

## BOOK REVIEWS

**De Waal, F.B. (ed.) 2002:** *Tree of Origin: What Primate Behaviour Can Tell Us about Human Social Evolution.* Harvard University Press, Cambridge. 311 pp., \$17.95. ISBN 0-674-01004-3.

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The evolution of man continues to fascinate the scientific community as much as the public, at least in places where evolutionary thinking prevails. There are different approaches to reconstruct the origins of our own species: phylogenetic relationships may be proposed based on fossil evidence, while the study of ancient DNA may shed light on migratory patterns and population dynamics. However, much of what makes us human lies not so much in our bones but in our brains, that is, in our social and cognitive abilities. Unfortunately, behaviour does not fossilize – therefore, if one is interested in human social evolution, one needs to turn to the study of the behaviour of our closest living relatives, the apes and monkeys. This idea has been around since the early 1960s when Louis Leakey and Sherwood Washburn suggested to use monkey and ape behaviour as a model for human social evolution.

Anyone interested in this topic should pick up 'Tree of Origin' for an enlightening and entertaining reading. The book came out of a meeting about Human Evolution held at Cold Spring Harbour in 1997. It was first published in 2001 and is now out in paperback. Frans de Waal assembled a fabulous crew of behavioural primatologists, all leaders in their fields, and asked them to present current lines of thinking in their areas of research. He actively encouraged them to speculate about the origins of human evolution, and asked them to write in an accessible and jargon-free style. These requirements are the foundation of both the strengths and weaknesses of this book: many chapters are easy to read and demonstrate that elegant, precise and simple writing are not mutually exclusive. On the other hand, readers with a scientific background are often left to wonder how much of what is presented is based on evidence, and how much springs from the author's more or less ingenious imagination, as references in the text are entirely lacking. A brief bibliography and an appendix with explanations of some technical details partly make up for this. Clearly, speculations can be very productive: they may promote discussion, cause changes in perspective and ultimately fuel empirical studies. On the other hand, if taken too far, they run the danger of discrediting the field. The lack of distinction between fact and fiction may however be acceptable given that this book has not been put together for the scientific community but instead reaches out to a wider range of readers such as interested lay people and first year students. As such, it does a great job.

The book centres on the following themes: sex and reproduction, social organization, social sophistication and cognition, and hominization. Most chapters discuss two or more of these aspects and their interdependence, and thus, the book provides a comprehensive view of the factors that probably played a role in human social evolution. Not surprisingly, apes feature in most of the chapters, and the topics range from Craig Stanford's discussion of the significance of meat-eating and meat-sharing for the evolution of sociality to the cognitive abilities underlying processing of food items by gorillas, as presented by Richard Byrne. I found Robin Dunbar's chapter particularly useful in which he outlines different approaches to the study of the evolution of human behaviour. Dunbar provides a good introduction to model building based on regression equations, and illustrates the use of this approach when he discusses the relationship between group size, brain size and the evolution of intelligence. Frans de Waal points out that using just chimpanzees as models for early human sociality may cause a tilted view – bonobos, who are as closely related to us as chimpanzees reveal a very different female-centred and relatively peaceful social organization. De Waal does not claim that bonobos provide a better model than chimpanzees but that the variation between the two species simply reminds us to be careful when we make extrapolations from their behaviour. Along the same line, Karen Stier argues that much can be learned from the study of primates other than apes. However, the same may be said about the study of other animals than primates. Recent studies of the

cognitive abilities of dogs and goats, for instance, highlight the dangers of a narrow primate focus when adopting the comparative approach. Richard Wrangham outlines his ideas about food hoarding and cooking for the evolution of human monogamy. Wrangham and his colleagues suggest that monogamy evolved because females who wanted to cook their foods and hence had to store it for brief periods of time near the hearth, needed strong males to protect them from scroungers who might sneak up and steal the food. According to this 'theft hypothesis', it was female-female competition for apt food-guardians that led to concealed ovulation and permanent pair-bonds. Although not everyone might find this argument fully pervasive, it at least provides fodder for a lively debate. Further contributions come from Bill McGrew, Anne Pusey, and Chuck Snowdon and deal with the evolution of culture, chimpanzee social organization, and primate communication, respectively. In summary, I can wholeheartedly recommend this book to anyone as a great introduction into the fascinating world of the study of human social evolution.

