Aquatic Mammals 2005, *31*(2), 268-270, DOI 10.1578/AM.31.2.2005.268

Book Review

THE BIOLOGY OF TRADITIONS: MODELS AND EVIDENCE. Editors: Dorothy M. Fragaszy and Susan Perry. Cambridge University Press, 2003. ISBN 0-521-81597-5, 456 pp., HBK, B&W figures.

Human culture sets us apart as a species, and the study of analogous phenomena in animals, variously identified as social learning, animal culture, or animal traditions as here, is an exciting, dynamic, and growing area of research. Perhaps the most exciting aspect of this area is as a point of interdisciplinary contact, with anthropologists, sociologists, psychologists, and biologists all having different perspectives. Unfortunately, these perspectives have remained too long trapped in their own "vertical" traditions (passed from generation to generation but without spreading "horizontally" to other disciplines). A current challenge is to bring these perspectives together as much as possible. The editors of this volume have risen to this with some success, bringing together workers from all the major concerned disciplines to produce a stimulating volume that is nonetheless, as the title suggests, firmly rooted in a "biological" (read, evolutionary and ethological) framework. That the cover is graced by a pair of bottlenose dolphins attests to the great strides marine mammalogists have recently made in this area as more and more compelling evidence for traditions continues to be presented; however, as relative newcomers to the field of animal traditions, we have much to learn, and there is much useful material here for anyone considering entering this field.

"Traditions" are defined early on by the editors (Chapter 1) as "enduring behaviour patterns shared among members of a group that depend to a measurable degree on social contributions to individual learning," and it is a concept that most contributors appear to accept. Of course, such phenomena in humans would be called "culture," but to use that word with respect to animals creates a little too much controversy for the editors of this book, who explicitly set out their case for avoiding the term in the introductory chapter. They avoid the "c-word" because it frames the debate in anthropocentric terms (Do animals measure up to us?), which they believe distracts from the underlying biology of the phenomenon. I can sympathise with the position, even if I disagree with the logic. The debate over animal culture is not going away, and the present volume will only fuel it; however, the editors explicitly decide to sidestep it, and so I will do the same here! The editors use the opening chapter to present their agenda for a biological study of traditions, exploring a conceptual "tradition space" that will greatly aid the thinking of anyone new to the topic, and laying out clearly and methodically the kind of evidence that is needed to demonstrate the existence of a tradition from both the experimental and observational perspectives. This latter deserves special attention from field researchers as an appreciation of the limitations of observational evidence is essential to productive field studies of animal traditions.

The style and content of the subsequent 13 principal chapters vary considerably, with some presenting substantial new data or analyses and others providing general overviews of specific areas or topics related to the study of traditions. There is a marked primate bias, with seven chapters devoted specifically to the results of primate studies, and therein lies my only major criticism of the volume. Although the authors have clearly tried for a broad taxonomic approach, they only partially succeed. Fish, for example, make only fleeting appearances, and the vast body of research on social learning in birds, vocal or otherwise, is condensed to just 1½ chapters. The volume has been professionally produced; there are few typographic errors; and the layout is pleasing, with sparing but appropriate use of figures.

There is a notional divide between chapters dealing with more "theoretical" issues and those mostly focused on data, although the divide is not always convincing. Laland & Kendal (Chapter 2) kick-off with a competent overview of what existing theory tells us about traditions. Their discussion is concise and at a conceptual rather than mathematical level, which many will find refreshing. Encouraging more interaction between modellers and data collectors is essential, and Laland and Kendal are right that there has been too little interaction in this field. Simon Reader then used literature surveys to test comparative hypotheses about the evolution of traditions; the results were not always intuitive. For example, there is no support for a relationship between social learning frequency and social group size. Of course, one must keep in mind the "literature-filter" inherent in such work as publication bias can work in unpredictable ways. Equally solid is the chapter

by Lefebvre & Bouchard in which literature surveys are again employed in a comparison of social learning in birds and primates. Their results suggest that while birds are clearly highly innovative, innovations are more likely to be subsequently socially transmitted in primates. This is puzzling because birds are known to be capable of social learning from experimental studies, so why are reports of social learning so rare in the wild? The authors suggested several factors that could productively be tested. Gwen Dewar (Chapter 5) introduced a theoretical framework that seeks to predict social learning based on "cue-reliability." The concept is simple: Individuals should only learn socially when social cues are sufficiently reliable to produce a positive outcome. The power of this framework is its flexibility in potentially explaining a wide range of social learning (or absence thereof). The disadvantage is in the quite detailed data required to input into the modelling; it will only be useful in a subset of cases. Nonetheless, this chapter presents an imaginative and positive contribution to thinking about when animals should learn from others.

