13. The fast *versus* the furious – On competition, morphological foraging traits, and foraging strategies in stingless bees

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Abstract
Stingless bee pot-honey is a valuable product with a long tradition of harvest and consumption in Central and South America. The differences found among meliponine honeys concerning physiochemical composition, sugar content, and floral origin depend, to some extent, on the bee species. In the present chapter we outline some basic principles underlying foraging specialization by stingless bees, mainly morphological and behavioural differences among species. Both morphological foraging traits and foraging strategies influence meliponine colony decisions to collect a particular food source while ignoring others, which in turn contributes to honey quality, considering floral origin and sugar content.
Key words:
body colouration, body size**,** exploitation of food sources, food niches, foraging strategies, stingless bees

Introduction
Some pot-honeys are sweeter than others. Stingless bee pot-honey is a valuable product with a long tradition of harvest and consumption in Central and South America (Camargo and Posey, 1990; Crane, 1999; Vit et al., 2013). Diverse meliponine species are kept by meliponiculturists all over Latin America to provide this precious gold. The differences found among pot-honeys with respect to physiochemical composition, sugar content, and floral origin depend certainly on the geographic region and also the stingless bee species (Barth, 1989; Souza et al. 2006; Vit et al., 2013). In the present chapter, we outline some basic principles on how competition for food shapes differences in spatio-temporal foraging preferences found among meliponine species, which can lead to a better understanding of why some pot-honeys are sweeter than others.

13.1 Competition for food, survival, and reproduction
The rich diversity of both flowering plants and flower visiting insects has rendered the tropics an ideal evolutionary playground for developing an overwhelming diversity of insect-plant interactions. Plants, on the one hand, have evolved a fascinating variety of floral shapes, flowering traits, and phenological strategies in order to prevail in the inter- and intra-specific competition for pollinators (Gentry, 1974; Waser and Real, 1979; Augspurger, 1980; Bawa, 1983; 1990; Frankie et al., 1983; Waser, 1983;

2001). Flower visiting insects, on the other hand, have developed a no less impressive diversity of strategies and mechanisms aiming at maximizing the exploitation of floral resources (Johnson, 1983; Roubik, 1989; Goulson, 1999; Jarau and Hrncir, 2009).

In the tropics, the most abundant flower visitors are eusocial bees, the stingless bees (Apidae, Meliponini), bumble bees (Apidae, Bombini), and honey bees (Apidae, Apini) (Heithaus, 1979; Roubik, 1989; Momose et al., 1998; Biesmeijer et al., 2005). In contrast to solitary insects that collect food for their individual survival and reproduction (*direct fitness*), social insects gather food to guarantee the survival and reproduction of their colony (*indirect fitness*) (Wilson, 1971; Michener, 1974; Jarau and Hrncir, 2009).

Tropical habitats are frequently shared by several dozen social bee species, most of which are considered generalist foragers, and diet overlap, therefore, is considerable (Wilms et al. 1996; Ramalho, 2004; Biesmeijer et al., 2005; Biesmeijer and Slaa, 2006). The generalized utilization of common floral resources results in pollen (a protein supply for brood rearing) and nectar (carbohydrate supply to satisfy energy-demands of non-foraging nestmates) competition between colonies (Johnson, 1983; Johnson and Hubbell, 1974; Roubik, 1980; Roubik et al., 1986; Wilms and Wiechers 1997; Biesmeijer et al., 1999a; Nagamitsu and Inoue, 2005). The selective pressure to maximize pollen and nectar collection led to the evolution of a rich variety of foraging strategies among social bees, which differ according to variation in foraging-related traits, such as morphology, aggressiveness, recruitment velocity, and recruitment efficiency (Lindauer and Kerr, 1958; Johnson, 1983; Roubik, 1989; Biesemeijer et al., 1999a; Biesmeijer and Slaa, 2004; Nieh, 2004; Willmer and Stone, 2004; Nagamitsu and Inoue, 2005; Barth et al., 2008; Hrncir, 2009; Jarau, 2009).

