CHAPTER 5

Primate Behavioral Ecology

This chapter addresses the following questions:

- What is comparative primatology, and how can it tell us about human behavior?
- What is behavioral ecology, and how does it help us understand the evolution of behavior?
- What are the general behavioral patterns in the living primates?
- What kinds of societies do primates have, and how can we use specific examples (macaques and chimpanzees) to help us understand primate patterns present in humans?
- How are human societies similar to and different from those of other primates?

We humans have long wondered what lies at our innermost core. What part of us is contributed by "nature," and what is the result of "nurture"? If a child were raised in isolation, without human contact, would we see in that child raw "human nature," untainted by education or culture? Of course we could not carry out such an experiment, but the folklore and literature of many cultures include tales of human children raised by wolves, apes, bears, or other animals. A few actual cases have also been recorded that offer insight into these questions.

In 1799 a "wild boy" was discovered in the French countryside in a forest of Aveyron. He seemed to be mute and behaved as though he had been raised by wild animals. Victor, as he came to be called, was taken to an institute for deaf-mutes in Paris and placed in the care of a physician named Jean Itard. Dr. Itard took the boy under his wing and tutored him in French culture, language, and manners. Victor never learned more than a few phrases, but he did learn to behave in a somewhat "normal" manner for his time. The French film director Francois Truffaut was so taken with this story that he made a movie about it in 1969, *The Wild Child,* using the boy's experience to explore the larger human experience.

In 1970 a "wild girl" was discovered in California. This girl, given the pseudonym Genie, was about 13 years old. For unknown reasons, her parents had isolated her in a small room and never spoke to her. She was restrained by a harness and at night put in an enclosed, locked crib (Curtiss, 1977). When she was discovered and rescued, she could not stand erect or speak. Genie was eventually treated and tutored by a battery of researchers who tried to teach her to speak English and behave in ways considered "normal" for an American child. Genie never learned to speak at more than a rudimentary level—she could not learn how to combine words in sentences—but she was able to effectively use tools, succeed at complex spatial tests, and easily master cause-and-effect tasks.

These two cases make it clear that human behavior results from the complex interaction of our morphology and physiology; our exposure to other humans, cultural patterns, and language; and our individual life histories. We cannot discover what it means to be human by stripping away any of these components to see what is left.

There is another place to look for answers to our questions, however. We can learn something about human behavior by determining what aspects of our behavior result from our evolutionary heritage as mammals, as primates, as anthropoids, and as hominoids. We can especially look to our primate relatives to understand what we all have in common and what patterns and processes in the past have influenced both general primate and specific human behavioral patterns.

In the previous four chapters we have focused on genetics, anatomy, and the processes of evolution, establishing a baseline for understanding how our bodies function, what forces have shaped the evolutionary history of our species, and how some aspects of behavior may be related to genetics and biology. In upcoming chapters, we will delve into the evolutionary history of the human species, from the earliest primates to modern *Homo sapiens*. We will explore in detail the evolution and characteristics of mammals and primates (chapter 6) and the emergence of humans and their ancestors (chapters 7–9). In this chapter, we examine our closest living relatives, the primates, to understand aspects of our own behavior. We call this approach **comparative primatology.**

comparative primatology
the study of our closest living relatives, the primates, for the purpose of understanding aspects of our own behavior

Strepsirrhini
primate suborder that includes the Lemurs, Lorises, and Galagos (the prosimians)

Haplorrhini
primate suborder that includes the Tarsiers, monkeys, apes, and humans

Comparative primatology provides insights into modern human behavior

In chapter 2 we described humans as belonging to the order Primates, the suborder Simiiformes (anthropoids), the family Hominoidea (hominoids), and the genus *Homo.* We also discussed the phylogenetic principles that biological anthropologists use to talk about the appearance and relationships of morphological traits, that is, ancestral, derived, and shared derived traits. Comparative primatology is based on these same principles, but here we are talking about behavior rather than morphology. Thus, instead of asking if brachiator anatomy (arm and shoulder morphology adapted to swinging through tree branches) is a shared derived trait for apes relative to other primates, we will be looking at behavioral patterns and asking about their relative presence among the living primates or subgroups within the primates.

The Living Primates Are Widespread and Diverse

The living primates represent nearly 300 species in two major suborders and about 15 families. The two suborders in the order Primates are the **Strepsirrhini** (also known as the prosimians) and the **Haplorrhini** (also known as the tarsiers, monkeys, apes, and humans). Primates live throughout the tropical and neotropical areas of the world (Figures 5.1, 5.2).

FIGURE 5.1
The primates are a diverse group of animals.

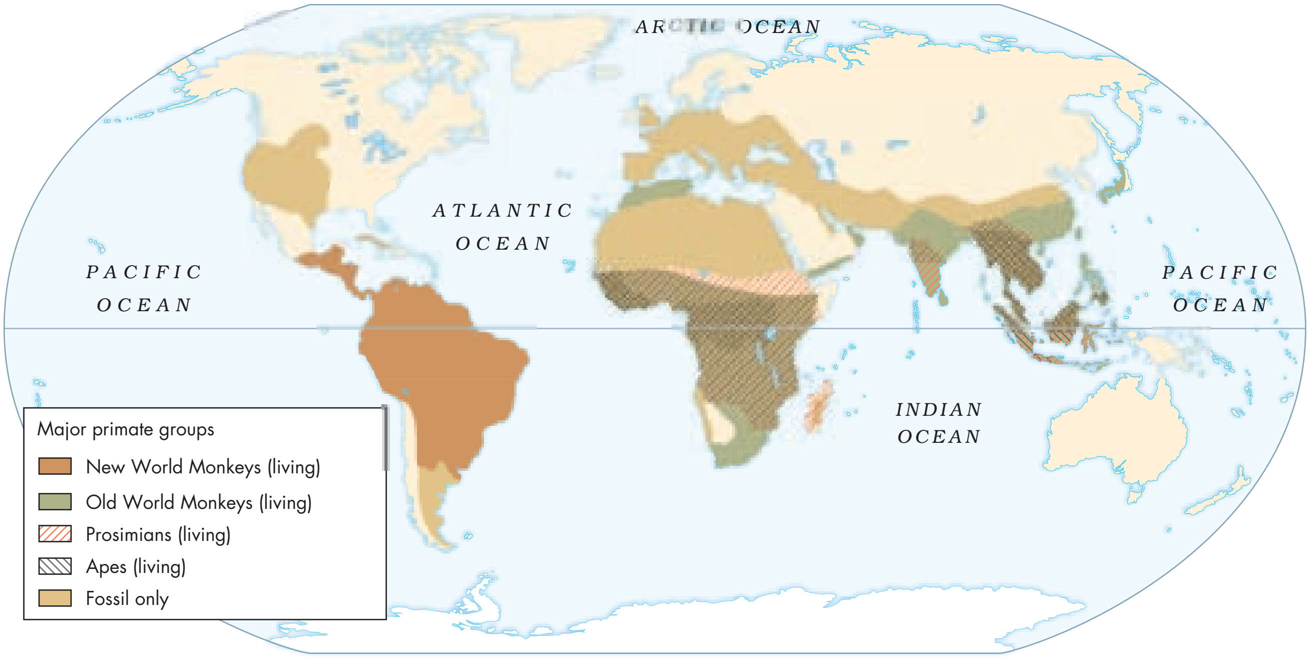


FIGURE 5.2
Geographic distribution of the living primates. Except for a few species of Old World monkeys, and humans, primates live in tropical regions.

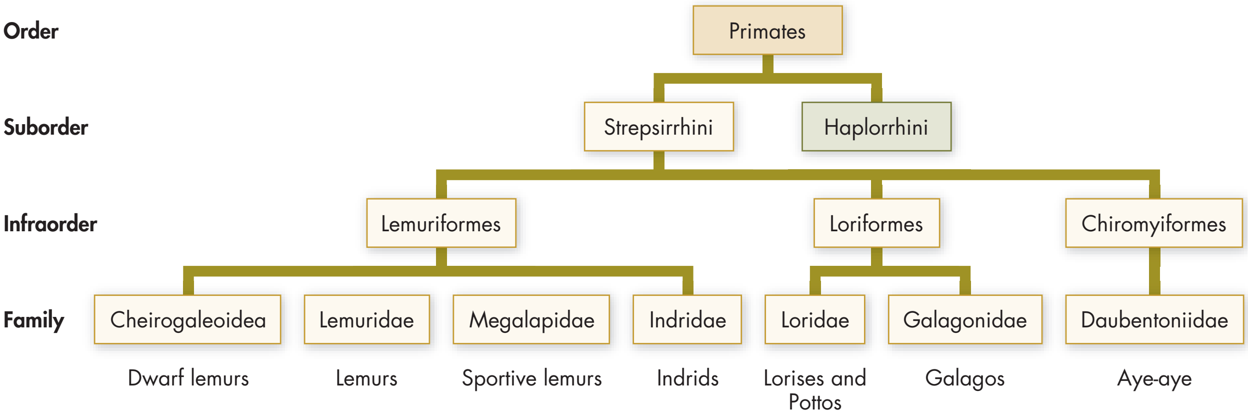


FIGURE 5.3
Taxonomy of the strepsirrhines to the family level. The strepsirrhines include lemurs, lorises, pottos, and galagos.

The Strepsirrhini, or Prosimians

The Strepsirrhini are divided into the lemurs of Madagascar and the galagos and lorises of Africa and Asia (Figures 5.3 and 5.4). The lemurs are a diverse group of primates that exist solely on the island of Madagascar. Like most strepsirrhines they have a special nail on their feet called a grooming claw and a modified set of lower incisors called a tooth comb that are used for cleaning their own and others' fur. Because there are no other primates (such as monkeys) on Madagascar, the lemurs have spread out and adapted to many available environments. This resulted in lemurs that fill the same environmental roles as some monkeys do on the African mainland. Before the arrival of humans a few thousand years ago, there were lemurs the size of bears and a diverse array of forms. Today, human hunting and forest conversion

(a) (b) (c) (d)

■ **FIGURE 5.4**
Strepsirrhines. Shown are: slender loris (a); indri with young (b); adult male crowned lemur (c); ringtailed lemurs (d).

have caused the extinction of a large number of lemur forms, but many species are still found in the forested areas of Madagascar.

