thoracic vibrations. Consequently, the recruits were thought to leave the nest with detailed information about the position of the visited food patch (Esch et al. 1965; Esch 1967; Nieh and Roubik 1998; Aguilar and Briceño 2002; Nieh et al. 2003). However, in spite of putative correlations between the duration of the vibratory pulses and the position of a food source (distance or height), convincing evidence is lacking that the foragers' sounds really constitute a form of referential location communication comparable to the honey bees' dance. Nieh and Roubik (1998) performed experiments in which they removed the recruiters—trained foragers (either ten or twenty individuals) collecting at an experimental feeder—during an ongoing recruitment process. From the observation that, after capturing the foragers, more newcomers arrived at the experimental feeder than at a control feeder (either at a different distance from the nest or a different height above the ground), the authors concluded that these bees had found the food source based on information provided by foragers inside the nest (Nieh and Roubik 1998). It remained unclear, however, for how long the newcomers had already been searching for the food source prior to alighting at the experimental feeder. Thus, it cannot be excluded that the bees had actually left the nest long before the experienced foragers were removed, and that their search had been biased by the presence of up to twenty collecting nestmates—as has been observed in honey bees (Friesen 1973).

So far, in fact, experiments have only undoubtedly demonstrated that the foragers' signals are followed by an increasing number of bees leaving the nest (Lindauer and Kerr 1958; Esch 1967; Pereboom and Sommeijer 1993) or by an increasing number of bees arriving at a food source (Lindauer and Kerr 1958, 1960; Nieh and Roubik 1995; Jarau et al. 2000, 2003; Nieh et al. 2003; Schmidt et al. 2006b, 2008). Furthermore, the recent findings that foragers of *M. seminigra* do not encode the visually measured distance of a food source in the temporal pattern of their thoracic vibrations (Hrnčir et al. 2004a) actually provide strong evidence *against* a referential location communication. In fact, all available experimental data corroborate the alerting hypothesis by demonstrating that (1) the recruiters' excitement strongly depends on the individually perceived value of a food source, and (2) the foraging motivation of bees depends on the nest-internal behavior of the recruiters. In addition, ecological considerations indicate that a quick activation of foragers is of considerable advantage for various species of stingless bees in order to exploit valuable food sources efficiently. It has to be kept in mind, however, that so far only a small percentage of the Meliponini has been investigated with regard to their recruitment communication, and that many surprises still might await discovery.

## ACKNOWLEDGMENTS

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