ORGANIZATION OF INSECT SOCIETIES

From Genome to Sociocomplexity

Edited by **Jürgen Gadau** and **Jennifer Fewell**

Foreword by **Edward O. Wilson**

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CHAPTER TWELVE

Convergent Evolution of Food Recruitment Mechanisms in Bees and Wasps

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THE STUDY OF FORAGING activation has played a crucial role in the theoretical development of sociobiology. In particular, explorations of the foraging and recruitment behavior of social bees and wasps have provided the groundwork for much of the theory on central place foraging. Advances in our understanding of foraging activation in bees (Apiformes) and social wasps (Vespidae) show fascinating convergent similarities within and between these groups, suggesting that they have found similar solutions to the problems of group foraging. Despite detailed studies of recruitment in individual taxa (Dornhaus and Chittka 2004; Dyer 2002; Nieh 2004; Raveret Richter 2000), the parallels between these different groups have not been ~~well~~ explored. In this chapter I compare and briefly, though not exhaustively, summarize what is known about food recruitment in bees and social wasps. The focus is on recent reviews and papers which are divided into two categories: (1) foraging activation (nest-based recruitment) and (2) local enhancement (information provided in the field, outside the nest). I also refer to nest-based mechanisms as "information center" mechanisms involving information transfer at a central location on or near the nest site. In general, I hope to stir up lively debate and future studies, particularly over two hypotheses that the shared behavior of foraging through flight is a basis for the parallel evolution of similar forms of (1) odor trail communication in bees and wasps and (2) acoustic communication in the corbiculate bees.

Phylogeny

The phylogenies of bees and stinging wasps (Hymenoptera, Aculeata) provide important information for understanding the evolution of foraging activation. However, as the phylogenies are not fully resolved, it is premature to map traits onto uncertain topologies. For example, there is controversy about the number of times that eusociality has evolved in the Apinae and whether stingless bee or orchid bees are the closest sister group to the honey bees (Cameron 1993). Similarly, the correct phylogenetic topology of the wasps is debated (Carpenter 2003). All social wasps are in the Vespidae with the exception of the primitively eusocial wasp, *Microstigmus comes,* which is in the Sphecidae. Within the Vespidae, sociality has evolved multiply (Schmitz and Moritz 1998). Furthermore, it is clear that sociality and thus cooperative group foraging have evolved independently between bees and wasps (Wcislo and Tierney 2007), and multiply within bees (Danforth et al. 2006) and wasps (Hines et al. 2007). Thus, even within the Apidae, some aspects of recruitment communication are likely to have evolved independently and not all similarities in communication mechanisms point to a similarly behaving ancestor.

Recruitment

Foraging Activation

Foraging activation is an increase in the probability of an individual leaving the nest to search for resources as a result of information received (at the nest) from successful foragers. This information can come from nestmates or non-nestmates (as in an information center), consist of cues (evolutionarily basal) or signals (evolutionarily derived), and indicate the general availability of resources or their specific location. Intranidal (within-nest) or at-nest communication of food location is rare in bees and undocumented in wasps.

Benefits of recruitment communication can depend on resource density. Specifically, honey bee location communication is advantageous if patches are variable, poor, and few, but not when resources are densely distributed (model results, Dornhaus et al. 2006). Thus communicating specific food location may not always be beneficial, even in species with this ability because additional nearby resources may be missed. Only honey bees and some species of stingless bees are known to communicate specific resource location at the nest (Nieh 2004; von Frisch 1967). Few studies have tested the ability of wasps to recruit to a specific location and to date there is no evidence that they can do so (Raveret Richter 2000).

Aggregations

An untested, though intriguing, possibility is that foraging activation exists among clumped nests of solitary bees. Mutual stimulation between solitary nesting bees could lead to foraging activation. Nesting aggregations occur among all taxonomic groups of bees, particularly soil nesters. Potts and Willmer (1998) report close spacing of up to 304 nests/m^2 with a nearest neighbor distance of 25.2±1.1 mm in the solitary ground nester, *Halictus rubicundus* (Halictinae). Given this population density, near neighbors could potentially monitor each other's departures. However, departure synchrony, or an increased rate of nest departures after the return of a successful forager, is not sufficient to demonstrate foraging activation because these effects may also arise from circadian rhythms and times of food availability on previous days. Some of these confounding factors could be eliminated with feeder studies (conducted during seasonal food dearth) using individually-marked bees whose daily foraging patterns are documented before, during, and after food is offered at unpredictable times.

