gold mine even for readers without sociobiological inclinations.

Koenig and Mumme begin with an overview of the characteristics of their population and emphasize the strong dependence of the acorn woodpecker on acorn crops and granaries. Granaries provide a focus for group activities and define territories that may last for 12 or more years. Both clutch size and reproductive success are most strongly correlated with the number and energy content of acorns stored. Nests fail and territories are abandoned when acorn stores run out. The authors next analyze the effect of nonbreeders on the reproductive success of the group and conclude that their presence has little overall effect in this species and probably in most other cooperative breeders. Males tend to profit directly from living in cooperative groups, male survivorship being positively correlated with group size. Virtually all nonbreeders that survive to their first spring eventually obtain breeding positions somewhere. Koenig and Mumme conclude that space competition per se is not the critical feature of cooperative breeding systems because many other territorial species also face space competition. Whether they are correct remains to be seen; I found discussion of space competition one of the few poorly argued sections of the book.

The authors thoroughly analyze territorial inheritance in acorn woodpeckers and find that, although either sex may inherit the territory, inheritance by males is more common because of demographic patterns. The probability of handing down high-quality territories (ones with large storage facilities) to descendants is high. To understand thoroughly how natural selection affects fitness of long-lived individuals such as acorn woodpeckers, one must measure lifetime reproductive success. Koenig and Mumme are among the first to have long-term data on individual reproductive histories, although most of their study animals are presumably still alive. They calculate effective population size and conclude that acorn woodpeckers are not prone to an unusually high degree of inbreeding, despite their social organization. The opportunity for selection is relatively high.

The latter part of the book addresses why offspring are retained in groups. As in other cooperative breeders, offspring are constrained from dispersing and breeding on their own by limitation of resources, in this case granaries. The authors' analyses indicate that dispersal when possible is a superior alternative to nondispersal and helping, and thus ecological constraints have been paramount in the evolution of nondispersal and delayed breeding. The role of indirect selection in the evolution of helping behavior is explored, and it appears that important gain in inclusive fitness results from delayed dispersal. The major way nonbreeders enhance their indirect fitness is by increasing the survivorship of male breeders. Koenig and Mumme suggest that there is no selective advantage to helping per se and that this long-debated phenomenon may be selectively neutral. I find this suggestion plausible, but it is not likely to be embraced by all sociobiologists interested in cooperative breeding. Finally, the sharing of mates and nests is explored, and the analyses reveal that males in mate-sharing duos and trios enjoy enhanced fitness over males nesting singly but that females who nest jointly have lower fitness than do females breeding singly. Why a substantial proportion of males still breed solitarily and some females still nest jointly is not clear.

One of the most perplexing results in the book is the calculation that stored acorns represent only 4.6 percent of an individual's total energetic needs between December and June. The authors conclude that stored acorns cannot be the only or even the major source of food, yet throughout the book the importance of acorn stores is made obvious. My guess is that the 4.6 percent figure is based on faulty energetic analyses of acorns (possibly because very few individual acorns were analyzed) and that acorn stores actually represent a much larger fraction of each individual's total energetic needs.

I found little to quarrel with in this magnificent monograph and was continually impressed with the depth and thoroughness of the analyses. The book is well written and, in keeping with Princeton's tradition, well edited and produced. At times there is an over-reliance on tables, and figures would have illustrated data more effectively. The tone of the book is a refreshing change from that of other recent literature on cooperative breeding that is marred by egocentric and vitriolic exchanges. This book has none of that and reviews other work fairly and adequately. It would have benefitted from a broader perspective in places; discussion of work on other social but non-cooperatively breeding birds and mammals would have provided interesting parallels. As their study continues, the authors should consider simple experimental manipulations. The study so far has been strictly observational and correlational, and the one experimental manipulation described (adding granaries) is inconclusive because of small sample sizes. Manipulating the number of breeders and nonbreeders in a territory, territory quality, and sex ratios of broods, to name just a few possibilities, could provide very interesting information.

