PRIMATE BEHAVIORAL ECOLOGY

SIXTH EDITION

Karen B. Strier

Primate Behavioral Ecology

This comprehensive introductory text integrates evolutionary, ecological, and demographic perspectives with new results from field studies and contemporary noninvasive molecular and hormonal techniques to understand how different primates behave and the significance of these insights for primate conservation. Each chapter is organized around the major research themes in the field, with Strier emphasizing the interplay between theory, observations, and conservation issues. Examples are drawn from the "classic" primate field studies as well as more recent studies, including many previously neglected species, to illustrate the vast behavioral variation that exists across the primate order. *Primate Behavioral Ecology 6th Edition* integrates the impacts of anthropogenic activities on primate populations, including zoonotic disease and climate change, and considers the importance of behavioral flexibility for primate conservation. This fully updated new edition brings exciting new methods, theoretical perspectives, and discoveries together to provide an incomparable overview of the field of primate behavioral ecology and its applications to primate conservation. It is considered to be a "must read" for all students interested in primates.

Karen B. Strier is a Vilas Research Professor and the Irven DeVore Professor of Anthropology and an Affiliate Professor of Integrated Biology at the University of Wisconsin-Madison, where she has been teaching since 1989. Her main research interests are to understand the behavioral ecology of primates from a comparative perspective, and to contribute to conservation efforts on their behalf.

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Taylor & Francis Group
http://taylorandfrancis.com

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Sixth Edition

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Routledge
Taylor & Francis Group
LONDON AND NEW YORK

Sixth edition published 2021 by Routledge
2 Park Square, Milton Park, Abingdon, Oxon OX14 4RN

and by Routledge
605 Third Avenue, New York, NY 10158

Routledge is an imprint of the Taylor & Francis Group, an informa business

First edition published by Pearson Prentice Hall 2000
Fifth edition published by Routledge 2017

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library

Library of Congress Cataloging-in-Publication Data
Names: Strier, Karen B, author.
Title: Primate behavioral ecology / Karen B. Strier.
Description: Sixth edition. | Abingdon, Oxon ; New York, NY : Routledge, 2021. | Includes bibliographical references and index.
Identifiers: LCCN 2020043958 (print) | LCCN 2020043959 (ebook) | ISBN 9780367222864 (hardback) | ISBN 9780367222888 (paperback) | ISBN 9780429274275 (ebook)
Subjects: LCSH: Primates--Behavior. | Primates--Ecology.
Classification: LCC QL737.P9 S764 2021 (print) | LCC QL737.P9 (ebook) | DDC 599.815--dc23
LC record available at https://lccn.loc.gov/2020043958
LC ebook record available at https://lccn.loc.gov/2020043959

ISBN: 978-0-367-22286-4 (hbk)
ISBN: 978-0-367-22288-8 (pbk)
ISBN: 978-0-429-27427-5 (ebk)

Typeset in Sabon
by SPi Technologies India Pvt Ltd (Straive)

Visit the companion website: www.routledge.com/cw/Strier

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Preface

I completed the revisions to this sixth edition of *Primate Behavioral Ecology* while under the "shelter-at-home" mandate imposed by the unprecedented COVID-19 pandemic of early 2020. Reading and thinking so intensely about other primates at a time of human vulnerability was a compelling reminder of the fragility and the resilience of the natural world and of our responsibility to protect it along with ourselves. This edition is dedicated to all of the people all over the world who expose themselves to personal risks in order to take care of others—both human and nonhuman—during the crises of our times.

This edition, like its five predecessors, is an introduction to the field of primate behavioral ecology and its applications to primate conservation. It integrates the basics of evolutionary and ecological approaches to the study of behavior with up-to-date coverage of how different primates actually behave. Examples are drawn from the "classic" primate field studies as well as more recent studies from diverse species across the Primate Order to illustrate both the vast behavioral variation that we now know exists, and the gaps in our knowledge that future studies will fill. Throughout the book, the interplay among theory, observations, and conservation issues is emphasized.

Readers will undoubtedly have different levels of familiarity with primate evolutionary history, the genetics underlying evolutionary processes, and basic behavioral ecology. For some, the background material covered in the early chapters will be an easy review, but the relevance of these areas to conservation deserves to be reinforced. Subsequent chapters are organized around some of the major research themes in the field. Most begin with an overview of theoretical approaches and then examine the comparative evidence that supports or challenges evolutionary-based predictions.

As one might expect for a field as vibrant as this, new discoveries continue to refine the ways we think about primates and the theoretical perspectives upon which these perceptions are based. Increasingly, however, anthropogenic activities are negatively impacting primate populations and their habitats. Although these changes put primates at ever-greater risks, they have also stimulated widespread interest and awareness in the remarkable behavioral flexibility that many primates exhibit. This combination of attention to the variation in ecological and demographic conditions, on the one hand, and the responses of primates to these variable conditions, on the other hand, has shifted some of the focus of primate behavioral ecology away from evolutionary adaptations per se, and more toward considerations of behavioral flexibility as a part of the primates' evolutionary heritage.

All of the material carried over from the previous editions has been updated so that it tracks the new directions in which primate behavioral ecology is moving. This has resulted in some substantive enhancements and additions to nearly every chapter. Some of the highlights of this edition include:

- Integration of methodological and technological advances including remote sensing tools and their implications for noninvasive studies of primate behavior, populations, and habitats.

- Syntheses of new insights from theoretical and analytical approaches including the extended evolutionary synthesis, social network analyses, reconsiderations of female dominance, multi-modal signaling, and ethnoprimatology.
- Expanded coverage of primate behavior, diet, microbiomes, and health in anthropogenic landscapes.
- Fully updated taxonomic classifications including new tables and an up-to-date Appendix, and greater integration of evolutionary history and conservation, including the Anthropocene.
- Focused attention on contemporary conservation issues throughout, including disease, climate change, forest corridors, and ecotourism.
- New boxes on drones, terminology in primatology, positional behavior and behavioral thermo-regulation, and zoonotic disease.
- Companion website with chapter summaries, flashcards, study and discussion questions, links to resources, recommended readings, and educational videos.

More than 300 new references provide authoritative sources and additional examples. However, I have also retained most of the citations to the original studies on particular topics to provide the historical context and time-depth we have in the field. In our digital age, it is more important than ever for newcomers to the field to learn about some of the classic studies that established the field and continue to shape it, but that were often published as books or book chapters and may therefore not be accessible online.

As with past editions, this edition benefited by help from many colleagues who answered questions, provided references, or offered feedback on the text or figures. This list must begin with Anthony Rylands, who contributed the taxonomic updates to this and all prior versions of the Appendix. Other colleagues who responded to queries about this edition and provided materials include (in alphabetical order): Ilianna Anise, Michelle Bezanson, Mary Dinsmore, Irene Duch-Latorre, Alexander Georgiev, A. J. Hardie, Michael Huffman, Jacob Kraus, Rebecca Lewis, Jonathan Marks, Fabiano de Melo, Sérgio Mendes, Russ Mittermeier, Carla Possamai, Robert Sapolsky, Stella de la Torre, and Toni Ziegler, plus the six anonymous (to me) reviewers for their incredibly helpful comments.

Many people also generously provided some amazing new photos and videos for this sixth edition: Mary Dinsmore, Irene Duch-Latorre, Pablo Fernicola, Chrissy Grebe, A. J. Hardie, Jacob Kraus, Fabiano de Melo, Sérgio Mendes, Carla Possamai, and Stella de la Torre. It is an honor to be able to include these new photos, along with the others carried forward from prior editions by other photographers: Susan Alberts, Thad Bartlett, Irwin Bernstein, Carla Boe, Sue Boinski, Jean Boubli, Robert Boyd, Diane Brockman, Heather Bruce, Richard Byrne, Christina Campbell, Ron and Anne Carlson, Cristiane Cäsar, Margaret Clarke, Marina Cords, Paulo Coutinho, Irven DeVore/Anthro-Photo, Nancy DeVore/Anthro-Photo, Luiz Dias, Kerry Dore, Robin Dunbar, Beth Erhardt, Daniel Ferraz, Mary Glenn, Cyril Gruenter, Sharon Gursky, David Haring, Peter Henzi, Roland Hilgartner, David Hill, Alain Houle, Michael Huffman, Ellen Ingmanson, Robert Jeanne, Peter Kappeler, Minoru Kinoshita, Amy Klegarth, Cheryl Knott, Kathelijne Koops, Melanie Krebs, Tim Laman, Joanna Lambert, Phyllis Lee, Marlon Lima, Brent Loke, Jessica Lynch (Alfaro), Katherine MacKinnon, Joe Manson, Richard McFarland, William McGrew, John Mitani, Florian Möllers, Jim Moore, Leanne Nash, Anna Nekaris, Marcello Nery, Ian Nichols, Ronald Noë, Claudio Nogueira, Maria van Noordwijk, Marilyn Norconk, John Oates, Adriana Odalia-Rímoli, Claudia Olejniczak, Marino Junio Fonseca de Olveira, Julia Ostner, Deborah Overdorff, Melissa Panger, Susan Perry, Jane Phillips-Conroy, Carla Possamai, Erika Patricia Quintino, Yaya Rayadin, Ulrich Reichard, Melissa Remis, José Rímoli, Martha Robbins, Elizabeth Rogers, Noel Rowe, Carel van Schaik, Joan Silk, Meredith Small, Craig Stanford, Thomas Struhsaker, Fernanda Tabacow, and Frans de Waal.

This edition would not have been possible without the many people whose encouragement and help with the content of prior editions deserves to be acknowledged, once again, here.

First, I extend my enduring gratitude to those friends and colleagues and my late father who provided extensive feedback on one or more prior editions: Irwin Bernstein, Jonathan Marks, William McGrew, Jim Moore, Sylvia Shepard, Murray Strier, and Robert Sussman. Thanks, too, to the many others for responding to past queries, offering tips and encouragement, or providing what were, at the time, anonymous reviews on earlier editions: Susan Alberts, Wendy James Aldridge, Jessica Lynch Alfaro, Jeanne Altmann, Michelle Bezanson, Júlio César Bicca-Marques, Sue Boinski, James Calcagno, Anne Carlson, Paulo Chaves, Marina Cords, Robin Dunbar, Karin Enstam, Linda Fedigan, John Fleagle, Beth Fox, David Frayer, Agustin Fuentes, Paul Garber, Paulette Goldweber, Reiko Matsuda Goodwin, Mark J. Hartmann, David Hill, Minna Hsu, Michael Huffman, Tony Ives, Patricia Izar, Clifford Jolly, Jason Kamil, Richard Kay, Andrew Klaber, Leslie Knapp, Cheryl Knott, Andreas Koenig, Tibor Koertylelyessy, Vincent Labb, Joanna Lambert, Katrina Larkin, Phyllis Lee, Robin Lee, Tom Martin, Fabiano de Melo, Sérgio Mendes, Lynne Miller, John Mitani, Russell Mittermeier, Cate Mitton, David Morgan, Sheri Morgenroth, Liza Moscovice, Anna Nekaris, Ronald Noë, Maria van Noordwijk, John Oates, Marin Oschmann, Deborah Overdorff, Melisssa Panger, Mary Pavelka, Carla Possamai, Anne Pusey, Alison Richard, Erin Riley, Martha Robbins, Norman Rosen, Anthony Rylands, Crickette Sanz, Ashley Sapieja, Carel van Schaik, Stuart Schimmel, Daniel Sellen, Hogan M. Sherrow, Richard Sherwood, Charles Snowdon, Elliott Sober, Stephanie Spehar, Phillip Stall, Laura Szymanski, Linda L. Taylor, Forrest D. Tierson, Matthew A. Tornow, Sarie Van Belle, Eduardo Veado, Kara Weiss, Michael Wilson, Patricia Wright, and Toni Ziegler. In addition, I thank Perry van Duijinhoven for his illustration, and Paulette Goldweber for her support with permissions.

