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FRUSTRATED FELINES AND EXCITED UNGULATES

A review of *Homosexual Behaviour in Animals: An Evolutionary Perspective* edited by Volker Sommer and Paul L. Vasey. Cambridge University Press (2006) 382 pages, £75 (\$125), ISBN: 0521864466 (hardback).

DAVID W. LAWSON

Human Evolutionary Ecology Group, Department of Anthropology, University College London, London WC1H 0BW, UK E-mail: d.lawson@ucl.ac.uk

Homosexual behaviour has been documented in practically every major taxonomic group in the animal kingdom, from *Drosophila* to *Homo sapiens*, yet a convincing evolutionary explanation for its occurrence remains elusive. At the theoretical level this is not for want of trying. As the editors of this new volume point out in their introductory chapter, testable hypotheses for the ultimate function of homosexual behaviour have long been in existence, and are now numerous (14 separate hypotheses are distinguished here). Rather, progress has been limited by the death of empirical research that is required to test competing hypotheses against one another. *Homosexual Behaviour in Animals* then makes a particularly welcome contribution to the literature by presenting almost a dozen research papers on a range of animal species in which sufficient data has been collected to warrant quantitative analysis.

The editors provide an engaging opening, reviewing the history of research into ultimate explanations for homosexual behaviour and discussing each of the principal hypotheses in turn. Following this introduction, the bulk of the book is composed of a series of contributed chapters, divided into two sections. The first set takes in studies of birds (geese and flamingos), cetaceans (bottlenose dolphins), ungulates (bison and deer) and carnivores (feral cats). The second half focuses on primates, including Old World monkeys (Japanese macaques, rhesus macaques and langurs monkeys) and apes (mountain gorillas and bonobos), and concludes with an essay on male homosexuality in humans.

Homosexual behaviour, of one form or another, is characterised as a routine behaviour for each of these animals. For example, we learn that male Indian Ocean bottlenose dolphins engage in more sexual encounters with same-sex than oppositesex conspecifics as calves (p. 126). While data from Sommer's well studied Indian

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langur population indicate that on average homosexual mounts account for 46% of a female's sexual interactions across her entire lifespan (p. 261). A high emphasis is given to this descriptive information, as often such data forms the first reliable frequency estimates of homosexual behaviour for each species. Even without the detailed analysis of the socio-ecological determinants of such behaviour elaborated in most chapters, this point serves well to illustrate the importance of this ambitious volume.

In general, each research chapter is well written and insightful. Janet Mann's study of bottlenose dolphins, Akihiro Yamane's study of Japanese feral cats and Barbara Fruth and Gottfried Hohmann's work on bonobos provide the highlights for this researcher, but reader preferences will likely vary with individual species of interest. Perhaps unsurprisingly, the editors own contributed chapters, both citing extensive observational data, are amongst the strongest in the volume.

Many contributors ascribe a socio-sexual function, such as reconciliation, status acknowledgement or alliance formation, to their findings on homosexual behaviour. Others argue that homosexual behaviour might be a relatively functionless by-product of the core adaptations relating to reproductive sex. As Vasey puts it in reference to his own study of Japanese macaques: "from an ultimate perspective, female-male mounting can be understood in terms of function and evolutionary history, but female-female mounting can only be explained in terms of the latter" (p. 216). Overall it is clear that multiple developmental pathways and evolutionary histories may underlie the occurrence of homosexual behaviour in animals. This only serves to make each individual study all the more interesting.

Dan Werre's essay on homosexuality in humans takes a suitably broad comparative perspective (if you discount the significant exclusion of the female sex). While solid in its own terms, an empirical study of human sexual behaviour would have perhaps been more in keeping with the ethos of the book (CAMPERIO-CIANI et al. 2004; VASEY et al. 2007, for some recent examples). After all, a number of instructive reviews of the human literature are already in print (e.g. KIRKPATRICK 2000). In this sense, researchers specifically interested in human homosexual behaviour are more likely to learn something new from the animal chapters.

The book is rounded off by a short discussion of the political sensitivity of research into homosexual behaviour by Sommer, and a summing-up chapter by Vasey. Sommer's chapter is concise and to the point, effectively dismissing arguments about the morality of human homosexuality that misguided individuals might attempt to make on the grounds of its existence in animals. Vasey's more crucial chapter, (aptly titled "Where do we go from here?"), while clearly written by a researcher with formidable knowledge and passion for the field, is somewhat of a mixed bag. On the one hand, it raises several exciting new questions based on the existing literature at large. For instance, in Japanese macaques males appear to actively compete with one female for sexual access to another (see also VASEY)

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1998). Using supportive evidence for a range of other studies, Vasey makes a convincing case for future research into such *inter-sexual* competition and its implications for our current understanding of reproductive strategies. On the other hand, Vasey's discussion is relatively ineffective at summarising the specific answers provided by the contributions to this volume.

This latter point is perhaps the focus to my most serious criticism. Despite the introductory chapter's lengthy discussion of alternative ultimate hypotheses for animal homosexual behaviour, throughout the volume it is difficult to keep track of the implications of each study either individually or as a whole. Perhaps this is a product of the sheer number of possibilities encountered, but there are also several factors which make it difficult to distinguish the precise nature of each hypothesis. Discussions do not always make clear which hypotheses are mutually exclusive and exactly what findings would be required to reject or strongly support each alternative. A reference table contrasting the predictions of each hypotheses related to socio-sexual function are often blended together. Vasey's concluding chapter would have been a good point to resolve these issues, but at this level presents a missed opportunity.

On occasion the editorial reigns also feel frustratingly slack. Several contributing chapters move at a leisurely pace that, while at times enjoyable, can distract from the questions at hand. Supplementary information on a species' socioecology might have been better referenced out and several discussions feel overlong and somewhat meandering. Structural flaws further drain clarity and focus. In particular, I found it confusing that in many chapters hypotheses and associated predictions make their first appearance in the discussion, rather than the introduction.

In conclusion, in comparison to BAGEMIHL'S (1999) recent encyclopaedic book on animal homosexual behaviour, *Homosexual Behaviour in Animals* can be seen as sacrificing breadth for depth, and it is all the better for it. While at times frustrating in its execution, the volume succeeds by shifting focus away from the anecdotal and speculative and towards directed empirical study. In light of this triumph, other criticisms can be seen as relatively minor. Sommer and Vasey have sharply steered the Darwinian study of homosexual behaviour out of its infancy and towards all the defining features of a mature science.

The volume collectively demonstrates that we can not afford to dismiss homosexual behaviour as either uncommon or of little consequence to wider social and reproductive strategies. For many species, its occurrence is surprisingly frequent and heavily patterned. For these reasons, the book deserves to be widely read by researchers interested in ultimate functions of human and animal behaviour alike. In particular, researchers who hope to make further empirical contributions to this exciting field will find *Homosexual Behaviour in Animals* indispensable. Readers may not receive all the answers they desire from this volume, but should be

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inspired by the laudable examples of the right way to ask and evaluate the questions.

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