At solitary bee nesting aggregations, cues such as floral odor adhering to returning foragers and, to a limited extent, visual and acoustic information could elicit foraging activation. Halictine visual acuity has not been measured, but may be similar to that of bumblebees, which can resolve a 2 cm object from 82 cm away (angular acuity of 0.36 cycles/degree, Macuda et al. 2001), and worker honeybees (0.26 cycles/degree, Srinivasan and Lehrer 1988). Such resolution should be sufficient to allow visual detection of near-neighbors exiting nests. It is not known if sounds produced by exiting Halictine foragers can activate neighbor foraging, but this hypothesis is testable.

Some wasp species exhibit foraging activation. Hrncir, Mateus, and Nascimento (2007) demonstrated foraging activation in the social swarm-founding wasp, *Polybia occidentalis,* by showing that newcomers only arrived at feeders after researchers trained foragers to the feeders. As with bees, there is no data on foraging activation in solitary wasp nest aggregations. However, solitary digger wasps (*Cerceris arenaria)* form dense nesting aggregations of up to 136.4 nests/m^2 over a 3.6 m^2 area. Moreover, wasps preferred to stay in their natal nests and in the natal nesting area, thus creating the potential for increased relatedness among neighbors (Polidori et al. 2006).

Mechanisms of Information Transfer

Several multimodal mechanisms of information transfer can activate foraging in social bees and social wasps. It is useful to consider these in detail, because information sources such as excitatory motions of returning foragers, colony resource levels, trophallaxis (food exchange), and olfactory cues (food scent) are likely basal, whereas olfactory signals (recruitment pheromones) and functionally referential communication are thought to be more derived (von Frisch 1967). For example, successful foragers of all eusocial corbiculate bees exhibit *increased movement rates* upon returning inside the nest. Increased food quality results in increased velocity and acceleration of movements by recruiting honey bees (Dyer 2002) and stingless bees (Schmidt, Zucchi, and Barth 2006). Bumblebees *(Bombus terrestris)* also perform excitatory runs inside the nest when returning from good food sources, and foragers increase their average speed when colony honey stores are experimentally depleted (Dornhaus and Chittka 2005). Given that such excitatory responses to food are widely observed in many insects, these behaviors are possibly basal (von Frisch 1967)

In wasps, Naumann (1970) reported a “departure dance” in which a rapidly running wasp forager was licked and antennated by nestmates. It would be useful to determine if these forager motions follow a similar pattern to that observed in recruiting stingless bees, which run in zigzag patterns interspersed with sudden turns (Nieh 2004). Stingless bee (Nieh 2004) and honey bee recruits (Rohrseitz and Tautz 1999) also frequently contact recruiters.

Excitatory buzzing runs during wasp swarming offers another parallel between bees and wasps. Although swarming is distinct from food gathering, it transfers information about a resource location, the new nest site. In stingless bees and honey bees, swarming and foraging use many of the same guidance and communication mechanisms (Roubik 1989). Excitatory buzzing runs are seen throughout the swarm in many wasp species (Naumann 1975), similar to the behavior of buzz runners in swarming honey bees (Seeley et al. 2003).

Successful foragers returning to the nest can produce *acoustic signals* in bumblebees (*B. terrestris;* Oeynhausen and Kirchner 2001), stingless bees (Nieh 2004), and honey bees (Dyer 2002). In these groups, thoracic muscle contractions can generate sound and vibrations that could increase forager conspicuousness to nestmates; however, thoracic muscle contractions can occur silently (Heinrich 1984) and thus a non-exclusive route for the ritualization of an acoustic recruitment signal is the buzz of foragers as they fly away from the nest. Wasp foragers are not known to produce foraging-related acoustic signals, although wasps produce a wide variety of vibrational signals including alarm tapping (Jeanne and Keeping 1995).

Trophallaxis between nestmates can result in foraging activation, particularly if successful foragers offer their food to nestmates. For example, trophallaxis increases after the return of a successful forager in *Megalopta* bees (Halictidae; Wcislo and Gonzalez 2006), honeybees (von Frisch 1967), and stingless bees (Hrncir et al. 2000). Returning foragers of the facultatively social *Megalopta genalis* and *M. ecuadoria* (Halictidae) regularly give nectar to nestmates. All females can participate in foraging, with the second oldest female usually making the most foraging trips (Wcislo and Gonzalez 2006). Thus, foraging activation following food exchange is possible. In other cases, such as *Xylocopa sulcatipes* (Xylocopinae), typically only one female bee forages and other females receive nectar trophallactically from her. This would not lead to foraging activation, but Velthius (1987) observed two-female nests in which both females foraged and could thus potentially activate each other.

In honeybees, trophallaxis from dancing foragers provides information about the odor and sweetness of the nectar, thus contributing toward a forager's decision to visit the advertised food source (Farina and Wainselboim 2005). No studies have shown that trophallaxis alone leads to foraging activation in naïve honeybees, although one suspects it may lead to foraging reactivation in experienced foragers. Similarly, no stingless bee studies have systematically examined the possibility of food alertment due solely to trophallaxis.

