Jürgen Tautz

The Buzz about Bees

Biology of a Superorganism

With Photographs by Helga R. Heilmann

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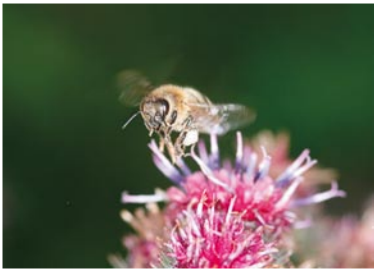
A bee colony—surely nature's most wonderful way of organizing matter and energy in space and time.

Dedicated to Martin Lindauer, mentor of the Würzburg BEEgroup, excellent scientist and splendid person



The Author

Jürgen Tautz is a professor at the Institute of Behavioural Physiology and Sociobiology of the University of Würzburg where he heads the BEEgroup. He and his team have two major goals: basic research on the biology of honeybees and the communication of knowledge about bees to a broad audience. During the last 15 years, Jürgen Tautz has contributed a significant number of discoveries that have considerably changed our view of honeybee biology. Published in top scientific journals (Proceedings of the National Academy of the USA, cover-stories in Science and in Nature) his contributions have earned him the ranking of the fifth most frequently cited behavioural biologist. It is nevertheless his didactic abilities that have brought him his highest accolades. Able to make the most complex principles understandable to all, his university lectures are remembered by students long after their studies, and his public lectures, of which he has given a large number, are always packed with enthusiastic audiences. His writing and popular lectures on organismic biology have been honoured by the European Molecular Biology Organization (EMBO) twice, in 2005 and 2007. He was singled out as one of the best scientific communicators in Europe.

A gifted communicator and leading scientist, Jürgen Tautz has much in common with Carl Sagan, Richard P. Feynman, Konrad Lorenz, Vince Dethier and others famous for their work in popularizing science and making it accessible to all.

The Photographer

Helga R. Heilmann is a photographer and works in the basic research team of the BEEgroup at the biocenter, University of Würzburg. She supports the public relations of the BEEgroup.

The Translator

David C. Sandeman has enjoyed a long career as a comparative neurobiologist interested in the anatomy and physiology of neural control systems underlying reflexive and compensatory behavior in insects and crustaceans. He obtained his first degrees from the University of Natal, South Africa, and his doctorate from the University of St. Andrews, Scotland, followed by a post doctoral period at the University of California, Los Angeles. He returned to Scotland to lecture in Zoology at the University of St. Andrews. Four years later he left for Australia to take up a Fellowship in the Research School of Biological Sciences at the Australian National University in Canberra. In 1982 he was appointed to a chair in Zoology at the University of New South Wales in Sydney. His collaboration with Juergen Tautz during this period resulted in some of the initial data on comb vibration described in this book. Retiring from Sydney and moving to Germany in 2002, he has continued to pursue his scientific interests and is presently a Research Scholar at Wellesley College, USA, where he is part of a team exploring the birth of new neurons in the brains of adult crustaceans. Resident in Laubach, Germany, he has two daughters, one in Australia and one in the USA, and six grandchildren.

Preface to the English Edition

This book, already translated into ten languages, may at first sight appear to be just about honeybees and their biology. It contains, however, a number of deeper messages related to some of the most basic and important principles of modern biology. The bees are merely the actors that take us into the realm of physiology, genetics, reproduction, biophysics and learning, and that introduce us to the principles of natural selection underlying the evolution of simple to complex life forms. The book destroys the cute notion of bees as anthropomorphic icons of busy self-sacrificing individuals and presents us with the reality of the colony as an integrated and independent being—a "superorganism"—with its own, almost eerie, emergent group intelligence. We are surprised to learn that no single bee, from queen through drone to sterile worker, has the oversight or control over the colony. Instead, through a network of integrated control systems and feedbacks, and communication between individuals, the colony arrives at consensus decisions from the bottom up through a type of "swarm intelligence". Indeed, there are remarkable parallels between the functional organization of a swarming honeybee colony and vertebrate brains.

The Buzz about Bees will appeal to many; natural historians will enjoy the exquisite photographs; students considering studying biology should read this book as a primer to appreciate the principles upon which the biological sciences are based, and to get a small taste of the fascination and complexity of biological systems. Apiarists will find here the underlying scientific principles of much of the behavior that they already know, and some basic information that may lead to a reconsideration of some traditional practices. Teachers will find easily understood, practical illustrations of basic biological principles, and an example of how understanding biological systems requires an integration of all scientific disciplines. Professional biologists will enjoy the restatement of evolutionary principles, the introduction of the bee colony as a superorganism, and the consequences of kin selection and natural selection for such systems. Those still persuaded by the creationist arguments and intelligent design may pause to think about the emergent properties of self-organizing and adaptive complex systems.

We are all becoming increasingly conscious of climatic change that is occurring in our world. Climate change brings home to us an awareness of which organisms are living at the edge. Highly specialized for their niches to which they have been adapted, even a very small environmental change over a relatively short time span spells the end for these living forms. Unable to complete enough generations in this time to take advantage of small genetic variation that may allow them to escape their niche, they die and join the long list of beings registered forever in the time capsule of the fossil world, or more recently, in the sobering records kept by mankind. It may be thought that organisms, like mankind and the honeybees, that can exert some measure of control over their immediate environment, would be advantaged. Highly mobile, we are able to move to where it is comfortable, and where it is not, to construct enclosures in which we live, that are. This is an encouraging but unfortunately oversimplified and misleading thought, because there is a great deal more to the interwoven web of life that includes us and on which we depend. We are all in this together and the greatest threat is our own staggering ignorance and cavalier treatment of the natural world to which we belong.

Our exploitation of natural systems without understanding them and their vulnerabilities in detail, has disturbed fine balances, established over thousands of years. Left alone, a new natural balance will, in time, be established, but this is often not to our advantage. Honeybees are important to us. No honeybees means no pollination of most of our crops. No pollination means no fruit, no seed—that simple. If honey bees are in trouble, so are we. And there is more than a little to suggest that honeybees are in trouble. We would do well to understand them, and through them gain a broader appreciation of the enormous complexity of the natural world. This book is a good place to start.

Würzburg and Laubach, January 2008
Jürgen Tautz, David C. Sandeman

Preface to the Original German Edition

Honeybees have fascinated mankind since the beginning of recorded history, and probably much longer. Bees have long been prized for their honey, and beeswax was recognized early on as a natural product of significant importance. The ordered communal lives of the thousands of bees in colonies, and the impressively regular geometry of their honeycombs have intrigued generations of observers. For modern man, bees serve not only as essential coworkers in agriculture, but also as indicators of the state of the environment, and witnesses of an intact association between mankind and nature.

Down through time, and for all cultures knowing them, honeybees are symbols of positive and desirable qualities such as harmony, hard work, and selflessness. Modern research exposes some details of the honeybee nature that may deprive them of this somewhat mythical status, but concurrently affords us with deep insights into the lives of one of the most amazing life forms we know.

This book aims to convey some of the fascination of honeybees, and at the same time to couple new perceptions with existing knowledge. It must be made clear, however, that we are a long way from knowing everything that there is to know about honeybees, and there are still many exciting discoveries to be made.

A dominant theme that runs through this book is that honeybee colonies share a set of characteristics with a highly developed group of organisms, namely, the mammals, but have combined these with the immortality of unicellular organisms. In this way, bee colonies have joined the survival strategies of both the multicellular and unicellular organisms, and hence occupy a special place among the living.

Pictures often say more than lengthy written descriptions, particularly in the Life Sciences; for this reason, we decided at the very beginning of this project to design a book with a strong emphasis on the alternation between text and figures.

We have purposely, with few exceptions, avoided references to the scientific literature, authors, and researchers. Instead, we have prepared an accompanying website for interested readers (http://www.beegroup.de), containing important additions and background material for each chapter, be these references to the literature, internet links, photographs, video clips, sound files, or similar material. We will update this website at intervals, in order to maintain the state of the art that this book represents.

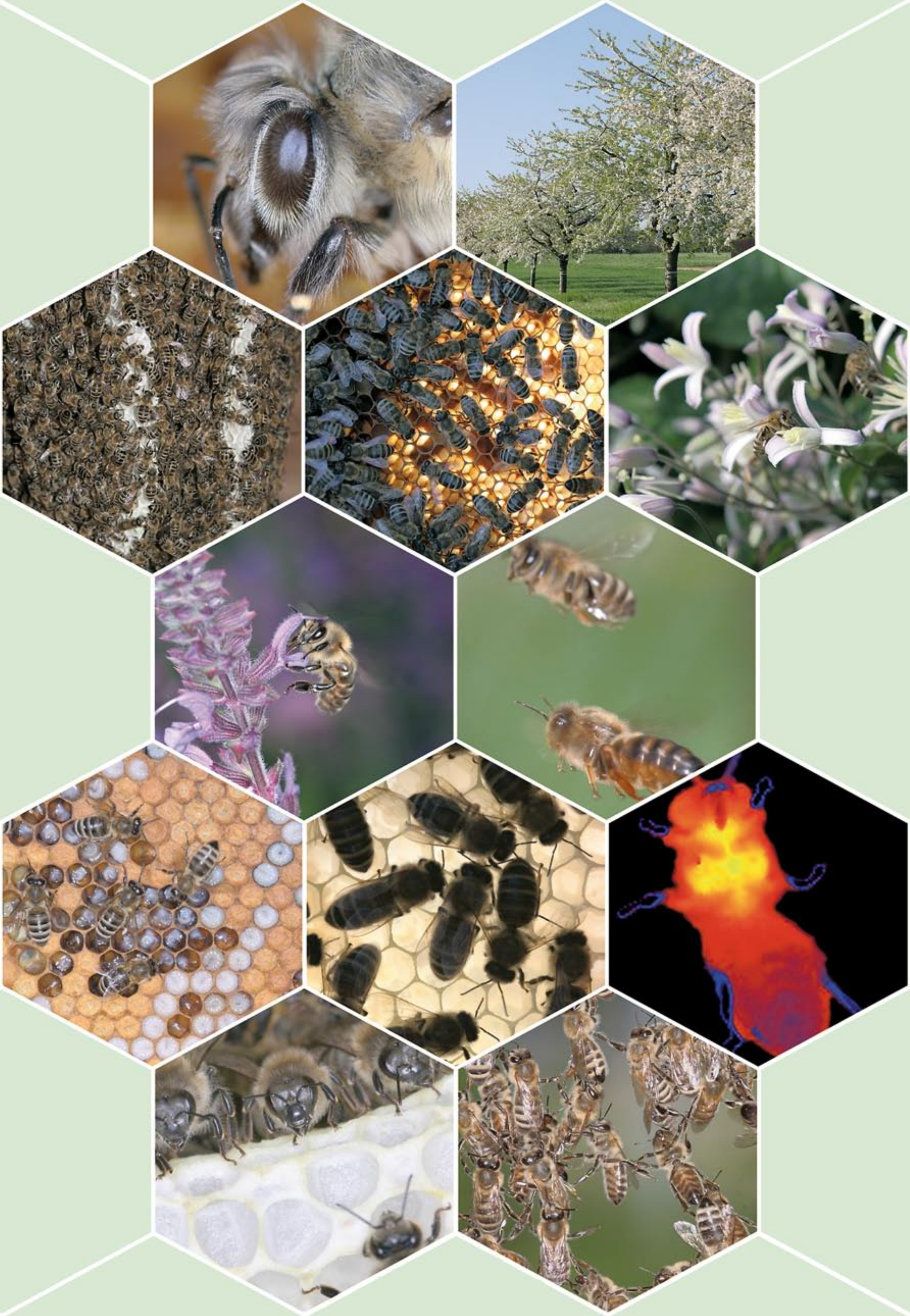
The honeybee is, for us, a "phenomenon" in the purest sense. The original Greek word, φαινόμενο (fenomeno), means something that shows itself, or appears, and we believe this term to be a perfect characterization of this so-called superorganism, its nature repeatedly exhibiting the characteristics of a "phenomenon". The steps we take toward unveiling this "superorganism", which so cautiously surrenders its secrets, are small. But what one can learn from the study of honeybees is so rewarding that it is worth every effort.

The more we are able to penetrate the hidden lives of the honeybee, the greater our amazement, and also the deeper our ambition to explore this wonder world. Karl von Frisch, grand old master of honeybee research, made the fitting comment that "The honeybee colony is like a magic well; the more one removes from it, the stronger it flows".

If, after reading this book, readers were to observe the next honeybee they came across for a little longer than usual, and perhaps remember one or other of the remarkable aspects of her life, then we have achieved a great deal.

We thank the members of the BEEgroup in Würzburg, and the team from Elsevier/Spektrum Akademischer Verlag for their support during the preparation and publication of this book.

Würzburg, November 2006
Jürgen Tautz, Helga R. Heilmann



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PROLOG

The Bee Colony— a Mammal in Many Bodies

Characteristics leading to the dominance of mammals can be found in a similar constellation in the bee colony superorganism.

According to all the usual criteria, honeybees are insects—of that, there is no doubt. And this has been so since their appearance in their present form, about 30 million years ago. Nevertheless, in the 19th century they were accorded the "status" of vertebrates, following a remarkable comparison made by the apiarist and cabinet maker Johannes Mehring (1815–1878). According to Mehring, a bee colony is a single "being" equivalent to a vertebrate animal. The worker bees represent the body organs necessary for maintenance and digestion, while the queen and the drones represent the female and male genital organs.

The concept of equating an entire bee colony to a single animal resulted in the term "bien", implying the "organic interpretation of an individual". The honeybee colony was seen to be an indivisible whole, a single integrated living organism. On the basis of his work on ants, the American biologist William Morton Wheeler (1865–1937) coined the term "superorganism" in 1911 for this special type of living form (origin: lat: *super* = above; grk: *organon* = tool).

Here, I would like to take the shrewd and basic observation of the old apiarist's concept of a bee colony to the extreme, and propose that a honeybee colony is equivalent not only to a vertebrate, but in fact to a mammal, because it possesses many of the characteristics of mammals. This may seem rather farfetched, but not if rather than concentrating on the phylogeny of the honeybee, one would focus on the context of those functional evolu-

Fig. P.1 Bee colonies raise only a few queens each year. The new queens develop in these specially constructed, thimble-shaped queen cells

tionary characters that have rendered the most recently evolved form of all vertebrates—the mammals—dominant.

Using a distinct set of criteria and novel features, mammals can be separated from other vertebrates—and directly compared with honeybees:

- Mammals have a very low rate of reproduction—so do honeybees (Fig. P.1, ▸ Chaps. 2, 5).
- Female mammals produce nourishment (milk) for their offspring in special glands—female honeybees also produce nourishment (royal jelly) for the offspring in special glands (Fig. P.2, ▸ Chap. 6).
- The uterus of mammals offers their developing offspring a precisely controlled and protective environment, independent of the control variables of the external world—honeybees provide the developing juvenile forms the same protection: the “social uterus” of the brood comb in the nest (Fig. P.3, ▸ Chaps. 7, 8).

Fig. P.2 Bee larvae live in paradise. They float on a nourishing jelly produced by nurse bees

- Mammals have body temperatures of about 36°C—honeybees keep the temperature of the brood combs containing the pupae at about 35°C (Fig. P.4, ▸ Chap. 8).
- Mammals with their large brains possess the highest learning and cognitive abilities of all vertebrates—honeybees possess a highly developed capacity for learning, and a cognitive ability that eclipses that of some vertebrates (Fig. P.5, ▸ Chaps. 4, 8).

It is of considerable interest to biologists that this list of novel and fundamental developments characterizing mammals, ourselves included, is found also for a honeybee colony.

The notion of honeybee colonies as "honorary mammals"—or better expressed, as having developed the same novel strategies as mammals have—suggests that there is more to this than a mere superficial similarity. And this is indeed the case.

To extract more information about this phenomenon, i.e., to go beyond simply relating surprising analogies, it is necessary to

Fig. P.3 The microclimate of the brood nest is precisely controlled by adult bees

question why these characters are shared. In this regard, I believe that it is helpful to look for significant "problems" for which animals have "found" the same solutions.

Initially, we could ask: "We can see the solution, what was the problem? We know the answer, what was the question?"

A group of organisms that undertake an evolutionary step forward can have an advantage over their competitors, depending on the extent to which their own existence is influenced by the random nature of the environment. Environmental factors vary unpredictably. Should these affect a broad palette of characters in a population, then these characters acquire a "value", because they will determine the reproductive success of the population. The better adapted organisms flourish, the less well adapted vanish. This is the nub of Darwin's theory on the mechanism of evolution.

Given the unpredictable direction or intensity of environmental change, an organism would therefore seem to be well advised

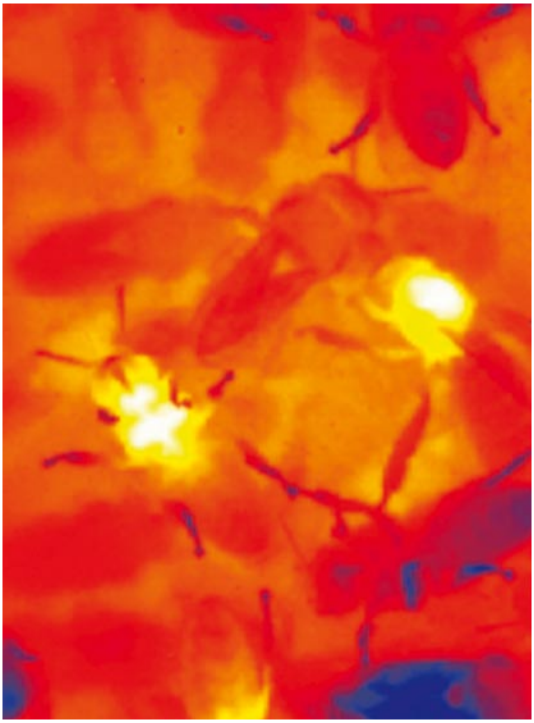


Fig. P.4 Heater bees keep the pupae at a body temperature that, in ideal situations, does not vary from that of mammals by more than 1 °C

to produce as many and varied progeny as possible, in order to prepare for many possible, unknown future scenarios.

When, through the course of evolutionary process, organisms adapt to, and can even control a significant number of environmental parameters, and thereby more or less free themselves from the dictates of the environment, they can afford to exploit this, and produce *fewer* progeny. Mammals and honeybees both belong to this special category of beings.

Independence from fluctuating sources of energy, and from a varying quality of nourishment through self-produced food, protection from enemies by the construction of shielded living space, and independence from the influence of weather by controlling the climate in the habitat—all are clear advantages over organisms to which such possibilities are not available.

All these “mammal-like” qualities guarantee mammals, as well as honeybees, a significant independence of prevailing environ-

Fig. P.5 Bees quickly learn where and which flowers have nectar, and how they have to be handled in order to extract the most from these

mental conditions. This is achieved through the existence of a complex social and behavioral organization enabling the effective application of available material and energy (▶ Chap. 10). A lower rate of reproduction can be adopted as a consequence of these optimally controlled living conditions. Organisms with low reproductive rates, and that are highly competitive, achieve a stable population size through the small number of progeny within a framework of possibilities offered by the habitat. Should the environmental conditions change, however, they would be poorly able to adapt, due to the limited number of offspring, unless they already have the critical environmental parameter under control by constructing a part of their own ecological niche for themselves to ensure their survival during difficult times.

As though not enough, honeybees go beyond the mere control of their environment: their colonies are, under optimal conditions, potentially immortal. The bee colony superorganism has found a way to continually alter its genetic equipment, like a “genomic chameleon" (▶ Chap. 2), so as not to enter an evolutionary dead end.

In general, control through feedbacks is indicative of living organisms. Each organism precisely controls its own "inner environment". Through this process, energy flow, and the passage of material and information within an organism are adjusted to appropriate levels. Body temperature is the result of energy addition and subtraction, while body mass is the result of a balance between the addition and removal of material. In 1939 in his book "The wisdom of the body", W.B. Cannon coined the term "homeostasis" to describe this regulation of body state. Physiology is the realm of biology concerned with investigating these kinds of regulated processes in organisms. Transposed to an analysis of the controlled conditions within a honeybee colony as superorganism, or" a mammal in many parts", sociophysiology is concerned with which regulatory quantities in a honeybee colony are adjusted homeostatically, how these are carried out by the bees, and the purpose this all serves (▶ Chaps. 6, 8, 10).

The physiology of mammals, and the sociophysiology of honeybees have arrived at remarkably similar interpretations. Comparable life strategies, evolved independently in different groups of organisms, are described to be analogous or convergent. The wings of a bird and those of insects are an example of such an analogy. The common problem, for which the invention of wings represents a solution, is "movement through air".

Given the common features shared by mammals and honeybees, we are led to ask: "What was the common problem to be solved by this collection of convergent strategies?". It is apparent that all these features allow mammals and honeybees a degree of independence from the environment, achieved by hardly any other groups of organisms. This independence does not necessarily extend over the entire lifespan of each individual, but rather is limited to particularly vulnerable stages in the life cycle of the organism (▶ Chap. 2).

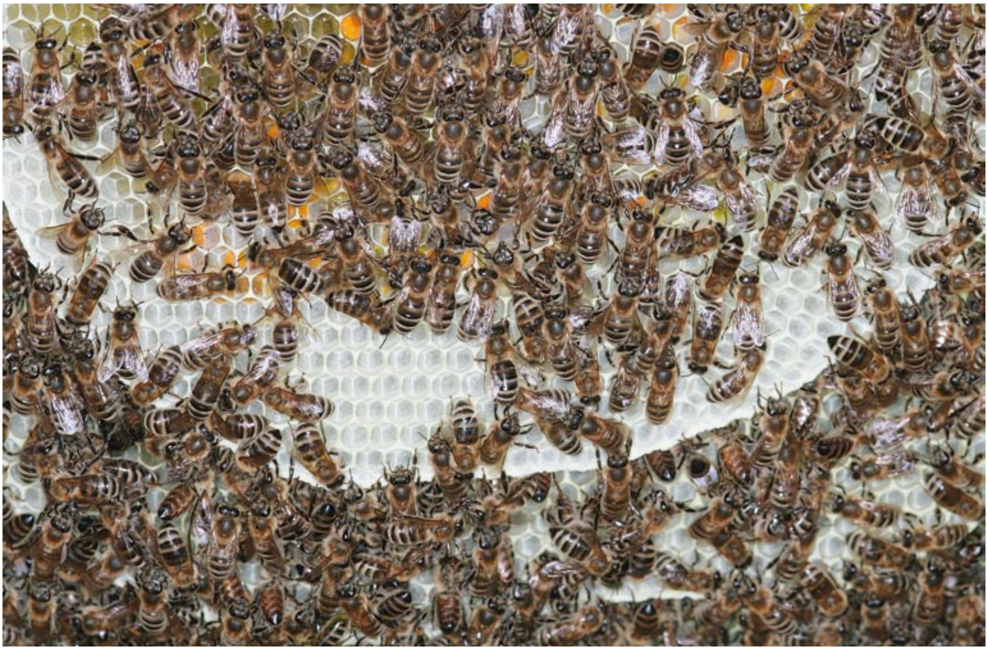
Honeybee colonies employ strategies remarkably similar to those of mammals, and raise relatively few, but extremely well-prepared and carefully protected reproductive individuals to release into the world. To this end, honeybees have developed specific abilities and behaviors that belong among the most amazing in the living world. We are only just beginning to understand this highly complex tapestry.

Man's Smallest Domestic Animal—a Picture Guide

Honeybees are not only fascinating models of evolutionary success; their pollination activities result in them being of considerable economic importance to man.

Honeybees …

… have the scientific name *Apis mellifera*, which means "honey-carrying bee"



… live in colonies of about 50,000 individuals in summer, and about 20,000 in winter

… visit flowers to collect nectar and pollen. They make honey from nectar; pollen is a protein-rich source of nourishment

… transport nectar in a crop, a special part of the gut, and carry pollen in small “baskets” on their hind legs

… build combs from wax that they produce from glands. They store honey and pollen in the six-sided cells of the comb, and also use comb cells as a nursery for their young

… serve mankind foremost as pollinators of crop plants

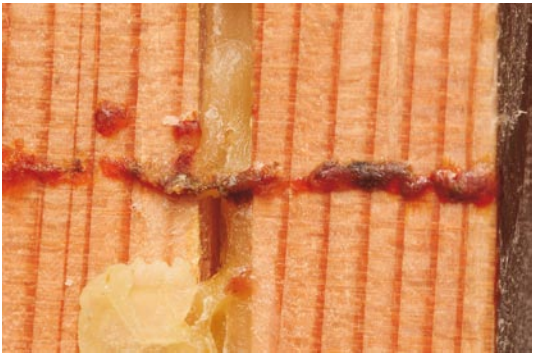
… are kept by humans in artificial hives from which the honey, pollen, propolis, and royal jelly are harvested

In the colony, all worker bees are sterile females

Male bees, or drones, serve only for reproduction, i.e., to mate with the females

Each colony has only one queen, easily recognized by the longer abdomen

Bees collect resin from the buds, fruit, flowers, and leaves of plants to make a caulking resin, called “propolis”, which they build into the hive. Humans use propolis from beehives for medicinal purposes



A queen bee lays only a single egg in each comb cell, but up to 200,000 eggs each summer

Bee larvae hatch out of the eggs, grow, and when large enough, pupate in the cells

Female bees develop from fertilized eggs, the larger male bees from unfertilized eggs

Worker bees pass through many occupational stages in their lives, for example, as cleaner bees, builder bees, brood care bees, and guard bees. Having reached seniority, they leave the nest as foragers

Brood care is the task of bees living within the hive

Foraging is the task of the bees that fly out of the hive

Honeybees communicate with one another through various chemical and tactile signals. The dance language is an important part of their communication system

In summer, the bees raise several young queens in specially constructed cells, and feed them a special diet. Young queens mate only once in their lives, during their nuptial flight, but with many drones

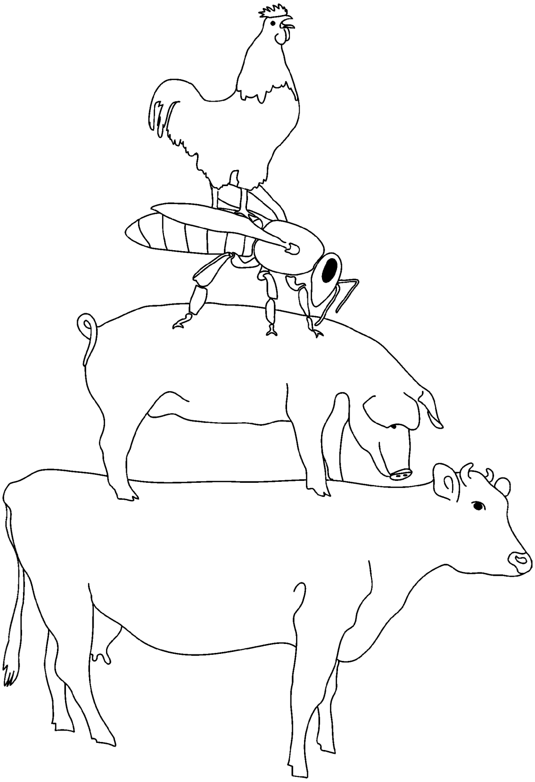
Honeybees feed their queen during her whole lifetime exclusively with royal jelly, and assign court bees to provide her with particular attention and care

Honeybees swarm to propagate their colonies. The old queen leaves with a large proportion of individuals from the original hive

Honeybees survive the winter as a complete colony. The bees collect together in a dense cluster, and keep themselves warm by vibrating their wing muscles. They use honey stores as energy source for this activity

Honeybees defend themselves with their stings

Through their pollination of crop plants, honeybees are the third most valuable domestic animal in Europe



The honeybee is the most important agent in the maintenance of flowering plant diversity

1 The Inevitable Honeybees

Honeybees must have evolved under suitable conditions.

The development and dispersion of life on our planet has been taking place according to unchanging principles since its very beginning, an estimated four and a half thousand million years ago. Following a set of basically simple rules and easily understood recipes, an organismic world of breathtaking diversity and incredible complexity has unfolded.

The driving force for the dynamics of this explosion of life is the "will to survive", in which "survival" is to reproduce faster than the competitor. Reproduction, from an abstract point of view, means making copies of oneself. When using the term "copy", one really implies "clone". For only in this sense in the world of the living can the hereditary material produce true copies of itself. Nucleic acids, macromolecules that are assembled from a large number of links to form a chain, have prevailed as the only hereditary material. Each link in this chain consists of four different organic bases, a sugar and a phosphoric acid. Should any of these bases be freely available in the environment, and close to an existing chain, it will bind specifically with only one of the other base types, known as its complement. When all the bases in the chain are bound, each with its specific complement, a "negative" replica of the original is the result. Separated from the original template, this "negative" will produce a perfect copy of the original chain when complementary bases bind to it.

Following the development of these types of molecules on earth, and their dominance over possible (but to us unknown) alternatives, an exciting perpetualism arose: copies of copies constructed an unbroken line of hereditary material over thousands of millions of years, extending to the organisms living today.

It is not difficult to imagine that those molecules that were making copies of themselves were already in competition with one another for basic resources for their replication. Raw materials were scarce even then, and became more so the greater the demand for these became. Molecules that enlisted enzymes to enable a quicker and more efficient construction of copies overhauled competition. To develop novel molecules, however, copying should be precise but not totally free of mistakes. A tolerable level of errors in copies guarantees the chance of variability. Without this, there can be nothing new.

Nothing has changed over the millennia. Mutations traced to errors in copying are an important source for the appearance of new living forms. Through the continuous production of new "versions" that are either disadvantageous and so vanish quickly, or that survive because they are useful, a wealth of variation in nucleic acids has resulted. These different chains contain the instructions that constitute the genetic information, or genome, of particular organisms, and that lead to the huge diversity of living forms.

It cannot be ignored that after the scarcely imaginable time of more than 4,000 million years, the world is crawling with nucleic acid molecules, the chains of which have links that are arranged in very different combinations. These chains do not exist free in the environment, however, but have "acquired" highly variable forms of "packaging". What is the reason for this sequestered existence of nucleosides, hidden deep within the organisms? It is by no means a shy retirement. Rather, these nucleic acids are continuously and boldly occupied with improving their own performance relative to that of similar nucleic acids in direct competition. How does the "packaging" help with this?

Life Gets Complex

If we look for features that arose through evolution from the original naked and self-reproducing hereditary material (the nucleic acids) through to the present forms, the following is evident:

- ever more complex structures appear over time
- the structures achieve more as a whole than do the single elements of which they are constructed

- the structures can determine the behavior of the elements of which they are made

The hereditary material itself becomes in no way more complex. The three statements above summarize the apparent tendency in evolution for the development of the "packaging", or so-called phenotype, of the organism that the hereditary material (the "genome") uses to carry it into battle with other organisms, and "survive and reproduce more successfully than the competitor".

The first cells representing an early, complex form of organization were formed about 3,500 million years ago, and included a number of important functional elements, although the genome was not enclosed in a nucleus. These were free-living, independent cells that took the material and energy they needed for the reproduction of their genome from the surrounding environment. Free-living single cells exist today, and play an important part in the natural economy. These are the bacteria, and as unicellular organisms, they have remained at this basic stage of evolution and can obviously compete with multicellular organisms. Otherwise, they would no longer be there. The evolution of multicellular organisms first began about 600 million years ago, about 3,000 million years after the unicellular life forms. In this next great leap, the originally independent unicellular organisms banded together into multicellular beings. Entering this next level of complexity, cells did not at first give up their separateness, but merely lived alongside one another in colonies. Through this "accident", the advantages of two critical properties were "discovered": the division of labor, and cooperation. Thus, a "vehicle" arose with features that the molecules of the genome could better use for the reproduction of their own diversity. Through the aggregation of available building blocks, complex structures were developed. This is unarguable. But why should complex body forms have an advantage? And if so, what are these?

One clear advantage lies in the opportunity to delegate different tasks to different single elements. This kind of specialization then permits different problems to be solved simultaneously, rather than serially, which is the case with unicellular creatures. The moment specialists arose, such as the different cell types in multicellular organisms, so did the possibility of integrating their activities, opening radically new avenues for interaction with the environment. This was clearly a highly successful step, because multicellular organisms determine the present appearance of the living world.

Planned death came with the arrival of multicellular life forms. The vehicles that the genomes had created in the form of multicelled organisms were mortal. One may think that this was not a good beginning for a long-term competitive struggle for survival. The way out of this dilemma was to protect a small proportion of body cells from death, and use these to establish the "eternal" line of copies, thereby trading off the gain in efficiency provided by the multicellular organization against their limited lifespans. Many-celled animals, therefore, delegate the transfer of the genome to specialized cells, the male and the female germ cells. From these, the lineages that bind generations over time arose, and passing on the genome became independent of the death of their carriers.

The construction of complex subsystems from stable elements therefore led to multicellular organisms, and a solution to the problem of genome mortality.

The Germ Line

The evolutionary quantum leaps described above have one factor in common: the molding of basic and available building materials into ever newer and more complex structures. New levels of intricacy were added, and each of these added possibilities in the world of the living that were previously unavailable. Following the logic of organizing elements into ordered substructures, the next quantum leap would be the creation of even more complex systems by the aggregation of individuals into superorganisms (Fig. 1.1). An observer, having understood the first steps in this evolutionary progression on earth, may have predicted the appearance of the superorganism. This step had to occur sooner or later. The only condition was the availability of appropriate raw material. To follow these thoughts further: at some time, the superorganisms themselves will band together to form the next level of being that would dominate the superorganism. Evolution has not proceeded this far—yet. Will it ever? There are signs—in

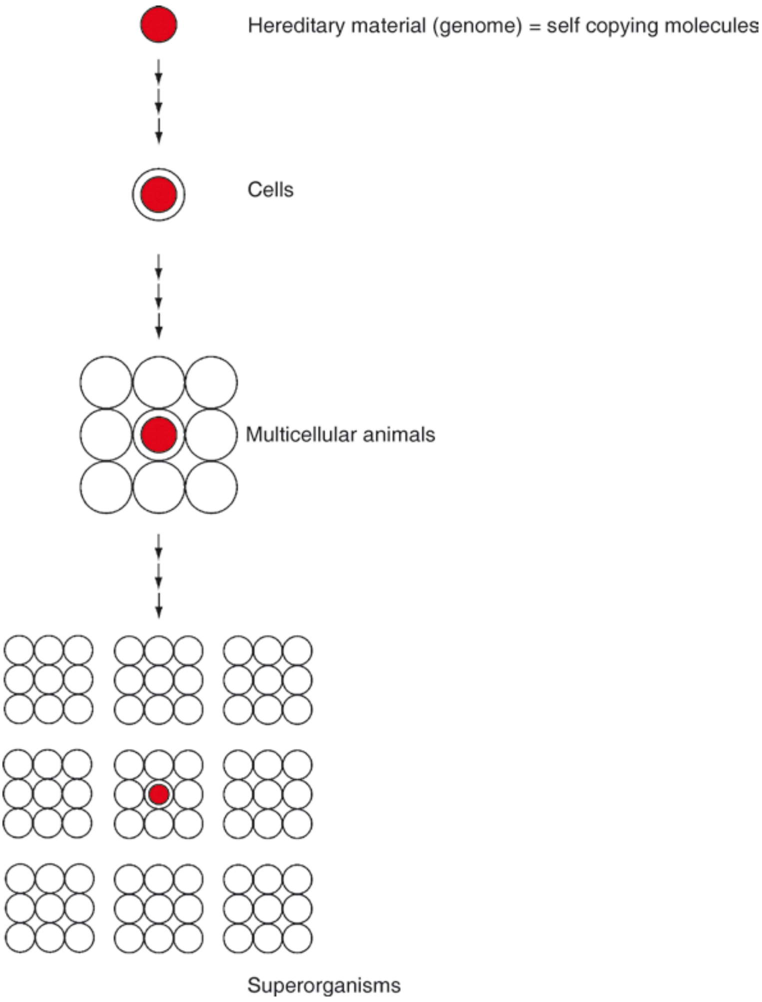


Fig. 1.1 Significant quantum leaps in the evolution of complexity in organisms. An unbroken line of elements that arise from copies, and continue to live as copies (shown here as *red circles*) could exist without interruption from the beginning of life to the present day. Initially, single cells carried the eternal line in their nucleus, passing the genome on from generation to generation. When these single cells came together as organisms, they surrounded themselves with ever increasingly complex, mortal structures, but the line was continued by their germ cells. Superorganisms, such as honeybee colonies, arose from single organisms, in which only the reproductive queens and drones were responsible for the continuation of the germ line. In single organisms, the somatic cells form the support system; in the bee colony superorganism, this role is undertaken by the worker bees. *Unfilled circles* in the diagram represent the elements that are not able to make copies of themselves, but were developed to support those that can

particular, species of ants—that the required developments could already be underway.

The Superorganism

Honeybees, as they appear today with a history of about 30 million years, were almost inevitable. They had to "happen" at some stage. The details of their body form could have differed; they did not have to look like our present-day honeybees, but there is no competitive alternative to the basic organization of the "honeybee colony superorganism".

Honeybees could nevertheless "happen" only because they brought the necessary conditions with them. To theoretically propose the appearance of a superorganism is one matter, to actually find it is something else. Superorganisms of notable significance in the natural world are found, with the exception of the taxonomically separate termites, only in the hymenopterans and more specifically the ants, honeybees, bumblebees, and wasps. The answer to what the required conditions are for the appearance of a superorganism will be described in Chapter 9. For now, we will interest ourselves in the present, and put off our consideration of the past for later.

In the honeybee colony superorganism, we have a highly complex system, but like more simple systems, it is merely the vehicle for the genome. Even in this refined packaging, the genome "pursues" the same goal as that of molecules in the primeval soup, namely, that their proliferation be more successful than that of the competitor. Molecules are, of course, not actually "pursuing" a goal. But if one observes the flow of the evolutionary process, elements that survive behave as though they have actively followed the goal to repeatedly copy themselves. This expression is a description of the process, but we simplify the concept by using anthropomorphic terms such as "… the molecules strive toward …", or "… they want …", or "… they have a goal …".

Specialized individuals in superorganisms adopt the role of handing on the genome, just like the germ cells in multicellular organisms. Colonies are created with a few sexually active individuals concerned with the direct transmission of the genes, and a majority of individuals that do not reproduce, but carry out important tasks in the upkeep of the colony, such as the rearing and quality control of sexually active individuals.

Can the more complex structures, as maintained above, really achieve more than the single elements of which they are constructed? And is this also true for honeybees? Complex structures, because they are made up of elementary units, possess more components than do more simple ones, and hence the possibility of an interaction of the components within them. For this reason, complex structures under certain conditions exhibit properties that cannot be explained by the properties of their single elements: that the whole can at times be more than the simple sum of its parts was known and expressed already by Aristotle. So it is that, on the basis of information flow between all individuals, as a single unit a honeybee colony is able to "make decisions" that autonomous honeybees would be unable to make. The gain that the honeybee colony has acquired through the collection and fusion of the different abilities of individuals is presented in detail in Chapter 10, "The circle closes".

Can a complex system really influence and determine the properties of its own components? This, too, is relevant for honeybee colonies. The characteristics of individual honeybees are determined by living conditions that, in turn, are controlled by the honeybees themselves. Chapters 6 and 8 cover in detail these options that are essential in the biology of honeybees.

2 Propagated Immortality

The biology of the honeybee is constructed around using energy and material from the environment, and organizing these to ensure the propagation of daughter colonies of the highest quality. This insight is the key to understanding the amazing achievement and performance of honeybees.

Reproduction and sex are two different and essentially independent processes. Reproduction can occur without sex, and sex without reproduction. Reproduction is duplication. The simplest way to achieve duplication is through cell division. Sexual procedures, on the other hand, are based on the fusion of germ cells from two differently sexed individuals and lead, through these combinations, to an increase in diversity in a population. This diversity is important, because it offers the process of selection a broad palette of possibilities from which to choose and maintain an evolutionary progression. Mutations in the genome have the same effect, but these cannot be induced, and they occur and are allocated randomly. Sexuality is not dependent on such chance, and results with certainty in new types with every fertilization.