**Kareiva, P. & Levin, S. A. 2003: The Importance of Species: Perspectives on Expendability and Triage. Princeton University Press, Princeton. 427 pp., \$35.00. ISBN 0-691-09005-X.**

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There is a surge of conservation interest among animal behaviorists, as evidenced by numerous symposia, workshops, reviews and edited volumes by ethologists hoping that their science might be applied to saving and managing biodiversity (see the conservation section at <http://www.animal-behavior.org> for relevant references). A major impediment to the etho-conservationist is that policy or management decisions are usually made based on landscape or species level considerations (or even more mysterious entities such as 'evolutionarily significant units') that are not common to our training. Most ethologists focus their studies on variation in the behavior within or between individuals. This edited volume, a festschrift in honor of the seminal contributions to ecology of retiring University of Washington Professor Robert T. Paine, may be helpful to ethologists trying to understand how their own speciality might be useful to conservation biology. In his classic studies of the rocky intertidal communities of the Pacific Northwest of the United States, Paine showed experimentally how temporal and spatial variation in species distributions were, in part, the result of species interactions (i.e. predation, competition, etc). This volume assembles prominent and lesser-known (to me) North American ecologists who employ empirical and theoretical approaches to address how species interactions might inform us about the ecological (not economic) value of individual species within communities. This is mostly achieved by considering how species extinctions or introductions change the quality or quantity of species interaction.

Given the cost of efforts to conserve threatened species, politicians and the general public often ask 'Do we really need species X?'. Value systems are already employed in conservation decision making: international biodiversity 'hotspots' are prioritized for preservation in national parks, monotypic taxa are of greater conservation concern than speciose taxa, and the endangerment of charismatic mega-vertebrates attracts more public interest than the loss of plant species. The authors in this volume find that some species, as measured by their contribution to community stability, nutrient cycling and biomass production, are not particularly valuable. The 17 chapters are grouped into three oddly named 'parts' [(i) Using Experimental Removal of Species to Reveal the Consequences of Biodiversity Depletion, (ii) the Anthropogenic Perspective, and (iii) Linkages and Externalities], each separated by a helpful introduction from the editors. The organization of chapters leaves the impression that the volume was not carefully crafted to achieve some goal other than making sure that symposium participants had an opportunity to publish their presentations. Typographical errors are uncommon but also lend the impression of inattention by the editors.

The chapter topics run the gamut of examining how the presence of native thistles might assist insect predators to control invasive exotic thistles, to determining fish species' characteristics that contribute to their invasiveness. The approaches include field experiments, philosophical discussion, mathematical modelling, comparative analyses and literature review. Gratefully none of the authors concludes that any species is ecologically unimportant and should not be conserved; only that some contribute very limited or redundant ecological services that could be compensated for by other species. Notably, the chapter by S. R. Palumbi cautions that even ecologically unimportant species may have unforeseen evolutionary potential to restore biodiversity through adaptation and speciation.

Several chapters conclude that too few studies collect relevant data to adequately address the ecological consequences of extinction or species introduction. I found it necessary to consult with my community ecologist colleagues in order to fully understand chapters that had an ecosystem focus. Despite the global nature of the biodiversity crisis and the presence of excellent ecologists elsewhere, the list of 28 authors are all from the USA (an author based in Canada and another at the Smithsonian Tropical Research Institute in Panama are technical exceptions), primarily coastal California and Washington. No doubt these contributors are former students and collaborators of Dr Paine who wished to honor him by attending the symposium. However it is not unreasonable to expect the volume editors to solicit additional chapters to provide a broader, multi-cultural perspective on species expendability.

There are only a few places in the book where a need for behavioral data is mentioned, mostly in the guise of natural history information. In addition there are numerous places in the text where I found myself remarking on how behavioral studies would be helpful in resolving the management problem. For example, Ruckelhaus and colleagues mention that while salmon normally return to their natal streams to spawn, they spawned in alternative drainages when their home streams were decimated by the volcanic eruption of Mount St Helens. Interestingly, the fish recolonized the old streams when the waterway had recovered ecologically. One wonders if mating competition or condition-dependent behavioral tactics might be involved in allowing some individuals to behave in ways that have not been thought of as typical for the species, but that were essential to the persistence of regional salmon populations. Nevertheless, the potential value of this book to the aspiring etho-conservationist does not lie in what it has to say about animal behavior (which is virtually nothing). Instead its value is in showing us how ecologists have attempted to apply the approach and findings from their tests of ecological hypotheses to an applied, environmental policy concern, species expendability. It is not an important volume for the ethologist's bookshelf, but most university libraries should probably purchase it for ecologists, thus making it available for perusing by the behaviorists as well.

