

BOOK REVIEWS

Boinski, S. & Garber, P. A. (eds). 2000: *On the Move. How and Why Animals Travel in Groups*. The University of Chicago Press, Chicago, London. 824 pp., Cloth Hb £ 66.50, US\$ 95.00. ISBN 0-226-06339-9; Paper Hb £ 24.50, US\$ 35.00. ISBN 0-226-06340-2.

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I read this book under ideal circumstances – in the field. I spent part of each day following baboons outside of Amboseli National Park. The baboons rose just after dawn, spent nearly an hour resting and socializing, and then moved out onto the savanna to begin the day's work – finding food. These daily expeditions gave me ample opportunity to ponder the questions raised in this impressive volume: Why do the baboons choose one foraging site over another? How do the baboons know where to find food? How do they know how to get from one feeding site to another? What behavioral mechanisms do baboons use to maintain cohesion and coordinate travel from one place to another? What constraints limit their options? Observers of primate groups have entertained these questions for decades, but had made little progress in answering them. In the last few years, however, an important body of information has been compiled about the ecological, behavioral, social, and cognitive factors that influence group movements in primate species. The 22 chapters that comprise this edited volume provide encyclopedic coverage of these topics, making this an essential resource for anyone interested in how and why primates travel in groups.

The book begins with a consideration of the ecological factors that shape movement patterns in primate groups. These include the demands of finding food, avoiding predators, defending territories and/or avoiding neighbors, and finding mates. The chapters in Part I reveal that primatologists have made considerable progress in understanding how these factors jointly influence the economy of social life. Faced with ecological challenges and energetic constraints, selection favors cognitive adaptations that enable animals to make efficient use of available resources while maintaining group cohesion. This is the subject of Part II. A fascinating body of new work on the cognitive mechanisms that underlie home range use is described in Part III. Some of this work employs innovative experimental methods, such as Menzel et al.'s analysis of homing abilities in semifree-ranging tamarins, and Garber's analyses of how tamarins and capuchins use spatial and temporal information to generate foraging rules. Part IV focuses on the nature of social processes that influence group movement, including coordination of the timing and direction of travel and leadership. Here careful ethological work documents the subtle dynamics of how decisions about movement are reached.

One of the most interesting conclusions that emerges from this book is that low-cost vocal and postural signals play an important role in group movement in many species. Although the role of such signals has been well-documented by researchers (reviewed here by Boinski), the extensive list of these signals provides a counterpoint to the prevailing wisdom that all honest signals must be costly. Boinski suggests that the paradox is resolved because these are cooperative signals, which enhance the welfare of all group members. However, she and many of the other contributors document the extensive conflict of interests among group members who have different energetic needs, reproductive interests, and constraints. Cooperation is not the operative concept when conflicts of interests exist. Low cost signals can evolve when there are conflicts of interest, if coordination is sufficiently valued (Farrell & Rabin 1996). Signals need not be costly because deception is not profitable. Thus, if one monkey wants to move to the nearest fruit tree and another wants to continue resting, they have no reason to lie about their preferred destination. They will, however, need to reach a decision about where to go, a process that may involve conventional asymmetries (older animals decide), dominance (high ranking animals decide), or motivational differences (hungeriest animals decide). These decision-making processes are still poorly understood in most species.

Most of the chapters in this book focus on nonhuman primates, but there are also chapters on cetaceans, social carnivores, social insects, birds, fossil hominids, and modern nomadic pastoralists. This section of the book is least satisfying. Editors of books on primates always seem compelled to include chapters on other taxa, as if it is necessary to remind our colleagues that we know that primates

are subject to the same evolutionary constraints as other animals. However, comparative analyses are only valuable if they enlighten us about the ecological, behavioral, cognitive, or selective processes shaping the phenomena of interest. Thus, our confidence in the relationship between sexual dimorphism and social organization is enhanced by the demonstration that this relationship has evolved independently in several different taxa. Similarly, comparative data suggest that the cognitive abilities that underlie group movement in primates do not differ qualitatively from those of animals with much smaller brains, and this in turn implies that encephalization in primates does not reflect an adaptive response to challenges that arise from navigating large home ranges. Barton arrives at the same conclusion from neuroanatomical evidence.

Not all of the comparative chapters contribute directly to an understanding of group movement in primates. For example, Dyer's chapter on group movement in social insects is meant to provide 'a valuable guide to primate researchers by outlining a set of concepts regarding possible mechanisms underlying spatial orientation' (Dyer, p. 164), but does not explicitly consider the implications of the fact that 'insects are unlikely to provide a useful model of the underlying mechanisms in other animals' (Dyer, p. 164). Greenberg's chapter on mixed species associations in birds makes no effort to compare the ecological forces shaping mixed species associations in birds and primates, and does not refer to Cords' excellent summary of information on mixed species associations among monkeys. It is not clear how McCabe's chapter on the Turkana, who are nomadic pastoralists, contributes to our knowledge of group movement in nonhuman primates, although McCabe does demonstrate that ecological, social, and cultural factors guide the Turkana's movements in ways that fit behavioral ecological paradigms. The most useful comparative chapter focuses on social carnivores. Here, Holekamp et al. explicitly compare social carnivores to nonhuman primates and humans, focusing on some of the same questions (e.g. coordination of travel, leadership, factors influencing party size, cognitive mechanisms) that were raised in earlier chapters.