Trophallaxis and grooming activity can increase after a *Mischocyttarus* or *Polistes* forager returns to the nest, and one or more foragers may then leave (Jeanne 1972). However, we do not know if these forager departures occur because of food received from a successful forager. Aggression can activate wasp foraging, and provides an interesting parallel to aggressive behavior in bees of dominant *Megalopta* females. In the wasp *Polybia occidentalis,* O'Donnell (2001) found a positive correlation between foraging and the rate of being bitten, with some workers leaving to begin foraging activities immediately after being bitten. Here, the aggressed wasp does not offer food to the aggressor, as in the *Megalopta,* but the aggressed wasp does leave the nest, presumably to obtain food. Biting may be an example of foraging activation, but it is unclear if the biting wasps had recently discovered food.

Stored food levels, as assayed through gustation, touch, and olfaction, provide an information reservoir that can modulate foraging activation. Communal food provisioning can allow individual foragers to assess colony food levels and learn about resource availability. Food levels alone can inform nestmates of colony need and alter foraging, thus modulating foraging activation. For example, honey bee colonies increase pollen foraging when pollen levels decrease (Fewell and Winston 1992). The rate of bumble bee *(B. terrestris)* exits increases and successful returning foragers spend more time running excitedly when honey pots are depleted than when they are full (Dornhaus and Chittka 2005). We know little about the effects of communal food provisioning on foraging in other bee groups. This is somewhat surprising given that communal provisioning is widespread among bees such as Anthophoridae (genus *Exomalopsis*; Michener 1974); Halictidae, (genus *Lasioglossum*; Richards, French, and Paxton 2005); and Euglossini (limited cross-provisioning in *Eulaema nigrita*; Zucchi, Sakagami, and Camargo 1969).

Non-food related stores might also affect foraging decisions, although the influence of non-food supplies on colony foraging has received less attention than food stores. In the orchid bee, *Euglossa townsendi* (Euglossini), resin is reused from old cells and taken from resin dumps created by foragers near the nest entrance (Augusto and Garófalo, 2004). Whether resin foraging activation occurs remains to be determined. In *Eulaema nigrita* (Euglossini), foragers created separate piles of building materials (resin, mud, and feces) that were used communally to seal cracks in the nest and to complete brood cell construction (Santos and Garófalo 1994). It is unknown if non-food stores can influence Euglossine colony foraging. In stingless bees, foragers are known to collect salt, water, urine, feces, resins, bark, leaves, and mud (Lorenzon and Matrangolo 2005). In honeybees, Nakamura and Seeley (2006) found that *Apis mellifera* foragers perform waggle dances for resin sources deep inside the nest where the resin is typically used, thus facilitating resin use and direct sensing of its need by collectors. Similar studies in stingless bees would provide useful comparative information. Like bees, social wasps need to forage for food, water, and nest materials (Raveret Richter 2000).

Olfactory cues and signals can activate foraging. A cue~~, e.g. Food odor~~^ can reactivate experienced honey bee foragers to visit their former feeding site (Reinhard et al. 2004). Whether food odor alone can lead to foraging reactivation in other social bees deserves investigation. The bumblebee *B. terrestris* releases tergal gland pheromone during the excitatory movements of a successful returning forager (Dornhaus and Chittka 2004). One primary function of these movements may be to disperse the recruitment pheromone. Recruiting honey bees also produce volatile compounds, and a synthetic blend of these compounds increased the number of bees exiting the hive (Thom et al. 2006). Stingless bees may also use intranidal recruitment pheromones, although this awaits experimental evidence.

Olfactory cues can also lead to wasp foraging activation. Overmeyer and Jeanne (1998) showed that inexperienced *Vespula germanica* foragers prefer to visit feeders with the same scent as that carried back to the nest by successfully foraging nestmates. Foragers based their preference on scent alone because the authors eliminated visual local enhancement, unlike previous studies. There is no evidence that wasps produce an intranidal recruitment pheromone, but no published studies have examined this possibility.

Forager temperature inside the nest may contribute toward foraging activation. Returning foragers have intranidal thorax temperatures that are elevated over ambient air temperature (ΔTth) and correlate with collected sugar concentrations in honey bees (Stabentheiner 2001) and stingless bees (Nieh and Sánchez 2005). The function of elevated ΔT_{th} has not been determined, but it may keep thoracic flight musculature at higher temperatures and thus facilitate a more rapid return to higher quality food (flight facilitation hypothesis). Other testable hypotheses are that it attracts potential recruits to foragers advertising high quality food (attraction hypothesis), or enhances the release of food odors or foraging activation pheromones (odor signal modulation hypothesis). Research using artificially heated bees could help to distinguish between these different hypotheses. Successful *B. terrestris* foragers returning from a rich sucrose solution produce a foraging activation pheromone; the resulting higher body temperature could enhance recruitment pheromone release. We do not know if this species has elevated intranidal ΔT_{th} corresponding to food quality; but in *B. wilmattae,* ΔT_{th} is correlated with sucrose concentration in bees feeding within a foraging arena (Nieh et al. 2006).