Until recently the only prominent areas of applied animal behavior were for the management of farm and companion animals. Now field ethologists will increasingly find themselves being asked to explain why behavioral diversity is of importance to human society. They will also be asked to reshape their data collection methods to include the 'natural history' results that this book's authors often found to be missing. The 'Importance of Species' is a worthy read for the etho-conservationist because it demonstrates the difficulties and surprising results that are generated when 'pure' scientists attempt to apply themselves to real-world problems. For the promising field of etho-conservation to succeed, it would be best that we have our eyes open to the unique demands of environmental decision makers before we make promises that we cannot keep.

**Hardy, I. C. W.** (ed.) 2002. *Sex Ratios – Concepts and Research Methods*. Cambridge University Press, Cambridge. 424 pp. \$48 paperback, \$120 hardback. ISBN 0-521-66578-7.

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Darwin (1871) tackled the problem of sex ratios in the 'Descent of Man'. He had noted an approximately equal number of males and females in those domestic animals for which data were available. He discussed the outlines of a model and considered that an excess of one sex would be 'superfluous and useless', and considered that natural selection would restore the equilibrium. In the more widely read revised version of 1874, however, this section was largely deleted (Darwin 1874). He wrote 'I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see the problem is so intricate that it is safer to leave its solution for the future'.

It is clear from this volume edited by Ian Hardy that it is an intricate problem and also one that is fascinating. The developments since Darwin's attempts have been remarkable. They started with a much neglected mathematical approach by Düsing (1883), which sets out fitness as a function of the sex ratio of the parent's progeny in a given population sex ratio. This argument was central to the well-known treatment by Fisher (1930). Other major contributions have followed, notably but not exclusively by Hamilton (1967) and Charnov (1982). These and other advances have been documented and developed in the first section of Hardy's book. We also have a section on statistical methods for the analysis of sex ratio data that will be essential for all workers in the area. The genetics of sex ratio and

sex determining mechanisms are considered in the next section, followed by two sections on particular groups of animals, plants and protozoa. A section that covers applications of the theory closes the book.

There are no weak chapters. I found all to be of great interest, although my work in the area of sex ratio is limited. I was impressed by the care of editing and the uniform style. In particular, each has a summary and clear introduction that enables a swift comprehension of the content. It is difficult to pick out any chapter above the others. Throughout, there are clear explanations of theory, methodological approach and some wonderful examples. The ideas of local mate competition, local resource competition and local resource enhancement are simple elegance in the complexities of evolutionary biology. Descriptions of the wasp *Nasonia vitripennis*, in which sib-sib mating occurs, leading to competition between brothers for access to sisters are staples of undergraduate lectures. Females thus produce a large clutch with a strong female bias when eggs are laid on unparasitized hosts, as the additional females will produce more grandchildren and thus offer a higher fitness gain than would 'spare' males. However, these same females produce a small clutch of males when they encounter a previously parasitized host. In the latter case these few males will hatch into a female-biased local population and males offer a greater fitness gain than would females. The adaptive shift in the sex allocation of Seychelles warblers when offspring of one gender may enhance or reduce future success is another fine example. It makes the study of sex ratios the 'jewel in the crown' of evolutionary biology and my undergraduate students are captivated by these studies. This book encourages me to expand this area of my teaching. It collates examples and clarifies theory in a way that should be accessible to students and researchers alike.

There is a sting in the tail, however, with the penultimate chapter by Orzack. He suggests that such is the clarity and elegance of the theory that weak data that are merely consistent with the theory are said to support it, and that data that are contrary to the theory are often ignored. Many of the claims concerning local mate competition, for example, may not stand up to close scrutiny. Indeed wide gaps seem to exist between data and theory when many of us believed that there was close agreement. There is confusion about the mating systems of species that are popularly regarded as examples of sib-sib mating. Furthermore, *Nasonia* may still produce a small number of male offspring when they encounter hosts that have been parasitized by another species although those males will not benefit from a female-biased local population. The final impression is that we now have good theory and that methods of investigation have been vastly improved but what is needed are rigorous tests of the theory. Hardy has brought us up to date with an excellent volume. However, it seems that Darwin is still right about the problem being intricate and that at least some answers are for the future.

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