The galagos are a group of small, nocturnal (nighttime active) strepsirrhines found across central African forested environments. They have specialized lower limb morphology that results in a great leaping anatomy. The galagos are largely fruit and insect eaters and spend a lot of their time involved in vocal and olfactory communication. Many researchers have argued that the galagos are nocturnal to avoid competition with the larger bodied diurnal (daytime active) monkeys that share the same forests and overlap in diet and habitat use.

The lorises consist of the Asian lorises (usually called slow and slender lorises) and the African pottos. Like the galagos, these strepsirrhines are mostly nocturnal and fully arboreal. However, the lorises tend to have diets that are made up largely of insects and other small animals. Unlike the galagos, the lorises do not leap in the trees; rather they move (usually slowly) by using all four limbs to grasp branches and "clamber" through the trees. The

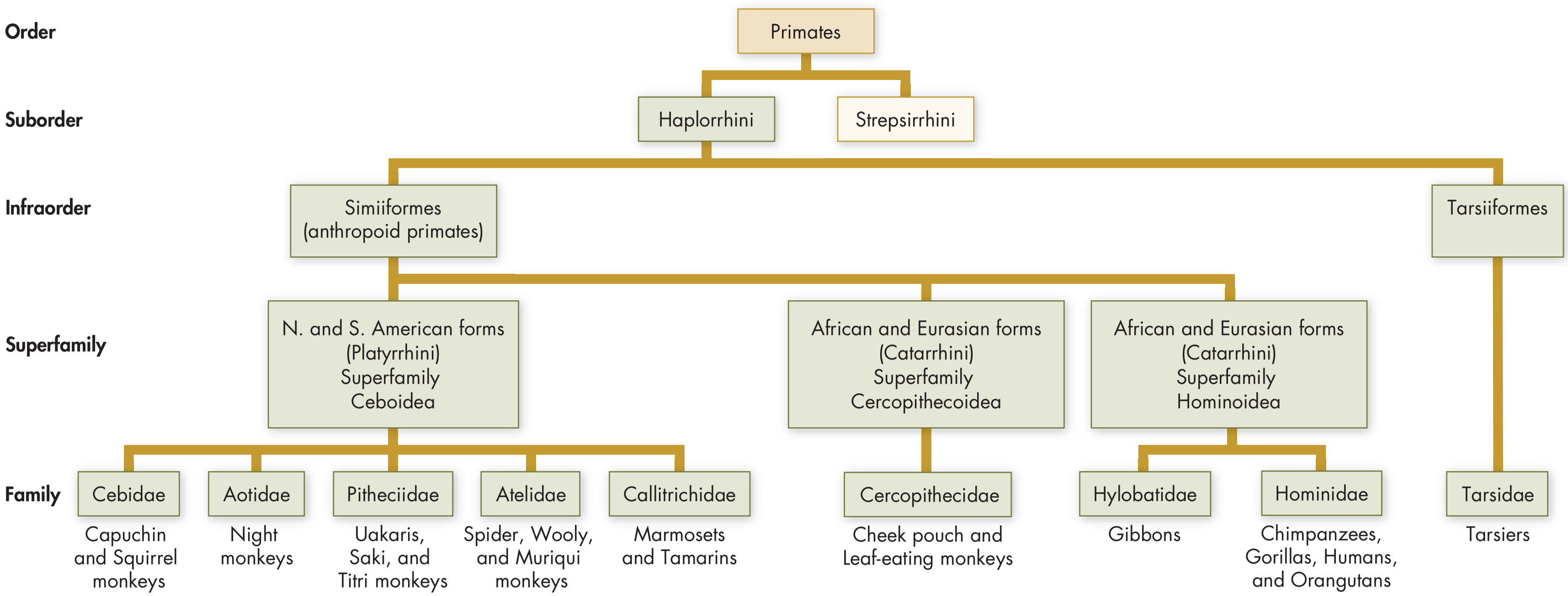


FIGURE 5.5
Taxonomy of the haplorrhines to the family level. The haplorrhines include tarsiers, New World monkeys, Old World monkeys, apes, and humans.

lorises are the most widespread of the strepsirrhines and are found across Africa and into southern and Southeast Asia.

The Haplorrhini, or Tarsiers, Monkeys, Apes, and Humans

The Haplorrhini are divided into two infraorders: the Tarsiiformes and the Simiiformes. The Tarsiiformes are made up of the tarsiers (family Tarsiidae). The Simiiformes are made up of three superfamilies: **Ceboidea,** or monkeys of the Americas; the **Cercopithecoidea,** or Asian and African monkeys; and the Hominoidea, or apes and humans (Figure 5.5). In this book, we use two specialized terms to refer to the Simiiformes: **anthropoid** refers to all monkeys, apes, and humans, and **hominoid** refers to all apes and humans. We reserve the term **hominin** for the hominoid lineage that produced our own species, *Homo sapiens.*

Ceboidea
primate superfamily that includes all monkeys found in the Americas

Cercopithecoidea
primate superfamily that includes all monkeys found in Africa and Asia

anthropoids
all monkeys, apes, and humans

hominoid
member of the super-family Hominoidea

hominin
the division (called a tribe) in the superfamily Hominoidea that includes humans and our recent ancestors

The tarsiers are a group of small-bodied, nocturnal primates found in Southeast Asia. They get their name from having very elongated tarsal bones (see chapter 2) and lower limbs adapted for incredible leaping abilities (greater even than galagos). The tarsiers live in small groups, usually consisting of two adults and some young. They hunt small animals and insects and use a diverse array of vocal sounds to communicate. The tarsiers have extremely large eyes and are well suited to moving about through dense tropical forests at night. Tarsiers are particularly interesting, as they share traits with both the strepsirrhines and the Simiiformes and may even represent a third branch of primates outside of the haplorrhine/strepsirrhine dichotomy (Figure 5.6).

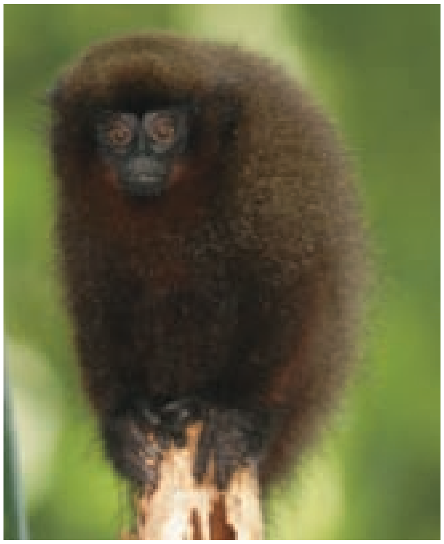
The Ceboidea, or New World monkeys, are a large and diverse group found in forested environments from southern Mexico to southern Argentina. The vast majority of Ceboid forms are fully arboreal and relatively small compared to the Old World monkeys and apes. The smallest Ceboids are as small as or smaller than the tiniest strepsirrhines (less than 250 g, or half a pound), and the largest are about the size of a middle-sized anthropoid (about 12 kg, or 26 lb). The Ceboidea share a set of dental and anatomical characteristics that differentiate them from the other anthropoids and unite them as a group. However, among the Ceboidea there are many morphological and behavioral variants. A group of small-bodied Ceboidea known as the Callitrichids always give birth to twins, and one genus, *Aotus,* is the only nocturnal monkey. Additionally, a few genera of Ceboids are the only primates with truly prehensile (or grasping) tails (Figure 5.7).

FIGURE 5.6
A tarsier. Notice the large eyes and elongated tarsal bones.

The Cercopithecoidea, or Old World monkeys, include all of the monkeys found in Asia and Africa. These monkeys are divided into two subfamilies: the colobinae and the cercopithecinae. The cercopithecines are the baboons, macaques, and related forms of both Africa and Asia. These range in size from a few pounds (~1 kg) to over 60 pounds (~28 kg). They include both terrestrial (ground using) and arboreal species. All, however, are diurnal. The cercopithecines are also called "cheek-pouch" monkeys, as they have small pockets inside their cheeks in which they can store food. The other subfamily of Cercopithecoidea, the colobines, are more arboreal than the cercopithecines and do not have cheek pouches. However, they do have large "sacculated" stomachs with multiple folds that act as reservoirs for special bacteria that help the colobines digest leafy matter. For this reason the colobines are also known as the leaf-eating monkeys,

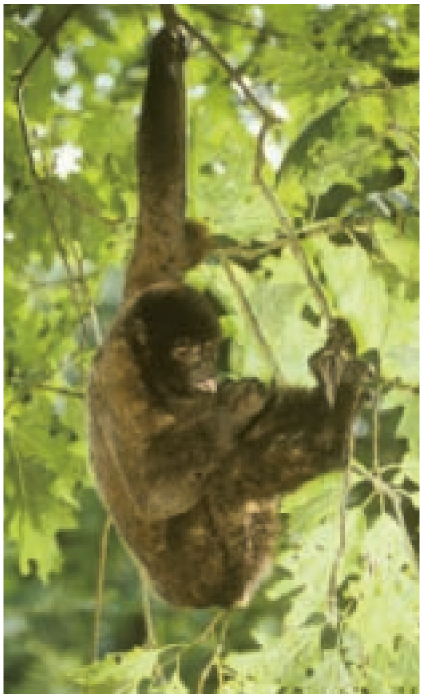
(a)

(b)



(c)

(d)



(e)

FIGURE 5.7
New World monkeys, or Ceboidea. Shown here are: spider monkey (a); capuchin monkey (b); titi monkey (c); cotton-top tamarin (d); and wooly monkey (e).

and many species specialize in hard-to-digest leaves and plant matter that other primates cannot eat (Figures 5.8).

The Hominoidea include the African and Asian apes and the humans. The African apes include the chimpanzees and gorillas; the Asian apes are the orangutan and the gibbons. Relative to the other primates (especially the monkeys), the living Hominoidea have very few species that have survived into the modern era. As you will see in chapter 6, the Miocene period (~22–5 million years ago) was a time of great diversity of hominoid forms. The hominoids are mostly large bodied (except for the gibbons) and have relatively large brains (much larger relative to body size than other primates or most mammals). The apes

FIGURE 5.8
Old World monkeys, or Cercopithecoidea. Shown here are: black and white colobus (a); olive baboons (b); hanuman langurs (c); and guenon (d).

and humans also lack external tails and have adaptations in the upper body that allow a wide range of movement in the arms and hands (Figure 5.9).

