PRIMATE BEHAVIOR AND HUMAN ORIGINS

GLENN E. KING

COMPANION WEBSITE

ROUTLEDGE

Primate Behavior and Human Origins

This comprehensive introduction demonstrates the theoretical perspectives and concepts that are applied to primate behavior, and explores the relevance of non-human primates to understanding human behavior. Using a streamlined and student-friendly taxonomic framework, King provides a thorough overview of the primate order. The chapters cover common features and diversity, and touch on ecology, sociality, life history, and cognition. Text boxes are included throughout the discussion featuring additional topics and more sophisticated taxonomy. The book contains a wealth of illustrations, and further resources to support teaching and learning are available via a companion website. Written in an engaging and approachable style, this is an invaluable resource for students of primate behavior as well as human evolution.

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To the people who have meant the most to me –

In my professional life
Sherwood L. Washburn
William A. Lessa
William P. Mitchell

and in my personal life
Barbara Barrett
Cynthia King
David King
Kimberly Spurgeon
Edith King

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Preface

In graduate school primate behavior lured me away from other fascinating specialties and actual experiences did nothing to change that feeling. The first was a sweltering summer in New Mexico, observing a colony of captive chimpanzees that impressed me with their intelligence, strong personalities, and complex relationships. Next, I studied three kinds of baboons (a loose term for certain large monkeys) in the Los Angeles Zoo. The fog of rising at dawn began to lift when Billy, the adult male mandrill, gave me the seemingly fearsome snarl that is really a greeting in his species (Figure 0.1).

Figure 0.1 A male mandrill "grins"—a friendly expression. © abzerit via iStock

In Africa I observed baboons in their natural setting. Expected behavior patterns were spiced by unusual occurrences, such as a male baboon lifting an infant over his head in a movement reminiscent of a human father's play. Ordinary events sometimes assumed unexpected dimensions—the simultaneous crunching of crisp fruits by 30 or 40 baboons became hilarious. And there were close encounters like those at the Serengeti Lodge, where a vervet strolled into the restaurant and a baboon tried to become my roommate.

Primate studies also bring you into contact with interesting people, many of them nice. I was swindled in Nairobi, but invited to a dinner of roast goat by a chance acquaintance. I was bawled out by a pompous minor official in a Tanzanian park, but invited to share meat ("Karibu chakula") with a hospitable game warden. I was frustrated by elusive baboons in South Africa, but comforted by one of the best cooks and one of the kindest couples I have ever met. And I learned that two people can communicate about important things despite rudimentary knowledge of one another's languages.

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William A. Lessa provided a floundering new graduate student at UCLA with support and direction, nurturing a continuing interest in cultural anthropology. Sherwood L. Washburn opened a new world of primate behavior in relation to human evolution. He guided me to my doctorate at Berkeley, along with Phyllis Dolhinow. William P. Mitchell escorted me through the intricacies of professorship at Monmouth University and became a good friend along the way.

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Many people encouraged me in the long trek to this book. Foremost is my fabulous wife Barbara Barrett, who was always there with whatever I needed most, whether it was techinal advice, a loving word or a snarky remark. I'm also grateful to Cynthia King, Al King, Jack Bufton, Mary Carol Stunkel, and many others at Monmouth University in New Jersey and St. Mark's Episcopal Church in Highland, Maryland. Special thanks go to the Department of History and Anthropology at Monmouth and to Dr. Kenneth Stunkel, who again provided both moral and immoral support.

Brian Barrett made valuable comments on parts of the manuscript. Lin Gaylord midwifed the project. Katherine Ong and Lola Harre of Routledge guided it to maturity with cheerful skill and great patience. It has been a great pleasure working with them.

An undertaking like this one requires ready access to an enormous and varied professional literature. I am deeply grateful to the following individuals for making the resources of the Monmouth University Library available to me: Dr. Thomas Pearson, Provost; Dr. Ravindra Sharma, Dean of the Library; and Grey Dimenna, Esq., University Attorney.

I'm very thankful to all the colleagues who have made their work available via mailed reprints in the past and online in more recent times. The personal and laboratory websites of colleagues have been enormously helpful and ResearchGate and Academia.edu. have also been of great value. For images in this book I want to acknowledge the generosity of Yvonne de Jong and Tom Butynski; Rhett Butler and Mongabay, and with special thanks, Stacey Tecot, Eric Matthews, Chimpanzee Sanctuary Northwest, and Curt Busse.

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Introduction

A Book about Humans and Other Primates

This book will introduce the reader to our closest living relatives. Monkeys and apes are the most familiar members of a large group that includes lemurs, lorises, and tarsiers. Primates are fascinating animals that are worthy of study in their own right. Nevertheless, due to shared ancestry, we have many physical and behavioral features in common with other primates and this is also a legitimate focus of scientific inquiry. Information about other primates is widely used to shed light on human evolution and modern human characteristics.

This text is unusual in the extent to which it combines the study of nonhuman primate behavior with applications of that study to understanding our ancestors and ourselves. Probably every introduction to primate behavior gives a nod to the subject's anthropological relevance, but this book makes it an important theme. All major groups of primates are covered, but there is an overall emphasis on the ones that are more relevant to understanding humans and their ancestry.

Organization of the Book

The first chapter introduces the primates in a general way. The second surveys methods, concepts, and general theories used in the study of primate behavior. Chapter 3 describes behavior patterns that occur in many or most of the species and introduces additional theoretical perspectives. The rest of the book covers important features of major subgroups with emphasis on relatively distinctive traits. Each chapter discusses theoretical perspectives that are helpful for understanding the described behavior.

This survey of nonhuman primates leads up to a review of how the data are used to better understand recent humans and their prehistoric ancestors. Three chapters deal with the last common ancestor shared by humans and nonhuman primates, the further evolution of our early ancestors, and the continuing influence of this evolutionary heritage on the behavior of recent and contemporary humans. These chapters give critical consideration to relevant primate models. The text follows the convention of using the word *primate* alone to stand for nonhuman primates. Where humans are included in a statement, this is indicated where necessary by phrases such as *humans and other primates* or *primates, including humans*.

The final chapter attempts an overview of primate conservation, including common problems and some distinctive issues arising from primate diversity. I hope that concern for the conservation of primates will have been heightened by contact with their fascinating behavior and their relevance to understanding ourselves.

Reading the Text

The descriptions of primate behavior are arranged under four headings: Ecology, Sociality, Life Cycle, and Cognition (Table 0.1 summarizes the definitions for easy reference). This will facilitate comparison of the various primates described in the book. *Ecology* encompasses all the relationships between a kind of animal and everything in its environment. *Sociality* refers to interactions among members of a group and the group structure that this behavior represents. The *Life Cycle* is the typical path of an individual's development from infancy to death. Each stage has its distinctive behaviors and relationships. *Cognition* is used broadly here to include all mental capabilities and processes, ranging from intelligence to emotion. Social traditions are based on mental capabilities, so they are considered under this heading.

Table 0.1 Categories of Behavior

Ecology	Relationships between a kind of animal and relevant features of its environment.
Sociality	Interactions among group members and the group structure that this behavior represents.
Life Cycle	Developmental stages of the individual from birth to death.
Cognition	Mental capabilities and processes, including transmission of traditions.

In comparative studies it is important to have some idea of how widespread behavioral patterns are. Several non-technical terms, as defined for this book, will be used to provide a rough idea of trait distributions (Table 0.2 summarizes the definitions for easy reference). This is intended to provide a feeling for the frequency of the behavior patterns without using misleadingly precise formulations. *Ubiquitous* behavior patterns are defined here as being found in virtually all well-studied species of a particular taxon. This term is used instead of *universal*, because it is impossible to establish that there are no exceptions to a widespread pattern. *Typical* behavior patterns are widely distributed throughout a taxon, but with a significant number of exceptions. A *recurrent* behavior pattern occurs several times in a taxon without being frequent enough to be called typical. Because it is often difficult to distinguish typical from recurrent behavior patterns with available evidence, the word *common* is used for a behavior pattern that is at least recurrent and possibly typical.

