The Buzz about Bees

Jürgen Tautz

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Biology of a Superorganism

With photographs by Helga R. Heilmann
Translated by David C. Sandeman

Springer

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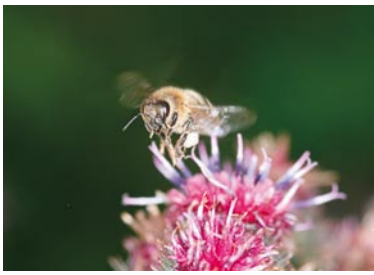
A bee colony—surely nature's most wonderful way of organizing matter and energy in space and time.

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.

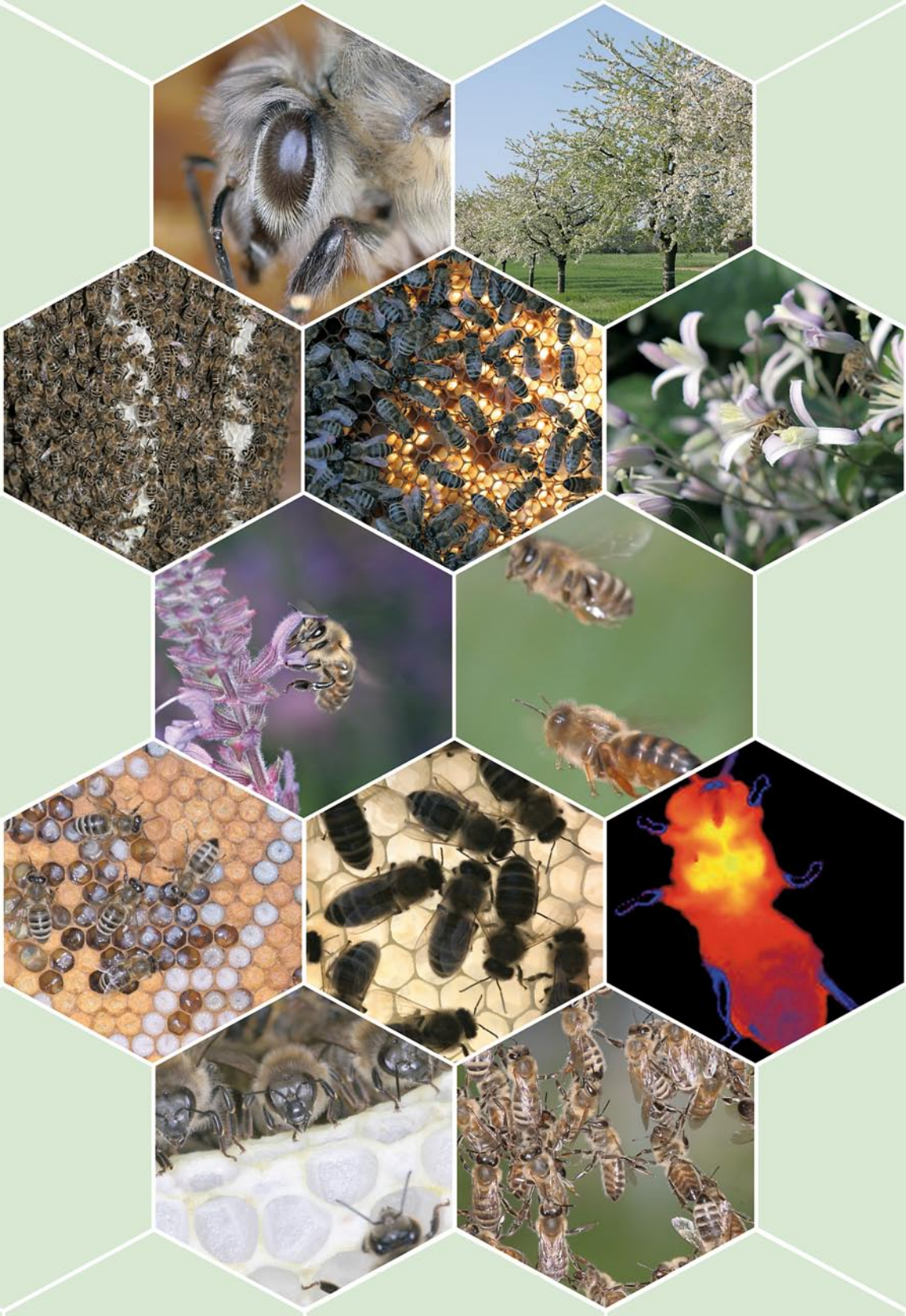
The honeybee is, for us, a "phenomenon" in the purest sense. The original Greek word, φαινόμενο (fenomeno), means something that shows itself, or appears, and we believe this term to be a perfect characterization of this so-called superorganism, its nature repeatedly exhibiting the characteristics of 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



