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Honeybee Ecology

1 Introduction

Why Study the Ecology of Honeybees?

The honeybee is a wonderful example of adaptation. In this it resembles all forms of life, but because it is an extremist its adaptations are striking. The honeybee's waggle dance, with which forager bees share information about the locations of new patches of flowers, is unsurpassed among animal communication systems in its capacity for coding precise yet flexible messages. Honeybee workers display an extraordinarily elaborate division of labor by age, switching their labor roles at least four times as they grow older. When a honeybee colony needs a new home, several hundred scout bees comb some 100 square kilometers of forest, discover a few dozen possible nest cavities, and harmoniously choose the best dwelling place through a sort of plebiscite. In winter, the thousands of honeybees in a colony form a tight, well-insulated cluster and pool their metabolic heat—fueled by about 20 kilograms of honey stores—to keep warm despite subfreezing temperatures, a method of winter survival which is unique among insects. The honeybee, then, has an extremely elaborate social life. It is therefore an unusually rewarding subject for ecological studies of social behavior.

Besides possessing a wealth of adaptations associated with group living, the honeybee's attractiveness for ecological investigation is heightened by the remarkable ease with which it is studied. Honeybee colonies thrive as managed colonies in apiaries or as wild colonies in nature, or both, throughout most regions of the world. Unlike most other social insects, honeybees prosper in brightly illuminated, glass-walled nests and so allow humans to observe easily the internal operations of their societies. Furthermore, individual honeybees are relatively large social insects, large enough so that colony members can be labelled with color codes for individual identification. This sets the stage for truly detailed observations of interactions among colony members. Countless experimental manipulations of the honeybee's social environment, such as colony fusions, brood transplantations, and alterations of nest design, were made possible by the invention of hives with movable combs in the mid 1800's. Nests which are readily dissected and reassembled also facilitate the collection of such basic ecological data as colony population size, age structure, and metabolic rate. Even manipulations of the kinship relations among colony members are possible with honeybees, a fortuitous byproduct of instrumental insemination techniques developed for bee breeding.

Given the richness of the honeybee's adaptations for social life and its advantages as a study animal, it is somewhat surprising that a strong imbalance exists between mechanistic and functional studies of honeybee sociality. We know a great deal about how honeybee societies work but comparatively little about the forces of natural selection which have shaped their finely tuned social systems. Perhaps the most vivid illustration of this imbalance is found in our understanding of the honeybee's social organization for food collection. The central mechanism of their foraging strategy is recruitment of nestmates by successful foragers via the dance language. The physiological processes underlying the dance language have been the prime subject of investigation by several dozens of researchers over four decades, and the dance is certainly one of the best understood examples of animal behavior. In contrast, our knowledge of how foraging efficiency is enhanced by this social machinery is still nascent. Undoubtedly there are numerous reasons for this difference in emphasis between physiological and ecological approaches. In part, it is a reflection of the history of scientific studies on animal behavior, which focused first on questions of behavioral mechanisms and only relatively recently on topics of behavioral ecology. Perhaps more importantly, though, it reflects the ease with which one can culture honeybees in apiaries and perform experiments with them. Thus honeybee scientists seem to have been consistently attracted to experimental studies conducted in man-made environments, rather than broadly observing the organism living undisturbed in nature, the essential first stage of behavioral-ecological studies.

This book is an attempt to redress the imbalance between physiological and ecological studies of honeybee social life by emphasizing ecological studies of the honeybee societies. It will focus on how honeybees live in nature and why their social organization has the design that it does. Honeybee research has historically been concentrated in Europe and North America, and so has inevitably emphasized just one species of honeybee, *Apis mellifera*, and the way it lives in the northern latitudes of these regions. Unless stated otherwise, the discussion can be assumed to refer to these studies of the temperate-zone races of *A. mellifera*. However, in the final chapter, I will emphasize the ecology of the other species in the genus *Apis* and the races of *A. mellifera* having non-European origins. Though the mechanisms of honeybee social life will not be the prime subject of this book, they will be discussed frequently, since understanding the minute operational details of an adaptation often casts light on underlying selective pressures. Moreover, knowledge of the machinery of an animal's behavior provides behavioral ecologists with ways to probe the adaptive significance of the behavior experimentally. Reciprocally, the ecological view illuminates the path to understanding the mechanisms of social life. By studying how an animal lives in its natural environment, a biologist gains a clear picture of its full behavioral repertoire, and develops a heightened intuition for the physiological processes which underlie its behavioral adaptations. One main theme of this book is, therefore, to exemplify the synergism which arises from a balanced combination of physiological and ecological studies of social behavior.