Many parts of the preparation of the manuscript in its various drafts and editions were aided by others. Andreia Oliva helped with the initial bibliography and Bob Becker (Wisconsin National Primate Research Center) played a critical role in reproducing most of the photographs for the first edition. Larry Jacobsen, Ray Hamel, and staff at the Primate Center Library helped in locating essential reference material. Jennifer Jacobson, my last editor at Allyn & Bacon, was critical to the completion of the third edition. Without Jen, there would not have been a fourth edition, for which Nancy Roberts, my editor at Pearson, was essential. The fifth edition gained a third publisher, a consequence of the publishing business that I believe has worked to my great advantage. In moving to Routledge at Taylor & Francis Books, I gained a remarkable editor, Katherine Ong, who did everything possible to smooth the book's transition. Katherine's assistant, Lola Harre, was essential in moving the fifth edition forward to production, where marketing assistant Staci Custus, copy editor Cinqué Hicks, the proofreader Helena Power, editorial assistant Marc Stratton, and especially production editor Anna Callander, each played essential roles.

I was very fortunate for this sixth edition to still have Katherine Ong as my editor and main champion, and her assistant, Stewart Beale, who helped with permissions and other details. I was also delighted to be working once again with Anna Callander as production editor, and with an outstanding copy editor, Liz Dawn. I am very grateful to Anna, who shepherded the sixth edition into its final product.

Other friends and family members have been uniformly encouraging and tolerant of my concentration on this project, and I thank them for their kindness, patience, and support. I am grateful to the students in my classes, especially those in the Primate Conservation seminar, for their stimulating discussions of recent literature, and to the members of my lab, for their critical feedback during this project. I am also appreciative of the University of Wisconsin-Madison and my Vilas Research Professorship, which facilitated much of the research that went into this edition. Finally, a second and very special thanks to Anthony Rylands (Global Wildlife Conservation) for once again generously sharing his evolving taxonomic lists and permitting me to include them in the Appendix, and for all of his help in clarifying taxonomic questions.

This book, like its predecessors, was only possible because of the many primates who have continued to let so many of us into their lives. I hope that by sharing what we have learned, this book will inspire a new generation of primatologists to study and conserve them.

Chapter 1

Introduction to Primate Studies

The tropical forests where most primates live are humid, shadowy places. More often than not, there is a humming in the background from the hordes of mosquitos and other insects hovering about. Fieldworkers' clothes get torn and snagged from thorny plants that thrive on the forest floor, and our skin is often covered with itchy scabs from the microscopic ticks that invariably find their way to the warmest parts of our bodies to feed on our blood. Putting up with these discomforts can be trying at times, but it is a small price to pay for the privilege of studying the world's wild primates.

Primates are special animals. Visitors flock to their exhibits at zoos, record numbers of viewers watch televised documentaries about the most intimate details of their lives, and newspaper headlines and all forms of social media now routinely cover their latest antics. This broad public appeal of primates no doubt stems from the fact that we humans count ourselves among them (Table 1.1) and see aspects of ourselves in them (Figure 1.1).

Primates are as fascinating to scholars as they are to the general public. At major colleges and universities throughout the world, primates occupy a unique niche in research and teaching curricula as examples of highly intelligent, social animals and as members of the long evolutionary heritage to which we belong. Primatologists employed in academia are housed across departments of biology, psychology, anthropology, and anatomy, where they bring their own disciplinary perspectives to bear on uncovering and understanding the patterns that describe primate adaptations. Accumulating data from long-term studies of familiar primates and new data from recently established field sites on rare and unfamiliar primates continue to shift our understanding of what it means to be a primate in provocative ways.

As study subjects, primates are special in two additional respects. First, because their geographic concentration in the tropics has placed many **species*** at risk of extinction from deforestation and hunting pressures, knowledge about primates is now widely recognized as being

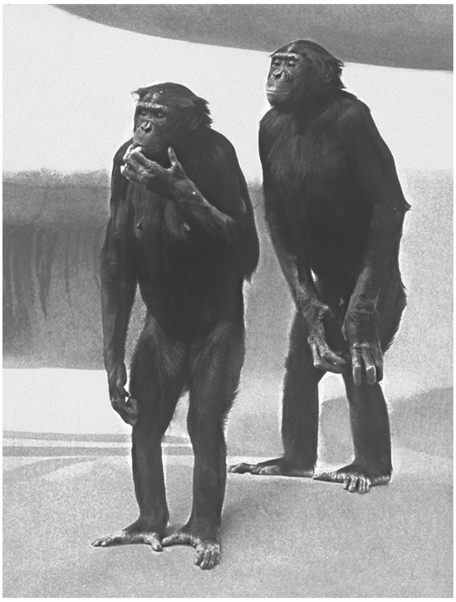

Figure 1.1 Bipedal bonobos (*Pan paniscus*) at the San Diego Zoo. Female is on the left, male is on the right. From *Peacemaking among Primates* by Frans de Waal (1989). Photo by Frans de Waal.

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* Key terms appear in boldface the first time they are mentioned in the text, and are defined in the Glossary.

essential to conservation efforts on their behalf. The relevance of primatology extends beyond science to its applications to mainstream societal issues, where primates are serving as flagships for their own and others' benefits, and where our discoveries about primates are being translated directly into saving endangered species and their habitats. Second, their biological similarities to humans have put primates into the position of contributing to biomedical advances (King et al., 1988; Sapolsky, 2005). Rapid advances in **comparative genomics** continue to be made as the number of primate genomes that have been sequenced has grown (Siepel, 2009; Rogers and Gibbs, 2014; Rogers 2018), challenging the ethical as well as biological limits of what it means to be human. Knowledge about primates is helping to determine guidelines for the use of animals in experimental research, and catalyzing public awareness and action about sensitive biomedical ethics and animal well-being. It is also stimulating greater concern with protecting wild primate populations, which may hold the keys to understanding the origins and spread of many human diseases, including highly infectious ones such as HIV, Ebola, and coronaviruses (Moore, 2004; Rouquet et al., 2005; Weiss and Heeney, 2009; Rockx et al., 2020) and even older diseases such as malaria (Tung et al., 2009; Varki and Gagneux, 2009).

My own biases in this book will be immediately apparent. Trained as a biological anthropologist, my original interest in primates for what they can teach us about the evolution of human social behavior led me to study them in their natural habitats, where ecological and social pressures interact. My first field experience was as an undergraduate assistant on the Amboseli baboon project in southern Kenya (Figure 1.2; see also Box 9.2). It was during this decisive six-month assignment that my early views of how nonhuman primates were supposed to behave took shape. By 1982, when I began my long-term field study of the critically endangered northern muriqui monkeys in Brazil's Atlantic forest (Figure 1.3), I was intent on testing comparative models of primate behavioral ecology and on applying this knowledge to their conservation. Muriquis represented an ideal test case because their elusive habits had left them out of the comparisons on which the models proposed at the time were based. In addition, their endangered status meant that everything learned about them had the potential for practical as well as theoretical applications.

Figure 1.2 Yellow baboons (*Papio cynocephalus*) at Amboseli National Park, Kenya. Mt. Kilimanjaro is in the background, the author is to the left. The baboon troop was habituated to human researchers, and only researchers were permitted to follow the baboons. Photo by K. B. Strier.

Table 1.1 Classification of some familiar living genera in the Primate Order

Suborder	Infraorder	Parvorder	Superfamily	Family (N of genera)	Subfamily (N of genera)	Genus (Subset of total)	Common name*
Strepsirrhini	Lemuriformes		Cheirogaleoidea	Cheirogaleidae (5)		*Microcebus*	Mouse lemur
						Cheirogaleus	Dwarf lemur
			Lemuroidea	Lepilemuridae (1)		*Lepilemur*	Sportive lemur
				Lemuridae (5)		*Lemur*	Ring-tailed lemur
						Eulemur	Brown lemur
						Varecia	Ruffed lemur
				Indriidae (3)		*Indri*	Indri
						Propithecus	Sifaka
	Chiromyiformes			Daubentoniidae (1)		*Daubentonia*	Aye-aye
	Lorisiformes		Lorisoidea	Galagidae (6)		*Galago*	Galago (bushbaby)
						Galagoides	Dwarf galago
				Lorisidae (4)		*Loris*	Slender loris
						Nycticebus	Slow loris
Haplorhini	Tarsiiformes			Tarsiidae (3)		*Carlito*	Philippine tarsier
	Simiiformes	Platyrrhini				*Tarsius*	Tarsier
				Callitrichidae (8)		*Callithrix*	Common marmoset
						Saguinus	Cotton-top tamarin
						Leontopithecus	Lion tamarin
				Cebidae (3)		*Cebus*	Capuchin monkey
						Sapajus	Tufted capuchin monkey
						Saimiri	Squirrel monkey
				Aotidae (1)		*Aotus*	Night (owl) monkey

				Pitheciidae (6)		*Callicebus*	Titi monkey
						Pithecia	Saki monkey
						Cacajao	Uakari
				Atelidae (4)		*Alouatta*	Howler monkey
						Ateles	Spider monkey
						Lagothrix	Woolly monkey
						Brachyteles	Muriqui
		Catarrhini	Cercopithecoidea	Cercopithecidae (23)	Colobinae (10)	*Semnopithecus*	Sacred langur
						Colobus	Colobus monkey
						Piliocolobus	Red colobus monkey
						Rhinopithecus	Snub-nosed monkey
					Cercopithecinae (13)	*Macaca*	Macaque
						Mandrillus	Mandrill
						Papio	Baboon
						Cercopithecus	Guenon
			Hominoidea	Hylobatidae (4)		*Hoolock*	Hoolock gibbon
						Hylobates	Agile gibbon
				Hominidae (4)**		*Pongo*	Orangutan
						Gorilla	Gorilla
						Pan	Chimpanzee
						Homo	Human

Adapted from Anthony Rylands (Primate Specialist Group, SSC/IUCN), following Mittermeier et al. (2013), and other key sources (e.g., Groves, 2001, 2005; Rylands and Mittermeier, 2009). Older, alternative taxonomies (e.g., the position of tarsiers, and the separation of the great apes in the Pongidae instead of Hominidae) are discussed in Chapter 2 and shown in Figure 2.10. For a complete list of living primate species and taxa, see the Appendix to this book. *Common names to the familiar species in the genus; **Number of genera shown here includes humans. (For additional discussions about other taxonomic revisions, see Leakey et al., 2001, Marks, 2005, Di Fiore et al., 2015).

Figure 1.3 Two northern muriquis (*Brachyteles hypoxanthus*) at the Reserva Particular do Patrimônio Natural (RPPN) Feliciano Miguel Abdala (a Private Nature Heritage Reserve named after the man who preserved it; previously known as the Estação Biológica de Caratinga while Senhor Feliciano was alive), located on Fazenda Montes Claros in Minas Gerais, Brazil. Muriqui taxonomy, like that of many other primates, has been revised since the early 1980s and the northern muriqui is now considered a separate species from the southern muriqui, known as *B. arachnoides.* Photo by A. Odalia-Rímoli.

