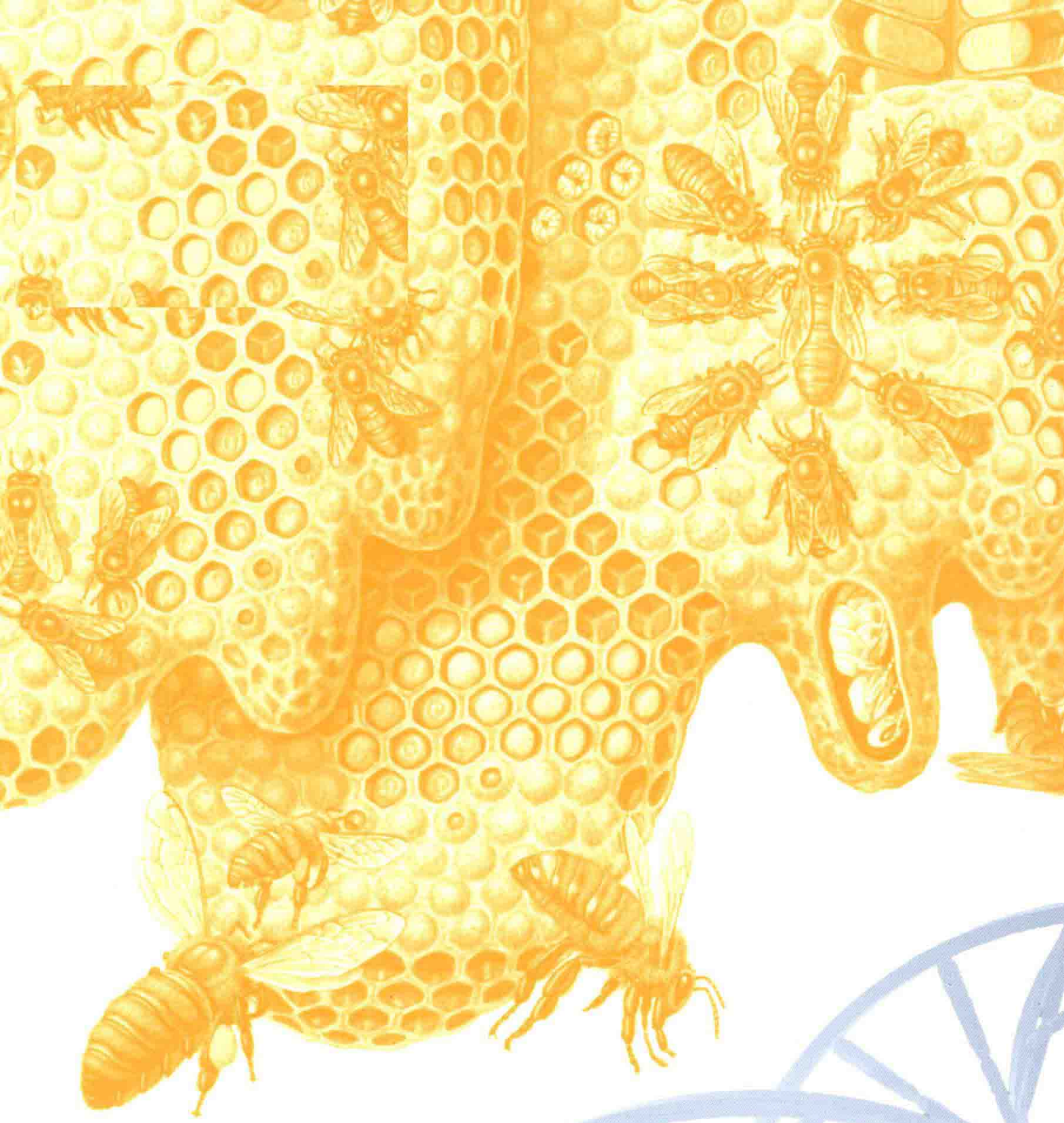

The Spirit of the Hive

THE MECHANISMS OF SOCIAL EVOLUTION

Robert E. Page, Jr.

Foreword by Bert Hölldobler

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The Mechanisms of Social Evolution

Robert E. Page, Jr.

