

Preface

When the renowned fossil hunter Louis Leakey arranged for Jane Goodall to begin her field study of wild chimpanzees in East Africa, he hoped that her observations would shed light on the evolution of human ancestors. In the nearly six decades since, chimpanzees have become the most studied nonhuman mammal species in the wild and our primary model for thinking about how the last common ancestor of chimpanzees and humans may have behaved.¹ The list of intriguing discoveries about these African apes is long and still growing: wild chimpanzees are prodigious tool users, they form and manipulate coalitions to achieve social status, they hunt in groups for large mammal prey, they occasionally kill their neighbors, and they exhibit persistent group-level differences that are reminiscent of human cultural variation, to name a few of their most notable features. Revelations such as these offer important clues about the early stages of an evolutionary voyage that would lead to modern *Homo sapiens*, the most intelligent and socially complex animal in the history of life.

How sobering, then, to contemplate that these intelligent and socially complex apes, our closest relatives in the animal kingdom, are poised for extinction in their natural habitat. Chimpanzees form large, mixed-sex groups, or "communities," that aggressively defend extensive feeding territories where they find the ripe fruits that constitute the mainstay of their diet. When they reach sexual maturity, females typically disperse from these groups to breed in neighboring communities. In order for genetically viable populations to thrive, therefore, chimpanzees require intact forest areas that encompass multiple contiguous territories between which females can move. Habitat loss and fragmentation inevitably have devastating effects on chimpanzee populations, reducing food supplies, constricting mating

opportunities, and forcing lethally antagonistic groups either into close contact with one another or into fringe habitats where they have access to only remnant patches of forest. Since the equatorial African rain forests on which chimpanzees rely continue to be harvested for timber and cleared for agriculture, their survival prospects are truly grim.²

Long-term research projects play a key role in chimpanzee conservation efforts. Protecting chimpanzee populations relies partly on having detailed and comprehensive information about their social behavior, their ecological requirements, and the limits of their social and ecological flexibility. Since chimpanzees are long-lived animals and tropical forest habitats vary greatly and change over time, this necessitates the establishment and maintenance of decades-long field studies. These studies involve numerous researchers, students, and field assistants monitoring known individuals across as many generations and in as many habitats as possible. Long-term projects also include natural scientists studying a wide range of topics in forest and community ecology, and sometimes social scientists exploring aspects of animal-human conflict, land history, and government policy. This interdisciplinary collaboration is essential for establishing successful forest preservation and management guidelines and for developing policies and practices that promote the coexistence of chimpanzees and the human neighbors with whom they periodically come into contact.

Long-term field projects also provide key conservation services beyond generating behavioral and ecological data.³ The sustained presence of research staff in a forest deters encroachment and poaching by people from surrounding areas. Successful projects can employ dozens of local workers, providing an economic alternative to extracting forest resources. At the same time, researchers have the opportunity to collaborate with local people and, ideally, arrive at a mutual understanding of conservation goals and practices. Local field assistants and staff often develop more sympathetic attitudes toward forests and wildlife and share these attitudes with their communities. Researchers can educate themselves about community needs and historical land use patterns, an understanding of which can be critical to developing sustainable conservation schemes. Finally, scientific findings generate descriptions of chimpanzee social life that capture public attention, inspire students to pursue research, and attract donor support and tourist dollars. All in all, long-term field projects now constitute a bedrock component of chimpanzee conservation work.

This book provides an up-to-date synthesis of research on chimpanzee social behavior documented primarily from the seven field projects where it has been possible to monitor known individuals the most continuously for the longest time. Studies at these locations have been ongoing for more than twenty-five years; at two, research has been conducted with few interruptions since the 1960s, and at a few sites it has been possible at times to monitor neighboring communities simultaneously. These projects have collectively produced a rich picture of chimpanzee social life in the wild, based on hundreds of thousands of hours of observation by hundreds of researchers, and they continue to generate a steady flow of new data and surprises on this extraordinary species. There are also several other sites where wild chimpanzees have been fully habituated to the presence of researchers and can be followed at close range throughout the day. Relevant results from these projects are mentioned sporadically throughout, particularly when they reveal behavioral and technological diversity.

My goal is to provide a concise overview of wild chimpanzee behavior that is accessible to specialists and nonspecialists alike. I have therefore elected to keep the body of the text comparatively brief and to put citations, data, and supplementary information in endnotes. The number of scientific publications on chimpanzees is vast, and it is often difficult to keep track of which results come from which sites, what behaviors have been documented in all populations, and what questions remain to be examined in which communities. Therefore, where multiple studies on a specific topic are referenced, I list the studies in the endnotes by field site and always in the order that the long-term projects were initially established, i.e., Gombe studies first, then Mahale studies, and so on. In this way, it is immediately clear where the most work has been done and where information is lacking. For those interested in more detailed descriptions of particular chimpanzee communities, excellent volumes are available that document research on specific populations.⁴ Likewise, readers can consult additional sources for descriptions of a second species of chimpanzee, the bonobo (*Pan pansicus*).⁵

I devote comparatively little attention to studies of captive chimpanzees, the literature for which is also vast and would require a book-length manuscript of its own to summarize. Behavioral research on captive chimpanzees, including widely publicized efforts to teach them rudimentary aspects of language, has contributed greatly to our understanding of chimpanzee cognition.⁶ In addition, with the establishment of large groups housed in naturalistic conditions, researchers

have been able to explore key aspects of development, the formation and maintenance of social relationships, and coalitionary behavior.⁷ Nevertheless, although studies in captivity have the advantage of affording reliable observation conditions, their utility for exploring the evolution of species-typical behavior patterns is handicapped by the fact that captive animals are inevitably influenced by human contact and rearing conditions. Although at times I draw on insights gained from the study of artificially housed chimpanzees, for captivity often reveals the enormous behavioral potential of animals,⁸ my focus is on behavior under natural conditions.

The book begins with an overview of the primates, situating chimpanzees within the order and describing the behaviors that researchers define and measure to quantify primate social behavior. This is followed in Chapter 2 by brief descriptions of the seven long-term field studies that have generated the most detailed information about chimpanzee social behavior in the wild. Nine subsequent chapters summarize well-researched areas of behavior, together constituting a coherent picture of chimpanzee social life in the wild across much of the species range. Results of studies on each behavior type are presented for each field site, to reveal both species-specific trends as well as inter-site variability. The Epilogue offers some final thoughts on chimpanzee conservation and the relevance of long-term field research. Lastly, the Appendix provides a brief description of field methodology for readers unfamiliar with animal behavior research in general and chimpanzee field research in particular.

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Finally, teaching keeps me in touch with the fascination that drew me to the study of chimpanzees, and reminds me constantly of how transporting it is to track and observe them in the wild. With the pressure to publish scientific papers on exceedingly narrow topics, it is easy to forget the quiet sense of wonder that permeates even the most rigorous days collecting field data. I am indebted to my undergraduate students for inspiring me to attempt a synthesis of wild chimpanzee behavioral research that would offer readers the opportunity to enter into the astonishingly complex social world of these intelligent apes and to reflect on the differences that make humans so unique.