Comparing the Primates Helps Us Understand Behavior

Studying primates is interesting in itself, and it teaches us a great deal about our own species. In comparative primatology we are looking for three things: primate-wide trends, hominoid-wide trends, and unique hominin or human characteristics. *Primate-wide trends* are those behaviors or behavior patterns that occur in all, or most, primates. We assume that their universal presence in members of the order Primates indicates that they are ancestral traits that have maintained themselves in all cases due to their selective benefits. In other words, behaviors that have some genetic basis and have done well for

■ **FIGURE 5.9**
Hominoids. The hominoids include apes (gibbons, orangutans, gorillas, chimpanzees) and humans. Shown here are: gorilla (a); orangutan (b); chimpanzees (c); gibbon (d); and humans (e).

CONNECTIONS

Monkey See, Monkey Do, and Humans Too?

If chimpanzee groups fight each other, is it the same as human war? When two gibbons live together for a long time, is it like human marriage? No; in both cases these are not homologous behaviors. While we have made a big deal about how similar humans and other primates are, we have to be careful not to fall into the trap of superficial similarity when it comes to complex social and behavioral scenarios. Human biocultural reality is more complex than that of other primates. Our evolutionary and social histories have created a whole range of options for us that are not available to other primates (see chapters 6–11). Wars occur for reasons that are simultaneously economic, political, and philosophical—all reasons that other primates do not have. A war is never simply about two groups fighting when they encounter one another (as chimpanzees will do). When two gibbons form a small group and mate together, they are not entering into a social, legal, and religious association (marriage). They are pair-bonding, as many primates do, and living in a small group that usually has only two adults and their offspring. There are no vows, no parties, no societal expectations of the pair. There are many behavioral overlaps between humans and other primates, but these tend to be in basic trends and patterns, not complex culturally defined events. Comparisons between us and other primates are as likely to show us what is unique about humans as they are to show us what is common among all primates.

primates are expected to be favored by natural selection and maintained across primate species.

Hominoid-wide trends are those behavior patterns that we see in all, or most, hominoids but not in other anthropoids or other primates. We assume that these behavior patterns arose since the evolutionary split between the hominoids and other anthropoids in the earliest Miocene, about 22 million years ago (as we will discuss in chapter 6). These behaviors are those that distinguish the apes and humans from other primates. Finally, looking at our primate relatives and ourselves, we will find that many behaviors occur only in humans, not in other primates. These behaviors are *unique to humans* and thus have arisen since our split with the apes in the terminal Miocene, about 6 million years ago (as will be discussed in chapter 7). Looking at these trends allows us to begin to reconstruct the evolution of our behavior.

CONNECTIONS

See chapter 7 (pages 206–209) to read about some of the hominoid behavior patterns and how our early ancestors modified them.

To Study Behavior, We Have to Measure It

To scientifically investigate behavior we have to be able to test hypotheses about it; to do that, we have to define it, quantify it, translate it into units of data, and develop tools to record it. Most broadly, behavior is defined as all the actions and inactions of an organism. It may seem counterintuitive to include inactions in this definition, because we tend to think of behaving as engaging in an active state, such as running, talking, fighting, eating, and so on. However, sleeping is also a behavior (a very important one), as are not running, not talking, not fighting, and not eating. In other words, inactions can be as important as overt actions. All are forms of behavior, especially in such complex social organisms as primates.

■ **FIGURE 5.10**
The author observes a macaque in the field. Both qualitative and quantitative methods are used to study primate behavior.

Specific Methodologies Are Used to Measure Primate Behavior

A *methodology* is a set of means used for data collection. Both quantitative and qualitative methods are used in comparative primatology. In *quantitative methods,* data are recorded in a standardized format such that actual numbers (individual data) can be compared across time and place. This type of data can be analyzed statistically and therefore tested most effectively. In *qualitative methods,* data are not collected in specific, standardized formats. These data may enlighten the observer about the behavior of a particular organism, but they cannot readily be used to test hypotheses across different studies. Qualitative data are valuable because they can frequently fill in gaps in more standardized data by adding context and offering a glimpse of the "bigger picture" (Figure 5.10).

To collect quantitative data, researchers use a specific sampling protocol, a fixed pattern for data collection. For example, they might follow a single individual, record the behavior of a whole group, or take snapshots of behavior every 5 minutes of the day. Such studies can be long term (some chimpanzee studies have lasted more than 40 years) or short term (some studies last only a few weeks), depending on the questions being asked and the methods used. Primate studies are done both in captive situations (laboratories, zoos, captive colonies of primates) and in free-range situations, where the researchers go to the locations where the primates live naturally.

A Behavior Can Be Viewed from Five Perspectives

Once you have recorded a behavior, you will want to ask questions about it. A useful approach is to think about behavior from five different angles: phylogeny, ontogeny, proximate stimulus, the behavior itself, and its function (Bernstein, 1999; Tinbergen, 1963). As an example, let's consider the behavior of eating. When you are hungry, a set of chemical and nerve responses stimulates you to look for food. When you obtain food, you use your hands and mouth to process it. These are observations we might make about eating if we are considering it in terms of *phylogeny,* its evolutionary history. The behaviors of using your hands to get your food to your mouth and then chewing it have an evolutionary past that includes the morphology and anatomy of your digestive system (recall chapter 2), hands, fingers, mouth, teeth, and so on. The combination of these features is not unique to you or to humanity; rather, it arose among the earliest primates, who used their hands to manipulate food items, and it is common to all primates.

In contrast to the phylogeny of a behavior, the *ontogeny* of a behavior includes all the factors that have influenced an organism since its conception, that is, learning and life experience. For example, when you are hungry, you go to certain places to get food—if you are at home, you go to the refrigerator or cupboard—and you eat certain sets of food but not others—you select specific items to consume. Food preferences and knowing where to go for food are learned behavior patterns and important parts of ontogeny.

If we think about eating from the perspective of *proximate stimulus,* we consider the trigger event that initiated the behavior. For example, you may

be out and about and pass a hot dog stand, which smells quite good (assuming you have learned to like hot dogs). The aroma stimulates your hunger and you move toward the stand to feed. If we think about eating from the perspective of the *behavior itself,* we look at the behavior of feeding: Once you have the hot dog, you eat it. Finally, and importantly from an evolutionary perspective, we are also interested in the *function* of a behavior, that is, its impact on fitness (or lifetime reproductive success, as discussed in chapters 1 and 4). The function of a behavior, its evolutionary consequences, can be significant when we are trying to understand why a behavior is common or rare or even why it appears at all. From this perspective, we might consider the effects on overall fitness of relying on a diet of fast food.

When we collect behavioral data, then, we ask one or more of these five questions in an attempt to better understand the behavior itself. In the overall picture of biological anthropology, we are most interested in behaviors that seem to serve some function and therefore add to potential lifetime reproductive success. Just as in our earlier discussions of Darwin's finches, we are interested in what facets of our behavior have evolved over time—behaviors that have at least some genetic basis such that natural selection would have favored them over the last several million years, influencing the patterns we see in humans today.

Behavior and Genetics Are Interconnected

In chapter 3 we saw that all aspects of an organism have some genetic component. When it comes to behavior, however, identifying the underlying genetic basis is extremely difficult, because behavior is not directed by one or two genes or a few chemical or neurological impulses (although we assume that there is some heritable component to at least some behavior). Most, if not all, behavior is a complex series of interactions among morphology, learning, experience, circumstance, and chance events. This complexity makes it difficult to assess the function (or evolutionary impact) of any behavior and to understand the biological basis or genesis of a behavior. Many behaviors may also reflect exaptations, the use of certain behavioral capabilities in novel ways. These complex factors do not mean that we cannot attempt to answer these questions.

CONNECTIONS

See chapters 3, pages 88–89, and 4, pages 106–108, for discussions of genetics and behavior.

Some behavior patterns that are widespread in a taxonomic group serve clear functions. These patterns are easily observed, described, and tested, and we assume that they are adaptations. The flight/fight/startle response in mammals is an example of such a behavior. We see this response when a zebra standing on the savannah looks up from the grass it is eating to see a lion charging at it, mouth open and teeth glistening. The zebra immediately stops eating and starts moving. Its heart beats faster, the blood flows away from its stomach and intestines toward its legs, and it sprints away as fast as it can. If successful, it escapes the lion and then slowly calms down and returns to eating. If the situation is slightly different—for example, the lion has cornered the zebra and her offspring—the zebra may choose to stand and fight. Either way, the physiological response (changing heartbeat and blood flow) is the same and is part of the zebra's phylogeny. The decision to flee or fight is based on experience/learning and is part of the zebra's ontogeny.

A similar pattern happens in humans. If a friend (or foe) sneaks up on you and scares you, your heart pumps faster, your stomach feels queasy, and you may yell or jump. A whole genre of movies (suspense/slasher movies) relies on

STOP & THINK

What does it mean for us that modern humans can induce these stress responses just by worrying about jobs, moneys, families, and other aspects of our lives?

this startle response for its success. The fight/flight/startle physiological pattern and its generalized behavioral response are very old and are found in most animals. Why? It stands to reason that those individuals who did not respond to predators in this way with relative frequency did not do well in the overall evolutionary picture. We hypothesize that this combined physiological and behavioral response pattern is an adaptation because it is widespread and potentially results in a selective benefit for an organism.

There are several such behaviors common to mammals and other organisms. In this chapter we are going to focus specifically on the nonhuman primates and their general behavior patterns. From assessment of these general patterns and a look at a few groups of primates, we stand to learn something about human behavior.

Behavioral ecology provides the basis for evolutionary investigations of behavior

behavioral ecology
the study of behavior from ecological and evolutionary perspectives

foraging
the act of seeking and processing food

Behavioral ecology is the study of behavior from ecological and evolutionary perspectives (Strier, 2006). In later chapters we will be looking at how ecological pressures and evolutionary patterns have shaped morphology, but in this chapter we examine how these pressures and processes affect behavior. By obtaining a general understanding of how aspects of ecology challenge organisms, we can model ways in which organisms might deal with these pressures through behavior as well as morphology. In other words, the behavioral ecological approach seeks to understand the selective pressures on organisms and hypothesize about how the behaviors they exhibit today have arisen in response to current and past ecological pressures.