Harvard University Press
Cambridge, Massachusetts
London, England
2013

Printed in the United States of America

Library of Congress Cataloging-in-Publication Data

Page, Robert E.
The spirit of the hive : the mechanisms of social evolution / Robert E. Page, Jr.
pages cm
Includes bibliographical references and index.
ISBN 978-0-674-07302-9 (alkaline paper)
1. Honeybee—Evolution. 2. Honeybee—Behavior 3. Beehives.
4. Pollen. I. Title.
QL568.A6P24 2013
595.79'9—dc23 2012044923

The Spirit of the Hive

To Harry Laidlaw (1907–2003)
My good friend, teacher, and mentor

Foreword

The late Larry Slobodkin, the distinguished evolutionary geneticist and theoretician, once said, "Nature defeats theory." I was frequently reminded of this wise revelation when I read *The Spirit of the Hive*. This book provides an avalanche of hard facts. Yes, it contains models too, but models that are based on solid scientific facts to serve as tools to design new experiments and to investigate unknown perspectives of the regulatory networks that constitute the foundation of division of labor in honey bee societies.

This concisely written book by Robert Page opens a window for a deeper view of the genetic and physiological architecture of the life of the honey bee and its society. Whereas other recently published books on honey bees inform us about the ways an insect society of about 40,000 individuals organizes division of labor, how its members communicate with one another, and how they make collective decisions, this challenging book by Robert Page explores the genetic and physiological mechanisms on the individual and colony levels that underlie the evolution and workings of honey bee society. It presents new, exciting insights concerning the so-called building blocks, the raw material, on which natural selection operates during the evolution of eusocial behavior. Although, as Robert Page states, the word *superorganism* hardly appears on the pages of his book, his work is deeply intertwined with the superorganism concept. In fact, this book offers the most thorough analysis of the physiological mechanisms and genetic substrate that underlie the emergence of colony traits, and it provides the best experimental evidence for colony-level selection, which of course, does not contradict inclusive-fitness theory, as other authors occasionally have erroneously claimed. The intricate social interactions within honey bee society deeply affect development and ontogeny of all its members and lead to the manifestation of robust colony traits.

This is an important scientific book. It covers the lifetime work of Robert Page and his impressive, international group of collaborators, mostly his former doctoral and postdoctoral students. The results of these far-reaching experimental studies, obtained during the past 30 years, have been published in many first-rate journals, such as *Nature, Science, Proceedings of the National Academy of Sciences of the United States of America, Genetics,* and *Insect Molecular Biology,* but this volume presents the first comprehensive synthesis of this important work. The book is written for scientists, but it is also very suitable for graduate student courses in biology. Each chapter offers plenty of material for discussion with advanced students.

The book is exemplary in its focus on collaborative research and in using interdisciplinary approaches to make new progress in understanding complex adaptive systems. Although the statement appears obvious, it cannot be emphasized enough that the scientific enterprise is conducted by people, and success in this endeavor very much depends on the quality of human interactions, be they competitive or collaborative.

Bert Hölldobler

Preface

In 2009–2010, I spent 10 months as a fellow at the Wissenschaftskolleg zu Berlin (Institute for Advanced Studies) in Berlin, Germany. I was part of a study group that investigated developmental evolution in social insects. Although writing a book is the normal activity of WIKO (the familiar name for the Wissenschaftskolleg) fellows, I arrived with the explicit and frequently announced plan that I would not write one. In the biological sciences, research papers are the coin of the realm, and there is little to gain with respect to advancing one's career by writing books. However, my good friend, colleague, and author of the foreword of this book, Bert Hölldobler, had encouraged me for several years to write one. He thought that the body of work produced by my lab and colleagues over the past 30 years or more was too widely scattered—across many research papers in journals spanning multiple disciplines—and should be consolidated into a single, coherent volume. But I resisted.

While I was at the WIKO, I was invited to give the annual Ernst Mayr Lecture to the Berlin-Brandenburg Academy of Science. The title of my talk was "The Spirit of the Hive," and its theme was developmental evolution. The academy publishes a small booklet for each lecture. Afterward, Bert suggested that I take the booklet derived from the lecture as a starting point and write the book. I gave in and began writing in January 2010, and by the time I left WIKO in mid-July, I had a first draft. Completion of the book has been a much more laborious process requiring frequent revisits to Berlin.