As a rule, higher animals couple their reproduction with sex, so that an independence of sex and reproduction may not appear to be feasible. However, sex without reproduction is practiced by unicellular life forms: two unicellular organisms fuse with one another, exchange genetic material, and then separate. The result of this fusion is again two unicellular organisms, so no reproduction has occurred, but due to the exchange of genetic material, genetically novel types arise and consequently the diversity in the population is enhanced.

Reproduction and Sex

Due to their unusual reproduction and sex, honeybee colonies, and colonies of related stingless bees of the tropics take a special place in the animal kingdom. Normally, sexually propagating animals pair with one another, and the offspring from this coupling, given the opportunity, also propagate and so raise the next generation.

Honeybees, however, are different.

Let us undertake a small thought experiment: if all the infertile individuals in a honeybee colony were suddenly made invisible to an observer, a single lonely female, the queen, is all that would be seen in the entire hive. Once a year, this female would raise one to three daughters that, 1 year later would, either in the old hive or in some new place, each propagate in the same way. Each summer, thousands of male bees, the drones, would appear and leave the hive to mate with the young queens from neighboring hives (Fig. 2.1).

From this point of view, the sexual behavior and propagation of honeybees would be unremarkable were it not for the surprisingly small number of reproductive females, the fact that these females live for many years, whereas the males are present for only a short period, and that there is an extreme imbalance of females to males. Also remarkable is that successive generations of reproductive females are separated by alternating short and much longer time periods.

Two to three daughters per propagation period is remarkably little, compared to other insects where a single female can produce up to 10,000 fertile offspring, subdivided approximately equally into males and females. Female animals are clearly more valuable in the propagation process than males, because males are the source of the cheap, mass-produced sperm cells, whereas females provide the comparatively small number of expensive egg cells. From a purely technical point of view, very few males in any population would be sufficient for the fertilization of all the females.

This makes the situation that we find in honeybees, with so few females and so many males, even more surprising. The reverse condition would be easier to understand, because a few males could produce enough sperm for the fertilization of all the egg cells. The regular succession of short and long periods

Fig. 2.1 If all the sterile bees in the nest were made suddenly invisible, only the queen, and now and then a couple of drones would be seen, as in this picture

between the appearance of fertile females, the queens, is also a cause for wonder. Into a given time period, most other animals pack as many generations as their physiology and the environment allow. Why have honeybees chosen this unique path?

The rearing of so few female offspring is, in many respects, extremely risky. According to Charles Darwin, an overproduction of many different offspring is an important requirement for evolution. This is modest in honeybees, and it follows that there is only a limited palette of honeybee variation, providing the process of selection with only a small number of possibilities to choose from. In addition, the small number of offspring could be destroyed entirely, and their genes would vanish from the gene pool.

However, animals that take intense care of their progeny, and thereby provide them with a safe start in life, often have few offspring. In optimal cases, the parental care extends up to the sexual maturity of the young. Secured and protected, the progeny carry the genes of the population more certainly into the next generation, compared to those that are abandoned at the mercy of the environment. In this context, one is reminded of the large mammals in which pregnancies result usually in the birth of only one or two offspring, but these receive continuous care over a long period—the smaller the number of young, the longer and more care they receive.

Is the situation comparable in honeybees? This is indeed the case, and honeybees employ an impressive system of optimal care of long duration for their young fertile females.

But to return to our experiment: if we now allowed all infertile honeybees in a colony to be seen, the hive would suddenly be populated by many thousands of sterile females (Fig. 2.2).

Daughter Colonies

The many sterile female honeybees offer the queen a safe environment, and provide each new young queen with a dowry of a complete colony when the old queen leaves the nest, with about 70% of the worker bees. The young queen remaining in the hive, the reproductive daughter of the old, departed queen, receives a gift of not only a third of the worker bees, but also combs filled with honey, pollen, and developing larvae. One cannot imagine a better start to a queen bee's life.

A single honeybee colony can supply more than a single swarm. After the departure of the primary swarm, there are often enough bees remaining in the nest for these to be subdivided again between two young queens. Should this happen, the secondary swarms that gather around each of the queens are then not as large as the primary swarm. Their ability to survive depends on their size; the chances of survival of very small secondary swarms are slender.

The production of a very small number of reproductive females in honeybees is reflected in the division of the hive into very few daughter colonies, each grouped around their new queens.

Reproduction by establishing a complete daughter colony is an unusually extravagant strategy, and within the insects is known to occur only in honeybees, stingless bees (which adopt the role of honeybees in the tropics), and some ants in which reproduction takes the form of a nest division.

Fig. 2.2 A fertile queen, many sterile female workers, and a large number of drones at mating time are the "building blocks" of the bee colony superorganism

Swarming takes place in the period from April to September, depending on geographical latitude. New queens are produced when the development of individual numbers in the hive has reached a maximum, and enough brood is available to replace the loss of adults in the original colony after the primary swarm has departed. Preparations for swarming can be recognized 2–4 weeks before this dramatic departure, by the construction of queen cells that hang like small open thimbles from the lower edge of the combs (Fig. 2.3).

These small cuplike cells can be present for long periods in the colony, but eggs are laid in them only during the preparation for swarming. As many as 25 of these cells with potential queens have been found in a colony, but most of these will not survive. The time to swarm arrives when the first of these larvae is large enough to have its cell closed by workers, and enter the pupation phase. The old queen leaves the nest a few days before the new queen emerges in the darkness of the hive.

Immediately before departure, the workers that will accompany the old queen fill their crops with honey from the stores in the nest (Fig. 2.4). These provisions will last at most 10 days, a time span during which it is essential to find a new nest site, and to reestablish a regular colony life.

Shortly before leaving the hive, swarming bees run about in an agitated fashion, produce high-frequency vibrational signals, and animate the swarming queen by biting and pulling on her legs and wings. A torrent of honeybees begins to flow out of the hive (Fig. 2.5), filling the air around the nest with their buzzing as a large cluster forms nearby (Fig. 2.6), which will serve as the base from which the search for a new home will begin. The swarm cluster contains a good cross section of the individuals that belonged to the original hive, although the very young and oldest bees are left behind.

Should the original hive containing the new queen be insufficient to sustain further division after the departure of the primary swarm, the worker bees in the hive destroy any remaining queen cells, including the larvae within these. Once the hive has reestablished its size, they will begin again to rear new larvae in queen cells.

Propagation via a few but complete and fully functional daughter colonies has dramatic consequences for the entire life of

Fig. 2.3 The colony constructs new queen cells as the first step in preparation for swarming. Several queen cells are established along the lower margins of the combs

Fig. 2.4 Worker bees fill their crops with honey before swarming. A new home must be found and occupied before these supplies are exhausted

honeybees: the process bestows on them a potential immortality, and enables the release of complete colonies as "immortal copies" into the world.

The resulting daughter colonies will not, however, end up as genetic copies of one another. Each new superorganism possesses its own genetic makeup. The individuals in a colony are all

Fig. 2.5 Swarming bees literally "flow" out of their nest

Fig. 2.6 The swarm settles near the old nest, and sends out scouts to search for a new home

children of the same mother. Only those genes that the mother carries—in her eggs, or in the male sperm in her sperm storage gland—can be present in the children making up the genetic profile of the colony. Even if the new queens were identical twins, they could not produce colonies with the same genetic makeup, because the suicidal mating behavior of the males, in which the male mates once and then dies (▸ Chap. 5), ensures that the offspring of two queens will never be the same.

That part of the colony remaining after a swarm is, of course, identical to the one that left, because they all descend from the same, now departed, mother. This changes the moment the new young queen begins to lay her own eggs. Once all the original individuals have died, the changeover to a new genetic makeup is achieved. A honeybee colony that has occupied the same nest over an extended period of time therefore will have changed itself, like a genetic chameleon, with each new queen. The superorganism is the same, and yet not the same.

The primary swarm of the old queen, on the other hand, retains its genetic makeup until the time comes for her to be replaced.

The Life Cycle of the Superorganism

Each generation of multicellular organisms passes through a life cycle that consists of four stages: the cycle begins with the single-cell stage, usually the fertilized egg cell. A second stage of growth and development follows. The third stage begins with the advent of sexual maturity. The last stage, often coincident with the third stage, is the period of reproduction. The four stages constitute a single generation. The time taken for subsequent generations within animal species can vary, because the individual stages are dependent on the environment. The seasons, and the associated climatic conditions with their direct and indirect influences, are a powerful factor in determining the duration of a generation.

The individual generation time of a honeybee queen, starting with the embryonic development of the egg and extending to mating, takes at most 1 month. But this does not mean that a new generation of queen bees is produced every 4 weeks, because their generation time is complicated by being divided into alternating phases of different lengths: an initial phase of 1 month, and a second phase that has a duration of almost a year. One month is the actual generation time from the laying of the egg destined to become the new queen, to the successful mating of the new queen. The second phase of the generation time, nearly 1 year, lasts until this queen lays an egg that will become a new queen from whom the next generation will develop. In this fashion, a rhythm is established in which successive queen generations are separated by periods of very different duration.

This alternating sequence of generation times is a strategy possible only in superorganisms: the queen continuously produces eggs that develop into females. These remain sterile. Reproductive females are produced only when they are needed, by worker bees feeding a special diet to larvae housed in queen cells. Worker bees can raise new reproductive individuals at almost any time, because except for a few weeks in winter, there are always larvae present in the hive. Usually, new queens are raised once a year, and after their short development from egg to mating, will then lay eggs throughout the long summer.

The worker bees in the colony therefore determine the dynamics of the successive generations, actively manipulating the temporal rhythm of the generations, and extending the temporal pattern of a physiologically short queen generation time into a rhythm with a period of 1 year. This manipulation enables honeybees to couple the generation time of the reproductive animals to the rhythm of division and separation of the colony by swarming. The division of the honeybee colony into daughter colonies is carried out at the level of the entire colony, and leads to a different and simpler cycle than that of single organisms. The colony circumvents the single-cell stage, and also does not exhibit a true growth stage. Only the size of the colony undergoes changes that are associated with an increase or decrease in individual numbers over the seasons: a buildup of numbers in spring, a (strongest) decline through swarming in early summer, and individual die-off in winter. In principle, the colony is able to divide almost all the time. However, certain preparations have to be made before this step can be taken.

Why don't most other multicellular animals go the same way? Why don't they just divide like unicellular organisms do?

The development and differentiation of elements in a multicellular organism, starting from the single-cell stage, is a costly and complex process. Achieving immortality through a simple and even division of these highly specialized individual cellular components is not like subdividing between essentially similar and physically separate bees in a beehive. Nature did not avoid complicated sex by producing dividing and immortal cats, because this is technically far too difficult.

Genetics provides an explanation for the general preference for a four-staged life cycle. As we have already explained, reproduction coupled with a sexual process increases diversity in a population, an essential condition for evolution and recognized by Darwin. Sex, and the specialization of a few body cells for propagation in multicellular organisms, nevertheless brings with it the death of all other body cells. The division of labor into germ cells and body cells that we find in multicellular organisms brought the principle of death onto the stage of life, not through accident or misfortune, but as a programmed and general principle (▸ Fig. 1.1).

Honeybees have found an ideal way for themselves in this difficult evolutionary landscape. They have achieved one advantage without losing the other, reproducing the entire colony by simple division (swarming), and simultaneously raising reproductive individuals whose generation time is synchronized with the cycle of this division. By retaining the reproductive individuals, they have safeguarded the option of genetic variability. Honeybees therefore avail themselves of the continuous germ cell lineage, like all other sexually reproducing animals and plants (▸ Fig. 1.1). In contrast to other multicellular animals, they enclose these immortal germ cell lines in a likewise immortal superorganism, the colony. The strategy of reproducing the colony by division has the consequence of simplifying its life cycle and making it, in principle, immortal.

The principle of becoming immortal through binary fission is therefore found in the simplest life forms of unicellular organisms, and also in the most complex, the superorganisms.

Death and Immortality

As humans, we are proud of the ancient establishment of our cities, marked by a history of thousands of years and 500-year anniversaries. Of course, the original houses and streets are no longer there, nor the same citizens, but at least the settlements and geographic locations that have been continuously occupied as units. Honeybee colonies are a continuous unity in the same sense.

The eternal bee colony is made possible through an ongoing replacement of its members. Worker bees are replaced every 4 weeks to 12 months, depending on the season, and the queens every 3–5 years. Drones survive only 2–4 weeks, and are as short-lived as many of the workers. In a colony of 50,000 bees, and with a daily death rate of 500 individuals, this amounts at a daily replacement of 1% to a replacement of the entire colony, with the exception of the queen, within about 4 months. This continual change does not alter the genetic identity of the colony.

The genetic makeup of the colony is completely changed, though, when a new queen becomes responsible for the offspring. This step is the beginning of the creeping "genetic death" that occurs at this time in a colony. The new queens are, in their eggs and in the sperm of the drones with which they have mated, equipped with a new genetic constitution, and this is true for all their offspring, which over time populate the colony and replace the original bees. This changeover occurs regularly when a new young queen is raised, and the colony divides by swarming. The same genetic renewal and reconstitution of a colony takes place when, in an emergency (such as the accidental death of the queen), the colony is compelled to rear a new queen from available larvae (Fig. 2.7). This backup also allows the colony to replace an old queen, now ineffective, by a new queen that, during her mating flight, will gather new sperm and begin to rear worker bees. A honeybee colony residing at a single locality, and that changes queens each year through the natural swarming behavior, changes

Fig. 2.7 In answer to an emergency, additional queen cells are hurriedly constructed in the brood nest

its genetic "color" each year. The potential immortality of resident colonies would raise a problem for colonies new to the area, and for which there is no suitable space. In practice, however, this does not arise. Diseases, parasites, plunderers, famine, water shortage, or real catastrophes such as forest fires have a regulating effect, leading often enough to the end of a potentially endless existence, and leaving room for newcomers. The chances of survival of swarms leaving a colony are also not very high. About every second swarm fails to establish a new colony, particularly where a weak secondary swarm is concerned, and when these are surprised by bad weather (Fig. 2.8). Those swarms that do survive the first season, however, have a good chance of continued existence.

The Organization of Materials and Energy

The slow but continual departure of numerous, fully functional daughter colonies has its price for the founding colony.

The creation of daughter colonies is not undertaken as a side issue, and the entire biology of honeybees is focused on exploit-

Fig. 2.8 This swarm did not find a home in time to escape a storm

ing the material and energy from the environment, and manipulating these to produce daughter colonies of the highest quality. This is the key to understanding the nature of the honeybee's capabilities and performance.

Honeybees leave behind the self-sufficiency and protection of their nests to gather material and energy to keep themselves alive, and to prepare for and carry out the division of the colony each year.

How do honeybees manage the flow of this material and energy through a colony?

All earthly life is dependent on the sun. This provides plants with the power to capture and fix energy from the sun, and synthesize organic matter. The resulting plant material, and the energy stored in it, is then used by animals. This is particularly true for the maintenance of a bee colony, and for the production of daughter colonies. For this, honeybees are entirely dependent on flowering plants (Fig. 2.9).

Flowering plants are not unilaterally exploited by bees. Flowering plants and bees support one another in the most important task of all living forms, that of propagation. Bees that visit flowers carry pollen from one to the other, and so perform the sexual exchange necessary for the flowers to develop fruits containing seeds. The daughter colonies are the "fruit" of the bee colony, the

Fig. 2.9 Honey is the solar energy source in the darkness of the hive. Solar energy is captured by plants, and chemically transformed into the sugar of nectar. Honeybees take the nectar into the nest, and store the chemically bound solar energy as honey

production of which depends on the harvested nectar and pollen. To extend this obviously highly simplified analogy with plants, the reproductive individuals embedded in the daughter colonies are the “seeds” of honeybees (Fig. 2.10).

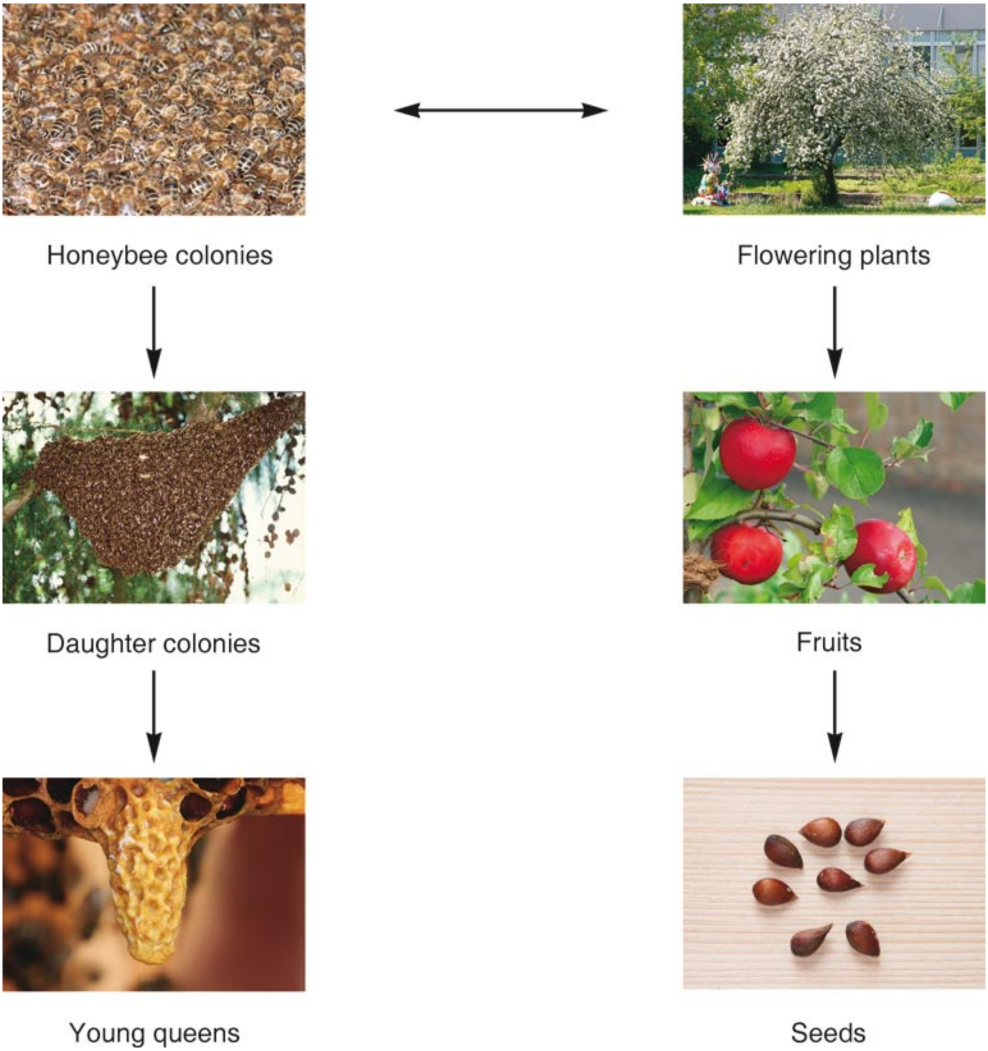


Fig. 2.10 The biology of bee colonies and many flowering plants are tightly interwoven. Bee colonies produce daughter colonies with young queens carrying the female germ cells. Flowering plants produce fruit containing seeds. The uninterrupted flow of material and energy from the flowers to the bee colony enables the continuous replacement of the members of the hive, and thereby an “eternal colony” that brings forth a perpetual stream of daughter colonies

3 Honeybees—a Model for Success

Although a relatively species-poor group of animals, honeybees exert an extensive influence on the biotope.

Species diversity amongst honeybees is remarkably small. Only nine species of the genus *Apis* are known, not exactly a record for insects. These are grouped together with the bumblebees into the family of true bees (*Apidae*). Eight genera of honeybees live in Asia, while only one species, *Apis mellifera*, is present on the two continents of Europe and Africa. There they have formed many races that can interbreed with one another. *Apis mellifera* has been secondarily distributed worldwide by mankind.

Only a single species throughout two continents conjures the picture of an unsuccessful and insignificant fringe group. It would be a mistake, however, to dismiss honeybees as an unimportant fringe group because of their extremely small species diversity. One only has to consider what the similarly species-poor group, *Homo*, has contributed to the appearance of our globe. The nature and extent of the human role is comparable with that which honeybees have had in the domination of the world's vegetation by flowering plants (Fig. 3.1).

From Destruction to Gentle Pollination

Flowering plants have existed for about 130 million years. Initially, the wind alone was the "postillon d'amour", and the sexual exchange was somewhat inefficient, requiring huge amounts of pollen that were dispatched on an uncertain, and in most cases unsuccessful journey. In wind-still areas, this did not work at all.

Fig. 3.1 The almost inconceivable diversity of flowering plants stands in stark contrast to the very few species of honeybees that will pollinate them

A significant advance accompanied the discovery of pollen as a source of nourishment by insects, which then simply devoured the pollen-bearing anthers (Fig. 3.2). By feeding on the anthers of a number of flowers, enough pollen was transported from the anthers of one plant to the stamens of neighboring plants. This somewhat cavalier treatment of flowers is still practiced by rose beetles to the present day.

From the plant's point of view, a more satisfactory situation would be the reliable transport of pollen between blooms, but without collateral damage. In honeybees, flowering plants have found a partner with whom they have reached close to an ideal relationship after a long co-evolutionary period.

Christian Conrad Sprengel was the first to describe this partnership in a wonderful book in the year 1793. He entitled his

Fig. 3.2 Rose beetles are today as cavalier with flowers as insects were at the beginning of their association with plants: they devour them. The head shield of the rose beetle forms a scoop to gather the anthers together, before cutting down as many of them as possible

book “Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen” (The discovered secret of the nature of the construction and fertilization of flowers). As much as we now admire his genial insight, Sprengel himself gained little from his efforts. His opinions remained completely ignored by the professional world, and indeed were attacked because of his “immodest” accounts on the sexuality of innocent flowers. Stimulated by Sprengel’s writings, no lesser man than Charles Darwin himself experimented in 1860 with flowering plants that he covered with nets to exclude pollinating insects. When he saw that, in contrast to the uncovered control plants, these failed to produce fruit, he came to the obvious conclusion.

The pollination system developed by flowering plants has resulted in a dependency on insects that choose between various offers, like at a marketplace in which flowering plants compete for their customers.

As suppliers, plants differ in the quantity and quality of nectar they offer their visitors. Pollen content also varies from flower to flower. Even the temperature of the nectar may be an important criterion of quality that plants exploit. Bumblebees (Fig. 3.3), at least, prefer flowers with warm nectar, and obtain direct physical warmth in addition to chemical energy in the form of carbohydrates. It is suspected that, given the choice between nectar at different temperatures, honeybees will not behave any differently than bumblebees, and will prefer flowers that offer warm nectar.

Many of the “cries” of these vendors at the flower marketplace are focused on the visual and olfactory world of honeybees. The necessity of offering the bees something particularly attractive increases with the number of competitors all blossoming at the same time where the bees forage. What is particularly attractive to honeybees is determined by their powers of discrimination, and the extent of their “intellectual” abilities. In Chap. 4, we will consider these in detail.

With the advent of clearly less destructive pollinating insects, plants relocated the germ cell-bearing parts of their flowers to shielded interiors, to protect these and their products from wind and weather, and from devastation by pollinators for whom pollen is merely a source of nourishment. With this came flowers having unusual visual and olfactory properties that serve to attract the desired customers.

Fig. 3.3 A thermocamera image of a bumblebee collecting nectar from a Compositae flower. Bumblebees, and probably also honeybees prefer flowers with warm nectar

Honeybees are the most important pollinators in most regions of the world where flowering plants exist, but are by no means the only insects that play this role. Flies, butterflies, beetles and other hymenopterans related to bees, such as solitary bees, wasps, bumblebees, and even ants can pollinate plants. Very few flowers are dependent on a single insect species, although no other pollinators are as effective as are honeybees. In all, 80% of flowering plants worldwide are pollinated by insects, and of these about 85% by honeybees. As many as 90% of fruit tree flowers are dependent on honeybees. The list of flowering plants pollinated by honeybees includes about 170,000 species. The number of flowering plant species that are dependent on honeybees, and without which they would fare badly, is estimated to be about 40,000. This worldwide sea of flowers is pollinated by just nine species, and in Europe and Africa by only one, which is indispensable for most flowering plants. This extreme numerical imbalance between plant clients and pollinators is remarkable, and suggests that honeybees are so successful in this area as to leave little room for the coexistence of similarly occupied competitors.

This is globalization and monopolization in the animal world.

And, indeed, the honeybee colonies with their enormous diligence can teach their competitors a lesson. A single colony of honeybees may well visit several million flowers on a single working day. Because the bees inform one another about newly discovered areas of flowers, visits to all flowers are rapidly achieved. Hardly a single bloom remains unattended. Bees are also generalists that can cope with just about all flower types, so that all have the same chance of being visited by bees.

The high amount of flowers visited, the rapid recruitment of an appropriate number of foragers, and the enormous adaptability of single bees, and of the entire colony to the continuously changing flowering "situation" in the field make honeybees ideal partners for flowering plants. Flowering plants have done their best to make themselves interesting for honeybees. Losing pollen to visiting insects was nothing new to flowers, but bees at least are gentle—the pollen simply sticks to the thick tufts of branched hairs covering their bodies (Fig. 3.4).

These reliable and considerate pollen transporters enable these flowers to produce far less pollen than those that depend on wind pollination, and certainly less than those depending on flower-eating beetles.

Because the flowers then limited their production of pollen to a minimum, during their evolution bees developed equipment that enabled an efficient collection and transportation of pollen that had clearly become scarce. The fore, middle, and hind pairs of legs work together to produce firm pollen packets in a manner that would do justice to every automatic harvester. At the end of the process, a massive ball of pollen is fastened to the outside of each hind leg; there it is stowed, surrounded by bristles arranged around the edge of the tibia, the so-called pollen basket (Fig. 3.5).

The Sweet Temptation

During co-evolution with flowers, the form of the honeybee was not developed only for pollen transport. Flowering plants have much more to offer: ferns, which populated the earth long before the flowering plants, excrete large quantities of sweet sieve tube juice as a by-product of photosynthesis. Flowering plants have retained this process, and have made nectar out of the original waste product, purely for consumption by bees (Fig. 3.6).

To exploit this attractive source of nourishment, honeybees have developed appropriately formed mouthparts, and a part of the gut as a small reservoir that, in a bee with a body weight of 90 mg, can accommodate up to 40 mg of nectar, i.e., almost half

Fig. 3.4 Much of the precious pollen adheres to the body hairs of honeybees

Fig. 3.5 Pollen is brushed up, and compacted into the pollen baskets on the hind legs, in preparation for the flight home. Bees can return from a pollen-collecting flight with up to 15 mg of pollen. In this way, a bee colony will transport about 20 to 30 kg of pure pollen to the hive in a single year

the body weight of the bee herself. The contents of this reservoir, or crop, is the common property of the colony. The bees need only a small fraction of their harvest for themselves, which when needed, is passed on through a small valve lying between the crop and the digestive midgut.

Flowers do their best to attract bees. A single cherry blossom can produce more than 30 mg of nectar per day, and an entire cherry tree, almost two kg. The amount that a single foraging bee will bring home with each flight can reach 40 mg, about the daily production of a single cherry blossom. At 2 mg of nectar per blossom, a far larger number of apple blossoms need to be emptied, and the crop of a forager holds the result of about 20 days of the flowers' production. However, a bee needs to visit more than only two cherry blossoms or 20 apple blossoms to fill her crop. For each visit to the flower, the bee can take only that small

Fig. 3.6 A rare forager collecting pollen and nectar simultaneously, with a large drop of nectar in her mouthparts. This drop will be swallowed, and transported in the crop. In the hive, she will regurgitate the nectar, mixed with enzymes, for receiver bees to store in comb cells

amount of daily supply made available at that time, and which is then replenished when she leaves. The estimated record for a bee is having visited 3,000 flowers in a single day (Fig. 3.7).

This record does not imply 3,000 trips from the hive and back, because the forager will visit many flowers on each flight. In this respect, bees are inclined to be lazy. The number of flowers that a forager visits on her relatively few daily tours will be greater if the flowers offer only small amounts of nectar each time the bee visits.

Single flowers do not place an inexhaustible supply of nectar at the bee's disposal. The production of nectar is a strategy to lure bees, and costs the plants in the form of raw material and energy that have to be invested in this commodity. A cost-efficiency estimate from the flower's point of view would show that it is more effective, through a gradual excretion of nectar, to achieve a high

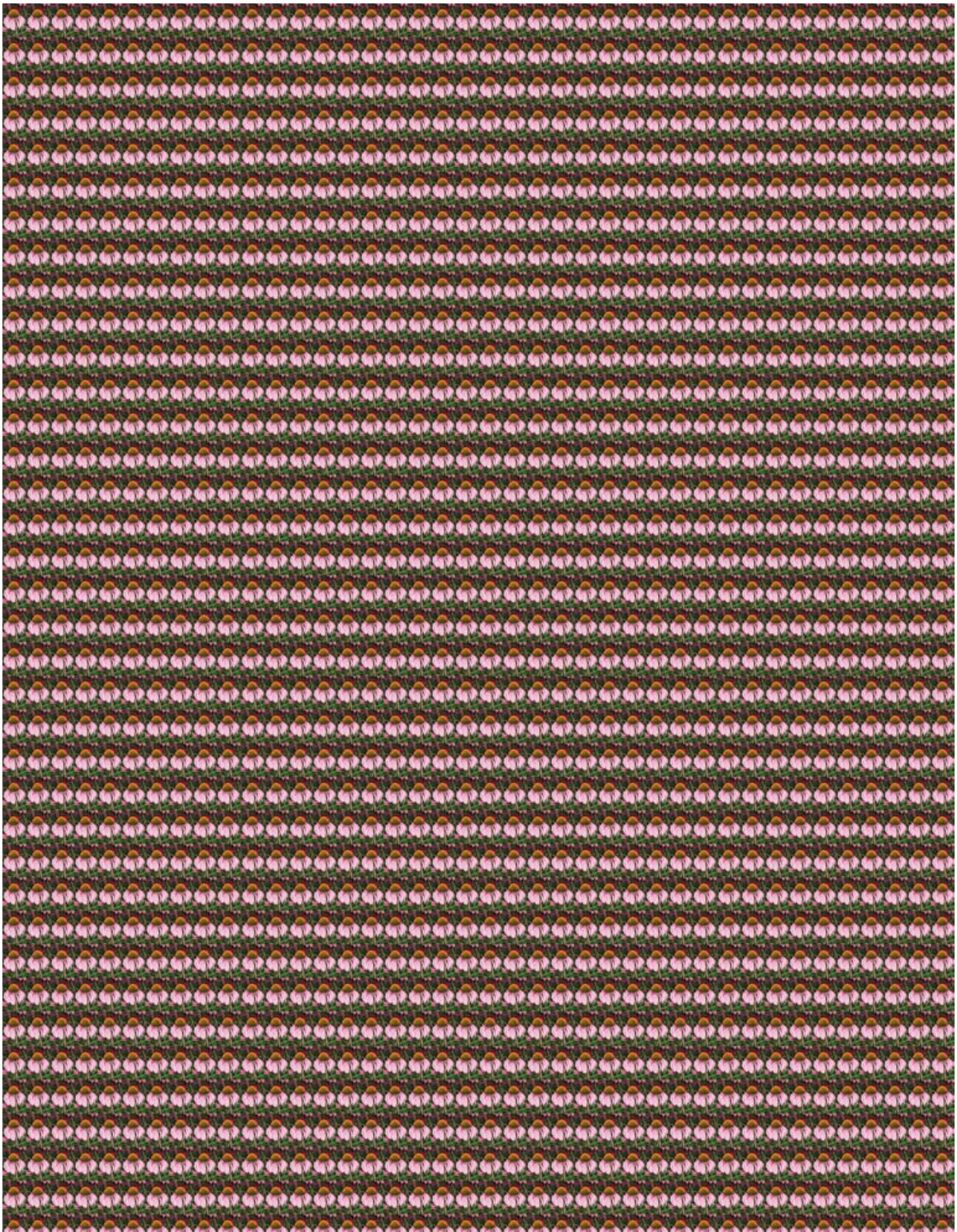


Fig. 3.7 A representation of a bee's visits to flowers over half a day. A single bee can visit up to 3,000 flowers in a single working day, although this many visits would be limited to short flights to flowers, yielding small amounts of nectar

frequency of visits: a large number of arrivals and departures by bees results in effective pollination, with the least possible cost in nectar. Nevertheless, flowers cannot take this thriftiness to an extreme, because then the customers will stay away, and turn to the more generous flowering competitor.

Industrious Honeybees

Honeybees must leave the comfort and safety of the nest during the mating period, and more often to harvest material and energy. The foragers of a colony undertake reconnaissance flights, and establish a fine network that covers the vicinity of their nest. Every available flower is enclosed by this invisible net.

For most flowering plants, this means they do not need to depend on other pollinating insects. A colony of honeybees could, theoretically, cover a region of up to 400 km^2 around the nest, if the maximum distance that a bee can reach from the hive is included in the estimate. This is about 10 km in direct flight. A bee that fully replenishes her honey energy reserve in the hive can just reach this distance. Bees undertake such flights only when the need for nectar is extreme. Over such long-distance flights, the energy used is almost as much as that gained, and an energy debt is only barely avoided. For most of their flights, the foragers cover between 2 and 4 km from the nest. This is an economically tolerable distance, in terms of energy in the form of honey used as fuel, and of energy gained in the form of nectar brought home.

Foraging is probably the most demanding period in the life of a honeybee. Perhaps it is then no surprise that a pronounced state of sleep has recently been discovered and described to occur in foragers (Fig. 3.8). Young bees sleep for shorter periods, and not in a day/night rhythm. Foragers sleep longer, and largely at night. Bees sleep in the hive, but sleeping bees can also sometimes be seen outside the hive (Fig. 3.9). Sleeping bees can be identified by a posture reflecting a lack of muscle tonus, in which the antennae hang down, and the legs are folded beneath the body. Why foragers in particular must sleep is as difficult to answer as for many other organisms. That this is so obvious in the foragers implies the importance of sleep for the physical demands of their service outside the hive.

Fig. 3.8 Worker bees sleep mainly at night in communities along the peaceful areas at the edge of the comb

Fig. 3.9 Occasionally, a forager can be found asleep on a flower in the field

Flowers are not always available at all times and localities within a colony's territory. Depending on the geographical region, either the flowers are seasonal—and so, when present, then everywhere—or they are present during the entire year, but concentrated in certain areas.

The former situation affects bees at temperate latitudes, the latter, in the tropics. The discovery and harvesting of resources present honeybees, regardless of the nature of their environment, with a series of problems. A regionally limited appearance of flowers, the timing of which is unpredictable for bees, would considerably raise the level of competition among bee colonies in the area. This situation is represented by flowering tropical trees that occur in an otherwise flowerless sea of green leaves; bees can find a flowering tree at all times of the year, but sometimes here and sometimes there. Honeybees evolved under these conditions, and focused their harvesting strategy through an ingenious communication system. When bees spread from the tropics to the temperate latitudes, they came fully prepared. For the efficient exploitation of the flower resource, the bee colony also has developed the ability to distribute precisely the correct number of foragers in an area, relative to the productivity of the flowers there. Attractive and fruitful sources are visited frequently, and less productive sources are not ignored but visited by a smaller workforce. Exhausted sources are not visited at all.

How Much, and Where?

If humans had to optimize their harvest in terms of the availability of nectar and pollen, and distribute their available workforce appropriately, their strategy would depend on extensive information regarding the production of these resources in the field. The situation also changes continuously, so that a running update would be indispensable. To this must be added a necessary overview of the stores at home, because when these are full, much less needs to be collected.

The number of bees deployed as foragers fluctuates strongly, and is subdivided into various proportions of nectar and pollen collectors. Indeed, there are only very few foragers (at the most, 15%) carrying out the simultaneous gathering of both nectar and pollen (Fig. 3.6). Most of the honeybees underway collect either nectar or pollen.

No individual bee in a colony has an overview of the supply and demand, and takes the responsibility of distributing the workforce. Nevertheless, from observations and experiments it is known that a honeybee colony optimally apportions its foraging force in the field. How can this work, when none of the individuals in the colony has the faintest notion of the overall situation?

The answer lies in a decentralized, self-organizing distribution mechanism. Decentralized means that there is no leading authority that "gives orders". Self-organizing means that the pattern of deployment of the workforce as a whole results from the many small contacts between the individuals. These small contacts serve to exchange single elements of information concerning the millions of flowers out in the fields. The honeybee colony casts its net across many hundreds of square kilometers, pulls the meshes close where a visit is worthwhile, and allows the mesh to open where there is little to gain. Scouting honeybees, usually about 5–20% of those bees that fly out of the colony, search continually for new sources of nourishment, and share the new discoveries with their nest mates.

The foraging effort of a colony with a higher requirement is not regulated by an increase in the efforts of the already active foragers. The foraging intensity of different individual bees is also not the same. There are lazy foragers that are content with a mediocre one to three foraging trips a day. There are also true honeybee workaholics that achieve ten or more foraging flights per day. The different personalities of the apparently identical members of a colony are revealed only after long-term observation of their behavior. By affixing a tiny RFID (radiofrequency identification) microchip to the back of the thorax of every bee in a colony at birth, it is possible to monitor the behavior of each individual over its entire life (Fig. 3.10). Individual bee personalities, in all their facets (industrious, lazy, peaceful, aggressive, warmth-seeking, cold-preferring, etc.), can be observed in such "transparent" colonies. The differences between individuals are nevertheless relatively small, so that the wide dynamic range of behavior displayed by a colony cannot be explained by this approach. Tightening the foraging net in the field is more often the result of an increased recruitment of additional foragers that fly to the profitable source. The presence of inactive foragers, and their deployment according to need, is the secret that enables a colony to optimally exploit a source of blossoms in their territory, despite their lack of a "director". In this way, a few hundred active and successful foragers can lead to the mobilization of a third of the entire colony.

The co-evolution of bees and flowers has resulted in a relationship not marked by mutual generosity, but rather by mutual exploitation. This launched a positive spiral that resulted in a won-

Fig. 3.10 The lifelong foraging activities of bees can be measured by attaching a microchip to them as they emerge from the pupa. In this way, differences between individual bees can be established, and factors that influence their foraging activity studied

derful partnership in which bees and flowers have shaped one another, becoming so inextricably interlaced that bees leave little room in their servicing of flowers that could be filled by other insects. One of the very few opportunities available for other competitors is related to the temperature at which bees begin to forage. Honeybees are able to fly when external temperatures reach about 12°C. For bumblebees that compete for the same flowers, and can fly at about 7°C, this provides a window of opportunity for undisturbed visits.

Resin is a third and important plant-derived product collected by bees, which they convert to propolis to apply around and in the nest. Only a small proportion of the resin collected comes from flowers; most is from buds, fruit, or leaves (Fig. 3.11). Plants do not seem to have any particular adaptations to cater for this need, but the possibility cannot be ruled out.

Fig. 3.11 A few bees specialize in the task of gathering resin from plants, and then transporting this propolis back to the hive on their hind legs

The foraging ability of a single bee depends, like that of the whole colony, on a range of variables. A simple approach is to describe the yearly foraging performance of a colony, which is largely dependent on its size.

The approximate quantities of nectar harvested by a typical colony can be estimated as follows:

- A single forager transports between 20 and 40 mg of nectar in her crop
- A single forager completes between three and ten flights per day
- A single forager collects over a period of 10 to 20 days
- A single colony deploys between 100,000 and 200,000 foragers per year

From the above, we can calculate the minimum and maximum values of expected nectar collection:

- Minimum value: 20 mg × three flights per day for 10 days × 100,000 bees would produce 60 kg of nectar.

