6 How to Tell Your Mates

Costs and Benefits of Different Recruitment Mechanisms

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CONTENTS

INTRODUCTION

The evolution of sociality has created the need for information transfer among group members. Insects that live in societies cannot behave as if they were solitary; rather, actions by different group members need to be integrated to achieve desirable outcomes at the level of the group. The ways in which individuals exchange information depends largely on the size of the society. Small societies can rely on all individuals having knowledge about which tasks need to be done and where to go, but global knowledge about all tasks needed by a colony is much harder to achieve once group size increases (Deneubourg et al. 1987). Groups comprising a large number of individuals cannot rely on all individuals having perfect information about their colony's needs, but must instead rely on their interactions with their peers as well as information directly obtained from their immediate surroundings. The result is self-organized emergence of adaptive behavior at the group level (Camazine et al. 2001).

Recruitment is an example of such self-organized behavior. Recruitment, a collective term for any behavior that results in an increase in the number of individuals at a particular place (Deneubourg et al. 1986), to food sources is probably the most widely studied, but recruitment also occurs in the context of building (e.g., Karsai and Penzes 1993; Bonabeau et al. 1998), excavation (e.g., Deneubourg and Franks 1995), defense (e.g., Millor et al. 1999), and nest site selection (Pratt et al. 2002; Visscher 2007).

Recruitment to food sources allows insect societies to forage efficiently in an environment in which food sources are patchily distributed or in which food sources are too large to be exploited by single individuals (Beckers et al. 1990; Beekman and Ratnieks 2000; Detrain and Deneubourg 2002). In addition, social insects that transfer information about the location of profitable food sources can exploit an area much larger than those that lack such sophisticated recruitment mechanisms. Honey bees are a prime example. Their sophisticated dance language (von Frisch 1967) allows them to forage at food sources as far as 10 km from the colony (Beekman and Ratnieks 2000).

The type of recruitment mechanism employed by social insects (see the next section) depends strongly on the size of the colony (Beckers et al. 1989). This is because colony size determines both the amount of food that is necessary for growth and maintenance and the number of potential recruits. In small colonies, individuals tend to explore the environment individually and do not recruit nestmates to food sources they find. For colonies of intermediate size, exploring individuals return to their colony once they find a profitable food source and recruit nestmates to that source. The larger the colony, the more recruitment relies on mass communication, mostly by means of a chemical trail, as in many species of ants and termites.

What are the costs and benefits of different kinds of recruitment mechanisms? This is the topic of our chapter. We will first give an overview of the different ways in which social insects recruit nestmates to food sources. In the rest of the chapter we will then mainly contrast the two extreme forms of recruitment mechanisms: mass recruitment via a pheromone trail, where individuals only interact indirectly via the trail, and the honey bees' dance language, where information is transferred directly from individual to individual. We will discuss how these two mechanisms allow the colony to adapt to changing conditions, the means insect colonies have evolved to overcome constraints imposed by their way of communication, and other implications of indirect and direct recruitment mechanisms. In the last section we will synthesize our findings.

THE TOWER OF BABEL: VARIETY IN INSECT LANGUAGES

Exact recruitment mechanisms vary greatly among the social insects but can be divided into two main classes: direct and indirect mechanisms. Mass recruitment via a chemical trail is an example of indirect recruitment. The recruiter and recruited are not physically in contact with each other; communication is instead via modulation of the environment: the trail. The recruiter deposits a pheromone on the way back from a profitable food source and recruits simply follow that trail (Figure 6.1). In a way, such a recruitment mechanism is comparable to radio broadcasting: information is disseminated without controlling who receives it. The other extreme is transferring information from individual to individual: direct recruitment. The best-known example of such recruitment mechanism is the honey bees' dance language. Successful foragers, the recruiters, perform a stylized dance that encodes information about the direction and distance of the food source found, and up to seven dance followers (Tautz and Rohrseitz 1998), potential recruits, are able to extract this information, upon which they will leave the colony and try to locate the advertised food source. Recruitment trails and the honey bee dance language can be seen as the two extremes of a whole range of different mechanisms used by social insects to convey information about profitable food sources. Let us now consider the variety of insect "languages" and how the type of recruitment mechanism depends on colony size.

INDIRECT RECRUITMENT: TRAIL-BASED FORAGING

In many ants, foragers lay trails from food sources back to their nest. These trails allow nestmates to locate and exploit the source easily. As more individuals collect food they reinforce the trail. Because the pheromone is volatile, it can only be maintained if sufficient individuals are using it. Hence, the use of a volatile recruitment pheromone imposes constraints on minimum colony size because a stable trail is only possible if the trail is reinforced before the pheromone evaporates

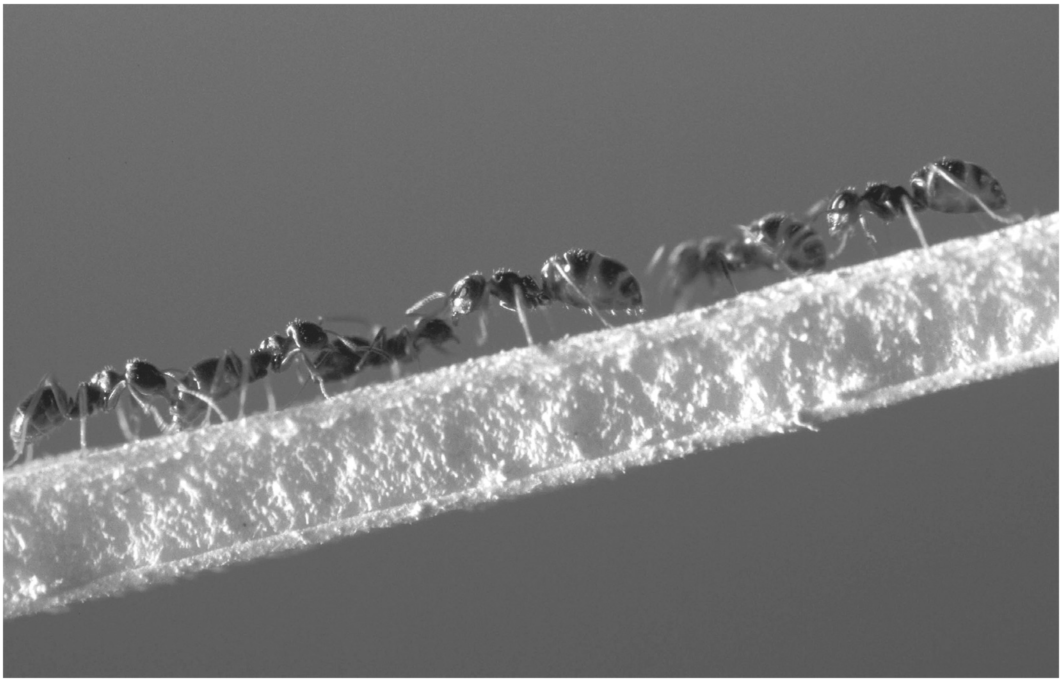

FIGURE 6.1 Ants on a trail. The ants coming from the right return from a food source, while the ants walking in the opposite direction come from the nest. Newly recruited ants are guided toward the food source by a chemical trail deposited by the ants that have been feeding at the source on their way back. See color insert following page XXX. (Photograph by Perrin Emmanuel, taken from CNRS Phototheque. With permission.)

(Beekman et al. 2001). To overcome the constraint on minimum colony size set by the volatility of the trail pheromone, ants could presumably evolve less volatile pheromones. However, this is maladaptive for ants that feed on ephemeral food sources because the trail would outlast the food source.

Ants have evolved various mechanisms to overcome the constraint set by minimum colony size on pheromone trail foraging. For example, Pharaoh's ants, *Monomorium pharaonis* (Fourcassie and Deneubourg 1994), and other trail-recruiting species (Detrain et al. 1991) deposit an attracting pheromone when exploring new areas, even when no food has been found (see also Chapter 2). This mechanism may serve to increase the local ant density, thus increasing the probability of forming a trail when food is found. Some species with intermediate-size colonies (*Camponotus socius*, Hölldobler 1971; *Tetramorium caespitum*, Verhaeghe 1977; *T. impurum*, Verhaege 1982; *Ambliopone* sp., Ito 1993; *T. bicarinatum*, de Biseau et al. 1994; for reviews see Beckers et al. 1989 and Hölldobler and Wilson 1990) use a combination of group recruitment, whereby a successful forager guides recruits directly to the food source (Beckers et al. 1989), and pheromone trails. Such a dual mechanism, combining both direct and indirect recruitment, with an initial period of group recruitment helps to establish a trail, thus overcoming the constraint set by colony size (Beekman et al. 2001).

Species that forage at food sources that are plentiful and stable, such as trees for collecting honeydew (*Lasius fuliginosus*, Quinet et al. 1997), leaves (*Atta* sp., Fowler and Robinson 1979; Shepherd 1982, 1985; Howard 2001), seeds (*Pogonomyrmex rugosus* and *P. barbatus*, Hölldobler 1976; *Pheidole militicida*, Hölldobler and Möglich 1980; *Messor barbarus*, López et al. 1994; Detrain et al. 2000; Azcárate and Peco 2003), or dead wood (termites, Grassé 1986), construct long-lasting trails (trunk trails) that connect the nest to foraging locations. In some species, *Formica* or *Pogonomyrmex*, for example, trails are more or less permanent due to the ants actively changing the environment by removing vegetation (Rosengren and Sundström 1987; Fewell 1988).