My approach in this book is different from that of most books on social insect behavior and evolution. I think that this is because of my background. I was not trained as an ecologist or behavioral ecologist. I am an entomologist trained in traditional breeding genetics, evolutionary population genetics, and mechanisms of behavior. As a consequence, after this preface, you will not see the words *kin selection* or *superorganism,* although they are interesting and important topics. This book is not about them. It is also not about behavioral ecology; therefore, it contains very little about how the external environment shapes the behavior of individuals or the social organization of colonies. Behavioral ecology is more the domain of the very interesting book by Tom Seeley, *The Wisdom of the Hive.* And although our titles are very similar, our books are very different. This book is about how social organization is linked vertically from genes to societies by mechanisms that evolve and operate within and between biological levels. I map out the architecture of traits and mechanisms and show how selection has altered them.

The main theme of this book is "the spirit of the hive." I explain it in Chapter 2 as the stimulus-response relationships of individuals with their environment. The book is centered on how those relationships shape individual and social behavior. I start with a "stone soup model" of division of labor and add complexity throughout the book. I present my view on models and modeling and develop heuristic tools along the way in an attempt to bring understanding to the mechanisms of social organization and their evolution and to generate new questions—a second theme.

I have not attempted to cite all the excellent work of all the researchers in the field. Instead, I support the content of each chapter with suggested readings listed at the end. I want this to be a book that is read for the story it tells, not as a collection of scientific references. This book is a tale of more than 30 years of research by my students, postdocs, colleagues, and me. The story is from my perspective, although the research ideas, development, and advancements were truly collaborative and shared by all. But I accept singular responsibility for the errors.

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Darwin's Dilemma and the Spirit of the Hive

Social insects have fascinated natural historians and philosophers since Aristotle and continue to fascinate us today with their self-sacrificing altruism, complex nest architecture, untiring industry, and division of labor. They presented Charles Darwin with special difficulties for his fledgling theory of evolution by natural selection. How can sterile castes, such as worker honey bees, wasps, and ants, evolve when they don't normally reproduce? The existence of sterile castes seems to be in direct opposition to a theory that requires differential survival and reproductive success. Darwin considered an even bigger difficulty to be the observation that the reproductive individuals in colonies are often anatomically differentiated from the sterile workers, showing adaptation of a sterile caste. However, he considered the biggest difficulty to be the anatomical differentiation within the worker caste that is dramatically demonstrated in many species of ants. Darwin waved his arms and invoked selection on families as an explanation, an explanation later shown to be too simplistic.

Social insects provided additional difficulties for Darwin when he considered the architecture of the honey bee nest (Figure 1.1). Darwin asked a Cambridge mathematician to study the comb of the bee from an engineering perspective of strength and economy, concluding, "For the comb of the hive bee, as far as we can see, is absolutely perfect in economizing labour and wax." How could the wax combs be built with such precision to maximize the strength of the comb and at the same

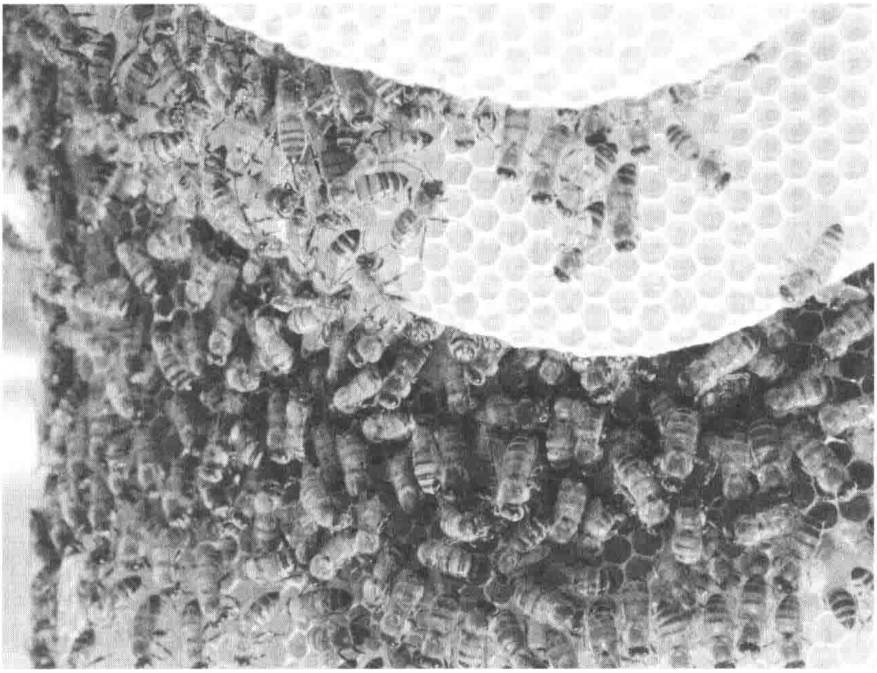

Figure 1.1. A colony of honey bees engaged in the construction of wax comb. Photo by Jacob Sahertian.