Particularly suited for studying the adaptive value of different food collecting strategies are the stingless bees, the largest and certainly most diverse group of eusocial bees (Michener, 2000; Camargo and Pedro, 2007; Vit et al., 2013). To date, only a handful of the more than 400 predominantly tropical species have been studied in some detail with regard to their foraging decisions, foraging strategies, and underlying ecological constraints (Lindauer and Kerr, 1958; Johnson, 1983; de Bruijn and Sommeijer, 1997; Biesmeijer et al., 1999a; Jarau et al., 2003; Slaa, 2003; Biesmeijer and Slaa, 2004; Nieh, 2004; Hofstede, 2006; Hrncir, 2009; Jarau, 2009). Besides

considerable similarities in food plant use (Biesmeijer and Slaa, 2006), species-specific differences in foraging traits allow successful partitioning of food sources among meliponine species. First, differences in morphological characteristics, such as body size and colouration, result in a spatio-temporal partitioning of food sources. Thus, one and the same plant may represent several different fundamental food niches for stingless bees (fundamental food niche: the ecological niche occupied by a species in the absence of competitors). Second, due to the fact that every foraging strategy (solitary foraging, foraging in small groups, mass-foraging, aggressive or unaggressive foraging, etc.) has its advantages under certain circumstances, differences in foraging strategies allow meliponine species to profit on food sources shared with competing species.

13.2 The fundamental food niche – resource use in the absence of competitors

13.2.1 Bees and flowers – mutualism and conflict

In the tropics, just as in every other terrestrial ecosystem, the reproductive success of many plant species with conspicuously coloured and/or scented flowers depends on bee pollination. Most bee species, in turn, depend on flowering plants as their principal food sources. In spite of this mutualistic relationship *par excellence*, there is an intrinsic conflict of interest between plants and their pollinators driven by the selection for increased exploitation of each other (Schoonhoven et al., 2005). Plants, on the one hand, need to receive as many conspecific pollen grains as possible on their flower stigmas and, in turn, transfer as much of their own pollen as possible to the stigmas of other conspecifics. Ideally, therefore, a pollination agent touches both anthers and stigmas of a flower, moves rapidly among plants, and visits exclusively conspecific flowers. In order to force bees to visit many flowers per foraging trip, selection favours the production of an amount of food sufficient to be attractive to the foragers, yet not so much as to satiate them during a single visit or a few visits (*selection for reducing reward*). Bees, on the other hand, following optimal foraging rules, try to collect as much food as possible while minimizing energy and time expenditure, and, consequently, should prefer flowers that offer large amounts of food (*selection for increasing reward*) (Real, 1981; Stephens and Krebs, 1986; Klinkhamer and de Jong, 1993; Schoonhoven et al., 2005).
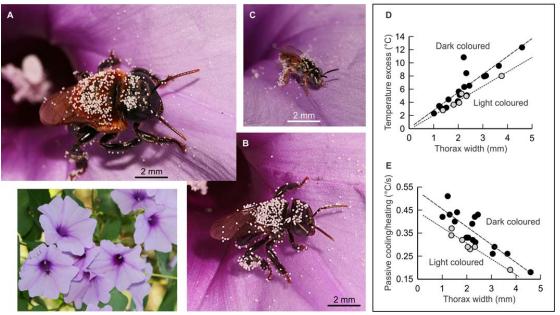
13.2.2 Spatio-temporal partitioning of food sources

A second major plant-pollinator conflict, the competition for effective pollination agents among

plant species, may be considered responsible for a plant's specialization on certain pollinator species or pollinator guilds (Schoonhoven et al., 2005; see however: Waser, 2001). Here, an efficient mechanism to restrict flower visits to certain pollinators, thereby avoiding competition with other plants, is flowering at a certain and limited time of the day. The segregation of food niches among pollinators is largely due to body size and body colouration, both of which are related to the thermal tolerance of a bee species and, consequently, may be the reason for both spatial and temporal foraging preferences (Biesmeijer et al., 1999a; 1999b; Pereboom and Biesmeijer, 2003; Hrncir and Maia-Silva, 2013) (Figure 1).

The flight activity of tropical and subtropical bees, such as the Meliponini, is constrained by high ambient temperatures when foraging (Heinrich, 1993; Biesmeijer

et al., 1999a; Pereboom and Biesmeijer, 2003). Small bees, in general, heat up and cool down more rapidly than large bees. Due to an elevated convective heat loss, however, small species rarely attain excessively high body temperatures (Digby, 1955; Pereboom and Biesmeijer, 2003) (Figure 1). Large bees, therefore, run a higher risk of overheating than small bees, in particular when foraging in full sunlight.

A second important parameter influencing the spatio-temporal foraging preferences of a bee is its body colouration. Physically, temperature excess and overheating are proportional to the absorbed thermal energy (high absorptivity for dark colours; low absorptivity for pale colours), and, consequently, pale-coloured bees heat up more slowly in full sunlight than dark-coloured bees (Digby, 1955; Pereboom and Biesmeijer, 2003) (Figure 1).