Although my firsthand experience on the Amboseli baboon project had given me an idea of what it took to conduct and maintain a long-term field study, I was totally unprepared for the behaviors I witnessed among muriquis. Unlike the **hierarchical** society of baboons, in which access to important resources such as food and mates is determined by **agonism**, or aggressive and submissive interactions between females and males, muriquis maintain nonhierarchical, **egalitarian** relationships with one another. Female baboons spend their lives in their **natal groups**, or birth groups, and maintain strong **affiliative bonds** with their closest relatives (Figure 1.4), but in muriquis it is the males that stay in their natal groups with their mothers and other male kin, or **patrilines**, and the females that leave their kin behind to pursue their reproductive careers in other muriqui groups. The peaceful social relationships at the core of muriqui society were an unexpected discovery that set muriquis apart not only from baboons, but also from nearly all other primates that were known at the time (Table 1.2). Indeed, the report of a case of lethal aggression in one population of the closely related southern muriqui (Talebi et al., 2009) makes the northern muriquis' pacific society even more striking today than it was at the start.

Had muriquis turned the evolutionary and ecological rules that predict competitive behavior in other primates to different ends? Or, did they represent just one example of a previously underestimated set of behavioral options available to primates? These were some of the questions that led me to pursue my long-term field study of the muriquis, and that ultimately inspired me to write this book. *Primate Behavioral Ecology* explores the diverse behavioral possibilities that are now known to exist among primates, and emphasizes the importance of preserving this diversity in the twenty-first century. Between threats from human population pressures and global climate changes, the challenge of protecting primates and their habitats from extinction has never been greater.

Figure 1.4 Yellow baboon (*Papio cynocephalus*) mother at Amboseli National Park, Kenya, is groomed by one daughter while a younger daughter suckles. Photo by K. B. Strier.

Primates as Study Subjects

Nonhuman primates have been described as representing the "boundary" that separates humans from other animals (Haraway, 1989). Primates bear the distinction of being the group of animals to which we belong and through which we trace our **phylogeny**, or evolutionary history. Because other primates are the closest living links we have to our extinct ancestors, they can make excellent models for identifying our ancestral traits. But even without their connection to us, primates are interesting in their own right. As a diverse group of long-lived, socially complex animals, they provide some of the best insights into the evolutionary and ecological processes that affect behavioral variation (Rowell, 1993). In fact, studies of primates have contributed to, as well as benefited from, advances in our comparative understanding of the evolution of animal, including human, behavior (Harcourt, 1998).

Despite these continuities in behavior, deeply rooted perceptions about the similarities and differences between humans and animals have influenced the history of primate studies in significant ways. From the kinds of questions asked of primates, to the species most widely studied, to the methods employed, and interpretations of results, academic traditions in the social and natural sciences have left their distinct disciplinary marks (Richard, 1981; Strier, 1993a, 1997a, 2011a; Riley, 2019).

Most questions in primate behavioral ecology require **ultimate** levels of analyses. This typically means asking **functional** questions about *why* primates have been selected to behave as they do under particular conditions, but it can also involve asking **phylogenetic** questions about *how* the evolutionary history of a particular trait or behavior accounts for its distribution among closely related species. Other questions require **proximate** levels of analyses that many contemporary primatologists incorporate in their research. Asking *what* are the underlying neural, chemical, physiological, or immediate causes for a particular behavior requires a **causal** level of explanation. Discovering the developmental trajectory of *when* a particular trait or

Table 1.2 Northern muriqui society compared to the societies of other well-known primates, including savanna baboons

Variable	Northern muriqui	Savanna baboon[1]	Chimpanzee[2]	Mountain gorilla[3]	Ring-tailed lemur[4]
Group composition:	multi-male, multi-female	multi-male, multi-female	multi-male, multi-female	uni- or multi-male, multi-female	multi-male, multi-female
Grouping pattern:	cohesive, fluid	cohesive	fluid	cohesive	cohesive
Natal group dispersal:	female-biased	male-biased	female-biased	both sexes	male-biased
Female relationships:	indifferent	matrilineal, hierarchical	indifferent, weakly hierarchical	indifferent, weakly hierarchical	matrilineal, hierarchical
Male relationships:	patrilineal, egalitarian	hierarchical	patrilineal, hierarchical	hierarchical in multi-male groups	hierarchical
Male–female relationships:	egalitarian	males dominate	males dominate	males dominate	females dominate

[1] The societies of Japanese macaques, rhesus macaques, vervet monkeys, and capuchin monkeys are similar, although in contrast to baboons, among these monkeys, some females can dominate all but the highest ranking "alpha" male. The societies of hamadryas baboons differ from those of savanna baboons, as explained in later chapters.

[2] Bonobo societies are now known to differ from those of chimpanzees in that female relationships, although not kin-based, can be highly affiliative. Male relationships are only weakly hierarchical, and females are not subordinate to males. Spider monkey societies are more similar to those of chimpanzees.

[3] The societies of howler monkeys and many langurs are similar to those of mountain gorillas, although in Hanuman langurs (now called Bengal sacred langurs) natal group dispersal is male-biased. Also, female relationships tend to be hierarchical in both howler monkeys and langurs.

[4] Although other species of lemurs live in different kinds of groups including fluid ones with fission–fusion dynamics (Baden et al., 2016; Agnani et al., 2018), none is known to be patrilocal.

behavior emerges during an individual's lifetime involves an **ontogenetic** level of explanation (Tinbergen, 1963).

To clarify the subtle differences between these levels of explanation, we can look at an actual example of sex differences in behavior. Consider the case of female chimpanzees at Gombe National Park, Tanzania, who use twigs to "fish" for termites that build earthy, mound-like nests (Figure 1.5). Females use these and other tools more frequently than males (McGrew, 1979; Lonsdorf et al., 2004). If we were interested in why these female chimpanzees are more avid tool-users, we might develop and test several predictions, such as that termites provide protein and lipids and other nutrients that are more essential to female reproduction than to male reproduction. To understand this sex difference at a phylogenetic level, we might examine whether there is evidence for sex differences in food procurement and object manipulation in other populations of chimpanzees and in other primate species. If we were concerned with what produces this sex difference in behavior, we might examine whether males and females differ in their fine-grained motor coordination or physiology to obtain an understanding of the proximate mechanisms that affect behavior. Ontogenetic approaches might lead us to explore when male and female chimpanzee behavior begins to

Figure 1.5 Chimpanzee (*Pan troglodytes*) mother with infant fishes for termites. Photo by Jim Moore/Anthro-Photo.

diverge, or whether mothers provide their daughters more opportunities to observe the practice of termite-fishing than their sons.

Many of the questions we ask about the evolutionary function of particular behaviors require multiple levels of analyses to address. For example, in hierarchical societies like those of savanna baboons, adult males can be ranked on the basis of the outcomes of agonistic interactions among them. Fights can result in debilitating wounds, so why do they engage in this behavior? Hypotheses about the functional significance of agonistic interactions have focused on the possible reproductive advantages that high status confers on the males that manage to attain it. Yet, it has only been through the use of genetic paternity analyses that the hypothesized positive relationship between male rank and reproductive success could be tested. Combining different levels of analyses is the most powerful way to understand why and how different primates behave as they do.

Descriptive Studies

The early years of primate field research were characterized by descriptive, **ethnographic**-type reports. Like contemporary fieldworkers, pioneering researchers went to remote locations to find wild primates, and eventually, through hard work and persistence, succeeded in winning the trust of the primates they had gone to study. Once primates are **habituated** to the presence of an observer, they go about their business as usual instead of fleeing or halting their activities when humans are near (Figure 1.6). Habituation is essential for seeing how primates behave when they're not on their guard. Primates with little or no prior experience of humans may exhibit more curiosity than fear, as was documented when the chimpanzee population inhabiting the remote Goualougo Triangle of the Republic of Congo was first contacted. Instead of fleeing when the researchers were near, these chimpanzees stared, vocalized, approached, and

Figure 1.6 Masudi, an adult male chimpanzee (*Pan troglodytes*) at Mahale, Tanzania, and primatologist John Mitani. Masudi is fully habituated to the presence of human researchers. Photo by John Mitani.

even followed when the observers moved away (Morgan and Sanz, 2003). But with primates that have already learned to avoid humans who hunt them or disturb their habitat, the process of habituation can be especially challenging. Of course, the transition from panic and flight to indifferent tolerance is a gradual one, and it is not always clear when human observers are fully accepted by their study subjects. For primates that have grown up as the subjects of long-term studies such as my own, the presence of human observers may be all that they know. But even well-habituated primates may alter their behaviors in subtle ways when human observers are near (Jack et al., 2008; Strier, 2010; McDougall, 2012).

Unlike contemporary primatologists, who now collect most of their data in highly systematic ways, early primate field researchers focused on cataloging the behavioral repertories, or **ethograms**, of their subjects. These original reports continue to provide some of the most detailed descriptions of primate behavior, but comparisons across studies were difficult to make. Did one researcher's interest in aggressive behavior lead her to notice hair-raising fights more often than another researcher, whose interest in **grooming** behavior may have led him to pay closer attention to the meticulous service of removing ticks and burrs that one primate provides for another? Because standardized methods of behavioral sampling were rarely employed, no one could say for certain how much the observers' own biases and interests influenced their findings.

Anthropocentric Perspectives

The descriptive, ethnographic-type reports that characterized the early years of primate field research grew partially out of widespread **anthropocentric** interests in primates. Anthropocentric approaches, which examine primates to understand more about humans, date back to the beginning of primate field research, when curious naturalists first set out to observe wild primates. In the 1920s and 1930s, Yale University psychologist Robert Yerkes began sending students to conduct naturalistic studies of primates as part of a larger agenda in comparative psychobiology, which included chimpanzees and mountain gorillas. But in many respects, it was when

Figure 1.7 Male mantled howler monkey (*Alouatta palliata*). Photo by Margaret R. Clarke.

Clarence Ray Carpenter went to Panama that the scientific study of wild primates got underway (Carpenter, 1934, 1964).

The howler monkeys that Carpenter studied are **arboreal**, or tree-dwelling, creatures, which, along with the other New World monkeys in Central and South America, share only a distant ancestry to humans (Figure 1.7). Nonetheless, Carpenter's depictions of their complicated family lives captured the attention of Kinjii Imanishi, a Japanese ecologist who, with colleagues at Kyoto University, launched his own detailed investigations into the societies of Japanese macaques in the late 1940s (Matsuda, 1997). These macaques, along with some of the other Old World monkeys of Asia and Africa, are **semiterrestrial**, or partially ground-dwelling, monkeys (Figure 1.8). They also share more traits with humans than the howler monkeys, in part because of their adaptations to life on the ground.

In the late 1950s, US physical anthropologist Sherwood Washburn recruited Irven DeVore to apply the ethnographic methods and theory employed by social anthropologists to study wild baboons, another semiterrestrial Old World monkey. Baboons had even stronger claims than macaques as possible models for human ancestors because baboons occur throughout sub-Saharan Africa, where the fossil trail of human origins begins (Figure 1.9).