time save costly building materials? And, as he pointed out, "this is effected by a crowd of bees working in a dark hive" (Darwin 1998, pp. 348–349). How could they achieve this architectural masterpiece with instincts alone, working without any central control of construction tasks? Darwin experimented with honey bees and demonstrated to his satisfaction that bees could construct combs using just their instincts and local information regarding cell construction, thereby solving his dilemma of perfection and instincts.

The Nobel Laureate poet, playwright, and author Maurice Maeterlinck was also fascinated by social insects. In his wonderfully romantic book *The Life of the Bee,* originally published in 1901, he noted that there was no central control of cooperative behavior, thought by many to be the domain of the queen, and stated, "She is not the queen in the sense in which men use the word. She issues no orders; she obeys, as meekly as the humblest of her subjects, the masked power, sovereignly wise, that for the present, and till we attempt to locate it, we will term the 'spirit of the hive.'" (pp. 38–39; English translation 1903). Here he resorted to a mystical vitalism to explain how colonies full of individuals working in the dark organize into a cooperative whole, and he left it for someone else to identify the "spirit of the hive" and where it resides.

How do insect societies evolve complex social organization? There is a hierarchy of organizational levels from genes to the society, but there is no centralized control of behavior, and there is no social genome controlling the society on which natural selection can act. Yet it happens. Insects display the most complex and fascinating social organization known, enough to capture the minds and fantasies of both Darwin and Maeterlinck. In the following chapters, I will define the genetic, physiological, and behavioral mechanisms behind the mystical "spirit of the hive" of Maeterlinck. In Chapter 2, I will show how division of labor among worker honey bees arises from the simple result that bees, like all other animals, respond to stimuli in their environments and, as a consequence, change the stimulus environment. In Chapter 3, I show how genetic variation within colonies resulting from the polyandrous mating behavior of queens—queens mate with many males—contributes to variation in the stimulus-response relationships of workers within a nest and contributes to their social organization. Thus there are consequences of polyandry. In Chapter 4, I propose that polyandry may have evolved in response to its effects on within-colony genetic variation and social organization and dynamics, although there are many competing hypotheses.

Chapters 5 and 6 focus on results of a selective breeding program that has continued for more than 20 years, designed to study the effects of selection on a single colony-level trait, the amount of surplus stored pollen. This trait is a consequence of the complex interactions of thousands of individuals who share the nest. I present the phenotypic architecture—the correlated changes in many different behavioral, physiological, and anatomical traits of worker honey bees—of pollen hoarding and then genetically map the traits to reveal the underlying genetic architecture, which is an extensive network of interacting genes having effects on many correlated traits.

Mapping the phenotypic and genetic architectures suggested that foraging division of labor in honey bees is derived from networks of genes and hormones involved in regulating reproduction, giving rise to the reproductive-ground-plan hypothesis of Chapter 7. Selection for pollen hoarding has changed the reproductive anatomy of workers, and Chapter 8 shows how the developmental mechanisms that give rise to the different female castes (workers, and queens) were used to generate workers with different-sized ovaries, which in turn affect their responses to environmental stimuli and thus their behavior as foragers and the amount of stored pollen.

Chapter 9 is an attempt to use what we know about stimulus-response relationships, pollen and nectar foraging, and the phenotypic and genetic architectures of pollen hoarding to build a model of the regulatory architecture of pollen hoarding. It is obviously a far more complex task than I can actually manage, but I hope that the process will serve to illuminate what we don't know and help guide future research. Chapter 10 completes the organizational structure of a scientific paper that my mentor Harry Laidlaw taught me: (1) tell them what you are going to tell them (Chapter 1); (2) tell them (Chapters 2–9); and (3) tell them what you told them (Chapter 10).