Photography: M Hrncir

Figure 1. Morphological foraging traits (body size and colouration) underlying spatio-temporal foraging preferences of stingless bees. (**A**-**C**) Three meliponine species of different body size foraging at *Ipomoea bahiensis* (inset) in Northeast Brazil (Mossoró-RN). The sequence of arrival was: (**A**) *Melipona subnitida* (around 7:00 a.m.), (**B**) *Partamona* sp. (around 7:30 a.m.), and (**C**) *Plebeia* sp. (around 8:15 a.m.). Photos by MH. (**D**) Correlation between body size (thorax width) and temperature excess (maximum difference between thoracic and ambient temperature), and (**E**) Correlation between body size and passive cooling/heating (cooling constant K) of 24 species of stingless bees. Light-coloured bees (grey-filled circles) have a lower temperature excess and cool down (and warm up) less rapidly than dark bees (black-filled circles) of similar size. Dashed lines indicate linear regressions for light-coloured and dark-coloured bees. Data (**D**-**E**) from Pereboom and Biesmeijer (2003). Figure (**D**-**E**) adapted from Hrncir and Maia-Silva, 2013.

In compliance with the thermal characteristics assigned to body size and colouration, stingless bees show a spatio-temporal partitioning of food sources (Willmer and Corbet 1981; Biesmeijer et al. 1999a; 1999b). Body size is the main factor responsible for the temporal segregation among species. It has been repeatedly demonstrated that large Meliponini start foraging earlier during the day, and at lower ambient temperatures, than smaller species (de Bruijn and Sommeijer, 1997; Pereboom and Biesmeijer, 2003; Teixeira and Campos, 2005) (Figure 2).
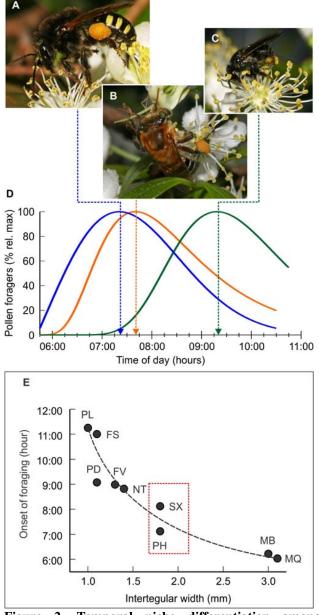

Figure 2. Temporal niche differentiation among stingless bee species differing in body size and colouration. (**A-D**) Pollen collection of three stingless bee species (**A**: *Melipona quadrifasciata*; **B**: *M. scutellaris*; **C**: *Scaptotrigona* aff. *depilis*) at mass-flowering *Eugenia uniflora*. (**D**) In August 2009, pollen collection of 4 colonies of each species was observed for 6 days at the campus the University of São Paulo in Ribeirão Preto, Brazil. The graph shows log-normal regression models of the number of foragers (percentage relative to maximum) returning to colonies with pollen loads between 6:00 a.m. and 11:00 a.m. for each species. Arrows indicate the time of maximum foraging— Maia-Silva, *unpublished data*. Photos by MH. (**E**) Foraging onset of 9 stingless bee species differing in body size (given as inter-tegular width); MQ, *Melipona quadrifasciata*; MB, *Melipona bicolor*, PH, *Partamona helleri*; SX, *Scaptotrigona xanthotricha*; NT, *Nannotrigona testaceicornis*; PD, *Plebeia droryana*; FV, *Frieseomelitta varia*; FS, *Friesella schrottkyi*; PL, *Plebeia lucii*. Note earlier foraging of dark-coloured PH compared to the similar-sized, light-coloured SX (framed red). Data (**E**) from Teixeira and Campos (2005). Figure (**A-E**) adapted from Hrncir and Maia-Silva (2013).

Large bees, due to their elevated mass of thoracic muscles, are capable of heating up their flight apparatus more efficiently than small bees. Consequently, they are able to attain ideal flight temperatures even at low ambient temperatures and can initiate foraging long before the small species are sufficiently warmed up (Heinrich, 1993; Teixeira and Campos, 2005). Additionally, body colouration might play a decisive role concerning the onset of foraging, particularly so for the small bee species. Due to the fact that dark-coloured bees heat up faster than light-coloured bees (Figure 1), dark species are able to initiate foraging earlier in the day than pale-coloured species (Figure 2).