Indirect Recruitment: Airborne Pheromone Trails

Even though odors play an important role in the location of food sources in many social insects, stingless bees are the only bees known to produce odor trails that can begin near the nest (but do not necessarily) and extend to the food source (Nieh 2004; for a critical review of pheromone trail use in stingless bees see Chapter 12). Such an odor trail is produced by foragers depositing odor droplets on vegetation along the vector from a food source to the nest (Lindauer and Kerr 1958). Unlike ant and termite trails, stingless bee odor trails are not continuous, and therefore need to be easy to find by unemployed foragers. It is probably for this reason that successful foragers leave their odor droplets on prominent vegetation (Nieh 2004). Judging from what we know of the physicochemical properties of stingless bee trail pheromone compounds that have been identified to date, it appears that their volatility makes them well suited to attract bees over longer distances (see Chapter 12).

Direct Recruitment: Dancing Bees

Upon returning to her colony, a successful honey bee forager may perform a recruitment dance that informs her nestmates of the presence of the profitable food source. The dance encodes two main pieces of spatial information: the direction and the distance to the target. During a typical dance the dancer strides forward vigorously shaking her body from side to side (Tautz et al. 1996). This is known as the waggle phase of the dance. After the waggle phase the bee makes an abrupt turn to the left or right, circling back to start the waggle phase again. This is known as the return phase. At the end of the second waggle, the bee turns in the opposite direction so that with every second circuit of the dance she will have traced the famous figure-eight pattern of the waggle dance (von Frisch 1967).

The most information-rich phase of the dance is the waggle phase. During the waggle phase the bee aligns her body so that the angle of deflection from vertical is similar to the angle of the goal from the sun's current azimuth. Distance information is encoded in the duration of the waggle phase. Dances for nearby targets have short waggle phases, whereas dances for distant targets have protracted waggle phases.

Dance followers need to be in close contact with the dancer in order to be able to acquire the directional information (Rohrseitz and Tautz 1999), especially in cavity-nesting species such as *Apis mellifera* and *A. cerana*, where dancing is performed in the dark.

All species of *Apis* use the dance language to communicate directional information of food sources, although different species differ slightly in their dance details (Oldroyd and Wongsiri 2006). It is interesting that only honey bees have evolved a dance language; why not stingless bees? After all, many species of stingless bee have colony sizes comparable to those of *Apis* (Michener 2000), and both originated in the tropics, the environment in which the dance language is thought to provide the most benefits (Sherman and Visscher 2002; Dornhaus and Chittka 2004; see also Chapters 1 and 7). It could be that this fundamental difference in recruitment mechanism between honey bees and stingless bees is due to their difference in foraging range. *Apis* exploit a vast area (Beekman and Ratnieks 2000), whereas stingless bees forage at a much shorter range (Roubik and Aluja 1983; van Nieuwstadt and Ruano 1996). However, this is an obvious chicken or egg problem: Do honey bees forage over a large range because they communicate effectively, or did the evolution of the dance language allow them to forage farther afield?

Recently it was hypothesized that the honey bee's dance language evolved not in the context of foraging but as a means to communicate the location of new nest sites (Beekman et al. 2008; Beekman and Lew 2008). Honey bee swarms go through a period of homelessness when they leave the mother colony and form a temporary cluster. Scout bees search the environment for a suitable new home (reviewed in Winston 1987) and need to provide spatial information about the location of potential nest sites found to other bees in the swarm, which they do via recruitment dances (Lindauer 1955). In contrast, stingless bees move into a new nest gradually over several weeks or months (Michener 1974). Most likely pheromone marking is used to mark the chosen nest, in a way similar to the marking of food sources. Thus, stingless bees do not need a symbolic dance mechanism in order to communicate the location of new nest sites (Lindauer and Kerr 1958).

Direct Recruitment: In-Nest Excitation

The only reason why flowers smell is to attract pollinators. It is therefore not surprising that odor plays an important role in foraging in the social bees. In Chapter 9, Judith Reinhard and Mandyam V. Srinivasan describe the importance of floral odors in honey bee foraging where the scent of past-profitable sites triggers renewed interest by foragers in flowers that carry that scent (Reinhard et al. 2004; Beekman 2005). In honey bees floral odors serve as a means to reactivate foragers, but successful foragers themselves also produce odors that entice more foragers to leave the colony (Thom et al. 2007). In bumble bees the transfer of scent from a returning forager to unemployed bees is the only means of recruitment. Bumble bees returning from profitable forage sites perform excitatory runs upon their return to the colony and carry with them the odor of the plant species they have visited. Unemployed foragers receive information not only about the presence of profitable forage sites but also about the smell of the plants in flower. Even though such recruitment mechanism does not convey directional information, it is remarkably effective: when presented with artificial feeders with different odors, recruits mainly visited the feeder at which the initial foragers had been foraging (Dornhaus and Chittka 1999). The same mechanism is found in some species of stingless bee (Nieh 2004; see also Chapter 12), where, in addition, the activation of the forager force is particularly enhanced though mechanical signals (see Chapter 11).

In some species of ant returning foragers perform excitatory displays while facing nestmates. This behavior motivates nestmates to follow the forager when it leaves the colony, and up to thirty ants will follow the experienced ant to the food source (Hölldobler 1971; Lenoir and Jaisson 1982). In some mass-recruiting species, only ants that have been stimulated by this in-nest excitation will follow a pheromone trail (*Formica fusca*, Möglich and Hölldobler 1975; *Myrmecocystus mimicus*, Hölldobler 1981). In other species, such excitation increases recruitment efficiency because it alerts a large number of individuals to leave the colony (*Monomorium venustum*, *M. subopacum*, Szlep and Jacobi 1967; *Camponotus pensylvanicus*, Traniello 1977; *Neivamyrmex* sp., Topoff and Mirenda 1978; *Pheidole pallidula*, Detrain and Pasteels 1991).

Direct Recruitment: Tandem and Group Recruitment

Because the use of pheromone trails is only possible in species with large colonies, ants with small colonies such as ponerines and *Temnothorax* often use tandem or group recruitment in which the returned forager directly guides one (tandem) or several (group) individuals toward the food source (Hölldobler and Wilson 1990). In this way, recruits are taught the route to the food source. Similarly, in some species of stingless bee, foragers were observed to actively guide recruits toward food sources, for example, by flying in a zigzag manner toward the food (Nieh 2004). These recruitment mechanisms are relatively short range and are most likely used in combination with scent marking of the food source and its surroundings (see Chapter 12).

STABLE VERSUS DYNAMICALLY CHANGING ENVIRONMENTS

The decentralized nature of most recruitment mechanisms allows an insect colony to choose the best forage site out of several alternatives. This is achieved without individual foragers directly comparing the quality of the sites on offer. Instead, positive feedback mechanisms ensure the collective choice of the best site (Bonabeau et al. 1997; Camazine et al. 2001).

Most studies on the allocation of foragers to food sources have used stable environments in which the feeders or forage sites were kept constant (e.g., Beckers et al. 1990; Seeley et al. 1991; Sumpter and Beekman 2003). However, natural conditions are rarely stable. Can we predict how a particular mechanism will work when conditions are not stable but change dynamically? How should recruitment mechanisms allow the optimal exploitation of food sources when conditions change?

When conditions are stable the optimal solution from the colony's point of view is to focus solely on the best food source (provided this food source is sufficiently large that it allows all recruited foragers to feed at it without crowding). As soon as conditions are unstable, however, it becomes important to have mechanisms that allow swapping to an alternative food source or food sources when they have become more profitable or when the initial food source has been depleted or has become unattractive because of competition with other species or other colonies. This means that in order to do well in a dynamically changing environment, insect colonies must allow storage of information about food patches that are currently exploited while at the same time allowing exploration for new sites, and retaining knowledge about previously profitable sites if they are likely to become profitable again.

At first sight it appears that direct and indirect recruitment mechanisms differ fundamentally in their ability to adapt to changing conditions. In indirect recruitment systems, information about forage sites is retained within the trail. Such systems are resilient to loss of individual foragers. In direct systems a colony can adapt more quickly to changes in the environment, but can render it more vulnerable to the loss of individuals. Consider a honey bee foraging site that is suddenly no longer profitable. Recruitment to that site ceases immediately, as returning foragers cease dancing for that site. Unemployed foragers are then recruited to alternative sites if these are available. The discovery of a new profitable site by just one forager is sufficient to initiate recruitment to that site. Pheromone trails, in contrast, are likely to outlast the food source even though trail pheromones are volatile. Consequently, there is a period in which the trail is still present when the food source has been depleted. Similarly, the formation of another trail to a newly discovered food source is likely to be slow until the old trail has sufficiently evaporated. On the other hand, the removal of a few individuals from an ant trail removes hardly any information, while the removal of a single honey bee returning from a forage site can destroy all information about that site.