Individual-Level versus Colony-Level Selection

The logical first step toward understanding adaptation in honeybees is to identify the level (or levels) of biological organization at which natural selection operates in social insects. Since the founding of the theory of evolution by natural selection, most biologists interested in insect sociality have emphasized selection at the level of colonies (Darwin 1859, Weismann 1893, Wheeler 1911, Sturtevant 1938, Emerson 1960, Wilson 1971, Oster and Wilson 1978). According to this view, the morphology, physiology, and behavior of an individual social insect are adapted to benefit its colony's reproductive success, not necessarily its own. This is a group-selection view of evolution, but one which is at least plausible, given that social insect colonies are discrete groups and that they possess variation, heritability, and fitness differences—three properties an entity must possess if it is to evolve by natural selection (Lewontin 1970). Relatively recently, students of the social insects have emphasized colony-level selection less and have focused attention instead on individual-level (or even gene-level) selection (Hamilton 1964, 1972, Williams 1966a, Alexander 1974, West Eberhard 1975, Dawkins 1976, 1982). According to this view, each member of a social insect colony has been selected to maximize its own reproductive success (inclusive fitness), even if this creates inefficiency and reduces its colony's overall fitness. The impressive group behaviors of social insects, such as cooperative food collection and precise control of nest temperature are, according to this viewpoint, simply statistical summations of many individuals' ultimately selfish actions.

There can be little doubt that individual-level selection is important in social insect evolution and therefore that colony-level selection is not of universal importance. Proof of selection having operated on individuals comes from numerous reports, involving a wide array of species, of workers laying eggs (reviewed by Hamilton 1972, Oster and Wilson 1978) or of dominance interactions among colony members (reviewed by Wilson 1971; see also Cole 1981, Franks and Scovell 1983). Such behaviors certainly decrease efficiency at the colony level but make sense in terms of individuals competing for reproductive success.

In honeybees, there are two dramatic examples of conflict among individuals that leads to a decrease in colony efficiency. The most familiar is the fights to the death (by stinging) among newly emerged queens. The benefit to an individual queen of killing her rivals is clear: undivided motherhood of the colony's next crop of reproductives. However, this combat between queens may work to the detriment of the colony if all the queens kill each other, or if the lone survivor is later preyed upon when she ventures outside the nest for mating. A second, even clearer product of individual-level selection is the behavior of workers in a colony that loses its queen and fails to rear a replacement. The best thing that the workers can do in this situation in order to maximize colony fitness is to produce one final crop of male reproductives reared from the unfertilized eggs which workers can lay. But rather than rear these males as cooperatively and efficiently as possible, disharmony erupts in the nest as workers compete to provide the eggs that will produce the males. Workers with active ovaries are mauled by workers with inactive ovaries (Sakagami 1954, Korst and Velthuis 1982). Frequently a half a dozen or more eggs will be laid in each cell in the broodnest, in stark contrast to the orderly one-egg-per-cell pattern when a queen is present and despite the fact that only one drone at a time can be reared in a cell (Fig. 1.1). A third possible product of individual selection among honeybees is the production by some colonies of several small reproductive swarms following the large primary swarm (Allen 1956, Winston 1980). Although no data are available to prove the point, it seems likely that these "afterswarms" are detrimental