Above all, Koenig and Mumme's book underscores the value of long-term field studies, not only for the study of cooperative breeding but for an understanding of animal demography and social organization in general. Many critical questions in population biology can be answered only by such studies. This book is a landmark achievement and will have a major impact on population ecology and sociobiology. With Woolfenden and Fitzpatrick's equally impressive *Florida Scrub Jay*, also published by Princeton, cooperative breeding is now one of the better understood forms of vertebrate social behavior.

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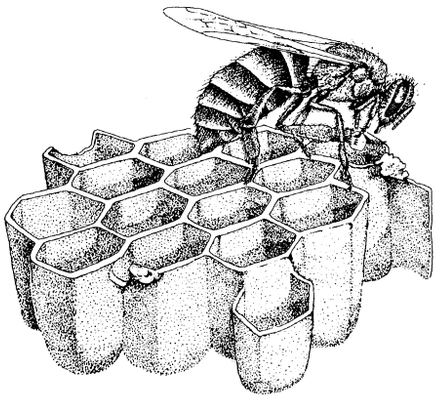
A Social Insect

The Biology of the Honey Bee. MARK L. WINSTON. Harvard University Press, Cambridge, MA, 1987. xii, 281 pp., illus. $29.95.

In 1954 the Bee Research Association published *The Behaviour and Social Life of Honeybees* by C. R. Ribbands. Partly because Ribbands's book itself stimulated research it soon became out of date, past the stage when it could readily or usefully be revised. For many years there has been no single volume in English that deals solely and comprehensively with the biology and behavior of the honey bee. Mark Winston's book is an admirable and worthy successor to Ribbands's. If anything it has a somewhat wider scope, especially in dealing with the origin and evolution of honey bees and with honey bee anatomy.

I greatly enjoyed reading each chapter. But of particular interest to me were the sections on the division of labor among worker bees, swarming and reproduction, and the behavior and biology of tropical honey bees, which contain much that is recently discovered and reflect the special research interests of the author.

Winston provides one of the most masterly reviews I have read of the age-related activities of worker honey bees and how they can be adjusted to a range of interacting colony and environmental conditions, including amount and type of brood to be fed, adult population, amount of comb available, nest characteristics, amount of stored food, available forage, temperature and weather, and the colony's racial origin. It illustrates the complexity of the information we already have but strongly indicates that we still know remarkably little about how the individual bee actually perceives the task



Wax manipulation and cell construction by a honey bee worker. [From *The Biology of the Honey Bee*]

needing to be done, and indeed how it sorts out and decides among the various stimuli impinging on its sense organs. Thus, we do not really understand how a worker honey bee knows when a particular larva needs feeding or how much food to give it, why some workers respond to their queen's proximity and others do not, or why some workers leave the hive to forage for themselves while others wait to be directed by dancing companions.

Everybody associates honey bees with swarming, so it is perhaps surprising that the factors that induce a colony to swarm have not been determined for certain, although Winston provides us with a comprehensive account of the circumstances that contribute to it. With swarming, as with other aspects of honey bee biology, it remains extremely difficult for us to understand how the individual workers measure, appreciate, and communicate so many varied pieces of information available to them and act in collaboration as a result.

The spread of Africanized honey bees in South and Central America has aroused much interest in the characteristics of African races of bees, especially in how their behavior differs from that of European races. These differences are mentioned at appropriate places though the book; for example, evidence has recently accumulated indicating a surprisingly low rate of survival of swarms in cold temperature climates relative to that in tropical conditions. A final chapter is exclusively concerned with comparing the biology of temperate and tropical honey bees and with the extent to which the differences in their aggression, reproduction, absconding, and colony foraging behavior have been selected by differences in predator pressure and resource abundance in the habitats in which they have evolved.

