

**John C. Mitani, Josep Call, Peter M. Kappeler,
Ryne A. Palombit, Joan B. Silk (eds):
The Evolution of Primate Societies**

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Twenty-five years have passed since the publication of *Primate Societies* (Smuts *et al.* 1987). In that time primatology has changed a great deal in its theoretical underpinnings, its technical possibilities and methods, the nature and extent of its empirical scope, and sadly, in the status of its subjects in the wild. Intended as a follow-up synthesis of the field, *The Evolution of Primate Societies* aims to provide an integrated overview of the state of play in primatology. With 32 extensive chapters written by many of primatology's most established authorities, we should start by saying that this book really is a tome, and we doff our collective caps to the editors. Putting this together was clearly no small effort, and our field owes them a great debt for their dedication and service.

The book is organized in five “parts.” These represent an overview of the primate order (Part 1, titled: “Primate Behavioral Diversity”), survival and development (Part 2, titled: “Surviving and Growing Up in a Difficult and Dangerous World”), reproduction (Part 3, titled: “Mating and Rearing Offspring”), sociality (Part 4, titled: “Getting Along”), and cognition (Part 5, titled: “Cognitive Strategies for Coping with Life’s

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Challenges”). After a Foreword by Richard Wrangham, and both a Preface and an introductory chapter from the editors, Part 1 consists of five chapters summarizing different primate taxonomic groups, while Parts 2–5 each consist of multiple chapters on nonhuman primates before a final chapter that covers human issues in the appropriate area. We will briefly review each part in turn.

Chapters in Part 1 helpfully have the same macrostructure (Diversity and Biogeography; Ecology and Life History; Evolution of Social Systems, and Summary and Conclusion). Part 1 begins with a thorough and detailed overview of the behavioral ecology of strepsirrhines and tarsiers (Chapter 2: Kappeler). When it comes to social structure, the author explicitly focuses on group-living lemurs given the poorly understood nature of nocturnal strepsirrhine and tarsier social systems, which highlights the need for further work in these areas. Chapter 3 (Fernandez-Duque, Di Fiore, and Huck) discusses New World monkeys and nicely summarizes the extent of new data on platyrrhines since Smuts *et al.* (1987), which includes big advancements in our understanding of molecular phylogeny and taxonomy and the diversity of social systems. Chapter 4 (Sterck) covers colobines, especially considering their role in helping us to develop current theories of socioecology and the selective pressures that structure primate social organization and style. Chapter 5 (Cords) is a comprehensive review of cercopithecines that draws attention to areas in need of further exploration. Chapter 6 (Watts) reviews the many detailed studies of apes. Owing to the number and range of field studies of species such as chimpanzees, there is a particularly rich dataset to describe and perhaps here more than anywhere do we get the impression of the extent of intraspecific variation among primate species. All Part 1 chapters provide a great deal of useful background information, and the authors make a good effort to be evenhanded with the treatment of different species. Inevitably when trying to review so many subject areas, species, and studies in one short piece, the chapters make some generalizations across species and populations, but they make excellent introductory starting points for further reading. The fact that strepsirrhines, tarsiers, and platyrrhines get only two chapters between them, while colobines, cercopithecines, and apes get a chapter each, is unfortunate, but probably does reflect the taxonomic bias of the literature.

Part 2 of the book focuses on survival and development. Chapter 7 (Chapman, Rothman, and Lambert) begins by describing primate nutritional requirements, foods, and digestive strategies, and then discusses three key research areas in primate foraging ecology: how foraging affects primate: 1) ecology and distribution, 2) movement, and 3) social organization. The chapter features a critical consideration of two frequently used terms in primate ecology: keystone and fallback foods, rejecting the long-held view that figs are keystone foods in tropical forest environments, while pointing out that fallback foods tend to be classes of foods rather than any particular species or food part. Chapter 8 (Fitchel) examines predation and features excellent resources including a comprehensive table covering observed primate predators. The author emphasizes perception in the role of different sensory modalities in detecting primates, noting that olfactory cues (as usual) have been neglected. Similarly, predation on nocturnal primates has been relatively little studied. Chapter 9 (Schülke and Ostner) gives an overview of socioecological theory and contains helpful definitions of terms such as social organization, social structure, and mating system, before covering ecological effects on these areas. Usefully, the authors cover research on nocturnal primate socioecology. The authors critique the “phylogenetic constraints” criticisms of the