- Maximum value: 40 mg × ten flights per day for 20 days × 200,000 bees would produce 1,600 kg of nectar.

Conversion of a single unit of nectar into honey reduces the amount to about half, so that one could expect between 30 and 800 kg of honey per colony each year.

The minimum amount calculated here is probably too low, and the maximum too high, but the values show the range in which the real levels of nectar collection and honey production must lie. In Chap. 8, we return to a consideration of the amount of foraged material that is really necessary for a honeybee colony.

A medium-sized colony collects about 30 kg of pollen each year—considering the relatively "weightless" nature of pollen, this is an astounding quantity.

The amount of resin that a bee colony brings into the hive lies at several hundred grams.

4 What Bees Know About Flowers

The visual and olfactory world of bees, their ability to orient in space, and a greater part of their communication revolve around their relationship with flowering plants.

Pollen and nectar are naturally renewable raw materials for bees, and are the essential basis on which the construction and function of the colony depends.

Flowers are not always present nor limitlessly available. They are the irreplaceable resources for which bee colonies compete, among themselves and with other insects. To this end, honeybees have developed some astonishing abilities enabling them to be the first to reach and harvest flowers.

Knowledge is power. This applies to honeybees as well. But what must bees know about flowers? And where did they get their information?

There are, in principle, three ways to obtain knowledge:

- Information is inherited, embedded in the genome (instinct)
- Information is gained from experience (learning)
- Information is gained from other experienced members of the species (communication)

Sense organs provide the essential link with the environment, for learning and communication. Sense organs are not passive windows onto the world; instead, together with sensory integration centers in the central nervous systems, they establish categories that are biologically important, but which in some circumstances do not exist as physical realities. Color is an example of being able to experience something that does not objectively exist. Colors do not exist outside the perceptive world of living organisms. Electromagnetic waves, to which light belongs, are part of a continuous spectrum. Only that part of this continuum that stimulates the sensory cells of an animal will be perceived as light. Colors are included in the perceptive world of organisms by different receptor cells being sensitive to different regions of the light wave spectrum. The color categories that have persisted in the course of evolution depend on the characteristics of the sensory equipment of organisms, and on how important these colors are for their survival and propagation.

The sensory world of honeybees is superbly adapted to the signals transmitted by flowers. Flowers, through their colors, stand out from a forest of green leaves—bees can see colors. Flowers are scented—bees have a very highly developed sense of smell.

Honeybees have an innate sense of color. Given the choice of various colors, naive bees will fly toward blue and yellow. Blue and yellow hues occur very frequently in flowers, and many other flower colors contain strong elements of the blue and yellow wavelengths.

Most important for the honeybee is the ability to assign different meanings to different colors in learning tasks. The acquisition of this skill through experience plays such a dominant role for bees that, with their ability to learn, they occupy a special place among insects. Communication, the highest level of information flow between members of the same species, is also unusually highly developed in honeybees.

An innate sense of color, the ability to learn from experience, and the ability to then communicate this information form the basic triangle of bee “wisdom”. The insights that we have of what bees “know about flowers” are particularly detailed.

To appreciate the complex behavioral performance of honeybees in their search and harvesting of flowers, it is helpful to subdivide the behavior related to visits to flowers into several functional steps.

Tasks that foragers must perform to effectively exploit the floral resource are as follows:

- recognize the flowers as such
- distinguish between different kinds of flowers
- recognize the state of the flower
- know how to work the flower effectively with legs and mouthparts
- determine the geographic location of the flower in the landscape

- determine the daily time window in which various flowers produce the most nectar
- share the information with nest mates as a messenger in a communication system
- receive and understand such information oneself in this communication system of where to find flowers

The World Is Made Not Only of Flowers. A Problem for Honeybees?

It is not obvious how honeybees recognize what is, and is not a flower. That they do this without any difficulty is clear from observations of their visits to flowers in the field. So, where's the problem?

We are also able to recognize flowers. But do bees experience flowers the way we do?

At this point, we could become a little philosophical. We can experience the nature of the world only from what we perceive. Perception is mediated by a general knowledge that, in the course of evolution, has proved to be essential for the survival and propagation of particular species. Our perceptions are conveyed through sense organs, and the subsequent processing of these sensory signals in our brains. This subjective experience cannot be transmitted from person to person. We call a certain color "violet" because this is what we have been taught, but we do not have the ability to see this color through the eyes of another person, and so confirm that their impression of "violet" is the same as ours. How can one transfer oneself inside the head of a bee to appreciate how they perceive the world?

It is possible to gain a certain impression of this by studying the sensory world of bees, and the performance of their brains. A combination of anatomical, physiological, and behavioral studies of bees has shown that the features of flowers and the perceptive performance of bees are tightly coupled.

Two important sensory modalities are matched between bees and flowers: vision, and olfaction. Our overall concept of flowers is also determined by colors and scent. But bees experience flowers in a completely different way. Humans, whose esthetic sense is considerably influenced by flowers, are merely perceptive parasites on features that bees have bestowed on flowers in their co-evolution.

The visual system of bees differs from ours in many ways. Each of their compound eyes is composed of about 6,000 single eyes (Fig. 4.1). A picture of the surroundings is put together from many, quite large, separate single points. Our own eyes construct a single complete image on the retina of each eye, formed by a single lens.

The poor optical acuity of bees means that they can resolve the fine details of objects, and flowers, only when they are a few centimeters away (Fig. 4.2).

Bees need to inspect the details of a flower from close-up before being able to recognize which blob in the landscape is indeed a flower. Color contrast will make flowers stand out from the green leafy background, in the same way that birds and primates quickly detect ripe colored fruit, which in turn is important for the dispersal of a plant's seeds by fruit eaters. However, before the seeds can be dispersed, the flowers must be visited by the pollinators. To ensure this, plants employ the same strategy as for their fruit: color as an advertisement. What's the color world of bees like?

A comparison with the ability of humans to see color is helpful. A rainbow appears: we perceive the long wavelengths as red, the short as violet. All the other colors lie between (Fig. 4.3).

Light at the red end of the spectrum is less interesting for bees, and only very weakly stimulates their visual receptor cells. An object reflecting a wavelength that does not stimulate the visual receptors appears black. To bees, a field covered with red poppy blooms appears as an area spotted with black blobs (Fig. 4.4). The lack of red sensitivity in bees is compensated by a gain in sensitivity to the short wavelengths of the visual spectrum: bees can see ultraviolet light, which we are unable to detect without technical help.

The petals of many flowers have some surfaces that strongly reflect ultraviolet light, and so form patterns for a bee eye that remain invisible to us (Fig. 4.5). Such patterns could serve as landing aids for approaching foragers, but may also enable bees to discriminate more easily between different kinds of plants.

The significance of certain aspects of the sensory systems of animals can be explained in detail by their relevance in a biologi-

Fig. 4.1 Honeybees possess two large compound eyes, and three small ocelli. Each compound eye produces an image that is constructed from a rough array of dots of different colors and intensity. The eyes of drones (the drone shown here has only just emerged from the pupal case) are larger than those of workers and queens

cal context. Bees use the short wavelengths of sunlight for their orientation in flight. Flowers exploit the visual sensitivities of bees by presenting their pollinators with areas on their petals that reflect short wavelengths, as attractive signals.

It becomes more complicated: the colors bees see depend primarily on the light's wavelengths, but also—and this is hard for us to imagine—on how fast the bee is flying. Even the behavioral task that a bee undertakes can influence her color vision.

When bees are flying across the landscape, they do this at about 30 km per hour. At this speed, their color vision is switched off—they are colorblind (Fig. 4.6, lower panel).

Fig. 4.2 A consequence of the rough array of dots in the visual world of a bee is that optical details of an object, such as a flower that they are approaching in flight, are resolved only when they are close to it. *Above* This is how a bee sees a flower scene from several meters away. *Center* At 30 cm away, the flowers will appear like this. *Below* Details of the flower are recognizable for the bee only from a distance of 5 cm

Not until the approach and slow circling of the blooms do the colors appear to them. This phenomenon is biologically meaningful. For a bee in rapid flight, the colors of objects are apparently unnecessary information. The small bee brain has to concentrate

Fig. 4.3 The rainbow reveals: humans see only a small portion of the sun's electromagnetic waves. In contrast, the color spectrum seen by honeybees is shifted toward the short wavelengths. Red disappears, and at the other end of the rainbow color spectrum, an ultraviolet band appears in their field of vision

on other matters that are important during rapid flight, such as the recognition of structural details in the surroundings: where are obstacles? Where are the landmarks that show the way? The detailed visual perception of many colorless objects and patterns in rapid succession is more important for bees than a colored but blurred landscape, such as we see when we are in rapid motion.

Bees, like many other insects, see things in "slow motion". Rapid movements that appear blurred to us are perceived clearly at each stage by bees (Fig. 4.6, lower panel). Sudden hand movements, like those that fearful people make when fending off bees

Fig. 4.4 Bees perceive long wavelengths as black. Flowers that reflect long wavelengths of light—we see these as red—are seen by bees as black

and wasps, offer the most easily recognizable goals for attack. Stings in the area around people's mouths are caused mainly by movements of the lips while speaking.

Even the flight goal itself has an effect on the ability of bees to discriminate between colors. The flight from the nest to the feeding site, and from the feeding site back to the nest are two quite different situations for bees, and this not only because they are in different directions. Approaching a flower, bees exhibit an excellent ability to discriminate between colors. Having terminated their visits to flowers, and having started back to the colony

Fig. 4.5 Many flowers have patches on their petals that reflect ultraviolet light. In this way, visual patterns appear to bees (*right*) that cannot be perceived by humans (*left*)

with a full crop, color vision plays a distinctly less important role. It is very difficult to train bees to colors they experienced once departed from the feeding site. Consistent with this, bees have difficulty, even in slow flight, in discriminating colors on their way home. The highly developed capacity of bees to recognize and discriminate between optical *patterns*, however, is unaffected by the final goal of their flight. Colorfully painted beehives are esthetically attractive for human observers (Fig. 4.7). In contrast, bees perform poorly when their ability to discriminate between the different colors of the hives are tested. They recognize only blue, prefer this to other colors, but cannot easily discriminate between these other colors—quite in contrast to their behavior at the feeding site, where they are able to separate the smallest differences between colors. Hive markings in the form of patterns, such as horizontal or vertical bars, better aid the bees to find the correct nest. Colored pictures, and particularly, attractively presented entrances to hives—a classic decoration of beehives in many regions—is optimal for both bees and people, because they offer bees an easily learned and recognizable pattern, and at the same time present the human observer with a pleasing picture (Fig. 4.7).

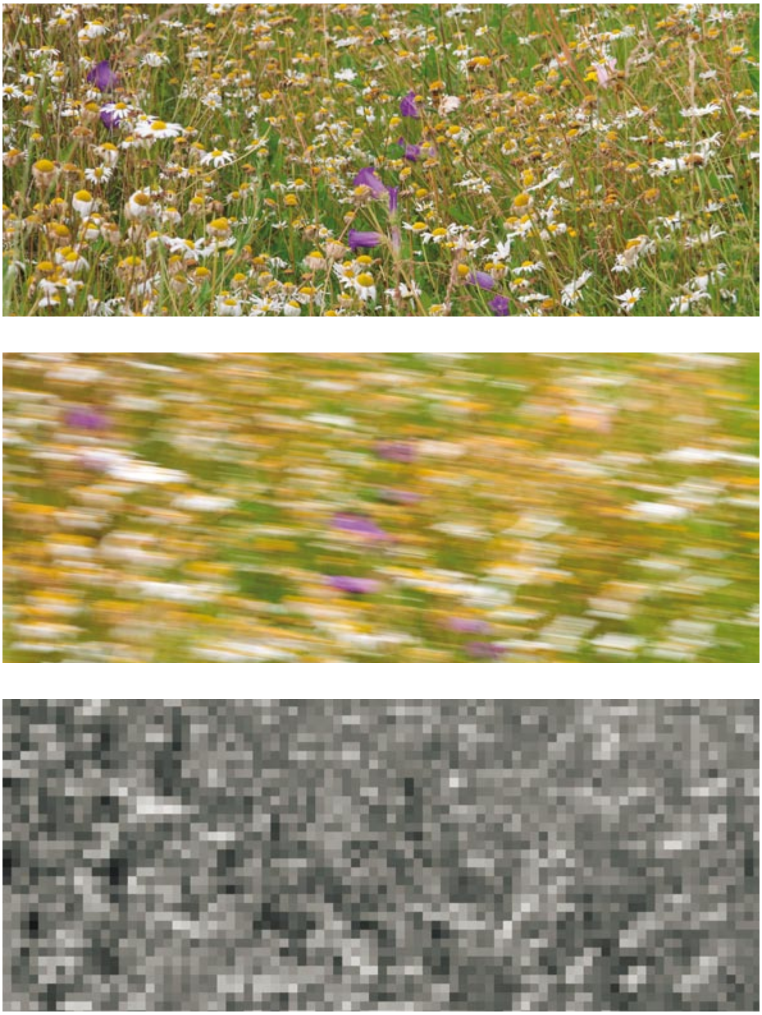


Fig. 4.6 Rapidly flying bees are colorblind. Color information is less important in this situation, and not processed. A colored field of flowers (*above*) appears blurred, but still colorful to a person moving past it (*center*). In contrast, a bee flying past the same field at the same speed will perceive: (1) a picture composed of a rough array of dots of different intensity, (2) a picture that is sharp, (3) a picture that is black and white (*below*)

Fig. 4.7 Artificial hives decorated with colored pictures (*above*) provide a better orientation aid for bees than do areas of plain color (*below*)

The behavioral context—expressed here as the opposed motivational situations for bees flying either to the feeding site, or back to the hive—determines the worldly experience of bees.

The visual perception of a rapid sequence of images is important not only when the bees are flying rapidly through the landscape, but also when they need to recognize other rapidly flying bees that they are then able to follow. This is true, for example, during mating behavior when worker bees either accompany, or follow a queen on her mating flight, or as described in Chap. 5, when the workers follow drones in flight. The same is true for swarming behavior when bees band together to fly to a new nest site, or for the flights of small swarms of newly recruited foragers and experienced bees to feeding sites.

Flowers are sedentary, and so it is surprising that bees have a high visual sensitivity to motion. This is exploited by some flowers, to their advantage. Different plant species compete for vis-

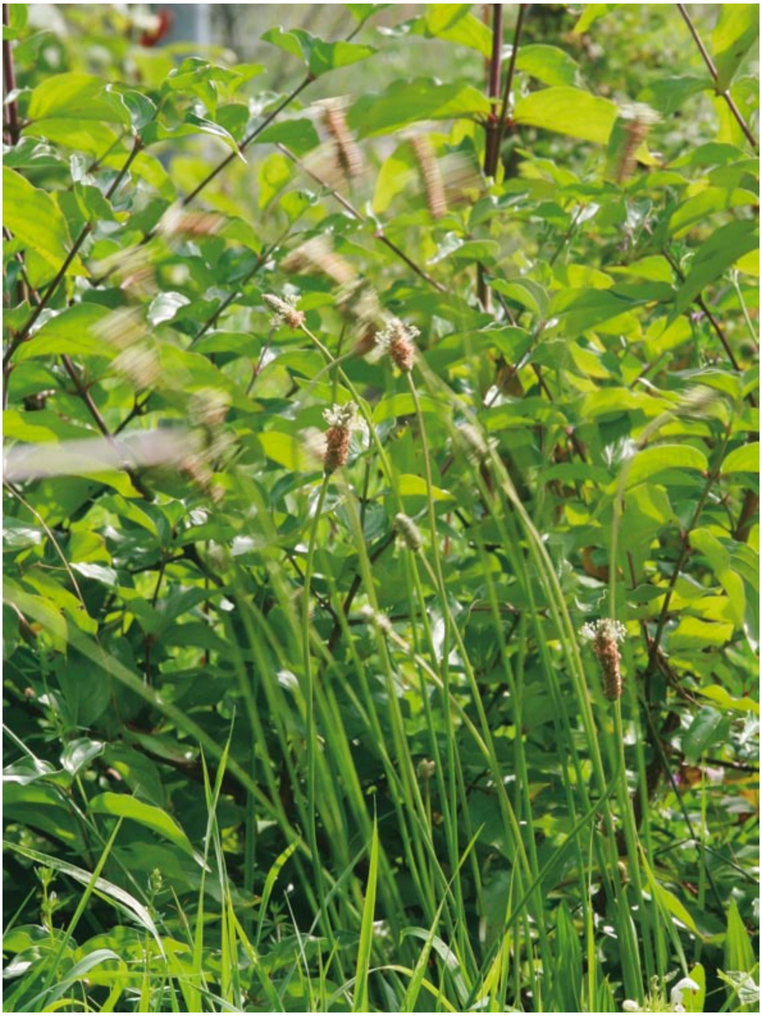


Fig. 4.8 Small flowers on thin stems move with the slightest breeze, attract the visual motion detection systems of bees, and are therefore noticed despite their diminutive size and pale colors

its from bees, as do bee colonies for access to flowers. Bigger and more colorful flowers should be more attractive for bees, and so lure more visitors than do their competitors. How, under these circumstances, can plants with tiny flowers attract bees? Small flowers are often supported on thin flexible stalks; the slightest breeze sets them in motion, attracting the attention of bees (Fig. 4.8).

Flowers are not only colorful, but also advertise themselves with distinct odors that even we are able to detect. The honeybee is again the most important target group. The "nose" of the honeybee is represented by many thousands of single sensory cells

Fig. 4.9 The antennae of honeybees are crammed with a variety of sensory receptors (*right*). Sensitivity to touch, temperature, humidity, and above all, odor is located here. The different appearance of these thousands of sensilla mirrors the breadth and diversity of their sensitivities. Different forms of some of these receptors can be seen in the 400 times enlargement shown on the *left*

on their antennae; the diversity of these sensory structures is revealed in scanning electron microscope images (Fig. 4.9).

The scent of flowers can lure bees over considerable distances, in contrast to their visual appearance that bees perceive only when they are very close and approach in slow flight. Under wind-still conditions, odors disperse evenly and are not much help for orientation, but should the air move and transport the odor molecules, it can lead bees to the goal. In general, bees land on a flower against the wind. This has nothing to do with the strategy of human pilots that land against the wind in order to slow their landing speed; nectar-seeking bees are following an odor trail leading them to the flower. Foragers that have already experienced the odor of a feeding site, but not its location in the field, will very quickly reach their goal if an airstream flows from the flowers to the nest. In such cases, they may circle in the air until they come across a breeze bearing the scent that will lead them to the feeding site.

When Is a Flower Not a Flower?

The features "visual appearance" and "scent" can be combined in different ways in flowers. Color, shape, and odor complement one another, resulting in a specific flower character that the bees recognize, and use to discriminate between different kinds of flowers. This discriminatory ability is the prerequisite for an important phenomenon for both bees and flowers, known as "flower constancy". Foragers do not indiscriminately visit every flower they come across, unlike butterflies and flies, but collect predominantly from those flowering plants with which they start their harvesting each day (Fig. 4.10).

For plants, this flower constancy has a significant advantage, because their pollen will not be wasted on the stigmata of flowers of a different species. For bees, flower constancy brings with it the possibility of adapting to the currently visited flower type, and quickly obtaining the nectar.

Color, shape, and odor can, in principle, be combined in an endless number of permutations. The storage capacity of the bee genome, though, is not large enough to provide the bee with an innate knowledge of the nature of all possible flower forms. Instead, bees have a genetically determined ability to learn the assembled visual and olfactory features that make up a flower's character.

The learning abilities of honeybees is highly developed. A single experience with a particular odor can be learned, and subsequently used to discriminate against other odors, with 90% certainty. This is true for simple chemical odors, as well as for those consisting of many components. Following two or three positive experiences with such odors, bees can become error-free in their choices. This learning ability is the basis of the high significance of odors in the perceptive world of the honeybee.

Shape and color are not learned as quickly as odors, taking three to five training sessions to achieve proficiency.

The ability to learn, and to discriminate between olfactory and visual stimuli is so pronounced in honeybees that in experimental situations (Fig. 4.11), some cognitive aspects have been revealed, equivalent to those of lower vertebrates. Even "intellectual" abstraction, the biological significance of which is not clear, can be demonstrated: bees in flight are able to recognize particular pat-

Fig. 4.10 Bees exhibit flower constancy, and continue to visit the same type of flowers, while others in the neighborhood are ignored, although they would also be worth a visit. In the patch of flowers shown here, blue and yellow blooms are mixed. Bees that first started foraging on the yellow flowers ignored the adjacent blue flowers (*upper*), while those that began with the blue flowers ignored the yellow flowers (*lower*)

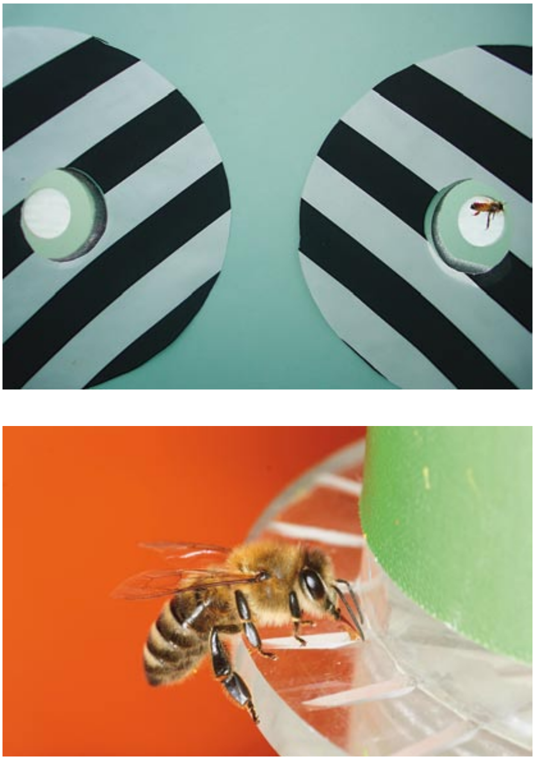


Fig. 4.11 Behavioral experiments designed to test the cognitive abilities of bees: if the bees choose the correct pattern to which they have been trained, they will be rewarded by finding a feeding dish behind the marked wall

terns in space independently of their own body orientation; certain trained behavioral activities of bees lead to the interpretation that they are aware of the abstract concepts of "left" and "right", "symmetrical" and "asymmetrical", as well as "odd" and "even". Bees can discriminate between "more" or "less", which may be regarded as a type of simple counting. Bees can derive certain rules of behavior from experience, and to then apply these rules to completely new situations. They will, for example, very quickly learn which sign to follow in order to find their way through an unknown labyrinth, when this labyrinth is equipped with appropriate signposts.

Better still: honeybees rapidly learn to associate different localities and different times with particular decisions. Flowers at different localities produce different amounts of nectar at different times of the day, a factor accounted for by bees when planning the most productive foraging flights. Honeybees will follow a daily work program, and carry out the correct task at the right locality at the right time (also see below).

This is "bee intelligence" at its best.

Is There Nectar in the Flower?

A foraging bee flying around a stand of flowers on a nectar or pollen search does not look into every flower. It is not immediately obvious that an optimal search strategy is being pursued here, in which the best way to save time and energy is not to visit every flower. The problem for the bee is comparable with the famous strategy planning game in which the most efficient way has to be devised for a traveling salesman to visit his customers. Bees, however, are guided by "messages" that the previous visitors leave behind on flowers, to inform those that follow. There are many foragers underway in the harvest area, and some flowers need time to replace the store of nectar that has been removed. Foragers that take the last drop of nectar mark the flower with a chemical "empty" signal. The chemical signal fades about as quickly as it takes the flower to replenish the nectar store. Bees that approach such flowers get the message before they land, and do not waste time trying to extract nectar from an empty flower.

The Way to the Nectar

The diversity of flower forms presents bees with a practical problem: every flower provides the bee with its own specific challenge on her way to the nectar, to ensure that she brushes past the stigma and anthers (Fig. 4.12). Obstacles have to be pushed aside, and the nectar glands of different flowers are located in different places. The quickest and most energy-efficient access to the drop of nectar, and the best strategy to collect the pollen are discovered by bees through trial and error.

Fig. 4.12 The enormous diversity of flower forms presents bees with a practical problem of devising an optimal time and energy strategy for harvesting

Regular visits to the same type of flower, through flower-constant foraging, improves the bee's performance, and optimizes the time and energy required to reach the nectar.

Where Are the Flowers?

The honeybee colony has a fixed address, leading a sedentary existence. This is not a problem as long as one stays at home, and for the greater part of their lives, the bees do not leave their nest. A flow of material and energy must nevertheless be maintained, and the foragers have no choice but to fly out into a dangerous world in search of flowers. They also have to find their way back to the colony after their excursions, and if they have discovered a particularly abundant collection of flowers, they must be able to find these again.

Bees use earthbound and celestial cues as aids to orient themselves outside the nest, and will make their way from one landmark to the next along each part of the journey to the goal. For this they use trees, bushes, and other conspicuous features in the landscape, and their visual and olfactory senses are of extreme importance. This method of orientation depends on the bees being in known and local territory that they have previously explored, by undertaking short orientation flights around their hives as new foragers. During these orientation flights, which initially do not last longer than a few minutes, bees leave the hive each time in different directions, and so map the location of the nest relative to its surroundings. To help the young foragers find their way home, older bees occasionally stand in front of the hive entrance, open the Nasanov glands at the ends of their abdomens, and release a scent called geraniol, a chemical compound that smells like geraniums. The geraniol is spread through the area by scenting bees fanning their wings (Fig. 4.13).

Bees that fly long distances to feeding sites will learn the location of landmarks they pass on their way from the hive to the food source.

A compass is a helpful device if one wishes to follow a direct path through an unknown landscape. The sun provides bees with

Fig. 4.13 Young bees returning to the hive receive help in landing from older hive bees that release an attractive scent from the Nasanov glands in their abdomens, and disperse this by fanning their wings

a celestial signpost, and they orient themselves relative to its position. If the sun is hidden, then the polarization pattern of the sky produced from light passing through the earth's atmosphere can be used. Non-polarized light from the sun becomes polarized when it passes through the earth's atmosphere, and the sky shows a visual pattern that can be detected by the human eye if aided by an appropriate device. Such a device, or analyzer, is built into the bee's eyes, and enables them to discriminate polarized from non-polarized light. The polarization pattern in the sky is, however, subject to distortion through differences in air density following changes in temperature and humidity. To be useful, an orientation aid needs to be reliable and unaffected by such distortion, and it so happens that the sky's pattern of polarization for shorter wavelengths is more stable, and so better suited as an orientation cue. Foragers need to find their way home to the colony, and the development of a sensitivity to ultraviolet light providing use of the sky's stable polarization pattern carried with it an obvious selective evolutionary advantage. This ability of bees, which initially arose as an aid for their orientation, has been exploited by flowers, many of which include UV-reflecting patterns on their petals. These offer the bees visual landing aids, and also make it possible for them to discriminate between different kinds of flowers.

Time Signals

The use of celestial signposts in the form of the sun's position, and the polarization pattern of the sky for orientation require that bees take into account the changes that accompany the daily the rotation of the earth. Bees have a sense of time that allows them to compensate for the continual change in the location of their signposts, even after pauses in the hive of a few hours between successive excursions. The bees then "calculate" the original direction on reemerging from the hive, despite the new relative locations of the orientation cues. This feature of honeybee behavior provided Karl von Frisch (1886–1982) with a critical insight into the communication of the bee dance: foragers that visited the same feeding site for the entire day danced in different directions in the morning and in the afternoon. The position of the sun relative to the hive is dependent on time, and von Frisch concluded that the sun was being used to aid orientation.

The sense of time also makes it possible for bees to adjust to the limited "open periods" of flowers. In order to decrease competition among themselves, certain plants will produce nectar only at certain times of the day, and bees are able to learn such a timetable. They adjust their visits, and turn up at appropriate flowers at the right time (Fig. 4.14). Even when many flowers are mixed together at localities visited by bees, the bees learn not only at which site they should be at what time, but also which flowers they should visit at particular times and places.

They also quickly recognize sources that are no longer worth visiting (Fig. 4.15).

A forager that visits a previously prolific source in good flying weather, and finds nothing there, will rapidly erase this from

Fig. 4.14 A forager arrives too early at a flower that she successfully visited the day before

her memory, and not visit again. On the other hand, when bad weather prevents foragers from leaving the hive, they will remember the location of recently visited feeding sites, and immediately visit there with the return of fair weather. Learning and "forgetting" are perfectly adapted to each biological situation.

How Bees Talk to Each Other About Flowers

Flowers have to be found, before these treasures can be raided. A small percentage of older bees act as scouts, and search the area for new flowers. Flowers that have attracted the attention of these pathfinder bees will receive visits from an increasing number of bees, from a few minutes to about half an hour after their discovery. The increase in the number of visits is too rapid to be the

Fig. 4.15 Faded flowers rapidly loose their attraction for bees

result of each bee having found the site on her own. Instead, the newly arriving bees have been informed about the discovery in the hive, and recruited to help.

The communication that takes place between the "informed" and the "uninformed" bees is highly complex, and still not satisfactorily understood. It consists of a chain of behavioral patterns that are played out in the hive and in the field. Just *one* link in this chain is the so-called dance language that Karl von Frisch discovered, and which has become one of the most intensely studied forms of communication in animals.

A bee that has discovered a flowering cherry tree, for example, will return to the nest with some of the nectar. She transfers the nectar to a receiver bee, and leaves the nest again to return to the same cherry tree. This is repeated several times, each trip being completed more rapidly, presumably because the flight path becomes more direct with each trip. Once the quickest way has been found, which can take up to ten flights, the bee will begin to dance.

Fig. 4.16 A forager has discovered a food source close to the hive, and carries out a round dance

For feeding sites less than about 50 to 70 m from the hive, Karl von Frisch discovered that bees perform a round dance (Fig. 4.16).

A round dance contains only some information about the quality feeding site. An indication is merely given about what to look for, and that this source can be found close to the nest. A bee that returns from visiting a cherry flower will smell like cherries, and a cherry tree can be found easily enough after a few flights around the hive.

Should it lie at greater distance from the hive, an indication of the location of the source is helpful, and would spare long search flights. Bees seeking to enlist the help of others provide this information in the waggle dance. Aspects of the path followed in this dance have been found to indicate the location of the feeding site relative to the hive.

The remarkable sequence of events in a waggle dance is so intense and regular that it has attracted a great deal of attention in behavioral research. Modern technical aids, such as close-up, slow-motion videos, record amazing details: the waggle dance gets its name from a part of the dance behavior in which the bee standing on the comb shakes her body from side to side, at a rate of about 15 times a second. She then runs in a circle back to the point where she started waggling, repeats the waggle “phase”, and

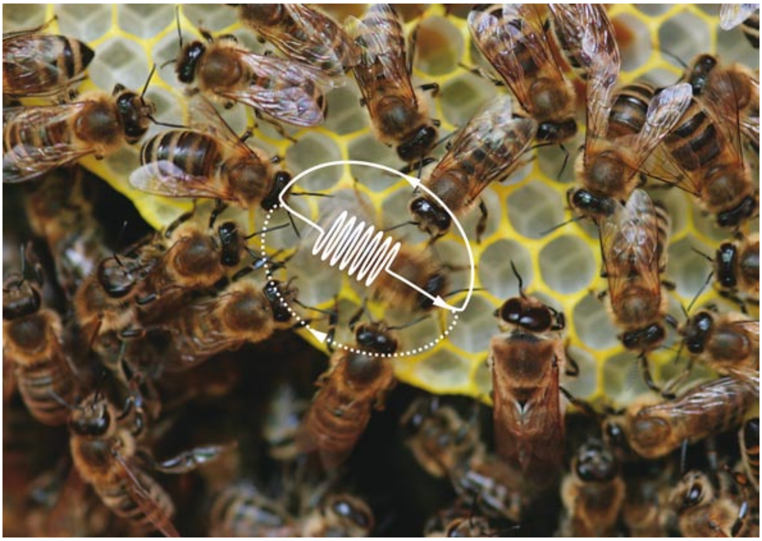


Fig. 4.17 A forager has discovered a distant food source, and performs a waggle dance

again runs a full circle, but this time in the opposite direction to the starting point, so that the two paths together approximate a figure of eight lying on its side (Fig. 4.17).

A complete dance cycle lasts only a few seconds, and is played out over an area of about 2 to 5 cm in diameter. The details of the small and rapid movements were first revealed in slow-motion film recordings. These showed that the original impression that a bee runs over the comb during the waggle phase is an optical illusion, caused by the bee leaning forward during the rapid lateral oscillation of the body. The bees are really performing a “waggle stand”, rather than a “waggle run”, during which they remain anchored to the substrate as long as possible with all six feet, leaning forward. Some bees become detached for a moment from the comb while they search for a more stable grip, and when stretching forward do need to move one or other of their feet, but at the most one or two steps (Fig. 4.18).

Bee dances take place almost exclusively in a small area close to the entrance of the hive. Dancers meet foragers that are interested in their messages on this “dance floor”, which is apparently chemically signposted by the bees. If this part of the comb is cut out and put back in a different place in the hive, bees will search until they have found its new location before they perform their dance.

Fig. 4.18 Communication by dancing requires that the legs of the dancer remain firmly anchored to the comb. Hence, the dancer carries out a "waggle stand", rather than a "waggle run". Her six feet (marked here with *white points*) maintain contact with the rims of the cells, while her waggling body leans forward over her stationary feet (shown by the *arrow*)

Dancers and their followers, of which up to ten can crowd around a dancer, perform a ballet in which the movements of the partners taking part are all precisely choreographed (Fig. 4.19).

Like the movements of the dancer, those of the followers are precisely programmed. The sequential placement of the feet and turning of the bodies are stereotypic. The complex pattern of the followers' movements, much less obvious than those of the dancer, can be detected only in the analysis of slow-motion recordings. From such analyses, it is clear that only those followers correctly performing all the detailed sequence of movements, including moving each time around the head of the dancer on the inside of the return cycle, can keep "in time" over several sequential rounds of the dance.

How does one, in general, describe the path to a goal? A set of directions can be built up from several detailed descriptions of parts of the journey: go 100 m along Station Street until the first traffic light, go left to the second crossroad, follow this right to the pub "Honeybee". Then take a right at the first street after the

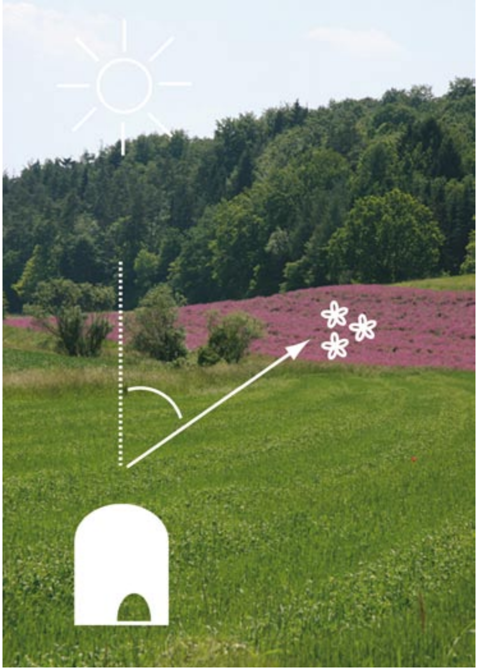
Fig. 4.19 Only dance followers whose movements are stereotyped and precisely tuned to those of the dancer, and that follow the dancer over several rounds, receive information about the location of the food source

pub, and after about 200 m the post office is on the right-hand side of the street.

Such a complex set of directions, which may not be a problem for us, is beyond the ability of the small bee brain. They are also not necessary, because bees can fly in a straight line. This shortest of all possible ways can be described by a single direction, or vector, pointing directly to the goal; by its length, it can show how far away the goal is (Fig. 4.20).

Flying bees use this method. After many patient hours of observing waggle dances, it occurred to Karl von Frisch that the direction the bees faced during the waggle phase on the combs changed continuously during the day, although the same bees from the same hive were visiting the same feeding site. With the direction of the waggle phase in the dance, the only feature that changed was the movement of the sun across the sky. Von Frisch recognized that changes in dance direction were correlated with the sun's position at different times of the day, and established that directional information is contained in the dance.

Fig. 4.20 Bees find their way to the food source by means of a sun compass. A vector at the hive indicates the location of the food source relative to the position of the sun



Direction is always relative, and a point of reference must be provided. The position of the sun, or the angle of the sky's polarization pattern provide these points of reference outside the hive. The dances, though, take place on the vertically hanging combs within the dark hive. Here, the downward direction of gravity is the only point of reference. Bees in flight outside the hive see the position of the sun. They translate the angle that was indicated to them in the waggle dance relative to gravity, into the corresponding angle between the hive and the sun, and this leads them to the food source (Fig. 4.21). The polarization pattern of the sky gives them an indication of the position of the sun when the sky is overcast.

Coding the direction in the waggle dance depends on the availability of a dependable point of reference, such as gravity, to which the directional messages can be referred. The precise

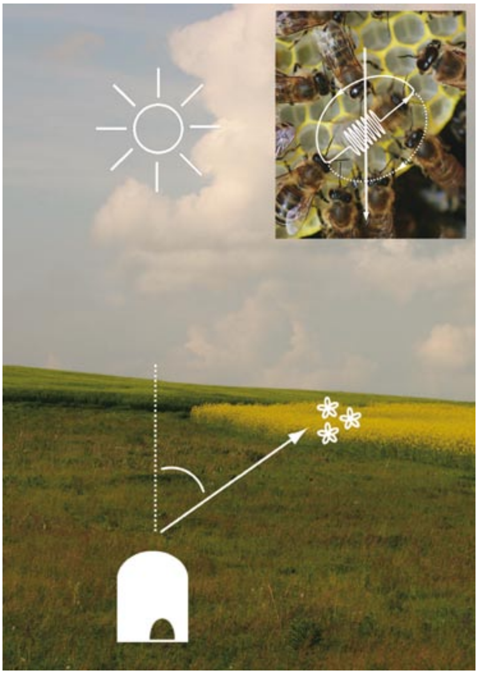


Fig. 4.21 The path of the waggle dance contains instructions about the direction and the distance of the food source from the hive that the dancing forager has measured during her flight through the landscape. In the darkness of the hive, the direction of gravity is substituted for the direction of the sun, registered by the forager during her outward flight (*arrow in inset*)

coding of the path to the food source is possible only if the comb surfaces hang exactly vertically, without which this type of communication would not have occurred; indeed, there is no such form of communication in colony-building insects such as bumblebees, wasps, and most tropical stingless bees, which have no vertical surfaces in their nests. A few stingless bees have been reported to build vertically hanging combs, and it would be worth investigating these species to see if they have developed a dance language similar to that of honeybees.

The waggle dance of honeybees also contains information about the distance between the hive and the feeding site. This is almost a luxury, as far as finding a feeding site is concerned. A recruit that followed the indicated direction to a food source with the same odor as that of the dancer could reach the goal with this information alone. Distance information in the dance, in contrast to the directional information, is associated with a number of problems that are considered below.

Some unambiguous correlations can be noted: with basically the same frequency of waggle movement, the longer the waggle phase of the dance lasts, the further the bee has to fly to the source. However, the duration of the waggle phase increases proportionally to the distance only over the first few hundred meters; thereafter, it increases more gradually, and the distance information to remote goals is consequently less precise. It is scarcely possible for a human observer of the waggle dance to determine the difference between a dance for 1 or for 3 km.

An additional difficulty arises from the bees' use of a visual odometer to determine the flight distance that is communicated in the dance. The data delivered by this odometer are relative to the structural nature of the surroundings through which the bee flies.

When flying through a structured environment, the images of objects move across the facets on the surface of the compound eye of the bee. This result in an "optical flow" in the visual field of the bee, which helps the bee determine her flight speed. We are also able to do this quite well—for example, when watching passing images from a moving railway train. Based on optical flow, bees are also able to derive the distance they have flown, something we do poorly, if at all.

