



# The NONHUMAN PRIMATES

Phyllis Dolhinow & Agustín Fuentes



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*To all those we study, may they prosper  
and survive long into the future.*

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## Preface

Primatology, the study of primate behavior, ecology, and biology, is a large and ever-growing discipline. No one book can hope to cover more than a modest portion of all the topics and species of nonhuman primates investigated by people in many fields. We invited a broad range of expert researchers to write essays specifically for this book that would provide an introduction to the nonhuman primates: their past, present, and future. By bringing together this array of experts in one volume, we hope to offer a cutting edge overview of our closest relatives: the prosimians, monkeys, and apes.

We have much in common with these mammals because of our shared evolutionary history. We also share this planet and, as a result, to an alarming extent we control their future. If we learn to appreciate the nature, value, and richness of their lives, perhaps we will take care to ensure their continued survival. Some of them, those closest to us, can be of great usefulness in helping us reconstruct aspects of our past adaptations and behavior. They can also offer us an important set of comparisons as we investigate our present patterns of life.

## ORGANIZATION

The book is divided into two parts. Part 1, "The Nonhuman Primates," describes who they are, where they live, and how well or precariously they are surviving in their present habitats. The first section of Part 1 discusses primate diversity, taxonomy, and phylogeny. Our approach throughout the book is an evolutionary one, and to illustrate this point of view we present a model system for the study of adaptation at the molecular level. The next sections introduce and describe representative nonhuman primates, starting with apes, then Old World monkeys, New World monkeys, and finally, prosimians. Because a particular species is omitted does not indicate that it has not been studied or that it is in any way less important than another species that has been included. In an introductory text one is forced to make choices due to space limitations. In some instances we have selected primates because the studies on them are very recent or the work is ongoing and steadily adding new information to what we know of primates. The final section of Part 1, "Primate Conservation," addresses vitally important issues of survival for the living nonhuman primates. These essays

cover the primate status in Asia, a case study of the impact humans have on a species of macaque monkey, and the use of translocation and rehabilitation as conservation tools.

Part 2, “The Realm of Primate Behavior,” introduces the reader to the study of different aspects of primate behavior from the evolution of social organization to reconstructing the behavior of our ape ancestors. In addition, special topics of social behavior such as aggression, reproduction, kinship, social dominance, communication, and aging are investigated in some detail. These are the essays that will provide a view of what life is really like for a prosimian, a monkey, or an ape. The distinctive biology of each kind of primate is used as the basis for understanding the dimensions of its social experience. The section concludes with a review of part of the history of primate studies to show the reader how much influence the investigators’ training and interests have on their work. The last essay illustrates some of the important roles primates have played in many aspects of human culture.

## FEATURES

Several key features distinguish this introduction to primates:

- *A flexible organization.* The sequencing of the essays can be rearranged easily to suit the structure of the course, whether it be by topic or by taxa. Essays address issues and examples that will hold the interest of beginning students, and primate taxa are introduced in a complete section. Some may find it convenient to start with the individual primate species and then move to their evolution and questions of conservation. Other sequences could work equally well because no section requires another as background. A topical table of contents suggests various ways in which each essay may be used to illustrate topics ranging from behavioral ecology to conservation and evolution.
- *Currency and breadth of coverage.* Because the contents of this book are derived from recent or ongoing studies, the essays will be of interest to readers with diverse backgrounds in primatology or animal behavior, as well as to the reader who is being introduced to the field. By mixing paradigms, styles, and levels of analysis, this collection reflects the growth and diversification of the field of primate studies.
- *Abundant pedagogical support.* To help students better comprehend what they read, this collection includes illustrations; worldwide distribution maps of the primates; an index; an extensive bibliography; part and article introductions; and a 16-page, full-color portfolio of primates. The glossary provides definitions of terms that appear in individual essays and offers additional information. Readers wanting to know more about specific kinds of nonhuman primates not discussed in this book are encouraged to follow Suggested Readings offered at the end of the book. This list of supplementary readings is included to assist in locating related information about species and topics introduced in each essay.

The published results of modern primate studies are scattered widely in the literature—often in very specialized and highly technical journals and books. This text presents current views and information in a manner reflective of the variety of perspectives and approaches that characterize modern primate studies. Our purpose in putting together this selection of leading research is to provide all who are interested in and fascinated by primate behavior with a well-rounded sample of information that is new and exciting.

## ACKNOWLEDGMENTS

We wish to express our thanks and appreciation to all those at Mayfield who helped make this book possible. Jan Beatty, our sponsoring editor, translated our early conversations and perceived needs into a real project, allowing, encouraging, and guiding us the entire way. Her understanding of anthropology and its relatedness to the behavior of all primates made our volume a reality. Linda Ward, our production editor, guided us step by step through the maze that ended in the book and did so with patience, good humor, and diplomacy. Kay Mikel, our copy editor, translated our verbiage into Standard English with helpful nudges and consistent effort. And, to the many other people that make up the Mayfield team, we give our sincere thanks.