socioecological model and call for the model to be expanded and evaluated with more empirical data. In Chapter 10 van Schaik and Isler address primate life history by first placing primates in the context of mammals and then by examining their life histories as they relate to ecology and behavior and, in an extensive final section, to brain size. Chapter 11 (Lonsdorf and Ross) covers development and discusses the extended pre-reproductive period in primates, including a comprehensive section on mother–infant relationships and mothering styles. In Chapter 12, Di Fiore examines the relationship between primate social systems and genetic structure, discussing why the relationship is important and emphasizing its role in testing many of our most foundational hypotheses. The chapter features a very useful summary of molecular studies of dispersal in wild primates and a discussion of important and developing issues in this area. Chapter 13 (Gurven) is the first of four chapters devoted to humans, meant to link nonhuman and human primate research by theme. Gurven refers back to Chapters 7 (diet), 8 (predation), 10 (life history), and 11 (development) but mainly presents studies of human behavioral ecology. This is a good review of this area, though further natural links between human and nonhuman primate research on life history, survival, and development could potentially have been highlighted. Overall, Part 2 is a comprehensive review of different areas related to processes of natural selection.

Part 3 comprises chapters on reproduction. It begins with Chapter 14, in which van Noordwijk thoroughly reviews maternal investment in the context of parental investment theory and parent–offspring conflict, with an interesting section on seasonality of reproduction and the income–capital breeding continuum. In Chapter 15, Pusey focuses on variation in female reproductive performance, citing data largely from long-term studies of catarrhines. The chapter features extremely useful tables summarizing effects of both age and dominance (separately) on female reproductive rates. Chapter 16 (Kappeler) focuses on mate choice, presenting theoretical arguments on why mate choice may be rare in primates and, conversely, why it may be common. The author focuses on female mate choice (which theory predicts should be much more frequent), considering the types of direct and indirect benefits for which females might select males, and the mechanisms by which they might do so, before finishing with a discussion of the evidence for male mate choice and its inherent costs. Chapter 17 (Muller and Emery Thompson) considers male parenting and reproductive strategies, beginning with an extended discussion of paternal care and a very valuable summary table of studies that have documented direct paternal care. The chapter then goes on to discuss male reproductive strategies in detail, covering everything from ornaments to canine dimorphism and alternative tactics. Chapter 18 (Alberts) discusses variation in male reproductive performance, with an interesting discussion of how it might be measured, and lengthy consideration of the effects of factors such as longevity (where few data are available) and differences in infant survival. In Chapter 20, Palombit discusses infanticide, including adaptive theories for its evolution. The evidence for infanticide in primates, and evidence for counterstrategies in females, are considered at length, and there are two particularly extensive tables that summarize the available data for both these phenomena. The section on reproduction closes with a chapter on humans (Chapter 21, Marlowe), which covers topics including human mate choice, ovulatory signaling, sexual division of labor, and parental investment. Taken as a whole, Part 3 is an extensive overview of primate reproduction. Some chapters feature overlap (e.g., sexual swellings and paternal care of infants are discussed in more than one

chapter), but the topics covered are diverse, and the authors include examples from throughout the primate order.

Part 4 deals with sociality in primates, emphasizing cooperation (with the part titled “Getting Along”). In Chapter 21, Langergraber provides a systematic review of the evidence for cooperation among kin, with most cited examples coming from anthropoids. In Chapter 22, Gilby does the same for cooperation among non kin, discussing mechanisms such as biological markets, contingent reciprocity, and mutualism before concluding that no single mechanism can explain the observed variation in primate cooperative behavior. In Chapter 23 (Aureli, Fraser, Schaffner, and Schino), the authors discuss the formation and regulation of social relationships, covering topics such as affiliation, aggression, and postconflict mechanisms such as reconciliation. Their approach is based on a perspective developed from earlier work by Hinde (e.g., 1979) on description and Kummer (1978) on function, while integrating the proximate mechanisms of emotion. In Chapter 24, Silk summarizes the associations between group size, brain size, and the presence or absence of social cognitive abilities, and then reviews recent studies on the effects of group sizes and structures on fitness. As the author notes, the evidence for sociality’s effect on fitness comes almost exclusively from a few species of Papionins, and data from a wider range of species are needed to evaluate this potential link across the Primates. Chapters 23 and 24 both present frameworks that should aid future researchers in describing the maintenance and character of social relationships, respectively. In Chapter 25, Jensen considers the psychological adaptations that may underpin cooperation, discussing concepts such as social regard, including a three-page table summarizing all experimental primate studies that have researched this phenomenon. Much of this chapter focuses on approaches from experimental psychology and cognition, making this a natural link toward the next section of the book on cognition. Finally, Chapter 26 (Alvard) reviews studies of human sociality. This chapter includes extensive discussion of concepts of cultural group selection in human societies, with the author arguing that cultural group selection does not suffer from many of the theoretical problems that may characterize genetic group selection and that the exceptional life history of humans creates a number of unique selection pressures to consider. Overall, Part 4 is a coherent and well-structured summary of research into primate social behavior.