Some simple experiments carried out on the bee odometer have provided a number of insights into the perceptive world of the honeybee. Honeybees that fly to the feeding site through a narrow tunnel with patterned walls experience an artificially increased optical flow along a short distance of the path they have to fly (Fig. 4.22).

These bees have been deceived, and translate the increased optical flow into a longer distance, resulting in a correspondingly long waggle phase. This simple deception in terms of estimated distance opens a window into the subjective experience of bees, in which measurements of the length of the waggle phase are an indication of how far the bees believe they have flown.

The application of the "deception tunnel" confirmed some old ideas, disproved others, clarified disputed points, and provided the following new insights:

Fig. 4.22 Foragers trained to fly through a narrow tunnel with patterned walls, on their way to the food source, experience a rapid sequence of images as they fly close to the walls. The resulting high optical flow leads to a waggle dance in which the actual distance flown is incorrectly translated

- Refuted the opinion that bees use energy consumption as a measure of flight distance.
- Confirmed the use of the visual odometer.
- Confirmed the old suspicion that distance measurements are made on the outward, not on the return flight.
- Explained and settled the decade-long controversy about the waggle dance, in which it was disputed whether or not the recruited bees followed the information coded in the waggle dance. The tunnel enabled one to produce bees that made errors, visiting feeding sites 6 m from the hive, but in their dance signaling a distance 30 times longer. Searching recruits were not found flying around where the dancing bee really came

from, but in an area much further away where there was nothing of interest. Information from the dance is used.
- Led to the realization (with the help of colored patterns in the tunnel) that, of the three color-sensitive visual receptor cells in the complex eye of the bee—which individually react best to either ultraviolet, blue, or green—only the green receptor is used in measuring distance.

The simple manipulation of the bee dance by means of tunnel flights demonstrated that the distances that the visual odometer was indicating to the bees were influenced by the structure of the landscape along the flight path. In a test of this idea, a flight path that passed through a landscape of even appearance was found to result in a dance with a short waggle phase, whereas a flight path of the same length through a complex, structured landscape led to a long waggle phase. Should bees fly to feeding sites that are the same distance from the hive but lie in different directions, the waggle phases of their dances, and so the indication of the distance, can differ by a factor of two. A waggle phase of 500 ms (millisecond) could, in the case of a flight to the south, mean a distance of 250 m, and for a flight to the west from the same hive, 500 m (Fig. 4.23).

From this, we can draw two conclusions:

- The odometer of bees does not deliver absolute distance information, and is useful only when the followers leave the hive in exactly the same direction (and altitude) as the dancer.
- There needs to be a reevaluation of the idea that in the translation of flight paths of the same length, bees of different races differ in the duration of the waggle phase, because their dance languages have different "dialects".

The duration of the waggle phase exhibits only minimal differences when the dances of different bee races are compared for one and the same flight path. A comparison of the dances of bees of the same race for the same distance, but over different terrain, reveals the landscape-dependent differences to be significantly greater than the race-dependent variation. In assessing the coding of the flight path length in the bee dance of different races in different areas, one is therefore comparing the visual properties of the landscape, rather than the properties of bee races.

Fig. 4.23 The view from the beehive is seldom the same in all directions. Different details of the landscape over which bees fly evoke optical flows of variable intensities, and lead to differences in the length of the waggle dance for the same distances flown in the field

A critical condition for the translation of the relative distance information in the dance is that the dance followers keep to exactly the same route as that flown by the dancer. Therefore, there is high selection pressure on the exact transmission, and subsequent execution of the directional information contained in the waggle dance.

Dancers transmit other important details about the flight path and the food source, in addition to the location of the source. Attractive sites lead to lively dances. In lively dances, the dancers complete the return phase to the start of the waggle phase very quickly, while in less lively dances they return relatively slowly to the starting point. The duration of the waggle phase that contains the distance information is not influenced by the attractiveness of the food source.

What constitutes an attractive food source?

Bees integrate a number of different impressions into an overall picture. Included are not only the quality of the food, but also features experienced along the route: a high concentration of sugar in the nectar raises the liveliness of the dance; difficulties on the way to the site, such as strong wind, recognizable threats from enemies, or narrow entrances, reduce it. Lively dances attract the interest of a larger number of followers than do less lively dances, and bring more recruits to the particular feeding sites.

A dancer knows what she has to express from information she collects during the flight between the hive and the feeding site. But how do the followers read this message? Extreme slow-motion video recordings have provided valuable insights. The dance followers use their antennae to detect the message from the magnitude of movements coding the direction and distance in the repeated sequence of the dance.

Using the tactile sense of their antennae, the dance followers detect the message in the repeated sequence of the dance choreography, which allows only differences in the magnitude of movements coding the direction and distance. Correctly stationed dance followers stand still during the dance, with their antennae stretched out stiffly in front of them at an angle of about 90 to 120° to one another. They are so close to the dancer that her laterally moving abdomen rhythmically displaces the antennae. During the waggle phase, both antennae of a dance follower will be simultaneously displaced when she stands at right angles to the dancer, and alternately when she stands directly behind the dancer. For locations between these two, there will be correspondingly different combinations of antennal displacement (Fig. 4.24). The dancer leans forward during the waggle phase, while the dance followers stand still, so the pattern of antennal displacement changes in a predictable fashion. Each dance follower is aware of her own position on the comb, because she has gravity detectors (▶ Fig. 7.12). She can determine the attitude of the dancer on the comb if she combines the information about her own spatial orientation with the received pattern of antennal displacement. The duration of the waggle phase that codes the flight distance corresponds to the duration of the dance follower's antennal stimulation.

Fig. 4.24 In the dark hive, the antennae of the dance followers are used like a blind man's cane to detect the movements of the dancer. The rhythmic back and forth oscillations of the dancer's body tap out the waggle rhythm on the stiffly outstretched antennae of the dance followers. A unique pattern of contact between the dancer's body and the dance follower's two antennae characterizes each position of the follower relative to the dancer. Information about the duration of the waggle phase (the distance to the food source), and the location of the dancer relative to gravity (the direction to the food source) is thus encoded

Not all the questions about these interactive dances have been answered. Today, we have the same situation as that prevailing after the initial discovery of the dance: we have a clear correlation between the locations of the dancer and the dance followers, and know the pattern of antennal displacements that results from this. That the antennal displacements are used as information has still to be confirmed.

Dancing and follower bees meet on chemically recognizable dance floors that may be purposely marked by them (see also Chap. 7). While the message about the location of the food source is most likely received over the antennae, an important link in the procedure is missing: how do interested bees find dancers on the busy, crowded, and dark dance floor?

High-tech eavesdropping, in combination with behavioral observations on physical details of the waggle phase have played a significant role in recognizing the importance of comb vibration. The chemistry of the dance floor can lead the communication partners into the same area; the physics of the comb is responsible for leading the partners to a direct contact. In the darkness of the hive, vibrations of the comb direct prospective dance followers, already assembled on the dance floor, to the dancer. These vibrations are transmitted over the thickened rims of the comb cells, which together form a "net" on the surface of the comb described in Chap. 7 (Fig. 4.25 and ▸ Fig. 7.23).

Bees produce vibrations by means of the thoracic flight musculature, the most powerful they possess. The bees run these muscles at full power, but with the wings uncoupled so that they move only slightly. The flight motor does not contract and relax continuously, but produces pulses that are in most cases synchronized with the maximum left and right excursions of the abdomen during the waggle dance. The basic frequency of these vibrations lies between 230 and 270 cycles per second.

In some cases, "silent" dances can occur that are no different in their appearance for human observers, but from which the flight motor vibrations are missing. Silent dancers fail to attract, and consequently no foragers are recruited. The remarkable waggle motion is apparently being employed as a mechanical strategy to introduce the flight muscle vibrations into the comb through the legs. A lightweight dancer standing, or even running over the ridges of the cells would not transfer energy of any significance to

Fig. 4.25 The thin walls of the wax comb cells terminate along their upper edges in a thickened bulge. Together, these form a continuous mesh that rests on the surface of cell walls

the comb over her thin legs. During the waggle motion, however, she is anchored to the rims of the cells with her feet, and so places the cell rims alternately left and then right under tension with her feet. This tension is highest at the reversal point of the waggle motion, because that is when the bees pull most strongly on the cell rim. And at precisely this moment, when the rim is under the greatest tension, the vibration is introduced into the comb. The bees emphasize each reversal of direction of the abdomen with a vibratory pulse.

The vibratory signals that the dancers produce are nevertheless very weak, compared to the constant and powerful background noise of a buzzing hive. Communication systems, both natural or artificial, are designed to achieve the highest possible signal-to-noise ratio, and the relevant signal has to be strong enough to be recognized in spite of the background noise. Loud buzzing is continuous in a beehive, and the waggle dance vibratory signal from a single bee is too small to be detectable above this noise.

How do interested bees detect even the presence, let alone the location of a dancer, given such weak signals and high background noise? A physical peculiarity of the vibrational properties of the comb is critical here, and this will be explained in detail in Chap. 7. It appears, though, that the pattern of vibration in the horizontal plane, which each bee detects from the rims of the

Fig. 4.26 Interested bees in the dark hive detect the position of a dancer from a distance, through the two-dimensional oscillatory pattern of the cell walls. The walls of the cell outlined here in white move in opposite directions. The cell walls of all the other cells move in the same direction as each other (▶ Fig. 7.27). The bees detect the vibration of the cell walls with their legs. Once they have interpreted this information (like the bee in the picture touching the cell *outlined in white*), they turn their heads in the direction of the dancer, rotate their bodies, and then run toward her and join in the ballet as a follower. The distance from which a dancer can be localized in this fashion is highly dependent on the physical construction of the comb on which the dances take place. The image of the dancer whose vibrations are leading to the oscillation patterns in the cells is blurred by her rapid movement

cells with her six legs (▶ Fig. 7.27), describes the direction and the distance of the dancer on the comb relative to herself (Fig. 4.26).

The comb vibrations serve only to lead the follower to the dancer. They contain no information about the location of the feeding site.

In spite of what is known about the dance language, many important questions have still to be answered. There are some surprising anomalies related to elements of the waggle phase, and the location of the food source:

- The direction of sequential waggle phases, danced for the same goal, differ from one another.

- The duration of the waggle phase that codes the distance depends on the visual structure of the landscape between the hive and the feeding site.
- The representation of the flight distance becomes less precise as the distance increases. Dances for a 2- and a 3-km flight path—which is about the limit for normal foraging flights—are almost the same, although bees can be found foraging at distances of 10 km from their hives. Such extreme excursions cannot be very accurately communicated in the dance.

How do recruits find feeding sites with such inaccurate instructions?

Recruits, Please Follow the Signals

The observation of recruits that have followed a dancer for many rounds is informative. To reach the feeding site on her first flight from the hive, such a bee takes up to 30 times as long as a bee that has already visited the site. A bee with local experience can cover the distance in 40 s; a newcomer leaving the nest for the first time after witnessing the dance can take up 20 min (minute) to reach the feeding site. A significant decrease in the newcomer's flight time occurs if the feeding site is attractively scented, and if the wind carries the scent directly to the hive. Dancers visiting unscented feeding sites provide clear evidence that contact and communication are practiced by bees in the field. Bees with and without local experience, at least when flying to a feeding site, form small mixed groups of up to about ten individuals. Those with local experience land first, followed soon after by the inexperienced bees (Fig. 4.27). Tandem landings sometimes occur—the experienced bee below, and the inexperienced bee on top.

How do such groups of foragers form? Our knowledge about this is meager, but it appears that bees that dance in the hive will help the recruited bees in the field. A bee that has visited a feeding site and not danced in the hive will fly in a straight line back to the site where, upon arrival, she lands immediately. A forager

Fig. 4.27 Newcomers are led to flowers by experienced bees. This often results in tandem landings by foragers and newcomers

that has danced, however, will circle the goal in large loops while producing a loud buzzing. These buzzing flights led Karl von Frisch, before he had discovered the dance communication, to consider the possibility that bees were acoustically leading their nest mates to the feeding sites. The low velocity of the "buzzing flights" allows an observer to notice light-colored stripes on the abdomen of the buzzing bees. These are the exits of the wide-open Nasanov glands found between the last two segments of the bee's abdomen. An open Nasanov gland extrudes the scent of geraniol, which is important in several behavioral contexts (see also Fig. 4.13). Non-buzzing bees, which land without circling the site, and without company, keep their Nasanov glands closed. Buzzing foragers land in the company of recruits. No groups of experienced and newly recruited bees leave the hive together to fly to the same goal; these must form somewhere between the hive and the feeding site.

Fig. 4.28 Experienced foragers that have visited the same feeding site often keep close together as a group in the hive, and form a communal ballet corps at the dances

There is also a group of bees, however, which very quickly and without any help turn up at the indicated feeding site after following a dance in the hive. These are experienced foragers that already know about, and have visited the site, sometimes up to several days earlier. Foragers that collect from the same site, and that are marked with a small paint spot, can be observed to stay close to one another in the hive, and even spend the night in the same cluster (Fig. 4.28). Such groups of bees are often also found taking part in the same dances, where one of them will be the dancer and the others the dance followers (Fig. 4.29). Dancers therefore do not recruit only newcomers, but experienced foragers as well, even those that have visited the same site as the dancer herself. In this way, experienced foragers are possibly alerted to the replenishment of an already well-known source.

Bees have no true sense of hearing, and so “buzzing flights” in the vicinity of the feeding site cannot be perceived acoustically by

Fig. 4.29 Experienced pollen collectors in a group of dance followers that have visited the same pollen source as the dancer

follower bees, and used for orientation. The flights are nevertheless visually striking, and would optimally stimulate the motion-detection abilities of the bees. The "buzzing" sound of the flights is probably an unintentional result of the way the wings are employed to produce turbulence. This turbulence can, like the wake of a ship on the water surface, or the eddies behind an airplane, remain stable in the air for some time, capturing pheromones from the Nasanov glands and providing chemical signposts as additional guides for the newcomers.

Many elements of the communication used to recruit miniswarms to feeding sites are also observed in "true" swarming behavior. Miniswarms of foragers are not placed under the same selection pressure as are true swarms, because the fate of the entire colony is not at stake. A truly swarming colony has to be quickly led to a new home, or it will perish (▸ Fig. 2.8). The behavior used to recruit to food sources possibly developed from the "true" swarming behavior.

Recruitment of newcomers to feeding sites is a highly complex behavior in which bees in the hive and in the field communicate with one another. Flowers add important aids, such as the odors absorbed onto the body of the dancer, which in addition to those borne in the wind, serve as olfactory signposts. With sufficient natural resources, bee colonies will develop normally even if the ordered dances are completely disoriented by tipping the hive on its side, and so removing gravity as a reference point, and the ability of the dancers to convey information about direction. A colony that is surrounded by sufficient and spatially evenly distributed resources is not disadvantaged by this treatment, and will find enough flowers to satisfy its needs, by chance in searching and by the detection of odors. The dance communication becomes critical when resources are spatially confined and less abundant. Focused recruitment will then considerably improve the harvest.

5 Honeybee Sex, and Virgin Brides

We still are guessing more than we know about sex in the private life of honeybees.

Sex maintains the diversity and variety of characters in a population. It achieves phenotypic heterogeneity by joining an egg and a sperm cell, and combining the hereditary material of each in a unique way in the genotype of a new, young female or male individual. Honeybees are no exception to this general rule, but as in many other aspects, they nevertheless present us with the unusual.

Female organisms generally produce relatively few gametes, but these are large, richly supplied with nourishment, and valuable. This is the biological definition of "female". Males, on the other hand, produce minute sperm cells, and because these are reduced to virtually a "genotype with an outboard motor", a very large number can be created. From a "gameto-technical" point of view, a few males in any population would be able to fertilize all the females.

In honeybees, however, we find the opposite situation. For the ten young queens that a hive can maximally produce, there are between 5,000 and 20,000 drones in any honeybee colony.

Without going into the question, at this stage, about the reasons for this imbalance (it will be considered again in the last chapter), it is still of interest to consider a situation in which we have the same number of females and males in a population. We could imagine that this would lead to the males competing for the females, because only a few males are needed to produce sufficient sperm for all the females, thereby making most of the males superfluous. Such competition is, of course, well known in such populations, and expresses itself in behaviorally recognizable mating displays, or contests between males.

In honeybee colonies, there are, by and large, about a thousand males for a single female. The competition should be gigantic, but as we will see, the issue is remarkably peaceably settled.

To answer the question “how do bees do it”, we find some explanations in the unusual details of honeybee sex. The study of this has yielded new insights in this area of bee biology, and uncovered gaps in our knowledge.

Only a few of the approximately 1 million daughters that a queen produces during her life will mate, because it is exclusively the young queens that undertake a “nuptial flight”—and then only during a single period in their lives. The situation is not much better for drones, and for the greater majority of the drones, in fact far worse. Of these only a few dozen, if that, will ever be involved in the mating procedure. And then they pay on the spot with their lives.

The Nuptial Flight

Many myths surround the mating behavior of honeybees, mainly because it is very difficult to observe, and this has made it somehow mysterious. Drone assemblies, marking the locations where mating takes place, are almost mystical. New drones become sexually mature about a week after hatching, and collect year after year at precisely the same places, where they buzz around in concentrated, noisy masses in the air, waiting for the arrival of young queens.

But how does a queen, sometimes transported by apiarists to a place where she has never been before, find a drone assembly? Why is there no aggressive competition between the drones in their hives, or between those from different colonies in their attempts to mate with queens? And why do worker bees remain apparently indifferent to the exciting events involved in the mating procedure? Does it really make sense for a colony to raise only a few new queens, and then let these valuable individuals—on which the reproduction within the colony depends—go off alone in a dangerous and unknown world?

Questions upon questions, the answers to which come slowly and gradually. But there are some fixed reference points in this puzzling world of bee mating. Drone assemblies, for example, have been observed in many parts of the world, and can extend over areas that range from 30 to 200 m across. These form in a landscape that usually contains clear visual features that apparently attract the drones. Such features can be large trees, or aspects of the horizon, such as dark objects in front of a bright sky, or bright gaps in a dark barrier. Flowing water, both above and below ground, has been proposed as a possible orientation aid.

Surprisingly though, such assemblies are not essential, because mating will take place also where no drone assemblies have ever been seen. This leads one to suspect that drone assemblies are a result of the landmark-based aggregation behavior of drones occurring where landmarks are at hand. If the appropriately conspicuous landmarks are present, a drone assembly will form; if not, mating will take place in any case.

Even in those regions where drone assemblies are found, it is possible to observe that the flying mass of drones is not stable in its location, but drifts relatively rapidly across the landscape. Drone assemblies have been seen to disband, reassemble in a short space of time at another location, disband, and appear yet again at a third location. The area where drone assemblies occur appears to be covered with a diffuse network of drones in which tight clusters form from time to time.

Drones do not, as was previously supposed, remain continuously in the air after leaving the hive. They can be found resting in the vegetation on the ground, or on the leaves and branches of trees (Fig. 5.1), and not only during the so-called drone eviction when, at the end of the mating season, the drones are turned out of the hives (Fig. 5.2).

So what are the drones that are sitting or flying outside the hive waiting for? The young queens, of course.

Virgin queens that are about a week old leave their hives once, or more often, for periods of usually only a few minutes (but possibly up to an hour), and return to their colonies after successful mating. A queen can leave the hive several times on nuptial flights, and will continue with the flights until her sperm reserve gland is filled. A single drone can deliver up to 11 million sperm cells. At the end of a single nuptial flight, the queen will retain a maximum of 6 million sperm cells, but this is only about 10% of all sperm cells with which she is finally impregnated. These she stores in her sperm reserve gland, and takes them back to her

Fig. 5.1 Drones are highly effective flying machines, but do not fly without stopping. They can be found resting in the vegetation even during the mating season

Fig. 5.2 Drones become superfluous at the end of the mating season. Those that remain are no longer fed, are expelled from the hive, and die

hive. The sperm is kept fresh in the queen's sperm gland over several years throughout her life—a natural sperm bank from which around 200,000 eggs are fertilized per year.

Drones leave the hive from late in the morning to the middle of the afternoon, coinciding with queens that leave the hive at the same time. While the young queens, if their first flight is successful, do not need to leave the hive again, the drones leave the hive every day, regardless of whether young queens are about or not. The daily drone flights are undertaken in most cases without mating, and are an indication of considerable competition between drones of different colonies in any particular region. The mostly fruitless mass exodus of the drones from the hive each day, and which continues over several weeks, nevertheless reduces the risk of missing a young queen that is outside the nest—a huge effort, but the possible reward, in the form of fathering thousands of bees, is high.

The massive investment in the number of drones and their flight activity may be coupled with the lack of aggression between the drones. An interesting contrast is found in solitary species where rivalry between the males is conducted at the level of the sperm cells themselves, a process known as sperm competition—within the female sexual organ, a physical contest takes place between the sperm cells for access to the egg. Here, the recipe for success lies in the sheer amount of sperm that is inseminated.

In the bee colony superorganism, drones are virtually flying sperm carriers. They go off in their masses to the mating grounds, and have the same function as that of individual sperm cells in sperm competition within the female of solitary species: displacement of their rivals through overwhelming numbers.

When they are outside the hive, the queens use an olfactory lure to which the drones are highly attracted. But only outside the hive. Within the nest, they ignore each other although living for weeks within touching distance (Fig. 5.3), and breeding is avoided.

From genetic studies it is known that a queen will mate with a number of drones during her nuptial flight, which can be the only flight of her life. In flight, the drones approach the virgin queens against the wind, lured by the "queen substance" exuded from her mandibular glands. Within the nest, this same substance suppresses the development of the ovaries of the workers.

Once the drones have caught sight of a young flying queen, they rapidly fly after her, guided by their visual systems, and appear as though fastened to the queen by an invisible thread. If they catch up with her, they grasp the queen with their legs, and latch on to her genital organ with their mating apparatus. They extrude about 50% of the endophallus, and then just hang passively on the queen. Once the drone has become passive, the complete extrusion of the endophallus (see Fig. 5.4), and the transfer of sperm cells are undertaken by the queen herself, through a strong contraction of her abdominal muscles. It is not unusual for this

Fig. 5.3 Virgin queens and drones live platonically with one another in the hive

process to result in the explosion of the drone's abdomen, with a sometimes audible snap while still in the air. The bursting of the drone's abdomen results in his immediate death.

The endophallus, part of the male sexual organ, initially remains attached to the queen. It constitutes the so-called mating sign, is very attractive for pursuing drones, and consists of mucus from slime glands, the chitin strap of the endophallus, and an orange-colored and sticky (UV-reflecting) coating, the cornua (Fig. 5.4).

The firmly attached endophallus (Fig. 5.5) is not, however, some kind of chastity belt that blocks the access of subsequent drones to the queen, but just the opposite: the odor of the mating signal, and its specific reflection of the ultraviolet component of sunlight, to which the eyes of drones are particularly sensitive, lure more drones to the queen. They remove the plug, or so it is supposed, and after mating replace it with their own seal.

It is remarkable that successful drones leave a signal to show successors the way to copulation. What possible advantage can they gain from this, and from the complete absence of aggressive competition? A possible answer to this question is provided in Chap. 9.

Fist-sized groups of drones lying on the ground with a queen at their center is not an unusual sight in the mating season. A mating couple, consisting of a queen (a poor flier, in comparison

Fig. 5.4 A drone has extruded his large mating organ. The large white bladder contains the sperms cells. The two downward-facing hooks latch the drone to the queen during mating

Fig. 5.5 After successful mating, part of the endophallus remains in the sting chamber of the queen, and is brought back to the nest after the nuptial flight, as a sign that fertilization has occurred

with the workers) carrying a passive drone, is not particularly good in the air and often lands on the ground. Other drones are attracted, in the hope of also being able to mate. All other species related to honeybees, such as bumblebees, wasps, and ants, copulate on the ground (Fig. 5.6).

Much remains unknown about mating in honeybees. An important question, for example, is whether the majority of the colony—namely, the workers—are really indifferent, and entirely uninvolved in the crucial affair between the queens and the drones?

Worker Bees as Bridesmaids

The nuptial flight is an extremely risky undertaking for the queen, and for the entire colony for which the queen is essentially a single "flying gamete". Bees in flight are preyed upon by many. And here one should not think only of the "bee wolf", large wasp, the

Fig. 5.6 Colony-forming hymenopterans such as wasps or bumblebees mate on the ground, and never in flight

females of which catch single bees and bury these in tubes in the ground to provide food for their larvae. Many birds catch honeybees, and learn how to cope safely with their stings. Should this single young queen, this thin thread on which the future of the colony is suspended, the result of the combined effort of all the bees in the colony, be allowed to be underway completely alone in the dangerous world outside the hive?

Hard to imagine. Bee colonies have developed optimal solutions to every imaginable problem, and one may ask if they have really not found a more certain way to conduct this key event on which the future of the hive depends. A phenomenon called "mass orientation flights", long known to beekeepers as small swarms of bees clustered in front of the hive, has thrown some light on this question. During a particular time of the year, and just at that time of the day when young queens and drones are expected to leave the hive, clouds of bees that continuously take off, and land again can be seen at the entrance to the hive (Fig. 5.7).

Fig. 5.7 During the mating season, so-called mass orientation flights take place in front of hives, and foraging activity is considerably reduced

A proposed explanation for this behavior is that it represents orientation flights of young bees. There is, however, based on simple experiments and the careful observations detailed below, another explanation suggesting that mass orientation flights have a completely different, and more focused significance in the honeybee mating process.

For example:

- If young bees are marked as they emerge from the hive, and records are kept of the time of day at which they undertake their first flights, it is found that they leave the colony, undertake their first orientation flights, and return to the colony over the entire duration of normal flight times between sunrise and sunset, and not only during mass orientation flights. Nor is there a concentration of young marked bees during the time that mass orientation flights take place.
- If an entire mass orientation flight swarm is captured, and its members examined, young bees are certainly present but in small numbers, which is to be expected if they are active at all times during the day. The majority of bees in the mass orientation flights turn out to be old and experienced forager bees, evidenced by their tattered wings or worn-off bristles. These old foragers certainly do not need to undertake orientation flights. Indeed, some captured in the mass orientation flight swarm have come directly “from work”, and can be recognized by their full pollen baskets and nectar-filled crops.
- Normal mass orientation flights take place at the usual time each day in colonies that contain only old forager bees.
- No mass orientation flights take place in a colony in which, over several weeks, there has been no queen, but to which young bees are added regularly in an amount approximating the normal birth rate were a queen present.
- If a queenless colony in which no mass orientation flights take place is provided with a queen, then mass orientation flights take place from the first day onward of the queen’s presence.
- Mass orientation flights occur only at that time of the year when the drone flights take place, and when the young queens leave their colonies on their nuptial flights. Earlier and later in the year, the colony produces many new worker bees that have to undertake normal orientation flights, but that never form mass orientation flight swarms.

- The foraging activity of the colony is temporarily, but nevertheless clearly reduced during the occurrence of mass orientation flights.

The theory that mass orientation flights represent the orientation flights of young bees is obviously untenable. What then is the reason for these mass orientation flights, if they occur only in the presence of a queen?

With patience, it has been possible to witness a young queen emerging from the hive for her nuptial flight, and see how she walks to a point in front of the entrance accompanied by a retinue of up to 20 workers, before flying off together with the entire group (Fig. 5.8).

Coincident with this departure of the queen and her retinue, the mass orientation swarm also disappears, to appear again in front of the hive the moment the queen returns (Fig. 5.9). If the queen does not appear and fly out of the hive, the mass orientation swarm disbands within about half an hour, but returns the following day to repeat the performance.

After returning and landing, the queen immediately retires to the safety of the hive, with her closely accompanying group of worker bees. Many of the bees in the newly formed mass orientation flight swarm also enter the hive (Fig. 5.10), and the mass orientation swarm rapidly disperses.

A queen returning from a successful nuptial flight will often carry the endophallus of the drone that sacrificed himself in the last mating, attached to her sexual organ (Fig. 5.11). This “mating sign” is removed from the queen by worker bees in her retinue, either before returning to the hive (Fig. 5.12), or immediately after she is within the nest (Fig. 5.13).

Just what happens out in the field, and what role is played by the worker bees that accompany her, is still unknown. Nevertheless, a picture is slowly developing from the analysis of an extensive number of recorded observations of individual beekeepers.

A beekeeper, not depending on artificial insemination of his queens, has two options for the fertilization of queens from his hives: (1) local mating, where he leaves the pairing process up to the young queens and drones, relying on the presence of fully developed colonies already established in the area, and (2) transportation of the young queen with a “minicolony” of a few hundred

Fig. 5.8 A virgin queen, accompanied by a group of workers, leaves the hive to fly off to her nuptial appointment

Fig. 5.9 On her return to the nest the queen is, as when she left it, accompanied by a group of workers

Fig. 5.10 A newly fertilized queen lands, and enters the hive with her retinue. She may not leave the hive again until a year later, during the swarming season

Fig. 5.11 A queen sometimes returns to the nest carrying part of the endophallus of the last drone with whom she mated, as a mating sign

Fig. 5.12 Should the queen vanish rapidly into the nest, the mating sign is removed there, and not in the open

worker bees, housed together in a small mating box (Fig. 5.14), to a so-called mating station where large colonies with many drones are known to be established.

Interestingly, the loss of queens seldom occurs in local mating situations, and virtually every queen returns fertilized and healthy to the hive from her nuptial flight. On the other hand, about one of every three queens that have been transported to a different area, and that fly out from minicolonies, is lost. Under natural conditions, such a 30% loss would be potentially serious, considering the very few queens that are produced in any season by each colony.

What causes this difference in the survival of the queens? Perhaps the size and abilities of the group accompanying the queen on her flight? A queen flight led by forager bees would make a lot of sense. The queens have either no knowledge at all of the area outside the hive, or at the most a poor impression gained from a few orientation flights. Experienced forager bees have the geography of their habitat in their heads, and can provide a guide, especially for the return to a hive that they have recently left. For the security of the queen, this return needs to be rapid and direct. Young queens are the most valuable commodity that a honeybee colony produces, and great care must be taken for their safety.

Fig. 5.13 A worker removes the mating sign from the genital opening of the queen

A small titmouse, lured by the flying spot of a queen against the bright sky, can threaten reproduction within the colony. Group flights can help not only with orientation, but may also provide a measure of protection through the “herring shoal effect”. The larger the number of worker bees that populate the mating area, the greater will be the protection through this effect, a possibility supported by the observation that all the queens of large colonies usually return from their nuptial flights, whereas in small colonies only two of three return.

Fig. 5.14 Beekeepers arrange the mating of free-flying young queens at so-called mating stations where a mini-colony, consisting of the young queen and a few hundred workers, is set free in an area where there are resident colonies with many drones

One could propose an even more active role for worker bees in the mating process: it is known that if a young queen is placed on a leaf out in the open, and does not immediately fly away, she will be surrounded within a few minutes by a small group of worker bees, although she may be several hundred meters away from the nearest hive. Drones, which are attracted by the receptive queen and arrive a little after the workers, are aggressively driven off, and even pursued as they fly away. Such pursuit flights, in which worker bees are chasing drones, would appear to an observer just like drones chasing queens, unless the entire development of this behavior had been continuously recorded.

The aim of the worker bees is not clear, nor is it known whether this behavior is an exception, or the rule. Nevertheless, it would appear that workers closely associated with the queen allow some drones access to her, and others not. The possibility that the workers are selecting which drones will mate with their queen raises some exciting questions for future research. Is this another safeguard against inbreeding?

After the nuptial flight, the queen will not leave the nest again until about a year later, when her colony adopts a new queen, and when she leads a swarm of followers to find a new home. The sperm cells that are taken up by the queen in the initial pairing remain viable for years. Should the sperm reserve be exhausted, though, the queen will lay only unfertilized eggs that develop into drones, and she will have played out her role in the immortality of the colony.

Whole-animal Gametes

But let us return to the matter of raising sexually active individuals in the colony: the first sign that a colony has begun to raise drones and queens—in terms of the hive as a superorganism, these are virtually "whole-animal gametes"—is provided by changes in the architecture of the comb. Queens are raised in queen cells, of which a small number are usually constructed along the edge of the comb. The larvae that reside in this royal accommodation are at first indistinguishable from those that will turn into future workers. The exclusive diet of "royal jelly" that the larvae in the queen cells are given, however, results in their developing into queens. The old queen is treated less well. She is given progressively less of the royal jelly, and in the end has to live partly on honey, slimming her down in preparation for her departure from the hive with a primary swarm of workers. About a week after the old queen has departed with about half the colony in a primary swarm, the first of several young queens emerges from her cell (Fig. 5.15).

Young queens that come across each other in the nest will fight until one of them is dead (Fig. 5.16). Raising young queens that then kill one another, though, is not particularly productive, and most contests of this nature are avoided when the first young queen to emerge quickly leaves the nest like the old queen did before her, but with another portion of the original colony in a secondary swarm. Sometimes a second queen born shortly after the first will join the secondary swarm. The unfortunate result is that the inevitable deadly dual is simply moved to another venue.

Fig. 5.15 A new queen sees the light of day. Emergence from the cell, however, like everything else in the hive, takes place in complete darkness

The fatal combat between valuable young queens is sometimes averted by another remarkable behavioral mechanism: the first emerging queen engages in a vibratory dialogue with the queen still enclosed in her cell. The signals used in this communication are loud enough to be heard some distance from the hive. The firstborn queen "toots" after she emerges from her cell. Workers helping the next queen in emerging become motionless when they receive this signal. Occasionally, the "toot" is answered with a "quack" from the queen still in her cell. The curious duet delays the emergence of this second queen, and avoids the conflict that would follow if she did.

The appearance of drones is also announced by architectural changes in the comb. When there is no reason to raise drones, which outside the mating time would only be idle mouths to feed and a drain on the colony's resources, worker bees build comb cells that have a diameter of 5.2 to 5.4 mm. If drones are needed, however, then a few thousand extra cells are added to the edge of the comb, which have a diameter of 6.2 to 6.4 mm, and can make up about 10% of the whole cell number of the colony (Fig. 5.17).

Fig. 5.16 A deadly duel ensues when two young queens meet one another, in which the poisonous stings are used without mercy

The queen uses her forelegs to gauge the size of the cells. If she comes across a cell of small diameter, she lays a fertilized egg that will develop into a female individual; if she finds a large cell, she lays an unfertilized egg that will develop into a drone. The machinery in the sexual apparatus of the queen bee, which can allow a few sperm cells access to the egg, or prevent this, must be very reliably controllable. Nevertheless, it is not the queen that decides on the sex of the offspring and the eventual consequences, but rather the workers of the colony. The queen is merely their instrument.

Setting a High Standard—Removal of Inadequate Queens

The colony also decides when it is advantageous to change queens. As a rule, it is an old queen that is replaced. This is logical, because the sperm cell stores that were established during the nuptial flight will sooner or later be used up. The queen produces

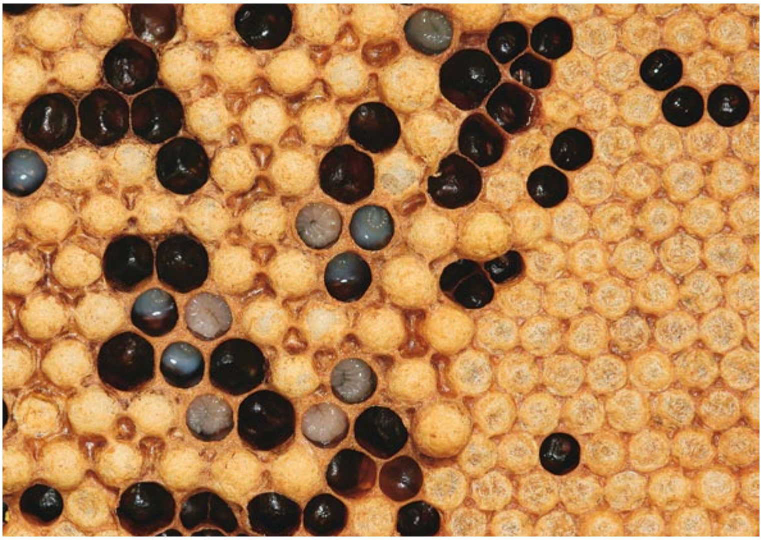


Fig. 5.17 Capped brood combs with flat lids on the worker cells (*on the right*), and rounded lids on the drone cells (*on the left*). The small worker cells and large drone cells determine the egg-laying behavior of the queen. She lays fertilized eggs in the small cells, and unfertilized eggs in the large cells

a special pheromone. "Court" bees, grouped around the queen, frequently lick her body and take up the queen odor from her body surface (Fig. 5.18). These bees then spread her pheromone throughout the hive via the continuous exchange of food that occurs between workers, and with it, information about the presence and condition of the queen.

Should the concentration of the queenly perfume decline to below a particular level, as happens when a queen becomes older, a replacement queen is reared.

Initiation of the queen replacement process does not require the occurrence of an extreme situation. Minor handicaps that appear relatively trivial to a human observer can lead to queen replacement. A queen without a leg, provided this is not the foreleg used for measuring cell size (Fig. 5.19), is not handicapped, and is able to ensure the production of the next generation despite this loss. Clearly, though, the standard for a perfect queen is high, and such a small departure from normal can result in a new queen being raised, with the predictable demise of the old queen. Such a "quiet revolution" can sometimes result in the old queen continu-

Fig. 5.18 Worker bees of the queen's court lick her body, and ingest her pheromone. Through trophallaxis, or food exchange between bees, the queenly perfume is distributed through the colony

Fig. 5.19 This five-legged queen has not met the criterion for perfection required by her colony, and the workers have begun a "quiet revolution": they have raised a new queen

ing to lay eggs without being disturbed for a significant period, even after a successful nuptial flight of the new queen.

Replacement queen cells are unlike those used for normal queen rearing, in that they do not hang along the edge of the comb, but are constructed in the middle of it. Replacement queen cells are produced by extending the walls of a normal-sized comb cell (Fig. 5.20).

The replacement process also functions in emergencies, such as the sudden death of a queen, but can occur only if the colony also has larvae at this critical moment. All larvae that are 1.5 to 3 days old potentially have the possibility of a royal career, should they be placed on the special diet. Their cells would be hurriedly enlarged, and transformed into queen cells. In such emergencies, there is often not enough time to activate the wax glands on the workers' abdomens, needed to produce the fresh beeswax for the cells, and therefore old wax is scraped together and reworked to build replacement queen cells. Should a queen die when there is no appropriate brood, this means the end of the colony. In general, honeybees do not allow such a situation to develop.

The young replacement queen emerges and departs on her nuptial flight, and with the hereditary material that she brings back with her, ensures the continual flux of the gene pool that will determine the characteristics of the colony.

Fig. 5.20 Should a queen suddenly die, an emergency queen cell is constructed of old, scraped-up wax, and a replacement queen raised as quickly as possible

6 Royal Jelly—Designer Diet in Bee Colonies

The larvae of honeybees obtain their nourishment from a glandular secretion of adult bees, the function of which is comparable with the mother's milk of mammals.

Honeybees are insects that undergo a complete change during their development. The well-defined steps are the egg, several larval stages, the pupa, and finally the adult bee. In this respect, bees follow one of the standard paths of insect metamorphosis. Insect larvae obtain nourishment from either plant or animal tissues that they collect themselves, or which are provided by the adults. Honeybees nourish their larva with a secretion produced by nurse bees in special glands in their heads, a sort of surrogate mother's milk. This made-to-order nutrition provides opportunities to manipulate the nature of the resulting adults; the production of a new queen is one of the more striking uses of this option.

In summer, the queen lays between 1,000 and 2,000 eggs every day, each in its own cell (Figs. 6.1, 6.2). At one to two eggs per minute, the queen lays about the equivalent of her own body weight each day. Translated into human terms, this would mean about 20 babies per day for an entire summer.

Cells are thoroughly cleaned by young bees before the eggs are laid in these (Fig. 6.3).

The Larvae

A tiny larva leaves the egg case after a 3-day-long embryonic development period within the deposited egg (Figs. 6.4, 6.5).

