

Literature

Engels, Wolf (ed.) 1990: Social insects. An evolutionary approach to castes and reproduction. 264 pp. Springer-Verlag, Berlin. ISBN 3-540-50812-0. Price (hardcover) DEM 89.

This recent volume edited by Professor Wolf Engels of Tübingen covers thoroughly all groups of social insects. The subtitle, however, confines the scope of the book to caste formation and reproductive strategies, which alone are certainly worthy of an even thicker volume. While many other books dealing with castes and reproduction concentrate mainly on termites and ants, in Engels' book these groups merit one chapter each, and refreshingly the rest of the chapters present reproductive strategies and regulatory mechanisms of social wasps and bees.

"Caste system" in social insects refers to the fact that the members of the colony can be divided into fertile sexual and specialized infertile individuals, such as workers and soldiers, which in most cases are females incapable of reproducing. According to noted biologist E. O. Wilson, the caste specialization and individual altruism of social insects are unparalleled in the animal world. The termites, ants, social wasps and social bees are fascinating study-objects which interest both basic and applied researchers because of the great economic importance of such insects.

Although termites and ants are in the minority as far as page-numbers are concerned, this does not mean that any important aspects are missing. In his article Charles Noirot shows how different termite workers and soldiers are developed and what the underlying genetic and neuroendocrinal mechanisms are. The main elements of population dynamics (fecundity, longevity, mortality) are discussed both at the individual and society levels. The complexity of the termite caste system (having both male and female castes) compared with that of social Hymenoptera calls for more studies of termite societies, especially in the field of population genetics.

The social hymenopterans have only female castes, which, for instance in ants, are usually

characterized both by form and function. Moreover, the colony system varies from monogynous to polygynous and from a single nest to polydomy. Alfred Bushinger presents the reproduction strategies in these colonies and discusses caste formation in different cases. Genetically mediated caste formation seems to be near the author's heart and receives relatively much space. Those interested in the other aspects of the ant castes can read the excellent and updated book by Hölldobler and Wilson (*The Ants*, 1990, Belknap).

Alain Strambi's chapter about social wasps, the caste-formation of which is probably most poorly studied of social insects, shows that especially in Polistinae wasps the morphological differences between queens and workers are nonexistent, and *Polybia dimidiata* workers may be even larger than queens. Vespine queens are induced when the larvae are fed more and richer food while on the other hand, in polygynous Polistinae the caste system is regulated endocrinally.

In Charles D. Michener's two chapters about primitively social bees, those belonging to Halictinae and Xylocopinae, he updates information in his textbook of the social behaviour of bees (1974) by presenting detailed examples of species in which caste differentiation and larval care has been observed.

Bumblebees are presented by Peter-Frank Röseler and Cor van Honk. Their queens have characteristically a larger size and longer lifespan than workers. The authors mainly emphasize the hormonal control and dominance hierarchy in the worker caste, using *Bombus terrestris* as an example. Their dominance hierarchy means that although there are several groups among workers, only the highest, the "elite group", will lay eggs and, when necessary, replace the queen. The "elite group" is characterized by large size,

high juvenile hormone titre in haemolymph and a tendency to remain in the nest leaving the foragers to serve as "common workers". Although the dominant individuals are the ones most likely to start ovipositing, the presence of ovaries is not necessarily connected with dominance behaviour. In queenless colonies the dominance hierarchy among workers is established by means of aggressive behaviour.

Wolf Engels and Vera Imperatriz-Fonseca write interestingly about the reproductive strategies and castes of honeybees (Apinae) and stingless bees (Meliponinae), putting both under the same heading. The queens in both these eusocial groups are incapable of founding a colony alone, and the drones form aggregations before mating. Moreover, nest-foundation is preceded by colony fission. The main difference between the groups is that stingless bees produce queens throughout the year, and honeybees only seasonally; however, most of the meliponine queens are later eliminated by the workers, which leads to an oligogynous status. The authors present three modes of gyne production in which the queen larva eats either from two cells (some Trigonini), from one large cell (most Trigonini and Apinae), or from the cells which are of equal size to the worker cells (Meliponini); in the latter case queen-formation is controlled by internal determination (genetic caste determination) and by environmental conditions. This long and thorough chapter ends with remarks about the evolutionary trends in both subfamilies.

The honeybees and stingless bees have the main roles also in the last two chapters. Hayo Velthuis, Friedrich Ruttner and Robin Crewe introduce a peculiar honeybee race, the South African *Apis mellifera capensis*, the workers (or false queens) of which can produce female offspring. The intermediate caste may even act as a facultative parasite of *A. m. adansonii*. The behav-

ioral factors affecting the life of workers are connected with the food available.

Klaus Hartfelder gives a very detailed picture of corpora allata activity and juvenile hormone synthesis during the larval life of stingless bees and honeybees. Differences occur between workers and queens in the timing of hormonal activity; the peaks in ecdysteroid activities also differ between castes. The endocrinal system of these eusocial bees are compared with that of the ants, in which the soldier caste may be explained by the early effect of maternal hormones on larvae. In all, such evolutionary comparisons as these would have clarified the ideas throughout the book because most of chapters concentrate on details of a certain genus or even a species (Fig. 8-53 in Hölldobler & Wilson exemplifies how to show variation in timing of caste-formation among social insects).

Social Insects is a book where much is said concisely. Many details and thoroughly investigated case studies are presented. The book is partly based on symposium papers and perhaps for that reason no-one has written a concluding chapter showing, for example, the effect of food or hormones on caste formation in different insect groups. I also have a couple of typographic comments on the book: all taxa above genus level (tribes, subfamilies, families, orders) are printed in capital letters, so that they really leap from the text. On the other hand, in the list of contents the subtitles and the page-numbers are connected with so limited number of dots that a ruler is needed. The number of resembling terms is high, and although the terminology is consistent, a short glossary would have helped one to keep definitions in mind. There is no index. In spite of these minor remarks I would like to recommend the book to all those interested in social insects.

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