Part 5 is on the topic of cognition and begins with Chapter 27 (Menzel), which reviews cognitive adaptations for solving ecological problems, presenting both wild and captive data that assess the abilities of primates to develop spatial maps for finding food and coordinating movement. A number of other cognitive adaptations for obtaining food (e.g., tool use), not considered in depth in other chapters, might have best fit into this chapter. Chapter 28 (Seyfarth and Cheney) focuses on the social intelligence hypothesis and social cognition with a large part of the chapter devoted to reviewing the ways in which nonhuman primates recognize and use social relationships. Here, the authors acknowledge alternative interpretations of data while at the same time making a persuasive case for their own perspective. Chapter 29 (Zuberbühler) discusses primate communication in the three main signaling modalities: olfaction, vision, and audition. The sections on the latter two modalities usefully adopt the same structure, which helps to enable easy comparison. The focus on visual signals here is on flexible signals that are decisions of the individual rather than morphological signals, with the section on vision exclusively considering gestural communication

rather than discussing well-studied morphological visual signals such as sexual swellings. Chapter 30 (Call and Santos) examines the evidence for the ability of nonhuman primates to understand the mental states of others, focusing on results from lab studies, which the authors argue are likely to be less familiar to primatologists than field studies. Overall this chapter presents the controversial evidence on primate minds in a balanced way with regard to the different potential interpretation of results. Chapter 31 (Whiten) addresses nonhuman primate culture and social learning mechanisms, with the author arguing that the study of culture should not be separated from the rest of biology, while discussing studies from a range of primate species. As is often the case, the author notes that we have barely scratched the surface of primate social learning and culture. Given that the first two papers ever published in a primatology journal were on this topic (Imanishi 1957; Yamada 1957), this is a somewhat depressing thought! Finally, Chapter 32 (Herrmann and Tomasello) reviews human cognitive processes, primarily covering the similarities and differences between humans and other primates (usually chimpanzees) and studies on the evolution of human social cognitive abilities. The authors argue that humans do not differ much from other great apes in the basic cognitive skills used to deal with the physical world, but that we are set apart by our “cultural intelligence.” Overall, Part 5 is a very useful summary of the literature on primate cognition, though many chapters do rely heavily on evidence from chimpanzees and a few other catarrhines (all but one of the chapters have a first author who studies chimpanzees as one of his/her main study species), and several chapters might have benefited from broader comparative perspectives.

Some potential criticisms of the book could include that, on the whole, not much extra-primate literature is cited. Some years after calls for better integration of primatology into the wider animal behavior literature (Harcourt 1998), this is still something where collectively as a field we might do more. The absence of a section on conservation might also irk some, but given that this is a book about primate sociality, this seems to make sense. On the whole, the structure of the book flows nicely, though the chapters on humans (although an extremely laudable idea) can sometimes feel disconnected from the overall thread. Nonetheless, *The Evolution of Primate Societies* is a must have: many chapters feature extremely valuable and comprehensive tables packed with information and references that should be very useful to junior and senior researchers alike. Moreover, in an age in which primatology books can often seem extortionately priced, softcover copies of the book are widely available for around \$40, making this an essential and affordable purchase.

It seems apt to finish by wondering where we might be in another 25 years. Will we have made the same range of technological advances as in the previous 25 years, and will we be able to study our subjects with ever increasing detail and sophistication? What will such methods reveal about primate sociality, dispersal, communication, and other key elements of primate lives? What new primate species might be discovered (e.g., Lesula: Hart *et al.* 2012), and how might this impact our understanding of primate diversity and biogeography? Will we be able to start slowing the decline of wild primate species and stabilize their populations? Though the challenges ahead for primatologists are daunting, many of them are also extremely exciting. While writing their chapters, the authors of *The Evolution of Primate Societies* were fortunate to have the legacy of *Primate Societies* and all that has come since to build upon. So too will the next generation of primatologists have *The Evolution of Primate Societies* to guide

them in the future, as they seek to understand our fellow primates, and protect them from the overwhelming forces that threaten their survival.

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