
Social Insects and the Exploitation of Food Sources

Concluding Thoughts

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“...think of an insect colony as a diffuse organism, weighing anywhere from less than a gram to as much as a kilogram and possessing from about a hundred to a million or more tiny mouths. It is an animal that forages ameba-like over fixed territories...”

Edward O. Wilson, 1971

In social insects, foraging individuals gather food that predominantly supports the rearing of the brood and satisfies the energetic demands of nonforaging individuals. Thus, the foragers' activities serve the benefit of the colony rather than their personal profit. Food collectors sometimes even “sacrifice” their individual performance and gather food at suboptimal rates (Núñez 1982; Roces and Núñez 1993), in exchange for a faster return to the colony and the activation of additional foragers (Roces and Núñez 1993; see also Chapter 14). At the individual level, therefore, social insect foraging does not necessarily fit into “simple” concepts, theories, and models of “optimal foraging” (Pyke 1984; Stephens and Krebs 1986) or “social foraging” (Giraldeau and Caraco 2000), which have been developed for vertebrates (or vertebrate groups) that optimize their food-collecting activity in accordance with their individual needs. Yet, the optimality of food exploitation in social insects has to be considered at the level at which natural selection takes place—that is, the entire colony.

In analogy to higher organisms that are composed of numerous single cells, colonies of eusocial insects have frequently been considered “superorganisms” (Wilson 1971; Seeley 1989; Moritz and Fuchs 1998), in which the workers adopt the role of the somatic cells. In contrast to multicellular organisms, however, colonies of eusocial insects have no (or only a weak) central control that regulates and coordinates the behavior of their subunits. The decision of workers to start, continue, or stop a specific task, e.g., foraging, is based on local stimuli, such as the interactions with nest-mates or cues from the environment (Seeley 1989; Biesmeijer et al. 1998; see also Chapter 2). Thus, because of the lack of a central control and the individual decision-making by foragers, it is quite astonishing that social insect societies are able to coordinate their foraging forces for an optimized exploitation of food sources at the colony level.

The amazing coordination among the individuals is a result of self-organization processes through interactions, feedback loops, and local information transfer among workers. The principle of self-organization was originally introduced in physical and chemical systems in order to explain the emergence of macroscopic patterns (e.g., rippled sand dunes) from interactions at the microscopic level (e.g., between sand grains). This concept has been adapted to describe how complex collective behaviors in social insect colonies arise from interactions between individuals that follow rather simple behavioral rules* (Bonabeau et al. 1997). In their book, Scott Camazine and his co-authors

* It should be kept in mind, however, that the principle of self-organization largely ignores the complexity and variability that occurs at the individual level in social insects, and allows them to adapt to changing environments (see also Chapter 6).

give a fascinating and detailed overview of self-organization in biological systems (Camazine et al. 2003), including the emergence of foraging patterns in eusocial insects. Using nectar source selection by honey bees, trail formation in ants, and swarm raids of army ants as examples, the authors demonstrate that colonies are able to efficiently solve particular foraging problems in spite of the fact that the single individuals do not possess a global knowledge of the “problem” at hand.

An important prerequisite for the emergence of self-organized patterns is the interaction among the subunits of a system—in regard to our book’s topic, the workers of a social insect colony. The two basic modes of such interactions are positive and negative feedback loops (Camazine et al. 2003), in which the activity of an individual is affected by the performance of others. Robin Moritz and Stefan Fuchs (1998) defined these feedbacks as follows: “Workers are engaged in a specific activity and by doing so, modify the local conditions to exceed the stimulus response thresholds of other workers (positive feedback). Also the opposite can be possible: the activity of a worker reduces the stimulus below the response threshold which then stops being involved in that task” (Moritz and Fuchs 1998, p. 12). Hence, positive feedback between subunits, in general, promotes changes within a system, whereas negative feedback helps to stabilize certain processes (Camazine et al. 2003). Such feedbacks might be particularly adaptive for the emergence of colony-level foraging patterns when single workers have different thresholds for a particular task. A threshold variability among the individuals of a colony has, for example, been demonstrated to be related to caste differences (e.g., the different response thresholds for recruitment displays found in the different castes of *Pheidole pallidula* ants; Detrain and Pasteels 1991), or to a genetic variability among individuals (e.g., foraging thresholds in pollen- or nectar-collecting honey bee workers; Fewell and Page 2000; Pankiw and Page 2000).