Socioecological Pressures Affect Organisms in Five Areas

General socioecological pressures can be divided into five main arenas: nutrition, locomotion, predation, intraspecific competition, and interspecific competition (Figure 5.11). *Nutritional ecology* refers to the pressures that organisms face in obtaining sufficient food and water. Whether a primate feeds on fruits, leaves, insects, or other mammals makes a substantial difference in how it **forages**—that is, how it goes about finding food, where it looks for food, and how it captures and processes food. This pattern is an important element in the primate's behavioral ecological profile.

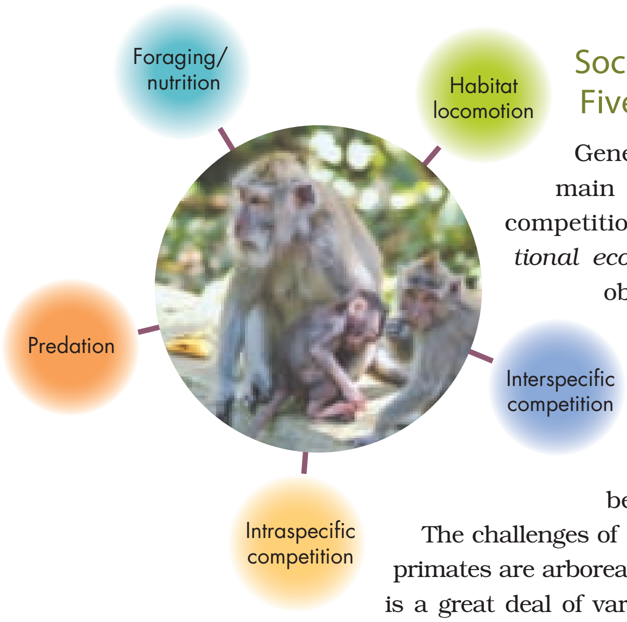


FIGURE 5.11
Socioecological pressures. All animals are subject to five basic kinds of challenges: the need to obtain food, to move around their habitat, to protect themselves from predators, and to compete for resources both with members of their own species and with other species.

The challenges of *locomotion* involve how an animal moves about. Generally, primates are arboreal, terrestrial, or both. Within each of these categories there is a great deal of variation. One arboreal primate may use the lower limbs of trees and move about in dense foliage, while another arboreal primate may use the upper extremes of the forest, moving by leaping between trees and using the smaller terminal branches as its pathways. Both of these primates are arboreal, but the pressures on their bodies and behavior are substantially different, based on the surfaces they use in their arboreal environment (Figure 5.12).

Predation is another important selective force. If an organism is eaten, its reproductive success is drastically diminished, to say the least. If there are predators in the environment, we would expect primates to deal with this

threat in some way. Most primates have very little defensive morphology (aside from large canine teeth), so we would expect to see some behavioral means of avoiding predators. In fact, that is what we find. Most primates have vocalizations and specific behaviors that they use to respond to predators. Sometimes, primates will mob predators as a group. The pressure of predation is thought to be so important in the evolution of behavior that it is often proposed as one of the reasons that many animals live in groups. This idea is referred to as the *selfish herd concept.* If an individual is in a group, the odds of its being eaten are reduced by the number of other individuals in the group. Additionally, with more eyes and ears, predator detection increases. On the other hand, the larger the group, the easier it is for predators to detect it. Clearly, there are trade-offs in the evolution of behavior, just as there are trade-offs in the evolution of morphology, as we will see in upcoming chapters.

FIGURE 5.12
Modes of locomotion. These two arboreal primates move very differently. The prosimian (indri), top, moves by leaping between branches and clinging. The anthropoid (baboon), bottom, moves by quadrupedal walking along the branches. Note the anatomical differences in their upper bodies and lower legs.

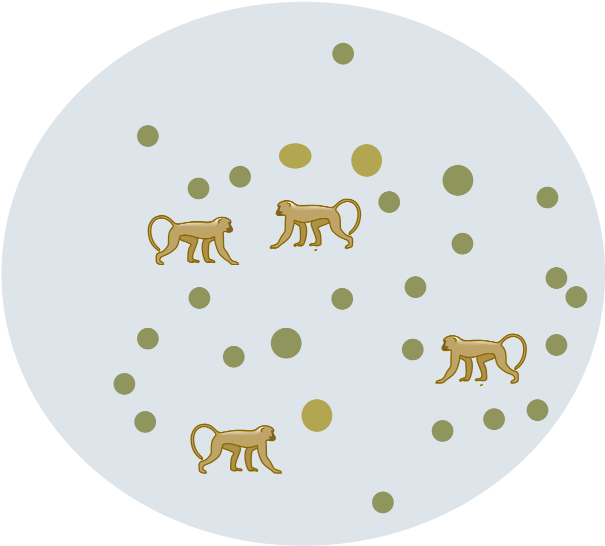
There are many ways that competition can be an important selective force on primates. *Intraspecific competition* refers to contests among members of the same species or even the same group. *Interspecific competition* refers to contests between different species for the same resources (for example, competition between monkeys and birds over the same fruit source). A distinction is also made between contest competition and scramble competition (Sterck, Watts, & van Schaik, 1997; van Schaik, 1989). *Contest competition* occurs when the resource being fought over can be monopolized by one or more individuals. For example, if there is a relatively small prize fruit tree, one or a few individual monkeys can potentially dominate access to it and keep others away. The contest is then between individuals or groups to see who can hold the tree and defend it from others. *Scramble competition* occurs when a resource is not effectively defensible by one or a few individuals (for example, a whole orchard of fruiting trees), and thus all individuals are really racing against time to see how much fruit they can gather before it is all gone. Each of these types of competition exerts slightly different pressures on organisms. Consequently, we would expect that behavioral adaptations to these pressures would also vary. Figure 5.13 illustrates these two types of competition.

Success of a Behavioral Adaptation Is Measured in Terms of Energy Costs and Benefits

Primatologists use the concept of costs and benefits to describe an organism's behavioral responses to ecological pressures. In chapters 1 and 4, we discussed the concept of *fitness,* which we can define here as a genotype's contribution to net lifetime reproductive success relative to other genotypes. In terms of behavioral ecology, we seldom actually measure an organism's

STOP & THINK

Do humans today still have to worry about these basic pressures?



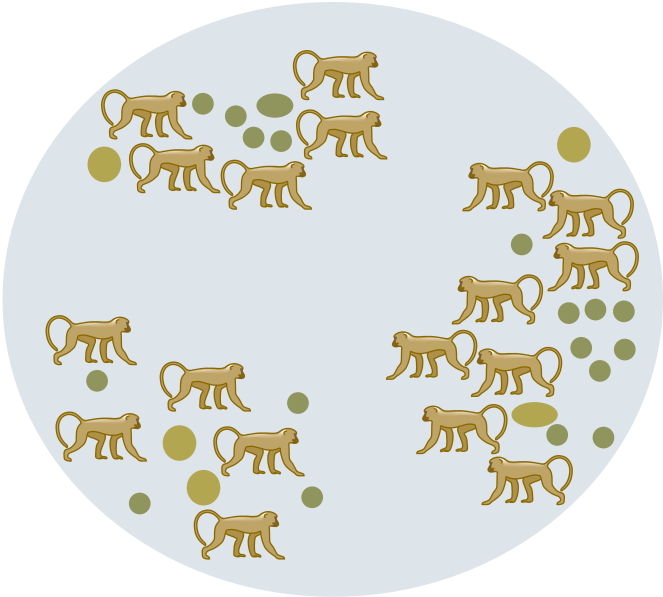


FIGURE 5.13
Scramble competition: dispersed food, difficult to monopolize

Contest competition: clumped and defendable food sources

overall lifetime reproductive output; rather, we model the amount of energy that an organism uses in any given behavior and try to determine whether the organism gets back what it expended (neutral behavior), loses energy in the behavior (a cost to the organism), or gains energy in the behavior (a benefit to the organism).

CONNECTIONS

See chapter 4, page 103, to tie this into modern evolutionary theory.

Because it costs energy to reproduce and to live from day to day, the core assumption of behavioral ecology is that organisms will try to maximize their net energy gains and minimize their costs. Those organisms that do this most effectively will hypothetically have the most success in reproducing and thus leave more copies of their unique genotype in the next generation (the process we call natural selection). Notice that we assume that natural selection will favor those behavior patterns with the highest net fitness returns (as measured by energetic benefits and, ostensibly, reproductive output).

strategy
set of behavior patterns that has become prominent in a population as a result of natural selection

kin selection
behavioral favoring of one's close genetic relatives

altruism
acting in a way that has a net loss of energy to the actor and a net benefit in energy to the receiver

If a set of behavior patterns becomes prominent in a population as a result of natural selection, we call this pattern a **strategy.** Thus, competition among behavioral variants leads, over time, to the overrepresentation of the better-fit strategies in subsequent generations. Of course, this process is only possible via natural selection if the behavioral patterns in question are heritable, that is, they have a genetic component (or, as noted by Jablonka and Lamb in chapter 4, have epigenetic, behavioral, or symbolic inheritance).

Certain predictions about how animals should behave emerge from these basic notions of behavioral ecology. One of the most significant predictions is **kin selection,** the behavioral favoring of your close genetic relatives (Hamilton, 1964). Kin selection was proposed to explain the dilemma posed by altruism. **Altruism,** or acts that have a net loss of energy to the actor but a net gain in energy to the receiver, does not make sense if organisms only benefit by maximizing their own fitness. However, the idea of kin selection offers a simple equation that should predict when an organism might behave in a manner that looks altruistic. If the individual who receives the benefit from a behavior that costs you energy is your relative, then a certain percentage of your genotype (depending on the degree of relatedness) is still benefiting. Because

close relatives (parents and offspring, siblings) share much of their genotype, we would expect behaviors among them to be seemingly altruistic, as they frequently are. As individuals are more distantly related, we would expect to see less and less seemingly altruistic behavior among them.

Alternatively, even if organisms are not related to each other, we might still expect to see reciprocal altruism. In *reciprocal altruism,* an individual behaves in a way that benefits another at a cost to itself, and the other individual in turn benefits the original actor, either immediately or at some time in the future. These basic assumptions serve as a set of predictors that researchers use in attempts to explain the types and patterns of behavior they observe.