The resilience of interaction networks can be visualized by presenting the interactions among individuals, e.g., ants on a trail or bees on the "dance floor" (Seeley 1995), in a network graph. We have done this in Figure 6.2 for mass-recruiting ants (Figure 6.2a) and dancing honey bees (Figure 6.2b). Because the ants mainly interact with each other via the pheromone trail, the network appears unstructured, with most links being between two to ten individuals. A network of honey bee interactions, on the other hand, shows many nodes: individuals that have many interactions with many other individuals. These nodes represent the dancing bees that interact with dance followers. From these interaction networks we can see how the network will react against perturbation. If we remove one node (a dancing bee) from the network, we will greatly affect the network as the removal of a node destroys a large number of interactions. In an unstructured network, as in the ants, removing an individual will hardly affect the structure of the network because an ant only interacts with a small number of ants.

Some forms of recruitment, for example, tandem recruitment, may seem very inefficient, as only one individual is guided toward the food source. However, tandem recruitment certainly is the most reliable of all recruitment mechanisms, as it often comes with a feedback mechanism that prevents information from being lost. As soon as the leading individual, the recruiter, realizes that the follower or followers have lost contact, she will stop and emit a pheromone that will attract the follower or followers (Deneubourg et al. 1986). When an individual of a mass-recruiting species loses the trail, she will not be able to find the food source unless the trail is rediscovered. Similarly, information about the location of food sources is stored in the memory of the individuals in most species of social insects apart from those that rely on mass recruitment only, as here all information

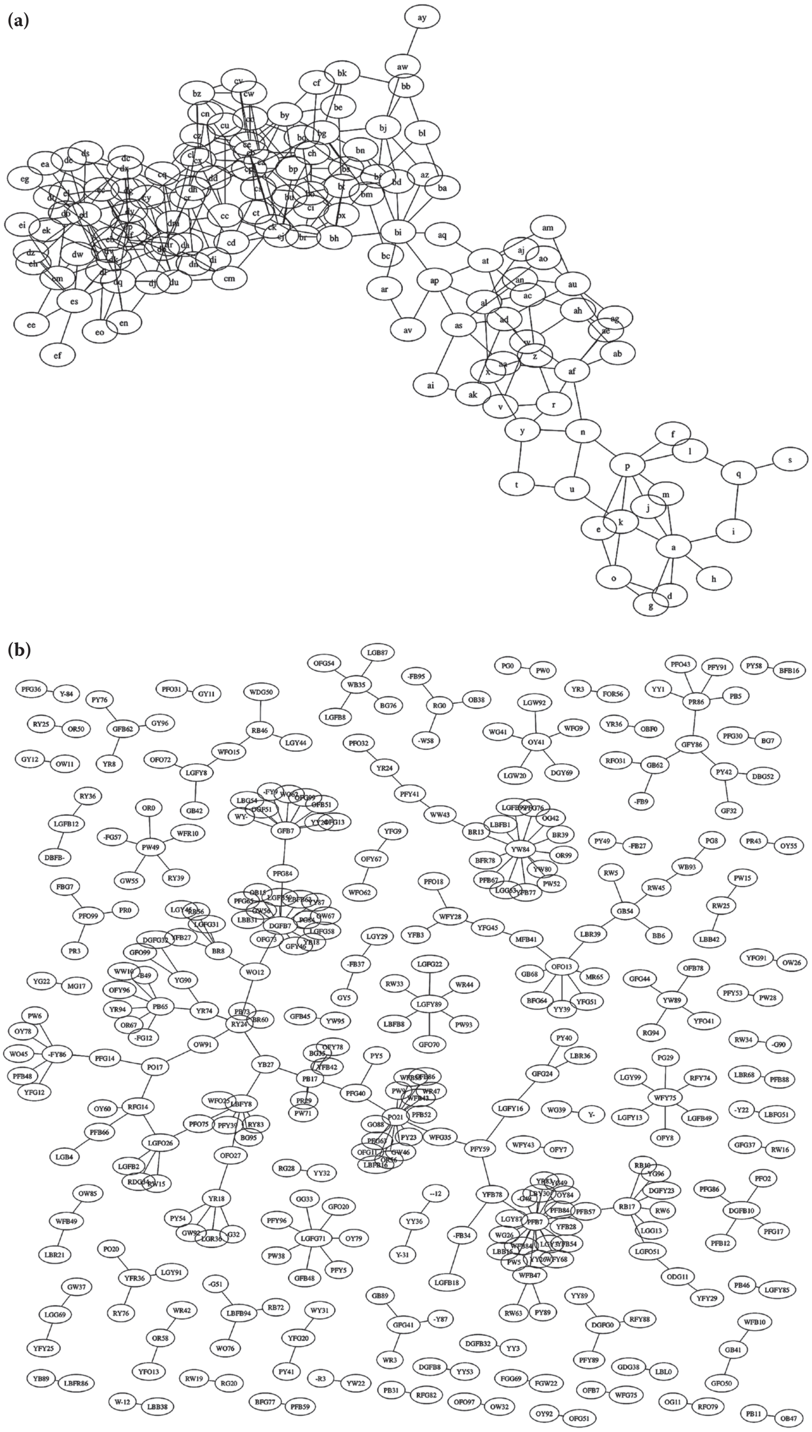

FIGURE 6.2 Network graphs for ants on a trail (a) and bees on the dance floor (b). When two individuals interact physically (ants) or when one individual follows a dance of another (bees), the two are connected by a line. Individuals are represented as eclipses, whereas the strings in the circles identify them. It is clear that most ants only interact with a small number of other ants, as the main means of interaction is via the trail. This contrasts with dancing bees, where some bees have many interactions as their dances are followed by a large number of other bees, which may dance in turn if they find the advertised food source.

is contained in the trail. Has the trail disappeared? Then so has the information of the food source it was leading to.

A comparative study by Beckers et al. (1990) indeed seems to suggest that the ability of ant colonies to adapt to changing foraging conditions depends on the type of recruitment employed. When a better-quality food source is introduced while a colony is already exploring a source of mediocre quality, *Tetramorium caespitum* (which uses a combination of group and mass recruitment) rapidly reallocates its foragers to the better food source. In contrast, *Lasius niger* (which depends solely on mass recruitment) is unable to shift its foraging efforts away from the mediocre food source. Likewise, workers of the stingless bee *Trigona recursa*, which uses scent trails for the recruitment of nestmates to food sources, failed to shift to a better food source when this became available after the bees were already foraging at a food source of lesser quality (Schmidt et al. 2006). The flexibility of *Tetramorium caespitum* colonies can be explained by two characteristics of its recruitment strategy. First, as soon as one individual has discovered the better food source, it can directly lead nestmates to that food source via group recruitment. This enables foragers to ignore the existing trail toward the less profitable food source. Second, individual workers modulate the amount of pheromone they deposit, depending on the quality of the food source found (measured in concentration of sugar) (Verhaeghe 1982). Hence, a pheromone trail initiated via group recruitment will rapidly build up to a better food source, resulting in a shift in the workers' collective foraging behavior without the system getting "trapped" into an existing pheromone trail toward a poorer food source.

A different way to achieve such flexibility is to use different chemical signals: a short-lasting trail pheromone and a long-lasting exploration pheromone. The latter acts as an external memory of the foraging environment (see also Chapter 2) and allows the colony to rapidly establish a new trail, whereas the former will quickly evaporate if it is no longer reenforced (*Pheidole megacephala*, Dussutour et al., unpublished data). In the Pharaoh's ants, *Monomorium pharaonis*, foragers can deposit a "no entry" signal when they return from an unrewarding food source, thereby allowing the colony to quickly reallocate its foragers (Robinson et al. 2005). These two examples indicate that ant colonies most likely have evolved multiple mechanisms for adapting to changing foraging conditions. The challenge now is to understand how different mechanisms have been shaped by natural selection to function optimally under particular ecological conditions.

STAYING INFORMED: SCOUTS VERSUS RECRUITS

The key to keeping track of changing conditions while gaining maximum advantage of existing food sources is the trade-off between exploitation and exploration: the use of existing information (exploitation) versus the collection of new information (exploration). How do different recruitment mechanisms allow for the discovery of new food sources? We will again discuss the two extreme recruitment mechanisms, trail-based foraging and the honey bee's dance language, and explore how both allow the discovery of new food sources.

The success of the pheromone trail mechanism is likely to be due, at least in part, to the nonlinear response of ants to pheromone trails where, for example, the distance that an ant follows a trail before leaving it is a saturating function of the concentration of the pheromone (Pasteels et al. 1986). In other words, the probability an ant will follow a trail is a function of trail strength (expressed as concentration of pheromone: the better the food source, the more pheromone the ants deposit; Sumpter and Beekman 2003), but ants never have a zero probability of losing a trail, irrespective of the strength of the trail. There will therefore always be a number of ants that become lost, and their number will be negatively correlated with the strength of the existing trail. Assuming that these lost ants are able to discover new food sources and thus serve as the colony's explorers or scouts, this "strategy of errors" (Deneubourg et al. 1983; Jaffe and Deneubourg 1992) allows the colony to fine-tune the number of scouts depending on the profitability of the food source that has already been exploited.