Probably the best-studied example concerning the importance of feedback loops for the emergence of self-organized patterns from the social insect world is the dance communication of the honey bee (*Apis mellifera*). Here, food-collecting workers inform unemployed foragers about the quality of a discovered food source through the liveliness of their waggle dance (duration and rate of waggle runs performed in the hive; Seeley et al. 2000; see also Chapter 6). This information from the dance, as well as gustatory information received through trophallactic interactions with an active forager (see Chapter 10), influences the decision of unemployed foragers whether to initiate foraging or to stay in the hive. In case the intensity of the information exceeds the foraging threshold of the bees, they will start collecting at the advertised food source. Thus, bit by bit, the colony’s foraging force will increase at this food source through an accumulation of attractive signals (positive feedback). Yet, if too many foragers have been activated, the nectar influx might exceed the food processing capacity of a colony. In this case, in order to maintain the food exploitation at an efficient level, the foraging activity should be downregulated, or alternatively, nectar processing should be enhanced. Here, information about the colony’s nectar processing status is provided to the foragers through the time they need to unload their crop (Seeley 1995). In case nectar foragers, which return from profitable food sources, experience long search times to find food receivers, they are stimulated to perform tremble dances. On the one hand, these dances activate additional nectar receivers and, consequently, increase the food processing capacity of the colony (positive feedback). On the other hand, the tremble dances have an inhibitory effect on waggle dances (negative feedback) so that no further foragers are activated and, consequently, the nectar-collecting rate is stabilized (Seeley 1995). As can be seen from this example, the emergence of feedback loops is directly related to the capacity of the individuals to process relevant information obtained both from other individuals and from the local environment. Thus, the management of information at the individual level constitutes the core of self-organized processes at the colony level.

Several models exist that attempt to link the pattern of task performance at the individual and colony levels in order to explain division of labor. These models are based on both external and internal factors, such as ontogeny, genetic components, motivation, experience, environmental factors, and probably most important, the flow of information between the individuals of a colony (for a comprehensive review see Beshers and Fewell 2001). It is apparent that the organization of foraging in honey

bee hives is largely based on *direct* social cues (interaction rate between individuals), such as encounters between nestmates and the concomitant direct exchange of chemical cues, which have also been demonstrated to be a major channel of information transfer in ant colonies (Gordon 1999; see also Chapter 2). However, as Claire Detrain and Jean-Louis Deneubourg illustrate in Chapter 2, foraging efficiency in ants is also considerably enhanced by the detection of *indirect* social cues, which can be by-products of the ants' activity or excreted compounds left behind. The use of indirect cues to estimate the activity or density of nestmates and foreign workers allows an asynchronous transfer of information. Basically, this means that such cues can contain the recent history of frequentation of an area. Furthermore, this information is available immediately, without requiring much sampling effort. Ants that use such indirect cues and accordingly tune their foraging and recruitment activities can increase their food collection efficiency at both the individual and colony level.

When looking at the adaptiveness of foraging strategies one must also consider sensory biases and learning abilities of the involved individuals. As demonstrated by Nigel Raine and Lars Chittka in Chapter 1, bumble bee workers from eight species (and from eight subspecies within *Bombus terrestris*) show a strong innate color preference for violet-blue, which therefore seems to be a phylogenetically ancient trait. Since violet and blue flowers also contain high nectar rewards in a variety of habitats, this innate preference likely is advantageous in terms of foraging success of bees (an innate violet and blue preference has also been demonstrated for *Apis mellifera*). Indeed, *B. terrestris* colonies with workers that showed a stronger preference for violet over blue flowers in a laboratory assay also harvested more nectar per unit of time in a natural habitat where violet flowers on average contained twice as much sugar reward than blue flowers (see Chapter 1 for details). Likewise, there was a positive correlation between the learning speed of the workers from different bumble bee colonies in the lab and their foraging performance (nectar intake per unit of time) under field conditions, indicating that learning speed is closely associated with colony fitness (Chapter 1).