Reality Is More Complex Than Suggested by Cost-Benefit Analyses

Organisms are constellations of traits, and often there are conflicting pressures on different traits. For example, if an organism used both arboreal and terrestrial environments, we might expect that arboreality would exert pressure favoring curved phalanges for better movement in the trees, while terrestriality would exert counterpressures favoring straighter phalanges (at least on the feet) for more efficient bipedal walking. The situation is even more complex when we try to understand behavior, especially complex social behavior.

Because there are no known direct gene–behavior links, it is likely that ecological pressures set up ranges of selection within which many behaviors can function, some better than others. Imagine a spectrum of potential behaviors influenced by a variety of factors (Figure 5.14). Natural selection (fitness costs/benefits) and other limitations (such as body size and shape) determine the ends of the spectrum—the limits of practical behaviors—and particular environmental stimuli or experiences elicit behavior from a specific part of the spectrum. As a simple example, think of femur length. In the fetus the mass of tissue that is eventually going to be the femur is controlled in part by genetic instructions, and during fetal development the general shape of that bone is influenced by cell–cell interactions and the interactions of proteins and tissues—epigenetic and developmental factors. After the individual is born, however, the rate at which the bone grows is powerfully influenced by the amount and quality of nutrition received. So although the potential spectrum of femur length for two individuals might be the same (especially if they were identical twins), different stimuli and experiences would result in different actual femur lengths.

We can refer to the spectrum as the **potential** for a trait and to the actual phenotype as the **performance** of that trait. As a behavioral example, consider physical aggression in humans. There is a range of possible types and patterns of physical aggression that any individual can exhibit. This broad potential is influenced by body

potential
the spectrum of possible expression created by morphology, evolutionary history, and other aspects of a genotype

performance
the actual expression of a trait or behavior

CONNECTIONS

See chapter 4, pages 16–108, and think about how this relates to epigenetic inheritance and niche construction.

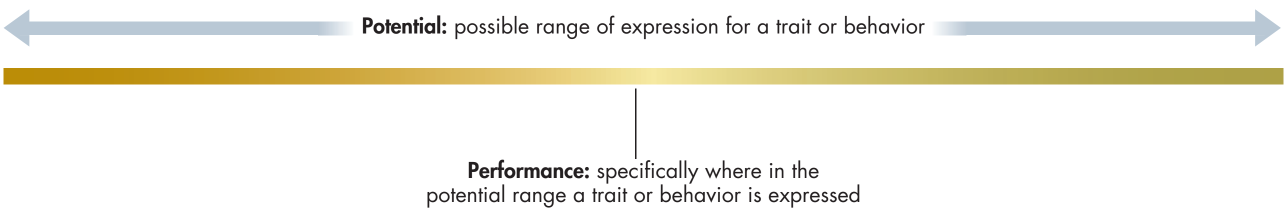


FIGURE 5.14
The spectrum of behavior. Natural selection and other limitations create the potential range of the spectrum. Particular environmental stimuli, experience, and physiological conditions determine where on the spectrum the behavior or trait occurs.

size, muscle density, and health, among other things. However, cultural patterns, life experience, and the availability of weapons or other tools can dramatically influence where in the potential spectrum an individual actually expresses physical aggression.

This example is simplistic, but it illustrates the complexity of understanding even one behavior. Although a behavioral ecological approach can be useful in modeling the function and thus the evolution of behavior, we need to remember that it is not individual behaviors or traits but whole organisms that face environmental challenges on a day-to-day basis. It is the overall lifetime reproductive success of those organisms that affects the next generation; our estimates of energy costs and benefits can easily oversimplify or miss the mark on lifetime patterns.

Adding to this complexity, factors other than natural selection affect behavior. Chance events (such as in genetic drift) can influence an individual's life in ways that we cannot predict based on energy models, giving rise to new behaviors. Some behaviors may be exaptations (behaviors that are co-opted for a new purpose); thus, a behavior that functions in a particular way today may have arisen for an entirely different purpose. And some behaviors may be by-products of other behaviors. The evolutionary biologist Stephen Jay Gould introduced the notion of **spandrels**—by-products of structural change—to account for some anatomical structures. The example he gave was the arch, which by its very structure creates two open spaces, or spandrels, in either corner (Figure 5.15). In terms of behavior, a spandrel pattern could mean that a given behavior produces other side behaviors that in themselves are not the result of selection. It might be very difficult for a primatologist to tease out the causes of such a behavior.

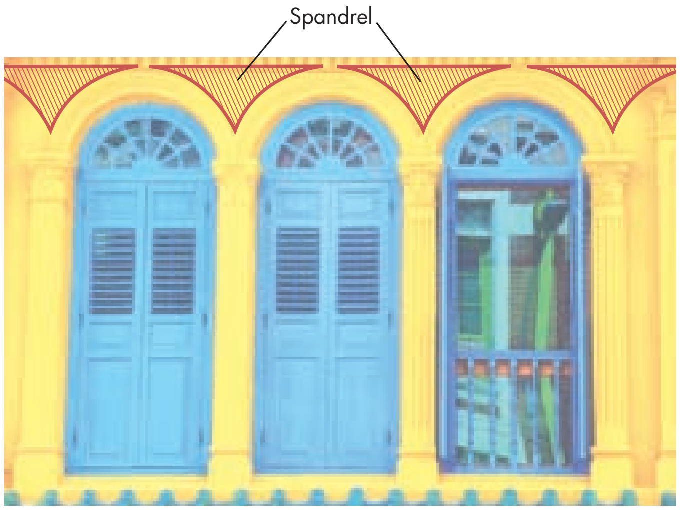
spandrels
by-products of structural change

Morphological constraints on organisms also limit the spectrum of potential behavior expression. For example, human morphology will not allow us to see certain wavelengths of light or hear certain ranges of sound; our behavior could not evolve in response to detection of those elements outside the ranges

CONNECTIONS

Are All Men Jerks?

Chimpanzee males often attack females just to keep them in line. Certain types of baboon males will bite and attack females to keep them from wandering toward other males. Human males in many societies occasionally attack and abuse women. Are male primates just jerks? No, but they have the potential to be very aggressive. In many societies, human and other primates, social cooperation keeps within-group aggression relatively low. However, in some species and in some contexts males can use aggression to influence other group members, including females. In many primate species males are larger than females and thus have an advantage when it comes to physical conflict. So in these species there is the potential for males to use physical aggression as a social tool, but they do not always do so. The difference between males having evolved aggressive responses and males using those aggressive responses is a good example of the potential and performance concept. The body size difference between males and females sets up the possibility that such behavioral patterns could emerge. However, many other factors, such as type of social system, makeup of the group, and tendency for coalitionary support in conflicts, all affect the performance (or emergence) of such aggression on the part of males. So, when it comes to aggression, males have the potential to be jerks, but they are not evolved to be that way.



■ **FIGURE 5.15**
The spandrel is the by-product of arch building. Just as building an arch creates spandrels, natural selection creates some behaviors that are merely by-products.

accessible to us. Finally, there are **phylogenetic constraints** on behavior, which are limits on our current behavior due to patterns and trends in our evolutionary past. Just as humans have five fingers because they are primates, they also have other morphological and possibly behavioral patterns that have been inherited from their distant ancestors.

phylogenetic constraints limits on current behavior or traits due to patterns and trends in an organism's evolutionary past

infant dependency period period during which the infant is wholly reliant on others for nutrition, movement, thermoregulation, and protection

General behavior patterns in the living primates

If we look across the primate order, we see that some behavior patterns are found in nearly all primate species. When we identify such widespread patterns, we assume that they represent ancestral characteristics and successful adaptations. Most of these behavior patterns stem from living in groups and negotiating the social relationships that group living creates.

Mother-Infant Bonds Are the Core of Primate Societies

In all primates, and in many mammals, the behavioral interactions between a mother and her infant establish the parameters for the offspring's later social relationships. Compared to other mammals, primates have a very long **infant dependency period,** the period during which the infant is wholly reliant on others for nutrition, movement, thermoregulation, and protection. Obviously, it is in the mother's evolutionary interest to enable her offspring to mature successfully. In primates, due to the long dependency period, this interest results in a patterned set of behavior we refer to as the *mother-infant bond.* This bond is characterized by very close spatial association (for years in human, ape, and some monkey societies), frequent physical and vocal contact, and the exposure of the infant to the mother's behavior and association patterns. The infant not only gains nutrition and protection from the mother but also acquires information about other group members, foods, ranging patterns, and behavior habits (Figure 5.16). We can see this as one of the major aspects of behavioral inheritance in primates. We might even consider the intense closeness of primate mothers and infants as building a

FIGURE 5.16
A female primate and her infant. These are macaques (*Macaca fascicularis*).

kind of social niche for the growing infant (remember niche construction from chapter 4).

Specific mothering behavior is not coded for by particular genes; rather, all female primates (and males in many species) have the behavioral capability to exhibit a set of caretaking behaviors. What type of behavior an individual exhibits depends on her or his previous experience (ontogeny). Infants act as a strong stimulus and always seem to generate much interest from members of a group; however, if a female has not had previous experience observing her mother or other group members handle infants, or if she herself has never interacted with young individuals, she may feel the stimulus but not be able to exhibit behavior that results in successful infant caretaking. We can hypothesize that the evolution of a set of physiological and behavioral patterns that predispose individuals to caretaking behavior (caretaking potential) exists as a result of natural selection. Life experience then enables the differential expression of those behaviors (caretaking performance). We could also expect that in many species the selection pressures for successful caretaking potential would be stronger on females than on males due to the fact that females give birth and must lactate and provide food if the offspring is to survive.

STOP & THINK

If we do not automatically know how to parent, then how do we learn?

There Are a Few Primary Grouping Patterns in Primates

Most primates live year-round in relatively cohesive groups, typically consisting of more than two adults and related offspring. Frequently, there are multiple adult females and males, although sometimes there is only one male and multiple females. In a few species there are groups with one adult female and multiple adult males. In about 3% to 5% of primate species, groups typically consist of one female, one male, and their offspring (Fuentes, 1999). Some primates, primarily prosimians and a few anthropoids, are also found in what is referred to as a *dispersed social group.* In this pattern, individuals rarely gather in the same place at the same time, but their individual **home ranges,** the areas they use regularly, overlap substantially. These individuals know each other and frequently interact via scent marking or vocalizations but rarely engage in face-to-face behavioral interactions (Figure 5.17).