Fig. 6.1 A queen shortly before laying an egg. Worker bees help align the tip of her abdomen, so that she can back into the chosen cell

The developmental paths for workers, drones, and queens are recognizably different from one another. All proceed through five larval stages (Figs. 6.6–6.8), but these are of different durations: larval stage duration is intermediate for the workers (Fig. 6.9), longest for the drones (Fig. 6.10), and shortest for the queens (Fig. 6.11). The weight gain of the larvae is prodigious. Within only 5 days, they increase their body weight by a factor of 1,000. Translated into human terms, this would mean that a newborn baby 5 days old would weigh 3.5 tons!

Fig. 6.2 Here, a queen has lowered her abdomen down to the bottom of a cell to deposit the egg

The rapid development of the queen is possibly a kind of temporal competition between the young queens: the first to emerge has the opportunity to sting the unborn competitors in their cells.

The last larval stage of all three bee types is so large that when stretched out, it fills the entire cell. At this stage, it spins itself a cocoon within the cell, from a thread secreted from a special gland, and the cell is supplied with a wax lid by the worker bees (Fig. 6.12), beneath which metamorphosis through the pupal stage to an adult bee takes place. The cell cap is porous, so

Fig. 6.3 A young worker bee thoroughly cleans an empty cell in the brood nest, in preparation for the queen to deposit an egg

Fig. 6.4 Egg-endowed cells in the brood nest. The freshly deposited eggs at first stand vertically, then sink slowly down, and lie flat at the bottom of the cell

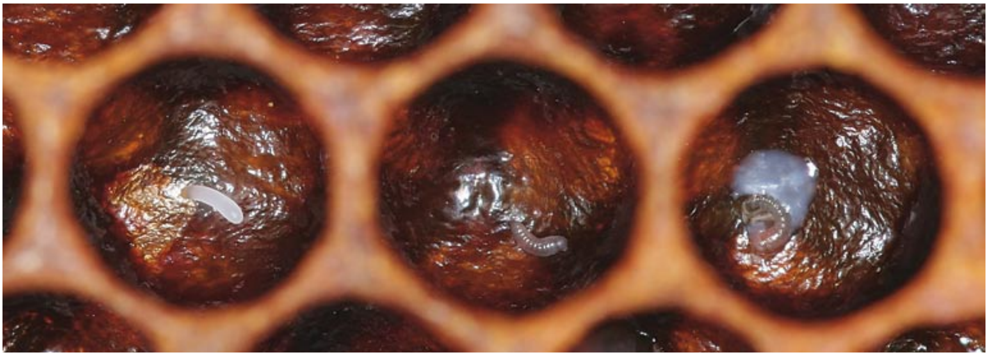


Fig. 6.5 The bee embryo develops within the egg over a period of 3 days (*left*). A small larval bee then hatches (*center*), and is immediately provided with food jelly (*right*)

that gaseous exchange is possible, and chemical signals can pass through it in both directions.

Bee larvae hatched from their eggs land in paradise, because nurse bees supply their cells with a thick soup of royal jelly. This is a mixture of secretions, the components of which are produced in the glands of the hypopharynx and mandibles in the head of the bee. Small drops of royal jelly are extruded from openings on the inner side of each mandible, into the cells containing the larvae (Fig. 6.13). Nurse bees are usually young bees that are between 5 and 15 days old, and consume a significant amount of pollen in order to provide their royal jelly glands with the necessary raw materials. These glands atrophy in worker bees not producing royal jelly—one example of the many kinds of plasticity expressed by the members of the bee colony superorganism.

The young larva are initially nourished exclusively with the royal jelly produced by the nurse bees. They live entirely on a designer diet. A similar form of nourishment of the very young is found in mammals. Bees are not fed mother's milk, but a surrogate produced by their sisters (Fig. 6.13).

A bee larva will consume about 25 milligrams, or 25 microliters, of royal jelly during its larval stage. With a yearly production of 200,000 bees per colony, the total amount of royal jelly will amount to about 5 l per year.

Fig. 6.6 Small larvae feed on food jelly, the so-called royal jelly, which is produced by glands in the heads of nurse bees

Making a Queen

As larvae become older, their diet of royal jelly is mixed with ever more pollen and honey, and the final larval stage does not receive any royal jelly at all. Larvae that receive royal jelly throughout their development develop into queens (Fig. 6.14), although this is not the only factor that determines if larvae will become workers or queens; the components of the royal jelly are also al-

Fig. 6.7 Larger larvae are fed increasing amounts of pollen and honey

Fig. 6.8 On their tenth day of life, the larvae stretch out and begin to spin a cocoon around themselves. Worker bees close the cell with a wax lid

Fig. 6.9 A young bee leaves her nursery

tered: a sugar content of 35% hexose results in a queen, but simple workers will develop should this ingredient amount to only 10%. The developmental program of bee larvae can apparently be switched by "sweetness".

Royal jelly is therefore one of the "environmental factors" that will determine the development of larvae into queens or workers. Infertile workers and fertile queens represent the two castes within the bee colony, and the path to one or the other is set by their diet. Queen larvae are also visited about ten times more fre-

Fig. 6.10 An emerging drone. The cell lid is opened from within by the emerging bee, aided by workers that gnaw at the lid from the outside

Fig. 6.11 A new queen leaves the specially constructed cell in which she has developed

Fig. 6.12 Worker bees close the cells with a wax lid at the beginning of the pupal stage. The metamorphosis of a bee takes place in strict isolation

quently by nurse bees than are worker larvae. Larvae that develop in the direction of queens accept greater amounts of royal jelly, and more often. The difference in the quantity, and also the quality of the diet initiates a complex cascade of biochemical reactions, and the amount and timing of hormone synthesis in the larvae play a decisive role in the establishment of the significant morphological differences between the two castes.

Royal jelly—as a designer diet in the beehive, and initiating the different developmental paths of the bee castes—is under the control of the bees themselves, and is an example of the uniqueness of bee colonies: bees determine their own developmental conditions. Royal jelly is also significant for the health of a bee colony. Like mother milk in mammals, royal jelly provides bee larvae in the first stage of their lives with an immunity against bacterial infection. One of the most prevalent pathways for the infection of the larvae is by the invasion of pathogens through their gut, but here the infections are countered by the royal jelly and its defensive proteinaceous components.

Fig. 6.13 Nurse bees produce the royal jelly for their siblings in their head glands. The jelly is excreted from the inner side of the base of the mandibles (*arrow*), collects on the tips of the mandibles (*inset*), and is packed into the cells with the larvae

Fig. 6.14 In contrast to those of workers and drones, larvae that develop into queens are fed exclusively on royal jelly even when they are large. The opening of the queen cells is downward (the picture is taken from below), but the sticky jelly prevents the larva from falling out

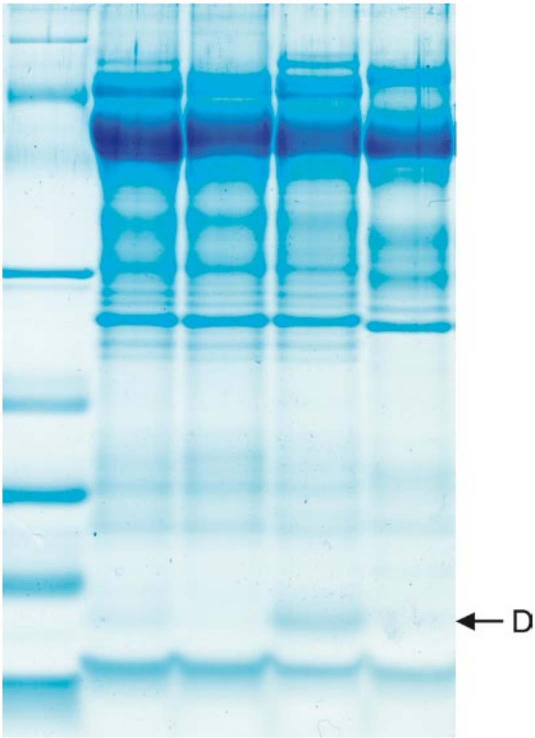


Fig. 6.15 Electrophoretic separation of royal jelly components shows the complex molecular nature of this substance. The single horizontal lines on the gels represent the different proteins. The band marked *D* is defensin, a protein that protects the larvae from infections. In this picture, the test sample run in the *left column* is a mixture of known substances that serve as a calibration. The other four separation columns are samples of royal jelly from different races of bees. The defensin referred to in the text, and marked here with an *arrow*, is present in all races of honeybees

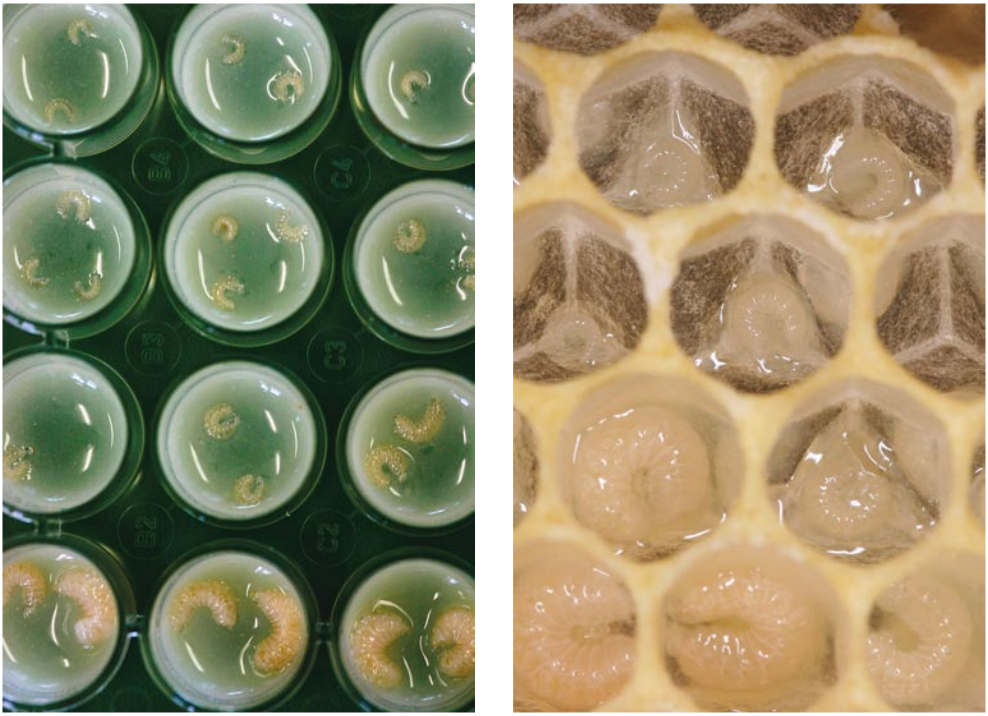


Fig. 6.16 Honeybees can be artificially reared from small hatched larvae, through the pupal stage to the emerged adult (*left*), and so imitate the conditions of the brood nest (*right*)

Honeybee Breeding Station

In terms of the development and health of bees, the significance of some elements found in the analysis of royal jelly (Fig. 6.15; see also the figures in the prolog) is still unexplained.

Honeybees can be artificially reared in the laboratory, from the time the larvae emerge from the egg (Fig. 6.16), through all the larval and pupal stages, to the adult bee. The role played by various elements of the royal jelly in the development, caste determination, and health of the bees can be studied under these conditions by experimental manipulation.

7 The Largest Organ of the Bee Colony—Construction and Function of the Comb

Properties of the comb are integral components of the superorganism that contribute to the sociophysiology of the bee colony.

The nest of honeybees plays a key role as the visible expression of the bee colony superorganism. Its significance for the function of bee colony is far deeper than that which comes to mind for nests in general, i.e., a shelter constructed out of materials from the environment. The comb of the bee nest is in a sense a part of the bees themselves. Even the expression that the comb is a "frozen image of bee behavior" does not completely capture the situation. The footsteps of gulls in the smooth sand of the seashore are also frozen images of behavior. These footsteps, however, have no further consequences for a gull's life, unless they attract predators. The honeycomb as the "spoor of bees", on the other hand, determines the nature and life of bees. A combination of existing hollows, at least in temperate climates, and waxy combs, the nest is not only living space, food store, and nursery, but also an integral part of the superorganism: skeleton, sensory organ, nervous system, memory store, and immune system. The comb and the wax from which it is constructed are not only entirely produced by the bees, but also an inseparable part of their lives, and bound up with the function of the superorganism.

Honeycomb, an Organ of the Superorganism

Material, energy, and information are the three basic pillars upon which all life is built. The physiology of single organisms describes how these fundamental factors are spatially and temporally organized. Physiologists examine in detail the forces and mechanisms that control and modulate these three very different foundations of life.

Honeycomb is an integral part of the bee colony because so many features of its structure play an essential role for the channeling of material, energy, and information in the hive. The nest is not a normal environment in a classical sense, to which bees have adapted themselves during the path of evolution; instead, as an environment constructed by bees themselves, it also has been subject to the forces of evolution, just like any other organ or character of bees. Even forager bees that leave the comb on foraging flights spend more than 90% of their lives within, or on the comb. The protracted amount of life spent on the comb provides countless possibilities for interaction between the bees and their combs, which together constitute the superorganism.

In the year 1850, the great French physiologist Claude Bernard (1813–1878) formulated the influential idea of the *milieu intérieur*, an "environment" within organisms that differed significantly from the environment outside the organism. The inner world is precisely regulated, while the outer one, the *milieu extérieur*, cannot be controlled by the organism. The regulated inner state is called homeostasis.

What, however, is the situation when homeostasis extends to a self-constructed environment, such as in the case of the honeybee? The difference between the *milieu intérieur* and the *milieu extérieur* no longer applies in a true sense. There is no clearly recognizable model of Bernard here where a distinct boundary between *intérieur* and *extérieur* is discernible, because the nest is an integral part of the larger entity, the bee colony superorganism. The nest, with all its features, has developed during the passage of evolution, together with the "bee component" of the superorganism. The properties of the nest are a part of the superorganism, and contribute as much as the single bees themselves to the sociophysiology and biological fitness of the bee colony—for example, in metabolism and communication. Just as evolution shaped the nervous system of bees, so it shaped the nest with its combs as part of an integrated whole.

The Wax Factory

Honeybees manufacture the material for the combs themselves, and in this respect belong to an elite among animals. Wax is produced in eight groups of glands arranged in pairs on the ventral side of the last four segments of the bee abdomen. This area, beneath which the wax glands lie, can be seen as smooth surfaces, the so-called wax “mirrors” (Fig. 7.1). The wax glands develop slowly, needing a few days before they achieve their full size. They reach their peak performance in worker bees, between about the 12th and 18th day of their lives, and then degenerate. Should the need arise, however, older bees can again become “wax gland young”: the wax glands of a significant proportion of the bees will regain their top performance in a colony that is artificially

Fig. 7.1 Eight smooth areas, the so-called wax mirrors, can be found on the ventral side of the worker bee abdomen. Wax from abdominal glands spreads over the mirrors, and hardens into small scales

Fig. 7.2 Worker bees activate the wax glands beneath their wax mirrors, and extrude up to eight plates of wax per day when there is a need to build combs in the hive

manipulated to contain only older bees. Plasticity of age-related abilities extends to many aspects in the life of bees, not only in the production of wax and its appropriate application. A high degree of plasticity in anatomy, physiology, and behavior are a characteristic feature of bee biology.

Once the wax has been extruded onto the body surfaces of the bee, it hardens into small, paper-thin scales (Fig. 7.2).

The controlled production of building materials from their own bodies is a peculiarity of honeybees, with far-reaching consequences for their entire biology. Bees can themselves determine the essential characteristics of the raw material for the construction of the comb. This is like a construction engineer that controls the physical nature of the building materials to suit the project in hand.

Wax scales that do not fall immediately to the floor of the hive are collected by the bee by means of a specially enlarged segment of the hind leg (Fig. 7.3), and passed forward to the mouthparts with the middle and forelegs (Fig. 7.4).

There, the scales are kneaded with the mandibles, mixed with a secretion of the mandibular glands, and brought to a consistency with which the bees can work. A worker bee needs about 4 min to complete the preparation of each scale of wax. About 8,000 cells are made out of 100 g of wax, and about 125,000 wax scales are required for this (Fig. 7.5).

Fig. 7.3 Wax scales are captured with an array of spiny bristles on the hind legs, and passed forward to the mouthparts

The wax production of a colony is particularly high after the move to a new home, and demands a significant input of energy. A swarm that has to construct an entire comb in a new nest must invest the energy from about 7.5 kg of honey in order to produce the 1,200 g of wax that is needed. From this 1,200 g of wax, the bees will, over time, build about 100,000 cells, which represents the content of a medium-sized nest.

Building the Comb

Directly after swarming, the honey provision that was taken on the journey delivers enough energy for the construction of about 5,000 cells, for a start. Foraging begins immediately, and further construction can be continued. Bees that embark on building a comb within a hollow begin on the roof, where they use their mouthparts to attach lumps of wax onto the surface. They may begin in several places at once for each new comb. The starting

Fig. 7.4 Workers knead small lumps of wax with their mouthparts, and add an enzyme that makes the wax easier to work

points for this wax deposition are chosen randomly (Fig. 7.6), but once established, they determine the subsequent activity of the comb builders.

The accumulating, thick lines of wax develop toward one another, because an approaching bee simply adds her parcel of wax

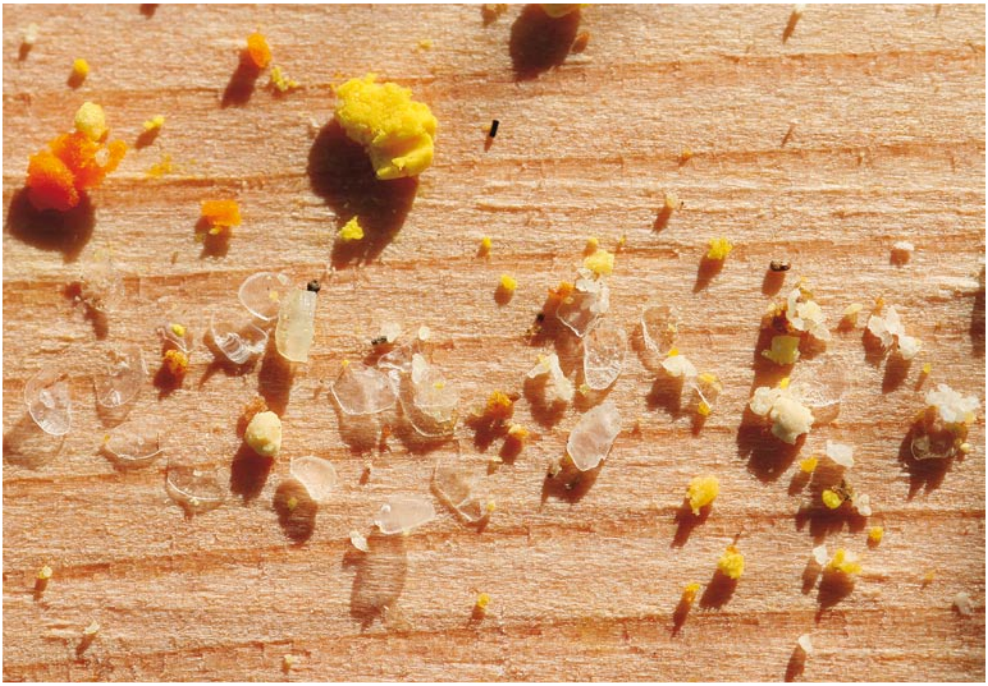


Fig. 7.5 Wax scales rain down onto the bottom of the hive in a colony busily engaged in comb building. These can be seen here lying among packets of pollen that have also fallen from above

Fig. 7.6 The construction of a new comb begins with randomly distributed lumps of wax stuck to the ceiling of the hive

to the already established line. In 1959, the French entomologist P.P. Grasse proposed the term stigmergy for such a mechanism, in which the building of structures requires no communication between the animals engaged in the task. The innate response of comb-building bees to add lumps of wax to already deposited wax results in the rapid formation of thick layers of this material. During comb construction, the bees gradually "stretch" the deposited wax into elongated cells.

Separate sectors of the comb meet so exactly that scarcely any irregularities can be found in the completed cell pattern (Fig. 7.7).

At this stage of comb building, a large number of bees form living chains between the edge of the comb under construction, and the wall of the hollow. They link their legs with one another and remain hanging, motionless, for long periods of time (Fig. 7.8). The meaning of this striking behavior is completely unknown. Do they serve as a rope ladder for bees that collect wax scales that have fallen to the floor, and bring these up to the building site? We do not know.

The appearance of the cells in a comb, with its unbelievably regular geometry, has intrigued all observers, and its pattern has been used many times for artistic ornamentation (Fig. 7.9).

Studying the comb geometry in more detail, our first impressions are confirmed: here is a structure of unbelievable precision that has resulted from the activity of an insect. The thickness of the individual cell walls, measured over a length of several centimeters, is exactly 0.07 mm. The angle between the smooth walls is 120° (Fig. 7.10), and the combs hang vertically. The cell floors are not perfectly horizontal, but slope gently downward to the cell base. The distance between the neighboring parallel combs is typically 8 to 10 mm.

Johannes Kepler, Galilei Galileo, and many other famous, mathematically interested visionaries were fascinated by honeybee combs, because it seemed difficult to imagine how, without an understanding of mathematics, such precise construction was possible.

Studies of the physiology of bees have provided insights into how the vertically hanging and parallel organization of the combs is achieved (Fig. 7.11).

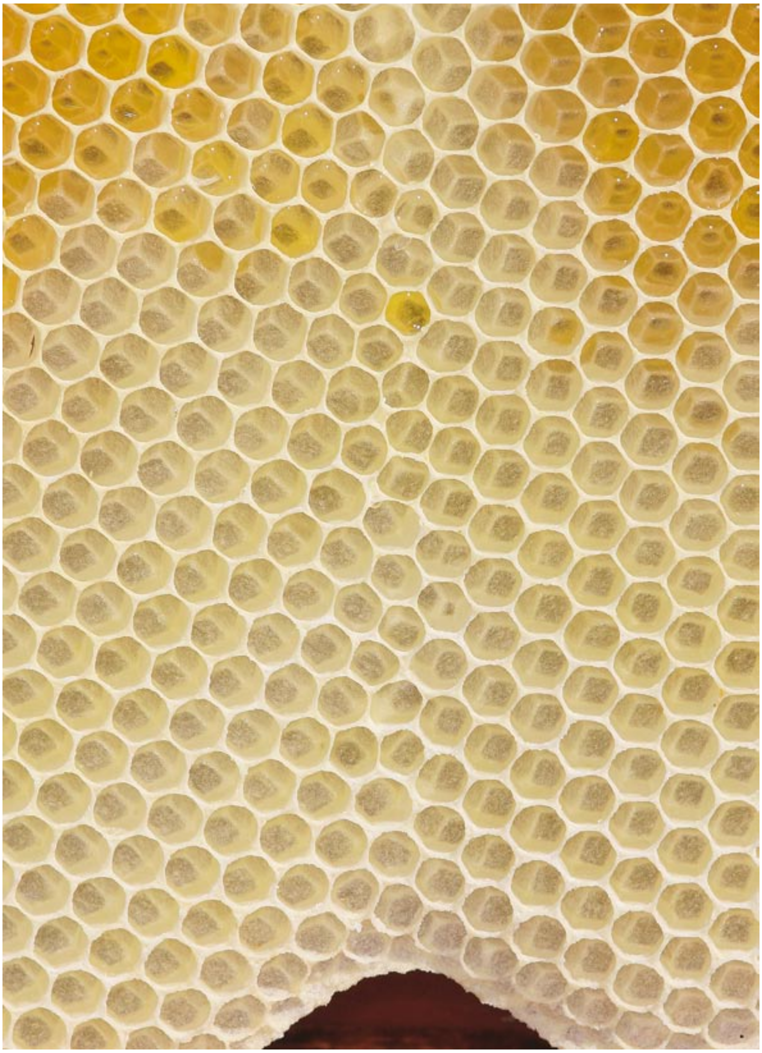


Fig. 7.7 Building troops often begin comb construction at the same time in different places. This does not lead to serious problems—the two separately built parts of the comb fit together as if with a zip fastener

Honeybees possess cushions of sensory hairs at all their joints. These are stimulated if gravity causes single parts of the body to move like a pendulum, or lever, relative to one another (Fig. 7.12). Sensory receptors in these cushions can in this way detect the direction in which the force of gravity acts. It is usually dark in the hollows where bees choose to build their nests, and so their visual sense cannot help them.

Fig. 7.8 The function of the living chain that is formed by bees where new combs are being built, or old combs repaired, is completely unknown

Guided by their sense of gravity, though, bees can maintain a comb construction that is vertical, and oriented downward from the roof to the floor. The distance between the combs results from the space a bee occupies when standing on the comb. When moving over the surface of neighboring combs, bees must be able to pass one another, back to back, without difficulty (Fig. 7.13), and this minimal distance is strictly maintained.

The resulting alleyways between the combs also provide the possibility of sending air currents through the nest to control its climate. Neighboring combs are not necessarily quite as flat as boards, but do run parallel to one another. The bees achieve this orientation by means of as yet undiscovered sense organs that detect the lines of the earth's magnetic field.

But how does the highly precise hexagonal pattern of the single cells emerge? It may be disappointing to learn that the mechanism that ensures the crystal-like exactness of the cell geometry is a process of self-organization that, apart from a small contribu-

Fig. 7.9 A new comb made of fresh white wax is an esthetically pleasing sight

tion from the bees, takes place entirely on its own. But here lies the ingenuity of honeycomb construction.

The key to the crystal-like precision of the comb cells lies in the properties of beeswax building material. Wasps also build six-sided cells, although their geometry is more crudely crafted, and the cells are actually in cylinders that have been set together (Fig. 7.14). The building material used by wasps is a pulp that they produce from wood fibers and saliva. The cell walls orient themselves, more or less regularly, under the tension exerted on these by neighboring cells, as can be seen in cells at the edges of the nest that bulge out on their free sides.

In contrast, the cells of honeybees are perfectly formed. Honeybees are in no sense more precise builders than are wasps, but their building efforts are aided by wax as an “active” building material. Beeswax contains more than 300 different chemical components. When mixed, these result in a substance with the physical properties of a liquid, even if it appears solid at lower

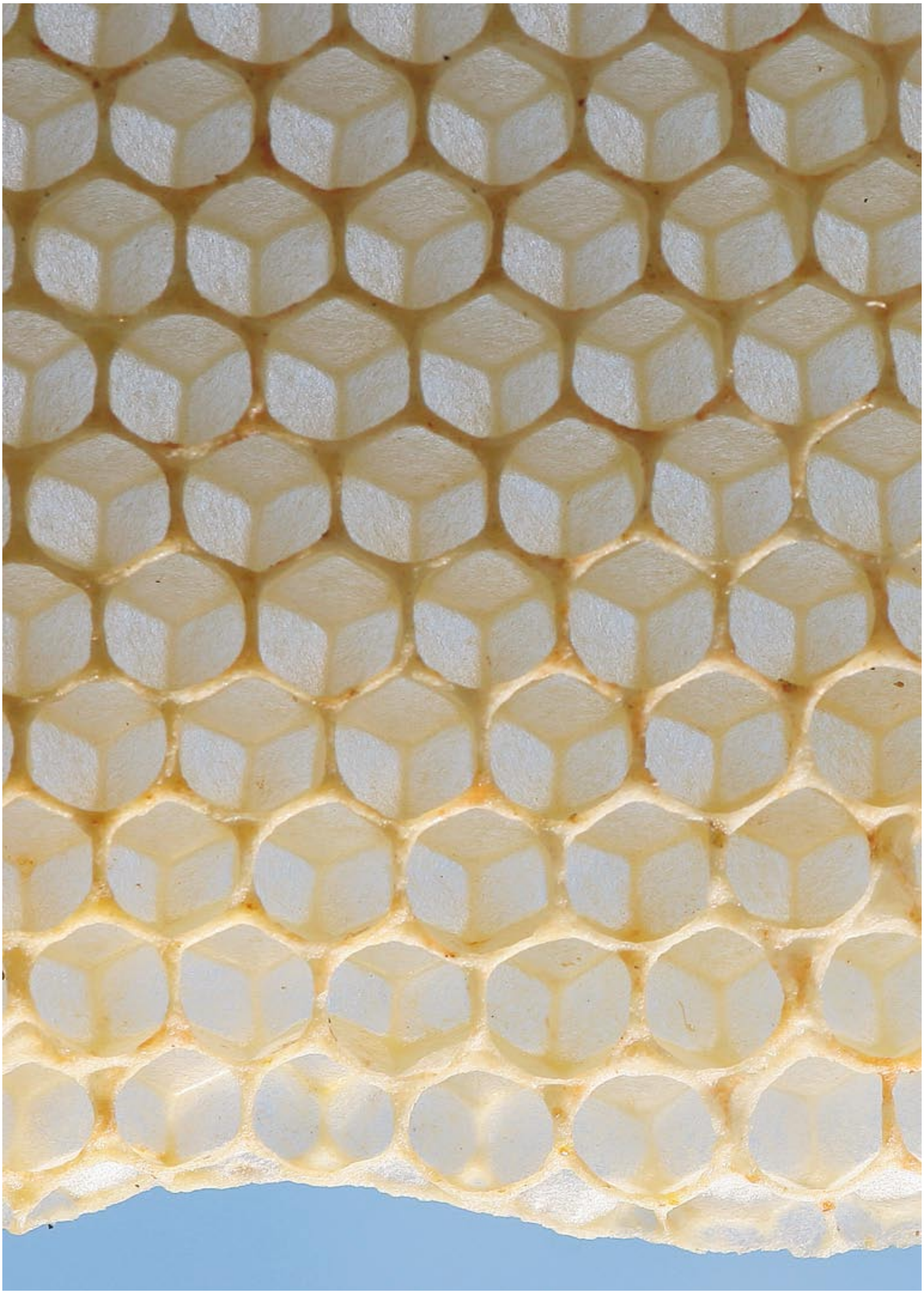


Fig. 7.10 Humans have long been fascinated by the geometric details of honeycomb

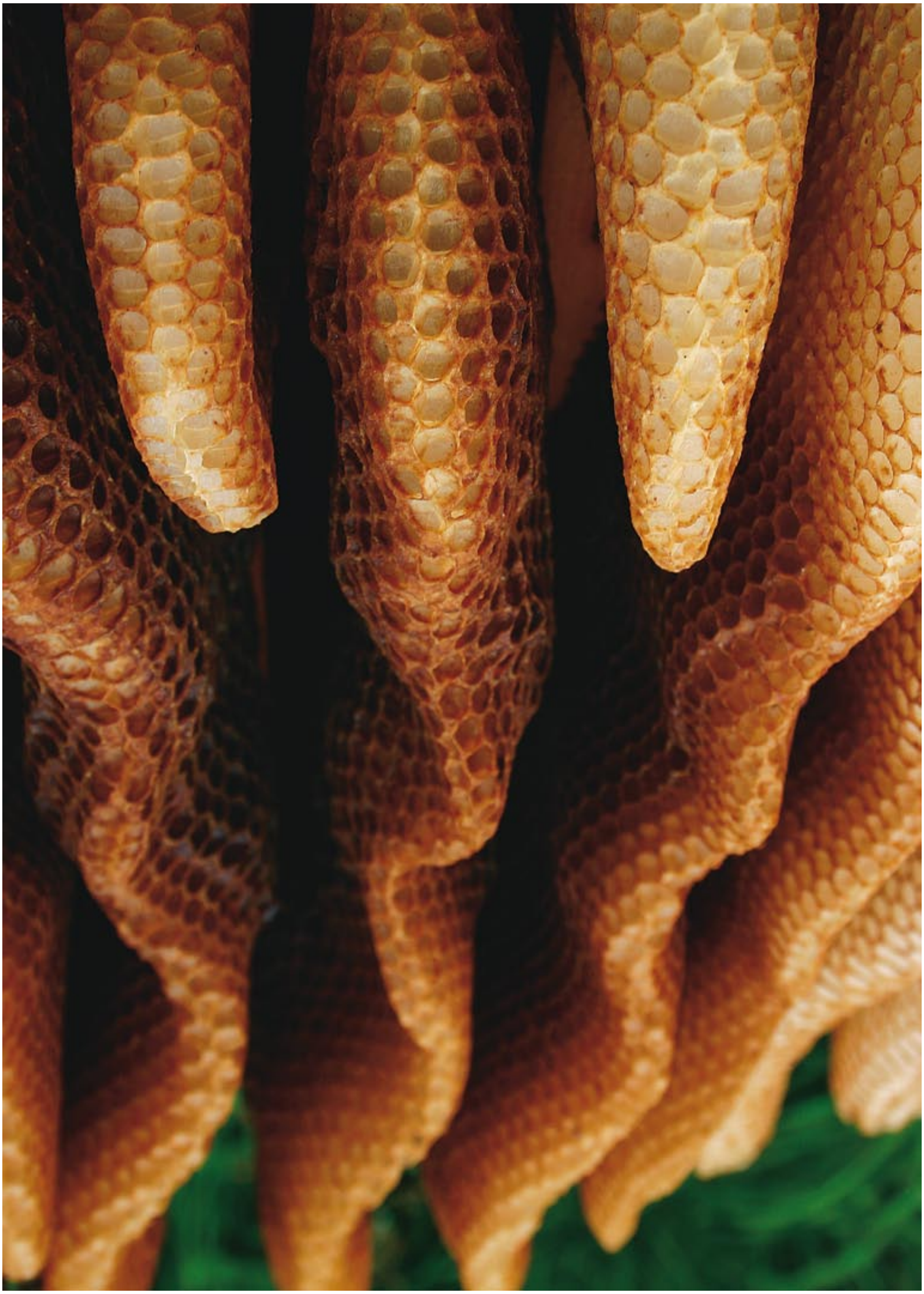


Fig. 7.11 Freely constructed combs hang vertically, and lie parallel with one another in the hollow of a tree

Fig. 7.12 Gravity receptor organs are located on all the leg joints, and between the head, thorax, and abdomen of bees. They use the information from these receptors to orient the combs vertically in the dark hive

Fig. 7.13 The alley width, or distance between neighboring combs, is set so that bees on opposite sides of the alley have enough space to pass each other back to back

temperatures. The same situation is found in glass—from a physical point of view, a liquid. Solid objects have a clearly defined melting point; glass, on the other hand, becomes increasingly fluid as it is heated. The same is true of wax. Nevertheless, the changes that occur in wax with an increase in temperature are not continuous. The fine internal structure of wax exhibits three basic states: a highly organized crystalline state, in which the wax molecules are all aligned exactly parallel to one another, and at the other extreme, an amorphous state in which the molecules

Fig. 7.14 Wasps construct their nests from pulp that they produce from chewed wood. Compared to the geometry of the comb of a bee colony, that of wasp combs appears less exact. Precise corners and sharp edges are absent

lie completely disorganized in every direction. A pseudo-crystalline state prevails between these two extremes, in which one finds both the amorphous and crystalline states lying adjacent to one another. Warm wax exhibits the amorphous structure. The change from the crystalline and pseudo-crystalline to the amorphous structure does not proceed gradually, but takes place in two steps, at about 25 and 40°C (the so-called transition temperatures). The mobility of the wax particles relative to each other changes abruptly at these transition points, which is expressed as a change in the malleability of the wax.

These physical properties of wax, and the ability of honeybees to raise their body temperatures to more than 43°C form the basis for the construction of such geometrically correct combs. In 1637, R.A. Remnant, without the help of refined technological assistance, observed and aptly wrote: "The heat of the bees makes the wax so warm and flexible that they can work with it and use it directly after collecting it". Remnant, however, labored under one of the misconceptions of the day: it was thought that bees collected wax from flowers.

Bees use their own bodies as a template as they begin to construct the walls of the cells, and build cylindrical tubes around themselves. The inner closed ends of the cylinders are smooth hemispheres, and remain as such for many weeks after their con-

Fig. 7.15 Comb cells are initially constructed as cylinders, and only during the passage of time do they assume their exact hexagonal shape

struction. The initially cylindrical, tube-like cells take on their typical hexagonal form (Fig. 7.15) only when the bees raise the temperature of the wax to between 37 and 40°C (Fig. 7.16). Cell construction sites viewed under a thermocamera glow from the activity of worker bees that heat the wax to the point where the thin wax walls slowly start to flow. Due to the inner mechanical tensions of the walls, the result—as one can observe also when two soap bubbles come in contact—is that the shared wall becomes perfectly straight. In this way, the sidewalls between the tightly packed wax cylinders are also stretched out in a straight line, gain a completely smooth surface, and a thickness of 0.07 mm, and form an angle relative to one another of exactly 120°.

Bees from which the last segments of the antennae have been amputated build imperfect cells with walls that are about twice the normal thickness, and that also have holes. The sense organs with which bees measure the ambient temperature lie embedded in segments of their antennae; most of these receptors are located

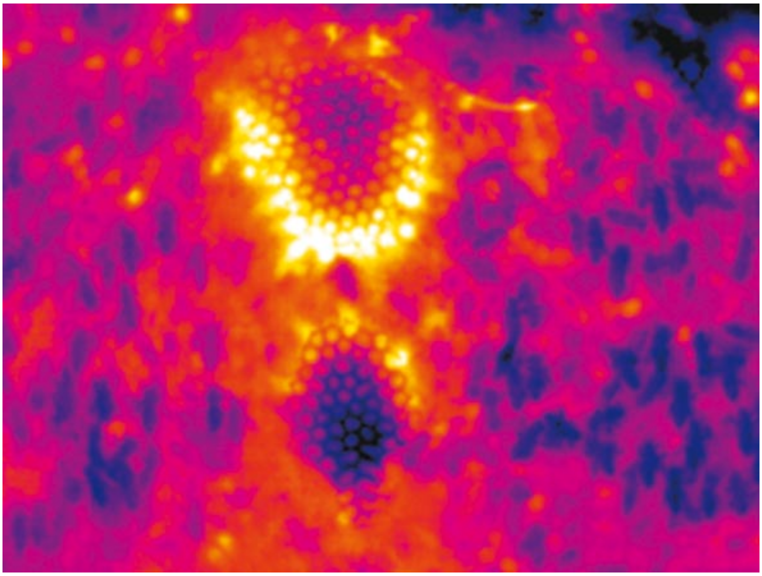


Fig. 7.16 This thermographic image shows two building sites where the builder bees heat the wax to a temperature at which it begins to flow, and forms regular six-sided cells in response to inner tensions

in the last segment at the tip of the antennae, fewer in the subsequent segments. Amputation of the antennae robs the bees of many sensory inputs, and also makes them insensitive to temperature. From this, one can speculate that the disabled bees, also responsible for warming the wax, are no longer able to correctly measure temperature.

Piece by piece, the crystal-like pattern of the comb cells forms on its own when the wax is warmed. Looking through a comb against the light gives the impression that the bottoms of the cells are composed of three rhomboids of equal size. In newly constructed combs, this is an optical illusion produced by the position of the hemispherical bases of the cells on the other side of the comb (Fig. 7.17).

With the passage of time, the bottoms of the cells become so thin that the same self-organizing principle explained for the walls also results in three rhomboids, and a perfect honeycomb.

The process can be modeled artificially with small wax cylinders packed close together and warmed. Slowly, a honeycomb with six-sided cells forms without the help of any bees. Comb cells built at zero gravity by a colony of honeybees aboard a NASA space shuttle flight in 1984 were as exactly formed as those made under earth conditions. The pattern-forming inner forces of the comb cells do not require any aid from outside, with the excep-

Fig. 7.17 The bottoms of newly built cells are hemispherical. Three rhomboidal images appear through the thin wall at the bottom of the cell formed by bases of the cell walls on the other side of the comb

tion of the addition of warmth by the bees. Only the orientation of the cells relative to the horizontal axis was disorganized in space—this was to be expected, view the absence of a directional gravitational cue.