Food carbohydrate levels can also affect wasp thoracic temperatures; for example, *Paravespula vulgaris* foragers increased ΔT_{th} when feeding on more concentrated sucrose solution (Kovac and Stabentheiner 1999). Currently, we do not know if ΔT_{th} elevation at the feeder persists at the nest and is thus a potential foraging cue for either species. This would be worth investigation. Moreover, the wasp data suggest that we should also examine the effect of pollen protein quality on social bee ΔT_{th}. Parallel effects may exist in wasps and bees, particularly if thermal hypothesis 1 is correct and the primary function of elevated temperatures is not signaling but facilitating flight.

Functionally referential signals occupy a behavioral continuum and are defined by two key features: they are stimulus-class specific (specific to the environmental information, event, or item being signaled) and context independent (the sender signals and the receiver behaves appropriately without the direct presence of what is signaled). Thus the honey bee waggle dance is functionally referential because it is (1) specific to the communication of resource location and (2) communicates spatial location and elicits appropriate receiver responses without the signaler and receiver being at the communicated location. In social insects, the information-rich honeybee waggle dance dominates the concept of functionally referential communication. Yet functionally referential communication, as understood in other animal systems, occurs in forms such as predator-specific alarm calls in ground squirrels (Blumstein 1999) and chicken food calls (Evans and Evans 1999). Thus the potential encoding of food quality in stingless bee sound pulses (Hrncir, Barth, and Tautz 2006) may also be an example of functionally referential communication. Researchers could demonstrate this if receivers that do not receive a food sample (context independence requirement) respond appropriately to this sound-encoded food quality information.

In stingless bees, the evidence for functionally referential communication is primarily based on correlations between sound pulse duration and food distance (Nieh 2004). Direct evidence is required to demonstrate functionally referential communication because it is also possible that these sounds activate foraging without communicating distance. Functionally referential foraging communication has not been found or sought in wasps.

Local Enhancement

Local enhancement is the facilitation of learning resulting from an individual's attention being drawn to a locale and then reinforced with a reward (Roberts 1941). In social insects, this can occur when the presence of an individual high quality food attracts another individual, who thereby obtains a food reward. Local enhancement is a subset of *social facilitation*, which Wilson (1971) defined as "behavior initiated or increased by the action of another individual." Olfactory, visual, and acoustic information could lead to social insect local enhancement, although studies to date have not tested acoustic local enhancement. Local ~~evolutionary~~ enhancement toward visual and olfactory cues and piloting are likely basal conditions. ~~Target only olfactory signaling may have evolved subsequently, followed by odor trail communication as the most derived.~~

We do not know if local enhancement occurs in solitary bees; I therefore focus on social bees. Social insects are champion associative learners when it comes to food and local enhancement is thus likely to be more widespread than is currently documented. In general, visual local enhancement has been neglected in bee research. One exception is provided by Slaa, Wassenberg, and Biesmeijer (2003), who reported that newly recruited foragers of the stingless bee *Trigona amalthea* exhibited visual local enhancement, approaching nestmates on feeders. No studies have yet demonstrated visual local enhancement in bumblebees, honey bees, or non-corbiculate social bees.

Unlike bee research, wasp studies have focused more on visual local enhancement. Investigators used odor-extracted posed wasps and controlled for olfactory local enhancement by counting choices made in the absence of other live foragers. In this study, *Vespula germanica, V. consobrina*, and *Polistes fuscatus* foragers were attracted to extracted (odor-free) posed wasps on feeders or flowers over feeders or flowers without posed wasps. In *V. maculifrons,* attraction was density dependent because foragers were attracted to other foragers on a closely spaced feeder, but not to foragers on a widely spaced array (Raveret Richter 2000). Similarly, *Polybia occidentalis* newcomers were visually attracted to extracted wasp dummies placed on a feeder (Hrncir, Mateus, and Nascimento 2007).

Wasps can be attracted to the visual or olfactory presence of other wasps on food. Investigators trapped *V. germanica* and *V. maculifrons* foragers in pierced clear plastic containers that allowed meat bait and potential forager odors to escape and found that foragers were attracted to these baits over control baits with meat alone (Raveret Richter 2000). *Polybia occidentalis* and *P. diguetana* foragers were attracted to caterpillar baits occupied by a live forager over an unoccupied bait (Raveret Richter 2000). However, *V. germanica* were not attracted to potential odor marks deposited after 50 or 100 feeder visits (Raveret Richter 2000), therefore we do not know if wasps can deposit odors to mark good resources.