Stingless bee species of similar size, but differing in body colour, partition patches of the same floral resource according to sunlight incidence (spatial partitioning). In an experimental study on the foraging choice of the sympatrically occurring dark-coloured *Melipona costaricensis* (described as *M. fasciata*) and light-coloured *M. beecheii*, the dark species clearly preferred shaded food patches and avoided sunlit ones (Biesmeijer et al. 1999a) (Figure 3). This spatial separation among stingless bees may lead to differences between species concerning the nectar concentrations harvested (Biesmeijer et al., 1999b) (Figure 3). Differences in evaporation due to differences in illumination between patches result in more concentrated nectar in sunlit flower patches as compared to shaded patches (Willmer and Corbet, 1981). Accordingly, the light-coloured *M. beecheii*, who favoured sunlit patches, were found to collect more concentrated nectar from the same plant species and at the same time of day than the dark-coloured *M. costaricensis*, who preferred the shaded patches (Biesmeijer et al. 1999b) (Figure 3).
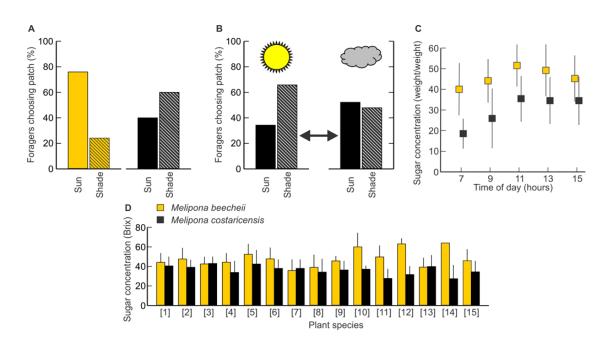
Figure 3. Spatial niche differentiation among stingless bee species differing in body colouration and its impact on the harvested sugar concentration from floral nectar. (**A**) Under clear sky-conditions, foragers of the light-coloured *Melipona beecheii* (yellow bars) preferentially collect at sunlit patches whereas the dark-coloured *M. costaricensis* (black bars) prefer food patches in the shade. (**B**) Foragers of *M. costaricensis* react immediately to switches from sunny to cloudy weather or vice versa with respect to their patch preference. Data (**A**-**B**) from Biesmeijer et al. (1999a). (**C**-**D**) Light-coloured *Melipona beecheii* (yellow bars and squares) collect nectars of significantly higher sugar concentration than dark-coloured *M. costaricensis* (black bars and squares). (**C**) Variation in sugar concentration (means ± SD) of nectar collected in a day. (**D**) Sugar concentration (means + SD) of nectar of different botanical origin obtained from foragers at the nest entrance. [1] *Oxydaea verbesinoides*; [2] *Vernonia patens*; [3] *Bidens squarrosa*; [4] type 11; [5] cf. *Heliocarpus*; [6] *Hyptis capitata*; [7] *Serjana* sp.; [8] *Mikania micrantha*; [9] *Bravaisia integerrima*; [10] *Schlegelia parviflora*; [11] cf. *Celtis*; [12] type 9; [13] type 16; [14] type 42; [15] type 50. Data (**C**-**D**) from Biesmeijer et al. (1999b). Figure (**A**-**D**) adapted from Hrncir and Maia-Silva (2013).

13.3 The realized food niche – resource exploitation in the presence of competitors

13.3.1 Mass-flowering foraging bonanzas – a good reason for competition

Whereas plants ensure successful reproduction through cross-pollination by increasing the movement of pollinators between patches, the pollinators' interest lies in obtaining food as quickly as possible, thereby reducing risk and energy expenditure (Real, 1981; Real and Caraco, 1986). Therefore, in order to increase collection efficiency in terms of time and energy, flower-visitors should opt for ample patches that offer large amounts of the desired resource.

Plants feature a wide variety of flowering patterns: Individuals of a population may flower for periods as short as a single day, or as long as an entire year; they may flower several times in the course of a year, once a year, once every few years, or once in a lifetime (Frankie et al., 1974; Opler et al., 1976; Bawa, 1983). Also, there is considerable variation among species concerning the number of flowers produced per unit of time. At one extreme we encounter species in which individuals produce small numbers of flowers per day but bloom for an extended time-period, lasting from several weeks to several months ("steady-state" or "extended blooming" strategy). At the other extreme, 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" strategy) (Gentry 1974; Augspurger 1980; Mori and Piploy, 1984; Bawa, 1983).

These two extreme modes of flowering, which represent merely the end points of a broad spectrum, constitute two distinct resource types for bees (Hrncir, 2009): (1) *Low profitability - long-lived resources*. Steady-state plants offer a small number of flowers per day. Consequently, bees occasionally have to move long distances between conspecific individuals to collect sufficient food (elevated search costs and risk of predation). However, as soon as a bee knows all, or many, patches of a steady-state species within its flight range, this plant represents a reliable food source due to a flowering period that often exceeds the foraging-life time of the bee; (2) *High profitability - short-lived resources*. Mass-flowering plants produce an excess of flowers each day[1]. Bees collecting at this kind of food source, therefore, are able to rapidly fill their crop with nectar, or load their corbiculae with pollen, during a single foraging trip[2] (low search costs and risk of predation). Consequently, mass-flowering plants offer an ideal opportunity for colonies to hoard large amounts of nectar or pollen within a short period of time, even if only for few days.