The combs that result from the self-organizational process described above not only have an impressive geometry, but also possess precise static and dynamic properties. These properties are continually controlled and corrected during the building process.

Mathematicians have repeatedly and convincingly calculated that the geometry of the bee comb represents the optimal solution when one wishes to enclose a largest possible volume with the least amount of wax. This first view stemmed originally from the Greek astronomer and mathematician Papus, of Alexandria (about 290 to 350 a.d.). These conclusions are certainly true for the section of the combs just below the cell rims. If the thick wax rim is included in the calculation, however, this additional 30% (sometimes as much as 50%) in the amount of wax used for a cell is no longer optimal in terms of storage capacity.

The comb does not consist only of wax. Bees also work with resin that they scrape off plants, as an additive to store on, as well as including in, the comb cell walls. Through this deliberate inclusion of resin on and in the wax, bees open the possibility of being able to adjust the properties of parts of the comb, depending on its various uses.

Functions of the Comb

With its 100,000 to 200,000 cells, the comb fulfills many functions, and provides:

- Shelter
- A place to produce honey
- Storage for honey
- Storage for pollen
- A nursery
- A telephone system
- Information storage
- A colony-specific identity
- The first line of defense against pathogens

The first four items on this list do not require building materials with any special properties, only an appropriate division of particular regions of the nest. The last five functions depend on special physical and chemical properties.

It All Depends on the Contents

Some combs serve mainly for the storage of honey. These storehouses are located at the periphery of the hive. The precious brood nest is located in the center of the hive where it may extend over several neighboring combs. Each of these combs is subdivided into three zones: (1) the cells with eggs, larvae, and pupae in the center; (2) a directly adjacent wreath of cells filled with pollen, and (3) a collection of normal cells around the outside, filled with honey. This pattern becomes more complex during the rearing of the reproductive individuals, when the somewhat larger drone cells are added (Fig. 7.18).

In contrast to the cells filled with nectar or honey, those with pollen are not sealed. The pollen is mixed with small amounts of nectar, and pressed firmly into the cells (Fig. 7.19). This solid mass, made from loose pollen collected from flowers, does not need to be stored hermetically.

Fig. 7.18 The comb is the nursery for all castes in a colony. Drone pupae develop in the large cells with bulging lids in the background, the worker pupae in the smaller cells with flat lids in the foreground

Fig. 7.19 Pollen is deposited in the cells either as large lumps, or packed together as a fine powder

The processing of nectar into honey requires evaporation. This is carried out by heating, using the body warmth of the bees.

When the nectar has been condensed to a satisfactory consistency, each cell is sealed by means of a wax lid. The horizontal long axes of cells in a comb are tipped slightly inward, so that the combination of gravity and surface tension prevents the nectar from flowing out of the cells before they are capped (Fig. 7.20).

A colony can produce up to 300 kg of honey during a single summer, of which almost all is used as fuel for heating (▶ Chap. 8). The storage of such an extensive supply of honey has its dangers. For example, microorganisms could flourish in this paradise. Bees prevent this by mixing antibacterial and antifungal peptides and enzymes from their salivary glands with the nectar.

Such a volume of sweet treasure also attracts plunderers, be these small members of other species, or competitors from neighboring colonies looking for an easy way to fill up their own stores, and it is mainly against other bees, in late summer or in times of poor harvest, that bees employ their stings (Fig. 7.21). If a bee stings another bee, she can retrieve her sting without any problem. That later in evolution, animals such as the mammals appeared with tissues from which the sting, with its barbs, could not be extracted was "unpredictable" for bees, and may be seen instead as an evolutionary "mistake" on their part.

Should the sting, with the attached poison gland, small muscles, and nerve cells, be ripped out of the bee, the stinger will die from the massive wound in her abdomen. The number of bees that lose their lives in this way is, nevertheless, so small that there has been no selection toward a barbless sting.

The small muscles of the detached sting system are still highly active, and continue to operate the different parts of the sting that move relative to one another. Their barbs drive into the tissue, and an alarm pheromone, released into the air from a gland beneath the sting, rallies the bee's hive comrades to attack. The main component of the alarm pheromone is isopentylacetate, a chemical responsible for the smell of ripe bananas. For this reason, it is not recommended to eat bananas in the direct vicinity of a beehive, unless one wishes to test the effect—on oneself—of alarming the bees.

The pattern of distribution of brood, pollen, and honey across the brood comb is biologically meaningful. The brood is placed

Fig. 7.20 Fresh nectar glistens in the cells

Fig. 7.21 Raids between hives to steal honey are common, should the harvest in the field be poor. Fights break out at the entrance to the hive, or within it

in the middle, for best protection; the pollen is packed in areas directly adjacent, to allow easy access for the nurse bees caring for the larvae, and the rest of the comb is filled with honey.

But how does this come about? Who has the overview, and coordinates the work to result in this pattern?

Again, bees provide an example of a decentralized, self-organizing mechanism.

The brood–pollen–honey distribution pattern is of multiple origin: the queen, by depositing eggs, the distribution of which can be corrected by the worker bees; the nectar-receiving bees, which take the nectar from the foragers and deposit this in the cells; and the pollen-collecting bees, which pack the pollen they have gathered into the cells themselves. The question about the origin of the distribution pattern is really a search for the rules that govern the deposition, or removal, of brood, pollen, or nectar from each cell.

Every cell in the comb can be used at different times to hold any of the three possible contents. Amongst comb builders, including also bumblebees, stingless bees, and wasps, honeybees are unique in this multiuse of the comb cells. In contrast to honeybees, the others use each cell for only one purpose.

A queen lays about one egg per minute in an empty cell during the peak summer season. She donates between 1,000 and 2,000 cells per day, but does not work her way in an orderly way across the comb, although this would be perfectly possible, given the regular geometry of the comb. Instead, she prefers empty cells that are close to those that already contain brood, beginning her egg laying in the center of the comb. In this fashion, centrally located and continuous areas of brood are produced. Integrated brood nests are significant for the sociophysiology of the bee colony. Pollen is then stored around the central brood, and a wreath of honey stores around the outside (Fig. 7.22).

The level of performance required to fill the honey and pollen stores in a hive is impressive. A bee colony produces up to 300 kg of honey during a single season. This takes about 7.5 million excursions, with a total distance of interplanetary dimension. In all, and assuming that each bee returns to the nest with a full crop, this amounts to almost 20 million km flown, which is about half the distance from the earth to Venus. The payload of a foraging flight can be calculated to be 40 mg of nectar, which is just a little more than half the body weight of a bee. Twenty-five flights are needed to fill a cell with honey, a calculation based on a special group of bees concentrating nectar of 40% sugar into honey of 80% sugar.

A pollen collector typically brings about 15 mg of pollen home, distributed between the two pollen baskets on her hind legs. A colony collects about 20 to 30 kg of pollen per year. About one to two million foraging flights are necessary to assemble these pollen stores.

The typical pattern of distribution of brood, honey, and pollen across a brood comb comes about by way of a self-regulating pattern-forming process.

In principle, there could be some unknown gradient that determines specific spatial location in a comb, and that would govern the distribution pattern. A chemical sign, or some physical feature such as the mechanical properties of the comb cells, or temperature are possibilities. This can be tested by disassembling a brood comb, as one would a puzzle, and reassembling it but in different way in a hive. In a very short time, the bees will have corrected this disorganization, restoring the original pattern.

Fig. 7.22 Brood, pollen, and covered honey are not randomly distributed over the comb, but form a distinct pattern

From this, it can be concluded that there are no patterns imprinted on the comb cells that label their location, and that bees could use as orientation. A few simple rules lead to the concentric distribution of the filled cells: the queen always lays her eggs in the neighborhood of brood. The flow of nectar into the hive is always greater than the flow of pollen, and the removal of honey from cells is more rapid than the use of pollen. Pollen and honey in cells near the brood are turned over about ten times faster than in cells further away. The pollen serves, as described in Chap. 6, for the production of the royal jelly. Honey, as will be explained in Chapter 8, is used for warming the brood. In contrast to the rapid turnover of the honey and pollen cells, the time span of brood development is relatively long, leading to the formation of a stable comb center. The number of eggs laid, and the amounts of honey or pollen produced and used play no role in the appearance of the pattern as such, but determine only the speed at which the distribution occurs.

The comb of honeybees is a communication network, and a memory store for the colony. As a wax telephone line, it transmits information between bees that are the elements of the superorganism. As a memory store, it contains chemically based data that bees use for spatial orientation and identification.

A Telephone Line

The upper edges of the cells in the comb end in a bulged rim (Fig. 7.23). Low-amplitude vibrations of these rims, which spread across the comb, play a significant role in the exchange of information between bees in the complete darkness of the nest, where no optical signals can be used.

Karl von Frisch speculated, 70 years ago, that vibrations may play an important role in the dance language, and recently his suspicions have been fully confirmed by the results of a simple behavioral experiment: bees that dance over cells that are empty and transmit vibration well recruit three to four times as many visits to a feeding site, compared to those that dance on the smooth surfaces of cells that have been sealed. The communication apparently functions far better on empty cells than on a firm flat surface.

Fig. 7.23 Comb cells of honeybees consist of very thin wax walls, the top edges of which bulge out into rims about 0.4 mm thick, and that together form a net with a six-sided mesh over the surface

The details of this communication pathway, insofar as they have been understood, indicate that the comb is not a defined transmission line for vibration, like a plant stem is for the tapped signals of some insects. Instead, it seems that bees have discovered a complex interaction between the physical properties of wax, and their own communication behavior.

The comb cells of the free-nesting giant and dwarf Asian bees do not have bulging rims. These freely nesting bees form colonies consisting of thousands of bees all clinging together in a living bag around the comb. Most of the communication takes place there, and not on the comb. In contrast, bees that nest in hollows spend the greater part of their lives directly on the comb. The thickened rims of the combs together form a network that rests on the thin cell walls, and is easily displaced over small distances in the surface plane of the comb, like the net of a football goal when its mesh is pulled aside. Such vibrations can spread across the entire comb, as displacements of the thickened cell rims. These are neither longitudinal nor transverse waveforms, but rather high-velocity deformations. This "comb-wide web" transmits best in a frequency range between 230 Hz (Hertz, cycles per second) and 270 Hz, and the amplitude of oscillations in this frequency window are even amplified, whether the cells are filled with honey or not. Capping the cells with a lid stops the spread of the oscillations, and no vibrations can be recorded from empty cells adjacent to the capped region when a dancer performs on capped cells. However, if a capped area of cells is located like an island surrounded by open cells, then the vibrations in the open cells travel around the island. The fact that the transmission of the best oscillation frequencies is independent of the cells being full or empty is surprising, and makes the structure of the comb an interesting study object for engineers. Honeycombs apparently possess not only structural properties that are worth emulating, such as enormous stability using a minimum of material, but for some technologies, also extremely useful dynamic properties. That mechanical loading has no effect on the dispersion of the signal in unexpected, and may have led to the development of this comb-wide communication system.

It is perhaps no surprise to find that the narrow frequency band of 230–270 Hz, which the comb transmits best, covers the range of oscillation frequencies that the dancer, in the form of short pulses, produces in the waggle phase of her waggle dance (see also Chap. 4). Honeybees, which control the construction of their combs in the smallest detail, seemingly lay their telephone network such that it conducts their own communication frequencies best of all. The properties of the material, architecture of the comb, and behavior of the bees are perfectly matched to one another.

There are three aspects that are worth closer examination:

- What possibilities are open to bees for the tuning of their telephone network?
- Are private lines possible in the telephone network, or do simultaneously occurring communications jam one another?
- How is the ever present background noise of 10,000 bees filtered out?

Tuning the Telephone Line

The temperature of the comb wax is the factor that has the greatest effect on tuning the telephone network. The mechanical resistance of wax to oscillation decreases with rising temperature, and it becomes increasingly easier for the bees to set the net on the rims of the cell walls in motion. This will work only to about 34°C, and the entire system breaks down if the temperature of the wax rises higher than this, because the wax becomes so soft that it is more likely to deform than to transmit vibration. After a cold start in the morning, the cell rim temperature of the dance floor of a bee colony is raised to the optimal range within the first hours of foraging activity of the colony. Bees will also correctly set the temperature of the dance floor using their temperature regulatory abilities.

Bees can be brought to the limit of their capacity to control the wax temperature if the entire bee colony be relocated and exposed to climatic extremes in which the entire nest is heated. In such a case, the bees employ a strategy known, to the building industry, as the use of material additives. If the wax temperature determining the oscillation properties of the cell walls is no longer appropriate, the bees mix propolis, as an additive, to the wax of the

Fig. 7.24 Bees reinforce cell edges that need mechanical support, with propolis

cell rims (Fig. 7.24). The proportions in which the wax and resin are mixed, and their spatial distribution, are adjusted so that the resonant properties of the wax lie in the correctly tuned range.

Propolis is added by kneading small strips into the wax. Rims and cell walls result that are constructed of a compound matrix, similar to that developed by human building engineers wishing to provide a large piece of concrete with high density, and tolerance to tension. Small pieces of metal are added to the liquid cement to reinforce it.

Prevailing climatic conditions are not the only factors that influence comb construction by bees. Some practices of beekeepers can unintentionally interfere with the telephone network of bees. Apiarists, in order to facilitate the removal of combs from the hive, surround these with wooden frames. A frame that completely encloses the comb on all sides restricts the motion of the surface network, which is not able to spread out across the rims

Fig. 7.25 Combs surrounded by wooden frames on all sides by apiarists: this prevents the horizontal displacement of the "comb-wide web", and communication is seriously compromised. Bees modify the combs on which dances are held, by introducing gaps between the comb and the frame, thus enabling dispersion of the vibratory signals

of the cells, there no longer being a free edge that can expand and contract. Bees on combs on which they do not dance are not disturbed by this. Such combs remain intact, and as the beekeeper installed them. On combs where dances do take place, bees introduce large gaps between the wax and the wooden frames (Fig. 7.25), and the signal transmission is thereby fully restored.

Private Lines of the Vibration Communication System

The smallest vibrational disturbance will disperse into all corners of the comb, over the surface network of the cell rims. How is mutual interference between groups performing different individual dances avoided (Fig. 7.26), when these are taking place simultaneously?

Fig. 7.26 At peak foraging times, several dancers, like the four marked performers shown here, will dance simultaneously, and often for different food sources

The problem is solved simply by the number of bees present at the sites. Displacements of the surface meshwork will travel far amongst bees gathered in loose groups, and with large spaces between them. In areas where the density of bees is high, the loading on the comb is also high, and this has the same effect as capping the cells with a lid. The oscillations are damped, and travel only a few centimeters. Hence, the range of the oscillatory messages, and consequently the area from which the recruits are gathered, is appropriately regulated.

Weak Signals in Noise—Aid from Comb Mechanics

Communication signals are normally stronger than those of ambient disturbances, or "background noise". This is not true for vibrations in the waggle dance of honeybees. Several thousand bees active on the same comb, and busy with their diverse projects produce a continuous background noise, and the communication signals do not rise above this. So, how are such weak signals recognized?

In radio-astronomy, the problem of detecting weak signals in noise is solved by interconnecting widely separated antennae. Signals from several sources can thus be compared, and faint regular events from very distant radio stars identified by their synchrony.

Every bee has, through its feet, six spatially distributed contact points with the cell rims. In this way, they can compare the oscillations in all six feet with one another, similar to the principle used in radio-astronomy.

Is it possible, by comparing different points on the network of cell rims, to recognize a vibration pattern in a honeybee comb that is not observable at any single locality?

What is found is that the oscillations that spread over the comb, as displacements of the cell rims, result in a remarkably regular spatial picture of cell rim motion: in the simplest case, the oscillatory displacement of only a single cell rim results in the opposite cell rims of a whole row of cells moving back and forth in synchrony with one another. In one single cell in this entire row, however, the bulged rims move in opposite directions to one another (Fig. 7.27). Because a dancer pulls on the cell walls with six legs, it is to be expected that the dancer, as transmitter of the oscillations, will have several "pulsating cells" around her. A follower bee receiving the comb vibrations stands on the rims of the cells, spanning up to three cell widths with her legs (▸ Fig. 4.26), and could detect the two-dimensional oscillatory pattern in the dark, using the vibration-sensitive sensory cells located in her legs. Behavioral analyses of video recordings support this proposal: video recordings of a dance follower that are played backward in time to the moment the dance began, or earlier, make it possible to determine the place on the comb from which the prospective follower first recognized the location of the dancer. She turns her head toward the dancer the moment she detects the direction in which the active dancer lies relative to herself (▸ Fig. 4.26). She thereupon turns toward the dancer, runs in the appropriate direction until she bumps into the dancer, and immediately takes part in the waggle dance. A coincident picture

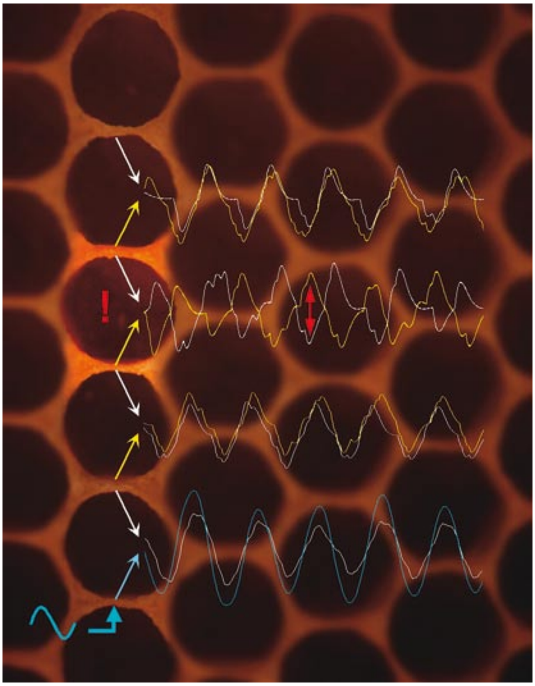


Fig. 7.27 Oscillations that spread out over the comb, as horizontal displacement of the cell rims, form a two-dimensional pattern that is determined by the physical and geometric properties of the comb, and that signals the location of an active dancer in the darkness of the hive. If the rim of a single cell wall (here, the one marked with the *blue arrow*) is made to vibrate, all the other cell rims in that row will also oscillate in the same direction, with the exception of one cell (*red exclamation mark*) where the walls move in opposite direction to one another. Because a dancer does not use one, but six feet to bring the cell walls into motion, several such "pulsing" cells may surround an active dancer

results from superimposing the positions of the "pulsating cells" detected by physical measurements, and the results of the behavioral analyses in which it was determined when the follower detected the dancer. The "pulsating cells" of the physical measurements, and the "I have detected a dancer" locations of the behavioral analyses are the same. Such observations indicate that it is highly likely that the two-dimensional pattern of oscillation in the comb leads bees to the dancer even on a noisy comb. Dances that take place on firm substrates, or on the bodies of other bees in a swarm cluster (see below) do not attract bees to the dancer from a distance.

The Chemical Memory Store

Beeswax alters its chemical composition with time, through decomposition of long chain carbohydrates, and the evaporation of wax components into the air surrounding the hive. Enzymes that the bees mix into the wax also alter its structure. In addition, the comb progressively becomes “dirty” (Fig. 7.28), through the effects of larval debris, excreta in the brood area, and imported pollen and resin. Initially chemically homogeneous honeycombs eventually turn into a chemically colored patchwork carpet.

By means of their antennae, honeybees are able to recognize even smallest differences in wax composition. They do not have to be in contact with the wax—the odor alone is enough for them to perform this discrimination.

For honeybees, the wax is a substance with history, the memory traces of which provide bees with information that help them orientate in the dark hive. Hence, the bees prefer to store nectar and pollen in older, rather than in newly constructed cells.

The body surface of bees is, like all insects, covered with a thin layer of wax to protect them from drying out. This cuticular wax is, in principle, the same as the comb wax, and wax-producing glands on the bee abdomen have their origin in structures that once served to produce cuticular wax.

The composition of the wax on the surface of bees is not the same for all bees. A genetically determined component ensures that the cuticular wax of full sisters is more similar than that of half sisters, i.e., those with the same mother, but a different father. The surroundings in which the bees live also influence the composition of the cuticular wax, because the wax layer over the surface of the bee’s body absorbs elements of the comb wax. This odor results in a colony-specific identity, making it possible for guard bees at the nest entrance to discriminate against bees that are strangers to the nest, and prevent their entry (Fig. 7.29).

Strangers to the colony are, though, not without a countermeasure to this strict entry control. Strangers bring a bribe with them, in the form of a large drop of nectar that they offer to the controlling guard bee, upon which their “false papers” are generously ignored and they are let into the hive (Fig. 7.30).

Bees can use the chemical characters of wax in an unmodified form, as they occur, but can also use the comb wax as a substrate

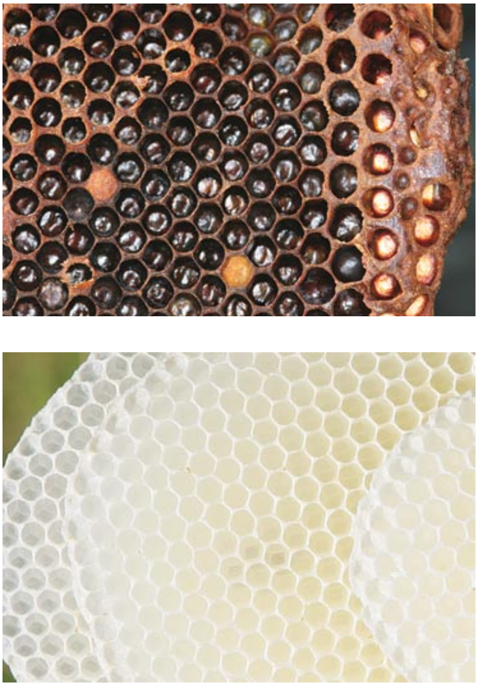


Fig. 7.28 Reflecting differences in age, or the inclusion of foreign substances, combs of very different chemical compositions can be found together in hives (*above* old wax, *below* new wax). This is also easily recognized by their color

to which they attach their own chemical labels. Such is the case of the dance floors on which the dancers of the colony are active.

Here, the exchange of danced messages about food sources takes place in an area of about 10 by 10 cm, in a hive with an overall comb area of 5 m^2. Motivated foragers meet dancers on these dance floors, to learn about the location of food sources out in the field. It is possible to carefully cut these dance floors out of the comb, relocate these, and neatly fill the hole with a different piece of comb. It is assumed that the dance floor has a chemical signal attached to it. The first forager that returns to the hive after this manipulation goes directly to the place where she last danced before the manipulation. She will not dance there, however, but searches the comb for the displaced dance floor. Once she finds it, she immediately begins to dance. Returning from the next excursion, she will go directly to the new location. If a new round of foraging occurs the following day, however, the dances will again be performed at the original location of the dance site.

These observations suggest that the dance floor carries a chemical marker the signal of which fades overnight when the

Fig. 7.29 Two guard bees in a typical interrogative attitude. Surveillance includes both ground and airspace

floor is not used, and that is newly applied the next day. Details of the chemistry of this marker are unknown.

Clean Space

Very few organisms live continually in such close contact with one another as do honeybees. This brings with it significant health risks for the superorganism. A strong selection pressure

Fig. 7.30 An interrogated bee (*left*) offers the guard bee (*right*) a drop of nectar as a bribe at the entrance to the nest

on preventing the spread of infection has led to highly effective and bee-specific solutions to the prevention and treatment of sickness. The comb assumes significance in the frontline defense against pathogens, and the thin carpet of propolis with which the cell walls of the brood nest are carefully coated is of particular importance. Propolis has antibacterial and antifungal properties, and prevents or reduces the risk of bacterial and fungal infections. Bees lay up large stores of propolis inside the nest, which can be accessed when needed (Fig. 7.31).

Large animals such as mice or shrews that force their way into the nest, and have been stung to death there cannot be removed from the nest by the bees. They present an extreme threat to the health of the bee colony. Bees solve the problem by covering the entire carcass with propolis, these mummified remains presenting no threat of infection for the colony. This behavior of honeybees is purported to have provided the ancient Egyptians with the idea of conserving their dead. Honeybees were certainly the first to practice mummification.

Fig. 7.31 Propolis is stored in various places in the nest

The Nest Hollow

Although honeybees can organize the interior of their homes, they are not able to excavate hollows that offer the bee colonies shelter. Here, they depend on what is available in the environment. Hollow trees typically offer an appropriate accommodation in temperate latitudes. Fissures between rocks are also considered. In highly cultivated landscapes offering little shelter, bees depend on the artificial housing that humans offer them, because they would otherwise not survive the winter, or even strong summer storms.

A swarm that leaves the hive has to hurry. The provisions for the journey, in the form of full crops, are limited, and a storm can dearly cost an unprotected swarm hanging from a tree. Up to 200 or 300 scouts search the land for possible nesting sites, and each successful bee that returns to the swarm cluster performs a dance on its surface (Fig. 7.32), in which, like the instructions given for a food source, the direction and the distance are coded.

Fig. 7.32 A scout bee (marked here with a *white spot*) has found a suitable nest hollow, and conducts a waggle dance over the bodies of her colleagues in the swarm. Unlike on the oscillating dance floors of a comb, only very few followers are activated. In contrast to the dances that take place on vibrating dance floors, only one or two dance followers pursue the movements of the dancer in the swarm

This message reaches only very few bees, in the immediate vicinity of the dancer, because the dance floor consisting of bee bodies transmits no vibration, and dance followers are not attracted. We have here the unusual situation that, in contrast to the recruitment to a feeding source, the entire colony needs to get the message but this is received only by very few followers.

Initially, there are as many potential nesting places being advertised in the dances as there are scouts that discover them, usually about 20 or so possible new addresses.

How can this "debate" over nesting places be resolved? There is only a single queen, so there can be only one address. Which site does the colony choose?

Bees that have discovered sites that are mediocre, or barely adequate, gradually become silent, and eventually dances are held that indicate only the best site. The bees that initially had promoted their own, but apparently less attractive sites join the others to form a majority.

The properties of the new hollow that appear to influence the decision are:

- the distance from the old home (not too near, not too far).
- the dimensions of the new hollow (not too large, but enough room for expansion in later years).
- the height of the hollow above the substrate (not too close to the ground).
- the structure of the entrance (not too small, in order to allow busy flight activity, but not too big, so that it can be easily guarded).
- the interior must be dry.
- the geographical orientation of the entrance (directed toward the south is preferred, in order to benefit from the warmth of the sun in early spring).
- the presence of old combs of previous inhabitants.

After the discovery of a hollow, the aspects that will determine its attractiveness are judged by scout bees flying slowly around the site, and intensively investigating the interior. The distances that the bees cover in their examination of the inner walls can amount to 50 m or more. No corner is ignored, and the state of the walls and the volume of the hollow are estimated.

The movement of 20,000 bees in a swarm to this spot in the landscape is no simple matter (Fig. 7.33), and various commu-

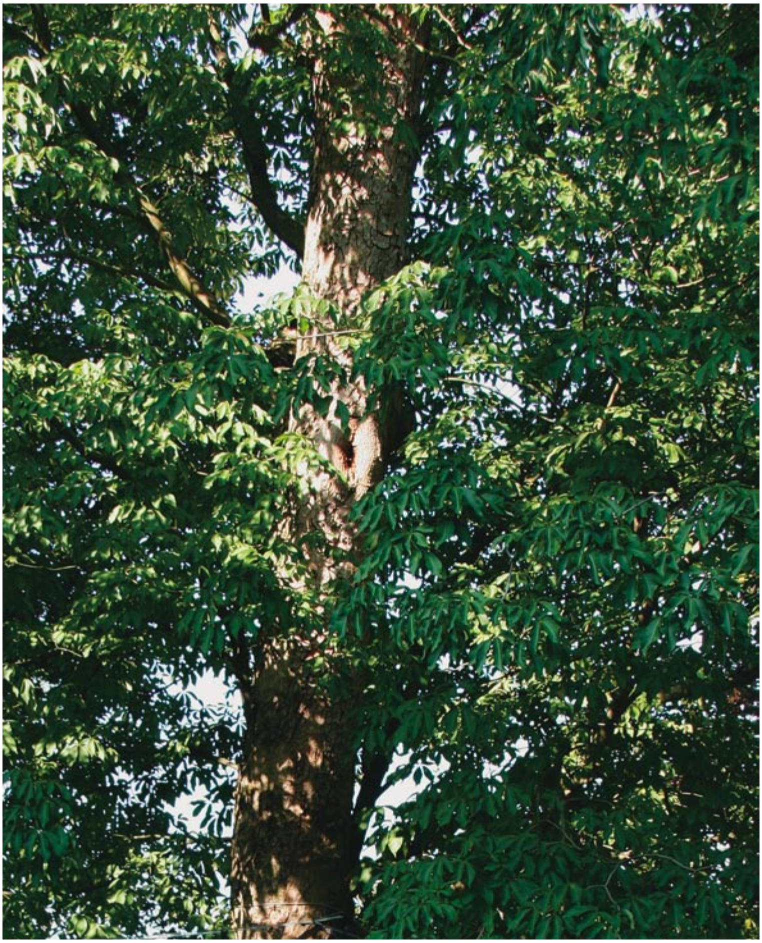


Fig. 7.33 Scout bees have found an ideal site in this tree for the establishment of a nest

nication mechanisms ensure its success. A relatively small and slowly growing group of bees are recruited to the new site by the bee that discovered it, and knows its location. In favorable cases, this can be perhaps 5% of the entire swarm. These bees fly back and forth between the nest hollow and the swarm, and continue to dance again and again on the surface of the swarm. Bees now remain close to the entrance of the new hollow, and circle around it in characteristic buzzing flights, marking the site with pheromone from the Nasanov glands in their abdomens. In this sense, the behavior is similar to that used by experienced forager bees to lure new recruits to a food source (▶ Chap. 4).

Because the dance floor of bee bodies transmits no vibration, and so attracts only a few followers, an extreme numerical imbalance between the few dancers and the many thousands of addressees results. It is practically certain that most of the bees, particularly those in the center of the swarm, have no idea about the dances occurring on the surface. So how can one motivate the swarm, with all the worker bees and the queen, to follow the right direction?

Gradually, all the dancers stop dancing, and force their way into the center of the swarm. There, they battle their way along complex three-dimensional paths through the mass of bodies, "beeping" at as many of their sisters as possible. This high-pitched tone is produced by their flight muscles, and is transmitted as a vibration to all they come in contact with. Each "beeped" bee then begins to raise her body temperature. Within about 10 min, the entire swarm begins gradually to "glow" (Fig. 7.34).

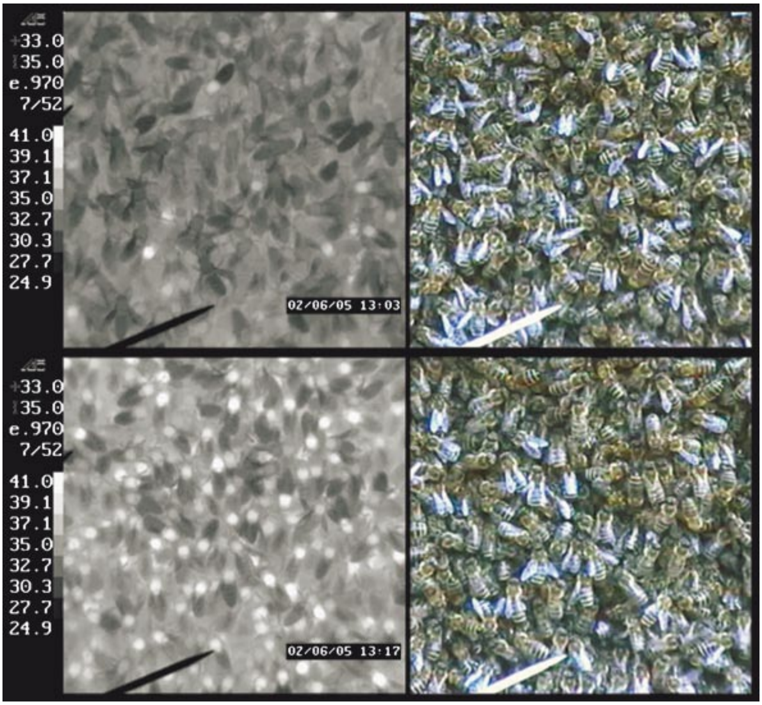
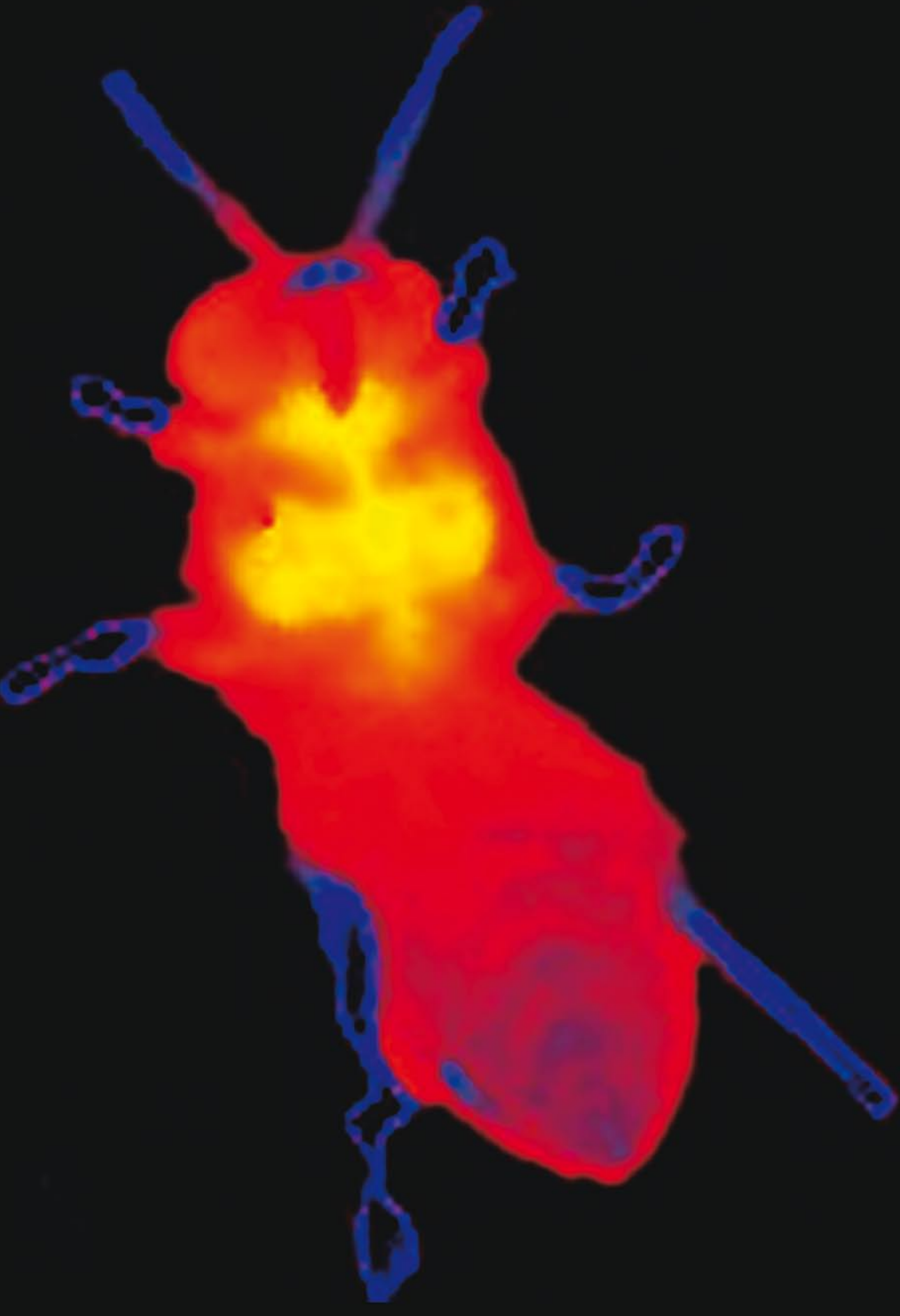


Fig. 7.34 Thermographic images (*left*), and conventional photographs (*right*) of a swarm cluster 15 min (*above*), and 1 min (*below*) before the swarm erupts. The conventional photograph shows no difference between the two exposures, but the thermograph shows the increased temperature of all "beeped" bees. The temperature of the bees can be read off the *scale on the left*. The pointers serve to identify individual bees

Once the whole swarm has reached a temperature of about 35°C, it literally explodes as all the bees take off into the air at the same time. A large, buzzing cloud appears, several meters in diameter, and consisting of slowly circling bees, with direction-indicating bees flying rapidly through it. These individuals, which know the location of the goal and will guide the swarm, shoot rapidly back and forth in a straight line through the cloud, the axis of which links the departure point with the new accommodation. The buzzing sphere of bees gradually changes its shape into that of a thick cigar, and sets off in the direction of the goal, led by the buzzing possessors of the new address. The entrance to the hollow has already been chemically marked for the newcomers, by scouts using the odor from Nasanov glands in their abdomens.

Having arrived in their new hollow, wax production begins immediately. Where necessary, the inner walls of the hollow will be smoothed by removing splinters of wood with the mouthparts. Where that is not possible, the walls will be covered with propolis. Draughty cavities will be sealed with propolis. Once all this has been completed, the new combs are built.

A new eternity can begin.



8 Cultivated Intelligence

The temperature of the brood nest is a controlling factor in the self-constructed environment with which bees influence the characteristics of their future sisters.

Organisms are exposed to the uncertain influence of their environment. Amphibians suffer from dryness, birds from lack of food, butterflies from the cold. The freedom to move provides most animals with the possibility of avoiding unfavorable situations, and searching for better conditions. Amphibians bury themselves in the earth; birds change their locality, and in extreme cases as for migratory birds, their continent; butterflies select sunny places. The environment provides possibilities from which animals choose the best solution. Selection ensures that species that have found an appropriate solution survive, whereas those that do not vanish completely.

The environment is not really only a palette from which organisms either choose well, or suffer unhappily. Environments can also be constructed. Earthworms form the substrate in which they live, through their feeding and burrowing habits. The leaves of trees shade, and thereby influence the leaves sprouting beneath them. Aquatic animals affect the acidity of small ponds by their excretions. Such influences on the environment, if not neutral, are followed by reactions that in turn impact on the animals involved. Such reactions are often negative: if the water in small ponds becomes too acid via the effects of animals living there, this kills the polluters.

But what if organisms could arrange their environment to their advantage, and include specifically manipulated positive effects? Would this not introduce an entirely new quality to the game of “environment, organism, and adaptation”?

And what if the environment shaped by the organisms could determine, or influence the characteristics of the organisms themselves? Would that not lead to a system in which cause and effect—and even the limits of the classical environment–organism model—become blurred?

In an evolutionary time span, an actively shaped environment that incorporated properties influenced by the organisms living within it would merge with the genes of the organisms that shaped it, resulting in a unity in which the elements would develop together.

Such organisms would have freed themselves from being slaves of an environment to which they had to adapt in order to survive and reproduce.

Steps toward independence from the environment have been taken by humans, but also by honeybees—comparatively, those taken by honeybees are perhaps more fundamental than those of humans. For us, the usual method of conditioning our environment is determined by constructional possibilities, and depends on the prevailing natural environment. It is possible that in conditioning our living and working areas, we merely achieve a feeling of comfort that satisfies an existing need, rather than truly changing ourselves over the short or long term.

In the 30 million years of their evolution, colony-building bees have achieved what is yet to be shown for humans—they can shape their environment to their own advantage.

We are gradually beginning to understand the highly complex and numerous feedbacks and interactions between bees and their self-controlled environment. One of the latest advances is the recognition that the temperature of the brood nest is of great importance for the entire biology of honeybees.

Hot Bees, and Warm Pupae

The brood nest of honeybees (Fig. 8.1) is an extremely important and sensitive part of their living world that they control with amazing precision, and the temperature of the area that contains the capped pupa cells is particularly exactly regulated.