This book is a valuable addition to the behavioral ecology literature, providing a comprehensive compendium of what we know and what remains to be found out about how and why primates travel in groups. It is essential reading for those interested in the intersection of ecology, behavior, and cognition and fascinating food for thought for fieldworkers who are simply curious about how animals make their way each day.

Reference

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Bennett, N., & Faulkes, C. (2000) *African Mole-rats: Ecology and Eusociality*. Cambridge University Press, Cambridge. xiv + 273 pp, 63 figs, 28 tables, \$59.95, £35.00. ISBN 0-521-77199-4.

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Ask your colleagues why honey-bees are eusocial and they will most likely tell you that 'it has something to do with haplodiploidy'. Even Bennett & Faulkes tell us in their new volume, *African Mole-rats: Ecology and Eusociality*, that 'haplodiploidy explains altruistic behavior in eusocial hymenoptera' (p. 189). This tidy genetic story has persisted for over 30 years despite the well-established facts that multiple mating by queens (Alexander & Sherman 1977) as well as equal investment sex ratios among alates (Crozier 1979) commonly remove the inclusive fitness benefit to workers (Andersson 1984).

In a similar fashion, the tidy inbreeding explanation for eusociality in the naked mole-rat is likely to persist long after the theoretical and empirical bases for this story have been removed. We now know that naked mole-rats do disperse in the lab (O'Riain et al. 1996) and in the wild (Braude 2000), that they prefer to mate with nonrelatives (Clark & Faulkes 1999; Cizek 2000) and that earlier estimates of inbreeding and relatedness were accidentally biased by sampling of a very recently founded population (Braude 2000). But if naked mole-rats are not eusocial because of inbreeding, why are they eusocial?

Bennett & Faulkes present a detailed case for an ecological explanation of mole-rat eusociality, the aridity food-distribution hypothesis (AFDH) in their new book.

The AFDH offers an explanation for the occurrence of eusociality in most of the African mole-rat species that occupy arid regions of Africa but solitary living in the species that occupy mesic habitat (Jarvis et al. 1994). According to the AFDH the large size and low density of geophytes on which Bathyergidae, African mole-rats, subsist makes random foraging too risky for small groups of large individuals but possible for large groups of smaller animals. Since Bathyergidae have a resting metabolic rate that does not scale with body mass, large numbers of small foragers can be produced. Lovegrove & Wisel (1988) suggest that this risk-sensitive metabolism is the reason that sociality has arisen multiple times in the Bathyergidae but not in other fossorial rodents.

Bennett and Faulkes build the case for the AFDH carefully. Their introduction to the African mole-rats reviews the general phylogeny and natural history of the various species (Ch. 1). Next they describe the general ecology of the subterranean environment (Ch. 2 and 3) and review the diversity of sociality and reproductive biology in the Bathyergidae (Ch. 4, 5, and 6). In Chapter 7 they review the literature on genetic structure of mole-rats and argue that 'an understanding of intragroup genetic relationships is clearly essential if we are to understand the factors involved in the evolution of sociality in the Bathyergidae' (p.189–190). Fortunately, they did not let the misunderstandings about naked mole-rats inbreeding at the time of publication mislead them from developing and presenting the rest of their argument. In the final chapter they pull together the various lines of evidence and make their case that the AFDH is the best explanation of bathyergid sociality.

Bennett and Faulkes also argue that the African mole-rats are a model system for the study of the evolution of eusociality because there is a broad range of sociality in the family. However, if the unique risk-sensitive metabolism of the Bathyergidae is necessary for the AFDH, their value as a model system is limited. Bennett and Faulkes do discuss the nonbathyergid fossorial rodents (*Thomomys*, *Spalax* and *Ctenomys*) but only for occasional comparison, and not systematically.

The authors point out how much work lies ahead in collecting basic information on the many solitary bathyergid species and it is disappointing that some of the basic foundations of the AFDH have not yet been tested. For example, the predictability of rainfall (Low 1978) has not actually been compared for habitats of the different species; instead, coefficient of variation in rainfall is used as an estimator of predictability. More importantly, the distribution of food has not been compared either within Bathyergidae or for any of the other fossorial and social rodents.

This book is valuable to all of us interested in the evolution of social behavior for its comprehensive references on the African mole-rats and it has the advantage over an edited volume of being clearly organized and having consistent style. However, it is not a comprehensive review of ecological hypotheses. Other ecological models, such as the group defense hypothesis (Alexander et al. 1991) and the pregnancy constraints model (Burda 1990), are noted and dismissed rather than examined in detail. The authors have also missed an opportunity to integrate the information on the Bathyergidae with the broader theoretical literature on ecology and social evolution, especially the highly relevant models of foraging and nutrition in the social insects (Hunt & Nalepa 1994) and in vertebrates (Rubenstein & Wrangham 1986). Yet, on the whole, *African mole-rats, ecology and eusociality* is an excellent review of the Bathyergidae and a well-crafted argument in support of the AFDH.

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