

BOOK REVIEW

GADAU J. & FEWELL J. (eds): ORGANIZATION OF INSECT SOCIETIES, FROM GENOM TO SOCIOCOMPLEXITY. Harvard University Press, Cambridge, MA, and London, UK, 2009, 617 pp., hard cover. ISBN 978-0-674-03125-8. Price USD 79.95.

This voluminous book presents a synthesis of the up-to date knowledge on a broad spectrum of aspects of social life in insects written by an international group of 49 researchers in the fields of molecular biology, evolutionary genetics, neurophysiology, behavioural ecology and evolutionary theory. The authors present their expertise and insight in a newly unified vision of social insect societies and what they can reveal about how sociality has arisen as an evolutionary strategy. The volume, which is a tribute to Bert Hölldobler, is well organized and edited by two scientists at the Arizona State University, Jürgen Gadau and Jennifer Fewell, with a foreword by Edward O. Willson.

The book is not a mere assemblage of review papers on various aspects of sociality in insects. It has a firm framework into which the authors shaped their contributions. Twenty-six chapters of the book are thematically divided into four sections, each one being introduced and summarized by a leading expert in the particular discipline. This greatly helps the reader to find particular topics of interest within the diverse content of the volume (as well as the reviewer to precisely characterise individual contributions). Part one, *Transitions in social evolution* deals with basic questions about the evolution of sociality. It begins with a brief but comprehensive review of the evolution of social insect mating systems and their variations in eusocial Hymenoptera. The authors of the first chapter review the current knowledge about the evolution of mating frequency by summarizing and evaluating the results of studies on genetic markers and multiple mating frequency, particularly that relevant to hypotheses about the evolution of mating systems, and discuss the significance of mating plugs in the context of multiple mating by males, sperm variation and sperm storage costs. Chapter 2 deals with the evolution of queen numbers in ants. Both chapters focus on transitions between different classes of mating frequencies or queen numbers per colony in order to understand the selective forces behind this transition. Chapters 3 and 4 deal with colony demography in bees and ants, respectively, and present the basic approaches used to study this important but so far neglected research area. Amazing differences in the mean life span of the honey bee queen and workers (that otherwise share the same genotype) are emphasized and the current mechanistic and evolutionary explanations for this social phenomenon are summarized. Control of caste differentiation in termites is the topic of Chapter 5, and an interesting interpretation of the factors important for the evolution of eusociality in termites is discussed in Chapter 6; ecological factors over kin selection are emphasized. The last chapter in this section is devoted to the evolution of communal behaviour in bees and wasps. The authors try to explain why communal behaviour should be considered the ultimate social phenotype equivalent to eusociality rather than an intermediate stage in the evolution of sociality.

Part two of this volume is devoted to *Communication*, which is a key to understanding how an insect society is organized and

how it functions as an integrated whole. Each member of the society needs to be informed how to behave so as to contribute to the common good. Each member has to be continuously well informed to be able to decide what action to take at any given moment. Therefore, communication is a prominent part of this book as it is a central feature of insect social life. Six chapters in this section highlight the directions in which the current studies on social communication in insects are going. Chapter 8 reports the diversity of cues used in nestmate recognition, a critical process for directing acts of altruism at relatives. Chapter 9 reviews the functional organization of olfactory systems in social Hymenoptera and shows how the anatomy of this sensory system has evolved to complement cast evolution in certain ant species. The authors of Chapter 10 review the current knowledge on the pheromones of queen ants that provide workers with chemical signals about their queen's fertility. They maintain that the cuticular hydrocarbons on their own provide reliable information about fertility and thus play an essential role in regulating reproductive division of labour. The authors also dispute earlier claims that queen pheromones have a coercive effect on the receiver (i.e., directly inhibit ovarian development) and consider them to be rather carriers of information that induce the receivers to behave adaptively. Chapter 11 is a review of what is known about vibratory signals of social wasps and their role in cast determination; interestingly, these mechanical signals may represent an alternative mechanism to chemical triggers in biasing the development of the first offspring toward worker-like behaviour and suppressing their reproductive function as adults. Chapter 12 makes a comparison of mechanisms of recruitment to food sources in bees and wasps. And the last chapter (13) in this section reviews the organization of foraging by ant colonies. The author draws the attention to the fact that the foragers bring home both food and information, and that their behaviour is likely to be adapted to optimize the intake of both commodities.

The five chapters in part three of this volume are on the *Neurogenetic basis of social behaviour*. The authors examine the mechanisms of social organization across levels of organization through genes to neuroanatomy and physiology. Chapter 14 discusses the genetic background underlying social traits. The authors make an appeal for comparative studies involving less advanced social species or closely related solitary species as well as comparative studies across greater phylogenetic distances. Sensory thresholds, learning and the division of foraging labour in the honey bee is the topic of Chapter 15. The authors present and analyze the relationships between response thresholds to stimuli and behavioural plasticity in the honey bee. Chapter 16 is devoted to the history of the evolution of social life from a solitary stage and concludes that "complex social behaviour as found in eusocial insects is derived from reproductive regulatory networks common to all insects. Small changes in the timing of expression of maternal care behaviour may be all that is needed to form reproductive and non-reproductive phenotypes, the basis of eusociality." In Chapters 17 and 18 behavioural and neural plasticity, and sensory response systems and behaviour, are discussed. The question of whether social insects have evolved a "social brain" is the focus of the former chapter. The social brain hypothesis of primates proposes that certain areas of the brain are enlarged as a consequence of adap-

tation to complex social life. However, anatomy of the brains of social insects does not accord with this hypothesis. Actually, the brain size of some casts may be reduced as a consequence of a reduced behavioural repertoire due to division of labour. The last chapter in this section looks at the timing of behaviour and its synchronization with a biological clock.

Part four contains contributions covering *Theoretical perspectives on social organization*. The section is introduced by a paper (Chapter 19) that frames sociobiological principles in the context of mathematics. The next chapter (20) illustrates how positive feedback, as the basis of self-organization, can generate complex behaviours within a social group. Two following chapters (21 and 22) explore these mechanisms and concepts by applying them to two general attributes of complex social systems: the division of labour and collective decision making. A substantial contribution to sociogenomics (molecular and genomic studies of social behaviour) is the subject of Chapter 23, in which the authors discuss cases that illustrate how reducing complex behaviour to simple behavioural modules can help determine how genes and molecular pathways contribute to social behaviour. The following chapter (24), using social insects as a model system, integrates socio-biology and epidemiological models to examine the relationships between social

complexity and disease. The final two chapters (25 and 26) of this book address the question of how we view social insects as units of selection and evolution. The central idea of the first is provocative as it argues that colonies are individuals, not super-organisms. The authors' arguments open up the concept of what constitutes an individual – and an organism. The book concludes with a paper that focuses on the evidence that integrated development and evolutionary trajectories of social insect colony phenotypes are an ideal model system for applying social behaviour to evolutionary development.

As is apparent from the above review of the contents this book is a rich and inspiring source of information mainly for professionals in various fields ranging from hard-core field entomologists to students of insect behaviour, experimental ethologists, socio-biologists, theoretical evolutionists and social philosophers. This book will undoubtedly become a standard reference work on the organization of insect societies for many years to come, and the source of new and often unorthodox ideas that will stimulate and provoke further research in the field. It should not be missing from the bookshelf of any serious student of social insects or socio-biology.

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