Certainly, learning (or more generally spoken, experience) strongly influences the foraging decisions of insects. In Chapter 7, Ellouise Leadbeater and Lars Chittka show that bumble bee workers, which have used the holes cut into broad bean flowers by previous nectar robbers, thus acting as secondary robbers, are more likely to cut a hole at the right place (the base of a flower's corolla) when subsequently visiting intact flowers than robbing-inexperienced bees. How well this transmission of social information—the use of holes cut by others—may guide the decision-making of social insect foragers is illustrated by the authors' observation that broad bean plants grown in the open may stay intact for weeks, but then, within hours, every flower can be robbed. Workers of certain ant species can learn the route to a food source by following experienced leaders (Chapter 7), and flower-visiting solitary and social bees learn to interpret scent marks left by previous visitors in accordance with the reward level of a food source—scent-marked flowers, which are depleted after a single visit, are avoided, whereas the odors left behind at *ad libitum* food sources attract the bees (see Chapters 9, 12, and 13 for honey bees, stingless bees, and bumble bees, respectively). The adaptive value of using scent marks to reject recently visited flowers is that the bees save time and energy that would otherwise be spent with landing and handling a depleted resource. Instead, they quickly fly on until rewarding flowers are encountered, thereby increasing their foraging efficiency. Scent marks left at *ad libitum* sugar solution feeders, on the other hand, are a reliable cue that indicates food, and bees learn to associate them with a reward, just as they do with other sensory cues (Menzel and Müller 1996). The duration of the repellent effect of the scent marks encountered on flowers may reflect their nectar secretion rate, and it seems possible that bees learn the appropriate concentration of scent mark as the threshold for rejection of a particular flower species (Chapter 13). It is tempting to speculate that a mechanism similar to ants' ability to use area markings might be at work: from the model presented by Claire Detrain and Jean-Louis Deneubourg in Chapter 2 we learn that ants may be able to estimate the original amount of area markings as well as the time elapsed since their deposition when such markings consist of at least two compounds with different decay rates (which they certainly do, in both ants and bees). In such a case, the ratio between the compounds will change over time, and the age of a marking can be deduced by the relative concentrations of its

single compounds. Within the perception thresholds for the single compounds and the compounds' ratio, respectively, an insect can potentially use this information. However, one problem with this idea in terms of scent marks left at flowers by visitors is that their original compositions already vary considerably at the time of deposition, depending on the species the depositor belongs to.

Due to the overlap of foraging ranges of neighboring social insect colonies with similar food requirements, both inter- and intraspecific competition for resources can be high. Not surprisingly, it is apparently widespread (although little studied) that foragers use information about the presence of other individuals—nestmates and non-nestmates alike—as an indication for food. As illustrated by Judith Slaa and William Hughes in Chapter 8, there are different ways such information can influence the foraging decisions of insects. The logic behind this is simple: where individuals are present, food may be as well. Thus, a food-searching worker can make use of visual or olfactory cues passively provided by nestmates or workers of foreign colonies, or even of other species, when deciding where to forage. Such local enhancement might facilitate the formation of feeding groups (if attraction is to nestmates) or simply the finding of food. Its use, however, will only be adaptive if a food source is large enough to support several foragers, or if the attracted individual can drive away the original exploiter. But where an insect feeds (or recently has fed), a resource might as well be depleted. In such cases, foragers are repelled by cues that indicate the presence of others, as in the example of repellent scent marks used by the flower-visiting bees mentioned above. Likewise, foragers may also avoid food sources occupied by more aggressive heterospecific foragers (see Chapters 3 and 8). Thus, local inhibition can lead to the avoidance of depleted resources and may help to evade direct competition. Several studies have demonstrated that workers of a particular wasp species avoid occupied feeders in areas where they co-occur with larger, more aggressive species, but are attracted to collecting foragers at sites where the dominant competitors are absent. As pointed out by Robert Jeanne and Benjamin Taylor in Chapter 3, this strongly suggests that the respective responses to other workers at food sources are learned, and depend on the local species composition. Here, the parallels to what is known about the resource-dependent interpretation of food-marking odors by bees (see Chapters 12 and 13) are noteworthy.