The regulation of scout numbers in honey bees similarly ensures a balance between the number of individuals allocated to exploration and exploitation. An unemployed forager (an individual that wants to forage but does not yet know where to forage) will first attempt to locate a dance to follow. If this fails because the number of dancers is low, she will leave the colony and search the surroundings, thereby becoming a scout (Beekman et al. 2007). As a result, the number of scouts is high when the colony has not discovered many profitable forage sites, as dancing will then be low, whereas the number of scouts will be low when forage is plentiful and the number of bees performing recruitment dances is high (Seeley 1983; Beekman et al. 2007).

In many social insects division of labor is thought to arise via individual differences in task thresholds—individuals with the lowest threshold for task X will be the first to engage in that task, therefore reducing the chance that other individuals, with a higher threshold for task X, will perform that task. The latter individuals are therefore more likely to perform another task, and division of labor results (Bonabeau et al. 1996; Beshers and Fewell 2001). Often this difference in individual thresholds has a genetic component; in species in which the queen mates multiply, different subfamilies (workers that share the same father) differ in their task thresholds (Robinson and Page 1989). Even though division of labor based on individual or subfamilial differences in thresholds has been shown for many tasks in many social insects (Oldroyd and Fewell 2007), such a mechanism does not seem to be flexible enough for the regulation of scouts and recruits (Beekman et al. 2007, but see Dreller 1998).

In the honey bee in particular, the “failed follower mechanism” provides the colony with the means to rapidly adjust its number of scouts depending on the amount of information available about profitable forage sites. Even when the colony is exploiting profitable patches, there may still be other, undiscovered, profitable sites. As soon as there is a reduction in the number of dances occurring in the colony, the probability that some unemployed foragers are unable to locate a dance increases, and the colony therefore sends out some scouts. Such fluctuations in the number of dances regularly occur in honey bee colonies, even when there is plenty of forage (Beekman et al. 2004).

Honey bees collect food over a vast area, often more that 100 km^2, changing their focus on a daily basis to adjust to the often-rapid changes in foraging conditions (Visscher and Seeley 1982; Schneider 1989; Waddington et al. 1994; Beekman and Ratnieks 2000; Beekman et al. 2004). This ability is the result of a sophisticated communication system in which foragers integrate a large amount of information about the conditions of the patch they themselves are exploiting, as well as information obtained both directly and indirectly from their nestmates. The failed follower mechanism is an elegant example of a regulatory feedback in this communication system (Seeley 1995; Fewell 2003; Sumpter 2005). Scouting is influenced by the amount of information, in the form of recruitment dances, being brought into the colony. When incoming information is low, the number of scouts is upregulated to gather more information. Potential scouts thus obtain a good estimate of the need to scout without leaving their colony.

THE INDIVIDUAL VERSUS THE COLLECTIVE

Bonabeau et al.’s (1997) influential paper on self-organization in social insects provided a clear thesis of the principles of self-organization that underlie many aspects of insect colony organization. Bonabeau et al.’s paper both summarized and stimulated the field of research as to how collective behavior is achieved through feedback mechanisms arising from the activities of individual insects (Camazine et al. 2001). Since then, self-organization principles have been used to study many other aspects than foraging, including nest construction (Camazine 1991; Karsai and Penzes 1993; Deneubourg and Franks 1995; Franks and Deneubourg 1997; Bonabeau et al. 1998), nest site selection (Camazine et al. 1999; Visscher and Camazine 1999; Mallon et al. 2001; Seeley and Visscher 2004; Pratt et al. 2005; Seeley et al. 2006; Visscher 2007; Janson et al. 2007), and coordinated movement (Couzin et al. 2005; Janson et al. 2005; Beekman et al. 2006). These studies have shown how, despite the simplicity of both the individuals and the rules they follow, social insects are capable of choosing the best nest site out of several possibilities, to build architecturally elaborate nests, and to coordinate the movement of largely ignorant individuals.

Despite the considerable progress in self-organization research, it has now become clear that self-organization principles are insufficient to explain many aspects of colony organization because self-organization explicitly ignores complexity and variability at the individual level. Consensus is now emerging that rather than considering individual insects as simple units that achieve complex collective behavior solely through feedback mechanisms, one should instead think of each insect as a relatively complex individual that directly exchanges information with other individuals (Mallon et al. 2001; Seeley and Buhrman 2001).

However, in ants at any rate, it appears that individual complexity decreases with increasing sophistication with respect to recruitment (Deneubourg et al. 1987). Solitary foragers cannot rely on a pheromone trail to find their way to and from the forage sites. Instead, they need to be able to navigate precisely, sometimes literarily counting their steps (Wittlinger et al. 2006). Interestingly, in bees the trend seems to be reversed. Honey bees have the largest colonies, the most sophisticated recruitment mechanism, and the individuals are relatively complex, integrating vast amounts of information from different sources (Seeley 1995). This difference between bees and ants is most likely the result, at least in part, of the dimensionality of their foraging environment. Ants, as they do not fly, are faced with a two-dimensional environment that allows them to easily modify the environment, by forming trails, to recruit nestmates. Hence, the more sophisticated the recruitment mechanism, the more it relies on trails, and the easier it is for ants to simply follow the trail without even really knowing where they are going. It is therefore not surprising that ants with the largest colonies and the most elaborate trail networks, the army ants, are almost blind (Gotwald 1995).

Bees, on the other hand, fly to and fro, which makes it far more difficult to modify the environment. Odor-based recruitment in some species of stingless bees (see above) is only effective over relatively short distances (Nieh 2004; see also Chapter 12). Moreover, most bees forage at flowers (but note that there are some obligate necrophages among the stingless bees: Roubik 1982; Camargo and Roubik 1991), and many flowers only produce nectar at a certain time of day. Hence, bees need to not only be able to navigate, using both the sun's location and landmarks, but also know the time. The larger the colony, the further the bees forage and the more resources they need to collect. And when the distance to a particular food source needs to be communicated to nestmates, as in the honey bees' waggle dance, an individual not only needs to be able to measure this distance but also needs to code this into a waggle phase of the correct duration. A solitary foraging bee, on the other hand, even though it still needs to be able to navigate to and fro, does not need all the information processing skills of honey bees.

USING MORE THAN ONE LANGUAGE AND USE OF THE SAME LANGUAGE IN DIFFERENT CONTEXTS

We have already seen that individual ants can modulate their trail-laying behavior depending on the quality of the food source they have found: when the sugar concentration is high, ants will deposit more pheromone than when they return from a poor food source (*Solenopsis saevissima*, Wilson 1962a, 1962b, 1962c; *Monomorium* and *Tapinoma*, Szlep and Jacobi 1967; *Tetramorium impurum*, Verhaeghe 1982; *Myrmica sabuleti*, de Biseau et al. 1991; *Lasius niger*, Beckers et al. 1993; *Acromyrmex lundi*, Roces and Núñez 1993). Some species modulate their trail depending on the level of starvation (*Solenopsis geminata*, Hangartner 1969; *Oecophylla longinoda*, Hölldobler and Wilson 1978), the distance between the nest and the food source (*S. geminata*, Hangartner 1969), the deviation angle from the axis of the nest to the food source (*L. niger*, Beckers et al. 1992; Devigne and Detrain 2006), or the presence of territorial marking (*L. niger*, Devigne et al. 2004; see also Chapter 2). The ants' environment can indirectly affect pheromone trails. For example, trails can decay at different rates depending on the substrate (e.g., roots, log, or rocks), thus affecting the range over which the trail is effective (*S. saevissima*, Wilson 1962a, 1962b, 1962c; *Eciton* sp., Togerson and Akre 1970; *L. niger*, Detrain et al. 2001; *M. pharaonis*, Jeanson et al. 2003). This can also apply to other information-carrying signals, such as vibrations produced by stridulating ants where the recruitment range might depend on the resonance properties of the substrate (Baroni-Urbani et al. 1988).

Although flexibility can potentially be achieved through the modulation of a single chemical signal, a process based on several signals seems intuitively more reliable. The modulation of a single signal needs to be precisely tuned to allow flexible foraging behavior, something that is difficult when the signal (i.e., the trail pheromone) is deposited on substrates that differ in their adsorption properties (Detrain et al. 2001). So far the use of different chemical signals has been poorly investigated (e.g., invitation behavior or trail pheromones that contain more than one component: Cammaerts-Tricot 1974; Hölldobler 1982a, 1982b; Vander Meer et al. 1988, 1990). However, some authors (Verhaeghe 1982; de Biseau et al. 1991; Dussutour et al., unpublished data) suggest that the use of two signals would allow the colony to adapt rapidly to changes in its environment.

Honey bees modulate their waggle dance depending on the profitability of the food source found. The more profitable the food source, the livelier and longer the dance (Seeley et al. 2000). As a result, bees dancing for highly profitable sites attract more dance followers than those that dance for mediocre sites.

Even though the honey bee's most famous dance is the waggle dance, other dances have been identified (von Frisch 1967). Of these, we only understand the meaning of the tremble dance, the "shaking signal," and the "buzz run." Tremble dances are performed by returning foragers when they are not able to find a receiver bee quickly to which to transfer their nectar. The result of the tremble dance is an increase in the number of receiver bees and a decrease in the number of foragers so to balance the processing of incoming nectar with the number of available individuals (Seeley et al. 1996). The shaking signal is used by bees to encourage nestmates to greater activity (Seeley et al. 1998). One bee will climb on top of another bee and shake her for a few seconds. Buzz running is used in the context of nest site selection. Bees that have perceived that the decision-making process has come to an end will perform buzz runs on the swarm so that the swarm can prepare itself for the flight toward the new home (Seeley and Tautz 2001).