For stingless bees, mass-flowering plants are the predominant source of nectar and pollen, contributing by up to 90 % to the annual nutritional input into the colonies (Wilms et al. 1996; Wilms and Wiechers 1997; Ramalho 2004; Hofstede 2006) (Figure 4). After discovering such a profitable food source, stingless bee colonies are able to collect at known feeding sites for several consecutive days. Yet, a rich resource seldom, or probably never, remains in the possession of a single flower-visitor. The news of available foraging bonanzas spreads fast due to the overwhelming multitude of chemical and/or visual cues, which attract a diversity of pollinators competing for the available food.
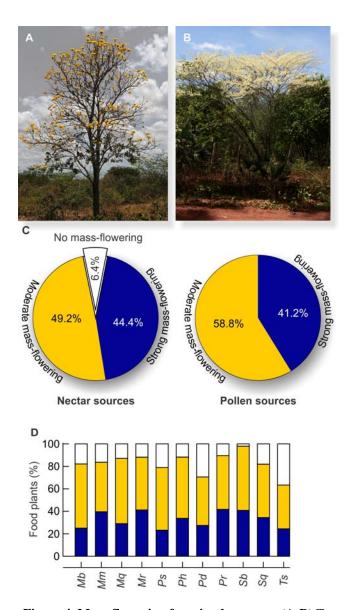
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[1] Mori and Piploy (1984) estimated about 500,000 flowers/day in the tropical tree *Miconia minutiflora*, Melastomaceae.

[2] Roubik and Buchmann (1984) calculated that foragers of *Melipona panamica* should visit an average of 15 flowers of the mass-flowering shrub *Hybanthus prunifolius* to fill their crops (average crop load: 25.8 µl), provided the bees removed all nectar from each flower (about 1.7 µl). Due to the high spatial density of flowers, each bee needs a mere 1.5 minutes to fill her crop (time to visit 5 flowers: 28.6 s; Roubik and Buchmann 1984).

Figure 4. Mass-flowering foraging bonanzas. (**A-B**) Two examples of mass-flowering tree species in Northeast Brazil (Mossoró-RN) that are important food sources for bee species (Barros, 2001; Maia-Silva et al., 2012): (**A**) *Tabebuia aurea*; (**B**) *Mimosa tenuiflora*. Photos by MH. (**C**) Mass-flowering plants are the predominant source of nectar and pollen for stingless bees. Pie-graphs show the percentage of mass-flowering plants (blue: pronounced mass-flowering; yellow: moderate mass-flowering; white: no mass flowering) contributing to the annual nutritional input into colonies, calculated from Wilms et al. (1996) and Ramalho (2004). (**D**) Food plants used by stingless bees in the Brazilian Atlantic rainforest. Given is the percentage of plants with pronounced (blue bars) or moderate (yellow bars) mass flowering, or without mass flowering (white bars), collected by: *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). Figure adapted from Hrncir, 2009.

13.3.2 Competition for food and foraging strategies in stingless bees

In every plant-pollinator system, even in those where the density of pollinators is low compared to that of the available flowers, competition for food exists. Yet, the degree of competition becomes more intense as the pollinator-to-flower ratio increases (Pleasants, 1983). In the Neotropics, frequently, one and the same habitat is shared by several dozen social bee species, most of them stingless bees (Roubik 1989; Biesmeijer et al., 1999a). The generalized utilization of common resources, such as mass-flowering plants, results in both interference and exploitative competition between species (Johnson, 1983; Biesmeijer et al., 1999a; Nagamitsu and Inoue, 2005), which reduces not only the foraging efficiency at food patches (Johnson and Hubbell, 1974; Roubik, 1980), but also diminishes the pollen and nectar harvest of colonies (Roubik et al., 1986; Wilms and Wiechers 1997; Nagamitsu and Inoue, 2005).

