

BOOK REVIEW

The social biology of *Ropalidia marginata*: towards understanding the evolution of eusociality

Raghavendra Gadagkar

Harvard University Press, Cambridge, USA, 2001. 368 pp. US\$ 90.00

Reviewed by OLIVER MAYO*

This book was clearly a labour of love for the author, and he has produced a work of substantial value in the study of the evolution of social behaviour in insects that is also a pleasure to read. The author has set out to demonstrate the value of his chosen insect, *Ropalidia marginata*, for research because of its small, open nests, primitive eusociality, extensive behavioural repertoire, and perennial, indeterminate nesting cycle (p. 74). He has certainly convinced me.

Gadagkar might have added that his wasp's predilection for building nests in close proximity to humans is a special advantage, but this he takes for granted, because his work is based on thousands of hours of close observation of the wasp, in natural and vespiary colonies and in carefully designed experiments. He has attracted students with the same willingness to undertake lengthy, laborious, meticulous observation. The result of his quarter-century's work is a real understanding of the behaviour of *R. marginata*, and an ability to use it to shed light on difficult questions in the evolution of social insects.

The book begins with a clear, careful, thorough introduction to eusociality. The author follows this with an introduction to the biology of *R. marginata* and to his approach to experimentation, which emphasizes the whole organism and its social context. He then works through the social structure of wasp nests, including caste differentiation, demography and ecology, to set a framework for his study of the evolution of social behaviour as elucidated through *R. marginata*. At each stage, he reviews the evidence and highlights what is unknown as well as what is known, and how his own work relates to both.

In particular, Gadagkar uses inclusive fitness, and Hamilton's rule for the increase in frequency of alleles predisposing towards socially beneficial behaviour of genes influencing such behaviour ($B/C > 1/r$, where B is the benefit to the recipient of the behaviour, C the cost to the performer of the behaviour, and r the coefficient of

relationship between recipient and performer), as a framework for his discussion. (This is expression 8.1 in the book; expression 8.2 appears to be in error, but the accompanying text is correct.) He produces a new parametrization of inclusive fitness, rbs , and an inequality $rbs > rbs$ (8.5) for the special case of workers in a colony compared with solitary (female) founders of new colonies. Workers will be favoured over such founders if this inequality holds. Here r is relatedness of worker to brood reared, b is intrinsic worker productivity, s is demographic scale (the weighting for b because the worker's lifespan may not match the brood's hatching time), and r , b and s are corresponding values for a founder.

Gadagkar then constructively applies this inequality to many problems in social evolution, attempting to estimate the six parameters or surrogates for them. For example, he shows that multiple colony founders show lower brood number variability (p. 225), clarifies the benefits of being workers (p. 233), and estimates s to assess a novel hypothesis relating to worker benefit (p. 255). Other reparametrizations have been advanced, however, and these might have been considered in some cases. They are not new (see, e.g. Mayo 1983 for discussion).

Gadagkar's experiments are remarkable for their elegance, provided one accepts the heavy observational load that so many of them demand (such as recording some 80 different behaviours at frequent intervals over many days, pp. 45–51). For example, his demonstration that *R. marginata* queens do not regulate forager activity is a model of clarity (pp. 162–164).

It could be said that *R. marginata* has directed the author to the conclusion that haplodiploidy, the fundamental phenomenon in Hymenoptera that has guided so much thinking about social evolution, has frequently been less important in determining the course of evolution than the range of ecological, physiological and demographic factors that he has investigated. Not everyone will share this view.

The book is a clear demonstration of the progress that can be made by largely noninvasive experimentation and observation. And it is a pleasure to read a work of evolutionary significance that is not dominated by comparison

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of DNA sequences. However, more use could have been made of genetics. For example, the remarkable finding, across several colonies in three independent experiments, that 50% of eclosing females can lay eggs and 50% cannot (pp. 234–239), could have been evaluated for genetic influences. Accurate pedigrees have been obtained by biochemical genetics in another case (pp. 160–170), and this method could have been applied. Similarly, the quantitative genetics of many traits could have been investigated where pedigrees were available.

In the investigation of polyandry, which necessitated accurate pedigree determination (pp. 160–162), the data are potentially of greater use than has here been made of them. For example, they might be further analysed in the light of the work of Crozier and Fjerdingstad (2001).

At times, Gadagkar's enthusiasm leads him close to anthropomorphism, as in the discussion of colony fission (pp. 279–283), but this does not influence his important conclusion that wasps can recognize individuals and alter their behaviour because of that recognition. Nevertheless, one should not lose sight of the caveat that an 'insect society more resembles a single animal body than a human society' (Fisher 1999, p. 181).

As his subject continues to develop, Gadagkar should produce a second edition. In this case, he should improve

the index. Among the topics not listed but considered in the text are: cladistics, inbreeding, nest building, phylogeny. He might also consider a glossary, for such items as gamergate, queenright (p. 6), Richard's gland (p. 18), van der Vecht's gland (p. 27), *ad libitum* sampling (p. 46), malaxation (p. 275; a word unknown to the reviewer). Preadaptation as a concept is something that should be clarified (pp. 21–22, p. 277).

I have read this book to learn about Gadagkar's work, not because I have expertise in social biology of insects. Indeed, it would be hard to compete with him in knowledge of *Ropalidia* spp. One can, however, ask whether he has successfully communicated the significance of his work, its factual and theoretical content, and his enthusiasm for the subject. I answer unequivocally: yes.

References

- Crozier R. H. and Fjerdingstad E. J. 2001 Polyandry in social Hymenoptera—disunity in diversity? *Acta Zool. Fennici* **38**, 267–285.
- Fisher R. A. 1999 *The genetical theory of natural selection. A complete variorum edition* (edited with an introduction and notes by Henry Bennett) Oxford University Press, Oxford.
- Mayo O. 1983 *Natural selection and its constraints*. Academic Press, London.