The baboons studied by DeVore just outside of Nairobi are found in the same types of open **woodland** and **savanna** habitats that our ancestors are thought to have occupied when they first made the transition to a **terrestrial** lifestyle (Figure 1.10). Similarities in the societies of baboons and macaques supported the idea that human sociality had been shaped by some of the same ecological pressures that influence the social behavior of these ground-dwelling monkeys. For example, primates on the ground are more vulnerable to attacks from predators such as lions and other large carnivores than their arboreal cousins, which may explain the fact that they live in large, coordinated troops (Washburn and DeVore, 1961).

Another early Washburn student, Phyllis Jay (later, Phyllis Dolhinow), conducted her research on Indian langurs, members of the other major group of Old World monkeys called colobines (Figure 1.11). Unlike baboons and macaques, langurs and other colobines spend most

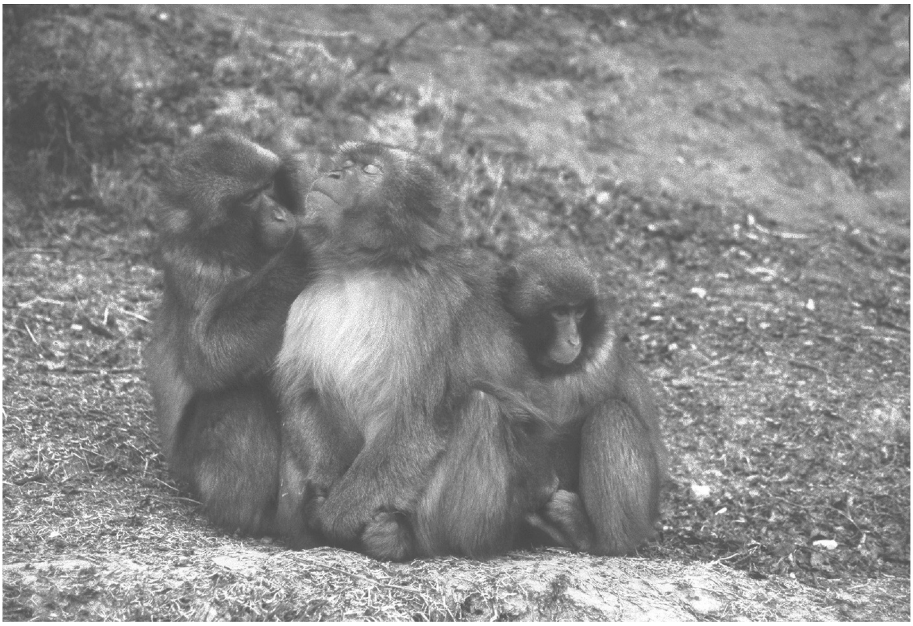

Figure 1.8 Japanese macaque (*Macaca fuscata*) matriline. Three generations of females of the "Mino" lineage huddled together on a cold January afternoon at Arashiyama, Kyoto, Japan. Photo by Michael A. Huffman.

Figure 1.9 Two male olive baboons (*Papio anubis*) looking at a pride of lions. Most primates can stand on two legs for brief periods of time, and do so to gain a vantage point when visibility is obscure. Photo by Irven DeVore/Anthro-Photo.

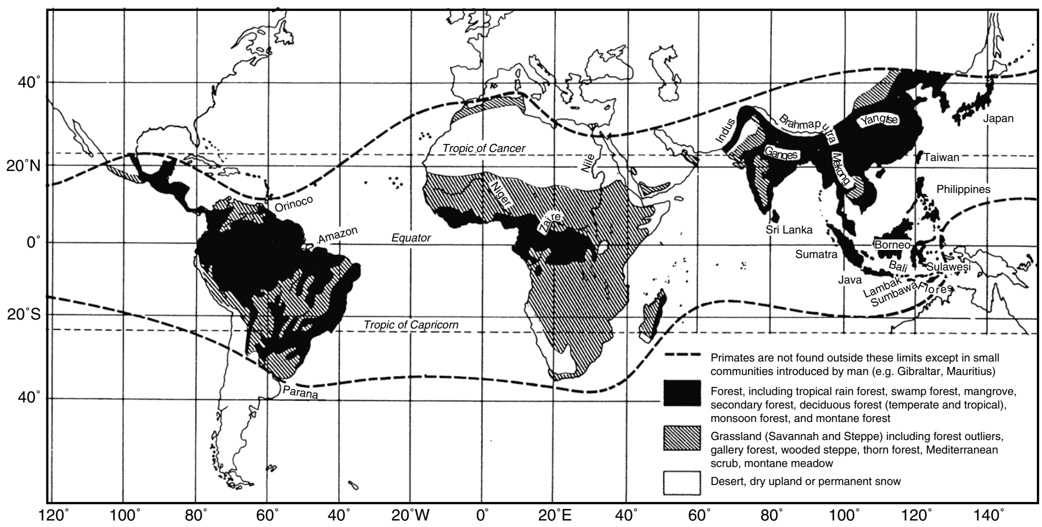

Figure 1.10 Distribution of major vegetation zones within the range of nonhuman primates. From Napier, J. R. and Napier, P. H. (1994). *The Natural History of the Primates,* Figure 1.2, p. 10. Cambridge: The MIT Press. Copyright © 1994, The MIT Press. Reprinted by permission of The MIT Press.

Figure 1.11 Malabar sacred langurs (*Semnopithecus hypoleucos*). Note that the langurs have undergone taxonomic revisions and many gray langurs were previously called Hanuman langurs, initially *Presbytis entellus,* and later *Semnopithecus entellus.* Photo by Robert L. Jeanne.

Figure 1.12 A male mountain gorilla (*Gorilla berengei berengei*). Photo by Martha M. Robbins.

of their time in the trees and have special anatomical traits that permit them to digest large quantities of leaves, which are usually found in abundance. Perhaps because of this, social relationships among members of langur troops were less hierarchical than those among macaques and baboons. Instead, Jay focused her studies on the processes of socialization and development within langur societies. Other pioneering field studies on langurs were also underway (e.g., Sugiyama, 1964), providing valuable comparative insights into the variation in langur behavior in troops that differed from one another in size and composition (Jay, 1968).

In the early 1960s, British paleontologist Louis Leakey helped establish long-term studies on three species of great apes, the closest living primate relatives to humans. First came Jane Goodall's studies of chimpanzees, then Dian Fossey's studies of mountain gorillas (Figure 1.12), and finally, Biruté Galdikas' studies of orangutans (Figure 1.13). Japanese primatologists also expanded their work to include African apes in the late 1950s and early 1960s, which they similarly expected would provide a deeper understanding of early human evolution (Azuma and Toyoshima, 1961/62; Imanishi, 1966; Matsuda, 1997). The great apes are thought to be most similar in size, biology, and behavior to the first human ancestors, and therefore hold keys to understanding our own behavioral evolution (Wrangham, 1987a; Moore, 1992b). Comparisons among apes and other, more distantly related primates provide perspectives on what is—and isn't—different about humans.

Comparative Biology

Biologists were equally active in the early days of primate studies, but their interest in primates extended beyond anthropocentric comparisons with humans to include those with other

Figure 1.13 A subadult male orangutan (*Pongo pygmaeus*) showing unusual limb usage (note the position of both arms and one foot). Photo by John Mitani.

animals. Biologists such as Stuart and Jeanne Altmann (1970) sought out the savanna-dwelling baboons whose complex social behavior could be readily observed in the open habitats they occupied. Others, such as Thelma Rowell (1966), who focused on baboons that spent time in forests, and Tom Struhsaker (1967a, 1969, 1997), who focused on semiterrestrial vervet monkeys (Figure 1.14) and their close arboreal relatives in the African rainforest, aimed to tease apart the ecological and phylogenetic determinants of social behavior. Comparisons among the same or closely related primates living in different habitats would reveal whether their behavior was responsive to the different ecological pressures they faced, or whether species-typical

Figure 1.14 Vervet monkeys (*Chlorocebus pygerythrus*; previously classified as *Cercopithecus aethiops*) at Amboseli National Park, Kenya. Photo by P. C. Lee.

patterns in behavior established during their evolutionary history prevailed (Rowell, 2000). Still others traced Carpenter's pioneering footsteps back to the New World to revisit howler monkeys and initiate comparative studies on other New World primates.

Early Classification Schemes

By the late 1960s, primate field research was no longer limited to the handful of monkeys and apes with clear ecological or phylogenetic connections to humans (Aldrich-Blake, 1970). Old World primates still dominated the literature, but a broader comparative framework for organizing primates had begun to take shape. Diverse species could be classified according to general ecological and social categories that clearly distinguished their lifestyles (Crook and Gartlan, 1966).

Many of these distinctions were, and still are, based on grouping primates into categories according to what the animals seem to do most of the time. As we'll see in later chapters, discrete categorical descriptions are artificial in a way, because we have no basis for knowing whether our cutoffs between categories are biologically meaningful (Clutton-Brock and Harvey, 1984; Moore, 1984) or whether the behavior patterns of a single study group or population at any particular point in time can be extrapolated to its behavior at other times or to other groups and populations living under different conditions (Strier, 2009). Nonetheless, classifying primates helps provide a basis for comparing different species and for identifying deviations among them that require closer scrutiny. The process of investigating unusual behavior patterns has played a major role in advancing our understanding of primate behavioral diversity and the underlying evolutionary and ecological factors that shape it. More recently, these investigations have extended to include the high levels of **intraspecific variation** observed in some behaviors across space and over time. As we'll see, the growing appreciation for the need to understand intraspecific variation presents both new challenges and new opportunities for discovery (Kappeler et al., 2013).

Activity Patterns. All primates must rest, eat, and travel between food sources, while also avoiding predators when they have them. Often both survival and reproduction also demand time-consuming sociality. How primates allocate their time to these essential activities, or their **activity budgets**, is highly variable among different species as well as among members of the same group. The amount of time they are active, as opposed to resting, is affected by climate as well as social conditions, and is one of the indicators of their behavioral flexibility (Korstjens et al., 2010; McFarland et al., 2014). Most primates are **diurnal**, meaning that they are active during the daylight hours and inactive, or sleeping, at night. Some of the primates living on the island of Madagascar are **cathemeral**, meaning that they have the capacity to be active by day or night. **Nocturnal**, or night-active, primates are thought to be the ancestral condition (Silcox et al., 2009), although there has been some disagreement about this (Tan et al., 2005; Chapter 2). They are turning out to be much more numerous than was previously thought (Bearder, 1999). Primates with different activity patterns are vulnerable to different kinds of predators and therefore vary in their **predator sensitivity**, or the degree to which they adjust their behavior to reduce their risks as prey (Miller, 2002). Those that made the move to more conspicuous diurnal lifestyles have had to shift from being fairly solitary and inconspicuous to a more social existence, in which extra pairs of eyes and ears can be advantageous for detecting, and defending themselves against, predators. This extra **vigilance** can mean the difference between life and death.

All primates devote considerable portions of their active hours to resting, but how much is essential and how much can be reallocated to other activities depends upon a variety of factors (Korstjens et al., 2010; McFarland et al., 2014). Many diurnal primates shift their activity patterns in dramatic ways in response to seasonal changes in day length, ambient temperature, and rainfall patterns that affect food availability and the corresponding energy balance. Some take long, leisurely siestas during the hottest hours of summer days, while on cold winter mornings they doze while soaking up the warmth of the sun on the tops of branches. The proportion of time different primates devote to their various activities coincides with divergent suites of behavioral and anatomical traits. For example, **energy minimizers** devote substantial proportions of their time to resting, and little time (and energy) to traveling. They rely heavily on foods such as leaves, which are relatively easy to find but are low in energy content and require both time and anatomical specializations to digest. **Energy maximizers**, by contrast, rest less and devote more of their time (and energy) to searching for and traveling between patches of foods. These foods, such as fruits, tend to be more widely dispersed than leaves, but they are also higher in easy-to-digest calories to fuel the extra energy required to find them.