Piloting is a form of local enhancement that can combine vision and olfaction. In social insects, piloting is perhaps the most basal recruitment strategy for an individual to lead one or more nestmates to a resource, yet it has been difficult to directly demonstrate piloting in flying insects. Honeybee scouts use piloting to help guide the swarm to their new home. The swarm relies on the conspicuous visual behavior of a relatively few fast flying "streaker" bees. Sealing the Nasanov glands of these guide bees does not impair swarm guidance, and thus honeybees evidently use vision, not olfaction, in swarm piloting (Beekman, Fathke, and Seeley 2006). Piloting has not been found in honeybee food recruitment (Riley et al. 2005). In stingless bees, Aguilar, Fonseca, and Biesmeijer (2005) found a close temporal synchrony in the arrival times of foragers and newcomers (recruits) in *Trigona corvina* and *Plebeia tica,* evidence that suggests piloting. Odor release may facilitate piloting. Kerr (1994) hypothesized that some meliponines deposit aerial odor trails, creating an "odor tunnel" as they fly to the food source during windless conditions under a dense forest canopy. To date, no studies have tested this hypothesis.

Partial piloting, in which foragers lead nestmates part of the distance to the food source rather than the entire distance, may occur accidentally if recruits lose track of the recruiter (a potential basal state), but may also be a consistent strategy, as is hypothesized for several species of *Melipona* (Kajobe and Echazarreta 2005). To date, no studies have directly demonstrated the existence of partial piloting (Nieh 2004), relying instead on indirect evidence that recruiters need some contact with recruits as they leave the nest (to communicate direction) and that recruiter and recruits often do not arrive in synchrony, as would be expected in complete piloting. Some form of piloting may exist in wasps, but this remains to be tested. As with some stingless bees, *Apoica pallens* wasps are hypothesized to use aerially released pheromones to help guide swarms, but this remains untested (Howard et al. 2002).

Target-only odor marking (i.e., odor-marking of the food source alone) is widespread among the social bees (Stout and Goulson 2001). I adopt this term to distinguish target-only odor marking from odor trails. The evolutionary precursor to food odor-marking may lie in nest entrance odors that help to orient returning bees. Nest entrance orientation marks have been found in solitary bees (Guédot et al. 2006), bumblebees (*B. occidentalis;* Cameron et al. 1999), honeybees (*Apis mellifera;* von Frisch 1967), stingless bees (Schmidt, Zucchi, and Barth 2005), and wasps (*Vespula vulgaris;* Butler, Fletcher, and Watler et al. 1969).

Some stingless bee species (Schmidt, Zucchi, and Barth 2005) and bumblebees (in foraging arenas; Schmitt, Lübke, and Franke 1991) can deposit attractive target-only odor marks by walking. In certain species, these "footprint" odor marks may be odor cues (cuticular hydrocarbons) or odor signals that are not specific to food. For example, the stingless bee *Nannotrigona testaceicornis* deposits attractive olfactory compounds by walking on food sources. These compounds are equally attractive as those deposited by bees walking at the nest entrance (Schmidt, Zucchi, and Barth 2005). On natural flowers, Eltz (2006) demonstrated that *Bombus pascuorum* foragers deposited lipid footprints with the same composition as cuticular hydrocarbons found on other parts of the foragers' bodies. Similarly, wasp foragers (*Vespa crabro* and *Vespula vulgaris*) can deposit cuticular hydrocarbons to create an intranidal orientation trail (Steinmetz, Sieben, and Schmoltz 2002).

Target-only odor marks deposited on food can also be aversive, marking food sources that have been depleted and should thus be avoided (Stout and Goulson 2001). *Xylocopa virginica texana* (carpenter bee) foragers visiting passion flowers deposited repellant chemical marks on depleted flowers (Frankie and Vinson 1977). Recently, Saleh and Chittka (2006) have shown that foragers can learn to positively or negatively associate these bee-deposited odors with rewarding or unrewarding flowers, respectively. Thus, the same odor can act as an attractant or a repellant. Depositing cuticular hydrocarbons may be an inevitable consequence of multiple visitations to a rewarding food source. It would not be surprising if several species of stingless bees and bumblebees were able to associate food quality (handling time, sugar quality, and travel cost) with tarsal deposits of cuticular hydrocarbons. The ability of bees to learn associatively can enhance the flexibility of their behavioral repertoire without necessitating the evolution of specific olfactory foraging signals. Cues can sometimes be sufficient.