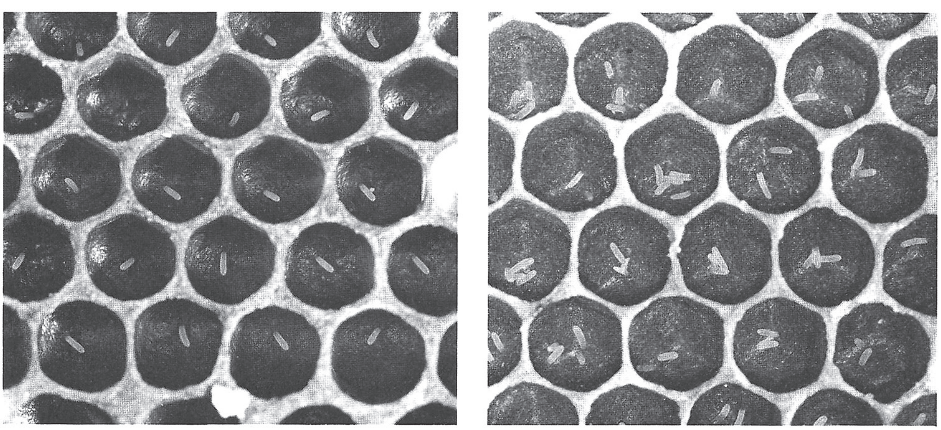

Figure 1.1 Comparison of egg laying patterns in queenright (left) and queenless (right) colonies. Queen-laid eggs are neatly deposited one to a cell, an arrangement which fosters efficiency in brood rearing In the absence of a queen, a less efficient pattern of multiple eggs per cell appears as the workers compete among themselves for reproductive success

to the parent colony, both because they further deplete the parent colony's worker force and because they are so small that they probably have little chance of surviving to maturity. On the other hand, the queen departing with an afterswarm may stand a better chance of survival than if she had remained to fight for control of the parent colony, and the workers closely related to her may achieve higher reproductive success by leaving with her to found a new daughter colony, as compared with staying with the parent colony and helping a more distantly related queen (Getz et al. 1982).

Clearly individuals are an important unit of selection in social insects, even in the honeybee with its complex colonial organization, but this by no means precludes the importance of colony-level selection. Just how potent is colony-level selection? Unfortunately, this question is not readily answered, in large measure because individual-level and colony-level selection should frequently promote the same pattern of adaptation. For example, in a queenright honeybee colony (one in which the workers are not laying eggs and thus achieve reproductive success indirectly via their mother queen [see Chapter 3]), both an individual worker's inclusive fitness as well as her colony's fitness are promoted by the worker performing such tasks as brood rearing, comb construction, and food collection as efficiently as possible. The larger the pool of resources assembled by the colony and the higher the efficiency of their use, the greater the number of reproductives the colony can manufacture and the higher each worker's inclusive fitness. In fact, it may be precisely because selection at individual and colony levels can operate in concert that certain species, such as the honeybee, possess such elaborate social organization. It might seem that a colony member working so as to decrease her inclusive fitness but increase colony fitness would prove the superior importance of colony-level selection. One could argue, for example, that this explains why workers refrain from rearing sons and instead help their mother rear their brothers even though they are more closely related to their sons than to their brothers (see Chapter 3). However, such apparently altruistic behavior can also be explained by adaptation at the individual level. One possible explanation is that the seemingly selfless worker simply has been manipulated by another individual seeking to boost its own inclusive fitness. The phenomenon of worker bees not laying eggs when a queen is in the nest could reflect precisely this process, with the queen perhaps dominating the reproductive activities of the workers via her inhibitory, "queen-substance" pheromone. In summary, I know of no observation on honeybee biology which unequivocally demonstrates the action of colony-level selection working at the expense of individual interests.

Our fascination with a colony of honeybees, army ants, or other advanced social insects is born largely out of curiosity about its overall achievements as an animal group. The intricate internal organization of a colony's foraging behavior, the efficiency expressed in nest design, the high precision of nest temperature control, all suggest functional, adapted organization of the colony as a whole. This intuitive feeling may be correct, but given that strong evidence exists only for selection at the level of individual social insects, it seems correct for now to explore adaptation in honeybees as far as possible in terms of individual-level selection, but also to keep in mind the possible role of colony-level selection, especially wherever individual and colony interests coincide.

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