Diets. Food is necessary for survival and reproduction. As we'll see in subsequent chapters, the ways that primate foods are distributed in space and time are among the most important determinants of their social lives. All primates eat a variety of different food items to obtain the carbohydrates, fats, and proteins they need. Energy and nutrient requirements vary with body size and metabolism, and, therefore, differ among individuals and species (Sussman, 1978). Diets are generally classified based on what the primates are eating most of the time. Those that devote significant proportions of their feeding time to consuming insects are called **insectivores**, those that consume non-insect invertebrates are called **faunivores**, fruit-eaters are called **frugivores**, and those that rely heavily on nonreproductive parts of plants such as leaves, stems, shoots, pith, and bark are called **folivores**.

As we'll see in Chapter 6, these simplified classifications can be highly misleading because they refer to the frequency with which different kinds of foods are eaten, which may or may not be indicative of their importance to survival. Moreover, most primates consume a variety of different food types, with the majority considered to be either insectivore-frugivores or frugivore-folivores because, while nearly all primates consume some fruit as their primary sources of energy, they differ in whether they rely on insects or leaves for their protein. Some primates consume prey items ranging from frogs and lizards to small mammals, such as hares, small antelope, or even other primates, along with their plant foods. Others supplement their diets with the gummy substance excreted by some tree species when their bark is punctured, as well as flowers and flower products such as pollen and nectar, bark, bamboo, and even dirt. The semiterrestrial primates may also include substantial quantities of grass and grass seeds or herbaceous vegetation in their diets.

Like their activity patterns, primate diets are strongly influenced by seasonal fluctuations in the availability of preferred foods. Recent analytical advances have made it possible to evaluate how primates balance their intake of nutrients in response to food seasonality (Rothman et al., 2012). Because of the importance of nutrition and **nutrient balancing** to survival and reproduction, identifying primate diets is essential to understanding many aspects of their anatomy and behavior, as well as patterns in their habitat use, ranging behavior, and social organization (Figure 1.15).

Habitat Use and Ranging. The semiterrestrial primates conduct much of their business on the ground, either feeding or traveling between their scattered food trees. Habitat use is more variable among arboreal primates depending on the level and kind of vegetation in which they spend most of their time. Indeed, contrary to what it might seem like at first glance, most of the tropical and semitropical forests inhabited by primates are a three-dimensional mosaic of different kinds of vegetation. Some primates find most of their foods in the **understory**, or the area below the trees but above the ground. The understory may be overgrown with dense impenetrable vegetation or fairly open depending on whether sunlight can penetrate or is blocked out by the leaf-covered branches overhead in the **canopy**. Other primates are stratified from the lower, to the main, to the upper canopy, and some even climb up into the **emergent** trees that tower above the rest of the canopy (Figure 1.16).

Figure 1.15 Gray-cheeked mangabey (*Lophocebus albigena*) consuming fig fruit (*Ficus sansbarica*) in Kibale National Park, Uganda. Photo © by Alain Houle.

Figure 1.16 Black and white colobus monkeys (*Colobus guereza*) by the Nile River in Murchison Falls National Park, Uganda. Photo by John F. Oates.

Primates must move through their habitats in search of food, while also managing to stay alive. The habits and habitat preferences of predators can make it risky for primates to travel through areas with poor visibility or few escape routes (Miller and Treves, 2011), and for arboreal primates there is always the risk of injury from falls. The distance traveled each day is measured in terms of **day ranges** or **daily path lengths** and the total area utilized is called the **home range**. Both daily path lengths and home range sizes are affected by the ways that foods are distributed in time and space. Differences in primate **locomotor** systems determine how quickly and efficiently they are able to move about in both two- and three-dimensional space (Garber, 2011; Blanchard and Crompton, 2011). The balance between the time and energy required to move between food resources and the nutritional quality of their foods affects primate daily path lengths.

When foods eaten over an annual cycle occur in concentrated clumps, primates can defend their food supply area from other members of their species. **Territorial** primates are those that defend the entire resource area they exploit from intrusions by other members of their species. This is usually only possible when their daily path length is roughly the equivalent of the radius of their home range (Mitani and Rodman, 1979). Nonterritorial primates have home ranges that overlap with the home ranges of other groups of their species. Some nonterritorial primates aggressively defend particular food sources, such as large fruiting trees, whenever they encounter other primates of their own or other species that compete with them for foods. But, because they require such large home ranges relative to their day ranges, they cannot keep intruders out of their home range at all times.

Territoriality is not necessarily a fixed attribute of a species. The same behavior, such as aggressive defense of food sources, may be territorial for a group of primates occupying a small home range but nonterritorial in a larger home range. Consequently, groups of the same species living under different conditions may be classified differently depending on the degree to which group home ranges overlap with one another.

Group Size. Most primates are **gregarious**, meaning that they spend most of their lives in social groups. **Solitary** primates are rarely seen with another individual except during brief periods to mate or during the period of infant dependency, when mothers are caring for their young. Gregarious primates form groups of various sizes made up of different age and sex compositions for a variety of reasons. One obvious advantage of a group is the increased ability to detect and defend themselves from predators. Another advantage of group versus solitary living is that groups include more individuals to find and defend food resources.

Groups can also be more conspicuous to predators, and competition for food can also impose limits on group sizes. Therefore, primates must balance the benefits of group living against the costs (Figure 1.17). Primate group sizes can vary tremendously between different habitats due to the effects of ecological variables, such as predator pressures and food availability, and **demographic** variables, such as population size and **population density**, or the number of individuals per unit area.

Primate groups also differ from one another in their degree of **cohesiveness**, or whether group members remain together on a routine basis. Chimpanzees, for example, have fluid, **fission–fusion** societies, in which group members split up into smaller parties and reunite in response to daily fluctuations in the availability and distribution of their preferred foods, whereas savanna baboons tend to stay together as a cohesive troop (see Table 1.2).

Grouping patterns, like ranging and territoriality, can differ from one population to another of the same species depending on the spatial and temporal availability of their foods, predation risks, and local demographic conditions. For example, chimpanzees living in predator-rich habitats, such as at Mt. Assirik, Senegal, join up in large parties and move rapidly and vigilantly when traveling long distances through areas where major predators lurk (Tutin et al., 1981, 1983). The grouping patterns of chimpanzees at the Taï National Park, Ivory Coast, also became more consistently cohesive over a ten-year period as the size of their community

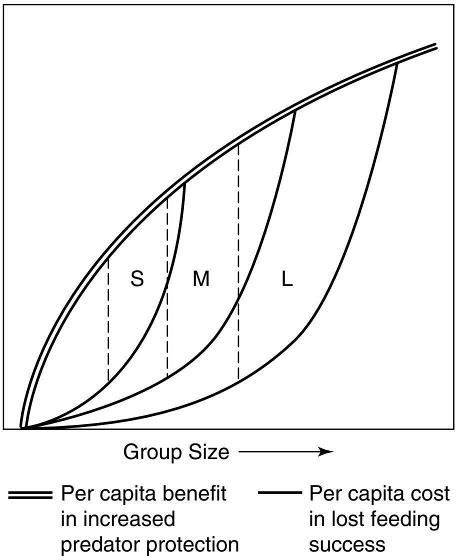

Figure 1.17 Model for optimal primate group sizes based on the compromise between costs of feeding competition and enhanced safety from predators. Dotted lines indicate the point of maximum benefits relative to costs when feeding on small (S), medium (M), and large (L) resources. Note that larger groups not only provide greater benefits against predators, but also have greater feeding costs, shown in key, and corresponding to the y-axis. From Terborgh, J. and Janson, C. H. (1986). The socioecology of primate groups. *Annual Review of Ecology and Systematics* 17: 111–135. With permission from the *Annual Review of Ecology and Systematics,* Vol. 17, © 1986 by Annual Reviews and the authors.

declined from 51 to 21 individuals and the number of adult males decreased from nine to two (Lehmann and Boesch, 2004). Conversely, the grouping patterns of northern muriquis at my field site at the Private Natural Heritage Reserve—Feliciano Miguel Abdala, in Caratinga, Brazil, have become increasingly fluid as the size of their group has increased (Strier et al., 1993; Dias and Strier, 2003). In addition, different social skills are required by primates who see each other sporadically, compared to those who associate continuously (Aureli et al., 2008). Exploring these differences provides insights into the role that sociality may have played in the evolution of primate cognition, as we'll see in Chapter 10.

Social and Reproductive Units. The composition of primate groups is affected by two factors. First, patterns of **dispersal** determine whether individuals of one or both sexes leave their natal groups to join another established group or form their own groups with other members of their species. Second, the ratio of females to males of reproductive age within groups, or the **socionomic sex ratio**, has profound effects on levels of mating competition (Dunbar, 1988). This can influence the degree to which males differ from females in body size and other traits that affect male competitive ability.

Male-biased dispersal was long thought to characterize most primates because of its prevalence among the Old World macaques and baboons that were regarded as "typical" primates (Moore, 1984; Strier, 1994a). However, we now know that female-biased dispersal or dispersal by both sexes are also widespread across primates. These varied dispersal patterns lead to very different genealogical relationships among members of primate groups. For example, in macaque and most baboon societies, females are **philopatric**, remaining in their natal groups for life. Dispersing males join groups composed of the extended, multigenerational **matrilines** formed by **matrilocal** females. When males are philopatric, like muriquis and chimpanzees, groups consist of **patrilocal** male kin that form extended patrilines. When both sexes disperse, groups will consist of unrelated or only distantly related members unless dispersing individuals transfer into the same groups as their kin. There are no known primate species in which both sexes routinely remain in their natal groups, a system that could lead to serious **inbreeding depression** (Chapter 4).

Understanding these differences in primate kinship systems is essential to understanding their social relationships (Altmann and Altmann, 1979; Moore, 1992a). Primates generally treat familiar individuals better than unfamiliar ones, and familiar biological relatives are generally the most reliable allies. Not surprisingly, whether primate societies are matrilineal or patrilineal affects female and male social options and the probability of having closely related allies on hand (Chapais, 2001). The number of breeding females and males in primate groups has traditionally been used to define their mating systems. Thus, whenever primate groups included a single adult male and female they were thought to be **monogamous**. The mating system of groups with a single male and multiple females was considered to be **polygynous**, while those with multiple males and females were thought to be **polygynandrous**. Among a few New World monkeys, groups with a single breeding female and multiple males appeared to have a **polyandrous** mating system.

These differences in the number of adult males and females in primate groups were once thought to be characteristic of different species and indicative of species differences in their mating systems. We now know, however, that the compositions of primate groups vary substantially in the same species living in different habitats and under different demographic conditions, and that the same groups may change in composition over time. For example, in an analysis of so-called monogamous primates, anthropologist Agustin Fuentes (1998) found that only 17 of 49 species previously considered to be monogamous were frequently seen living in two adult groups, and only seven of these were routinely monogamous (Chapter 5). In fact, the occurrence of single- and multi-male groups in the same populations has been documented in a variety of different species, and even groups with similar compositions, such as the multi-male, multi-female groups of chimpanzees, baboons, and muriquis, can exhibit quite different social and grouping patterns (see Table 1.2).

