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# Introduction

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Probably everyone who has set out for a relaxing picnic on a sunny afternoon has gotten into the annoying situation that, all of a sudden, he or she had to compete for the favorite salami (or something similarly delicious) with several dozens of ants, which apparently turned up out of nowhere. Whereas many people, for sure, are merely irritated by this, others might marvel at the agility and speed with which these tiny animals find and collect food. In fact, the fascination and knowledge about the foraging efficiency of eusocial insects, particularly of ants, dates back several thousand years and has, for instance, found its way into Aesop's fables and the Old Testament: "Go to the ant, thou sluggard! Consider her ways, and be wise: which, having no guide, overseer, or ruler, provideth her meat in the summer, and gathereth her food in the harvest" (Book of Proverbs 6:6–8).

Nowadays, the industriousness of ants no longer serves as a mandatory example of how to behave in human society. However, the efficiency with which eusocial insects exploit food sources has by no means lost its fascination. Far from it! More and more researchers are intrigued by the highly structured organization of foraging processes and by the way a social insect society is able to solve a variety of rather complex tasks in spite of the "simplicity" of its members and of the rules they follow. The way by which these animals share and collectively process information, thereby enabling a colony to function as a single purposeful unit, is not solely of interest to biologists. During the last decade, the functional principles of social insect colonies have greatly inspired the design of intelligent artificial systems that find application in communication networks and robotics (e.g., Bonabeau et al. 1999; Dorigo and Stützle 2004).

This recent development called for a sound biological basis, which consequently resulted in a constant and rapid increase in information about task organization and information management in social insect societies. Here, the exploitation of food is probably one of the best-studied examples. Yet, in consequence of the steadily increasing knowledge about food exploitation by social insects, one can easily get lost in the constantly growing network of scientific literature. The present book aims at providing a comprehensive overview of the most recent insights into social insect foraging by combining ecological, behavioral, and theoretical studies. This offers the possibility to take a look at the fascinating aspects of social insect colony organization and coordination from different points of view. For obvious reasons, however, a single book cannot contain *all* information available about social insect foraging. We therefore excluded topics that we think have already extensively been covered by excellent books or review articles, such as, for example, the dance communication of the honey bee,\* *Apis mellifera* (von Frisch 1965, 1967/1993; Seeley 1995; Dyer 2002). For readers interested in social insect foraging, we highly recommend the following publications:

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\* In our book, we will follow the "bee spelling rule" defined by Snodgrass (1956) as follows: "If the insect is what its name implies, write the two words separately; otherwise run them together. Thus we have such names as house fly, blow fly, and robber fly contrasted with dragonfly, caddicefly, and butterfly, because the latter are not flies, just as an aphision is not a lion and a silverfish is not a fish. The honey bee is an insect and is pre-eminently a bee." Accordingly, we adopted the terms *honey bee* and *bumble bee* for our book instead of the frequently used *honeybee* and *bumblebee*.

For ants:

*The Ants* by Bert Hölldobler and Edward Wilson (1990)

*Army Ants: The Biology of Social Predation* by William Gotwald (1995)

*Ants at Work: How an Insect Society Is Organized* by Deborah Gordon (1999)

For bees:

*The Social Behavior of the Bees: A Comparative Study* by Charles Michener (1974)

*Ecology and Natural History of Tropical Bees* by David Roubik (1989)

*The Wisdom of the Hive—The Social Physiology of Honey Bee Colonies* by Thomas Seeley (1995)

“The Biology of the Dance Language” by Fred Dyer (2002)

*Bumblebees—Their Behaviour and Ecology* by Dave Goulson (2003)

*Asian Honey Bees: Biology, Conservation, and Human Interactions* by Benjamin Oldroyd and Siriwat Wongsiri (2006)

For wasps:

*The Social Biology of Wasps* edited by Kenneth Ross and Robert Matthews (1991)

“Social Wasp (Hymenoptera: Vespidae) Foraging Behavior” by Monica Raveret Richter (2000)

For termites:

*Nourishment and Evolution in Insect Societies* edited by James Hunt and Christine Nalepa (1994)

*Termites: Evolution, Sociality, Symbioses, Ecology* edited by Takuya Abe, David Bignell, and Masahiko Higashi (2000)

