

CROZIER, R. H., AND P. PAMILO. 1996. *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection*. Oxford Univ. Press, Oxford. viii + 306 p. ISBN 0-19-854942-3. Paperback. \$35.00.

I had the privilege to be a graduate student in the late 1970s when the more modern stages of the neo-Darwinian synthesis were under frenetic construction. Excite-

ment, compelling theories and occasional data were the materials at hand for laying the foundations of Sociobiology and Behavioral Ecology. People lost considerable sleep pondering the grim intricacies of parental manipulation and the sudden understanding of kin-selection could arrive like a religious revelation.

Among the most respected thinkers of The Movement was Robert Trivers, a genius, then at Harvard, who regularly elucidated evolutionary concepts that altered many a consciousness. In 1976 he and H. Hare published what, in retrospect, seems to have been one of the last great ideas of the time. Social insects were, so to speak, on everyone's mind. They had proved to be important both as protagonists in the thought experiments of pioneering theorists and as subjects for the experimentalist who had begun to test the novel predictions the new theories had generated. Trivers and Hare had appreciated that sex ratios in ants could help resolve which of the competing theories of "parental manipulation" or "kin-selection" was best able to explain the evolution of eusociality, an issue understood to have implications beyond the Hymenoptera. Their predictions arose from haplodiploid sex determination creating asymmetries of relatedness. Simply stated, they argued that under kin selection queens and workers would be lead to invest differently in sons / brothers and daughters / sisters, i.e., a kin-selected colony under worker control could be recognized by its disproportionate production of females.

Criticism of Trivers and Hare came swiftly. Not the least of the objections concerned the usefulness of the data they used to support their hypothesis. However, there was a general feeling that with a little more time the required data would be collected and the issue concluded. This collection proved to be more complex than anyone imagined and 20 years later the question of who runs social insect colonies, the queens or the workers, is still an important theme of this very well written and interesting book by Ross Crozier and Pekka Pamilo.

The authors introduce their book by posing 3 major questions: 1) Who reproduces in the colony? 2) How are resources allocated between reproductive and non-reproductive functions (i.e., between the production of reproductives and colony growth and maintenance)? and 3) How are resources allocated between male and female functions? In the course of addressing these questions the authors first examine the concept of inclusive fitness, including such issues as caste determination. They then consider the evolution of eusociality in insects, and in the process offer explanations for striking phenomena such as the absence of male workers in the Hymenoptera contrasted with their presence in the Isoptera. Next is a discussion of the evolution of colony characteristics, which include worker reproduction and queen mating frequencies. This is followed by an examination of intra-colony conflicts over sex-allocation and finally a survey of colony-level variation of sex ratios.

The book is a product of a mature field, i.e., it contains a wealth of detail and a considerable amount of mathematics. The latter should not discourage natural historians with an interest in the former. The authors have the happy ability of presenting complex arguments in prose and there are graphs to help visualize some of the more difficult concepts. The literature review alone will be of value to those intrigued with insects or social behavior. It would not take away from the drama of reading the book to hint that there is a great deal more to be done before the relationship between sex allocation and kin selection is fully understood.

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