In the first "data" chapter, Galef (Chapter 6) reviewed his outstanding contributions to studying social learning in rats, asserting that no case of animal tradition has been as well studied. This is correct, but the concomitant devaluing of other studies is indefensible. The main problem with his perspective is not that it is wrong—he is right that traditions are more easily studied in laboratory rat populations than perhaps any other organism; the problem is that the approach is profoundly uninteresting and, as actually happens in this chapter, liable to hoisting upon its own pedantic petard. Despite 30 years of process-focused research on rat traditions, Galef is forced to admit both that we still do not know which processes "are actually responsible for feeding traditions in free-living populations" and that his research approach is essentially impossible for vast swathes of the animal kingdom, either because of legislative protection, expense, or sheer impracticality. One has to question the utility of a perspective that insists on understanding process before all else but is unable, after decades, to say anything meaningful about processes in the wild. This monolithic perspective is simply outdated and has thankfully been overtaken by more sophisticated and flexible approaches; the loneliness of the furrow is shown by the self-citation rate being nearly double that of most other chapters. Galef also sneaked the culture/not-culture debate under the editorial radar as a tradition/not-tradition argument, based on an entirely untested assumption that human traditions all involve active transmission; we should, he asserts, be sure to refer only to "animal traditions" to remind ourselves of the difference. Thank goodness we have Galef around to make sure we remember that we are actually studying animals!

Having railed so hard, it behooves me to note that a subsequent chapter by Boinski et al. (Chapter 13) proved that some of Galef's warning about naïve attributions of tradition are indeed still necessary as it seems some fieldworkers have still to learn the lessons. Boinski et al. found that brown capuchins in their single study site access fruit through tool-use and claim tradition, despite the fact that the behaviour is both ubiquitous and extremely invariant in that population. There is little here that qualifies as evidence for a tradition, and such claims undermine the hard work of other scientists who are striving to move the field study of traditions forward.

In other chapters of this second section, Visalberghi & Addessi (Chapter 7) presented sophisticated captive studies of capuchin monkeys that illustrate how the role of social learning depends on what is being learned about—it is easier to learn what is good to eat socially than what is not good. Janik & Slater (Chapter 8) provided a review of vocal traditions organised around different kinds of learning about vocal output and highlight that traditional variants may not always be functional and can sometimes be completely arbitrary, while Mann & Sargeant (Chapter 9) raised the cetacean banner by presenting substantial data on foraging specialisations in Shark Bay bottlenose dolphins, among the most compelling of cetacean cases given the known social learning abilities of this species. An interesting perspective was given by Huffman & Hirata (Chapter 10), who use the examples of stone-handling in macaques and leaf medication in African great apes to explore the factors affecting the spread of behavioural variants through three distinct phases—(1) transmission, (2) tradition, and (3) transformation—highlighting that traditions themselves have a kind of ontogeny, beginning with innovation. This is followed by an outstanding chapter by Carel van Schaik (Chapter 11), who presented compelling evidence for traditions in orangutans, taking the wholly sensible stance that field studies are "essential to demonstrate the . . . patterning of behaviour expected for traditions." The work is taken a step further though by considering an "opportunities for social learning" hypothesis, suggesting that "socially tolerant conditions should enhance the likelihood that naïve animals learn skills through some form of social learning." van Schaik then presented some reasonably convincing evidence that this is indeed the case in orangutans and chimpanzees. These considerations are echoed in later chapters when it is noted

that capuchin monkeys are extremely tolerant of others observing their food extraction activities and also show good evidence of traditions in food extraction. Anne Russon (Chapter 12) took a developmental perspective on traditions, noting that as individuals develop, their opportunities and abilities for social learning change, as well as what they need to learn (e.g., a post-weaning juvenile needs to learn how to extract food pretty quickly). She promoted a holistic view of traditions, noting that "immature apes experience a physical world that is selectively used, marked, and shaped by community members." Finally in this section, Susan Perry and colleagues (Chapter 14) presented results from data collected over 11 years on multiple social groups of white-face capuchin at four sites in Costa Rica. This kind of dataset is extremely powerful in identifying traditions, and marine mammalogists should recognise the benefits of pooling results in this way for their own investigations on traditions. Perry et al. highlighted several behaviours, which appear to qualify as traditions, being present in some groups but not in others. Intriguingly, they are all apparently arbitrary forms of interactions between individuals—hand sniffing, sucking of body parts—where the form of the behaviour is apparently less important than the shared participation. Arbitrary behaviour patterns like this are often the easiest to identify as traditional as they are not expected to be strongly influenced by local ecology in the way that feeding traditions would be.

I found this book a fascinating and stimulating read, even with the primate bias. I suspect it will have limited utility in teaching because of the specialised nature of the topic, although higher-level undergraduate and graduate courses could find it appropriate. I feel the primary importance will be to researchers, who either are already or are considering working in this area, as it demonstrates the range of perspectives and the types of data that are useful in studying animal traditions. These are exciting times in the study of marine mammal behaviour, and I sincerely hope this volume will stimulate more research on this fascinating topic in our own field.

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