Foraging strategies and underlying recruitment mechanisms are important factors influencing food source partitioning among social flower visitors. In stingless bees, foraging strategies can be described in terms of three basic foraging traits: recruitment ability (solitary foraging, foraging in small groups, mass-foraging), individual aggressiveness (present or absent), and local enhancement in heterospecific encounters (attraction or avoidance) (Biesmeijer and Slaa, 2004). Among the possible combinations of these traits, a highly successful strategy is aggressive mass foraging. Here, large groups of aggressive foragers "extirpate" (Johnson, 1983) less aggressive species at a specific food patch, and thus are able to monopolize clumped and rich resources (Johnson and Hubbell 1974; 1975; Johnson, 1983; Biesmeijer and Slaa, 2004; Lichtenberg et al., 2010). The trade-off for this elevated competitive ability is a reduced capacity to discover new food sources or even neighbouring food patches independently (Hubbell and Johnson, 1978; Slaa, 2003; Biesmeijer and Slaa, 2004). The secret of success, therefore, of non-aggressive species that forage solitarily or in small groups lies in their ability to discover as many food patches as possible within the colony's foraging range (Hubbell and Johnson 1978). Thus, when dislodged from a certain location by mass foragers, these species are able to switch the colony's foraging focus quickly to another food patch. Due to this agility in their foraging, non-aggressive species that forage solitarily or in small groups are also able to capitalize on rich food sources – but only as long as they keep one step ahead of the extirpators (Hubbell and Johnson 1978; Biesmeijer and Slaa, 2004; Hrncir, 2009).

Time is a crucial parameter for the success of those foraging strategies that involve the recruitment of additional foragers to a specific floral resource. For species that forage in small groups, on the one hand, a quick detection of many food patches and a quick activation of all available foragers are imperative to get a head start before being excluded from some of the patches by mass-foragers (Hubbell and Johnson, 1978; Hrncir, 2009). The strategy of mass-foragers, in turn, relies on the rapid mobilization of huge numbers of foragers to a rich feeding site and, consequently, dislodging other species from the patch. Recruitment strategies, therefore, should differ between species that forage in small groups and mass-foragers with respect to the information about the exact position of a feeding site (important for mass-foragers, useless for small-group foragers) (Figure 5) but not necessarily concerning the velocity of mobilizing the foraging force.

13.3.2.1 The fast – success through "first come, first served" strategy

[Genera described using this foraging strategy: *Melipona*, *Nannotrigona*]

In various species of stingless bees, the strategies facilitating the effective exploitation of profitable food sources involve the recruitment of nestmates (Lindauer and Kerr, 1958; Jarau et al., 2003; Nieh, 2004; Hrncir, 2009; Jarau, 2009). So far, studies aimed at investigating the mechanisms underlying the mobilisation of food-source-naive bees (foragers without previous contact with the food source in question), and experiments largely focused on the behaviour of a handful of recruiting foragers and the arrival of naïve foragers at a food patch (review by Nieh, 2004). Although this methodological approach certainly provides valuable insight into both nest- and field-based information used by inexperienced bees for their foraging decisions, it neglects, in fact, a significant fraction of the foraging force— the experienced foragers. In bees of the genus *Melipona* —small or non-aggressive species that forage in small groups— the last category of foragers has been shown to play a decisive role in food collecting processes at both natural and artificial food sources, once familiar to the colony (*Melipona costaricensis* [*M. fasciata*], *M. beecheii*: Biesmeijer et al., 1998; Biesmeijer and Ermers, 1999; *M. seminigra*: Hrncir and Schorkopf, 2011) (Figure 6). These experienced foragers have a crucial advantage over naïve bees: they know both the position of a collecting site and the time of resource availability (Lindauer and Kerr, 1958; Biesmeijer et al., 1998; Biesmeijer and Ermers, 1999; Biesmeijer and Slaa, 2004; Schorkopf et al., 2004; Murphy and Breed, 2008).
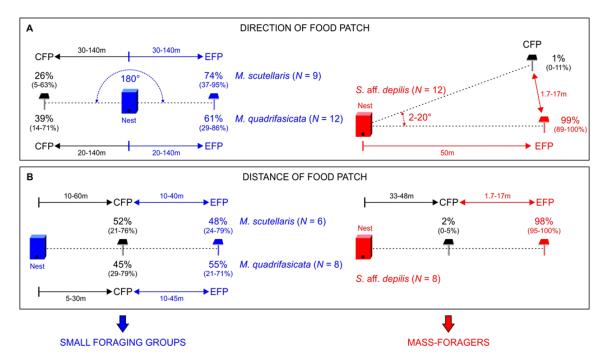
Figure 5. Accuracy of recruitment to a food patch. (**A-B**) Foraging strategies involving recruitment of nestmates differ between species that forage in small groups (left panels) and mass-foragers (right panels) concerning the information about the exact position of a feeding site. Shown are the results from recruitment experiments with two species that forage in small groups (*Melipona scutellaris* and *M. quadrifasciata*) compared to a mass-foraging species (*Scaptotrigona* aff. *depilis*). Five foragers (for *M.* sp.) or three foragers (for *S.* aff. *depilis*), trained to an experimental food patch (EFP), recruited their nestmates for three (*M.* sp.) or two hours (*S.* aff. *depilis*). Given are average percentages (minimum-maximum) of recruits captured at the experimental food patch (EFP) and at a control food patch (CFP) that differed from EFP either (**A**) in direction or (**B**) in distance. Values next to arrows indicate the distances of EFP and CFP from the nest, and the distances between CFP and EFP used in the respective studies. Note that, in contrast to the *Melipona* species, almost all recruits of *Scaptotrigona* aff. *depilis*. arrive at EFP. *N* indicates the number of experiments. Data for *M. scutellaris* and *M. quadrifasciata* from Jarau et al. (2000); data for *S.* aff. *depilis* from Schmidt et al. (2003).