For self-organization processes in various taxa:

“Self-Organization in Social Insects” by Eric Bonabeau, Guy Theraulaz, Jean-Louis Deneubourg, Serge Aron, and Scott Camazine (1997)

*Information Processing in Social Insects* edited by Claire Detrain, Jean-Louis Deneubourg, and Jaques Pasteels (1997)

*Self-Organization in Biological Systems* by Scott Camazine, Jean-Louis Deneubourg, Nigel Franks, James Sneyd, Guy Theraulaz, and Eric Bonabeau (2003)

“The Principles of Collective Animal Behaviour” by David Sumpter (2006)

Apart from the eusocial insects covered by these books and articles, and also by the volume at hand, there are several species that do not have distinct female castes and a strict division of reproduction and labor but still exhibit some sort of social behavior—including the use of food sources. A marvelous and extensive summary of the biology of these insects is provided by a book written by James Costa (2006), *The Other Insect Societies*.

The chapters brought together in our book basically look at two different levels of social insect foraging, which are, however, inseparably interlaced with each other. The first is the macroscopic or colony level. Like a solitary animal roaming for food, the colony adapts its foraging decisions and strategies to the respective environmental situation and its own physiological condition in order to optimize its food intake. The second level is the microscopic or individual level. Foraging decisions by individual workers are largely based on information from other individuals and/or the local environment, but they are also influenced by innate preferences. At this level the processing of relevant information is crucial for optimizing the colony’s food intake. Accordingly, the first part of the book (Chapters 1–5) focuses on *foraging decisions, patterns, and strategies* of social insect colonies, and the second part (Chapters 6–14) focuses on *information use and information transfer* by and between workers of social insects. Whereas these two sections contain information that is largely based on empirical studies, the third part of the book (Chapters 15 and 16) provides two examples of how this biological knowledge can be used as a basis for the construction of *mathematical and neural network models* that, in return, may help us to understand social insect foraging.

In Chapter 1, Nigel Raine and Lars Chittka address the question of how a particular foraging behavior contributes to the fitness of a social insect colony. Using a phylogenetic approach, the authors compare innate color preferences between different bumble bee species, and between different populations within a single species, respectively. If foraging preferences were adapted to the available food sources, local variations in flower traits (e.g., floral colors) should have driven selection of the bees' sensory bias toward particular colors. In addition, the authors evaluate how differences in learning performance among colonies of one bumble bee species affect their fitness. In order to examine to which extent a specific foraging trait is adapted to a given niche, the foraging success of an experimentally manipulated honey bee behavioral phenotype (directional information component of the dance language removed) is compared to that of the normal foraging phenotype.

In Chapter 2, Claire Detrain and Jean-Louis Deneubourg investigate in which way social cues influence the foraging patterns of colonies of trail-laying ants. Since in these species the efficiency of recruitment does not only depend on the behavior of the recruiting foragers, but also on the amount of potential recruits located within the trail's active space, the foraging dynamics should be particularly sensitive to the density of nestmates. Foraging individuals, therefore, should adjust their recruiting behavior and communication according to the social environment, which they can access via direct (contact) as well as indirect (area marking) cues from nestmates, but also from foreign ants.

In Chapter 3, Robert Jeanne and Benjamin Taylor explore how social foraging patterns can emerge in eusocial wasps, which apparently have not evolved specific signals to inform nestmates about the presence of valuable food sources. The foragers have to be highly sensitive to social cues, both in the environment and at the nest, as well as to the actual food availability within their foraging area in order to optimize the colony's food intake.

In Chapter 4, Flávia Medeiros and Paulo Oliveira illustrate the effects of seasonal changes of the environment on the foraging pattern of the Neotropical forest-dwelling ant *Pachycondyla striata*. This ant species shows a flexible foraging behavior that comprises a wide array of prey hunting techniques as well as the collection of plant material. It is, therefore, a suitable study object for improving our understanding of how ecological factors influence the foraging patterns and strategies of social insects.

In Chapter 5, Dave Goulson and Juliet Osborne evaluate different approaches to estimate the foraging ranges of bumble bees, comparing marking and homing experiments, theoretical calculations of possible flight distances, radar tracking, analyses of pollen collected from incoming foragers, and studies using molecular methods. The authors further discuss possible reasons for the observed differences in foraging ranges between different bumble bee species.