Table 0.2 Terminology for Frequency of Behavior Patterns

Ubiquitous	Found in virtually all well-studied species of a taxon.
Typical	Widely distributed in a taxon, but with numerous exceptions.
Recurrent	Appearing several times in a taxon, but not typical.
Common	Recurrent and possibly typical (data insufficient to distinguish).

Textbooks often present research data in their original precise form, e.g. "the average infant weighed 453.5 grams". This gives a misleading impression of exactness because the average from one study will not be exactly the same as the average in another. Most numbers in this book are rounded off. The infants cited above would be described as weighing "about 450 grams".

The most important terms in the text are emphasized in two ways. Those that are unfamiliar or that have a technical meaning are given in boldface the first time that they appear in the text (e.g. **catarrhine**). These are listed in the Glossary. The importance of some well-known terms is emphasized with the conventional use of italics (e.g. *only*). These do not appear in the Glossary.

Saving Space

This section describes several measures that have been taken to allow enough space for relatively comprehensive coverage of the subject. First, there are bibliographic liberties. The sources for each chapter have been divided into **Basic Bibliography** and **Additional References**. The Basic Bibliography consists of general works that provide fundamental information and concepts that are agreed upon by most experts. These are rarely given specific reference within the text. Additional References (mostly journal articles) are indicated in the text in parentheses (e.g. Jones 2013). These serve several purposes. Some augment the Basic Bibliography by providing additional information or updates. Others represent divergent opinions on controversial issues. Still others provide interesting sidelights, such as unique observations.

Many individual references have been shortened. Most of the journal titles have been abbreviated and Table 0.3 provides a key to those abbreviations. Book publishers have also been abbreviated and Table 0.4 provides a key. In any instance where a book has more than two editors or a paper has more than two authors, the additional individuals are indicated by 'et al.'. All sources can be found in their complete form at the Routledge companion website for this book [link here].

Table 0.3 Abbreviations for Journal Titles

AA	American Anthropologist
AJPA	American Journal of Physical Anthropology
AJP	American Journal of Primatology
AR	Anatomical Record
AB	Animal Behaviour
AC	Animal Cognition
AABS	Applied Animal Behaviour Science
BE	Behavioural Ecology
BE&S	Behavioral Ecology and Sociobiology
BP	Behavioural Processes
BL	Biology Letters
BMCEB	BMC Evolutionary Biology
CB	Current Biology
ESR	Endangered Species Research
EHB	Evolution and Human Behavior
EA	Evolutionary Anthropology
FP	Folia Primatologica
H&B	Hormones and Behavior
ICB	Integrative and Comparative Biology
IJCP	International Journal of Comparative Psychology
IJP	International Journal of Primatology
JAAWS	Journal of Applied Animal Welfare Science
JCP	Journal of Comparative Psychology
JEPG	Journal of Experimental Psychology: General
JZL	Journal of Zoology London
PTRSB	Philosophical Transactions of the Royal Society B, Biological Sciences
PRSB	Proceedings of the Royal Society B, Biological Sciences
YPA	Yearbook of Physical Anthropology

Table 0.4 Abbreviations for Book Publishers

California: UCP	University of California Press
Chicago: UCP	University of Chicago Press
CUP	Cambridge University Press
HUP	Harvard University Press
OUP	Oxford University Press

Beyond this Introduction, all Tables have been placed on the website to allow ample space for comparative data and the opportunity to update them as more information becomes available in the rapidly growing and changing field of primatology.

Companion Website

Additional resources to accompany the book are available at: **www.routledge.com/cw/king**

The website also provides the following lists as study aids for each chapter:

1 Study questions to guide reading.
2 Technical terms that were introduced in the chapter.
3 The most important hypotheses that have been introduced in the chapter. This includes all theoretical constructs, whether they have been designated as hypotheses, theories, models, or something else.
4 Additional readings with annotations.
5 Links to other websites that relate to the content of the chapter.
6 DVDs and online videos that relate to the chapter.

DVDs and online videos are briefly described on the website. Some are the direct product of researchers, but others are commercialized to varying degrees. Some of the latter are childish or exploitive, but many provide sound scientific information. There is one pervasive problem with the commercialized productions (many taken directly from TV shows), which is that even the best may be heavily edited to produce melodrama. One staple is the death of an infant or juvenile, which led one of my students to say in exasperation, "Why don't you just show us *Old Yeller*?" Of course, deaths do occur and this must be faced in order to achieve an understanding of the subjects. However, a balanced perspective is necessary.

Zoos are another obvious resource for the study of primate behavior. The animals can be seen alive and unedited and students can take notes on their behavior. However, zoo primates should be considered with caution because living conditions may drastically alter their behavior, varying from minimally modified natural behavior to severe pathologies. Fortunately for the animals and us, disturbed behavior has become less frequent and less intense as zoo conditions have improved. Some zoos with good primate collections are listed on the website.

1 The Primates

Meet Your Relatives

What's that thing? A monkey? An ape? It looks like my grandpa.

There are several hundred species of primates in the world today. Together they constitute what zoologists call an **order** of animals, which is a group with a common ancestor dating back tens of millions of years. This chapter surveys the primates in terms of their biological features, evolutionary origins, and main subgroups. The figures in this chapter and the next will illustrate the diversity of the primates.

Primate Biology and Behavior

Anatomical traits facilitate some behaviors and limit others. Wings make flying possible for most birds, but the reduced wings of ostriches show that flight is no longer possible for them. Physiology is also crucial: hormonal secretions (e.g. testosterone) and neurological processes shape behavior and vice versa. Biological traits raise issues of **function** and behavior, i.e. how the traits work and what the results are. For instance, birds must flap their wings in order to fly. Complex neurophysiological processes underlie the motivation to eat that we call hunger.

Common Primate Traits

Primate characteristics are illuminated by knowledge of the order's mammalian heritage. Some of these characteristics are shared, such as internal temperature regulation (warm bloodedness), live birth, and milk secretion. Other primate features contrast with those of most other mammals (Box 1.1). Some of these have been retained while other mammals changed. For instance, the five digits on each hand and foot contrast with specializations such as paws and hooves. Some distinctive primate traits are unusual innovations, such as the location of the eyes.

Compared to most other mammals, primate eyes are located closer together and toward the front of the head. This produces **binocular vision**, the ability to fix both eyes on the same thing simultaneously (Figure 1.1). The result is depth perception: getting two views of the same object allows the brain to calculate the distance to that object. Primates as a group have the largest binocular visual fields among mammals (Heesy 2004). Large eyeballs also enhance primate vision, and the visual centers in the brain are correspondingly large and complex.

Box 1.1 Distinctive Primate Traits

This table summarizes important features that are common among primates and relatively rare among other mammals. The broadly functional categories emphasize connections with behavior.

Grasping

- mobile digits, especially first digits of hand and foot
- flattened nails on some or all digits
- friction surfaces on tips of digits
- sensitive nerve endings on the surfaces of appendages.

Locomotion

- long, muscular legs
- hindlimb dominance (for both braking and acceleration).

Senses

- orbital convergence (for binocular vision)
- postorbital bone structure (protection of the eye).

Dentition

- four types of teeth: incisors, canines, premolars, molars.

Figure 1.1 A greater galago focuses its binocular vision. © Y.A. de Jong and T.M. Butynski, www.wildsolutions.nl

The **orbits** are the bony sockets that hold the eyes, and orbital convergence is a term for the relative closeness of primate eyes. Primate orbits are reinforced by extra bone at the rear that replaces the tough fiber found in most other mammals. This orbital closure creates a complete ring of bone around each eye and functions as protection against external dangers and/or unusual chewing stresses. Eye damage and loss are more critical for primates than for many other animals.

Primates are largely **arboreal**, meaning that they conduct most or all of their activities in trees. Their typical climbing pattern is distinctive. Rather than digging in with claws, they grasp with flexible extremities that can be called hands and feet rather than paws (Figure 1.2). Flat nails in place of claws support the fingers and toes. The five digits on each hand and foot (called **pentadactyly**) can be spread to facilitate gripping. Grip is further enhanced by friction surfaces with curved ridges on the digits and on the palms and soles. The term **dermatoglyphics** can be used for both the skin patterns and the study of them. Nerve endings in these surfaces provide feedback on how the appendages are interacting with the environment.