The text is written clearly, concisely, and with apt and refreshingly different metaphors and descriptions: prehistoric cave paintings of bees are regarded as "forerunners of the thousands of articles written" on bees; the uses of honeybee comb are said to range from "larval nursery to pantry to message center"; larvae themselves are described as "feeding mechanisms designed for rapid growth" and pheromones as "part of the social glue" that holds the honey bee colony together.

Where appropriate, techniques and methods used in particular studies are succinctly described, and where the available evidence is conflicting Winston suggests possible reasons and often provides a satisfying conclusion of his own. The book is illustrated with clear diagrams, tables, and figures. A glossary could usefully have been incorporated.

As a result of the vast increase in the literature on bees Winston has needed to be more selective than Ribbands in his choice of references. He manages in general to be unbiased, although there is a tendency to favor more recent North American work. Of the 853 papers cited in the references, 32 percent were published in the decade 1976 to 1985 and 21 percent in each of the two preceding decades. Because the dynamic growth of the subject is likely to continue I hope Winston will have the opportunity to provide us with a revised edition of his book before too long.

Without hesitation I recommend this book to a wide range of potential readers: to beekeepers because up-to-date knowledge of the underlying biology of the honey bee will enable them to increase their efficiency; to general biology students because the honey bee is surely the most fascinating of all insects and recent research on it exemplifies many new biological concepts; and to specialist students of honey bees and other social insects because it embraces much new research and many new ideas.

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Animal Relations

Kin Recognition in Animals. DAVID J. C. FLETCHER and CHARLES D. MICHENER, Eds. Wiley-Interscience, New York, 1987. x, 465 pp., illus. $77.95.

"Rarely in the history of biology has a domain of empirical knowledge followed so closely and fruitfully upon an abstract theoretical idea" as in the case of kin selection, writes E. O. Wilson in an introduction to this volume. Much of the scattered empirical literature on kin recognition has now been condensed, organized, and integrated in *Kin Recognition in Animals*, a book that examines kin recognition in invertebrates and vertebrates, including humans.

Specialists in kin recognition will notice that many of the most active researchers in kin recognition are absent from the list of contributors to the book. The editors acknowledge that they sometimes intentionally "bypassed eminent researchers who seemed to have had their say in favor of persons whose fresh ideas [might] be appreciated." Kin recognition has rapidly become a specialty, however, and several of the weakest chapters in the book are those written by behavioral biologists whose primary research area is not kin recognition. One cannot help believing that contributions from such researchers as Beecher, Getz, Holmes, Sherman, and Waldman would have improved the book.

In general, the chapters discussing kin recognition in specific taxa are reasonably accurate and comprehensive distillations of the published literature. The authors of the two chapters on social insects, who were faced with the difficult task of reviewing the voluminous literature on sweat bees, honey bees, social wasps, and ants, successfully uncovered both differences and broad patterns among the recognition mechanisms of the various groups.

There are several chapters that are especially absorbing. By far the longest (88 pages) chapter is by K. E. Linsenmair on the kin recognition system of a desert isopod. Although much of the chapter is based on unpublished work enough details of the methods and data analyses are included to permit one to judge that the experimental results justify the conclusions. By asking excellent questions and using numerous ingenious experimental designs, Linsenmair has teased apart various aspects of the mechanism of recognition in *Hemilepistus reaumuri*. As a result of his extensive studies over a period of 15 years, desert isopods almost certainly have one of the best-understood kin recognition mechanisms of any animal.

A stimulating chapter by E. B. Spiess brings the findings of research on mate discrimination in *Drosophila* to the attention of sociobiologists studying kin recognition. One may wonder how mate discrimination in a solitary fly is related to kin recognition in social animals, but the same mechanism may underlie both systems. In fact, several contributors, including Crozier, Michener, and Wells, have suggested that mate recognition on the basis of relatedness (or incest avoidance) likely served as an ancestral preadaptation leading to kin recognition.

One has to be impressed with the restraint displayed by J. R. Walters and P. A. Wells in