

Book Reviews

Nourishment and Evolution in Insect Societies.

Edited by J. H. HUNT & C. A. NALEPA.
Boulder, Colorado: Westview Press (1994).
Pp. xi+449. Price \$79.95.

For years Jim Hunt has been trying to awaken us to the importance of feeding and nourishment in the evolution of insect social behaviour (1982, 1991). Although others have shared his view that haplodiploidy and skewed genetic relatedness are neither necessary nor sufficient for the evolution of eusociality (Alexander 1974; Andersson 1984), they addressed a variety of extrinsic ecological factors without giving particular attention to the role of nourishment. Hunt & Nalepa have now provided us with a whole volume focused on the role of feeding and nourishment in the evolution of eusocial behaviour.

The editors realized that there are two ways to address such a broad topic: either research and write it themselves (analogous to cooking a nine-course meal for 100 friends) or pull together an edited volume (similar to 'pot luck'). The advantage of having chosen the latter is that we have *Nourishment and Evolution in Insect Societies* today. The disadvantage is some unevenness in the prose and internal structure of the chapters, as is often typical of edited volumes. It is possible, however, that much of the unevenness of content is due to the holes in our knowledge and points to areas ripe for further study. Fortunately, the 13 contributors did not all bring salads or desserts; there is a good mix of broad theoretical and taxon-specific contributions with plenty of examples and data.

The clustering of all but the first chapter is basically taxonomic (subsocial arthropods: chapter 2, termites: chapters 3–6, wasps: chapter 7, ants: chapters 8–10, and bees: chapters 11–13). Of these 12 chapters, three survey feeding in broad taxonomic groups (e.g. ants), five address much more specific groups such as fungus feeders, and four are more theoretical. The introductory chapter, by Hunt & Nalepa, sets the theoretical framework within which the other contributions should be viewed. They address feeding and nourishment as a major life-history component for insects and discuss the boundaries and options available. Variance in nourishment in societies and the modes of redistribution (i.e. cannibalism, oophagy, faecal pellet feeding and trophallaxis) have a major effect on social evolution. Trophallaxis, in particular, is key in the control of

nourishment redistribution and endosymbiont transfer. Hunt & Nalepa argue that although these components are crucial in the evolution of sociality across taxa, the interaction between morphology, physiology and nourishment in different taxa has followed different evolutionary pathways. Similar arguments about the importance of any particular life-history characteristic often degenerate into adaptationist story telling, but Hunt & Nalepa stop short of that in this chapter and let the contributors get on with giving us actual data, examples and cases.

Most of the contributors give lots of details of the role of feeding and nutrition in the social evolution of small taxonomic groups. Among the taxa reviewed are the soil-feeding termites, fungus-growing termites, fungus-growing ants, primitively social bees and stingless bees. Bignell's discussion of the soil-feeding termites and the constraints placed on them by their gut morphology anticipates Hunt's arguments about nutritional constraints in wasps in chapter 7. To my surprise and disappointment, only one chapter deals with wasps, and it is from a theoretical perspective rather than a review of a particular taxon.

The broad taxonomic reviews of nourishment in termites and ants cover major trends in these taxa. Lenz reviews constraints on colony size and caste due to food type and distribution across termite species. Wheeler gives a broad review of how ants and ant colonies use food. In contrast, Tobin has a narrower scope and looks at the role of ants as primary consumers. Similar reviews of wasps and bees would have been welcome additions to the book.

The theoretical chapters are a mixed bag. Those by Hunt (chapter 7) and Nalepa (chapter 3) are well organized and convincingly argued. Hunt's chapter 7 will probably be one of the most cited chapters in the volume and presents his argument that digestive tract morphology, maxillation, and sharing via trophallaxis are crucial characteristics leading to the evolution of social behaviour in Hymenoptera. On the other hand, Tallamy's chapter 2 on subsocial arthropods and the role of male parental care attempts to take a socio-biological approach, but he makes no reference to basic behavioural ecology in developing his model. The other problematic contribution is chapter 12, in which Moritz argues that the ability to store food is central to the evolution of social behaviour in insects. He attempts to find a pattern

from a suite of characters where it is difficult to determine which ones are just correlated and which have causal relationships.

In the light of Sherman et al.'s (1995) recent efforts to bridge the theoretical gap between the study of eusocial behaviour in insects and cooperative breeding in vertebrates, perhaps a good side dish to accompany this book would be Rubenstein & Wrangham's (1986) anthology on social evolution in vertebrates. Regardless of your usual taxonomic menu, I highly recommend adding Hunt & Nalepa's new book to the reading diet for all interested in social behaviour.

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Unravelling Animal Behaviour. 2nd edn. By MARIAN STAMP DAWKINS. Harlow, Essex: Longman (1995). Pp. vii+183. Price £12.99 paperback.

This second edition of Marian Dawkins' helpful textbook differs materially from the first: it is a genuine revision, not a repackaged updating. Two chapters have been deleted from the first edition and three new ones added, while the remainder of the text has undergone changes ranging from minor rewording of individual sentences to addition, deletion or substitution of whole sections. In a couple of cases a single new chapter has been formed by abbreviating and grafting together two former ones.

Of the chapters that have been removed, one dealt with a mixed bag of themes in classical

ethology, under the title of 'Some obstinate remnants'. Few will mourn its passing. The other deletion, 'Evolutionarily stable strategies', is more regrettable since ESS modelling still plays an important role in contemporary ethology, especially in thinking about communication. ESSs do not even appear in the index of the second edition. Perhaps Dawkins feels that ESSs are no longer sufficiently problematic to need explaining to students, but if my experience is anything to go by, undergraduates still have difficulty appreciating what game theory models have to offer and how payoff matrices are calculated. Recently, after I had patiently devoted an entire lecture to what I thought was a faultless step-by-step account of the hawk–dove model, a student asked me what was the point of the model since hawks and doves, being different species which eat different things, are not in competition with one another in the first place. If a second chapter had to be sacrificed to provide space for the new additions, I would rather it had been the one on optimality, which has undergone relatively little revision since the first edition.

The three new chapters are titled 'Cognitive ethology', 'Consciousness' and 'Animal behaviour and human behaviour'. The first and third of these are welcome additions, containing, amongst other good things, clear-headed accounts of cognitive maps, concept formation, and the problems besetting attempts to apply evolutionary thinking to human behaviour. I was less happy about the chapter on consciousness, which fails adequately to distinguish consciousness from intelligence and, in particular, motivation. The confusion with motivation comes in a section on animal suffering, where Dawkins advocates using elasticity of demand as a measure of an animal's motivation to procure something that is missing from its environment. Strength of motivation is irrelevant to the issue of consciousness and in the end Dawkins admits as much. However, this leaves one wondering why she introduced the subject in the first place.

Substantial revisions have been made to the chapters now entitled 'Inclusive fitness', 'Communication' and 'Sex and sexual selection', including the addition of new sections covering manipulation, handicaps, honesty of signals, and female choice. The discussion of handicaps is exceptionally clear and should be made compulsory reading. One of the best features of the first edition was its crystalline exposition of kin selection, and this has been retained and even improved in the second. It is a pity that the 'Inclusive fitness' chapter contains no mention of reciprocal altruism since it is in other respects a