The **hallux** (the same digit as the big toe in humans) is widely divergent in virtually all primates and is capable of a pincer-like grasp more powerful than that of the hands (Figure 1.3). In many primates the thumb is opposable to some extent: it diverges from the other digits and can rotate to make some degree of contact with them. Primates use their flexible hands and feet to grasp all sorts of objects, from branches to food items.

Primate limbs are also flexible. Paired bones in the forearms and lower legs allow a higher degree of rotation than in other mammals. The collarbone (absent from many other mammals) is a strut that allows the arm to rotate into a variety of positions. Climbing creates a tendency toward vertical posture, which also distinguishes primates from the majority of mammals.

Figure 1.2 A red-bellied lemur demonstrates its grasping ability. © Stacey Tecot

Figure 1.3 A chimpanzee shows its opposable hallux, the primate equivalent of the human big toe.
© Curt Busse

Primates appear to resemble other mammals in being **quadrupedal**, broadly defined as walking on four limbs on a relatively level surface (Figure 1.4). However, many components of primate quadrupedalism are especially suited to arboreal movement (Schmitt 2010). During each step the animal bends its arms and legs. This **flexion** reduces stress on the limbs (Larney and Larson 2004). It results in a crouching posture when walking on branches, which lowers the center of mass and enhances balance. Features of the primate hindlimbs and ankles facilitate leaping.

The primate forelimb is used for foraging and other manipulations, as well as diversified **locomotion** (any movement from one place to another). This requires mobility at the expense of stability, which makes the forelimb more vulnerable to stresses. Limb flexion alleviates some stress, but **hindlimb dominance** is also a factor: while most mammals place the greater part of their weight on the forelimbs, the distribution in most primates is roughly equal or is greater on the hindlimbs (Hanna et al. 2006). During arboreal movement the rear legs provide propulsion and a resting foundation, while the forelimbs provide guidance (Schmitt 2010).

Primates can process diverse foods because they have retained four kinds of teeth from their mammalian ancestors. The front teeth perform a variety of grasping functions. Incisors, relatively thin and flat, are used for nipping. The pointed canines can be used for fighting as well as food processing actions such as stripping bark. Premolars and molars (cheek teeth) are essential for chewing. Each has protruding structures, typically three or four, called cusps. Cheek teeth can pierce food with the cusps, shear with crests that link the cusps, and crush or grind between the occlusal surfaces. The pattern of molar cusps and their low profile in primates enhance crushing at the expense of other actions. This allows primates to obtain greater nutritional benefits from hard or tough foods such as nuts, seeds, roots, and insects with hard exoskeletons.

Figure 1.4 A captive monkey on a net displays the flexed limbs and crouching posture of arboreal locomotion. © Jaydenwong via iStock

The number of teeth in each category varies among primates. The typical array for a particular group is expressed by a **dental formula** that represents one side of the mouth, upper and lower. For example, the human dental formula is 2.1.2.3 / 2.1.2.3. Each quadrant of the jaw contains two incisors, one canine, two premolars, and three molars. Although some human individuals never grow third molars, this simply exemplifies the variation that exists in virtually every biological trait.

Primate Evolution and Classification

Evolution, as Darwin wrote, is descent with modification: the biological features of a group of organisms undergo hereditary changes across generations. There are several causes of evolutionary change but we will be concerned with **natural selection**, a process in which traits that favor successful reproduction become more common.

Evolution and Natural Selection

In modern terms evolution is a process of change in the characteristics of a breeding population, a group of organisms capable of reproductive interaction. Visible changes are the result of shifts in the **gene pool**, which is the totality of genes that are circulating among the members of the population, from one generation to the next. Evolution affects anatomy, which shapes and limits behavior, and affects behavior more directly through changes in the brain and the endocrine system.

Natural selection is an evolutionary process in which some genes become more or less common over generations because the traits that they influence affect reproductive success. Individuals who have more offspring than others in the same population because of genetic differences will transmit more genes to future generations, with the proviso that their offspring are **viable** (i.e. they can also reproduce). As a result of this process, the genes in question become more common and may ultimately be found in all members of the population.

Natural selection takes place in varied environments, so it usually favors traits that result in survival and reproduction in a certain kind of animal in a certain setting. An angry rabbit that fights a bobcat will probably do this only once. Rabbits that become frightened and run away are more likely to survive and reproduce. Those that start sooner and run faster are the ones most favored by natural selection. They transmit the genes underlying their anatomy and behavior to the next generation. Contrary to a widespread misunderstanding, it is the members of the same population (rabbits in this case) who compete for reproductive success. Predators (e.g. bobcats) are not competitors—they are part of the environment.

Evidence for evolution includes **fossils**, the physical remains of living things. Most of them are bones or teeth preserved by mineralization. However, fossils can also be other signs of the past, such as footprints. The fossil record has many gaps, so comparison of related living species has been used to infer evolutionary events. Since our main concern is the behavior of living primates, we will make little use of the fossil record throughout most of this book. Fossils will become more important when we look at reconstructions of our ancestors' behavior in Chapters 27 and 28.

Molecular primatology (Di Fiore et al. 2011), the comparative study of biomolecules such as DNA, makes vital contributions to our understanding of relationships between individuals, populations, and species. This approach to genetics illuminates mating systems, social structure, kinship, and emigration. It is essential to the reconstruction of population histories and phylogenetic relationships. Many consider molecular evidence to be superior to morphology for this purpose, because alternate forms are more clearly defined. One of the most important aspects of molecular studies is that they can provide dates for evolutionary events based on (assumed) constant rates of mutational change in the biomolecules of organisms.

In addition to DNA, chromosomes have long provided a molecular basis for inferences about evolution and behavior, and new techniques are making them more valuable. Increasing use is being made of RNA, enzymes, and proteins in cell membranes. **Genomics** goes beyond older molecular approaches, being the study of the complete DNA sequence of an organism. It promises more complete and sophisticated comparisons.

Classification

Biological **classification** is the ordering of living things into groups on the basis of their relatedness (Groves 2001). **Taxonomy** is the study and practice of classification. Groups that are formally classified according to these rules are called **taxa** (singular **taxon**). The definition of relatedness among taxa is the subject of some controversy, but most primatologists (and many other scientists) are interested in taxa based on **phylogeny**—that is, ancestor–descendant relationships. More concisely, a taxon is a group of organisms thought to have a common ancestor. This criterion is called **monophyly**, and a monophyletic group is called a **clade**.

Species in a clade share many traits due to common origins. If such traits have undergone little evolutionary change, they are described as **ancestral** or **primitive**. Such traits may have originated before the clade itself appeared (for example, the hairy integument that primates share with other mammalian orders). **Shared derived characters** identify a clade. This means that the common traits have changed from the condition of earlier ancestors, such as the differentiation of primate binocular vision from the visual apparatus of earlier mammals. Much taxonomic work involves distinguishing derived from ancestral features.

Classification is generally considered to be hierarchical in that each taxon can be subdivided into smaller ones (or conversely, nested within larger ones). The Order Primata, for example, can be divided into *suborders* and/or *infraorders*. Each of these can be divided into *superfamilies*, and so on. This raises the question of the level at which a given taxon should be placed. Levels are often identified by distinctive endings to taxonomic names (e.g. *-oidea* for a superfamily). If taxonomists change the level, the name changes (e.g. *-oidea* becomes *-idae* for the family level).

One criterion, influentially advocated by Groves (2001), is that the level of classification should reflect the age of the clade. However, this means that the name may fluctuate with new evidence and interpretations regarding the age of the common ancestor. It also means that those who reject the age criterion may use different terminology. This kind of problem applies at every level of classification. Another taxonomic issue is the identification and naming of new taxa within a recognized one, e.g. creating several new species out of a single one.