Where communication occurs in a network environment, there is also potential for parasitism on *signals* (as opposed to cues) released by individuals in order to recruit their nestmates. Non-nestmate “eavesdroppers” can capitalize on this information by following it to the indicated food source. Since the recruitment signals of others are a reliable signpost pointing toward the location of food, following them may be a beneficial strategy to find resources. So far, eavesdropping in social insects has been observed only in scent trail recruiting ants and a stingless bee, which likely is due to the nature of the longer-lasting chemical signals involved.

Another source of useful information is natural food odors, which are learned by (bee) workers and can play an eminent role in their foraging decisions. Our knowledge about the underlying mechanisms has advanced enormously during the past years (for honey bees see Chapters 9 and 10, for stingless bees, see Chapter 12; for bumble bees, see Dornhaus and Chittka 1999, 2004). Experienced foragers associate, and orient toward, the scents of rewarding flower species. In Chapter 9, Judith Reinhard and Mandyam Srinivasan show for honey bees that scent-associated memories of food sources can become quite complex, including not only a food source's nectar reward, but also its shape and color, its location in space, and even the navigational route to reach it. These scent-food associative memories can be recalled by the presentation of the respective odor in the hive, which quickly reactivates experienced foragers to revisit known food locations, thereby enhancing the foraging efficiency of the colony.

In Chapter 10, Walter Farina and Christoph Grüter emphasize the importance of trophallactic interactions within honey bee hives as a means of social information sharing. Recruited bees associatively learn food odors during trophallaxes with nectar-distributing foragers, and later arrive at flowers with the same odor in the field. Interestingly, the frequency of short trophallactic contacts that likely do not provide much nectar, but information about the collected food, increases with increasing food quality. This corroborates the idea that information about food quality is transmitted

via trophallaxis. Since food receivers also offer the food to other bees (second-order receivers), the incoming nectar is rapidly distributed among hive bees of all ages. Consequently, potential cues present in the collected food could rapidly be spread within the colony and serve as “global information” about the characteristics of currently available food sources. Yet, trophallaxis offers information not solely to the workers inside the nest, but also provides foragers with chemosensory information about resources collected by others. Based on such information, a forager may reevaluate its own food source and decide whether to continue exploiting it, abandon foraging, or switch to another, more rewarding food source.

Similar to the rapid propagation of information about food characteristics by means of trophallaxis in honey bee hives, the transport chains observed in leaf- and grass-cutting ants, through which a cut fragment is transported into the nest sequentially by a number of workers, may serve to transfer information about food quality and odor. As argued by Flavio Roces and Martin Bollazzi in Chapter 14, this could be of particular importance during the early phase of recruitment following the discovery of a food source. Dropped fragments along the trail may, for instance, act as cues that enable outgoing foragers to learn the odor of the harvested plant by contacting them, and then quickly locate it at the forage site. Thus, at the colony level, the increased rate of social information transfer may offset the suboptimal food delivery at the individual level. Analogous to these transport chains in leaf- and grass-cutting ants, foragers of *Macrotermes subhyalinus* termites also transfer a piece of food to other workers while returning to the nest, and then rapidly run back to the food source (Traniello and Leuthold 2000). While this behavior might speed up the food collection process, the possibility of information transfer via food cues during these interactions might well be worth consideration.

Of course, the foraging efficiency of social insect colonies depends not only on the use of information that emanates from cues. A large variety of true signals, which are deliberately emitted by an individual to communicate with its nestmates, have evolved among the social insects, e.g., trail pheromones in ants (Hölldobler and Wilson 1990; see also Chapters 2 and 6), stingless bees (see Chapter 12), and termites (e.g., Pasteels and Bordereau 1998; Traniello and Leuthold 2000); Nasonov pheromone released at food sources by honey bee workers; or their dance communication inside the nest (von Frisch 1965, 1967; Seeley 1995; see also Chapters 6 and 9). The social wasps, however, might be an exception here. As illustrated in Chapter 3 by Robert Jeanne and Benjamin Taylor, cues seem to be the primary information used to make foraging decisions in this group of insects. To date, only a single wasp species has been described to use true signals (an attractant pheromone) during the recruitment of nestmates (see Chapter 3 for details).