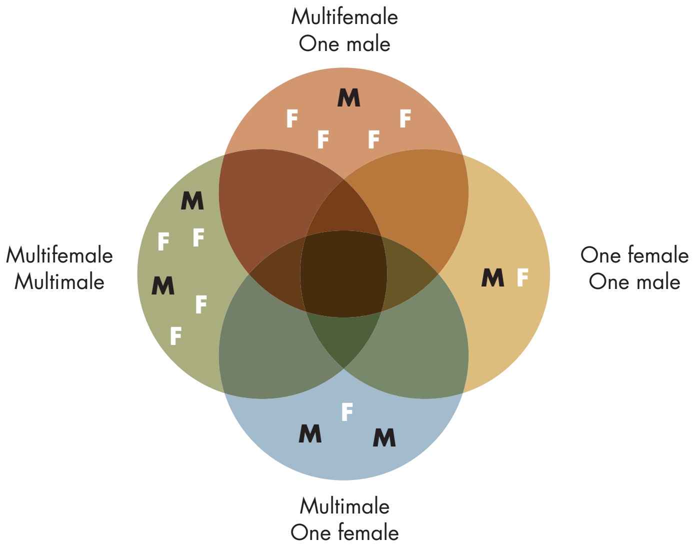
home range
area used by a primate group or community

affiliative
bond enhancing or prosocial ("friendly")

agonistic
aggressive or combative ("unfriendly")

Affiliation and Grooming Are Important in Primate Societies

Because primates live in groups and interact with one another frequently, social tolerance is extremely important. One way that individuals establish relationships with one another is through the use of space and a type of contact behavior called *grooming.* Space use is an indicator of the type of relationship between individuals. If individuals are frequently in close spatial association, we can say they have a tolerant and probably **affiliative** ("friendly") relationship. If two individuals avoid one another or engage in conflict over the use of the same area, we can say that they are less tolerant of one another and have an **agonistic** ("unfriendly") relationship.



■ **FIGURE 5.17**
Basic primate grouping patterns. Much of primate behavior stems from living in groups.

Primates establish and cement affiliative relationships through mutual grooming (Figure 5.18). Grooming is the movement of the hands and/or mouth through the fur to clean out particles of dirt, insects, and other debris. Obviously, this behavior has a hygienic function, but primates groom far more frequently than would be required for simple hygiene (McKenna, 1978). The physical contact involved in grooming appears to have a beneficial effect on both the groomer and the groomee. Especially in times of tension or strife, grooming can reduce stress and cement relationships. Individuals may spend more time grooming those with whom they want to associate, or they may refuse to groom those with whom they have agonistic relationships. The directionality of grooming can also be important. Who grooms whom and who initiates and terminates grooming sessions can reveal a great deal about the relationship between individuals.

Because grooming involves both morphological components (hands, mouth) and physiological components (the changes caused by touch and the effect that cleaning has on health), we can see the importance of selection in creating the parameters for its expression. At the same time, an individual learns during its lifetime which other individuals to groom, how to groom, and when to start and stop grooming. All primates groom—it is a primate-wide behavior pattern—but they vary in how they use social grooming.

■ **FIGURE 5.18**
Three macaque adults and a juvenile relaxing. The adult female on the right grooms the young juvenile.

Hierarchies and Dominance Help Structure Primate Societies

Most primate species exhibit a pattern of differential access to resources within a social group—in other words, some individuals get better food or more food, or better sleeping areas, than others. The set of relationships that results in different relative abilities to acquire desired goods is

called **dominance.** If an individual is dominant, or has a high rank, he or she can gain a favored resource more easily than an individual who is less dominant or lower ranking. The measure of access to desired resources by different individuals relative to one another is called a *dominance hierarchy.*

STOP & THINK

Do humans groom each other? Is physical touch the only way we might groom?

dominance
set of relationships that results in different relative abilities to acquire desired resources

philopatric
staying in one's natal group

Dominance hierarchies can take a variety of forms. Some species have relatively linear hierarchies, wherein one individual has priority access over most or all of the other members of the group. This dominant individual is called the *alpha* animal. In such a system there would also be a second-ranked individual who has access over all other members except the alpha, and a third-ranked individual, and so on. However, in most primate societies there is another level of complexity to dominance relations: They are contingent on coalitions and alliances (predictable and mutually invested relationships). Even in relatively linear systems, high-ranking individuals usually have one or more allies in the group with whom they interact frequently and who provide social support in contests for resources or even in direct physical fighting.

CONNECTIONS

See Chapter 7, page 208, and 8, page 226, to see how human ancestors might have changed the relationship between the sexes relative to other primates.

In many primate species, adult males and adult females have separate dominance hierarchies. Frequently, in one-on-one contests for resources, males are dominant over females, especially if the males are larger (sexually dimorphic). However, environmental and social selective pressures do result in systems in which females are dominant, in which males and females are co-dominant, or in which measuring dominance is difficult because individuals do not compete overtly with one another. Dominance is not a trait inherent in an individual; rather, it is a role that he or she occupies for a time. Primates move through different dominance ranks and roles throughout their lives, and each primate species has a different pattern according to which individuals attain dominance or interact with one another in competition for resources. Because dominance hierarchies are found primarily in adult primates, the system is one that young individuals have to learn to negotiate as they mature (Figure 5.19).

Dispersal and Life History Patterns Are Important to Social Behavior

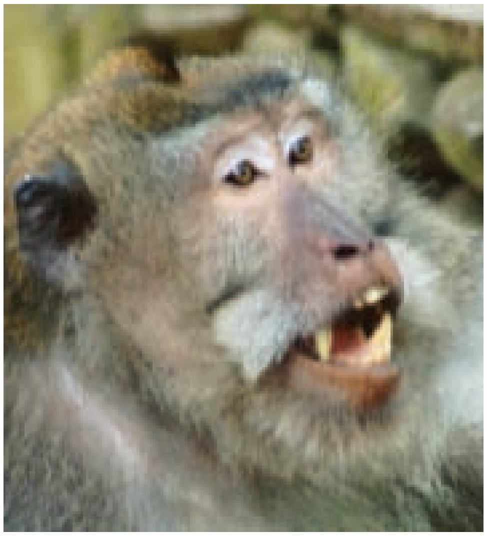


FIGURE 5.19
Dominance. A male macaque displays his canine teeth in a mild display of dominance.

When we want to understand the behavior of primates in an evolutionary context, we have to take into account the genetic makeup of the group they live in and the types of experiences they have across their life span. Understanding dispersal patterns is key to understanding these aspects of group living. For example, in most primate species, members of one sex disperse (leave their natal group, the group they were born into), and members of the other sex are **philopatric** (stay in the natal group). Members of the philopatric sex then have genetic relatives (siblings, parents, cousins) who live in the same group and theoretically have an investment in their survival (according to the kin selection hypothesis). Members of the dispersing sex have to enter a group in which they have no relatives and thus must forge relationships with nonkin. They cannot expect the "built-in" alliances and assistance that having kin around would provide. In some primate species, both sexes leave their natal groups, resulting in few kin bonds except those between mothers and offspring. Dispersal also has another cost: time spent alone, outside of a group. It is highly likely that dispersal can be very costly in an evolutionary sense, because the individual does not get the

benefits of living in a group and may be more susceptible to predation and less able to compete for access to food.

In some primate species, individuals of one or both sexes move among multiple groups during their lifetime, making and breaking alliances and relationships across groups and time. In some species, different types of groups exist within the same population. Hanuman langurs of India (*Semnopithecus entellus*), for example, have multifemale/multimale groups, multifemale/one-male groups, and all-male groups living in the same area. A male could move among three distinct types of group throughout his lifetime. His experiences in each of these group types would be very different and might require different social skills and patterns. We would expect to see a range of behavioral potential in species with this pattern, because the specific behaviors any individual would need to exhibit could change across the different social situations.

Cooperation and Conflict Are Integral to Primate Societies

Both cooperation and conflict play major roles in the lives of primates. Alliances and coalitions are core in social groups, and primates use social negotiation to establish, reinforce, and disrupt these relationships. Very few primates spend most of their time alone; therefore, they are constantly interacting with their group-mates. Because dominance relationships are pervasive in primate societies, serious fighting for resources usually does not occur. There are fights, but the overall time and energy spent engaging in serious aggression tend to be quite low (Sussman & Garber, 2007). This is not to imply that conflict is not important. It has been argued that social relationships between individuals are so important that the potential damage caused by conflict is serious and must be repaired. Many primate species display some form of reconciliatory behavior wherein they repair damage to relationships caused by conflict (Aureli & de Waal, 2000).

STOP & THINK

Do humans spend more time cooperating or fighting?

Social organization in two nonhuman primate societies: macaques and chimpanzees

It is evident that social organization is complex in primate societies. That is, their systems of living together, interacting with one another, acquiring sufficient nutrition, and ensuring safety from predators are quite intricate. We can envision social organization as being made up of the mating patterns, group structure, and individual behaviors of members of a species. Researchers generally agree that these constituent components of social organization have been, and are being, shaped by evolutionary pressures. Thus far in this chapter we have considered general patterns of primate behavior and briefly introduced the core aspects of behavioral ecology. In this section we examine two nonhuman primate societies—macaques and chimpanzees—and then briefly compare them with modern humans. Using the comparative approach, we hope to identify some behavioral patterns in humans that are primate-wide, some that are hominoid-wide, and others that are uniquely human.

Macaques: A Widespread Primate Genus

Macaque monkeys (members of the genus *Macaca*) are among the most widespread of any primate genus. In fact, of all the primates, only humans have a more extensive distribution on the planet (Figure 5.20). The genus *Macaca*

FIGURE 5.20
The distribution of the genus *Macaca*. Of all nonhuman primates, macaques have the widest geographical distribution.

is an excellent group to examine in a comparative perspective because the radiation of the genus in the Plio-Pleistocene, about 2 million years ago, is similar to that of the genus *Homo* at the same time. The macaques spread across much of Asia and into central Eurasia and even northern Africa. Today, their distribution remains widespread throughout eastern and southern Asia and into northern Africa. Macaques have encountered many diverse habitats. As a result, they reflect responses to a broader range of environmental pressures than nearly any other nonhuman primate group.