The same language can be used in different contexts. Ants use pheromone trails and honey bees use dances to recruit nestmates to new nest sites. Interestingly, bees modify their dance behavior when dancing for new nest sites. Whereas they will indicate the quality of a food source by dancing in a more excited way (Seeley et al. 2000), bees returning from a high-quality nest site will perform more waggle phases than bees that returned from a site of only mediocre quality (Seeley 2003). Each bee, irrespective of the quality of the nest site that she has discovered, will reduce the number of waggle phases performed after each return visit to the new nest site (Figure 6.3). As a result, individual bees dance for a limited period of time only (Seeley and Visscher 2004). This is in contrast to bees dancing for food, as a forager will dance for her site for as long as this site is profitable

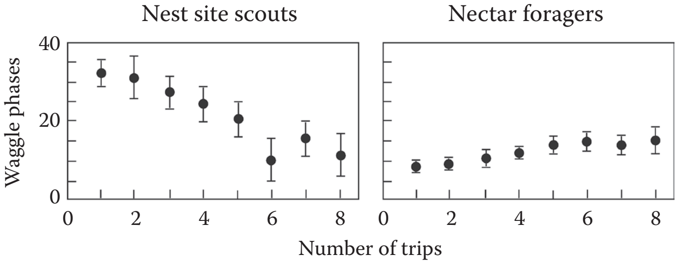

FIGURE 6.3 Number of waggle phases performed by bees that made successive trips to a potential nest site (left) and food (right). Bees visiting a potential nest site show a decline in the number of waggle phases performed, whereas foraging bees do not. (After Visscher 2007. With permission.)

enough (Seeley 1995) (Figure 6.3). It has been suggested that dance attrition is the crucial factor that allows a swarm to reach a decision about which nest site to move to (Britton et al. 2002; Myerscough 2003). If nest site scouts would not cease dancing, as we see in the context of foraging, all nest sites discovered will be advertised indefinitively and the swarm will not be able to select one only.

The ant *Temnothorax albipennis* uses a dual recruitment mechanism when recruiting to new nest sites. In the beginning of the process nestmates are recruited to potential new homes found by scouts via tandem recruitment. This relatively slow recruitment mechanism is abandoned as soon as the number of ants present in the new nest has reached a certain number (quorum). Once a quorum has been reached, individuals simply carry nestmates and brood to the chosen site, thereby significantly reducing the time needed to move into the new home (Mallon et al. 2001; Pratt et al. 2002, 2005). Such carrying does not take place in the context of foraging and is thus an adaptation to nest site selection.

For both the honey bee and the ant *T. albipennis* the context in which recruitment takes place, foraging or nest site selection, is clear. For honey bees it is clear because prior to selecting a nest site the bees comprising the swarm (the part of the colony that becomes homeless) leave the natal colony and form an interim cluster, while *T. albipennis* colonies tend to move home only when their old nest site has been destroyed. However, in many other social insects it may not be immediately obvious whether recruitment is for forage or nest site selection, especially in those species with colony fission, in which the move to a new nest site is a gradual process that can take days or even weeks. This raises the question of how recruited individuals know whether they are recruited toward a food source or a new nest site.

VARIATION IS THE SPICE OF LIFE

Insect colonies need to collect different resources, mainly carbohydrates (e.g., nectar) and protein (e.g., pollen or other insects). However, we know remarkably little about how a colony allocates its foragers over the two different types of food. Most, if not all, studies have focused on foraging for just one type of food (mostly carbohydrates) while offering the experimental colonies sufficient supplies of the other food source (protein). As protein is mainly used to feed the brood, the amount of brood must play an important role in determining how many individuals will devote their foraging effort to collecting protein (Sorensen et al. 1985). But how does the colony organize the simultaneous recruitment to carbohydrates and protein?

The division between nectar and pollen foragers in honey bees has a strong genetic basis (Calderone and Page 1988, 1991, 1992; Dreller et al. 1995; Page et al. 1995, 1998). Most likely this genetic component determines an individual's threshold to forage for either pollen or nectar, without completely excluding foraging for both when the need arises (Fewell and Bertram 1999). Honey bees have a relatively simple mechanism that they use to determine if there is a need to forage for pollen. If the pollen stores are above a particular point, the number of pollen foragers is reduced; conversely, if the stores are below that point, their numbers are increased (Fewell and Winston 1992; Camazine 1993). The honey bees' direct recruitment mechanism makes it relatively easy to simultaneously recruit to pollen and nectar at the colony level. Both nectar and pollen foragers will dance on the dance floor, and unemployed foragers that are stimulated to forage for nectar or pollen can simply choose to follow either a nectar or pollen dance (Oldroyd et al. 1991). Hence, the only direct competition between nectar and pollen foraging is via the number of available foragers, but it seems unlikely that their numbers are ever limiting.

Specialization on foraging for either protein or carbohydrates appears to be common in the Formicinae ants (Higashi 1978; Wehner et al. 1983; Traniello et al. 1991; Sundström 1993; Quinet and Pasteels 1996), but for all other ants we do not know how they are able to balance their nutrient intake. Although adult ants need carbohydrates as a source of energy, brood rely mainly on proteins (Sorensen and Vinson 1981; Cassill and Tschinkel 1999). We thus expect the ants' foraging patterns to track colony demography and larval growth. Thus, when the amount of brood is high, colonies focus more on collecting protein than when the amount of brood is low (Dussutour and Simpson 2008).

TRAFFIC JAMS

Because ants move through two-dimensional space, they are vulnerable to traffic jams, for example, when some sections of the trail are too narrow to allow a high volume of traffic or debris obstructs traffic flow. Overcrowding can slow down the speed of the ants and thus lead to a decrease in overall traffic flow (Burd et al. 2002; Burd and Aranwela 2003; Dussutour et al. 2005, 2006, 2007). Ants have developed particular strategies to prevent traffic congestion on recruitment trails. On long-lasting recruitment trails (trunk trails) they can remove debris or obstacles from the trail (Howard 2001) or widen the trail to allow for a higher traffic flow (Berghoff et al. 2002; for termites, see also Bruinsma 1979). On more ephemeral trails congestion can be reduced without decreasing the overall traffic flow. If the trail is wide enough, ants can be spatially organized with a distinct central lane of returning laden foragers flanked by two lanes of outbound foragers (army ants, Couzin and Franks 2003; leaf-cutting ants, Dussutour 2004). When the trail is too narrow to allow such spatial segregation, either the flow can be temporarily organized with alternating clusters of inbound and outbound ants (Dussutour et al. 2005) or part of the traffic can be diverted onto another path (Dussutour et al. 2004).

Interestingly, in leaf-cutting ants the foraging efficiency of the colony increases when individual ants experience crowded conditions on the trail. The number of leaf fragments brought back to the colony per unit time was shown to increase when the ants were forced to forage on a narrow trail compared with when they used a wide trail (Dussutour et al. 2007). This may seem puzzling, as the width of the trail strongly affects the traffic flow, with more ants being able to use a wide trail than a narrow trail. It seems that the enforced close encounters between empty (outbound) ants and laden (inbound) ants inform the outbound ants about the presence of food and most likely increase their motivation to forage.

The honey bees' direct recruitment mechanism does not lead to traffic jams, irrespective of the number of dancing bees, because there is never a "bottleneck" in the system. However, as we discussed earlier, the flux of returning nectar foragers can become so high that there are insufficient numbers of receiver bees to handle the incoming nectar. If this is the case, returning foragers will no longer recruit more foragers, but receiver bees until the balance has been reestablished. Because pollen foragers deposit their pollen load in the cells directly, there is no such feedback mechanism for pollen collection. Instead, pollen foragers will cease collecting pollen when the amount of stored pollen has exceeded their individual threshold (Dreller and Page 1999).

CONCLUDING REMARKS

By dividing the different recruitment mechanisms into two broad categories, direct and indirect, we can sum up the benefits and costs of both (Table 6.1). Obviously, such categorization is a gross simplification, as within each category we find many different mechanisms. Moreover, within the same category, for example, mass-recruiting ants, we find idiosyncrasies that may reduce a specific cost under certain conditions. We have seen that although trail recruitment may result in ants getting "stuck" in a suboptimal solution because they are unable to establish a trail to a better food source, some species can circumvent this problem by using two different pheromones or by adjusting the amount of pheromone produced, depending on the quality of the food source. Honey bees not only rely on dance information but also remember the location and smell of forage sites visited previously. How many sites they can remember is unknown, nor do we know how they balance private information (individual memory) with public information (dance communication) (Grüter et al. 2008).