Technical controversies about the grouping and naming of taxa can be very confusing to non-specialists. According to Groves (2001), this is how it must be. However, non-taxonomists hope for restraint and compromise (Asher and Helgen 2010; Bruner 2013). Untrammeled taxonomic change is a barrier to communication. At the foundation of this book is a simplified classification of living primates, which is intended to facilitate comparative learning about primate behavior (Box 1.2). It uses informal terms wherever such terms are available and unambiguous. Informal terms are likely to stay the same while formal terminology changes. For example, "Old World monkeys" (the monkeys of Asia and Africa) are the same group of species no matter what taxonomic level they are placed at or name they are given. However, since some contact with technical classification is unavoidable, particular issues and problems will be discussed in boxes throughout the book.

Box 1.2 A Simplified Classification of Extant Primates

This classification is based on Fleagle (2013), but is simplified to facilitate communication about behavior. It is intended to provide a framework for studying, understanding, and remembering broad patterns of primate behavior. The words in parentheses are informal terms that are used in the text. This classification differs from Fleagle in what is omitted (see website for a complete taxonomy). The omitted levels of classification will be discussed in the appropriate chapters later in the book.

SUBORDER <u>STREPSIRRHINI</u> (strepsirrhines)
- Infraorder *Lorisiformes* (lorisiforms)
- Infraorder *Lemuriformes* (lemuriforms)

SUBORDER <u>TARSIIFORMES</u> (tarsiers)
- Infraorder *Tarsiiformes* (tarsiers)

SUBORDER ANTHROPOIDEA (anthropoids)
Infraorder *Platyrrhini* (platyrrhines, i.e. New World monkeys)
Infraorder *Catarrhini* (catarrhines, i.e. Old World monkeys and apes)

The underlined taxa represent the three major clades introduced in this chapter. They have been formally recognized by experts other than Fleagle, but placed at different taxonomic levels with different labels, including "semiorder" (e.g. Masters et al. 2013).

Fleagle's suborders and infraorders provide the basic framework for this book, as will be seen in the arrangement of chapters. Lower level taxa are also used where they facilitate understanding of important variation in primate behavior. The relationships of this scheme to formal taxonomies (and the controversies they entail) will be discussed in boxes throughout the book.

Major Primate Taxa

Living primates can be divided into three major clades (or lineages) that emerged near the origin of the primate order and have continued to the present day (Beard 2013). In our informal terminology these are the strepsirrhines, tarsiers, and anthropoids. Tarsiers are sometimes treated as a **grade**, i.e. a notional intermediate stage between strepsirrhines and anthropoids. However, the fossil, molecular, and behavioral evidence all indicate that living tarsiers and their ancestors form a clade that reaches back almost to the origin of the primates. That is not changed by the fact that they form a larger clade with the anthropoids (called the haplorrhines) (Beard 2013). We are most interested in the distinctive behavioral outcomes of tarsier evolution. In addition to primitive features shared with strepsirrhines and derived traits shared with anthropoids, "tarsiers have many distinctive features all their own" (Fleagle 2013).

Strepsirrhines

Strepsirrhines (Figures 1.1 and 1.2) differ from other primates in several traits that they share with non-primate mammals. The majority of species are nocturnal, which means they are active mainly at night. The concomitant sensory equipment makes the strepsirrhine face resemble those of mammals such as dogs. The short snout ends in a **rhinarium**, a hairless and moist area around the nostrils that takes scent molecules from the air. Other information comes from prominent ears and from **vibrissae** ("whiskers") at the sides of the face. A bone called the postorbital bar protects each eye. This strut, probably an ancestral primate trait, bridges the gap in the rear of the orbit but does not form a complete socket like that of a human.

Strepsirrhines also display highly distinctive derived traits. The **toothcomb** is a dental structure in the lower jaw composed of incisors and canines that protrude at an angle. A strepsirrhine sometimes grooms itself by running the toothcomb through its fur. There is a hardened structure under the tongue (called the sublingula) that is used to remove the resulting debris from the toothcomb. The so-called **grooming claw** on the second toe of each foot is not really a claw like those of other mammals, because it is not sharp or bilaterally compressed. Rather, the strepsirrhine structures are elongated and curved nails that stand at an angle to the dorsal surfaces of the toes rather than flat on top of them.

Strepsirrhine eyes glow brightly when light strikes them in the darkness because the **tapetum lucidum**, a layer of tissue at the rear of the retina, reflects light back toward the pupil. This recycling effect allows the animal to see more in the dark. Other nocturnal mammals also have such structures, but the primate tapetum lucidum functions with different chemicals. This indicates a separate evolutionary origin.

Tarsiers

Living tarsiers are nocturnal, but lack the sensory equipment of strepsirrhines (Figure 1.5). Tarsier eyes glow in the dark, but with a dull orange color. Instead of a tapetum lucidum the eye has a **fovea**, a specialized section of the retina in which light-sensitive cells are closely packed. This intensifies images and gives tarsiers the most acute low-light vision among primates (Jablonski 2003). Each of the tarsier's eyes is larger than the animal's brain, which results in cranial proportions that are unique among the primates. The eye is protected by a postorbital flange, which covers more space than the strepsirrhine bar.

Figure 1.5 A tarsier in vertical clinging position. © Elecstasy via iStock

Tarsiers are less dependent on smell than strepsirrhines and lack the naked rhinarium and the philtrum. Instead, hair encroaches closely around the nostrils. Vibrissae are absent. Tarsier hands are proportionally longer than those of any other living primate, suitable for grasping prey and thin vertical substrates. There are large grooming claws on the second and third toes of each foot, contrasting with the single claw on each foot among strepsirrhines.

Anthropoids

Anthropoids are the most numerous of extant primates. Monkeys, apes, and humans are the living members. Monkeys are quadrupedal primates with (in almost all species) tails, found in the Americas and the Old World (Figure 1.4); apes are long-armed and tailless inhabitants of Africa and Asia (Figure 1.6).

Figure 1.6 A male chimpanzee illustrates ape characteristics: broad chest, long arms, and short legs. © Eric C. Matthews

Most anthropoids are larger than other primates and have relatively shorter trunks. Other than some species in one genus, all living anthropoids are diurnal. Like tarsiers (whose ancestors may have been diurnal), anthropoids have a fovea that intensifies images. Their visual acuity exceeds that of all other mammals and is matched only by birds of prey. Some form of color vision is also typical of anthropoids. Each eye is supported and protected by a **postorbital septum** that forms a complete bony cup behind the eyeball. As in tarsiers, the tapetum lucidum is absent and facial features indicate a shift away from olfaction. The anthropoid nose is dry and often covered with hair.

Summary

The Order Primata is composed of strepsirrhines, tarsiers, and anthropoids. The last lineage contains monkeys, apes, and humans. Primates have diverged into many species, so classification is essential to understanding their evolutionary relationships and doing comparative studies of behavior. The mammalian heritage of the primates is important, but the order also displays distinctive and unusual physical and behavioral traits. Primates climb by grasping. Binocular vision gives them depth perception, and diverse teeth facilitate omnivory. The three primate lineages are ancient, and each displays important features that distinguish it from the others.

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2 The Study of Primate Behavior

It took a little while to get used to the bright blue testicles of the vervet males, often seen as they ran away. Now the monkeys are used to the primatologist and he can focus on features that distinguish them as individuals. Understanding their complex relationships with other troop members is far more satisfying than any colorful novelty.

This chapter introduces the study of primate behavior in terms of *research* (observing, recording, and experimenting) and *interpretation* (using theory to understand the results of research). Watching primates for scientific purposes can be a more complicated and arduous activity than some people might imagine. It presents a variety of problems that call for a variety of techniques. Studies of wild and captive animals each have their own distinctive advantages and difficulties. They also have much in common and their findings often complement one another. Understanding what has been seen requires well-defined analytical techniques and reference to a variety of theoretical frameworks.

Fieldwork

C.R. Carpenter performed the first scientific field research on primates in the 1930s. Field studies burgeoned after 1950, led by Sherwood Washburn (baboons in Africa), Kinji Imanishi (Japanese monkeys), and their many students. Chimpanzee research started by Jane Goodall in the 1960s brought primate fieldwork to the attention of the general public. Since its early days, primate field research has gained enormously in complexity and sophistication.