There are about 19 macaque species, but they tend to cluster into a few major species groups. The rhesus-fascicularis group (primarily *Macaca mulata*, the rhesus macaque, and *Macaca fascicularis*, the long-tailed macaque) represents an extremely widespread species group wherein the different species can and do interbreed when they overlap in the wild (Figure 5.21). This occasional cross-breeding between species suggests that their speciation is relatively recent or that the species never diverged dramatically either behaviorally, ecologically, or physiologically.

Social Organization in Macaques

Female macaques range in body size from about 3 to 4 kg in some species to more than 12 kg (~27 lb) in others. Males are roughly 20% to 40% larger

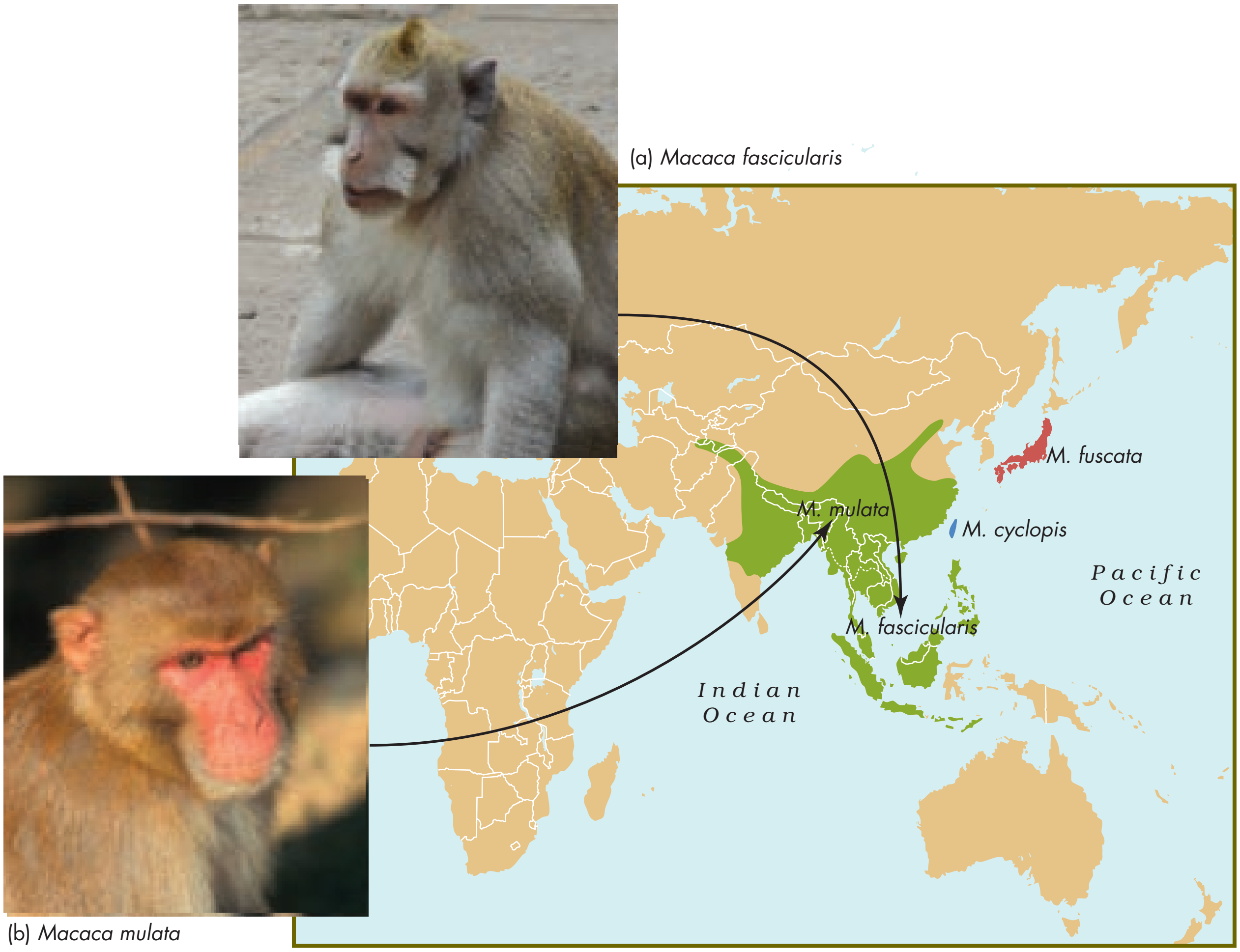


FIGURE 5.21
The combined ranges of *Macaca fascicularis* (a) and *Macaca mulata* (b). The rhesus-fascicularis group is a widespread species group of macaques.

than females (Rowe, 1996; Figure 5.22). Macaques are generalists in their feeding patterns, preferring fruit but eating a wide variety of foodstuffs, including leaves, insects, and occasionally vertebrates. They are full quad-rupeds and spend a good deal of time in the trees; however, most macaque species also use the ground for foraging and moving about.

The majority of macaques live in multifemale/multimale groups that can number from 10 to more than 100 individuals; the most usual group size is between 20 and 50. There are usually more adult females than adult males in these groups, and social activity revolves around clusters of related females (Thierry, 2010). In macaque societies, males tend to leave their natal groups and seek out other groups to join. Females, on the other hand, are philopatric and therefore are surrounded by their female relatives (sisters, cousins, aunts, mother, grandmother, and so on) throughout their lives. As we would expect, female macaques spend a great deal of time and energy associating and interacting with their maternal kin. Clusters of females and young can be seen in macaque groups huddling together in close proximity, grooming one another, and occasionally fighting (Figure 5.23). These clusters are called *matrifocal units* (Wheatley, 1999), indicating that they are generally made up of related females. A few adult males may be seen near and/or in the midst of the matrifocal units, but most males are relatively solitary, remaining on

FIGURE 5.22
Sexual dimorphism in *M. fascicularis*.

FIGURE 5.23
A macaque matrifocal unit. Female macaques spend a great deal of time interacting with maternal kin.

the outskirts of the groups and occasionally interacting with females and other males. Subadult (teenage) males may be seen together.

An explanation for these social differences between males and females can be found in the dispersal and dominance patterns that characterize macaque societies. Although there is a range of dominance patterns, from very strict linear (sometimes called "despotic") dominance systems to relaxed, "egalitarian" ones, the pattern of the rhesus-fascicularis group tends toward strict dominance patterns in females and males (Thierry, 2010).

Life for Female Macaques

The main arena of social interactions for female macaques involves female maternal kin. Depending on the size of the group, it will usually contain from two to six matrifocal units. There is a set of dominance relationships within and between each of these units. The more dominant matrifocal units usually displace the others from prime food sources, sleeping sites, and other preferred resources. This is partly because the dominant matrifocal units are also the largest. With more individuals in a cluster, they have a better chance of intimidating or outcompeting other, smaller clusters of individuals. This can often confer a slight advantage to infants born into higher-ranking matrilines.

Although there is strength in numbers, individuals are not always dominant on their own. Macaque females rely heavily on alliances with female relatives to gain access to resources and win competitions. A lone female from a dominant matrifocal unit may not be dominant when her relatives are far way (in another tree) and she has to contest with five or six females from a subordinate cluster. Usually, however, females do not stray far from their kin. Female dominance disputes typically involve vocalizations and threats and occasionally some physical fighting, but only rarely are participants seriously wounded.

In addition to the dominance relationships between units, there are dominance relationships within such a cluster. Generally, a prime-age female (about 8 to 14 years old) holds the highest rank within a cluster. In a system unique to macaques, youngest daughters inherit their mother's rank. It is not uncommon to see the 2-year-old daughter of a high-ranking female taking resources from a fully adult female who ranks lower than her mother. This rank relationship always transfers to the youngest daughter. Therefore, when the 2-year-old's mother has another female offspring, this youngest daughter will outrank her older sister. Why do we see this system of rank-reversal in macaque female social dominance? Probably partly because the youngest individuals are most in need of resources and partly because the mother offers greater protection to her youngest daughter than to other kin and intervenes more frequently on her behalf.

Life for Male Macaques

Life for male macaques is quite different from that of females. Males have clear linear dominance relationships that can change frequently. Because they leave their natal groups, they cannot rely on kin to assist them in conflicts and need to form associations with other males and with females in order to negotiate dominance disputes. High-ranked males often form coalitions with other, slightly lower ranked males, to defend their position and gain access to preferred resources. Because males may transfer groups multiple times during a lifetime, they can be exposed to risks, especially when they are between groups and on their own. This may be why there tend to be more adult females than males in macaque groups, despite the fact that the sex ratio is generally equal in young individuals.

There appear to be many ways for males to attain a high rank. Some males are extremely aggressive and use fighting and conflict to move up the dominance hierarchy. They rely on winning fights and intimidating others, including females, to gain access to preferred resources. Fighting in male macaques can result in substantial injuries; however, it is not clear how often these injuries result in deaths. Other males use association with females to form coalitions to create strong social bonds with other individuals. These males engage in a lot of grooming and other calm social interactions with females

and young, even including holding infants. In a sense they rely on the assistance of others to attain and maintain high rank. Because of the varied ways in which males attain rank, their ranks are fragile, and males may spend anywhere from a few months to many years at high rank (Berkovitch & Huffman, 1999).

Sexual Behavior in Macaques

estrus
behavioral and physiological sexual receptivity

Although sexual behavior can be varied, generally female macaques mate with more than one adult male and sometimes with all the males in a group. Many macaques are seasonal breeders, that is, females are receptive only during certain times of the year. During this period of **estrus,** or behavioral and physiological sexual receptivity, females actively seek males and solicit copulations with them. In some groups, high-ranking males can restrict access to females by fighting with other males or staying very close to the females (sometimes referred to as *mate guarding*), but in large groups, restricting access is very difficult. In slightly over half the macaque groups in which researchers have determined genetic relationships, high-ranking males fathered the majority of infants born during their tenure.

Other Patterns of Social Interaction

Interactions between groups of macaques are frequently aggressive. Disputes over favored resources (such as areas with food trees) are usually resolved by one group displacing the other. In areas where food resources are not limited, however, groups may tolerate one another's presence on occasion. It may be that the degree of territoriality and the way in which a group views a neighboring group are related to the relative abundance of food and the type of habitat in which they live.