The sheer fact that pheromone communication in connection with food collection evolved in such a vast number of social insects makes it quite plain that it must have an adaptive value. However, testing this assumption in nature is difficult. One possibility could be the application of a phylogenetic approach, i.e., studying related species with and without pheromone communication under the same conditions (as was done in studies on innate color preferences of bumble bees; see Chapter 1). This, however, might be critical, since several biological characteristics may vary between species apart from their mode of recruitment communication. Here, the modeling approach can provide valuable insights. In Chapter 14, Yoshiyuki Nakamichi and Takaya Arita present an agent-based evolutionary model, in which the agents (“ant foragers”) had to collect food items in a grid environment and store them in their nest. The agents could either deposit pheromone(s) or not, and their behavior was determined by neural networks, which evolved in the framework of a genetic algorithm and in accordance with their foraging activities. The outcome of this model not only affirmed that adaptive pheromone communication indeed evolves, but also demonstrated that agents with pheromone-inhibited sensors collected fewer food items than agents that could make use of pheromone information. Thus, the evolution of pheromone communication indeed increases foraging efficiency.

Whether social information use is adaptive in nature depends on the actual situation and environmental conditions under which the foragers act. In Chapter 6, Madeleine Beekman and Audrey Dussoutour demonstrate that the range of flexibility of social insects to react to changing conditions

(e.g., availability of rich food sources) largely depends on the recruitment mechanism they apply, which, in turn, likely is tuned to the environment in which they evolved. Experiments with honey bees, for instance, have revealed that recruitment through dances indeed leads to an increased foraging efficiency (nectar intake rate) when floral resources are clustered (tropical habitat or Californian winter), but not in landscapes with dispersed flowering plants (Central Europe and Spain, or Californian summer and autumn) (see Chapters 1 and 7). The stingless bees comprise many different species, most of which require similar resources. Competition for food, therefore, might be particularly high, and recruiting bees should rather aim at quickly mobilizing the available foraging force than spending much time with communication at pinpointing a particular food patch. This may be a good reason why a precise, but time-consuming, referential communication mechanism inside the nest, comparable to the dances of honey bees, has not evolved in this group of social insects. As Michael Hrnčir shows in Chapter 11, stingless bee foragers indeed quickly activate the available foraging force by jostling as well as by means of vibrations and sounds emitted inside the nest, when returning from rich food sources. Once activated, the recruits' decision on where to collect is largely influenced by field-based cues and signals, which are predominantly of a chemical nature (see Chapter 12).

The colony foraging patterns that emerge from the decisions of individual workers and from their interactions with each other are also influenced by the environment itself. In all ecosystems, the food availability is subject to changes in the course of the year. In addition to food abundance, abiotic factors such as temperature and relative humidity can vary on a daily and seasonal basis and, consequently, influence the foraging activity of social insects. In Chapter 4, Flávia Medeiros and Paulo Oliveira present a case study on *Pachycondyla striata* ants from a semideciduous forest habitat in southeastern Brazil, where summers are rainy and hot and winters dry and cooler. Their study shows that the ants adjust their foraging behavior to the different seasons, with higher activities and larger home ranges during the rainy season. The increased foraging activity corresponds to a three-fold increase in the abundance of potential litter-dwelling prey, mainly arthropods, which might well explain the observed differences. Changing foraging areas of single *Pogonomyrmex* harvester ant colonies were also revealed during a detailed long-term study in the Arizona desert (Gordon 1999). In addition to seasonal variations, the age, and thus the developmental stage of a colony, significantly affected the behavior of *Pogonomyrmex* workers, specifically in relation to territorial conflicts and the return rate to places where foreign ants were encountered (Gordon 1999). In analogy to the findings in ants, several species of termites also change their foraging patterns according to the season. Some species increase the collection of leaf litter with rainfall, whereas others show their peak foraging activity during the dry season (Bignell and Eggleton 2000). Without repeating all details here, these examples clearly show how foraging decisions of social insect workers, as well as the resulting foraging patterns at the colony level, are influenced by biotic (e.g., competition, natural enemies, availability of prey, age of a colony) and abiotic (e.g., temperature, precipitation, relative humidity) factors alike. One certainly has to keep this in mind when evaluating the foraging behavior of social insect workers and their activities at the colony level, especially in studies that are carried out during relatively short periods of time.