The environment for fieldwork can be anything from baking grasslands to leech-infested swamps. Primatologists have shown great fortitude and courage in their research. I write this with admiration, having worked in the highlands of Tanzania where dryness made temperatures of 90 degrees almost pleasant and the night air contained no mosquitoes because of the altitude.

The Goals of Fieldwork

The goal of field research may be **general study** or **hypothesis testing**. General study gathers data on a variety of observable behaviors. With sufficient information, later researchers can go into the field with particular questions in mind. These are best framed as testable hypotheses; that is, they are amenable to procedures used to decide whether a postulated relationship or explanation is probable beyond the level of chance.

Primate fieldwork shifted from general study to hypothesis testing in the 1970s and 1980s. However, there are arguments for renewed vigor in general studies. First, we still know very little. Many species remain unstudied, and in many cases where research has been done, we only know about one or a few populations or social groups. Second, many unstudied populations and taxa are rapidly disappearing due to human intrusions. Third, data recorded in general studies can be used to test hypotheses that have not yet been formulated. For example, the idea that primates have some kind of culture, now widely accepted, was originally based on data from prior general studies.

Making Contact

Making contact with the subjects can be a problem in fieldwork. There is some danger, but most primates are smaller than humans and even the most formidable (such as gorillas and baboons) will usually avoid humans rather than attack. Avoidance by the subjects is the greater problem for fieldworkers and requires **habituation**. This is the process in which the animals become accustomed to the presence of researchers so that they will allow sufficiently close observation (Figure 2.1).

Habituation demands patience, caution, and ethical concern for the subjects. The observer should be visible to the animals, but not close enough to disturb them. Eventually it may be possible to follow the subjects and stay near them or even walk among them. This process can take years, though it may be shorter for some species. The observer should not follow the subjects too persistently if they attempt avoidance or flight, because this causes stress and distorts natural behavior. Success comes from regular and frequent neutral contact with the same individuals. **Provisioning**, providing food on a regular basis, has been used

Figure 2.1 A fieldworker near habituated chimpanzees. © Curt Busse

in some field studies to bring the subjects close. However, provisioning is problematic because it creates dependence, alters normal behavior, and encourages dangerous interactions between primates and neighboring humans, such as crop raiding. Possible transmission of disease is an ethical problem because it is a danger to the subjects as well as the researcher.

Identification

Identification of individuals is necessary in many studies (in examinations of social relationships, for instance). This can come with familiarity, but photographs are helpful because they can be studied at leisure. Sometimes luck and insight combine to make things easier; for example, fieldworkers found that the nose of every gorilla forms a unique pattern (Fossey 1983; Schaller 1963). Marking of some kind may be necessary for species that are small or active, live in conditions of low visibility, are studied by different researchers, live in large groups or groups of changing composition, or do not have sufficiently distinctive individual characteristics. Marking methods include tattoos, ear tags, and collars or belts.

Marking raises questions about manipulating the animals, especially because it requires trapping. Traps should be humane for ethical reasons and also to avoid causing distorted behavior after release. A broad survey showed that humane trapping causes little or no change in primate behavior. The most common device is a cage baited with an attractive food. Primates present difficulties not found in other animals. Some can escape by raising the door with their hands. Some can learn to get the bait without entering the trap or without triggering automatic closure. On the other hand, some individuals become "trap-happy" and enter the cages more often than the researcher desires.

Anesthesia is needed for marking methods that are painful or animals that are hard to handle. It is usually needed to obtain information about physical characteristics, including measurements and collection of samples such as blood. Repeated capture increases risk of stress, injury, and death. Therefore, the maximum amount of information should be obtained whenever an animal is trapped and anesthetized for any reason.

Technology

Technology has become increasingly important and elaborated in fieldwork. Primatologists record behavior with photographs and video. They have long used recorded vocalizations and other sounds to study the reactions of their subjects. More recent is the use of **telemetry**, automatic measurement and transmission of data by wire, radio, or other means from remote sources to receiving stations. Telemetry provides identification and tracking of subjects collared with radio transmitters. Primate researchers now use the Global Positioning System (GPS) to demark locations on the ground more accurately and Geographic Information Systems (GIS) to create more accurate maps of primate habitats. Data recording by personal electronic devices saves an enormous amount of time and allows for protection of data by storage in more than one place.

Data Collection and Analysis

The researcher collects data by **sampling** the subjects—that is, by observing a number of individuals who accurately represent the total study population (Altmann 1974). This step may be simple (limited to adult males, for example) or complex (encompassing all age–sex categories), depending on the research question. One widely used technique is the **instantaneous scan**. The observer surveys the sample subjects at regular intervals and records what they are doing (or where they are) at each time. Continuous observation of particular individuals is required if the study question concerns the duration or rate of occurrence of a behavior. Instantaneous scan can cause brief but important behaviors to be missed. It is most useful in studying ordinary behavior in categories or groups such as *juveniles* or *cliques*.

Focal animal sampling records all the activities of a single individual over a predetermined period of time. When that time is up, the researcher follows another individual. This approach provides information about duration and frequency, but it requires that the behavior of other group members is ignored if they are not interacting with the focal animal. Another drawback is that results are invalidated if the researcher loses contact with the subject during the predetermined observation period.

Ad libitum sampling means the recording of behavior without a predetermined scheme. This may be part of a general study, but it is especially important with regard to rare and significant events such as the birth of an infant or an injurious fall from a tree. It is essential to break away from any scheduled procedure (or from resting or eating lunch) to record such events.

The collected data are quantified for statistical analysis. **Descriptive statistics** simply represent the behavioral patterns in the data, which are usually reported as frequencies. Percentages convey relative results, such as the amount of total daily active time taken up by a particular behavior. **Inferential statistics** explore the probability that a described relationship is *significant*, meaning that it is not due to chance.

Understanding behavior requires understanding the conditions that affect it. Fieldworkers record diverse aspects of the environment such as forest structure, daily light cycle, temperatures, and the availability and characteristics of plant foods and animal foods. Fieldworkers usually collect samples of plants and animals to be identified and/or analyzed in laboratories.

Dung samples are especially informative about behavior. They provide food remains with the assurance that the primates actually ingested that food (behavioral observations of feeding can be compromised by poor visibility). Feces can also be used to monitor hormonal changes in the subjects, which have implications for reproduction and for behavioral states like stress. Finally, the samples provide genetic material that can be used in studies ranging from phylogeny to kinship. The structure of scats can be used to assign them to a species, but association of a scat with a particular individual requires observation of the deed, or at least strong circumstantial evidence.

Captive Studies

Captive study refers to research on animals that are to some degree restrained by humans. This encompasses a wide variety of situations with a wide variety of effects on primates. The best case for the subjects is one in which they are maintained in a natural social group in an open-air enclosure in a favorable climate. This occurs at some research facilities and in some zoos. The main research advantages are that the animals can always be found, can be studied at any time, and in some cases can be seen from optimal locations. Some behavioral experiments can be performed, such as removing a particular animal to see how social relationships in the group are altered.

Manipulation of Captives

Researchers can subject caged primates to more extensive manipulation. This is considered vital because the scientists can then use numerous sophisticated techniques to record data (Stevens and Carlson 2008). Experiments may be relatively benign, such as a temporary set-up in which a female can choose between two potential sexual partners without being coerced by either. Most intelligence tests also fall into the benign category.

At the other extreme is the **deprivation experiment**, in which the opportunity to learn a behavior is taken away from the subjects. The usual goal is to explore which components of behavior are learned and which can develop without experience. In primates, for example, typical facial expressions are likely to appear despite deprivation.

In some experiments subjects have been deprived of all normal stimuli, resulting in severe trauma. Many primatologists oppose such experiments, as expressed in a letter signed by 56 students of primate behavior (King and LaFleur 2015). In a less drastic approach, humans care for the subjects in place of their mothers (e.g. Sugita 2008). Another method is **cross fostering**, in which learning deprivation is achieved by giving the subject a foster mother of a non-primate species (females of various mammal species readily accept such adoptions).