Beekeepers have long known about the warmth that is developed in the brood nest of honeybees, and that can be detected

Fig. 8.1 The brood nest of honeybees is that part of the comb in which each new member of the colony is individually cared for by a brood nurse during its development from larva, through the pupa to the adult bee

even with the bare hand. For some time, it was believed that the brood itself produces the localized high temperature, and that bees went there to warm themselves. This opinion was shown to be incorrect, and was replaced by a much more exciting insight into the biological significance of the nest climate of honeybees. The employment of heat-sensitive cameras in particular, coupled with patient behavioral observation and careful manipulation of bees and bee colonies, have provided completely new perspectives, the consequences of which are far from being fully appreciated.

Animals are able to produce warmth by metabolizing energy-rich substances such as fat and carbohydrates, or through muscular contraction, as we do when shivering with cold. Honeybees warm themselves by shivering with their flight muscles, which not only are used for flying, but as we have seen in Chap. 4, also are responsible for the production of vibratory pulses in waggle dance communication. Warmth is produced by these muscles in a slightly different way. Bees uncouple these muscles from the wings by means of the ingenious action of tiny steering muscles, and by contracting and relaxing these, increase their metabolic rate. Antagonistic muscles work against one another, and muscle trembles ensue that result in vibrations. These are far weaker than those produced by the dancers. In terms of heat production,

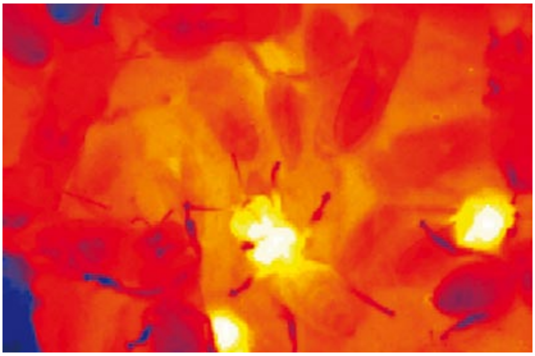


Fig. 8.2 The distribution of temperature in the bodies of heater bees becomes visible in thermographic images. The artificial coloring of the images indicates low (*blue*) and higher (*yellow*) temperatures. An ingenious employment of the counter stream principle prevents the passive dispersion of heat through the bee's abdomen, and warmth is confined to the thorax, where it is generated by strong flight muscle trembling

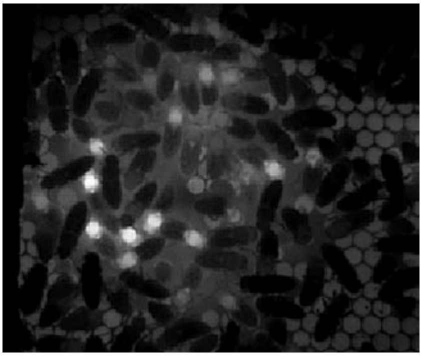


Fig. 8.3 Thermographic images show that "hot bees", with thoraces that appear *white* here, collect in the capped areas of the brood nest. The surrounding uncapped area of the comb, recognizable by the dark rims of the cell walls, is free of heater bees

the result of this trembling can be appreciated in pictures from a thermo-sensitive camera (Fig. 8.2).

Many insects, including honeybees, have developed the ability to heat their flight muscles through such contractions, to prepare themselves for flight. The solitary evolutionary predecessors of honeybees, which do not form colonies, probably already possessed this ability, and a possible way to control the nest temperature. This inheritance was one of the most important physiological requirements for the development of colony-forming honeybees.

Thermocamera pictures have been taken of many insects preparing to fly, and show that moths, for example, heat their flight muscles before they take off into the cool night air. The same warm-up occurs in the flight muscles of honeybees that are preparing to fly, and this is the original function of an ability that honeybees have exploited to achieve a very different end.

A view of the brood comb through the lens of a thermocamera reveals "hot" heater bees with "glowing" thoraces clearly outlined on the capped cell region (Fig. 8.3).

These bees press their thoraces down onto the cell cap that lies beneath them, and transfer their warmth to the pupae enclosed beneath the cell cap. This heating posture, in which they sit at least half a body height lower than other bees on the comb, is easily recognized (Fig. 8.4), and they will maintain this attitude, completely motionless, for up to 30 min. One could take these bees for dead. The antennae do not move, but are in held in contact with the cap of the cell in front of the bee, presumably to measure the temperature of the wax caps of the pupa cells, because the tips of the antennae carry the greatest concentration of heat-sensitive receptors.

To believe that the bees are resting, sleeping, or even dead would be doing them a great injustice. They are as active as a honeybee can possibly be. Only strenuous flying can match the energetic activity of a heater bee.

After maximally 30 min in this posture, and a heating performance corresponding to a body temperature of over 43°C, the animals are exhausted and interrupt the activity. The lid of the warmed pupa cell will "glow" for some time after a heater bee has completed heating, and has moved away (Fig. 8.5).

A heater bee can warm up only one pupa cell lid at a time, because this has the same dimensions as her thorax.

A heating engineer would wonder about the efficiency of a system in which warmth is transferred from the bee thorax to the single cell. Hot bees radiate heat from all sides, not only down to the pupae that need warming. They lose more warmth to the surroundings than they transfer to the underlying cells on which they have focused. This method of heating looks more like that of a hotel room with defective windows in former times of socialism: the windows were not repaired—the heating was just turned up.

A closer look at all the bees in the area of capped brood cells shows the efforts they indeed make to keep the loss of warmth as small as possible (Figs. 8.6, 8.7). Non-heating bees, for example, are thickly packed on the comb, insulate it, and reduce heat loss through radiation.

In addition, bees have adopted a far more ingenious and effective way to warm their brood, which is described below.

The Colony's Incubator

Bees always begin the establishment of the brood area in the center of the comb. This spreads out on all sides as the queen continues to lay eggs, and cells are closed with a lid during the

Fig. 8.4 A heater bee in typical heating posture can be seen in the center of the picture. Pressed close down onto the lid of a cell, she holds her wings firmly closed, and the tips of the antennae in continual contact with the lid of the cell. Bees can remain immovable for up to 30 min in this position, while the bustle of life on the comb carries on around them

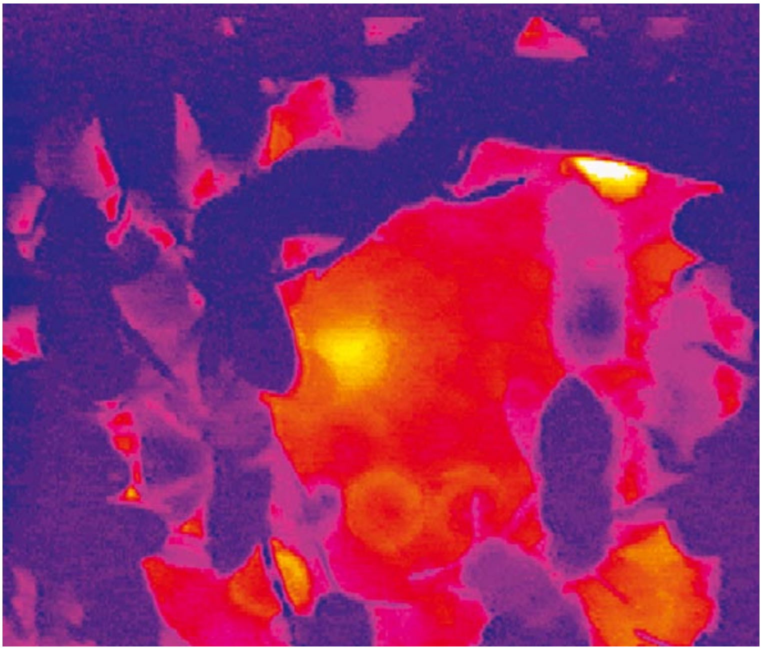


Fig. 8.5 If a bee that has been pressing herself down onto the lid of a cell for some time is moved aside, the thermocamera will detect a hot spot, precisely at the point where the bee's thorax had been, and seen here as a *yellow area in the center* of the picture

final larval stage so that they can pupate undisturbed. The capped area of the brood comb in honey bee colonies is not completely closed; empty cells, constituting 5–10% of the total number, are distributed among the capped cells. This percentage varies, depending on the outside climate.

Unused cells can be found in all stages of development of the brood nest (Fig. 8.7). A percentage of empty cells in a brood comb exceeding 20% of the total can be the result of unusual situations in the colony, such as the unwanted appearance of a large number of diploid drone larvae that the workers then remove from the brood nest.

Cells in the brood nest that remain empty can be found even after a queen has newly established a brood nest area (Fig. 8.8), and consequently after the emergence of the larvae (Fig. 8.9). This becomes functionally interesting when it is realized that (Fig. 8.10) these apparently empty cells are, in reality, seldom empty at all. Instead, they are frequently occupied by bees, lying headfirst in them (Fig. 8.11).

This behavior was initially described as "cell cleaning", or "resting", because it was not possible to determine what the bees were doing in these cells.

Fig. 8.6 Most of the bees are located in the region of the capped brood cells. The heater bees, with their bodies pressed down on the comb (four heater bees are marked here, see also Fig. 8.7), are partly hidden by a majority of standing, non-heating bees. The bodies of the non-heating bees form an effective insulating layer, and help to keep the warmth in the brood

Fig. 8.7 An enlarged view of the marked region in Fig. 8.6, with four heater bees pressing their thoraces down to transfer the warmth from their bodies onto the lids of the cells beneath them

Fig. 8.8 The queen does not lay an egg in every cell. Empty cells are scattered throughout an area in which a queen has deposited eggs

Fig. 8.9 Empty cells become conspicuous when the hatched larvae begin to develop

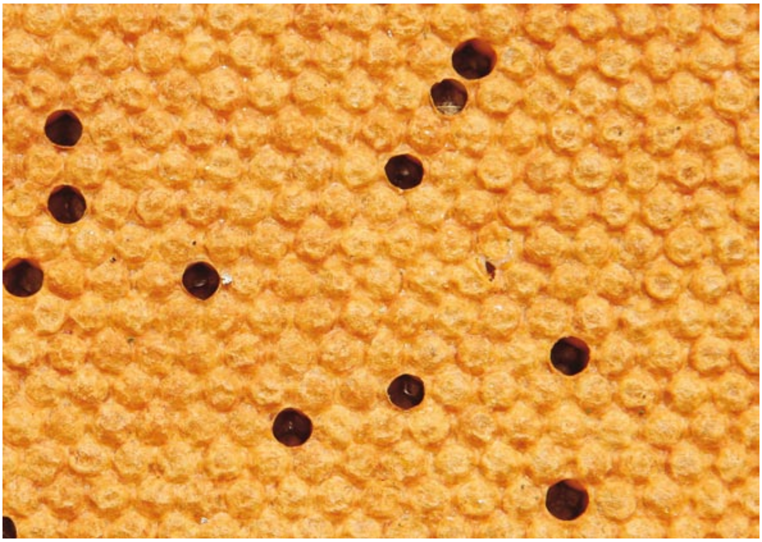


Fig. 8.10 About 5–10% of cells in the capped brood region are usually empty, a proportion that is ideal for warming the pupae

Fig. 8.11 Three workers, deep and headfirst in empty cells of a capped cell area of a brood nest

All that can be seen from the outside are the tips of the bees' abdomens, the ends of which are rapidly telescoping in and out, or show short periods of activity interspersed with long periods of rest. The rapidly telescoping activity is common across the brood area, the resting state, less so. Carefully opening the cells from the side exposes bees lying in the cells with their legs stretched out behind them. As pupae, they lie like this in cells with their heads

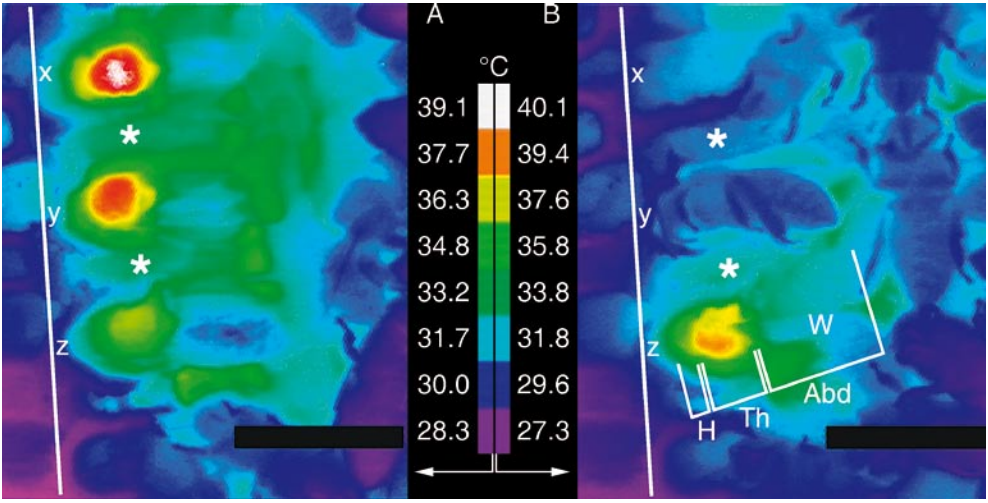


Fig. 8.12 A thermograph image of an area of a brood nest that has been cut open along the length of the cells. Four heater bees with different temperatures, and a resting bee at ambient temperature (*blue*, *y* in the group on the *right*) occupy cells close to one another. *x*, *y*, and *z* mark the bottoms of the six cells in which the bees are lying. The *asterisks* indicate the location of the pupae. *Abd* Abdomen, *W* wings, *H* head, *Th* thorax of the bees. The *scales* show the temperature calibration of the thermograph

facing out, but now the heads face in. The bees have an outward appearance of being completely at rest, apart from the pumping movements of the abdomen. A thermocamera directed at these bees shows a large difference in body temperature between individuals in the different cells (Fig. 8.12).

Strongly pumping bees have an average thorax temperature of up to 43°C, in contrast to bees in the resting state whose temperatures are the same as that of the ambient environment. The old interpretation that these bees are resting is true only for a small proportion of the cell inhabitants. All the others are actively heating. The behavior suggests a second heating strategy that is far more effective in transferring energy than is the case for pressing on the surface of cell caps. Measurements of body temperatures of the bees before they creep into the cells indicate that only those with high body temperatures slip into empty cells, and that they prepare themselves before entering the cells. Initially, they have the same temperature as the air in the hive, but before entering a cell, they run around rapidly over the comb, increasing the temperature of their thoraces to an appropriate level. Bees that have cooled down, after a period of 3–30 min, leave the cells. The effort of continuously maintaining the body temperature at such high levels costs an enormous amount of energy, and explains the limited occupation of the cell. The bees' reserves are exhausted after 30 min at most. Heater bees do not maintain maximal heating performance for the entire period they spend in the cells. Phases of activity of up to 5 min are interspersed with pauses during which the bees allow their body temperatures to sink by up to 5°C, before increasing these again to regain maximal heating performance. Such temperature troughs are expected in a controlled system that has to be maintained at a specified level. The application of heat is turned down when the desired temperature is exceeded, and reapplication occurs when the temperature has fallen below this level. This heating behavior is bound closely to the sociophysiological control of the brood nest climate (▸ Chap. 10).

Bees that are occupied as heaters—unlike many other activities in the lives of bees—belong to no particular age class. The youngest bees that undertake the heating task are 3 days old, the oldest 27.

Sweet Kisses for Hot Bees

Bees obtain the energy for heating from honey. A strong colony can produce up to 300 kg of honey during a summer, although only a small proportion of this can be found at any one moment in the nest, because the turnover is high. Honey is not food in the usual sense, for the maintenance of body functions of the bees, but is used mostly to warm the brood nest in summer, and to keep the bees clustered in the hive from freezing during winter. The large reserves of honey of a bee colony are therefore not food, but fuel. A few relevant data:

- The energy content of a full crop of nectar amounts to 500 J (joule).
- The energy cost of a forager amounts to 6.5 J per kilometer flown. It follows that for an average flight, she will need about 10 J. She therefore brings 50 times as much energy back to the nest as the flight costs.
- During an average lifespan, a forager carries 50 kJ back to the nest.

- The foraging force of a colony, involving more than 100,000 individuals during a summer, undertakes several million foraging flights, and carries about 3–4 million kJ of energy back to the hive.
- A milligram of honey contains 12 J of chemical energy, bound to sugar. The combustion of a kilogram of honey produces 12,000 kJ.
- A bee uses 65 mJ per second to achieve the heating performance needed for her thorax temperature to be raised to, and maintained at a summer ambient level of 40°C.
- Such a heater bee will have burned 120 J that she has drawn mainly from the sugar in her hemolymph, after a maximum heating period of 30 min.
- During the entire brood period, heater bees will burn about 2 million kJ, which is more than two thirds of the total energy used in a summer.
- The heat energy for the control of the brood nest temperature is equivalent to a continuous power usage of 20 W (watt). If bees were able to channel this energy into a light bulb, they could brightly illuminate their dark world in the nest.
- Also, 2 million J are burned for warming the cluster of bees in the nest in winter. The remaining fifth of the energy stores gathered by the bees over the summer provides the energy for all their other activities.

Honey reserves in the hive are usually located at some distance from the heated brood comb. “Filling station” bees are continuously underway to spare the heater bees the long trip to the honey stores, and particularly during cold weather, to avoid any interruption of heating activities. This group of bees deliberately search for heater bees, and transfer the honey directly to their mouths in a “sweet kiss”. The direct transfer of nectar or honey from one bee mouth to another is called trophallaxis (Fig. 8.13).

Filling station bees must find the exhausted heater bees, with their small residual body warmth, in the darkness of the hive, and the highly temperature-sensitive receptors on their antennae guide them in this search. Highly concentrated honey of maximum energy content is transferred between the members of this team, and not immature honey, or simply nectar, of which a considerable amount is exchanged between other bees in the hive.

Fig. 8.13 A donor bee (*below*) provides an exhausted heater bee (*above*) with a trophallactic "energy shot" of high-quality honey

Filling station bees load up from open, or already capped honey cells, the lids of which they must first remove (Fig. 8.14), and then go off in search of bees that need energy. This behavior is promoted by the higher air temperature in the brood nest—this is biologically meaningful, because usually the high air temperature in the brood area results from the activity of many heater bees, which are correspondingly hungry after completing their task. A certain provision for self-catering is also present in the brood area. Empty cells in the capped brood region are often used as depots, and filled with nectar (Fig. 8.15), only to be

Fig. 8.14 Bees whose task it is to supply and recharge the energetically exhausted heater bees in the brood nest are shown here opening capped honey cells

emptied again after a short time. These cells serve as local stores for energy-hungry bees, but do not offer the high-quality “energy shots” provided by the mature honey that is transferred from mouth to mouth.

The correct combination of empty heating cells among the brood, filled depot cells, and filling station bees is a consequence of ambient temperature. Should this remain low for a long period, many more empty heating cells are introduced; should it become high for a while, the extra cells are not used for heating, but as temporary nectar depots (Fig. 8.16).

Fig. 8.15 Nectar-filled depots in the brood nest

Fig. 8.16 Heater bees will serve themselves from depots in the brood nest when these are available to them. Such cells remain filled for short periods, and contain merely "thin" nectar, not honey

Bees that are not actively heating form a living layer over the comb, and do their share of temperature regulation through passive insulation. Such insulation can contribute both to reducing loss of warmth from within, and also to guarding against overheating from without.

Bees not only have to heat, but also cool, in order to keep the pupae at their optimal temperature. In central Europe, the latter is required significantly less than heating, but even a short heat wave can damage the sensitive brood.

Fig. 8.17 Bees search for water that they will then distribute in small drops and in a thin film on surfaces within the hive, if the hive becomes too warm

Fig. 8.18 Once the water collectors have spread a thin film of moisture, nest mates go into action as living ventilators. The streams of air they produce with their wings evaporate the moisture, and cool the surfaces

The method used to cool is the same as that employed by humans for their air-conditioners—evaporative cooling.

On hot days, specialized workers collect water from moist ground, and also from the edge of open ponds and waterways (Fig. 8.17).

They transport this into the hive, and there spread it as a thin film over the rims or caps of the cells. Martin Lindauer (1918–), a renowned bee researcher, recognized over 50 years ago that when bees ventilate the area with their wings (Fig. 8.18), the air

Fig. 8.19 If a general airing of the hive is required, the bees arrange themselves into a chain of ventilators in front of the hive, to draw out the old air that is too warm, or contains too much carbon dioxide

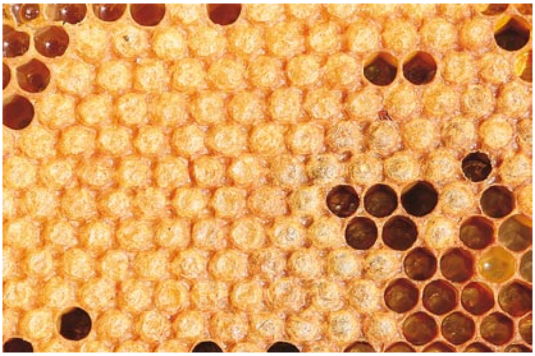


Fig. 8.20 The number of pupae that are adjacent to the empty cells in the brood nest partly determines the time a heater bee will occupy an empty cell. The more pupae in the immediate vicinity of the cell, the longer the cell will be occupied by heater bees

currents produced by this "stationary flying" evaporate moisture, causing the temperature of the hive to sink. Bees sitting either directly on the comb, or at the entrance to the hive create these air currents.

Ventilator bees will organize themselves into some spatial order, and combine their small individual efforts into a highly effective ventilation of the entire nest, should this be required (Fig. 8.19).

The body temperatures of the heater bees, and the time they spend within the cells set the temperature levels of very small, local areas in the brood nest. Both of these depend on the construction of the area around the empty cell.

An empty cell is used for heating only when it borders at least one pupa cell, and in such a case, the heater bee has an average temperature of 33°C. Heater bees raise their temperatures to 41°C if an empty cell is surrounded by the geometrically limited maximum of six capped pupa cells. Intermediate temperatures are applied when the empty cells are bounded by two to five pupa cells.

A clear relationship also exists between the cell surroundings, and the duration of heater cell occupation; those bordered by five or six capped pupa cells are occupied by heater bees for 100% of the time, energetically exhausted bees being immediately replaced by fresh heater bees.

Cells that lie next to only a single pupa cell are occupied during at the most only 10% of any observation period; those neighbored by three capped cells contain heater bees for up to 70% of the time (Fig. 8.20).

"Half-baked" Sisters, or "Genetics Is Not Everything"

In honey, the greater part of the energy stemming from high-energy sugar bonds in plant nectar is converted into heat (Fig. 8.21). This is not the usual, unavoidable loss that accompanies energy conversion and transport, because here the honey is metabolized with the express purpose of releasing heat energy.

What is the fundamental reason for this enormous investment of effort and time, on which so many areas of the biology of bees are focused?

Two possible explanations for the high temperature of the brood nest of honeybees can be considered:

- The first proposal: after winter, a high brood nest temperature enables bees a rapid start in spring, and so to exploit the resources of early flowering plants before their competitors. According to this hypothesis, the higher the brood temperature, the shorter the development time, and the quicker the colony will increase its population. Nevertheless, in any colony during the breeding season, young bees are produced continuously, and so do not follow one another in true generations. Hence, whether individual bees take 1 or 2 days more or less for their development, the situation is the same in terms of continuously replenished population numbers in all colonies. Compared to a brood nest temperature of 35°C, a brood nest temperature of 32°C, in which perfectly normal bees are produced, would enable a considerable economy in energy. So, why is the brood nest temperature so high?

  The queen has by far the shortest development time. Her pupa phase lasts, on average, 5 days, compared to 10 to 13 days for a worker. Is the temperature of the queen cell then so much higher than those of the workers? Not in the least. Measurements have shown that the temperature of the queen cell lies at 35°C, heated by bees that cluster around it.

  A positive correlation does exist between the duration of development, and the temperature of the pupae; this can be shown for all insects, and has a biochemical basis. As explained above, however, this aspect is unlikely to have been the driving force for the evolution of the heating behavior.

Fig. 8.21 To be precise, one should not describe flowers as the feeding sites of bees, and the collection of nectar as the harvesting of nourishment. Instead, these should be regarded as energy sources, and foraging as the acquisition of energy for the hive. Honey production in the nest is the refinery for the raw materials

- The second proposal for the use of the heating ability of bees is more convincing, particularly in temperate climate zones: honeybees first arose in the tropics, and evolved with brood nests at high and constant temperatures. Pre-adapted with a perfected heating system, they were well prepared to penetrate to temperate latitudes, with their hard winters. Here, they manage to keep the temperature of the outer layers of the closely packed winter cluster from going below 10°C, a temperature limit beneath which bees are no longer able to move. New brood can thus be started early in the year in the shelter of the winter cluster.

The second proposal does not answer the question of why the brood nest temperature of the pupa phase was already so precisely regulated in the tropics. To control the temperature of the pupa there, cooling is more of a problem than heating. Tropical bees, in their hot climates, have correspondingly smaller energy requirements, meaning less honey and storage.

The study described below, of the properties of honeybees that developed as pupae at different temperatures, has provided insights into the importance of social heating by honeybees.

Before manipulating the temperature of the pupae, it is necessary to establish the temperature regime to which the pupae are subjected in the undisturbed brood nest.

Tiny thermocouples installed into the capped cells, without damaging the pupae, produced three interesting results:

- The actual temperatures of the pupae in a natural brood nest are constant over a particular range, but nevertheless do vary slightly about a mean value in many cells. The duration of the single, very gradual variations lies between 30 min and an hour. The amplitude of the variations can be about 1.0°C in either direction about the mean.
- The average temperature of the pupae over time is constant for each individual pupa that was observed.
- The average temperatures of different individual pupae lie several degrees Celsius apart from one another. They range from 33 to 36°C.
- The direction of temperature change during the slow variations is not the same for all pupae, which it would be if the temperature of the entire brood nest varied as a single, inte-

grated unit. Instead, the temperature of an individual pupa may rise, while that of a pupa in a closely adjacent cell will fall.

In summary: worker bee pupae of honeybees (Fig. 8.22) receive individual and different "personal" heat treatments from heater bees.

Do these different treatments have consequences for the resulting bees?

The pupa phase of honeybees lasts about 9 days for the workers, about 10 days for the drones, and about 6 days for the queen. In this time, a bee transforms from a larva into an adult. The essential characteristics of the adult bee are established during this metamorphic change. These are typical of insects, and deviate less from the general basic form than is the case for many insects that are adapted to special ecological niches.

Behavioral plasticity is the distinguishing feature that tops the list for bees. During their lives, worker bees carry out a sequence of different tasks that depend on their age. There is a long list of tasks that bees undertake in an undisturbed colony. Arranged in the order of occurrence, these are: cell cleaning, capping the brood, caring for the brood, serving in the queen's court, receiving nectar, production of honey, removal of detritus, pollen pack-

Fig. 8.22 Pupae lie on their backs in perfect order in their cells

Fig. 8.23 In principle, each honeybee can carry out any task that has been observed in the hive. The quality of the performance, and the frequency with which the tasks are completed is nevertheless very different for different individual bees. Specialists go into action when the hive needs airing, in order to thicken honey, evaporate water for cooling, or exchange nest air that has a high concentration of carbon dioxide

ing, comb building, ventilation, entrance guarding, and foraging. Behavioral studies employing technology that can focus on single, individual bees have extended the list to include the heater bees, and the filling station bees responsible for providing the energy support for the heater bees (Figs. 8.23–8.26).

Different activities require very different behavior, and behavior is determined by the nervous system. The nervous system of honeybees must therefore possess a highly developed capacity for change. Unusual for insects, the amount of juvenile hormone increases with the age of the bee. As implied by its name, the amount of juvenile hormone is normally highest in young insects, and decreases during the life of the adult. The increasing levels of juvenile hormone during the adult life of bees may be responsible for the older forager bees being better able to learn than are the young hive-bound bees. Bees send their seniors out into an unfriendly world to cope with the dangerous and challenging tasks outside the nest.

Fig. 8.24 Pollen collection is carried out mostly by bees that specialize in this task. Only about five percent of the foragers bring both pollen and nectar back to the hive

Individual bees do not always take part in all the occupations listed above. For example, only a few bees are needed for the queen's court, or to guard the entrance to the nest; bees that are associated with a specific task perform it often, and their sensitivity to stimuli that evoke the task is critical. Highly sensitive individuals will react even to weak stimuli; insensitive bees will react only to strong stimulation, and be correspondingly less active (▸ Chap. 10).

A list can be drawn up for the frequency with which individual bees are engaged in various activities, and age and the social environment take on a primary role in determining their actual occupation. Here, too, a genetic component plays a role, but even more influential than the direct genetic contribution is the temperature at which the pupae developed into adult bees. Because the climate of the nest is controlled by the heater bees, whose own behavior and genetic disposition are determined by the conditions under which they developed, a highly complex interaction

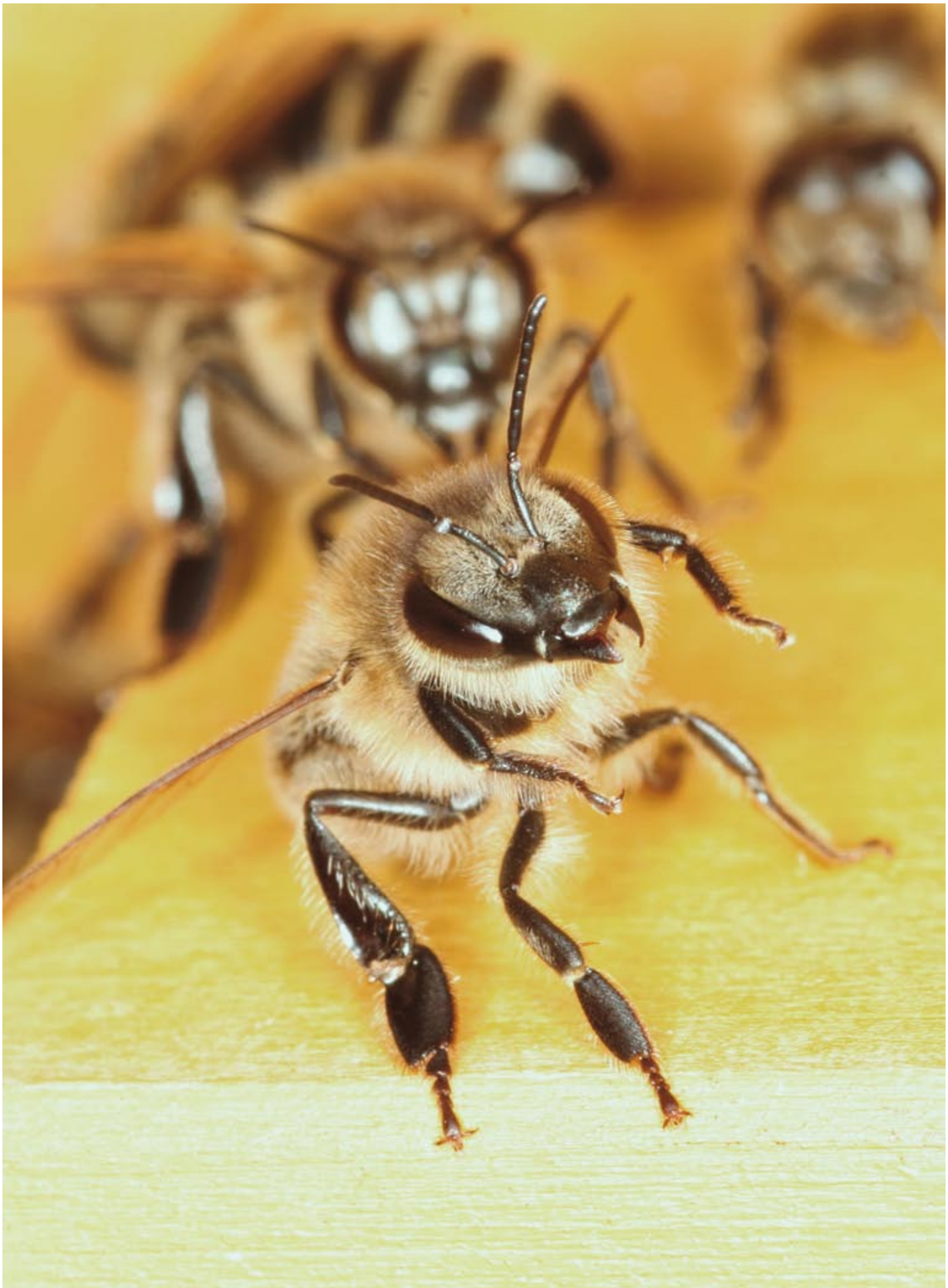


Fig. 8.25 Guard bees deny individuals from other colonies, and all other intruders, entrance to the nest, and will follow any strangers that pass them deep into the nest

Fig. 8.26 While building combs, bees form living chains, the function of which is completely unknown

of environment and genome provides the colony with a high level of adaptability.

Artificially rearing bee pupae at the different temperatures normally existing in an undisturbed beehive has shown that the frequency of the specific behavioral activities they undertake is dependent on the temperature at which they were raised. Bees that emerge from cooler pupae primarily undertake tasks that differ from those of bees stemming from warm pupae. Communication is critical for the successful foraging of a colony, and bees that can precisely communicate their message turn out to be those that develop at temperatures close to 36°C, the highest that has been found in the brood nest. This group of bees also possesses better learning abilities, and better memories than do their cooler sisters.

The temperature at which bees are raised also influences their lifespan. Adult foragers usually live for about 4 weeks, and are called summer bees by beekeepers. Individuals that survive the winter (winter bees), and are again active in the following season as foragers, can live up to 12 months. Pupae raised at the lowest temperatures in the brood nest are the most likely to become winter bees.

The influence of temperature on metamorphosis is known from many experiments on other insects. Unique to honeybees is that they themselves determine the temperature at which their sisters will develop. The old biological truth that environment and genome together determine the properties of an organism is extended here by honeybees, in their exploitation of a direct feedback between these two shaping forces.

9 Is Honey Thicker than Blood: How Important Is the Family?

The close family relationships in a beehive are a result, not the reason, for their formation of a colony.

The creation of the social form of the honeybee colony, as the most complex and highest level of organization yet achieved in the world of living organisms, was a step in evolution that one could have predicted (▶ Chap. 1). The question of when this step actually took place is closely related to the question about the conditions under which such a development could ever occur. A theoretical expectation on its own does not lead to reality when the appropriate conditions are not available. The quantum evolutionary leap to a superorganism was associated with the chance occurrence of a "technical prerequisite" that strongly favored the appearance of this life form. To provide an analogy: man long theorized about, and wished to fly before putting this into practice. The final step was possible only once the materials needed to build a functional flying machine had been assembled.

But what are the "technical" conditions for the creation of a colony-building honeybee? What do honeybees have that dragonflies, bugs, or beetles—which have not established superorganisms—do not?

The great evolutionary biologist Charles Darwin (1809–1882) did not accept that the appearance of colony-forming honeybees was inevitable; quite to the contrary, he saw a problem in the existence of honeybees that could threaten his entire evolutionary theory. According to his proposal, the first condition for evolution is that the number of offspring be greater than that needed to sustain the population at a constant level. Only when there are enough offspring, and these contain variations, can the next step, selection, take place. Honeybees confronted him with an organism in which all the females of an entire colony, except one, the queen, produce no offspring. In his book "The origin of species", he writes that the honeybee workers were difficult to include in his theory. They differ in form and behavior from the reproductive males (drones) and females (queens), but presumably cannot pass these characteristic differences onto the next generation, because they are sterile. But they quite clearly do … so, how do they do this?

Darwin found a solution that solved these challenging difficulties. The conceptual problem depicted above would be significantly reduced if one accepted that selection could act not only on the individual, but also on the entire colony. Seen in this light, entire colonies would compete for the largest number of daughter colonies that were reproduced, not of individual bees.

Modern evolutionary biology now includes the concept of colony evolution in the term group selection.

Darwin most likely was aware of the "collective" notion of a bee colony as an integrated being, which had been expressed by German apiarists. Consequently, such beings would be in competition with their equivalents, in the same way as are single organisms.

Just why it is that the individual workers of honeybees, and their relatives, bumblebees, wasps, and ants, do not compete against each other within the colony remains unsettled. Nevertheless, it is precisely this renunciation by the workers of producing their own offspring that the honeybees have used as successful strategy to propagate their own genome.

Special Genetic Relationships Between Bees

The unusual situation may be better understood in terms of a concept that has become popular through the work of an English biologist, William D. Hamilton (1936–2000).

The essence of Hamilton's idea is as follows: particular genes localized at the same place in particular organisms, and which influence the same character, are called alleles. Alleles can occur in different forms, and are the basis for variability in the gene. The alleles are not only passed directly onto the offspring, but copies of these exist also in their siblings and their children, cousins, aunts, uncles, and entire families. The likelihood of finding the same allele in individuals decreases the more remote the kinship of an individual is to the source. The carrier in which the allele resides is of little consequence for the success a single allele has in spreading as a competing allele in a population. A behavior in relatives that contributes to rearing the young, for example, can be of advantage to both the supporters and their alleles, even if the carriers have no offspring of their own. Such a sacrifice is then not a disadvantage, if the alleles occur sufficiently frequently in the family.

Kinship selection, a theory developed by John Maynard Smith (1920–2004) and William D. Hamilton, based on the distribution of alleles in groups of related organisms, has clear consequences for the appearance of cooperative, or in extreme cases, "altruistic" behavior in animals. This theory offers an explanation for single organisms that, like honeybees, have crossed the threshold from "loners" to social beings in the course of their evolution.

Alleles that are most successful in the branching family network exist "selfishly" at the expense of other alleles. The vision that alleles behave selfishly, and aim only to set as many copies of themselves as possible in the world, has been convincingly explained by Richard Dawkins (1941–), in his book "The selfish gene". To an observer, alleles appear as selfishly behaving single elements, exhibiting what could almost be termed a "propagative drive" in honeybees.

Honeybees have, like all other Hymenoptera, and many other insect species that do not form colonies, an unusual mechanism for determining the gender of the adults. Bees from unfertilized eggs have a single set of chromosomes, the haploid chromosome state. Bees from fertilized eggs have two sets of chromosomes, the diploid state. Honeybees possess a single gene for the determination of gender, which can appear in different alleles. An individual that is homozygous for this gene (the alleles are identical), which has to be the case for all haploid individuals (they possess only a single allele), will develop into a male. An individual that is heterozygous for this gene (all the alleles are different) develops into a female. A diploid individual homozygous for the sex gene, which very seldom occurs, is a diploid drone, and is usually killed by the workers in the larval stage.

This method of determining the sexes through the number of chromosome sets, or haplo-diploidy, has unusual consequences:

- Males have no fathers, because they come from unfertilized eggs. It follows that males have no sons, at the most, grandsons.
- Should a male and a female produce daughters, these daughters will share more common alleles than they would with their own children.

Approaching the concept in small steps allows a better understanding of these curious circumstances:

- In 1969, the French biomathematician Gustav Malecot (1911–1998) defined genetic kinships as "r", which is the average probability that a particular allele selected from an individual will also be found in a particular individual to which it is related.
- The value "r" is of biological significance from the point of view of the gene "spender", because this defines the direction of the gene flow.
- All the alleles of the haploid father will certainly be passed onto each daughter. The probability of occurrence of the father's alleles in the daughters is 100%, or, expressed differently, $r = 1.0$. The father will therefore find every one of his alleles again in every daughter.
- The statistical probability that the same alleles of the diploid mother will be found in her daughters lies at 50%, or $r = 0.5$, because a mother contributes exactly half of her alleles to each of her egg cells. A mother will therefore find, on average, half of her alleles again in a particular daughter.
- The probability that the same alleles will be found in a comparison between full sisters is given by a summary of factors relating to the father and the mother: half of the genome of a female bee comes from the father, and is identical in all full sisters. Mathematically expressed, this means that 100% of 50% of the sisters' genes are identical. The other half of the genome comes from the mother, and has only a 50% probability of being identical in the sisters, because for each gene the mother has one of two possibly different alleles to offer. In terms of the entire genome, this means 50% of 50%, or 25% are identical.