Consequently, this group of foragers arrives at a familiar feeding site far more quickly than inexperienced bees, which still have to search for it (Figure 6).

On the days following the discovery of a resource, part of the experienced foragers ("inspectors"; defined by Biesmeijer and de Vries, 2001), spontaneously revisit the known patch, investigating whether the feeding site is still profitable or whether it has become unavailable due to occupation by aggressive species or the end of flowering (von Frisch, 1923; zu Oettingen-Spielberg, 1949; Biesmeijer and de Vries, 2001). The main body of the experienced foragers, however, revisit the patch only after obtaining information about its availability from the inspectors (von Frisch, 1923; zu Oettingen-Spielberg, 1949; Biesmeijer and de Vries, 2001). In general, the scent of past-profitable forage, brought to

the colony by other bees, is sufficient to quickly reactivate experienced individuals to revisit a known food patch (Biesmeijer et al., 1998; Biesmeijer and Ermers, 1999; Hrncir et al., 2000; Grüter et al., 2008; Jarau, 2009; Reinhard and Srinivasan, 2009).

The foraging strategy of bee species that forage in small groups is tightly linked with rapid exploitation of known food patches (Biesmeijer et a., 1998; Biesmeijer and Ermers, 1999; Hrncir and Schorkopf, 2011). With such a strategy, these inferior competitors (Lichtenberg et al., 2010) are able to optimize foraging success at highly profitable, yet ephemeral and highly contested food sources, as is the case with mass-flowering plants. The colonies, apparently, invest little in searching for feeding sites besides those already being exploited (zu Oettingen-Spielberg, 1949; Lindauer, 1952; Beekman et al., 2003). Thus, a crucial pre-requisite for the success of
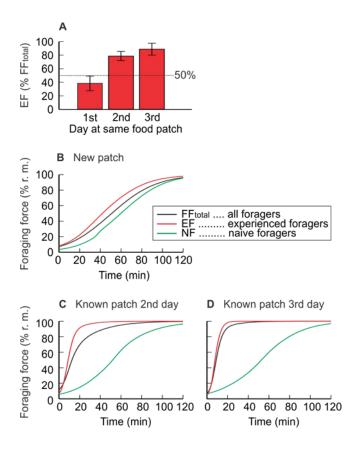
Figure 6. Importance of experienced bees for efficient resource exploitation. (**A-D**) Results from recruitment experiments with an unaggressive stingless bee species that forages in small groups (*Melipona seminigra*). (**A**) More than half of the foraging force at newly discovered food patches (of a known source) were inexperienced foragers (mean percentage ± 1SD; N = 32 experiments). From the second day on, however, the significant majority of bees collecting at the patch were experienced foragers (EF; mean percentage ± 1SD; 2nd day: N = 24; 3rd day: N = 13). The build-up of the foraging force is significantly slower at new food patches (**B**) than at known feeding locations (**C**: 2nd day; **D**: 3rd day at the same patch). Graphs (**B-D**) show the sigmoidal regression models of the average number (percentage relative to maximum) of all foragers (FF$_{total}$, black lines), and separately for experienced foragers (EF, red lines) and food-source-naïve forages (NF, green lines). Note similar build-up of NF at both new and known food patches. At known food patches, the rate of build-up of the entire foraging force increases with increasing proportions of EF (compare graphs of FF$_{total}$ on 2nd and 3rd day). Michael Hrncir, *unpublished data*.

a strategy based on the quick reactivation of experienced foragers is the initial discovery of as many food patches as possible (Hubbell and Johnson, 1978; Jarau et al., 2000). Here, location-specific

recruitment mechanisms like those found in scent-trial-laying stingless bees (Jarau, 2009) are of little use because they would restrict the foraging to one or few feeding sites (Hubbell and Johnson, 1978).