We also know that extrapolating from social groups to primate mating systems can be very misleading because primates don't always restrict themselves to choosing sexual partners that are members of their social groups (e.g., Cords, 1987). Behavioral observations indicate that many primates, including pair-bonded males and females, mate with individuals that are not members of their groups. In light of these findings, many of the early categorizations of primate societies are now being rethought (Kappeler, 2019). A good paradigm for thinking about the different components of sociality distinguishes between social organization, social structure, mating system, and care system (Figure 1.18). We can see that group size and composition describe the social organization, which is distinguished from the mating system. Adhering to this paradigm resolves many past confusions about whether pair-living primates are socially and genetically pair-bonded or not (Fernandez-Duque et al., 2020). It also helps in thinking about the evolutionary pathways from solitary and pair-living primates into group-living primates (Kappeler and Pozzi, 2019).

This paradigm is useful for thinking about the unusual **multilevel social organizations** that have long characterized hamadryas baboons, geladas, and snub-nosed monkeys, and have recently been described in Guinea baboons (Fischer et al., 2017) and Rwenzori Angolan colobus monkeys (Stead and Teichroeb, 2019). In these modular societies, there are three or four levels that increase in size and decrease in contact, beginning with the core, one-male unit (OMU) with one or more females, which may associate with groups of bachelor males in clans or with other OMUs as bands, which aggregate loosely as troops or herds (Swedell, 2012). The OMU is typically considered to be the reproductive unit, but in one population of golden

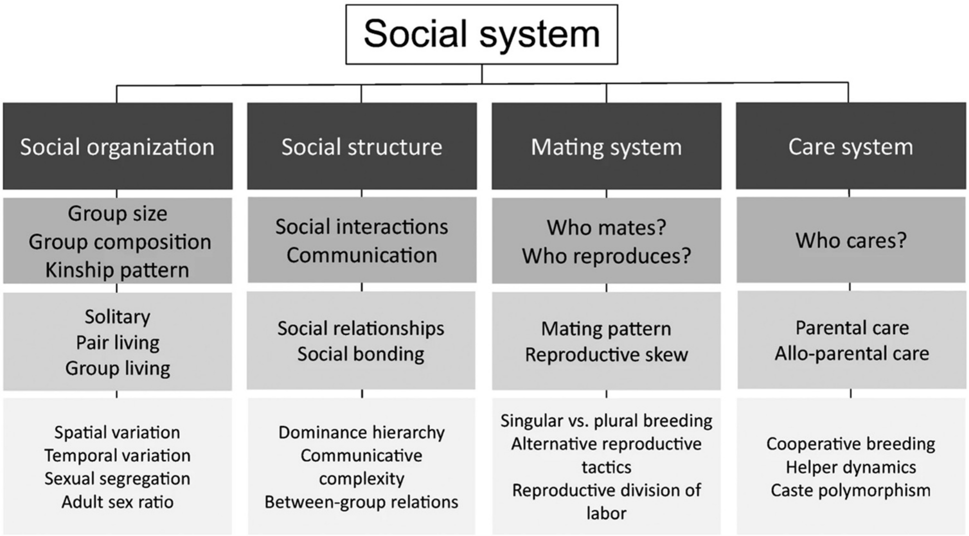

Figure 1.18 A framework for the study of social systems and social complexity. The first row indicates the four core components of a social system. The second row lists the main variables or questions addressed by each component. The third row contains key features of a social system that provide a general characterization of a given species. The differentiation between rows 2 and 3 is somewhat arbitrary, whereas the separation into different columns is not. Reproduced from Kappeler, P. M. A framework for studying social complexity. *Behavioral Ecology and Sociobiology* 73: 13 (2019). Springer Nature. https://doi.org/10.1007/s00265-018-2601-8. Reproduced under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/).

snub-nosed monkeys over a 17-year period, half of all infants were sired by extra-group males (Qi et al., 2020). We'll return to the significance of this kind of mating system when we consider baboon hybrids (Chapter 3) and primate social evolution (Chapters 4–8).

Field and Captive Studies

All of the aspects of primate behavior described so far, and most of the examples that follow in this book, come from studies of wild primates. But, it is important to realize that even when the first primate field studies were being conducted, there were few, if any, primate habitats that had not been altered in some way by human activities (Quiatt and Reynolds, 1993). Indeed, the effects of habitat disturbance are responsible for leading many primates to the verge of extinction. Nowadays, comparisons among primates inhabiting areas that have been subjected to different levels of disturbance are deliberately used to address questions about how primates adjust their behavior in response to local ecological and demographic conditions that can change over time (e.g., Sterck, 1998; Jones, 2005; Struhsaker, 2008; Strier, 2009). As a result, primate studies today may reach very different conclusions than they did in the past. During the early years of primate studies, however, such distinctions about the possible effects of human interference on primate behavior were rarely made.

In addition to the relatively naturalistic conditions of observing primates in the wild, there are more controlled ways of viewing them. **Provisioned** settings have designated feeding sites where food is provided, but the primates are otherwise free to come and go, or are restricted to large enclosures or islands where they have been introduced. In **captive settings**, they may be housed in large enclosures in either social groups similar to those found in the wild or in modified groups, or in solitary cages.

Studies on unprovisioned primates tend to be better suited than provisioned or captive studies for exploring certain kinds of questions, such as those about the relationship between the seasonal distribution of food and primate grouping patterns. However, provisioning can stimulate primates to interact more frequently than they do in the wild and can therefore accelerate our identification of social patterns. Once identified, these patterns can be studied more closely in unprovisioned groups where they are expressed at a slower pace. Captive studies that control and vary group membership and individual experience have been critical in calling our attention to many subtle behavioral phenomena, including the social suppression of reproduction, patterns of reconciliation after fights, and the ontogeny of vocal communication.

Captive studies also offer the advantage of better observation conditions and in many cases individual histories of the captive primates are known. However, there is always the possibility that the behaviors observed in captivity reflect extreme responses to their housing conditions instead of those that are most characteristic of them in the wild. For example, bonobos copulate at similar or lower rates during their swelling cycles than chimpanzees in the wild (Takahata et al., 1996; Furuichi and Hashimoto, 2002), but at other times, and in captivity, bonobos are much more sexually active than are captive chimpanzees. Captivity clearly has a different effect on bonobo sexual behavior than it does on chimpanzees, a discovery that could only have been made when field data and captive data on both species were compared (Stanford, 1998a).

Even under "natural" circumstances, we must be cautious in our observations and interpretations of primate behavior. This is particularly important when we know that their habitats have been recently altered and their behaviors may reflect recent responses to new challenges in these changed environments that may or may not be adaptive (Strier, 2009). The tremendous behavioral variation we now know primates exhibit also challenges our ability to generalize from the behavior of one study group to an entire species.

Many of our most important insights into the behavior of wild primates have come first from provisioned or captive populations. In the early years of her field study, Jane Goodall used bananas to lure the chimpanzees into her camp, where she could observe them more closely and begin to understand their social hierarchies. She also used the bananas to administer medication to chimpanzees ailing from illnesses they had acquired from the human settlements surrounding their forest (Goodall, 1971; Wallis and Lee, 1999).

Providing food to primates was also employed in the original studies on Japanese macaques. Fortuitously, provisioning the monkeys led to the adoption of novel techniques used by the macaques to wash sweet potatoes and sift sand out of wheat, providing some of the best examples for how innovative behaviors spread through primate societies to become **local traditions** (Kawai, 1965). Attracting primates to provisioned feeding sites is a powerful way of investigating the dynamics and negotiations of social relationships, and it was widely employed for studying primates whose elusive habits made them difficult to follow.

Captive studies provide opportunities to control and experimentally vary primate social and physical environments. Field studies provide opportunities to evaluate how behavior is affected by unpredictable ecological and demographic pressures, which more closely approximate the evolutionary circumstances under which primates evolved. Integrating data from both captive and field studies of the same species is a powerful approach (Bernstein, 1972), and it has become an increasingly important source of insights into what primates are capable of doing, and what kinds of stimuli trigger varied responses (Box 1.1).

Box 1.1 Clues from Captivity

Psychologist Charles Snowdon has pursued a rare breed of primatology. Most primatologists conduct either captive or field studies, but Snowdon has compared primates in both contexts. For many years, his laboratory at the University of Wisconsin-Madison housed colonies of two species of New World monkeys, pygmy marmosets, one of the world's smallest monkeys found throughout the Western Amazon, and the endangered cotton-top tamarin, found only in small remnant forest patches in northwest Colombia. Snowdon's students have studied both species in the wild, and now, the pygmy marmoset study, in collaboration with Ecuadorian primatologist Stella de la Torre, is being conducted entirely in the field.

Marmosets and tamarins belong to the Callitrichidae family, a diverse group of monkeys known for their high reproductive rates. Dominant female cotton-top tamarins give birth to twins, and sometimes triplets, at seven- to ten-month intervals in captivity. At birth, these twins weigh 19 percent of their mother's weight, the equivalent of a 120-pound woman giving birth to two 11½-pound infants. Unlike most primate mothers, marmosets and tamarins get help caring for their infants from adult males and older offspring in their families. These nonmother caretakers do most of the infant carrying and provide solid food at the time of weaning (Figure B1.1). As a result, callitrichid mothers can get pregnant within two to four weeks after giving birth.

The help that mothers get in caring for their infants is critical to infant survival. Snowdon and his colleagues have found in both captive and wild populations that infant survival does not approach 100 percent unless at least four helpers are present. Experience at taking care of infants turns out to be important, too, because adults that have not been helpers prove to be poor at parenting when their own offspring are born.

Female cotton-top tamarins reach puberty at 18 months of age, yet daughters living in captive groups never produce offspring of their own (Ziegler et al., 1987). Measuring hormones from daily urine samples, Snowdon's group found that these dutiful daughters don't even ovulate. There is nothing biologically wrong with these females, because as soon as they are removed from their family groups and paired with unfamiliar males, they ovulate and can become pregnant within eight days.

Pursuing the mechanisms behind this reproductive inhibition led Snowdon's group to discover that transfer of odors from the mother to newly paired daughters delayed the onset of ovulation and prevented pregnancy (Savage et al., 1988). Chemical signals have been shown to synchronize ovulation and menstrual cycles in women (Stern and McClintock, 1998), so it is not surprising that similar cues, known as **pheromones**, influence ovulation in monkeys as well. But exposure to novel males is also an important stimulus in tamarins. Daughters removed from their families, but paired with their brothers, failed to ovulate, whereas those paired with or even housed within sight and sound of a novel male rapidly ovulated (Widowski et al., 1990, 1992).

Reports from the field both support and conflict with these findings. Some wild cotton-top tamarin groups contain two pregnant females, but whether this only occurs after a novel male has joined the group is still not clear (Savage et al., 1996a, 1997). Reproductive inhibition is often observed in captive common marmosets (Abbott et al., 1993), but multiple pregnant females are relatively common in at least one wild population in northeastern Brazil (Digby and Ferrari, 1994; Sousa et al., 2005). Interestingly, when two wild marmoset females gave birth close in time, the dominant female directed aggression toward the infants of the subordinate female (Digby, 1995, 2000). But, aggression toward the subordinate female's infants is rare when births are separated in time. Moreover, in contrast to the dominant females, which mate mainly with group males, subordinate females mate mainly with extra-group males (Arruda et al., 2005).