Physically intrusive studies involve deliberate damage to the animal, such as lesions in particular portions of the brain in order to observe the behavioral effects. Alternatively, electrodes may be permanently implanted in the brain so that particular sections can be stimulated when desired. There is skepticism about conclusions based on animals traumatized by severe deprivation or by physical damage. Some observed behavioral deficits (inability to copulate, for instance) might be due to general pathology rather than specific lesions or rearing conditions. Many scientists also have ethical reservations about injurious experiments.

Distorted behavior can arise from the captive situation itself, and this may compromise both experiments and naturalistic observations. Captive animals expend little or no time and energy in foraging and feeding; they are protected from predators; and they are to a large extent protected from and treated for disease and injuries (Stevens and Carlson 2008). In addition to such drastic departures from normal ecology, captivity may alter social behavior; for example, heightened aggression may occur. Some such effects occur in laboratory groups, but not in zoos (Hosey 2005). Mallapur and Choudhury (2003) showed that primates confiscated from touring zoos, circuses, and animal traders exhibited higher levels of abnormal behaviors than did animals in larger, recognized zoos.

Anecdotes and Anthropomorphism

An **anecdote** describes a unique or unusual event. Any study of primates is likely to provide anecdotes because their behavior is so complex and variable. Researchers also get anecdotes from local residents in the field, staff in the laboratory, and a variety of other people. Non-scientists sometimes portray these accounts as proof of something, but a single case or a few unusual ones can never support a general proposition. However, it is important to distinguish between anecdotes mistakenly intended as evidence and anecdotes used for other purposes.

Some anecdotes point the way to future research. Accounts of tool use by chimpanzees were anecdotal in the beginning (van Lawick-Goodall 1968), but turned into one of our most fertile areas of research (McGrew 2004). A second benefit of anecdotes is that they can suggest the behavioral potential of a species. In a species that frequently uses tools to get food, a few individuals may also use objects to pick their teeth or clean their noses. Bates and Byrne (2007) argued that creative behavior occurs at low frequencies in nonhuman animals and is typically missed by standard observation methods. They provide criteria for the reliability of such anecdotes. First, they should be recorded immediately after observation. Second, the observer should be someone familiar with the species and the individuals involved. Third, separate reports should be collated to demonstrate a pattern.

Finally, anecdotes can amuse or touch us and remind us that the study of primate behavior is fun and can be enlightening in ways other than scientific. An example is Kortlandt's (1962) account of a chimpanzee that sat and watched a sunset for perhaps 15 minutes. This single incident can inspire humanistic consideration of the nature of art or religion and the nature of animals. Smuts (2001) described a comparable experience. Late in the day the baboons she was following sat down at the edge of a small, still pool and gazed into the water in complete silence for half an hour.

The last two examples raise the issue of **anthropomorphism**, the interpretation of animal behavior as if the subjects were human. The epitome of this phenomenon is cartoons where animals speak and behave exactly as if they were human. With regard to real animals, a frequent manifestation is the idea that animals found in pairs are mated for life and have a romantic relationship. Many such relationships fall far short of lifetime tenure and display little or no evidence for affectionate feelings.

Objections to alleged anthropomorphism are often couched in terms of **Morgan's Canon**. This rule, formulated by an early comparative psychologist, is often cited as prohibiting the attribution of so-called higher mental processes to nonhuman animals. Morgan actually argued that such attributions should not be made *without a strong foundation* (Karin D'Arcy 2005). The temptation to engage in anthropomorphism is greater with primates than most other animals because the primates really are so much like us. They share a real biological heritage with us, which provides the "strong foundation" needed for legitimate comparison. The argument often revolves around the idea that apes are like us, but it makes just as much sense to say that we are like apes. Interviews with prominent primate fieldworkers led Rees (2007) to the conclusion that "careful anthropomorphism" is valuable for the insights that it can provide. Lloyd Morgan did very little research with primates (Maple 1979). Had he done more, he might have qualified his rule.

Alleged anthropomorphisms are increasingly testable. For instance, the same areas of the brain may be activated in human and monkey mothers in comparable circumstances. At a minimum this indicates that both species possess the same motivational system. One might go further and infer that the monkeys feel much the same emotion as humans (even if calling it *love* might be going too far). The key, as in any scientific research, is to formulate a precise hypothesis and find a way to test it. A variety of scientific disciplines have developed ways to test hypotheses about animal behavior.

Explaining Primate Behavior

The Science of Primate Behavior

Primatologists generally regard their discipline as a science. Scientific thinking means a number of different things, one of these being objectivity. Complete objectivity is impossible for an individual, but it can be approached in science because diverse participants can counterbalance one another's biases. Primatology has been an international enterprise (Ji and Jiang 2004; McNeilage and Robbins 2006; Terry 1983), from the first field studies done by Americans, Europeans, and Japanese to increasing contributions from Indian, Chinese, and African scientists. Equally important, a male bias in the early years was offset by an influx of female scientists (Fedigan 1994). Some bias in the social structure of the field seems to persist (Addessi et al. 2012), but we have reaped the benefit of data and insights from female primatologists. Primatology as a field of inquiry seems well situated for the pursuit of objectivity.

The purpose of scientific study is explanation, which requires hypothesis testing. **Competing hypotheses** (alternative explanations for the same phenomenon) are an important part of this process. Some people will dismiss a hypothesis by saying that they already have an explanation for something and "don't need" the alternative. For example, they reject biological explanations for human behavior because social science already explains some of the facts. However, science is not about needs. It is about finding the best explanation for the currently known facts.

In evaluating competing hypotheses it is important to consider whether or not they are **mutually exclusive**; that is, whether acceptance of one precludes the other. Some apparently competing hypotheses are actually complementary. For instance, some scientists attribute color vision to the consumption of fruit and others to the consumption of young leaves. These views are not necessarily contradictory, because most primates eat both fruit and leaves.

Tinbergen's Questions

Many different scientific disciplines have contributed to hypotheses about primate behavior and the means of testing them. The lines separating the primatological fields have blurred because, regardless of emphasis, most practitioners appreciate the overlaps among them (Maestripieri 2003). Whatever disciplinary names they use, students of primate behavior are concerned with four or five kinds of explanation (though particular theorists often emphasize one over the others). This framework is largely based on the work of ethologist Niko Tinbergen (1963), who postulated four questions that have to be answered in order to fully understand a pattern of behavior (Barrett et al. 2013; Bateson and Laland 2013). The following summary combines Tinbergen's formulations with some newer concepts and terminology.

Proximate mechanisms are the immediate causal antecedents of particular behaviors in individuals. They include stimuli from the environment (e.g. the sight of a predator) and internal signals (e.g. feeling hungry). The threatened individual may flee and the hungry one will probably eat. Generalized internal factors such as hunger or fear can be considered motivational systems. These are often specified by terms associated with emotions, which can be considered the animal's subjective perception of the activated system. Cognitive processes—such as perception, memory, and reasoning—are also internal causes of behavior. The physiological basis for these causes lies in hormonal systems, neurological processes, and the interactions between them.

Other endogenous factors are more specific. **Attentional mechanisms**, for example, make certain stimuli (snakes, for instance) more likely to be noticed than others. Other mechanisms cause the form of some behaviors to be relatively stereotypical for a species (e.g. facial expressions). A behavior with such a stereotypical tendency is called a **modal action pattern** (abbreviated to MAP).

Functions (see Chapter 1) are the effects or consequences of behavior in relation to the physical and/or social environment. For example, the function of hunger is to motivate food acquisition and processing. The function of facial expressions is to communicate with others. The term function refers only to recent relationships and not to evolutionary origins. The current function(s) of a trait may not be the same as those it had in the past. Functional interpretation does not necessarily imply a genetic basis for the trait. "Current utility" has been suggested as an alternative that clarifies the issue (Bateson and Laland 2013).