- If one now adds up the values that come from the alleles of the father and the mother, and compares the sisters to one another, one gets 50% + 25% = 75%, or $r = 0.75$ genetic kinship.

Honeybee sisters therefore share a statistical average of three quarters of their alleles. In reality, this value swings between 50% of common alleles (only the alleles from the fathers are inherited), and 100% (alleles from both the father and the mother are the same).

Cloned animals are 100% genetically identical; their degree of genetic kinship is $r = 1.0$. Human children are 50% identical to their parents; here, the degree of genetic kinship amounts to $r = 0.5$. Honeybees, with their $r = 0.75$, lie between cloned animals and humans. From this perspective, the best thing that a female bee can do to propagate her genes is to renounce having her own children, and instead help her mother to bring as many sisters into the world as possible.

In order to propagate their alleles, the sterile workers should cooperatively support each other. This is exactly what happens in bee colonies, although the situation is a little more complex.

A queen on her nuptial flight usually pairs with about 12 drones, and their sperm fertilizes the eggs that will later develop into females. The workers in a bee colony all have the same mother, because they all stem from the same queen, but are from many fathers. Workers that are produced from the sperm of the same drone are full sisters. They are half sisters to those that have different fathers. Full sisters share more common alleles than do half sisters (Fig. 9.1), so they should support the half sisters less than they do other full sisters. A complex game of cooperation between the full sisters, and conflict between the full sister groups would be expected if bees supported their closest kin, although an interaction of this kind would depend on them being able to distinguish between full and half sisters.

Bees can determine a great deal about their conspecifics through their sense of smell. The decision of whether or not a bee that wishes to enter the hive belongs to the colony has fundamental importance. This check is undertaken by guard bees at the entrance to the hive (Fig. 9.2), which can smell a newcomer from a distance (▸ Fig. 7.29), and touch her with their antennae

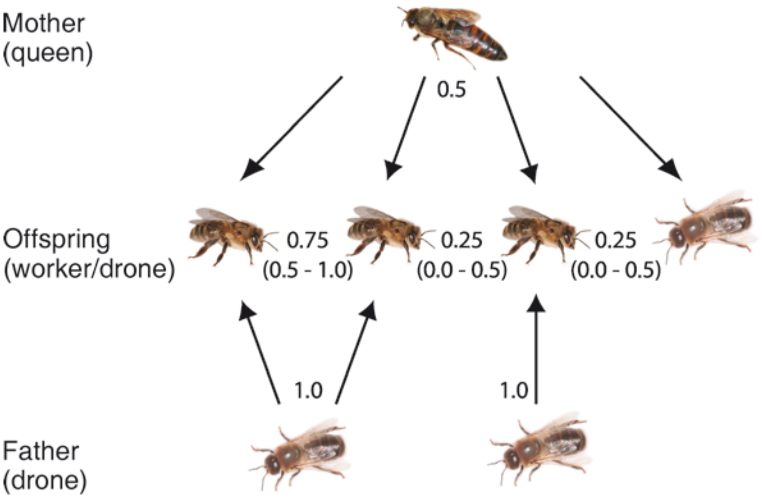


Fig. 9.1 There are many grades of genetic similarity within the bee colony superorganism, expressed by the degree of relatedness "r". The queen and all her children share in every case an r-value of 0.5. For full sisters (same mother and father), the r-values lie between 0.5 and 1.0, with a mean of 0.75. For half sisters (same mother, different fathers), the r-values lie between 0.0 and 0.5, with a mean of 0.25. Brothers and sisters share r-values in the range of 0.0 to 0.5, and with a mean of 0.25. Fathers share an r-value of 1.0 with their daughters. The larger the number of fathers of bees in a colony, the more diverse the relationships become. If the workers also begin to lay eggs, and so produce nephews, a further complication of the r-values ensues

when she lands. Chemo-sensitive sensilla in their antennae enable them to establish whether she belongs to the nest, or is a stranger.

If the odor signals "stranger", the newcomer will be aggressively chased off. She does, though, have the possibility of being granted entrance if she bribes the guard bees with a drop of nectar (▸ Fig. 7.30).

Conditioning experiments have shown that bees are able to distinguish full sisters from half sisters by the odor of their cuticle, the thin wax layer that covers all insects and protects them from dehydration. Do they use this ability, and if so, when would it be significant in terms of kin selection?

For kin selection, odor identification would be important when new reproductive animals are being reared, because the queens and the drones have a propagative future. The rearing of a new queen will set the genomic direction for the new colony, and

Fig. 9.2 Incoming bees are investigated at the hive entrance by guard bees to see if they belong to the colony, and so can be allowed in, or if they are strangers and need to be kept out

here there is a high potential for conflict between the different groups of full sisters in the nest.

We know virtually nothing about how a colony decides who the new queen will be. Do subtle conflicts and contests take place between the half sisters that we have not recognized? Do the still generally unknown, but often reported behavior patterns of workers, young queens, and drones on nuptial flights play a role?

Much of this is still a complete puzzle.

An additional area of potential conflict occurs when the workers themselves begin laying eggs. In European bees, this happens at a rate of 1 in 1,000. Such eggs are unfertilized, and result in haploid drones. In such a colony, therefore, drones can arise that stem from the queen, and have a degree of kinship with her of $r = 0.5$. Drones that stem from workers have a degree of kinship of $r = 0.5$ with their worker mothers. The degree of kinship between a worker and her brother is $r = 0.25$, and this value is independent of the number of queen pairings, because the mother passes her own genes onto her sons in the unfertilized eggs.

Things get really complicated when one calculates the degree of kinship between a worker and her nephew, the son of one of her sisters. The values that one obtains here are dependent on the number of pairings of the queen on her nuptial flight. If only one pairing took place, the worker would have a kinship of $r = 0.375$ with the sons of her sisters (and in this case, all the workers would be full sisters). With two possible fathers, the degree of kinship to the nephews sinks to $r = 0.1875$, which is below the kinship of $r = 0.25$ shared with brothers. If the queen had mated ten times, a kinship of $r = 0.15$ between workers and their nephews results. Purely theoretically then, and considering the usually typical multiple mating of the queen, it would be of genetic advantage to the workers to kill the sons of their sisters, but not their brothers, and on no account their sons, with a kinship of $r = 0.5$.

Workers should therefore suppress nephews that are genetically remote from them, and workers eat the eggs of other workers (Fig. 9.3). They should protect their own eggs, and those of their full sisters, while destroying those of their half sisters, but it is still not clear whether bees can distinguish between the eggs of their full and half sisters. Workers could also “make sure”, and simply eat up all the eggs that have not come from the queen.

Fig. 9.3 Worker bees eat the eggs that do not stem from the queen, or any egg that is defective, or shows signs of faulty development. In order to take these pictures, eggs in the cells were slightly damaged with a sharp needle. Minutes later, they were cleared out of the cells by worker bees (*above*, *white circle*), and eaten (*below*)

The quantitative determination of the genetic kinship between the members of a bee colony provides the basis for an ambitious theory. The degree of kinship "r" that is calculated is a statistical average that lies between widely separated extremes (Fig. 9.1). When a honeybee meets another bee, pupa, larva, or a different egg, she is not confronted with a statistical mean for "r", but with a concrete single "r". Can a honeybee determine this value when meeting another individual?

The destruction of haploid drone eggs by the workers shows that they can distinguish between the eggs of the queen and their sisters. The chance distribution of the alleles will, however, lead to situations in which a worker could come across a haploid egg from the queen with which she has nothing genetically in common, or an egg of one of her sisters with which she shares the maximum possible number of alleles.

For the theory to hold, it is not the origin of the egg that determines the action a worker should take, but the nature of the genome.

Just how well honeybees are in reality able to recognize, and use the degrees of kinship still needs to be demonstrated.

In the case of the destruction of worker eggs by workers, there is a simpler explanation: the consumption of eggs could be a purely hygienic precaution (Fig. 9.3). Very few of the larvae from worker bees molt, and embryonic development either does not start, or the embryo dies. In contrast to determining the degree of genetic similarity, worker bees are faced with the far simpler task of distinguishing dead from living eggs. It is also highly likely that eggs from the queen can be recognized by a protective odor provided by the queen when she lays these. Many questions remain unanswered.

The determination of sex in the form of haplo-diploidy in the Hymenoptera brought about the evolution of superorganisms, and provides an explanation for the change from living as an individual, through living in associations, to sociality and eusociality.

The reality of the presently living superorganisms does not support the theory that kinship alone is the explanation of bee biology. The difficulty of the enormous range of the r-value around the statistical mean has already been mentioned. This becomes even more complicated if the multiple pairing of the queen is taken into consideration when calculating the degrees of kinship. Hamilton's quantitative ideas would be valid only if all bees in a colony are from one mother and one father, but because many fathers leave their traces in a bee colony, this does not apply to the bee colonies that we find today. The workers of a colony are less genetically similar amongst themselves than they would be to their own daughters.

Perhaps we have, in the application of the theory of kinship selection to honeybees, a situation deserving T.H. Huxley's (1825–1895) remark that "The great tragedy of science is the slaying of a beautiful hypothesis by an ugly fact". The situation here, though, is not quite as severe. During the passage of evolution, kin selection and haplo-diploidy were needed for the bees, and other hymenopterans, to find their way to their superorganisms. Hence, when establishing nests, sisters would help one another in raising the young, just as we find today in wasps. But what keeps honeybees still at this level today, if kinship selection is no longer a significant basis?

Cooperation Is Always a Good Thing

What advantages are gained by bee colonies from their behavior, and in the workers in a colony stemming from different fathers, following the multiple pairings of the queen?

Because there is clearly no close family kinship between all members of the bee colony that can lead to the end of solitary organisms, some other aspects must be the center of focus preventing the collapse of the superorganism.

Once the first steps on the way to the superorganism were taken on the basis of kin selection, other changes occurred that offered advantages that more than compensated for genetically drifting apart, and that hold the organisms together in their superorganisms despite strong swings in kinship within them.

As each solitary organism has a physiology, so the superorganism has a superphysiology that extends from the properties and interactions of the colony members. It is this sociophysiology of a superorganism that, like parentheses, holds the colony members together, and it is their properties that are evaluated in the competitive selection between superorganisms. The characters of the entire group are the phenotype on which selection operates. Should an individual belong to a well-rated group, it is on the winners' side. Such workers have survived and propagated the alleles of their genomes, even if only indirectly through their mothers and brothers.

A significant cause for the massive genetic conflict within a bee colony is the multiple pairing of the queen. So, what does the superorganism gain from this multiple pairing when the result is internal conflict?

Many fathers means many different alleles, and that means workers with a correspondingly high number of different characteristics.

Differences between bees include their variable sensitivity to various environmental stimuli. Some fathers produce sensitive, others insensitive bees. The consequence of this is a large range of intensity with which a colony will react to external or internal disturbances. Certain individuals will begin to heat following even a very small drop in brood nest temperature. Others will join in only if the temperature falls further, and again others at still colder temperatures (▸ Fig. 10.6). The colony as a whole responds optimally in this graded way to disturbances, and exactly the right effort is mobilized that is appropriate to the level of disturbance. A broad spectrum ranging from highly sensitive to particularly insensitive bees leads automatically to the measured intensity of the colonies reaction.

The multiple paternal lines in a beehive, and the resulting character diversity of its members, has an impact not only on climate adjustment, but also on every aspect of the life of bee colonies.

The vulnerability to infection of a bee colony sinks with the number of fathers the daughters of which the colony is composed, although why such colonies are less susceptible to sickness—compared to artificially singly fertilized mothers—is not understood, considering the resistance to disease of single individuals. A genetically heterogeneous colony is possibly able to react more effectively to the various stresses presented by an infection. There are many interesting questions for future research on these aspects of bee biology.

10 The Circle Closes

The bee colony superorganism is more than the simple sum of all its parts. It possesses properties that one does not find in single bees, although many of the properties of single bees are determined and influenced by those of the entire colony, within the framework of its sociophysiology.

The Bee Colony Superorganism, a Complex, Adaptive System

The relationships and procedures in a bee colony are highly complex, because small behavioral building blocks are simultaneously and continually being contributed by thousands of individual bees to the collective behavior of the colony.

Complex biological systems, through their plasticity, adapt over the short term to relevant aspects of the environment, or over the long term through evolution.

Complex systems with adaptive abilities are found in many areas in nature and technology, and a general description of their properties is contained in the following broad definition taken from the computer scientist John N. Holland (1929–): a dynamic network with many participants (they could be cells, species, individuals, firms, or national representatives) that react continuously, and in parallel to that which the other participants are doing. The control of a complex adaptive system has the tendency to be distributed and decentralized. If an integrated behavior of the system is required, then this must come from competition and cooperation of the participants. The behavior of the system as a whole is a result of a large number of decisions that are arrived at by many single agents.

For a bee researcher, this is an exciting and challenging definition that has to be carefully considered to appreciate all its facets.

It provides a theoretical framework for the inclusion of the honeybee phenomenon within the framework of other complex systems, and confirms the intuitive impression obtained from working with honeybees. A bee researcher attempting to describe the particular nature of the bee colony superorganism would cover, point for point, Holland's definition:

"The bee colony is a complex adaptive animal community, consisting of many thousands of individuals that are continuously active and respond to the conditions of their surroundings and to the presence of their nest mates. There is no ruling body, instead the overall behavior of the colony results from the co-operation and competition between the bees".

Complex adaptive systems such as the bee colony exhibit the ability for self-organization and emergence. Other important properties of complex adaptive systems are communication (described for the bees in Chap. 8), spatial and temporal organization (described for the bees in Chap. 7), and reproduction (described for the bees in Chap. 2).

How is self-organization and emergence expressed in the bee colony?

Maintaining the Balance

The essential life processes in a healthy organism must remain in balance. To achieve this, there have to be mechanisms that actively restore the balance if it is disturbed by external or internal factors. Values that fall below a set level must be raised, if too high, then lowered. Such regulatory processes take place through negative feedbacks that establish the connection between the various components of a system and the external world, and maintain homeostasis. In a biological organism like a bee colony, homeostasis is the maintenance of a balanced state through self-regulation. The term balance may suggest peace and quiet. However, the balanced state of a bee colony is anything but "frozen". Set levels continually change, and are regulated through the constant activity of the colony, a situation better described by two Chilean pioneers, Francisco Varela (1946–2001) and Humberto Maturana (1928–), as homeodynamic, rather than homeostatic.

Regulated biological systems exhibit two basic features:

- First: The whole is more than the simple sum of the parts, and properties emerge that are not present at the level of the elements.
- Second: The whole, in turn, determines the behavior of the component parts.

The mutually coupled state between the whole and its parts is one of the fundamental tenets of organismic biology. To better understand the complex phenomena of living organisms, their functions and biological aims, an attempt has to be made in an all-encompassing study to appreciate the mutual interdependence of the separate parts on one another, and on the whole. Honeybees are particularly suited to this approach, because the two suppositions about the properties of living systems—that the whole is more than the simple sum of the parts, and that the whole influences the properties of the parts—are clearly demonstrated in honeybee colonies.

The First Basic Feature

Colonies of honeybees are highly complex systems containing the possibilities for many feedback loops. In the bee colony superorganism, we find homeostasis at the level of the body functions of individual bees, and also as a social homeostasis at the level of the entire colony. In terms of body functions, the individual bee is as balanced as every other healthy living being. Balanced states in the colony are achieved only through the collective action of all the colony members. Relevant here are comb construction, climate control of the nest, and hygiene. Abilities and properties that appear only as a collective effort, and are not achievable by single individuals, are the hallmark of the superorganism sociophysiology.

The Second Basic Feature

The sociophysiology of the colony exerts a significant influence on the properties of single bees, as in the case of "breeding" the characters of individual bees (▶ Chap. 8), or comb building (▶ Chap. 7).

Everything appears to be connected to everything else, making the isolation and study of single control loops very difficult.

The maintenance of brood nest temperature is a good example of control loops in the bee colony superorganism.

Not Too Warm, and Not Too Cold

By control, we mean the correction, in either direction, of the departure of a system from a specified value. The appropriate tools for temperature regulation (the regulation mechanism) have been identified in bees: the introduction of moisture and fanning to reduce temperature, and the production of warmth by the flight muscles to increase temperature. The warmth produced by bees is most efficiently applied to the pupae from cells within the brood combs.

The architecture of the brood nest also contributes here—it is constructed in a particular fashion to ensure constant and energetically optimal conditions for the brood. An optimal density of unoccupied cells in the capped brood area, which are used for heating from within, is established for every ambient temperature (Fig. 10.1). The effectiveness of heating decreases if there are too many, or not enough empty cells available. The proportion of unoccupied cells in the brood nests of healthy bee colonies is

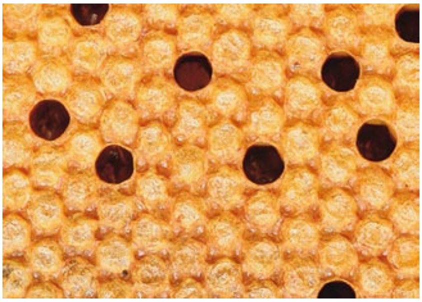


Fig. 10.1 The brood nest is a visible example of social homeostasis, and the result of the communal performance of all the bees in the colony. The energetically optimal heating of the pupal cells is a consequence of the architectural details of the brood nest, in which heater bees can apply the heat they produce from the 5–10% of empty cells distributed through the capped area

5–10%. Empty cells that lie between the capped pupa cells can also vary in number, depending on the average ambient temperature. Unfavorable conditions that per se would not be involved in the regulation of the nest climate can result in over 20% of the brood cells in the capped area being empty. For example, a high incidence of diploid drone larvae (▶ Chap. 9) that are destroyed by the workers, and removed from their cells, can lead to a strongly "holed" appearance of the brood nest.

The average temperature at which a pupa develops influences the characters of the resulting adult, and perhaps their ability to heat the brood, or build the brood combs. This, in turn, affects the nature of the next generation of pupae. Large and small control loops are interwoven in the brood nests.

Feedback loops are found in many forms in bee colonies. There are rapidly or slowly acting feedback reactions of both individual bees, and of the superorganism. Strong or weak correlations exist between negative feedbacks, and counteraction to disturbances.

Feedback loops act rapidly or more gradually, depending on the time it takes to determine the value of a particular parameter, and the speed with which this value can be communicated. If honeybees extract the information directly from a signal in their surroundings, counteraction is usually more rapid than when the information is transferred indirectly through communication signals. In contrast to the individually sensed information, activity that is induced and coordinated by communication signals has the advantage that the resulting response will be independent of the individual experience of each bee. The classical example here is the dance communication. In the brood nest heating behavior, we also find a phenomenon the details of which are still unknown, but which appears to operate through some kind of communication system: if the last antennal segment, which bears the temperature-sensitive receptors, is carefully removed from hundreds of heater bees, they will not behave noticeably differently within the nest, but they no longer heat the capped brood. A handful of intact heater bees added to this large group of temperature-insensitive bees results in all of them taking part in heating. The disabled bees are unable to directly measure the lowered temperature and respond, but communal heating behavior can be initiated through recruitment, and some form of communication. The small number of intact bees are able to animate a whole crowd of antenna-amputated bees to heat the brood.

The optimal value of controlled levels for any particular organism is found during the course of evolution through the process of change and selection. The most highly developed systems can not only comply with long-term constraints in the course of evolution, but can also alter the set points of control circuits over the short term, and adapt continuously to new conditions.

Specified levels in a bee colony, such as the optimal size of the brood nest, or the amount of pollen store, can vary considerably with the seasons, and the ability of the superorganism to continually adjust to these changes is an expression of its plasticity.

The superorganism has three ways to react to new requirements, or if the scale of an ongoing activity needs expanding:

- The individuals that are already busily involved with the task can increase their effort.
- Individuals that are occupied with other tasks can be redirected to the new activity, although this may lead to conflicts concerning the execution of the two different activities.
- Individuals from a "quiet reserve" can be deployed.

Honeybees usually respond by activating the quiet reserve, the maintenance of which they can afford through their strength in numbers.

The Control Circuit for Nectar Import and Honey Consumption

There are many preferred values in the bee colony. Thomas D. Seeley (1949–), in his book "The wisdom of the hive", describes his work on the exploitation of the food sources by a bee colony. An entire list of factors influence the optimal size of the honey reserves of the bee colony. The availability of storage space for honey in the comb, and the rate at which it is consumed by the bees, are two general factors that belong to these.

The extensive use of honey for heating the brood nest must be counterbalanced by the importation of nectar. This is done by the foragers. Control of the foragers must contain the two following aspects: an activation of foragers when the reserves in the hive fall, and there is a good supply in the field, and a decrease in foraging activity when there are sufficient reserves in the hive, or if the usual food sites fail. In both cases, the feedback takes place through communication mechanisms.

The dances activate the quiet reserve in the colony; reluctant receiver bees on the combs have the opposite effect, and down-regulate foraging activity. Such feedbacks allow a rapid response of the colony to each particular, new situation.

The details of the control are as follows: forager bees perform round or waggle dances if the nectar supply in the field is good. Their receiving nest mates are compelled to increase their intake of nectar. This increase in the importation of nectar is not because the foragers are collecting more diligently, but because the number of foragers increases. The bee colony has available to it a significant quiet reserve of inactive bees that are activated by the waggle dance. An accurate picture of the foraging activity of a single individual bee can be obtained from bees equipped at birth with a microchip (RFID = radiofrequency identification, ▶ Fig. 3.10). These record each foraging excursion she undertakes throughout her lifetime (Fig. 10.2), and show that on average a typical forager will undertake three to ten flights per day.

Receiver bees responsible for accepting the nectar from the foragers either no longer relieve them of their load, if all available storage areas in the nest are filled, or make them wait. Foragers then perform tremble dances, and signal the other foragers that further foraging is not required).

Foragers will also determine when a food site is failing, or that it is being visited by too many bees, leading to congestion and delays. On their return to the nest, these foragers press themselves against others, and give a short, high-toned beeping noise (Fig. 10.3).

This beep tone has a modulatory influence on both the waggle and the tremble dancers. “Beeped” waggle dancers stop dancing. Outside the area of the dance floor, the beeping and tremble dances recruit more receiver bees, in order to increase the processing capacity of the colony. The tremble dance both slows down foraging, and animates receivers. Waggle dances, tremble dances, and “beeping” stabilize the entire flow of nectar and its processing in the hive, and lead to smaller variations in both than would be caused if foraging behavior were governed only by swings of the supply in the field (Fig. 10.4).

Fig. 10.2 "Transparent bees": a small microchip, fastened to the thorax of bees emerging from pupae, allows individual bees to be identified and their activity monitored continuously throughout their lives

The spatial and temporal foraging activity of a colony is the result of a meaningful management of old and new feeding sites by the bees. The flow of information used to deploy the colony's work force depends on the dances, and on the behavior of the receiver bees that continuously compare the tastes of different food sources. In this way, the distribution of the foragers in the field can be optimally tailored to the supply.

The individual control circuits are also interconnected. The nectar-collecting control circuit is interwoven with the comb-building control system. If nectar-receiving bees that relieve the foragers of their loads, and then deposit these in cells, cannot find any storage space, their wax glands begin to produce more building material, which in turn releases a new wave of comb building, and so the creation of additional storage space, should the nest hollow allow such an extension.

A particular specified value in the colony is the temperature of the brood nest. Should this be too high, bees carry water into the

Fig. 10.3 Forager bees that have visited food sources that have become unattractive grasp other dancing foragers in the hive, and "beep" them with high-frequency tones. These immediately cease dancing. Should inactive receiver bees be similarly "beeped", they will become active and accept nectar from the foragers

hive, and spread this thinly over the edges and caps of the cells, while others on the comb produce a cooling air current with their wings (Fig. 10.5). If it is too cold, which is usually the case in the brood nest, the heater bees go into action (Fig. 10.6). We have two very different behaviors with opposite effects that are released by variations of the specified value.

But how is it that not only the direction of change (cooling or heating) is always appropriate, but also the exact value of the specified temperature is set? And how is it that exactly the right number of bees necessary to correct the unwanted temperature variation are activated?

The solution is simple, but very effective. Different individual bees have different thresholds to cues and signals that release behavior. Some bees start to fan their wings following even a very small increase in temperature. If this first group of coolers manage to contain the overheating, then all is well. If they do not manage, the temperature will increase still further, and the bees

Fig. 10.4 Two different behaviors represent the "volume control" for regulating the flow of nectar into the nest. *Above* Waggle dances recruit more foragers, and so increase importation of nectar. *Below* Tremble dances dissuade the foragers from further excursions, and so decrease the nectar import

that are the next most sensitive to temperature will also begin to fan with their wings (Fig. 10.5), and so on. When the temperature sinks, the individuals with the highest threshold to temperature, which were the last to begin fanning, will be the first to stop. The process is highly efficient, because the effort that is employed is exactly appropriate to the level of disturbance. The quiet reserve does not consist of bees with similar thresholds to stimuli nor with similar abilities, but is heterogeneous. This multitalented mixture of bees allows the colony to react appropriately to any kind of disturbance.

The threshold values at which the behavior is released in individuals are determined partly by the genome, and otherwise re-

Fig. 10.5 A few ventilating bees are active if the temperature of the capped brood nest lies slightly above the correct temperature (*above*); many are active if the temperature exceeds the required level by a significant amount (*below*)

sult from the multiple pairings of the queen bee. Different fathers lead to different daughters with different behavioral threshold values, and so a broad range of sensitivities. The wider this range, the more exactly the number of bees deployed can be tuned to the extent of disturbance, and the precision with which the colony can adjust.

Threshold values for particular actions can also be influenced by conditions in the brood nest. Unlike the genetic component,

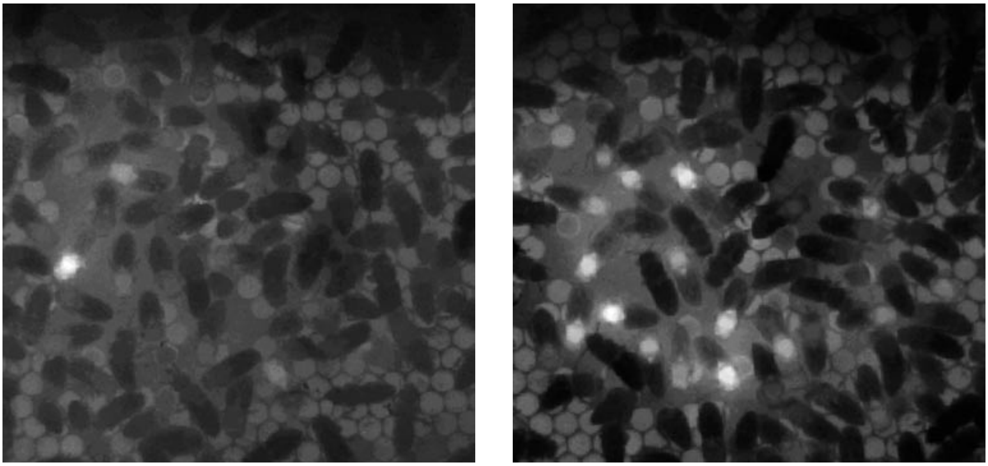


Fig. 10.6 A few heater bees are active in a brood nest that lies slightly below the required temperature (*left*); many are active where the temperature sinks significantly below the required level (*right*)

this is a slow feedback loop that is apparently developmentally manipulated by the bees themselves, and which plays the decisive role.

The hybridization of the European honeybee, *Apis mellifera carnica*, and the African honeybee, *Apis mellifera scutellata*, has resulted in the so-called African killer bees. Behaviorally, this hybridization manifests itself as a lack of fine control of the colony's response to an alarm. An enemy alarm signal, unlike the intimate dance communication, should in any bee colony activate a large number of colony members, but here, too, appropriate to the extent of the threat. The "derailed" alarm communication in killer bee colonies acts in an all or nothing way. The smallest trace of the alarm substance isopentylacetate, released from the sting apparatus of a bee, causes the entire colony to erupt from the hive to join in the attack, with frequently fatal results for the victim.

Sickness as a Maladjustment

Sickness can bring individual bees and whole colonies into difficulty. Bee illnesses are caused by pathogens or parasites, and fungi, bacteria, and viruses can all be considered as sources of

Fig. 10.7 Considering the crowded conditions in which they live, mutual grooming among the worker bees is an essential precaution against the outbreak of epidemics

infection for honeybees. Parasites such as the *Varroa* mite represent not only a direct threat in this regard, but can also carry pathogens.

Honeybees live in an unbelievably crowded world, and in constant touch with one another, and so it is no surprise that in the course of evolution a variety of mechanisms have been invented that can be employed to successfully prevent sickness.

To begin with, the outer covering of the bee, the cuticle, with its thin layer of wax, is difficult for pathogens to penetrate. Pathogens that do pass this barrier are confronted with the immune system, which relies on defensive cells in the hemolymph that possess innate molecular defense mechanisms. These obstacles are also found in the same, or similar forms in solitary insects. As a colony, however, honeybees have possibilities available to them that solitary species are denied, in particular the hygiene of the nest being carefully maintained through a number of specific behavioral patterns.

Worker bees frequently engage in mutual cleaning activity (Fig. 10.7), and the most valuable member of the colony, the

Fig. 10.8 The queen is cleaned almost without pause by her court bees. Of all the members of the colony, she can least afford to become ill

queen, is subjected to uninterrupted cleaning by her court bees (Fig. 10.8).

The future nursery is thoroughly cleaned before the egg is laid (Fig. 10.9).

Should a death occur in the hive, the corpse is removed from the colony as rapidly as possible (Figs. 10.10, 10.11).

Sick bees are recognized by bees working in the hive, and are aggressively treated, although it is not clear on what basis sick colony members are identified. Possibly these individuals are

Fig. 10.9 Thorough cleaning of the empty cells in which the queen will lay an egg is an important behavior for the health of the colony

noticed because of their altered behavior, or differences in the chemical nature of their body surfaces.

Bees also use foreign media in their defense against infections. Propolis, resin that has been collected by bees from plant buds, and built into the comb, has an antibacterial and antifungal action. Bees enter the apothecaries of the plant world, and there obtain their medications.

Diseases can, however, also alter behavior. In the Middle Ages, people left the towns for the open country in cases of epidemics, a strategy that slowed the spread of disease. Honeybees also exhibit changes in their behavior following the onset of a disease. Infections or infestation from parasites that affect the orientation abilities of individual bees is fatal for them. Sick bees cannot find their way back to their own colonies after a foraging flight. They stay out in the field, and die there.

This method of self-purification of colonies can lead to a problem if apiarists set the colonies so close together that sick bees find

Fig. 10.10 Dead larvae or pupae are rapidly detected, and removed from the hive

Fig. 10.11 Adult bees that die in the nest trigger cleaning behavior in bees that act as undertakers, and throw the corpse out of the hive

not their own, but other nearby hives that they enter (Fig. 10.12). Then, the mechanism designed by nature to isolate disease instead becomes a way of spreading infection to neighboring hives. The problem is somewhat alleviated by the activity of guard bees, but not entirely solved.

Fig. 10.12 Compared to wild populations, cultivated bee colonies are kept close together for convenience. This can result in the rapid spread of disease between the colonies

Division of Labor, Decentralized Control, and Emergence

Division of labor (▸ Chaps. 2 and 8) is one of the recipes for the success of colony-forming insects. In honeybees, this division of labor follows an age-dependent preference in carrying out particular tasks. Clearest to recognize is the activity of the older bees as foragers, but although this is true in principle for most of the special tasks in the colony, there is a high degree of flexibility. If all the young bees are removed from a colony, some of the old bees are "rejuvenated" and will develop active feeding glands, or even active wax glands. Removal of all the old bees results in the young bees very quickly becoming foragers. This adaptability of the system rests on a genetic component expressing itself in the deliberate raising of particular specialists in disproportionate numbers.

The presence of specialists does not guarantee their exclusive employment as such in a community. Honeybees of every age and occupation seem to know what has to be done, when to do this, where it is to be done, and how much to do. The sequence of age-dependent occupations in the life of a honeybee provides only the framework in which the bee colony can fulfill all its requirements. The extent and nature of the work done in a bee colony, and the amount of energy that is activated, are so closely linked that one must ask how the bees respond so appropriately to the need. Who gives the orders, and who ensures that they are correctly carried out?

The answer appears simple. They have a queen, who, at least one assumes from the term, heads the colony. However, no line of command can be found from the queen of a colony—with one exception: a fertile queen produces a so-called queen substance in her mandibular glands, which is distributed by trophallaxis to all the bees in the hive, and prevents the ovaries of the workers from developing. This guarantees her, apart from the very rare egg-laying workers, reproductive dominance in the hive.

This situation does not represent a command structure in the sense of decision making, only a physiological reaction of bees to pheromones, although the large number of bees that are influenced does give the impression of a ruling monarch.

Colonies are not organized as hierarchies. The collective behavior of bees is decentralized. Each individual bee behaves as though she herself has come to a decision. The results of these decisions are small, local changes in the colony. These small changes are, in turn, stimuli for other bees that adjust to the new local situation, and make their own decisions. The observable macro-behavior of the colony results from these many small decisions. Swarming, comb building, comb use, and investigation of the surroundings of the hive are all such macro-behaviors of the colony (Figs. 10.13–10.16).

Qualitatively new properties that appear following interaction of the participants in such a system are described as emergence. The macro-behavior of the system appears as the emergent result of many small steps from the bottom upward, and not from the top downward.

Emergent properties that are not of advantage to the system are as pointless as the wonderfully emergent patterns of a snow crystal. Natural selection among bee colonies ensures that their macro-behavior is adaptive, and useful for the colony.

The behavior of superorganisms may appear intelligent to an observer, because they seem to find appropriate solutions to tasks and problems. This behavior of superorganisms is termed collective intelligence.

The study of the collective intelligence of superorganisms delivers exciting insights to biologists, and is also pursued with great

Fig. 10.13 Honeybee swarm formation has lead to the term "swarm intelligence"

Fig. 10.14 Comb building is a tangible expression of the communal activity of the colony members

Fig. 10.15 The use of the comb is optimized through the mutual interactions between the bees

interest in many mathematical and technical sub-disciplines. In superorganisms, small elements of limited abilities that interact with their environment, and to which other similar elements belong, lead through these micro-actions to micro-patterns, forming the basis for the "artificial intelligence" of machines, to which the special case of "swarm intelligence" belongs.

Fig. 10.16 Communication is the basis of behavioral coordination

Insights from mathematicians and engineers that occupy themselves with complex computer systems have brought biologists to the point where they, too, search for mechanisms with formal principles and rules that nature has successfully built into her own complex superorganisms.

Honeybees are not only fascinating and important agents of the natural environment. Their networked control systems allow observations of solutions to complex tasks that can serve as exemplary models in technology—another exciting facet of the honeybee phenomenon.

AGTTCATCACCTCGAGTCCGAATGAAGACGAGAAGGGGAA
GAGAGACGCGGTCAAGGGACCGAAGATATCGATCATCCTG
AAACTATCCACGACGTAGGGATCGTCGGCAGCGTTTTTTT
AGTGTTTCGTCGTGTGTCCCTCCCCCGTTGCTCGGGGAT
GGCCGGCGACTTTGGTTACCGAAGAAGAAGGAGGAGAAGG
TGAGCGTAGGAGGGAGGAATCGAGGGGAAGGAATCGGG
GGTAGGTTTACGGAATCGATGCGTGGCCCCATGGTTGG
GTGTCGGACGCTTGACTCGGGGATTTGAAACTTAACCCTG
ATTTCTCTTTTTTCCCCCGCGAGCATTTCGGTGAAAAAT
TCGTATTCGTATCGACCTATTTCGATCCGATTCAAAATAT
AAATAAGAAGGAAAGATTCGGATAATTCGAANAAAATAAA
ACCTCGAGCGAAGGATGGATCCCGACGAATTCACCGATTC

AGTTCATCATTTTATCTTCCAAAACTTCAGAAGCAAATCC
AGTCGAAG GACCCCGCAA
GACGCGAT GGAGGGATTC
GGCGAGAT GGTCGTCGGG
TTTCTCCT CTTTTTTTCT
GGCGAAC GGATTGGAAG
AGCAATCC CAAATCGTTA
TCTTTCTT TTTCTAATAA
AATTCAC GACAACGATG
CATTTGAAATTCAAATGTATATCCGTTTCTTCTTTGTTTT
GTTATTATTAGATTCGTCTCGTTCAACTATACATATCTTT
TTATAATCCCTTGCTGAATAATTTTACACGATTCTCTA

The honeybee genome has been completely decoded. Letters stand for the bases Adenine, Guanine, Cytosine and Thymine and the sequence of the letters is the text which is translated into protein building blocks. Reproduced on the page here is the part of the genome used by honeybees to build elements of the Royal Jelly, stored in their mandibular glands (▶ Chap. 6).

AGTTCATCAAATTTTTCAAATTGGGGAGAGAATTTTCAA
CCGTTTTCGTGACGGATACTTATACCGATGCAGTGAAAAT
GTCTCACTTTACGATGTATCGTGATATTATACGTTGAGGA
ATAAAAATAAGGAGGAGGAGGAATTGATAAAAATAAGGAG
AGGAANNGANAAAAAGAANGATTTTTTTTTAANAAAAGGG
TGGTTGGAGAGGGAGGAGGGGTATTGGGAATTGGATT

EPILOG

The Future for Bees and Mankind

Mankind's interest in honeybees is ancient, and bees were of importance to our forefathers mainly for their honey and wax. In modern times, the interest in bees has undergone a true renaissance for very different reasons. Albert Einstein (1879–1955) is reported to have said: "When bees vanish from the Earth, mankind will have just four more years to live; no bees, no pollination, no plants, no animals, no humans …". This sentence should not, at least as far as the time frame is concerned, be taken too literally, but the statement carries more than a little truth. Bees are sensitive indicators of an intact environment, and as essential and persistent shapers of the environment, have a significance that cannot be estimated highly enough.

- We increasingly understand how important honeybees are for the maintenance of biodiversity. Even if an esthetically beautiful, and colorfully flowering meadow is not a good argument for some, the fact that the activities of bees reach as far as the steak on our plates should make us thoughtful. The quality of beef rises with the presence of honeybees, because they ensure the diversity of plants in the fields. This is just one example of the widely ramifying impact of honeybees on natural and manmade ecosystems.
- Without honeybees at our latitudes, management of increasingly important renewable resources will not be possible. Mankind and honeybees are dependent on each other, and there can be no enduring agriculture without honeybees.
- The health of honeybees is used as an indicator of the state of the environment made by man, and in which he must live.
- Honeybees excite and challenge the interest of young people in complex biological interactions, so that in time they can themselves accept the responsibility of taking over, and maintaining an environment worth living in.

- In basic research, the honeybee is an inexhaustible source from which ideas for applications in technology, and insights into the inner organization of biologically successful superorganisms can be won.
- Honeybees offer a long list of possibilities for basic research in the biomedical field: research into their immune systems promises important knowledge for humans, and is well suited for the study of fundamental issues. The extreme differences in the lifespans of bees with the same genetic makeup when exposed to different environmental conditions offer opportunities for research on ageing. The optimal rearing temperature for bee pupae, which is noticeably close to our own body temperature, leads to a host of interesting questions.

The ecology and economy of many regions of this earth depend heavily on a large and general presence of healthy honeybees. This presence can be maintained only if we understand the inner life and functions of the bee colony superorganisms so well that we are able to support and protect them when needed, in a focused way. A closer collaboration between basic researchers and practicing apiarists is essential, and the holistic approach of organismic biology offers the framework within which we are able to understand honeybees, using the most modern physical and molecular biological methods.

By supporting honeybees, we support ourselves.

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Photograph Sources

Brigitte Bujok, BEEgroup: Picture Guide page 26, Figs. 1.1, 8.5, 10.6
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