Since eusocial insects are central place foragers, the foraging range is a fundamental aspect of their ecology. Whereas it is relatively easy to investigate how far ants walk when searching and collecting food (Gordon 1999; Chapter 4), insects that forage on the wing cause a bit of a problem, because it proves difficult to follow their flight path. Not surprisingly, therefore, our knowledge about foraging ranges in bees is poor, the main exception being the honey bees, which encode the distance of visited food sources in the length of the waggle run performed by a returned forager inside the nest, where it can be measured by an observer (e.g., von Frisch 1965, 1967; Seeley 1995; Oldroyd and Wongsiri 2006). In Chapter 5, Dave Goulson and Juliet Osborne review what we know about foraging ranges in bumble bees. This problem was approached by a variety of methods, which all have their drawbacks. Nevertheless, all available studies indicate that bumble bees do not necessarily forage at the food plants closest to the nest. Goulson and Osborne argue that the most likely

explanation for the low worker densities near their nest could be that flight to and from food patches is relatively cheap compared to the energy spent within a patch, and that intracolony competition would be quite high if many workers stayed close to the nest (see Chapter 5). This assumption seems to be supported by the evidence that the foraging ranges of different bumble bee species are positively correlated with their respective colony sizes (adult worker populations). In this regard, it would be very interesting to study the third group of eusocial bees in the tribe Apini, the stingless bees. Since this bee group shows a great variability in colony and worker sizes among the several hundred known species, they would be well suited to test the assumption brought forth for bumble bees by Goulson and Osborne. Unfortunately, the few data available on flight distances (rather than foraging distances) of stingless bees do not yet allow coming up with a meaningful interpretation of the distribution of foragers in relation to their colony characteristics.

One critical aspect that certainly has to be considered when thinking about foraging ranges of insects is how they navigate, which, in turn, may influence not only their ability to find a resource without prior knowledge of its location or to return to a known feeding site, but also their ability to find their way back home after food uptake. Thus, in order to fully understand how an insect manages to carry out its day-to-day foraging activities, knowledge about the underlying medium-range navigation mechanisms is required. Apart from the empirical studies carried out on a few species, different mathematical and neural network models have been developed to address this question, many of which are reviewed by Allen Cheung in Chapter 16. As argued by the author, models dealing with navigation systems often treat them in isolation (i.e., not in a foraging context), whereas most of the available models of social insect foraging greatly simplify the details of biological navigation systems (which likely is due to our incomplete understanding of insect navigation). But still, from the models presented in Chapter 16 we can learn, for instance, how the competitive ability and information state of a foraging insect can affect the probability of its presence at a resource patch, how a forager's age might influence its threshold to accept a resource of lower quality (e.g., in honey bees due to higher flight costs caused by accumulating wing damage), or how it may find its way back home according to the navigation strategy applied (e.g., path integration, view-based homing, map-based navigation). It is clear that much of the success of a foraging strategy depends critically on the accuracy, reliability, and efficiency of the underlying navigation system. In social insects, foragers can also potentially gain useful navigational (foraging) information via interactions with nestmates.

To come to a close, we think that the most significant recent advance in our understanding of the mechanisms underlying the foraging decisions and recruitment behavior of social insect workers, and ultimately foraging patterns of social insect colonies, is the recognition that, aside from true signals, learning and the context-dependent interpretation and use of cues play a central role. It is also clear that foraging patterns at the colony level are not fixed features, but underlie a strong influence of environmental as well as current colony conditions, and that the workers' ability to search the nest's surroundings for resources and to successfully return with food depends on their navigation mechanism(s). We may still be far from providing a complete picture of how all these mechanisms work together to produce the collective, self-organized foraging processes observed in social insect societies. Yet, we expect that the combination of empirical ecological and behavioral studies with theoretical models will prove to be a fruitful approach to get us further toward a profound understanding of how social insects exploit food sources.

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