Odor trails are a form of local enhancement because they draw a recruit's attention to a rewarding location. In many cases, odor trails are observationally associated with some degree of piloting (stingless bees, Nieh 2004; wasps, Jeanne 1981). Some stingless bee species can produce an odor trail consisting of odor droplets deposited a few meters apart on vegetation between a feeder and the nest, even up a vertical substrate such as a tower. Some meliponine species also deposit partial odor trails consisting of odor marks deposited in decreasing spatial density extending from the feeder in the direction of the nest, but not the entire distance to the nest (Nieh 2004). In at least two meliponine species these partial odor trails are polarized, allowing foragers who enter the odor trail to determine the correct endpoint (the food source) without first traveling to one of the endpoints. Stingless bees deposit these odor trails by briefly landing, often on the edge of leaf or twig, and rubbing their mandibles against the substrate. Schorkopf et al. (2007) showed that this odor trail is composed of labial gland secretions in *Trigona recursa.* To date, odor trail studies have investigated only recruitment to nectar sources, although meliponine odor trails may also indicate resources such as pollen, resin, and building materials.

Bumblebee (*B. terrestris*) workers deposit short odor trails between the nest and the nest entrance (tested in a 100 cm diameter foraging arena, Cederberg 1977). The Amazonian bumblebee, *B. transversalis,* clears short trails (2–3 m) that extend from the nest and facilitate nest material gathering. Foragers followed the trail by keeping their antennae just above the substrate surface and crawling forward, moving in a sinusoidal fashion. This is reminiscent of how ants follow odor trails. Such a trail may be useful in nature when foragers negotiate obstacles to find the entrances of their subterranean nests. It is not known if these trails are odor-marked (Cameron et al. 1999). *B. impatiens* foragers also deposited odor trails within a foraging arena and were able to use these trails, in darkness, to walk to food sources (Chittka et al. 1999). Similarly, Steinmetz et al. reported that wasp foragers (*Vespa crabro* and *Vespula vulgaris*) can use odor trails to navigate through dark entrance tunnels within the nest. As in some stingless bees (Schmidt, Zucchi, and Barth 2005), these intranidal wasp odor trails may consist of cuticular hydrocarbons deposited by walking foragers (Steinmetz, Sieben, and Schmoltz 2002).

Some wasp species use odor trails to guide swarms or to assist orientation within nest cavities. Although odor trails are not known to be involved in wasp foraging (Raveret Richter 2000), foraging in many tropical species with large colonies (and thus a potential need for mass recruitment) remains to be studied. Moreover, the similarities between how wasps and stingless bees deposit odor trails are fascinating, because flying insects must confront the same problems of how to deposit and orient toward an odor trail that consists of small odor deposits widely spaced.

Substrate-deposited exocrine gland secretions are involved in the formation of some wasp swarm clusters and in the subsequent guidance of the swarm to a new location. Swarming *Polybia sericea* adults dragged their gasters over leaves and other substrates around the swarm cluster, depositing a substance similar in odor to an exocrine gland at the base of the fifth gastric sternite. Only wasps in a swarming behavioral state were attracted to extracts of this gland when it was smeared onto filter papers (Jeanne 1981). We do not know if wasp trails are polarized. Brazilian *Synoeca septentrionalis* wasp workers chewed and licked leaves on swarm routes (Jeanne, Downing, and Post 1983), a behavior with clear similarities to meliponine odor-trail marking (Schorkopf et al. 2007). Given that swarm founding evolved four separate times in the Vespidae, abdominal rubbing to mark the route to a new nest is widespread and has evolved independently multiple times (Smith, O'Donnell, and Jeanne 2002).

