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## **The Biology of Traditions**

### **Models and Evidence**

Socially maintained behavioral traditions in nonhuman species hold great interest for biologists, anthropologists, and psychologists. This book treats traditions in nonhuman species as biological phenomena that are amenable to the comparative methods of inquiry used in contemporary biology. Chapters in the first section define behavioral traditions and indicate how they can arise in nonhuman species, how widespread they may be, how they may be recognized, and how we can study them. The second part summarizes the latest research programs seeking to identify traditions in diverse taxa, with contributions from leading researchers in this area. The book ends with a comparison and evaluation of the alternative theoretical formulations and their applications presented in the book and makes recommendations for future research building on the most promising evidence and lines of thinking. *The Biology of Traditions* will be essential reading for students and researchers in the fields of anthropology, biology, and psychology.

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# The Biology of Traditions

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Models and Evidence

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In loving memory of my mother and father, Joan and Russ Munkenbeck, and my sister Lynne and brother-in-law Jim Wallace, whose traditions, as well as *joie de vivre*, I try to maintain. *Dorothy M. Fragaszy*

In memory of Guapo, Lomas Barbudal's great innovator, and the other capuchin monkeys whose striking social conventions opened my eyes to the importance of traditions as an exciting research topic. I thank my husband Joe and daughter Kate for their patience as I worked on this project. *Susan Perry*

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## *Preface*

For many decades, the scientific discussion about social learning in nonhuman animals has been dominated by two concerns: (1) whether any nonhuman species, but ape species in particular, possess “culture”, and (2) which nonhuman species exhibit imitation, assumed by many to be a prerequisite or at the least an important support for culture. However, from a biological point of view, these questions only narrowly address fundamental issues about social learning in nonhuman animals. Their link to functional, developmental, and evolutionary questions is not obvious, for example. We wanted to know about these latter topics, as well as more broadly about mechanisms supporting social learning, so we set about asking our colleagues what they thought. We got many answers that we felt were worthy of better dissemination than they were receiving in the literature or in the classroom. This book is the result.

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This book is intended for individuals interested in understanding social learning (the common short-hand phrase for what is more precisely called socially aided learning) in animals from a biological perspective. We focus on one outcome of social learning, traditions, as an element in behavioral ecology. By tradition, we mean a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning. The process of social learning does not lead inevitably to enduring traditions, however. Ultimately, we would like to understand how particular environments, social attributes, and life ways contribute to the appearance and persistence of traditions in particular taxa. Such an understanding will help us to appreciate the contribution of social learning to biology. It will also help us to appreciate the roots of human traditions in the intersection of particular social

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propensities and ecological circumstances in the past and present of our species.

Traditions have long been considered as one element of culture, and the relationships among social learning, traditions, and culture in primates have been hotly debated (e.g., Boesch and Tomasello, 1998; Matsuzawa *et al.*, 2001; McGrew, 1998; van Schaik, Deaner, and Merritt, 1999). Efforts to analyze traditions in nonhuman primates began with studies of Japanese macaques but recently have focused particularly on the great apes, and, more particularly, on a single species in one genus of great apes (the common chimpanzee, *Pan troglodytes*). Collations of findings across the several sites where chimpanzees have been studied for decades have documented many instances of putative traditional behaviors (Boesch and Tomasello, 1998; Whiten *et al.*, 1999, 2001). Unfortunately, the intense focus on a single species, and on a single issue (the degree to which chimpanzees possess “culture”), has restricted discourse about social learning in nonhuman animals in an unhealthy manner. A truly biological understanding of social learning requires broader treatment, both taxonomically and theoretically (cf. Marler, 1996; Kamil, 1998).

The contributors to this volume broaden the playing field for discussions of “culture” in nonhuman animals by considering the evidence for traditions in nonhuman primates alongside the evidence for traditions in two other orders of mammals (rodents and cetaceans) and one other class of vertebrates (birds). The contributions in this volume do not focus exclusively on transmission patterns within one group (the usual focus of experimental social learning studies) nor exclusively on intraspecific variation across groups (the usual focus of observational studies in natural settings), but rather the intersection of the two topics.

In the early chapters (Chs. 1–5) of the book, we highlight theoretical and conceptual issues in the study of traditions, and of social learning in general, in nonhuman species. We begin by presenting an explicitly biological approach to the phenomenon of traditions. We lay out what kinds of empirical evidence are necessary and sufficient to conclude that behavioral variants within or between groups reflect social transmission (i.e., are traditions), and we review the options for obtaining these sorts of evidence from nonhuman animals in common research settings (in nature and in the laboratory). Two contributions review general theoretical models for investigating the circumstances under which individuals are expected to rely on social learning. The authors devote particular attention to considering how these models can be operationalized to make

specific predictions that can be tested in real-world settings: that is, setting the research agenda to make use of the power of general models. Lastly, two contributions examine the relations among relative brain size and the distribution of reports in the peer-reviewed scientific literature about social learning and unusual (innovative) behaviors in nonhuman primates and in birds. In Chapters 6–14, we present empirical evidence for within- and between-group variability that may qualify as traditions in rodents, cetaceans, birds, and primates (Japanese macaques, orangutans, chimpanzees, and capuchin monkeys). The contributions span laboratory and field studies and include a wide spectrum of interests and methodological approaches. Three chapters concern capuchin monkeys, a genus of special interest to the editors of this volume, and one which we believe will be very rewarding to study in this regard. In the concluding chapter, we highlight the shared viewpoints and findings presented by the contributors to build a picture of the state of the science in this area. Then we consider how most productively to test theoretical models and point out some areas where we think critical thinking is needed to make headway in this area of science. We intend that our readers will come away from this book with a richly synthetic appreciation of social learning and of traditions as potential outcomes of social learning. We also want our readers to appreciate that traditions in nonhuman animals have important implications for biology, including evolution and ecology. We will have succeeded if our efforts inspire vigorous and rigorous examination and refinement of this view of traditions.

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