It seems likely that the exact recruitment mechanism employed by a particular species is tuned to the environment in which it evolved. So far, however, the types of environments in which recruitment

TABLE 6.1
Broad Benefits and Costs of Indirect and Direct Recruitment Mechanisms

Recruitment Mechanism	Benefits	Costs
Indirect mechanisms	Robust to the removal of individuals (persistence of information)	Information (trail) can be altered by the environment
	Ability to focus on best food source under static conditions	Less flexible under dynamic conditions without extra mechanisms; trapped in suboptimal solution
	Rapid exploitation at food source (amplification phenomena)	Constraints on minimum colony size
	Reduction in individual complexity (ants)	
Direct mechanisms	Well-adapted to dynamic conditions without the need for extra mechanisms	Unable to focus on one source only under static conditions
	No constraints on colony size	Sensitive to the removal of individuals
		Slow build up to food source

Note: Indirect mechanisms include foraging trails, while direct mechanisms include the honey bees' dance language as well as tandem and group recruitment. See text for more details.

mechanisms have been studied are rather limited, and experiments have mainly focused on static environments. We thus have inadequate knowledge about the capabilities of social insects to optimally adapt to changes in their environment. Thus, the time has come to study precisely the extent to which social insects with different recruitment mechanisms are capable of solving more realistic foraging problems. Only by offering species with distinct recruitment mechanisms similar foraging problems can we truly identify the costs and benefits of different communication mechanisms in the social insects.

REFERENCES

Azcárate FM, Peco B. (2003). Spatial patterns of seed predation by harvester ants (*Messor* Forel) in Mediterranean grassland and scrubland. *Insect Soc* 50:120–26.

Baroni-Urbani C, Buser MW, Schilliger E. (1988). Substrate vibration during recruitment in ant social organization. *Insect Soc* 35:241–50.

Beckers R, Goss S, Deneubourg JL, Pasteels JM. (1989). Colony size, communication and ant foraging strategy. *Psyche* 96:239–56.

Beckers R, Deneubourg JL, Goss S. (1992). Trails and U-turns in the selection of a path by the ant *Lasius niger. J Theor Biol* 159:397–415.

Beckers R, Deneubourg JL, Goss S. (1993). Modulation of trail laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *J Insect Behav* 6:751–59.

Beckers R, Deneubourg JL, Gross S, Pasteels JM. (1990). Collective decision making through food recruitment. *Insect Soc* 37:258–67.

Beekman M. (2005). How long will honey bees (*Apis mellifera* L.) be stimulated by scent to revisit past-profitable forage sites? *J Comp Physiol A* 191:1115–20.

Beekman M, Fathke RL, Seeley TD. (2006). How does an informed minority of scouts guide a honeybee swarm as it flies to its new home? *Anim Behav* 71:161–71.

Beekman M, Gilchrist AL, Duncan M, Sumpter DJT. (2007). What makes a honeybee scout? *Behav Ecol Sociobiol* 61:985–95.

Beekman M, Gloag RS, Even N, Wattanachaiyingcharoen W, Oldroyd BP. (2008). Dance precision of *Apis florea*—Clues to the evolution of the honey bee dance language? *Behav Ecol Sociobiol* DOI:10.1007/s00265-008-0554-z.

Beekman M, Lew JB. (2008). Foraging in honeybees—When does it pay to dance? *Behav Ecol* 19:255–62.

Beekman M, Ratnieks FLW. (2000). Long range foraging by the honey-bee *Apis mellifera* L. *Funct Ecol* 14: 490–96.

Beekman M, Sumpter DJT, Ratnieks FLW. (2001). Phase transition between disordered and ordered foraging in Pharaoh's ants. *Proc Natl Acad Sci USA* 98:9703–6.

Beekman M, Sumpter DJT, Seraphides N, Ratnieks FLW. (2004). Comparing foraging behaviour of small and large honey-bee colonies by decoding waggle dances made by foragers. *Funct Ecol* 18: 829–35.

Berghoff SM, Weissflog A, Linsenmair KE, Hashim R, Maschwitz U. (2002). Foraging of a hypogaeic army ant: A long neglected majority. *Insect Soc* 49:133–41.

Beshers SN, Fewell JH. (2001). Models of division of labor in social insects. *Ann Rev Entomol* 46:413–40.

de Biseau JC, Deneubourg JL, Pasteels JM. (1991). Collective flexibility during mass recruitment in the ant *Myrmica sabuleti* (Hymenoptera: Formicidae). *Psyche* 98:323–36.

de Biseau JC, Schuiten M, Pasteels JM, Deneubourg JL. (1994). Respective contributions of leader and trail during recruitment to food in *Tetramorium bicarinatum* (Hymenoptera: Formicidae). *Insect Soc* 41: 241–54.

Bonabeau E, Theraulaz G, Deneubourg JL. (1996). Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies. *Proc R Soc Lond B* 263:1565–69.

Bonabeau E, Theraulaz G, Deneubourg JL, Aron S, Camazine S. (1997). Self-organization in social insects. *Trends Ecol Evol* 12:188–93.

Bonabeau E, Theraulaz G, Deneubourg JL, Franks NR, Rafelsberger O, Joly JL, Blanco S. (1998). A model for the emergence of pillars, walls and royal chambers in termite nests. *Philos Trans R Soc Lond B* 353: 1561–76.

Britton NF, Franks NR, Pratt SC, Seeley TD. (2002). Deciding on a new home: How do honeybees agree? *Proc R Soc Lond B* 269:1383–88.

Bruinsma OH. (1979). An analysis of building behaviour of the termite *Macrotermes subhyalinus*. Doctoral thesis, Agricultural University of Wageningen, The Netherlands.

Burd M, Aranwela N. (2003). Head-on encounter rates and walking speed of foragers in leaf-cutting ant traffic. *Insect Soc* 50:3–8.

Burd M, Archer D, Aranwela N, Stradling DJ. (2002). Traffic dynamics of the leaf-cutting ant, *Atta cephalotes. Am Nat* 159:283–93.

Calderone NW, Page RE. (1988). Genotypic variability in age polyethism and task specialization in the honey bee, *Apis mellifera* (Hymenoptera: Apidae). *Behav Ecol Sociobiol* 22:17–25.

Calderone NW, Page RE. (1991). Evolutionary genetics of division of labor in colonies of the honey bee (*Apis mellifera*). *Am Nat* 138:69–92.

Calderone NW, Page RE. (1992). Effects of interactions among genotypically diverse nestmates on task specialization by foraging honey bees (*Apis mellifera*). *Behav Ecol Sociobiol* 30:219–26.

Camargo JMF, Roubik DW. (1991). Systematics and bionomics of the apoid obligate necrophages: The *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). *Biol J Linnean Soc* 44:13–40.

Camazine S. (1991). Self-organizing pattern formation on the combs of honey bee colonies. *Behav Ecol Sociobiol* 28:61–76.

Camazine S. (1993). The regulation of pollen foraging by honey bees: How foragers assess the colony's need for pollen. *Behav Ecol Sociobiol* 32:265–72.

Camazine S, Deneubourg JL, Franks NR, Sneyd J, Theraulaz G, Bonabeau E. (2001). *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.

Camazine S, Visscher PK, Finley J, Vetter RS. (1999). House-hunting by honey bee swarms: Collective decisions and individual behaviors. *Insect Soc* 46:348–62.

Cammaerts-Tricot MC. (1974). Piste et pheromone attractive chez la fourmi *Myrmica rubra. J Comp Physiol A* 88:373–82.

Cassill DL, Tschinkel WR. (1999). Regulation of diet in the fire ant, *Solenopsis invicta*. *J Insect Behav* 12: 307–28.

Couzin ID, Franks NR. (2003). Self-organized lane formation and optimized traffic flow in army ants. *Proc R Soc Lond B* 270:139–46.

Couzin ID, Krause J, Franks NR, Levin SA. (2005). Effective leadership and decision-making in animal groups on the move. *Nature* 433:513–16.

Deneubourg JL, Aron S, Goss S, Pasteels JM, Duerinck G. (1986). Random behaviour, amplification processes and number of participants: How they contribute to the foraging properties of ants. *Physica D* 2: 176–86.

Deneubourg JL, Franks NR. (1995). Collective control without explicit coding: The case of communal nest excavation. *J Insect Behav* 8:417–32.

Deneubourg JL, Goss S, Pasteels JM, Fresneau D, Lachaud JP. (1987). Self-organization mechanisms in ant societies (II): Learning in foraging and division of labor. In Pasteels JM, Deneubourg JL (eds.), *From Individual to Collective Behavior in Social Insects*. Basel: Birkhäuser, pp. 177–96.

Deneubourg JL, Pasteels JM, Verhaeghe JC. (1983). Probabilistic behaviour in ants: A strategy of errors? *J Theor Biol* 105:259–71.

Detrain C, Deneubourg JL. (2002). Complexity of environment and parsimony of decision rules in insect societies. *Biol Bull* 202:268–74.

Detrain C, Deneubourg JL, Goss S, Quinet Y. (1991). Dynamics of collective exploration in the ant *Pheidole pallidula*. *Psyche* 98:21–31.

Detrain C, Natan C, Deneubourg JL. (2001). The influence of the physical environment on the self-organised foraging patterns of ants. *Naturwissenschaften* 88:171–74.

Detrain C, Pasteels JM. (1991). Caste differences in behavioral thresholds as a basis for polyethism during food recruitment in the ant, *Pheidole pallidula* (Nyl.) (Hymenoptera: Myrmicinae). *J Insect Behav* 4: 157–76.