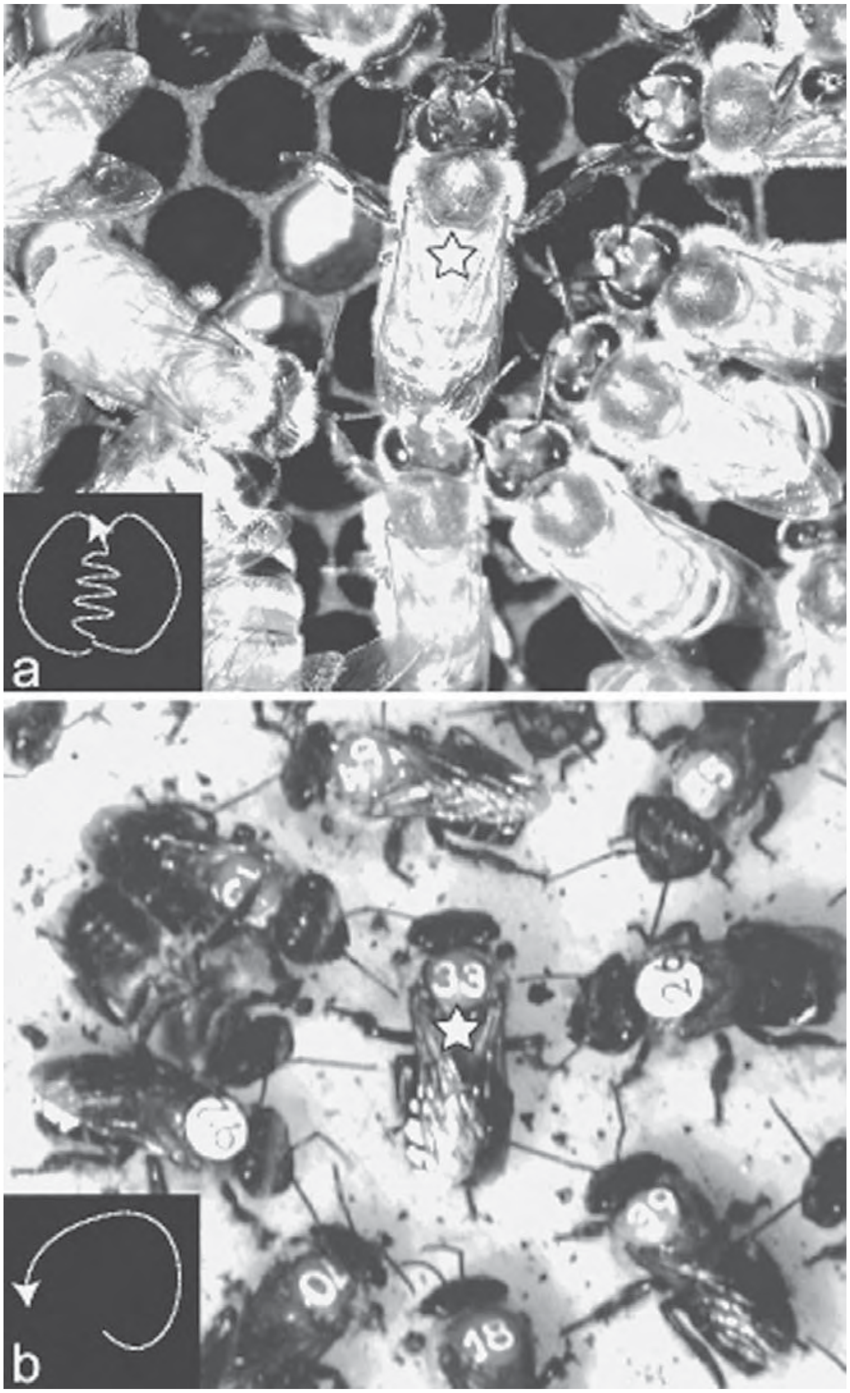
Ritualization of Excitatory Movements and Sounds

Esch (1967) proposed that the honeybee waggle dance may be a ritualized representation of the outbound and inbound flights of a forager to a food source outside the nest. I would add the possibility that these circular motions, found in honeybees and stingless bees, evolved from the ritualization of the cycle of entry, unloading, and exit *within the nest.* In the honeybee round dance and waggle dance and in the semicircular spins executed by foragers of some stingless bee species, one may see the generalized looping motion of the forager entering, unloading, and then exiting the nest (Figure 12.1). In addition, exiting acoustic cues from the flight departure sound or from pre-flight warm-up sounds (von Frisch 1967) may have evolved into signals. For example, recruiting *M. panamica* foragers return through the narrow nest entrance facing away from the entrance, and then must turn toward it to exit, all the while producing loud buzzing sounds (Nieh 2004). The repetition of these motions and sounds may have been ritualized into the spinning recruitment motions and buzzes found in some social bees.

More generally, this hypothesis could be extended to the evolution of non-referential excitatory motions in bees and wasps. At the most basic level, a forager of a social bee or wasp colony returns to the nest, unloads her food, and then returns to gather more food, thus describing some form of loop at the nest. Agitation and excitement upon the return of a successful forager is thought, in many cases, to be expressed through various running, spinning, and zigzag motions inside the nest (von Frisch 1967). Contact with nestmates, perhaps initially through trophallaxis, or even accidentally during this process, may have become ritualized because such contact provided increased nestmate exposure to information that good food sources can be gathered as well as information about that resource (odor, quality, and resource type), thus increasing colony foraging efficiency.

Conclusions and Future Directions

In both social bees and social wasps we know that visual local enhancement and odor trail communication exist, although odor trails have thus far been documented only for swarming, not foraging, in wasps. The convergent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evolution of food recruitment mechanisms in both groups may be due, in part, to the shared characteristics of foraging through flight, colonial life, and excellent associative learning.