We thank our colleagues Mark Taff, Robert Sussman, and many others for their generous sharing of ideas. Many disciplines and backgrounds are represented as well as differing points of view. We're especially grateful to the following reviewers of the manuscript: James M. Calcagno, Loyola University Chicago; Laurie Godfrey, University of Massachusetts; Deborah J. Overdorff, University of Texas, Austin; R. W. Sussman, Washington University; and Linda D. Wolfe, East Carolina University.

This set of essays would not have taken its present shape without the tremendously important stimulus of our students over the years. Their interests and questions about the nonhuman primates have helped structure the design of this book. Students at both University of California, Berkeley, and Central Washington University played an important role in its production. Katie MacKinnon, Erin Gemienhart, and Professor Fuentes's Spring 1998 primate behavior class are among them. Elsworth Ray, Allisa Carter, and Melissa Panger, contributors to the book, also helped in other ways. Penelope Anderson of Central Washington University provided excellent secretarial assistance.

Phyllis Dolhinow is grateful for the encouragement and support of Jack and Becky and appreciates the diversion provided by a miscellaneous group of non-primates. Agustín Fuentes thanks his parents, Elizabeth and Victor, his family in Espana and the United States, his partner Devi Snively, and Audrey the wonderdog for support and inspiration. Agustín Fuentes especially thanks Phyllis Dolhinow for being a friend and mentor.

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# Introduction

The field of primate studies has escalated in size and scope at an exponential rate since its inception in the early part of the twentieth century. The initial focus on a few field observations in Africa, Asia, and Central America and ethological investigations with captive apes has grown to encompass field and captive research of more than one hundred species at locations across the globe (see Fedigan and Strum for a historical review, Essay 33). The breadth of modern primate studies encompasses specializations that include ecology, genetics, physiology, neuroanatomy, biomechanics, and behavioral ecology/socioecology. This rapid growth has made it impossible for texts and overviews of the field to keep pace without an annual edition, and even then several volumes would be required.

Having acknowledged the impossibility of doing justice to all that is happening in modern primatology, we have elected to rely on the power of sampling to produce a small survey of what we know and think about the nonhuman primates at the end of the twentieth century. We have been delighted with the generosity of good advice and enthusiasm from our colleagues and contributors—each of whom is an expert in his or her own area. However, we offer the usual caveat and take full responsibility for omissions and commissions in this volume. Far more has been left out than has been included; dozens of volumes are possible.

The prodigious growth in information on many primate species in numerous locations has simultaneously aided and complicated our efforts to understand those that share our order. In our search for generalizations the untidy nature of the facts often defies organization into easy, manageable categories. It was a far simpler task when we knew far less. As we study more primates for longer periods of time, and in different locations, our conception of normal or usual is stretched further and further to include substantial variability even within a single species. We have tapped an enormous diversity of behavioral and ecological patterns. Although we persist in our attempts to analyze and generalize, we are faced with an ever increasing challenge to identify the genesis of diversity, to place it within ecological and evolutionary contexts.

In these essays the contributors present a view through a small window into the fascinating world of nonhuman primates—incomplete, to be certain, but representative. There is considerable variation in emphasis and theoretical position among the contributors, and as a result, you can expect an occasional contradiction in conclusions. All, however, seek to understand primate behavior

using the tools at their command. A diversity of academic backgrounds (for example, anthropology, biology, psychology, zoology, animal and human medicine, mathematics, and linguistics) and diverse theoretical orientations both contribute to the strength of the field of primatology. The contributors to this volume include a fair sampling of academic training and technology, of biases and beliefs.

The book has been organized in parts to incorporate the wide variety of viewpoints and the differing fields of emphasis within the study of nonhuman primates. The essays are succinct and readable and avoid discipline-specific jargon. The essays sample a wide array of primate field studies—some complete, some in progress, others just beginning. By introducing our subjects we hope to fire the imagination that will drive future studies. We are at a complex intersection in our study and understanding of primate behavior. New techniques of investigation and insights into the causes and effects of behavior are increasing our comprehension of what we see and measure.

We begin with a brief overview of the primates—who they are and when they came into being. This sample of primate evolutionary history sets the stage for a discussion of the modern primates. What we see today does not exist merely in the present but is part of a long and well-documented history. Relationships between the living primates present us with a family picture of the primate order, a cluster of taxonomically and phylogenetically related groups.