Detrain C, Tasse O, Versaen M, Pasteels JM. (2000). A field assessment of optimal foraging in ants: Trail patterns and seed retrieval by the European harvester ant *Messor barbarus. Insect Soc* 47:56–62.

Devigne C, Detrain C. (2006). How does food distance influence foraging in the ant *Lasius niger*: The importance of home-range marking. *Insect Soc* 53:46–55.

Devigne C, Renon AJ, Detrain C. (2004). Out of sight but not out of mind: Modulation of recruitment according to home range marking in ants. *Anim Behav* 67:1023–29.

Dornhaus A, Chittka L. (1999). Evolutionary origins of bee dances. *Nature* 401:38.

Dornhaus A, Chittka L. (2004). Why do honey bees dance? *Behav Ecol Sociobiol* 55:395–401.

Dreller C. (1998). Division of labor between scouts and recruits: Genetic influence and mechanisms. *Behav Ecol Sociobiol* 43:191–96.

Dreller C, Fondrk MK, Page RE. (1995). Genetic variability affects the behavior of foragers in a feral honeybee colony. *Naturwissenschaften* 82:243–45.

Dreller C, Page RE, Fondrk MK. (1999). Regulation of pollen foraging in honeybee colonies: Effects of young brood, stored pollen, and empty space. *Behav Ecol Sociobiol* 45:227–33.

Dussutour A. (2004). Organisation spatio-temporelle des déplacements collectifs chez les fourmis. Doctoral thesis, University of Toulouse III, France.

Dussutour A, Beshers S, Deneubourg JL, Fourcassié V. (2007). Crowding increases foraging efficiency in the leaf-cutting ant *Atta colombica*. *Insect Soc* 54:158–65.

Dussutour A, Deneubourg JL, Fourcassié V. (2005). Temporal organization of bi-directional traffic in the ant *Lasius niger* (L). *J Exp Biol* 208:2903–12.

Dussutour A, Fourcassié V, Helbing D, Deneubourg JL. (2004). Optimal traffic organization in ants under crowded conditions. *Nature* 428:70–73.

Dussutour A, Nicolis SC, Deneubourg JL, Fourcassié V. (2006). Collective decisions in ants when foraging under crowded conditions. *Behav Ecol Sociobiol* 61:17–30.

Dussutour A, Simpson SJ. (2008). Carbohydrate regulation in relation to colony growth in ants. *J Exp Biol*, in press.

AU: Please update.

Fewell JH. (1988). Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. *Behav Ecol Sociobiol* 22:401–8.

Fewell JH. (2003). Social insect networks. *Science* 301:1867–70.

Fewell JH, Bertram SM. (1999). Division of labor in a dynamic environment: Response by honeybees (*Apis mellifera*) to graded changes in colony pollen stores. *Behav Ecol Sociobiol* 46:171–79.

Fewell JH, Winston ML. (1992). Colony state and regulation of pollen foraging in the honey bee, *Apis mellifera* L. *Behav Ecol Sociobiol* 30:387–93.

Fourcassie V, Deneubourg JL. (1994). The dynamics of collective exploration and trail-formation in *Monomorium pharaonis:* Experiments and model. *Physiol Entomol* 19:291–300.

Fowler HG, Robinson SW. (1979). Foraging by *Atta sexdens* (Formicidae: Attini): Seasonal patterns, caste and efficiency. *Ecol Entomol* 4:239–47.

Franks NR, Deneubourg JL. (1997). Self-organizing nest construction in ants: Individual worker behaviour and the nest's dynamics. *Anim Behav* 54:779–96.

von Frisch K. (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.

Gotwald WH. (1995). *Army Ants—The Biology of Social Predation.* Ithaca, NY: Cornell University Press.

Grassé PP. (1986). *Termitologia, Tome 3: Comportement, Socialité, Ecologie, Evolution, Systematique*. Paris: Masson.

Grüter C, Balbuena MS, Farina WM. (2008). Informational conflicts created by the waggle dance. *Proc R Soc London B* 275:1321–27.

Hangartner W. (1969). Trail laying in the subterranean ant, *Acanthomyops interjectus. J Insect Physiol* 15:1–4.

Higashi S. (1978). Task and areal conservatism and internest drifting in a red wood ant *Formica* (*Formica*) *yessensis* Forel. *Jpn J Ecol* 28:307–17.

Hölldobler B. (1971). Recruitment behavior in *Camponotus socius* (Hym. Formicidae). *Z vergl Physiol* 75:123–42.

Hölldobler B. (1976). Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex. Behav Ecol Sociobiol* 1:3–44.

Hölldobler B. (1981). Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 9:301–14.

Hölldobler B. (1982a). Chemical communication in ants: New exocrine glands and their behavioral function. In *Proceedings of 9th International Congress of IUSSI*, Boulder, pp. 312–17.

Hölldobler B. (1982b). The cloacal gland, a new pheromone gland in ants. *Naturwissenschaften* 69:186–87.

Hölldobler B, Möglich M. (1980). The foraging system of *Pheidole militicida* (Hymenoptera: Formicidae). *Insect Soc* 27:237–64.

Hölldobler B, Wilson EO. (1978). The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 3:19–60.

Hölldobler B, Wilson EO. (1990). *The Ants.* Cambridge, MA: Harvard University Press.

Howard JJ. (2001). Costs of trail construction and maintenance in the leaf-cutting ant *Atta columbica. Behav Ecol Sociobiol* 49:348–56.

Ito F. (1993). Observation of group recruitment to prey in a primitive ponerine ant, *Amblyopone* sp. (*reclinata* group) (Hymenoptera: Formicidae). *Insect Soc* 40:163–67.

Jaffe K, Deneubourg JL. (1992). On foraging, recruitment systems and optimum number of scouts in eusocial colonies. *Insect Soc* 39:201–13.

Janson S, Middendorf M, Beekman M. (2005). Honeybee swarms: How do scouts guide a swarm of uninformed bees? *Anim Behav* 70: 349–58.

Janson S, Middendorf M, Beekman M. (2007). Searching for a new home—Scouting behavior of honeybee swarms. *Behav Ecol* 18:384–92.

Jeanson R, Ratnieks FLW, Deneubourg JL. (2003). Pheromone trail decay rates on different substrates in the Pharaoh's ant, *Monomorium pharaonis*. *Physiol Entom* 28:192–98.

Karsai I, Penzes Z. (1993). Comb building in social wasps: Self-organization and stigmergic script. *J Theor Biol* 161:505–25.

Lenoir A, Jaisson P. (1982). Evolution et rôle des communications antennaires chez les insectes sociaux. In Jaisson P (ed.), *Social Insects in the Tropics*. Paris : Université Paris-Nord, pp. 157–80.

Lindauer M. (1955). Schwarmbienen auf Wohnungssuche. *Z vergl Physiol* 37:263–324.

Lindauer M, Kerr WE. (1958). Die gegenseitige Verständigung bei den stachellosen Bienen. *Z vergl Physiol* 41:405–34.

López F, Acosta FJ, Serrano JM. (1994). Guerilla vs. phalanx strategies of resource capture: Growth and structural plasticity in the trunk trail system of the harvester ant *Messor barbarus. J Anim Ecol* 63:127–38.

Mallon EB, Pratt SC, Franks NR. (2001). Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behav Ecol Sociobiol* 50:352–59.

Michener CD. (1974). *The Social Behavior of the Bees: A Comparative Study.* Cambridge, MA: Harvard University Press.

Michener CD. (2000). *The Bees of the World.* Baltimore: Johns Hopkins University Press.

Millor J, Pham-Delègue M, Deneubourg JL, Camazine S. (1999). Self-organized defensive behavior in honeybees. *Proc Natl Acad Sci USA* 96:12611–615.

Möglich M, Hölldobler B. (1975). Communication and orientation during foraging and emigration in the ant *Formica fusca. J Comp Physiol* 101:275–88.

Myerscough MR. (2003). Dancing for a decision: A matrix model for nest-site choice by honeybees. *Proc R Soc Lond B* 270:577–82.

Nieh JC. (2004). Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). *Apidologie* 35:159–82.

van Nieuwstadt MGL, Ruano ICE. (1996). Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie* 27:219–28.

Oldroyd BP, Fewell JH. (2007). Genetic diversity promotes homeostasis in insect colonies. *Trends Ecol Evol* 22:408–13.

Oldroyd BP, Rinderer TE, Buco SM. (1991). Intracolonial variance in honey bee foraging behaviour: The effects of sucrose concentration. *J Apic Res* 30:137–45.

Oldroyd BP, Wongsiri S. (2006). *Asian Honey Bees. Biology, Conservation, and Human Interactions*. Cambridge, MA: Harvard University Press.

Page RE, Erber J, Fondrk MK. (1998). The effect of genotype on response threshold to sucrose and foraging behavior of honey bees (*Apis mellifera* L.). *J Comp Physiol A* 182:489–500.

Page RE, Waddington KD, Hunt GJ, Fondrk MK. (1995). Genetic determinants of honey bee foraging behaviour. *Anim Behav* 50:1617–25.