The ability to follow a flying forager and the difficulty of leaving a persistent odor trail in the air give rise to common solutions. Descriptions of piloting in bees and swarm-following in wasps suggest that slowing flight or increasing the conspicuousness of flight behaviors (meliponine zig zag flights, Esch 1967) may facilitate following. Moreover, depositing substrate-borne odor trails (odor droplets widely spaced each few meters) may enhance piloting. In ants, odor trails may have evolved from tandem-running, a form of piloting (Hölldobler and Wilson 1990). Bee and wasp odor trails may thus be more derived than piloting behavior, although supporting evidence awaits studies on a wider variety of species.

Colonial life has led to the evolution of sophisticated chemical signaling in bees and wasps. Nonetheless, we have yet to fully explore the role of odor cues. For example, the activating effect of food odor in bees and wasps may have evolved convergently because the association between food odor and foraging success is an important field cue, and thus extends easily into the nest, where it can cue nestmates to the success of compatriots. We now know that cuticular hydrocarbons, which facilitate nest and nestmate recognition, are also deposited on food and can therefore be learned by foragers as cues—guideposts to the rewarding and unrewarding.

A virtually unexplored area is the role of associative learning in local enhancement. Wasp and bee foragers can easily learn the appearance of food. Do they also learn that nestmate presence signals food? Work on relatively well-studied bee groups such as honeybees and bumblebees has not yet examined the role of visual local enhancement, something better documented in wasps. On the other hand, very little is known about the possibility of location-specific recruitment in wasps. Our understanding of the evolution of recruitment communication would benefit greatly from pur-

Figure 12.1. Recruitment communication movements of highly social bees inside the nest. Signal sender is indicated with a star and is surrounded by signal receiver~~t~~s. A: Honeybee waggle dance (movement pattern shown in inset). B:Stingless bee *(Melipona panamica)* dance phase (movement shown in inset). In both cases, the signal sender is shown just before she is about to turn. In both species, the signaler is producing sounds by vibrating her wings and thorax and is attended by followers (signal receivers) ~~who can detect near-field sound vibrations with their antennae~~ (photos by J. Nieh).

Table 12.1 Foraging-related information transfer mechanisms in bees and social wasps

Category	Bees	Social wasps
Foraging activation		
Solitary aggregations	?	?
Trophallaxis	Halictidae[1], Meliponini[2], Apini	Mischocyttarini[1]*, Polistini[1]*
Excitatory nest behaviors	Bombini, Meliponini, Apini	Epiponini* (Protopolybia[4], Polybia[3])
Referential communication	Meliponini[5], Apini	?
Local enhancement		
On resource	Meliponini	Vespidae, Polistini*, Epiponini*
Piloting	Meliponini[6], Apini[7]	Vespidae[8]
Partial piloting	Meliponini	?
Target-only odor marking	Xylocopini, Meliponini, Bombini, Apini	?
Partial odor trails	Meliponini	?
Complete odor trails	Bombini	Epiponini[7]*, Vespidae[10]

* Belongs to the subfamily Polistinae (Arévalo et al. 2004)

1. Not known if this behavior leads to foraging activation
2. Not known if this behavior leads to foraging activation, but likely
3. Inferred from foraging activation in *Polybia occidentalis.*
4. Excitatory behavior observed for successful foragers, but increase in foraging activation not documented.
5. Correlations between the distance to food and recruitment sound pulse duration reported in several species (no direct tests)
6. Indirect evidence
7. Only known in the context of swarm guidance
8. Likely exists in the context of swarm guidance
8. Suggested
9. Guidance within the nest and short trails (a few meters) extending from the nest
10. Guidance within the nest

suing these questions. Thus, in many respects, our understanding of social wasp and bee foraging activation is at a similar and tantalizingly incomplete stage.

There are many gaps in our knowledge of social bee and wasp foraging (Table 12.1), but I have selected five particular questions that will enhance our understanding of basal and derived recruitment mechanisms. In some cases, I have listed suggested study species based on preliminary published observations or biological characteristics of these species.

1. Is there neighbor foraging activation in nest aggregations of solitary bees or wasps?
2. Do wasps perform excitatory foraging activation behaviors at the nest?
3. Foraging activation based on the scent of collected food has been demonstrated in wasps and bumblebees, and foraging reactivation in honeybees. Do foraging activation and reactivation via food scent occur in the Halictidae, Meliponini (*Frieseomelitta silvestrii, F. flavicornis,* and *F. freiremaiai*), or Euglossini (*Euglossa townsendi* and *Eulaema nigrita*)?
4. Can some wasp species (*Polybia occidentalis, Brachygastra mellifica, B. lecheguana,* or *V. germanica*) recruit nestmates to a specific location? If so, do they use mechanisms analogous to those known for social bees?
5. The captivating honeybee waggle dance provides an astonishing example of functionally referential communication. However, do other, perhaps less information-rich, examples of functionally referential communication such as food quality or alarm signaling exist in bees (*Melipona panamica, M. quadrifasciata,* and *M. seminigra*) and wasps *(Polybia occidentalis)*?

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