In Chapter 6, Madeleine Beekman and Audrey Dussutour investigate the costs and benefits of different recruitment mechanisms, how they allow insect colonies to adapt to changing conditions, and how social insects overcome constraints imposed by their ways of communication. After giving an overview of the different ways in which social insects recruit nestmates to food sources, the chapter mainly focuses on a comparison of two extreme and well-studied examples: mass recruitment via pheromone trails, where individuals only interact indirectly through the trail, and the honey bees' dance communication, where information is transferred directly from individual to individual.

In Chapter 7, Ellouise Leadbeater and Lars Chittka evaluate under which circumstances—and how—social learning and social information transmission (“teaching”) add to the successful exploitation of food sources by foraging insects. By reviewing studies dealing with a variety of species, they reveal that, in spite of the high effectiveness of such social information systems, the underlying mechanisms are surprisingly simple.

A further and important aspect of social information use is discussed by Judith Slaa and William Hughes in Chapter 8, in which they outline the use or even exploitation of passively provided cues and of actively emitted signals from nestmates or non-nestmates, respectively. Although the role of local enhancement and local inhibition (use of social cues) as well as of eavesdropping (use of another colony's or species' signals) is relatively understudied in comparison to active recruitment

systems, it is quite clear that these mechanisms considerably contribute to the foraging ecology of social insects.

In Chapter 9, Judith Reinhard and Mandyam Srinivasan investigate the role of scents in food collection processes of honey bees. While these bees employ a highly complex referential communication system to recruit nestmates to food sources, the dance “language,” scents are important factors for the foraging and recruitment success of honey bee colonies. After a brief description of the morphology and neuroanatomy of the honey bees’ sense of smell—the necessary basis to understand how bees learn odors and how they use them during foraging and recruitment—the authors explore the honey bees’ world of odors, which are either of floral origin or emitted by other workers.

Inside the hive, honey bee workers learn the food odors while receiving nectar samples from foragers. The role of these trophallactic interactions for the exchange of chemosensory information between members of a colony is the topic of the contribution by Walter Farina and Christoph Grüter. In Chapter 10, they discuss which kind of information, in addition to the food’s scent and taste, is transferred from foragers to receiver bees, and from the receivers on to other colony members—thereby creating information networks that connect the different groups of workers.

Far less studied than the honey bees are their mainly tropical relatives, the stingless bees. In Chapter 11, Michael Hrnčir explores the potential messages and meanings of mechanical signals (jostling runs and pulsed thoracic vibrations) generated by stingless bee foragers during food exploitation processes. Due to the high competition over resources in the tropics, the strategy of these bees should aim at a quick increase in collecting foragers at valuable food sources once these become available. And indeed, empirical evidence indicates that the nest-internal behaviors by collecting bees mobilize additional foragers rather than inform recruits about the location of a food patch, as is known from honey bees.

In Chapter 12, Stefan Jarau reviews how odors, which originate from a variety of sources, are used by stingless bees during food exploitation processes. In addition to food odors, olfactory cues left by nestmates at food sources influence the decision of searching foragers on where to collect. Furthermore, several species employ pheromone marks at and near the food source, or even short pheromone trails, to guide recruits toward a specific food patch, and foragers of some stingless bees emit allomones to disrupt an organized defense by workers of nests they raid.

In Chapter 13, Dave Goulson shows how nectar foraging bees make use of olfactory cues left behind by previous visitors to decide whether to probe or reject a flower. Mainly focusing on bumble bees, he looks at the chemical compounds of scent marks, potential mechanisms that underlie the bees’ behavior, and at its biological significance.

In Chapter 14, Flavio Roces and Martin Bollazzi describe the trade-offs underlying the organization of collective foraging processes in grass- and leaf-cutting ants by discussing different hypotheses why foragers of these ants cut leaf fragments below the size that would maximize the individual’s delivery rate. After exploring the criteria used by workers during the selection of fragment sizes, they look at the adaptive value of cooperative vegetation delivery by means of transport chains, which might either serve to maximize the colony’s leaf intake or improve the information transfer between workers.

