



Book Review

The Evolution of Social Wasps. By JAMES H. HUNT. Oxford: Oxford University Press (2007). Pp. xxi+280. Price \$99.50.

I will open by making a strong recommendation: this is an important synthetic work, one that should be read by all students of animal behaviour and of related disciplines. It is an exemplar of the adage that one should not judge a book by its cover (an attractive macro photograph of a *Polistes* paper wasp, probably mounted upside down), or, in this case, by its title. To read or characterize this as a book about wasps is to miss the main point. The book is organised into 11 chapters, grouped in three sections: part I on History, part II on Dynamics, and part III, enticingly titled 'Paradigm Lost... and Found?'. The final 69 pages of text (the final chapter of part II, and all of part III) are a general exploration of the state of theory in the fields of animal behaviour and behavioural ecology. This latter part of the book makes a compelling case for fundamentally rethinking our models of behavioural evolution, particularly the evolution of social behaviour. Therein lies the book's most general appeal and impact.

In the beginning (chapters 1–7), this is a book about social wasp evolution. Hunt uses the earlier part of the book to build a case for a particular model of the evolution of sociality in paper wasps (presented in chapter 8, the final chapter of section II). The point of spending most of the book (and, for Hunt, most of a career) on the topic of wasp sociality is that although paper wasps provide a fascinating example of sociality and a range of social complexities, they are not mole rats, or scrub jays, or bonobos or humans. Are social wasps models for understanding the evolution of sociality? More generally, can any taxon serve as such a model? In some senses the answer seems to be yes. When sociality appears within animal clades, the social endpoints do show some compelling commonalities, such as dominance and division of labour. In important ways, the answer is also no. Careful and thoughtful biological analysis (like that presented by Hunt) shows that the devil is indeed in the details. One of the main theses of this book is that biology matters; the particular physiology, behaviour, genetics, life history and ancestral properties of a taxon affect not only the hows, but also the whys, of its evolutionary trajectory. This principle applies to social evolution every bit as much as it does to other traits: to the evolution of locomotion, of excretion, or of central nervous system architecture.

I agree with Hunt that this central point, that biology matters, has been lost on many animal behaviourists, including more than a few social insect researchers, for a number of years. It is time to come back to the light. This is why Hunt spends the first 133 pages of the book

exploring social wasp biology in a thorough yet concisely written review. This is a large literature with a long history. As a fellow student of social wasp behaviour, I found this part of the book a pleasure to read. It reacquainted me with some details I had forgotten and introduced me to some literature that was not familiar. A perusal of chapters 1 through 7 gives a good indication of Hunt's integrative agenda. Leafing through these pages reveals phylogenetic trees (in abundance), scanning electron micrographs, anatomical drawings and diagrams of antennal movements and of nest architecture (behaviour made solid). Larvae and adults are displayed. There is also a solid consideration of population dynamics, for both solitary and social species. This is an important piece of the evolutionary puzzle that is too often absent from the social insect literature. The chapters end with a presentation of remaining questions that may stimulate further investigations. One of the most exciting novel insights of this section of the book, later supported by phylogenetic evidence (Hines et al. 2007), is that sociality arose more than once in the Vespidae. I also particularly enjoyed the review of idiobiont parasitoid biology and its relevance to understanding the likely evolutionary base from which vespid sociality arose.

I do take exception to some of Hunt's ideas. As a tropical paper wasp biologist, I suspect that his emphases on seasonality and diapause as central factors in the evolution of reproductive caste (e.g. pp. 144–148) are misguided. At least some tropical social paper wasps do not show diapause, and the origins of wasp sociality in temperate or strongly seasonal tropical environments is open to question. These are largely empirical issues, and Hunt's book has framed the importance of testing them.

The latter part of the book is most likely to generate controversy and is therefore of great general interest and importance. Approach with care, or at least with an open mind. It contains some potentially explosive material; for example: 'Western culture has been shaped by the dualism of spiritual and material worlds... Behavioural ecology, but almost no other branch of science, has its own variation on this higher/lower theme: ultimate and proximate' (page 191). Some readers will no doubt bristle; others, like me, will rejoice that Hunt has laid down the gauntlet. I urge all animal behaviour researchers to carefully read pages 185–187, where an often-misunderstood passage from Darwin about social insects is quoted at length and thoughtfully analyzed. The end of the book questions the validity and utility of models and assumptions that have guided much behavioural ecology work since the 1970s. Finding these models lacking, particularly those of inclusive fitness maximization for all social partners, Hunt proposes an alternative approach. The proposed new

paradigm incorporates colony-level selection and the evolution of phenotypic plasticity as central elements. I find it satisfying that natural history research, and quantification of naturalistic behavioural variation, are recognized as important to making progress.

I will echo Hunt by ending with a bold assertion. There is a sea change occurring in the study of animal behaviour. Excessive focus on individual selection, and its evil twin, overzealous application of inclusive fitness maximization, are giving way to recognition that multilevel selection analysis is valid and appropriate to understanding social evolution (Wilson & Wilson 2007). This shift in theoretical focus has far-reaching implications, as Hunt's book makes clear. Rather than a universal functional model for social evolution, students of animal behaviour will seek understanding via an integrative approach to their study taxa. They will analyze genetic relatedness, yes, but also gene expression, endocrinology and signalling, development, nutrition, aggression, seasonality and natural enemies. I believe that this change in focus toward vertical integration of research questions will strengthen our ability to understand the evolution of complex traits, such as sociality. The work will be harder than we expected. We will have to proceed case by case, or taxon by taxon, and we will not be able to ignore physiology,

morphology and development on the way. To quote from one of Hunt's earlier works, '...nobody ever said life was fair.' (Hunt 1991, page 450). We will gain a deeper and more integrated biology of behaviour as a result.

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