13.3.2.2 The furious – success through dominance at a feeding site
[Genera described using this foraging strategy: *Oxytrigona, Partamona, Scaptotrigona, Trigona*]
When two or more stingless bee species simultaneously exploit the same clumped, profitable food patch, differences in level of aggression among species determine who stays and who abandons the patch (Johnson and Hubbell 1974; 1975; Roubik, 1980; Johnson, 1983; Roubik et al., 1986; Lichtenberg et al., 2010). Hence, less aggressive species are usually excluded from the most profitable feeding sites and need to switch to less profitable patches or even other food sources (Johnson and Hubbell, 1974). Aggression, however, should not be used as a direct measure for dominance of a bee species. Rather, dominance should be interpreted as the suppression or exclusion of one species by another (Johnson and Hubbell, 1974; Lichtenberg, 2010). In this context, an important factor is superorganism size. Independently of whether a species is aggressive or not, colonies that are able to quickly recruit large numbers of foragers to a feeding site (mass-foragers) tend to dominate a patch (Lichtenberg et al., 2010). Other species are often at a loss due the sheer fact that they cannot find a free spot to land and feed (Johnson, 1983; Biesmeijer et al., 1999a; Hrncir, 2009)[3].

13.3.2.3 The insinuators – success through persistence
[Genera described using this foraging strategy: *Frieseomelitta, Plebeia, Scaura, Tetragonisca*]
The term "insinuators", coined by Edward Wilson (1971) for small ant species that "*rely on small size*

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[3] Leslie Johnson (1983) related an observation, where two unaggressive mass-recruiters, *Partamona orizabaensis* (as *Trigona testacea*) and *Scaptotrigona mexicana* (as *Trigona mexicana*) numerically dominated the inflorescences of a *Bactris* palm tree. Although both species did not exclude each other from the food patch, insinuators (see 13.3.2.3.) did not find space to land at the inflorescences. More surprisingly, even an aggressive group-foraging species, *Trigona silvestriana*, was competitively outnumbered by the mass of bees and, consequently, left the patch (Johnson, 1983).

and stealthy behavior to reach the sugar baits" (Wilson, 1971; p. 447), was later adopted by Leslie Johnson (1983) for unaggressive stingless bees with little or no recruitment activity (Lindauer and Kerr, 1958; Jarau et al., 2003; Biesmeijer and Slaa, 2004). These usually very small meliponine species remain competitive through their nervous persistence in collecting at a food patch even if crowded by aggressive mass-foragers. When attacked by the dominant species, the insinuators fly off the patch, yet quickly return to the same site or nearby flowers and continue feeding as if indifferent to the aggressors (Johnson, 1983). Because insinuators are small species and few in number, the species dominating a food patch probably would spend more resources, in terms of energy, chasing off these visitors than they would lose by letting them feed. Thus, the adaptive strategy of the dominant residents is to attack insinuators rarely, yet sufficiently to prevent the insinuators from exploiting the food patch more fully (Lichtenberg et al., 2010).

13.3.2.4 The gleaners – success through cleaning up the leftovers
[Genus described using this foraging strategy: *Trigonisca*]
Similar to the insinuators, gleaners are usually very small stingless bee species. In strict contrast to the insinuators, however, the strategy of gleaners is to avoid crowded feeding sites. These species arrive at food sources after their attractiveness and occupancy have peaked, and harvest the leftovers (Johnson, 1983; Biesmeijer and Slaa, 2004). The secret of success of the gleaner is their small body and colony size. Due to the fact that these bees are tiny in relation to flower size, even the smallest amount of leftovers considerably increases the colony's food intake (Johnson, 1983).

13.4 Concluding remarks
The differences found among stingless bee pot-honeys concerning physiochemical composition, sugar content, and floral origin depend on geographic region and, within one geographic region, on the bee species. The struggle for sufficient food to guarantee colony survival and reproduction shaped a rich variety of foraging traits among the meliponine bee species. In the present chapter we outlined some basic principles underlying foraging choices of stingless bees, among them morphological and behavioural differences among species. On the one hand, species partition food sources according to body size and colouration (spatio-temporal resource partitioning): big species start and stop collecting

earlier in the day than small species (temporal resource partitioning); light-coloured species may collect in full sunlight whereas dark-coloured species prefer shaded food patches (spatial resource partitioning). On the other hand, some food sources, particularly mass-flowering plants, simultaneously attract several different species. Here, resource partitioning is facilitated through differences in foraging strategies among stingless bee species. Both morphological foraging traits and foraging strategies are among the main reasons why meliponine colonies decide to collect at particular food sources while ignoring others, which helps to understand the differences between honeys concerning their floral origin and sugar content.

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