Pasteels JM, Deneubourg JL, Verhaeghe JC, Boevé JL, Quinet Y. (1986). Orientation along terrestrial trails by ants. In Payne TL, Birch MC, Kennedy CEJ (eds.), *Mechanisms in Insect Olfaction*. Oxford: Oxford University Press, pp. 131–38.

Pratt SC, Mallon EB, Sumpter DJT, Franks NR. (2002). Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav Ecol Sociobiol* 52: 117–27.

Pratt SC, Sumpter DJT, Mallon EB, Franks NR. (2005). An agent-based model of collective nest choice by the ant *Temnothorax albipennis*. *Anim Behav* 70:1023–36.

Quinet Y, de Biseau JC, Pasteels JM. (1997). Food recruitment as a component of the trunk-trail foraging behaviour of *Lasius fuliginosus* (Hymenoptera: Formicidae). *Behav Process* 40:75–83.

Quinet Y, Pasteels JM. (1996). Spatial specialization of the foragers and foraging strategy in *Lasius fuliginosus* (Latreille) (Hymenoptera, Formicidae). *Insect Soc* 43:333–46.

Reinhard J, Srinivasan MV, Zhang S. (2004). Scent-triggered navigation in honeybees. *Nature* 427:411.

Robinson EJH, Jackson DE, Holcombe M, Ratnieks FLW. (2005). "No entry" signal in ant foraging. *Nature* 438:442.

Robinson GE, Page RE. (1989). Genetic basis for division of labor in an insect society. In Breed MD, Page RE (eds.), *The Genetics of Social Evolution.* Boulder: Westview Press, pp. 61–68.

Roces F, Núñez JA. (1993). Information about food quality influences load-size selection in recruited leaf-cutting ants. *Anim Behav* 45:135–43.

Rohrseitz K, Tautz J. (1999). Honey bee dance communication: Waggle run direction coded in antennal contacts? *J Comp Physiol A* 184:463–70.

Rosengren R, Sundström L. (1987). The foraging system of a red wood ant colony (*Formica* s. str.)—Collecting and defending food through an extended phenotype. In Pasteels JM, Deneubourg JL (eds.), *From Individual to Collective Behavior in Social Insects*. Basel: Birkhäuser, pp. 117–37.

Roubik DW. (1982). Obligate necrophagy in a social bee. *Science* 217:1059–60.

Roubik DW, Aluja M. (1983). Flight ranges of *Melipona* and *Trigona* in tropical forest. *J Kansas Entomol Soc* 56:217–22.

Schmidt VM, Schorkopf DLP, Hrncir M, Zucchi R, Barth FG. (2006). Collective foraging in a stingless bee: Dependence on food profitability and sequence of discovery. *Anim Behav* 72:1309–17.

Schneider SS. (1989). Spatial foraging patterns of the African honey bee, *Apis mellifera scutellata*. *J Insect Behav* 2:505–21.

Seeley TD. (1983). Division of labor between scouts and recruits in honeybee foraging. *Behav Ecol Sociobiol* 12:253–59.

Seeley TD. (1995). *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies.* Cambridge, MA: Harvard University Press.

Seeley TD. (2003). Consensus building during nest-site selection in honey bee swarms: The expiration of dissent. *Behav Ecol Sociobiol* 53:417–24.

Seeley TD, Buhrman SC. (2001). Nest-site selection in honey bees: How well do swarms implement the "best-of-N" decision rule? *Behav Ecol Sociobiol* 49:416–27.

Seeley TD, Camazine S, Sneyd J. (1991). Collective decision-making in honey bees: How colonies choose among nectar sources. *Behav Ecol Sociobiol* 28:277–90.

Seeley TD, Kühnholz S, Weidenmüller A. (1996). The honey bee's tremble dance stimulates additional bees to function as nectar receivers. *Behav Ecol Sociobiol* 39:419–27.

Seeley TD, Mikheyev AS, Pagano GJ. (2000). Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *J Comp Physiol A* 186:813–19.

Seeley TD, Tautz J. (2001). Worker piping in honey bee swarms and its role in preparing for liftoff. *J Comp Physiol A* 187:667–76.

Seeley TD, Visscher PK. (2004). Group decision making in nest-site selection by honey bees. *Apidologie* 35:101–16.

Seeley TD, Visscher PK, Passino KM. (2006). Group decision making in honey bee swarms. *Am Sci* 94:220–29.

Seeley TD, Weidenmüller A, Kühnholz S. (1998). The shaking signal of the honey bee informs workers to prepare for greater activity. *Ethology* 104:10–26.

Shepherd JD. (1982). Trunk trails and the searching strategy of a leaf-cutter ant, *Atta columbica. Behav Ecol Sociobiol* 11:77–84.

Shepherd JD. (1985). Adjusting foraging effort to resources in adjacent colonies of the leaf-cutter ant, *Atta colombica. Biotropica* 17:245–52.

Sherman G, Visscher PK. (2002). Honeybee colonies achieve fitness through dancing. *Nature* 419:920–22.

Sorensen AA, Busch TM, Vinson SB. (1985). Control of food influx by temporal subcastes in the fire ant, *Solenopsis invicta*. *Behav Ecol Sociobiol* 17:191–98.

Sorensen AA, Vinson SB. (1981). Quantitative food distribution studies within laboratory colonies of the imported fire ant, *Solenopsis invicta* Buren. *Insect Soc* 28:129–60.

Sumpter DJT. (2005). The principles of collective animal behaviour. *Phil Trans R Soc Lond B* 361:5–22.

Sumpter DJT, Beekman M. (2003). From non-linearity to optimality: Pheromone trail foraging by ants. *Anim Behav* 66:273–80.

Sundström L. (1993). Foraging responses of *Formica truncorum* (Hymenoptera: Formicidae); exploiting stable vs. spatially and temporally variable resources. *Insect Soc* 40:147–61.

Szlep R, Jacobi T. (1967). The mechanism of recruitment to mass foraging in colonies of *Monomorium venustum* Smith, *M. subopacum* ssp. *phoenicium* Em., *Tapinoma israelis* For. and *T. simrothi* v. *phoenicium* Em. *Insect Soc* 14:25–40.

Tautz J, Rohrseitz K. (1998). What attracts honey bees to a waggle dancer? *J Comp Physiol A* 183:661–67.

Tautz J, Rohrseitz K, Sandeman DC. (1996). One-strided waggle dance in bees. *Nature* 382:32.

Thom C, Gilley DC, Hooper J, Esch HE. (2007). The scent of the waggle dance. *PLoS Biology* 5:e228. DOI:10.1371/journal.pbio.0050228.

Topoff H, Mirenda J. (1978). Precocial behaviour of callow workers of the army ant *Neivamyrmex nigrescens*: Importance of stimulation by adults during mass recruitment. *Anim Behav* 26:698–706.

Torgerson RL, Akre RD. (1970). The persistence of army ant chemical trails and their significance in the ecitonine-ecitophile association (Formicidae: Ecitonini). *Melanderia* 5:1–28.

Traniello JFA. (1977). Recruitment behavior, orientation, and the organization of foraging in the carpenter ant *Camponotus pennsylvanicus* DeGeer (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 2: 61–79.

Traniello JFA, Fourcassié V, Graham TP. (1991). Search behavior and foraging ecology of the ant *Formica schaufussi*: Colony-level and individual patterns. *Ethol Ecol Evol* 3:35–47.

Vander Meer RK, Alvarez F, Lofgren CS. (1988). Isolation of the trail recruitment pheromone of *Solenopsis invicta*. *J Chem Ecol* 14:825–38.

Vander Meer RK, Lofgren CS, Alvarez F. (1990). The orientation inducer pheromone of the fire ant *Solenopsis invicta*. *Physiol Entomol* 15:483–88.

Verhaeghe JC. (1977). Group recruitment in *Tetramorium caespitum*. In *Proceedings of the 8th International Congress of IUSSI*, pp. 67–68.

Verhaeghe JC. (1982). Food recruitment in *Tetramorium impurum* (Hymenoptera: Formicidae). *Insect Soc* 29:67–85.

Visscher PK. (2007). Group decision making in nest-site selection among social insects. *Annu Rev Entomol* 52:255–75.

Visscher PK, Camazine S. (1999). Collective decisions and cognition in bees. *Nature* 397:400.

Visscher PK, Seeley TD. (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63:1790–801.

Waddington KD, Herbert TJ, Visscher PK, Raveret Richter M. (1994). Comparisons of forager distributions from matched honey bee colonies in suburban environments. *Behav Ecol Sociobiol* 35:423–29.

Wehner R, Harkness RD, Schmid-Hempel P. (1983). *Foraging Strategies in Individually Searching Ants, Cataglyphis bicolor (Hymenoptera: Formicidae)*. Stuttgart: Gustav Fischer Verlag.

Wilson EO. (1962a). Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). 1. The organization of mass-foraging. *Anim Behav* 10:134–47.

Wilson EO. (1962b). Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). 2. An information analysis of the odour trail. *Anim Behav* 10:148–58.

Wilson EO. (1962c). Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). 3. The experimental induction of social responses. *Anim Behav* 10:159–64.

Winston ML. (1987). *The Biology of the Honey Bee.* Cambridge, MA: Harvard University Press.

Wittlinger M, Wehner R, Wolf H. (2006). The ant odometer: Stepping on stilts and stumps. *Science* 312: 1965–67.