» Contents

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

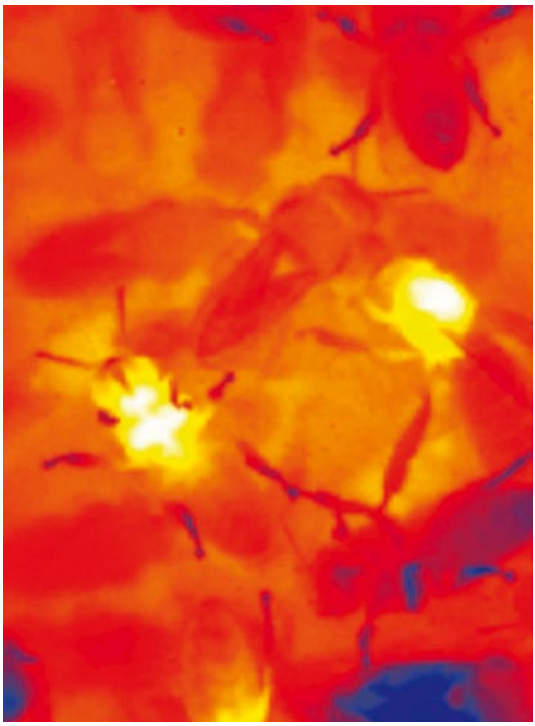


Fig. P.4 Heater bees keep the pupae at a body temperature that, in ideal situations, does not vary from that of mammals by more than 1°C

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 "ge-

nomic 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).

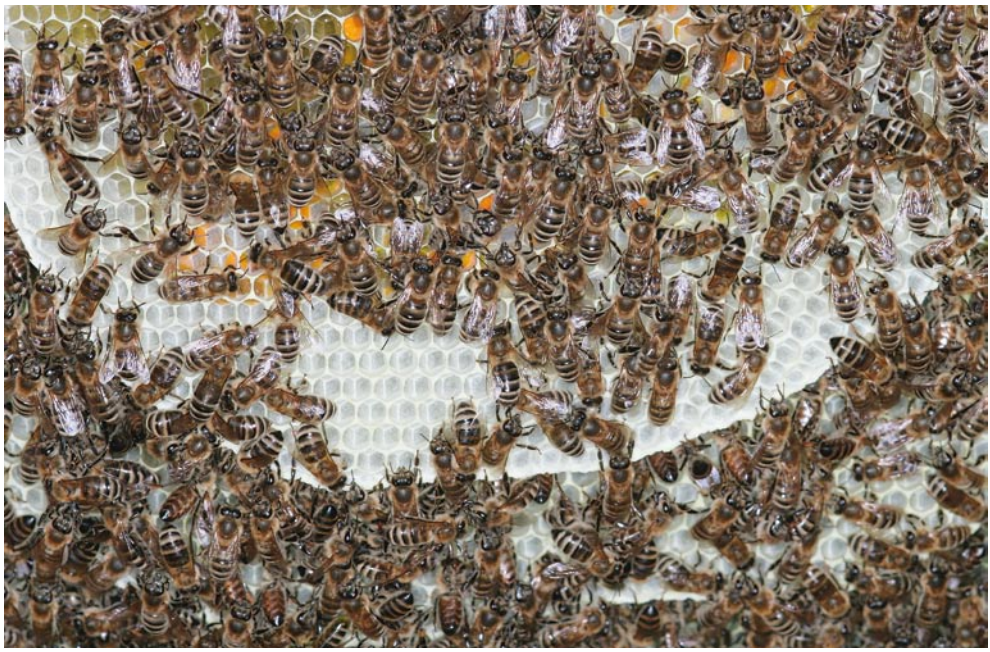
Honeybee colonies employ strategies remarkably similar to those of mammals, and raise relatively few, but extremely well-prepared and carefully protected reproductive individuals to release into the world. To this end, honeybees have developed specific abilities and behaviors that belong among the most 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