

**Social Insects—An Evolutionary Approach to
Castes and Reproduction**

W. Engels [ed.]
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THIS VOLUME examines phenomena at the reproductive/non-reproductive threshold in social insects. The multi-authored work is divided by taxon, with one chapter each on termites, ants, and wasps; four chapters on various bee taxa; and two short chapters addressing special topics on highly social bees. The authors are established, respected researchers with strong credentials for writing reviews of this kind. Although the volume is based on a symposium at the 1980 International Congress of Entomology, the contributions are up to date, with references in every chapter running to the late 1980s. The authorship is predominantly European, and this imparts a distinctive character to the volume. No chapter takes an inclusive fitness approach, and altruism is scarcely mentioned. The result, then, is a refreshingly unfettered overview of proximate factors affecting reproductive caste differentiation.

The most successful chapters are those on bees. That on Halictinae by Michener is a welcome update and status report on the now substantial body of rigorous and enlightening research on these primitively social bees as generated by the indefatigable Michener himself, his students, and a fraternity of distinguished colleagues. This chapter gives a clear exposition of the now well-supported contention that eusociality can arise in a single step from a solitary antecedent. We learn, in fact, that eusociality can have arisen hundreds of times in Halictinae! This remarkable state of affairs is interpreted as reflecting low selection intensity for the major switch mechanisms that regulate the expression of reproduction. Michener also clearly identifies inclusive fitness as nothing more than the best of a bad situation for a worker, and he emphasizes control of reproduction by a colony queen as perhaps the key to social evolution in this group. Indeed, control of reproduction is one of the recurrent major themes of the book. Michener writes, "All females have a tendency to develop into foundresses, and if they are to become workers, must be inhibited from following that course by general environmental factors and/or by environmental factors shaped by nestmates."

The different chapters of the book provide detail on the inhibition of reproduction and document inhibition to be based on behavior, pheromones, and/or nourishment, with mechanisms

and patterns differing for virtually every taxon. William Morton Wheeler may perhaps be responsible for the perspective that various sub-social and primitively social insect taxa are only stepping stones in the Aristotelian yearnings of every social lineage to achieve the sublime perfection of *Vespa*, *Atta*, or *Apis*. This volume is an antidote to that naive perspective, for it leaves little doubt that the proximate mechanisms of caste determination differ fundamentally in various taxa, and so those taxa are unique end points that are unlikely to be subsumed by a single evolutionary explanation.

The chapter by Engels and Imperatriz-Fonseca is an excellent, extensively documented review of caste determination and reproductive biology in stingless bees, with enough references to the better-known honey bee literature to maintain perspective and facilitate understanding. Their reporting of polygyny and of reproduction by workers as commonplace phenomena in stingless bees provides strong support for the perspective that inhibition of reproduction is the primary pathway to becoming a worker. The chapter by Velthuis, Ruttner and Crewe is an informative reporting of worker reproduction in the Cape race of honey bees.

The book will be most warmly embraced by entomologists with primary interests in bees as well as perhaps by insect physiologists, since there is much discussion of the role of hormones, especially JH, in caste differentiation. The chapter on wasps by Strambi is a strong example of the physiological approach. Students of non-bee taxa may be disappointed in the book; and evolutionary biologists in general will find themselves misled by the subtitle, for there is in fact very little direct address to evolution. Though this is true of most of the book, it is most obvious in the chapters on termites and ants. The authors of these chapters have faced the unenviable task of dealing with large and diverse taxa that lack primitively social and closely related non-social forms. One is struck throughout most of the book by the dire need for testable evolutionary hypotheses as might be generated by morphological cladistics or by molecular phylogenetics. Only with such a hypothesis, perhaps, will order be brought to the swirling variety of seemingly unrelated case histories in termites.

The book's focus on proximate factors is marred by some philosophical lapses. The editor incorrectly proposes in the preface that theoretical analysis of insect social evolution began with Hamilton; then his own excellent co-authored chapter concludes inappropriately by attempting, without apparent conviction or enthusiasm (not to mention relevant data), to shoehorn the analyses into an inclusive fitness, haplodiploid

context. A more egregious example of the same thought process is in the chapter by Noirot on termites, which seems to apologize that they aren't haplodiploid and then ends with a hope that an inclusive fitness theoretician on a white horse will ride to the rescue of all termitologists by explaining the population genetics foundation of the diversity of caste and reproduction systems in Isoptera. A major technical fault of the book is that there are numerous errors of spelling, punctuation, and syntax; these errors detract from the early chapters in particular. Terms are often used without definition.

The book will not resolve most readers' major questions on the evolution of the reproductive vs. non-reproductive dichotomy in social insects. It is a welcome volume of significant value, however, as a compendium of perspectives and references on proximate factors that affect the evolution processes.

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