1.1 Natural History of the Honey Bee

A honey bee colony typically consists of 10,000 to 40,000 worker bees, all females; zero to several hundred males (drones), depending on the time of year; and a single queen, the mother of the colony (Figure 1.2). The nest is usually constructed within a dark cavity and is composed of vertically oriented, parallel combs made of wax secreted by the workers (Figure 1.3, upper panel). Each comb can contain thousands of individual hexagonal cells on each of the vertical surfaces. The individual cells of the combs serve as vessels for the storage of honey (the carbohydrate food source for bees) and pollen (the source of protein) and as individual nurseries for developing eggs, larvae, and pupae. In addition, the combs are the social substrate of the colony. The nest has an organizational structure that is similar to concentric hemispheres, only expressed in vertical planes,

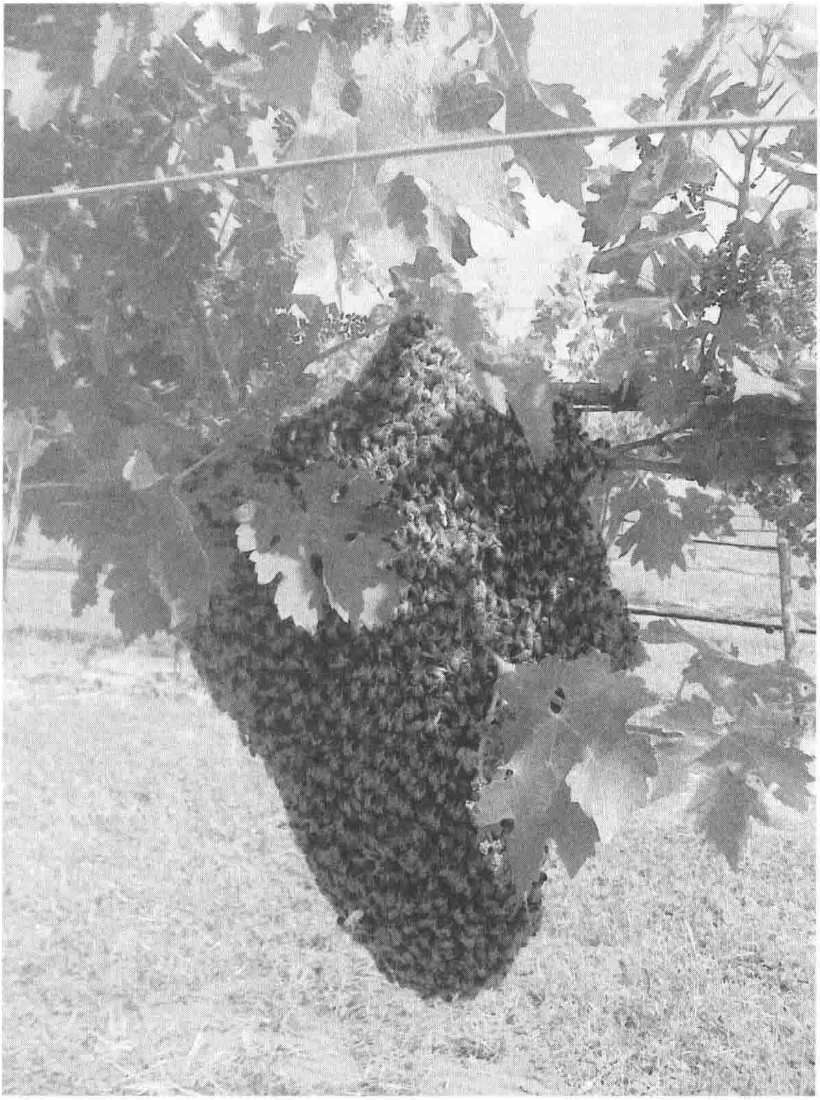

Figure 1.2. A natural swarm of honey bees. Photo by Kathy Keatley Garvey.

where the innermost hemisphere contains the eggs, larvae, and pupae (the brood), the next hemisphere above and to the sides of the brood contains the stored pollen, and the upper and outer regions contain honey that is derived from the nectar of flowers. If you remove a comb that is near, but to the side of, the center of the nest, it will contain three bands covering both sides: the outer band will be honey, the center band pollen,