Ultimate causes are the conditions thought to account for the origins of particular behaviors. These include past environments and the action of natural selection. Hypotheses of ultimate causation often assume that the behaviors in question are under some degree of genetic influence. Ultimate causation can provide an explanation for the functional significance of a trait; however, as noted above, functions may change over time.

The widely used word **adaptation** has been subjected to so much argument and redefinition that it may cause more confusion than it alleviates. Broadly speaking, an adaptation is a trait that facilitates survival and/or reproduction. The word is also used for the process or processes by which adaptations come into existence. Some scientists would reserve the term adaptation for the origin of a trait by natural selection, which is often highly speculative. Confusion about the meaning of adaptation can be alleviated somewhat by using the concepts of function and ultimate cause wherever possible.

None of this presupposes awareness on the part of the primates (including humans) that their behavior is related to natural selection. For example, the presumption is that primates (including most humans) seek sex because they are motivated to engage in that interaction (loosely speaking, they like it). They are not consciously trying to transmit genes to the next generation, although this may be the functional/adaptive significance of the behavior.

Misunderstanding arises in part because behavioral scientists often press everyday words into use when their connotations seem appropriate. An important example is **strategy**, which is a short way of referring to certain functions. For instance, to a primatologist, "sexual strategy" encompasses behavioral patterns that lead to a successful copulation (including searching for mates, selecting one, courting, and defeating competitors). The primary hypothesis is that this complex pattern of behavior is based on proximate mechanisms that were probably favored by natural selection. Many complex behavioral systems are based on a series of relatively simple proximate mechanisms (Kummer 2002).

Ontogeny refers to the growth and change of the individual from conception to death. **Development** is a similar concept, but is more often used for the period before maturity. Ontogenetic explanations explore the complex processes that link a growing individual to the proximate and functional aspects of behavior. This approach investigates the ways in which endogenous mechanisms are established during the growth and maturation of the individual.

Some behaviors appear at or shortly after birth (such as the grasping reflex in primates, including humans). Others manifest themselves somewhat later (for example, walking and language in humans). Early-emerging behaviors are especially likely to be under a significant degree of genetic influence, a condition that may be described as **innate**. Mameli and Bateson (2011) pointed out that the term has taken on a number of meanings. However, several of them connect closely with genetic influence, e.g. "developed without learning" and "history of natural selection". It might clarify some issues if we use *innate* to denote genetic influences on components of behavioral patterns, rather than whole patterns.

The mechanisms underlying innate components may be fully formed at birth but they are likely to require some degree of **maturation**; that is, they must undergo some development before they are fully operative. Learning is probably involved in the ontogeny of virtually all primate behaviors and is predominant in many, perhaps most. Following the development of a behavior gives us more insight into its components and causes, such as the balance between genetic and experiential factors. Genetic influences may make certain kinds of behavior relatively easy to learn. In some cases a behavior is readily learned only during a particular period of life, called a **sensitive period**. Imprinting in birds is a well-known example. For instance, newly hatched ducklings quickly learn to follow the first thing that they see (even a human).

Beyond limited phenomena such as sensitive periods, ontogenetic studies make us aware of broader stages in life. Some researchers have applied psychological concepts (such as those of Piaget) to the cognitive development of primates. Others have made it clear that adaptive behavior varies with an individual's stage of life. Annoying primate infants can expect a great deal of tolerance, for example, but juveniles must be more careful not to provoke adults.

Phylogeny is the pattern of evolution within and between taxa. It is popularly depicted as the branching of a tree, though this is often an over-simplification. Phylogeny is the basis for taxonomic classification. It is also a way to understand behavior. Phylogenetic analysis places the behavior of living animals in the context of evolutionary history (Ossi and Kamilar 2006). It postulates that ancestry can explain the distribution of behaviors among related species.

The **comparative method** is the vehicle for phylogenetic analysis. Variation of a trait is mapped onto the known phylogenetic relationships of living species. In its simplest form this guides us to the identification and explanation of evolutionarily conservative traits, such as climbing in primates. Facial responses to sweet and bitter tastes provide another simple example. A variety of primates (including human infants) display similar reactions, suggesting that they are phylogenetically connected (Weiss and Santos 2006). A further interpretation is that the shared response is part of a motivational system that originated as an adaptation for choosing or avoiding potential foods. Evidence for ancestral behavior can also provide a baseline for understanding derived behavior. Comparison of varying forms in living species can suggest the sequence in which the forms evolved.

Summary

Primate behavior is studied in the field and in captivity. Sampling and statistical analysis are essential. Recording and interpretation should avoid anthropomorphism, but recognize that we are primates and share traits with our close relatives. Causes of behavior are proximal, functional, ontogenetic, and phylogenetic. Hypotheses are tested and competing hypotheses are compared. Many primatologists consider their work relevant to understanding human behavior.

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3 Primate Ecology and Behavior

Common Features

A young primate moves aimlessly through the trees, emitting high-pitched sounds, desperately seeking the social group that it has lost. Eventually, the mother approaches and the youngster quiets.

This chapter tries to describe behavioral patterns that are common across the primate order. That is, they are widely recurrent, typical, or even ubiquitous among primates as a whole. An important caveat is that many published papers about "primates" are really about Old World anthropoids or even narrower groupings. This presentation is based on descriptions and explanations that seem widely applicable.

Primate Ecology

Most primates inhabit tropical and subtropical rainforests and woodlands. **Woodlands** are areas with varying proportions of tree and grass cover. A tropical **rainforest** is a more complex ecological community, consisting of vegetational layers called **strata** (Corlett and Primack 2011; Woodward 2012). The lowest level is the **understory**, which is sparse at ground level due to limited light and moisture. Farther up, a **canopy** or two are comprised of continuous layers of leaves. **Emergents** are widely spaced trees rising above the rest. Vines and similar plants are intertwined with the trees. Each plant species has its own distinct flowering and/or fruiting season(s). Dry seasons are usually brief and a complete cessation of rain is rare.

Primates are often called omnivores, meaning that they have diversified diets that include both plants and animals as food. Though broadly correct, this obscures enormous variation in particular foods and the ways they are used. **Preferred foods** are those eaten when there is a choice. These are of *high quality*, i.e. rich in protein and/or energy and easily digestible. Fleshy tropical fruits are an energy source containing vitamins that facilitate the body's use of energy. Figs, whether they are preferred or not, are common in primate diets for several reasons (Shanahan et al. 2001). The trees (*Ficus*) occur in almost every primate habitat, the only genus for which this is true. Figs are available throughout the year and present no defenses (such as hard shells). They contain a variety of nutrients (though particular species vary in food value).

Primates typically prefer young leaves to mature ones because the former contain more protein and are lower in **secondary compounds**. These are chemicals that plants secrete to protect themselves from destruction by animals: toxins (poisons such as cyanide) and digestion inhibitors (e.g. **tannins** that interfere with protein uptake). Other factors also contribute to diet choices. For instance, protein concentrations in some leaves vary through the day. Some taxa are called **folivorous** because they specialize in leaf consumption to varying degrees.

Primates are unusual mammals in consuming **exudates**, substances secreted by trees and some other plants (Burrows and Nash, 2010). **Gums**, the exudates favored by primates, are found immediately under tree bark where their function is to repair damage. They rival fruit in sugar content, but are more difficult to digest. At least 69 primate species eat exudates, some routinely and some opportunistically, mostly during dry seasons. Where rainfall is irregular, gums may be a more reliable and rapidly renewing source of carbohydrates than fruit. Feeding sites are small, but a single tree may contain numerous sites.

Primates select certain plants for mineral content: leaves are richest, followed by bark and fruit. Primates may also obtain minerals through **geophagy**, eating soils and clays (Ferrari et al. 2008). Other explanations for geophagy include toxin adsorption, control of diarrhea, and pH adjustment of the gut. These hypotheses are not mutually exclusive, and it is doubtful that such a widespread phenomenon has a single explanation (Krishnamani and Mahaney 2000).