In Chapter 15, Yoshiyuki Nakamichi and Takaya Arita present a model for the evolution of pheromone communication in ants based on computer simulations, in which neural networks of the agents evolve in accordance with their foraging success. The authors address the question whether this form of evolved pheromone communication is adaptive, and look at how the number of pheromones used by the agents influences their foraging efficiency. They end their chapter with a comparison of the effectiveness of the evolved pheromone communication with a human-designed one.

A critical aspect of social insect foraging is navigation. In Chapter 16, Allen Cheung provides an overview of various mathematical and neural network models for medium-range navigation in foraging insects. He compares different strategies to search for a resource without prior knowledge of its location (a new food source) and the principles of searching for a unique, stable target (like the nest), including path integration, map-based navigation (piloting), and grid-based navigation

(view-based homing). Since social insect foragers may obtain useful navigational information through interactions with other individuals, particular emphasis is given to the effects of such social interactions on the navigation behavior of food collectors.

In a final chapter, we present some concluding thoughts, which basically arose from working through the single contributions of the book at hand.

We are aware that this volume certainly cannot answer all questions on food exploitation processes in social insects. However, we could hope for nothing better than that the effort made by all authors who contributed to this work will stimulate others to continue the exploration of this fascinating aspect of our and the insects' world.

## REFERENCES

- Abe T, Bignell DE, Higashi M (eds.). (2000). *Termites: Evolution, Sociality, Symbioses, Ecology*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Bonabeau E, Dorigo M, Theraulaz G. (1999). *Swarm Intelligence: From Natural to Artificial Systems*. Oxford: Oxford University Press.
- Bonabeau E, Theraulaz G, Deneubourg JL, Aron S, Camazine S. (1997). Self-organization in social insects. *Trends Ecol Evol* 12:188–93.
- Camazine S, Deneubourg JL, Franks NR, Sneyd J, Theraulaz G, Bonabeau E. (2003). *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.
- Costa JT. (2006). *The Other Insect Societies*. Cambridge, MA and London: Belknap Press of Harvard University Press.
- Detrain C, Deneubourg JL, Pasteels JM (eds.). (1997). *Information Processing in Social Insects*. Basel: Birkhäuser Verlag.
- Dorigo M, Stützle T. (2004). *Ant Colony Optimization*. Cambridge, MA: MIT Press.
- Dyer FC. (2002). The biology of the dance language. *Annu Rev Entomol* 47:917–49.
- von Frisch K. (1965). *Tanzsprache und Orientierung der Bienen*. Berlin: Springer.
- von Frisch K. (1967, second printing 1993). *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.
- Gordon DM. (1999). *Ants at Work: How an Insect Society Is Organized*. New York: The Free Press.
- Gotwald WH. (1995). *Army Ants: The Biology of Social Predation*. Ithaca, NY: Comstock Publishing Associates of Cornell University Press.
- Goulson D. (2003). *Bumblebees—Their Behaviour and Ecology*. Oxford: Oxford University Press.
- Hölldobler B, Wilson EO. (1990). *The Ants*. Cambridge, MA: Belknap Press of Harvard University Press.
- Hunt JH, Nalepa CA (eds.). (1994). *Nourishment and Evolution in Insect Societies*. Boulder, CO: Westview Press.
- Michener CD. (1974). *The Social Behavior of the Bees: A Comparative Study*. Cambridge, MA: Harvard University Press.
- Oldroyd BP, Wongsiri S. (2006). *Asian Honey Bees: Biology, Conservation, and Human Interactions*. Cambridge, MA: Harvard University Press.
- Raveret Richter M. (2000). Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu Rev Entomol* 45:121–50.
- Ross KG, Matthews RW (eds.). (1991). *The Social Biology of Wasps*. Ithaca, NY: Cornell University Press.
- Roubik DW. (1989). *Ecology and Natural History of Tropical Bees*. New York: Cambridge University Press.
- Seeley TD. (1995). *The Wisdom of the Hive—The Social Physiology of Honey Bee Colonies*. Cambridge, MA: Harvard University Press.
- Snodgrass RE. (1956). *Anatomy of the Honey Bee*. Ithaca, NY: Comstock Publishing Associates.
- Sumpter DJT. (2006). The principles of collective animal behaviour. *Phil Trans R Soc B* 361:5–22.