With a background in primate evolution as a means of introduction to the order, we turn to the major divisions of living primates. There are many more prosimians and monkeys than are presented here, but these essays represent a range of ecological adaptations, behaviors, and lifeways. It is a sample—not random but deliberately chosen—that illustrates major geographical areas and well-studied species. Familiarity with the general ecology and behavior of these taxa will assist your understanding of the specific behaviors and physiological systems presented in the final part of the book.

After introducing the living nonhuman primates, we focus attention on the ever increasing serious threat to their very existence on this planet. The human primate is responsible for the loss or degradation of a multitude of habitats in which nonhuman primates cling to life. No scientist or even the casual observer or tourist can ignore the fact that the world's major primate habitats are shrinking at an alarming rate. If we are to continue to coexist, enjoy, and study prosimians, monkeys, and apes, we must move to conserve them. To do less will be to lose them forever.

Part 2, the realm of primate behavior, begins with an essay on general attributes of behavior and is followed by five groups of related essays. The different primates introduced and described in Part 1 provide a background for the special topics of behavior selected for discussion in each of the five sections. Evolution is a key concept for the first group of essays as we look closely at the broad arena of variable social organizations and then at specific patterns of behavior. Being our closest living relatives, the nonhuman primates serve as models for the reconstruction of the history of our own behavior.

The next section, on group living, concerns two central aspects of social life—kinship and social hierarchies—that are critical to our entire conception of

social life, for us as well as for them. Development, the life cycle, physiology, and anatomy provide the structure of the next group of essays. It is easy to overlook the fact that much of behavior results from and is facilitated by the physical structure of our bodies. To identify primate abilities and limitations, we must look closely at their capabilities and the environments in which they exist. These essays deal with specific cases and reflect the complex and engaging realities of the primate body.

From development and the body we move to the primate mind. The latter is no less critical to existence than is the body; indeed, they are inseparable. Primates are considered a relatively intelligent set of animals, and studies of cognition and language lend support to this evaluation. Finally, the last two essays provide us with an overview of the history of primatology and the place of our subjects in literature, art, and history. It is extremely important to appreciate how much the training and biases of the people who study a subject affect the results of their study. Just as evolution itself is a product as much of chance as any other factor, so too are the disciplines that produced the information on which this and all primate essays are based. It is fascinating to examine the focus and motivation of primate researchers. As to the pervasive and widespread place of primates in culture, this might surprise some of you. Our cousins have provided us with a panoply of gratifications, food for thought, and insights on the nature of life.

What would we like you to get from this book? Our goal is to provide an introduction to the nonhuman primates and to illustrate elements of their fascinating and complex social lives. You will learn who the primates are, where they live, and how they behave. You should come away with a feeling of what living in a group entails as well as an understanding of the evolutionary pressures and pathways that have shaped modern primate behavior. Finally, through general overviews and specific discussions alike, you will have the opportunity to discover the ordinary activities of their day-to-day existence. This is truly an exciting time to be studying the nonhuman primates. The field itself is a work in progress.





## P A R T 1

# The Nonhuman Primates: Who Are They, Where Are They, and How Are They Doing?

Part 1 of this book is divided into three sections: **taxonomy** and **phylogeny**, the living primates, and case studies of primate conservation. This effectively represents the past, the present, and the future of our **order**. We can see where we began and trace our route to where we are at present. Finally, we must become aware of the many challenges that exist today if we are to assure that all living primate species will continue into the future.

Essay 1 provides a historical or evolutionary background for the consideration of individual species in Essays 4–15. Sixty million years of change has produced the array of forms we study today. An understanding of the phylogenetic relatedness of primates provides guidelines for interpreting their current adaptations. Our understanding of the distribution, behavior, and ecology of living primates is enriched by knowing their place of origin and their evolutionary history. Essays 1, 2, and 3 outline the evolutionary history and genetic relationships of the primates as a basis for our overview of select living primate groups.

The next set of essays presents the results of field studies of a sizable (yet far from complete) sampling of the more than two hundred species of living nonhuman primates. These essays are divided into four sections with each section presenting examples from one of the four major divisions of the order Primates: apes, Old World monkeys, New World monkeys, and prosimians. Each section is preceded by a brief overview outlining the major subdivisions and groupings in the lineage and including general behaviors and ecological information. Many additional kinds of primates have been well studied in the field and in captivity, and it is only because of limited space that so few are presented here.

The final set of essays in Part 1 presents accounts of the conservation status of many primates and the often grim reality of the struggle for survival of some nonhuman primates. Many more could have been added to this short overview, but even this brief survey clearly illustrates the major issues confronting both human and nonhuman primates in a competition for living space and survival. Humans have changed the face of the planet, and adaptations that ensured survival in past times no longer guarantee life today. Knowledge is power. We can serve our close relatives well and ensure their continued presence and health if we attend to what we know to be their needs in concert with our own.