Animal foods provide primates with proteins and fats. Fat contains more than twice the energy of carbohydrates per unit of weight. Protein supplies amino acids for maintenance of the body. Most important to primates are nine amino acids that their bodies cannot synthesize. **Faunivory** denotes animal consumption by primates. The term **carnivory** is misleading due to the connotation of meat (vertebrate muscle tissue), which is limited or absent in most primates. Insects are the most important component of primate faunivory, but primates commonly eat other invertebrates, such as spiders and snails (McGrew 2014).

Primate prey are typically small and often cannot escape—for example, grubs, caterpillars, and insects that infest fruits. However, primates sometimes exert themselves to obtain animals like grasshoppers and rodents. Flexible hands facilitate capture, and the food value of larger animals can offset the energy costs of vigorous pursuit. If the prey can be controlled manually, the primate usually dismembers it or eats it whole. If it poses a danger (such as a bite) or is likely to escape, the primate will often kill or immobilize it quickly with a bite to the head and/or neck (King and Steklis 1984).

Some foods have a **patchy distribution**, meaning they exist in irregularly distributed clumps. Fruit distribution is patchy over a large area, but variation can occur within a single tree: warmer, drier upper crowns may produce bigger fruits at higher densities (Houle et al. 2007). Leaves may be everywhere, but the distribution of nutritious and easily digestible leaves can be patchy. Variation through time is also important. Seasonal cycles, rainy and dry for most primates, affect most fruit species. This is why the perpetual availability of figs stands out. Leaves are less affected, but they are not immune. Insect availability also varies, because insects depend on plant foods.

Fallback foods are eaten when preferred foods are scarce, usually during a dry season, and can be critical for survival. Fallback foods are inferior in terms of nutritional quality and/or the energy needed to process them. Proximately, these foods are less attractive due to taste and/or difficult processing. Fallback foods are sometimes conflated with *keystone resources*. The latter are theoretically critical for entire ecological communities. A fallback food may be important to just one species and it may not be essential to survival, especially if other fallbacks are available.

When primate species are **sympatric** (living in the same habitat), food competition is usually ameliorated by occupation of different **niches** (ways of relating to the environment). For instance, they may depend on different foods, forage at different times, or use different forest strata. Certain bats and squirrels also seek fruit, but birds are probably more important competitors.

Primates face a variety of dangers. Arboreal activity risks serious falls (Lovell 1991). Young individuals, less experienced and more likely to be careless, are particularly susceptible. Fighting and frights also result in accidents that cause death instantly, or through infection or susceptibility to predators. Predators may attack from any direction. Raptors can take primates from the trees (McGraw and Berger 2013). Cats and other terrestrial predators wait on the ground, and some can climb. Snakes eat a variety of primates (though none that weigh more than 13kg) and poisonous snakes may strike defensively (Headland and Greene 2011). An ongoing controversy addresses the possibility that orbital convergence and binocular vision are adaptations to snake detection (Wheeler et al. 2011). The degree of danger from snakes seems to vary by continent.

Fieldworkers found that their presence reduced attacks on primates by inhibiting the predators. This hampered assessment of the natural **predation rate**, the frequency of successful attacks on a group or population. **Predation risk** refers to the rate of unsuccessful attacks or other encounters with predators. Risk assessment includes primate responses to their perception of the danger (avoidance of a location, for example). If the predation *rate* for a given population or species really is low, it may be due to effective countermeasures by the potential victims rather than to low *risk*. However, even a low rate may be demographically significant because peaks in predator pressure can drastically reduce primate populations.

Vulnerability is the likelihood that a particular individual or kind of individual will be taken by a predator. Common sense may suggest that small-bodied species, and females and immatures in most species, are highly vulnerable. However, few field studies supported that idea and some found that large adult males were the most frequent victims. Relevant factors include greater visibility, more meat per kill, and/or availability because adult males sometimes confront predators.

Anti-predator behavior takes time from other activities, including foraging and social interaction, and can be costly in terms of energy expenditure. Primates in trees usually avoid raptors by moving lower and/or hiding in dense vegetation. Trees and cliffs provide refuge from terrestrial predators. **Alarm calls** are vocalizations that seem to warn conspecifics about predators. An alternative hypothesis holds that the calls notify the predator that the targets have been alerted. These functions are not mutually exclusive. Calling sometimes continues long after the predator has disappeared so that it no longer seems to be a warning; however, continued calls may convey that a predator has hidden rather than departed. A hypothesis of proximate cause is based on emotion: continuing alarm calls may express a high level of arousal that does not quickly subside.

Primates sometimes confront predators. In **mobbing**, the most common action, primates approach a potential predator and emit frequent loud calls while engaging in vigorous physical activity such as jumping (Crofoot 2012). An episode can last as long as 30 minutes. Mobbing is like an alarm call in that it notifies the predator that a sneak attack is impossible. It may confuse or even frighten some predators, especially younger individuals. Finally, it can teach young primates to recognize dangerous animals.

Vigilance, special visual attention to surroundings, seemed likely to function in predator detection. Doubts arose from the realization that vigilance could be directed internally, toward potential mates or competitors. This stimulated two kinds of problem-oriented research. Some fieldworkers looked for correlations between vigilance and natural predator encounters; others performed experiments simulating predator risk. These studies agreed that vigilance increases along with predator risk.

Van der Post et al. (2013) provided an additional perspective. This pertained to the issue of **free riders**, individuals who benefit from a behavior even though they never provide reciprocal benefit. If free riders benefit, the individual who performs a behavior has no selective advantage and the behavior should not evolve. The researchers postulated that predator detection is distance dependent, so that individuals closest to a given predator (and therefore more likely to become targets) would gain the greater survival benefit from vigilance. This mechanism seems compatible with others pertaining to predator defense.

Beyond predators, primates belong to larger ecological communities. Many primates contribute by dispersing the seeds in the fruits that they eat, propagating the trees and plants that they come from. The primates benefit, of course, but so do other frugivores and the plants themselves (Heymann and Hsia 2015). Less often noted is that there are some beneficial ways in which primate folivores alter the environment (Chapman et al. 2013).

Sleep ends a primate's day (Nunn et al. 2010). Most of its physiological functions seem to be characteristic of mammals generally, e.g. enhancement of the immune system and consolidation of memory. Two ecological hypotheses may have special relevance to primates. One holds that variation in sleep duration results from a trade-off between basic individual functions and ecological constraints on particular species (Capellini et al. 2008). The other hypothesis explains complete unconsciousness in sleep as a response to predation (Lima and Rattenborg 2007). Relative immobility reduces conspicuousness, and the period of helplessness is shorter because neural maintenance proceeds more quickly. Lighter sleep may have evolved to permit a quicker response to an immanent predator. Social contact during sleep may enhance relationships and provide thermoregulation, but it also increases the danger of disease transmission.

Primate Sociality

Primate groups differ from those of most other social mammals by integrating adults of both sexes on a long-term basis. Often the same individuals are together for years. Kappeler and van Schaik (2002) defined a **society** as a set of conspecific animals that regularly interact more with each other than with other conspecifics. **Social organization** denotes characteristics of a society, including size, sexual composition, and degree of cohesion in space and time. Other primatologists have included *relationships* (recurring patterns of interaction between individuals) and added that at least some interactions are affiliative (friendly or at least non-aggressive) (Mueller and Soligo 2005; Mueller and Thalman 2000).

Kappeler and van Schaik argued that the inclusion of mating patterns in social organization is neither necessary nor useful. Societies with similar patterns of day-to-day interaction may have different mating systems. In addition, mating with outsiders is a recurring pattern among primates, resulting from individuals seeking extra-group encounters or from temporary intrusions into a group.

Two main types of social organization recur throughout the primate order. One is based on a long-term relationship between a particular male and female, usually termed a **pair** (Figure 3.1). This kind of social unit is twice as common among primates as in other mammals. Pairs are usually accompanied by one or more offspring, and sometimes by one or a few other adults. I suggest the term **pair-group** to denote a social unit that is clearly centered on a single pair, but which may contain one or a few peripheral adults. The status of "extra" adults can be clarified by their interactions with others and by the demography of the population. There are also societies with multiple adults, ranging in size from a handful to several hundred. Such a society is commonly called a **troop** or **community** (Figure 3.2).