Figure B1.1 Breeding male cotton-top tamarin (*Saguinus oedipus*) carrying an infant. Photo by Carla Boe.

Multiple breeding females have also been observed in wild groups of buffy-headed marmosets (Ferrari et al., 1996; Guimarães, 1998), buffy-tufted-ear marmosets (Coutinho and Corrêa, 1995), saddle-back tamarins (Goldizen et al., 1996), and golden lion tamarins (Dietz and Baker, 1993; Baker and Dietz, 1996). In each case, the dominant female was the only one that reproduced routinely, but the variability in reproductive activity of subordinate females contrasts with the reproductive inhibition seen in captivity. Perhaps the suppressing effects of social or pheromonal cues communicated by dominant mothers are weaker or easier to avoid in the wild than in the closer confines of captivity. Perhaps more opportunities are available in the wild for females to locate unrelated males. Evaluating hypotheses about reproductive inhibition and cooperative infant care requires multifaceted approaches that combine field and captive studies and that integrate behavioral and hormonal data on proximate mechanisms and their functional, adaptive significance.

Evolutionary Models and Problem-Oriented Studies

During the 1960s, primatology was catapulted out of its descriptive, classificatory phase into a rigorous quantitative science. This transformation was based on the explicit adoption of rigorous methodological practices, in which behavior was sampled in a standardized way in order to minimize the biases and subjective impressions of observers (Altmann, 1974). Behavioral categories were carefully defined so that different researchers could use similar criteria for scoring an interaction or a behavioral event. Observation periods, or sampling schedules, were dictated arbitrarily by time intervals instead of by the primate's behavior or the observer's attention, making it possible to reliably calculate frequencies or rates at which particular behaviors occurred. Methods of collecting systematic behavioral data now range from the use of check sheets, to hand-written or tape-recorded descriptions, to digital recording devices. The best ways to collect data depend on the behaviors of interest, observation conditions, and logistical considerations such as terrain and the activity patterns of the animals (Paterson, 2001; Setchell and Curtis, 2011). The results obtained from these methods can then be compared across individuals in a study group, across time for the same study group, and across studies of other groups and species, including nonprimates (Harcourt, 1998).

The widespread adoption of these **systematic methods** of behavioral sampling also made it possible to objectively evaluate specific questions, which could be framed in terms of testable hypotheses, using comparative data. The theoretical shift of the seventies involved the incorporation of **evolutionary theory** to understand *why* individual primates behave as they do in the societies they live in, and *why* they live in their particular societies. From an evolutionary perspective, behaviors are treated like any other traits that are potentially subject to selection pressures for survival, which is a prerequisite for **reproductive success**, or an individual's direct genetic contribution to future generations. Evolution will act on social behavior if it is **inherited**, or has a genetic basis, and if it affects individual **fitness**. Individuals that behave in ways that increase their survival and reproductive success will pass on more of their genes than individuals that behave in less **adaptive** ways. For example, in contrast to solitary individuals, those that form groups in which individuals share the burden of watching for predators may be better able to avoid being eaten while also ending up with more free time for other essential activities, such as feeding, that improve their own reproductive success.

The difference in fitness between gregarious and solitary individuals will determine the strength of the selection pressures favorable to either type of lifestyle. The absence of predators might reduce the benefits of group living in one area, while the presence of predators might make group living highly advantageous in another area (van Schaik and van Noordwijk, 1985a). Even a shift from nocturnal to diurnal habits could be a recent response to relaxation in selection pressures from the extinction of diurnal predators (van Schaik and Kappeler, 1996).

Social skills associated with getting along in groups without being evicted, and for gaining access to the most or the best foods within groups, would also be favored by natural selection pressures (Dolhinow, 1972). And, because relatives share a proportion of their genes through common descent, individuals that choose to share vigilance and food with kin might benefit their own **inclusive fitness** indirectly through the reproductive success of their kin. Of course, keeping kin close at hand can also be risky because a catastrophe, such as a hurricane or drought, could potentially wipe out an entire genealogical line. In this case, it might be better for kin to disperse as far as possible, thereby hedging their bets in the fitness game. Indeed, many primates live in groups composed of nonkin. The trade-offs between extremes such as these are what we now think account for the patterns of behavior we observe. And, because there is no single rule that makes a particular behavior ideal under all possible circumstances, the fitness consequences of alternative behaviors can be difficult to predict and even harder to test (Bernstein, 1999a).

Evolutionary theory provided primatologists with a basis for developing predictions about primate behavior, which could then be evaluated quantitatively with data obtained systematically. The convergence of systematic methods and evolutionary theory launched primatology into a problem-oriented discipline in which comparative models could be tested and refined (Altmann and Altmann, 2003).

Sociobiology and Behavioral Ecology

These advances in evolutionary theory grew largely out of studies on insects, birds, and other nonprimates, which continue to exert a powerful influence on both theoretical and experimental approaches to primate behavior (Harcourt, 1998). Indeed, some of the most persuasive of these influences involved focusing on the evolution of female behavior, and how the behavior of females affects that of males (Figure 1.19). The development of evolutionary principles to understand the adaptive advantages of behavior under different ecological conditions is the basis for the field of **behavioral ecology** (Krebs and Davies, 1993) and its more controversial forerunner **sociobiology**, or the biological study of social behavior.

When Harvard biologist E. O. Wilson (1975) compiled the principles of evolutionary theory as they apply to behavior in his comprehensive book appropriately entitled *Sociobiology: The New Synthesis*, nonhuman and human primates were treated in sequence in the final two chapters. The idea that the evolution of human social behavior is continuous with that of other animals generated heated debate. For example, most behaviors of interest are complex traits, not simple ones controlled by single genes. The evolutionary process of **behavioral adaptation**, which is sensitive to the influence of environmental conditions, should not be confused with the misleading concept of genetic determinism, which would mean that behavior was entirely controlled—and predestined—by genes. In fact, evolutionary theory assumes that

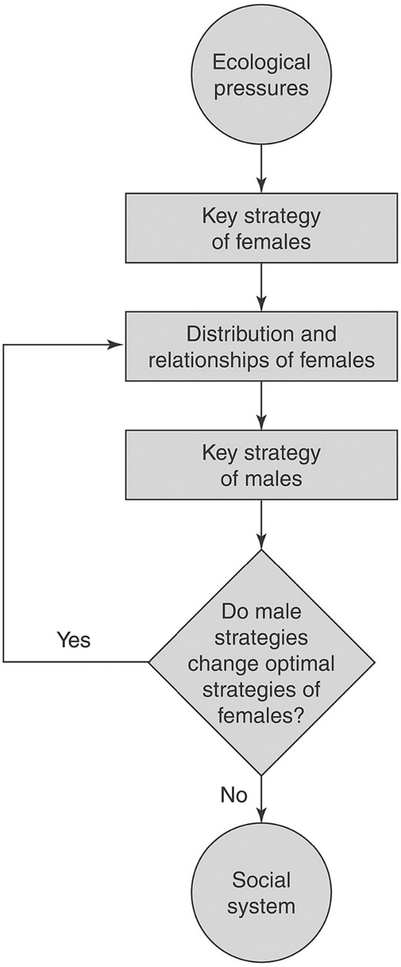

Figure 1.19 Female-focus view of social evolution. From Wrangham, R. W. (1982). Mutualism, kinship and social evolution. In King's College Sociobiology Group, eds., *Current Problems in Sociobiology.* Cambridge: Cambridge University Press, pp. 269–289. Reprinted with permission from the author and from Cambridge University Press. © 1982, Cambridge University Press.

behavior, like all other complex traits, has both a **genotype**, or genetic component, and a **phenotype**, which is the expression of an individual's genotype as it is affected by environmental influences.

What we see when we observe primates behaving is their phenotype, the product of the physical and social environment interacting with an individual's genetic makeup. Many aspects of primate behavior and biology exhibit high levels of **phenotypic plasticity**, or variability that may reflect adaptive responses to environmental changes over time (Fuentes, 2011). Nonetheless, in the shorthand of evolutionary theory, a behavioral phenotype is often described as if it were a **strategy**, shaped by the process of natural selection because of its advantages to individual survival and reproductive fitness. Although there are no assumptions of intentionality, there are references to **feeding strategies**, or behavior patterns involved in selecting different kinds of foods, and **social strategies**, or behaviors that lead primates to live in different kinds of groups and affect how they maintain their relationships within these groups. **Reproductive strategies** refer to behaviors that increase the likelihood of gaining access to mates and insuring their offspring's survival. **Life history strategies** are the trade-offs in patterns of development, from gestation length, to interbirth intervals, to age at first reproduction and life span, that influence the behavior of individuals at different times in their lives.

Early critics of evolutionary theory challenged the implication that ants, baboons, or even humans make conscious decisions or thoughtful calculations about how their behavior will affect their fitness (e.g., Sahlins, 1976). In fact, evolutionary theory does not make such untestable assumptions about conscious intentionality underlying the fitness consequences of behavior. In the jargon of behavioral ecology, *strategies* refer to behavior patterns that appear to increase fitness and therefore have functional, or adaptive, significance, and not to the mental processing of the fitness consequences by the organism (Box 1.2).

Box 1.2 Word Watching and Ethics

The words we use to describe the primates we study, the behavior patterns they exhibit, and their interactions with other species including humans in their communities carry underlying meanings we may not intend. Perhaps because of this, terms that have been directly or indirectly associated with sexist, racist, or colonialist implications in other fields of knowledge are increasingly being reconsidered by primatologists in response to increasing sensitivity about the power of our words. By the early 1980s, with the establishment of feminist theory and growing numbers of women in primatology, terms like "harems," which invoke descriptions of human societies in which despotic males control resources and female reproduction, were replaced with more objective descriptors based on the demography of these one-male (or uni-male), multi-female groups (Haraway, 1989; Fedigan, 2001).

Other terms, such as "weed species" or "agricultural pests," have been aptly applied to primates such as macaques in many parts of Asia and capuchin monkeys in South America, respectively, because of the capacity of these primates to survive in human-modified agricultural landscapes. However, these terms also carry unintended negative connotations that ignore the long histories of human–primate relationships in these and other parts of the world. Labeling these types of relationships under the rubric of "human–wildlife conflict" or "crop-raiding" carries other explicit meanings that may or may not accurately describe historical interspecific dynamics, particularly when human agricultural products (often planted on previously forested primate lands) are involved (Hill, 2017, 2018). Instead, and much like the efforts to eliminate terms with sexist associations from the primatological literature, a new set of more objective terms, including "sympatric primates," "provisioned primates," and "crop-foraging or urban foraging," are being increasingly adopted (Maréchal and McKinney, 2020). Situating primate–human relationships in more descriptively neutral terms is also less at odds with conservation agendas in which local human communities are involved.

There is an equally compelling argument for refining terms like "female dominance" to more accurately describe the different dimensions of intersexual power relationships (Lewis, 2018, 2020). Drawing on comparative analyses of the intersexual social dynamics of lemurs, University of Texas-Austin anthropology professor Rebecca Lewis distinguished the species and contexts in which females have superior fighting abilities over males from those in which females have greater power to control resources than males. As we'll see in later chapters, female primates often gain leverage over males, and therefore hold more powerful positions in their societies than traditional hierarchy-based language would imply.

There is current discussion among an international group of primatologists about whether historically colonialist designations of New World primates and Old World primates should be rethought. Although the current classifications will be retained in this book until a new consensus is reached, there can be no doubt that contemporary primatologists care about the sociopolitical contexts and broader ethical implications of how we communicate about our study subjects and our work (Riley and Bezanson, 2018; Norconk et al., 2020).

Testing Predictions about Behavioral Adaptations

It is important to emphasize that generating predictions about behavior based on evolutionary theory is not the same as testing or proving them. Behavioral ecologists must be wary of claims that assume all behaviors are adaptive, and, instead, focus on what our study subjects actually do. We must also be wary of generalizing from single observations, or anecdotes (Sarringhaus et al., 2005). But, it is important to recognize the value of anecdotes, which show us both the behavioral potential of primates and the complex contexts in which their behaviors take place, and can stimulate us to ask new questions (Ramsay and Teichroeb, 2019; Strum, 2019). Careful observation and critical assessment are essential to evaluating whether behavior conforms to predictions based on what other animals do under similar circumstances. Deviations from predictions can be exceptions, or they can indicate that our underlying premises are wrong (Fuentes, 1999; Thierry, 2008). It is not always possible to distinguish between these alternatives, as many of the primate examples described in this book will show.

Long-Term Field Studies and Individual Variation

Behavioral ecology opened up primatology to the value of broader comparative studies on a wider diversity of primates and other animals, and has helped to reinforce the value of in-depth, long-term studies. Long-term studies are particularly critical when primates are involved because of their long life spans, slow development, and slow reproductive rates relative to other animals of similar body sizes (Charnov and Berrigan, 1993). A 15 to 20-pound dog, for example, will be fully weaned within six to eight weeks of birth, and ready to give birth to her own pups within a year or two after that. A similarly sized female baboon, by contrast, will be dependent on her mother for at least six months, and won't be reproductively mature until at least four years of age. As a result of these **life history traits**, it takes many years to accumulate enough observations from enough individuals of different ages and sexes to be able to distinguish general behavioral patterns from individual variation under a wide range of contexts, as we'll see in Chapter 9.

Collecting longitudinal data on the same study subjects is a fundamental method in ecological studies of plant and animal communities and in professions ranging from economics to epidemiology. Marketing experts, stockbrokers, and meteorologists use longitudinal data to evaluate trends in their respective areas, which then form the basis for predicting future product sales, interest rate fluctuations, or global warming. Longitudinal data about primates provide similar bases for predicting individual behavioral strategies and testing hypotheses about behavioral adaptations.

Some of the most extensive long-term data for any animals come from the continuation of primate studies begun during the 1950s and early 1960s on macaques, baboons, and apes (Wolfe, 1987). Several of the original study groups that have been followed all these years have undergone major demographic changes resulting from births, deaths, and immigration and emigration events. Some groups have split up as they expanded in size, while others have been taken over by larger neighboring groups. Fifth-generation descendants of the original Gombe chimpanzees have joined their great-great-grandparents as *National Geographic* stars. Research initiated more recently on other primates in other locations does not yet match these original studies in duration, but as these newer studies move into their fourth and fifth decades, they are also contributing critical comparative insights into the dynamics of primate societies.

Primates are also subjected to complex ecological conditions, such as predictable rainy season and dry season fluctuations in the availability of food and water resources, as well as longer-term cycles in rainfall and food availability that span multiple years. Annual fluctuations in rainfall and food availability affect primate diets and reproduction, as well as their ranging, activity, and grouping behaviors. The effects of ecological fluctuations with even longer time frames require correspondingly longer periods to document. For example, when yellow baboons were first surveyed at Amboseli National Park, Kenya, in 1963 to 1964, there were over 2,000 individuals (Altmann and Altmann, 1970). By 1971, the area's baboon population had declined to about 200 individuals (Hausfater, 1975), and similar declines occurred in the local vervet monkey population as well (Struhsaker, 1973). These fluctuations have been attributed to alterations in the vegetation that baboons and vervets eat. Originally, shifts in underground water levels, which bring vegetation-killing salts to the surface in the volcanic soils at Amboseli, were implicated (Western and van Praet, 1973). Later, however, the role of elephants in destroying the vegetation has been implicated in contributing to the decline in the primate populations here (Western, 1997).

The Amboseli monkeys, like all primates nowadays, face additional challenges as their habitats and populations are modified by increasingly intrusive human activities. As humans clear forests for agriculture, some primates, such as rhesus macaques, have been able to adjust their diets to include cultivated crops (Richard et al., 1989). Some baboons at Amboseli have taken advantage of the garbage dump from a nearby tourist hotel, gaining a constant food supply that has given females in this troop some reproductive advantages, including faster maturation and shorter interbirth intervals, compared to females in troops that rely only on the wild foods in the park (Samuels and Altmann, 1991). Still other primates, including muriquis and some lemurs, appear to be able to survive at higher densities in forests that have suffered human disturbances than in more pristine forests where the diversity of food choices and the quality of food may be more limited (Pinto et al., 1993; Ganzhorn, 1995; Strier and Fonseca, 1996/97).

However, most primates rarely fare well when humans are near. Primates with highly specialized diets suffer from food shortages when their habitats are altered. Hunting and poaching pressures also plague primates, from mountain gorillas to marmosets. Often group members are slaughtered as they heroically defend prized infants from poachers who want to capture them for zoos or for sale as pets. Logging companies open roads into forests that not only alter primate habitats, but also make it easier for hunters to kill primates for food (McRae, 1997).

Destruction of surrounding areas causes what habitat that does remain to become saturated with primates, leading to significant behavioral changes, such as those described for Thomas langurs, an Asian leaf-eating monkey. Female langurs usually maintain casual, egalitarian relationships with one another, but their relationships may become more aggressive and hierarchically structured when they are forced by habitat disturbances to take refuge in saturated areas where opportunities for avoiding one another are limited (Sterck, 1998, 1999; Sterck et al., 1997). Documenting primate responses to both natural and human-induced changes in their habitats has become an urgent priority in primate conservation, and reinforces the importance of long-term studies that can identify the risks that habitat alterations pose for primates (Hockings et al., 2015; McLennan et al., 2017; Strier, 2017).

Comparisons among Species

Comparisons among different primate species are a powerful way to evaluate the adaptive significance of behaviors under different ecological conditions (Clutton-Brock and Harvey, 1984). Early anthropocentric approaches to primates were also comparative in their focus on those species that were thought to make the best **referential models** for humans because of parallels in their ecologies or their phylogenetic proximity. Seeking the best comparative reference for humans led to vigorous debates such as whether the societies of early human ancestors were hierarchical or egalitarian, or matrilineal or patrilineal (Fedigan, 1982). Particular species, such as baboons or chimpanzees, were promoted as the most appropriate candidates depending on the backgrounds and perspectives of the researchers studying them.

Some scholars have suggested that the reason aggressive competition among male primates received so much attention during the post-World War II years was a direct result of sexist attitudes about male dominance and the origins of human warfare and conflict (Haraway, 1989). Attention to the influential roles of female primates in their societies has also been attributed, in part, to the rise in feminist theory and influence in US society during the late 1960s and early 1970s. However, it is important to remember that this period also coincided with the explosion of evolutionary theory in animal studies, which also recognized the importance of females and their tremendous influence on males and their societies (Eisenberg et al., 1972; Emlen and Oring, 1977; see Figure 1.19).

Behavioral ecology helped to shift anthropocentric perspectives in primatology away from the focus on finding referential behavioral models for human social evolution (Richard, 1981). Instead, **strategic models**, which emphasized the evolutionary and ecological processes that affect behavior, were developed to provide an alternative way of understanding behavioral adaptations (Tooby and DeVore, 1987). For example, instead of extrapolating from the ranging patterns of chimpanzees to those of human ancestors, we might predict that primate day range lengths increase with the proportion of fruit in their diets because fruits occur in patchy, clumped distributions compared to other foods, such as leaves, which have more even spatial distributions and can be harvested within a smaller area (Moore, 1996). Comparing the diets and day ranges of various primates provides a way to evaluate this prediction, along with the broader underlying principle that primate ranging patterns reflect adaptations to their particular feeding strategies (Carbone et al., 2005).

Predictions about the adaptive advantages of primate sociality under different ecological conditions can be similarly tested with comparisons among species. Consider, for example, the societies that characterize chimpanzees and their closest relatives, bonobos, which unlike chimpanzees are found only in a small portion of the Congo Basin. In chimpanzees, male contests for dominance and status are so striking and so persistent that males have been described as having "demonic" streaks (Goodall, 1986; Wrangham and Peterson, 1996). Male bonobos, by contrast, seem to be much less excitable, in part because they spend more of their time around females, who play an active role in easing social tensions by engaging in sex (de Waal, 1987, 2005).

Differences in chimpanzee and bonobo patterns of association correspond to differences in their diets and are largely consistent with the ways in which feeding strategies affect social relationships in other primates (Chapter 6, Chapter 7, Chapter 8).

Evaluating the effects of demography on behavior can be equally informative, especially when the comparisons involve the same study subjects over time. Just as increases or decreases in group size can lead to correspondingly more fluid or cohesive grouping patterns, shifts in adult sex ratios, such as from female- to male-biased, can lead to corresponding changes in levels of male–male competition for mates, and even in deviations from the usual patterns of male- or female-biased dispersal (Hohmann, 2001; Strier, 2003a; Jones, 2005; Erhart and Overdorff, 2008).

Comparisons among primate species have become more sophisticated as predictions from behavioral ecology, often based on other animals, have become more specific and as the diversity of primates included in the comparisons has increased. Statistical methods are now used to control for the phylogenetic relationships among species so that comparisons can be made based on independent evolutionary events (Krebs and Davies, 1993; Nunn and Barton, 2001). In fact, focusing exclusively on comparisons between closely related species, such as chimpanzees or bonobos, can be misleading if the behavior patterns of interest are exhibited by other, more distantly related primates as well. For example, male bonding occurs in primates other than humans and chimpanzees, and nonreproductive sex occurs in primates other than humans and bonobos. Looking at a broader comparative sample of primates provides insights into the behavioral similarities and differences among them (Strier, 1994, 2001; Chapman and Rothman, 2009).

Part of the expansion in comparative primate studies has been due to explicit efforts to test existing models in primate behavioral ecology. Insights from these previously neglected primates generate new predictions, further increasing our understanding of the diversity of primate adaptations and refining our comparative perspectives.

The expansion of primate studies has also been stimulated by the increasing threats to primate survival. Elusive primates are often the ones with the most precarious futures, and learning about their adaptations is often the first essential step toward developing informed conservation management plans to protect them. As we will see in many of the examples given throughout this book, primate behavioral ecology and conservation are inextricably linked (Strier, 1997a, 2003b; Linklater, 2004).

Other Units of Comparison

The common anthropomorphic practice of distinguishing individual primates instead of lumping them together into age or sex classes was reinforced by, and contributed to, the focus on individual variation in evolutionary theory. Individual-level comparisons can involve the same individuals at different times, such as female diets during the rainy season versus dry season, or rates of social interactions among males during adolescence versus adulthood. Comparisons can also be made among individuals during the same period of time, such as male versus female diets during the rainy season of a particular year, or dominant versus subordinate female mating patterns during a particular breeding season.

The behaviors of individuals in select **study groups** are then pooled to develop the comparative species models that form the basis for our understanding of primate behavioral adaptations. However, it is important to remember that much of what we know about many primates still comes from single study groups during a short span of their histories, which may not be typical of the species. The question of whether one study group is representative or atypical is impossible to assess without comparative data from the same group over time and from other