Throughout Asia there are many sites, such as temples and even cities, where macaque monkeys live in and around areas also occupied by humans. In these groups, the macaques tend to exhibit high rates of object manipulation. They manipulate food and nonfood items in a variety of ways, such as rubbing objects together, rubbing them on the ground, and stacking and playing with stones. Some researchers suggest that these kinds of behavior arise in groups with very little food stress. Macaques have occasionally been observed using behavioral innovations to clean or access foodstuffs and even, in a few isolated cases, using tools.

Chimpanzees: Our Closest Relatives

When researchers ask comparative questions about the evolution of human behavior, the primate genus they probably use the most is chimpanzees. Along with the gorilla, the chimpanzee is our closest relative and therefore shares many ancestral (primate-wide) and shared derived (hominoid and hominine) morphological and, probably, behavioral traits with humans.

There are two species of chimpanzee: *Pan troglodytes,* frequently called the common chimpanzee, and *Pan paniscus,* frequently called the bonobo (Figure 5.24). They are found across central Africa (Figure 5.25). Chimpanzees are large primates, with female *P. troglodytes* weighing between 35 and 50 kg (~75–110 lb) and female *P. paniscus* between 32 and 40 kg (~70–90 lb). Males are about 10% to 20% larger than females in *P. troglodytes;* the sexual dimorphism is somewhat less pronounced in *P. paniscus.* All members of the genus *Pan* are heavily frugivorous (fruit-eating), and their lives are substantially affected by seasonality and fruit abundance.

(a) (b)

FIGURE 5.24
The two chimpanzee species, *Pan troglodytes* (a), and *Pan paniscus* (b).

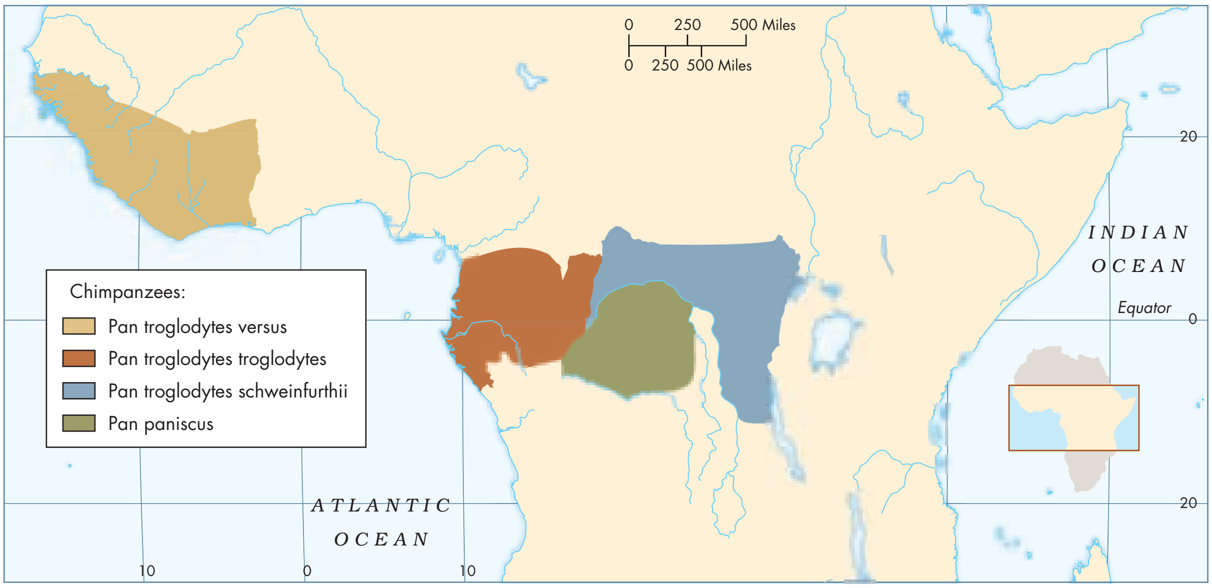


FIGURE 5.25
Distribution of the two chimpanzee species and the subspecies of *P. troglodytes*. They are found across central Africa.

Social Organization in Chimpanzees

Both species of chimpanzees live in multifemale/multimale communities ranging in size from 20 to more than 150 individuals. All these individuals are rarely, if ever, in the same location at the same time, however. This is because chimpanzee communities are characterized by a *fission-fusion* social pattern, meaning that individuals spend their time in various subgroups, which have variable compositions across space and time. Both species are characterized by female dispersal and male philopatry, although there is

some female philopatry in at least a few eastern chimpanzee populations (Stumpf, 2010).

Subgroups generally consist of mixtures of age and sex classes. Mother-offspring subgroups are made up of an adult female and her dependent offspring (usually a youngster under 7 years of age). Multifemale subgroups consist of multiple adult females and their offspring. Subgroups made up of clusters of related individuals consist of females and their offspring, some of whom may be adult or at least independent of the mother. All-male subgroups are made up of multiple adult and sometimes subadult (teenage) males. Heterosexual subgroups consist of adult males and females and frequently, young individuals. Consort pairs are two adult individuals (usually one male and one female) who separate themselves from other individuals in the community and spend a good deal of time mating. Finally, individual chimpanzees occasionally move around the range of their community by themselves.

The specific sizes of the different subgroups and the relative frequency of their occurrence vary by chimpanzee species, subspecies, and population. This variation is geographically pronounced, with the eastern populations of *Pan troglodytes* (*schweinfurthii*) having, on average, smaller parties than the other subspecies and than *Pan paniscus.* Overall subgroup size appears to be closely correlated with the availability of fruit and, in heterosexual subgroups, with the number of estrus females (females who are sexually receptive and have visibly swollen sexual organs, as discussed in more detail later in this section). The more fruit available and/or the more sexually active females present, the larger the subgroups tend to be.

Dominance Relationships in Chimpanzees

Although there are many similarities between the two chimpanzee species, there are also some important behavioral differences. Because both species are equally closely related to humans, it is worthwhile to examine the similarities and differences. One difference between the two species is in dominance relationships. In *Pan troglodytes,* males are, on average, dominant over females; however, both males and females compete with others of their sex and establish hierarchical ranks (McGrew, Marchant, & Nishida, 1996; Stumpf, 2010). Males attain high rank by forming alliances and coalitions with other males (frequently those of similar ages) and by using spectacular displays and other intimidation tactics, including serious fighting, to manipulate other members of their community into ceding access to favored resources. Male competition for rank can result in serious injuries and occasionally death. Some males attain rank through extreme aggression and maintain that behavior once they are high ranking. Others appear to rely heavily on coalition partners and mutual grooming and social bonding to achieve and maintain dominance status.

For females, dominance is associated with substantially improved access to food sources and high infant survivorship (especially in east African populations). High-ranking females tend to have a large number of offspring in the group, and occasionally mother-daughter pairs act together to achieve or maintain high rank. Females do achieve dominance via aggressive displays and occasionally fighting, but they do not do so as frequently or intensely as males (Figure 5.26).

In east African *P. troglodytes,* both males and females who are high ranking gain access to favored food sources and social partners and therefore have increased reproductive success. In west African forms, rank does not always result in increased reproductive success (Boesch, et al., 2002).

In *Pan paniscus,* dominance contests, dominance relationships, and the overall tenor of rank are different from those in *Pan troglodytes.* In this species, females are generally dominant to males and put on substantial dominance displays in which they drag tree branches or other objects behind them. However, dominance interactions rarely result in serious fighting. Rather, many of the dominance interactions and other conflicts in this species are resolved via genital–genital rubbing and other **sociosexual behavior** (nonreproductive sexual behavior that serves to resolve conflicts and/or reinforce alliances and coalitions) (Figure 5.27). Male bonobos also have an intrasexual dominance hierarchy, but they are seldom dominant over females. A male's rank is frequently tied to that of his mother. Males do compete with one another aggressively at times, but compared with *Pan troglodytes,* bonobos show lower overall rates of aggression (Stumpf, 2010).

■ **FIGURE 5.26**
Chimpanzees engaging in an aggressive encounter. This is one way to achieve dominance.

Although females disperse in both species, strong bonds between unrelated females are common in *Pan paniscus* and less so in *Pan troglodytes.* This difference may have to do with the differences in dominance systems and in the way that community members treat recent migrants in the two species.

Sexual Behavior in Chimpanzees

Female members of the genus *Pan* display distinct and easily observable signs of fertility. Their anogenital region becomes filled with fluid and very large and turgid during estrus. These sexual swellings provoke interest from other individuals in the community. Before, during, and after the period of peak swelling, females actively seek males and solicit copulations. In both species females mate with multiple males during these periods. In *Pan troglodytes*

sociosexual behavior
nonreproductive sexual behavior that serves to resolve conflicts and/or reinforce alliances and coalitions

■ **FIGURE 5.27**
Sociosexual behavior by *Pan paniscus.* Serious fighting is rare in this species.

males may attempt to mate-guard females. This usually takes the form of one or two high-ranking males staying very close to an estrus female and chasing away other males who try to approach her. *Pan troglodytes* males have also been reported to display high rates of aggression toward females. Some suggest that this aggression may be a coercive strategy to get females to mate with them. This is not the case in *Pan paniscus.* Female choice plays an important role in both species, but to date there is no evidence that bonobo males are able to effectively mate-guard or restrict females' mating choices. Some researchers have suggested that female chimpanzees mate with multiple males to confuse paternity and reduce the likelihood that any given male will treat them aggressively.

Although most copulation occurs during female estrus, members of the genus *Pan* do engage in sexual activity outside of estrus, especially in *Pan paniscus.* Bonobo females and males engage in frequent genital contact and stimulation as a means of social interaction. Conflicts among females are frequently followed by intensive sociosexual behavior. There are also indications that favored food sources (a kind of giant fruit) are shared among females and that the process of food distribution and sharing is mediated by sociosexual behavior.

Hunting and Meat Eating

Both species of the genus *Pan* hunt and eat other mammals, but *Pan troglodytes* do so more frequently than *Pan paniscus* (Boesch, et al., 2002; Stumpf, 2010). In some populations chimpanzees hunt frequently and have a high success rate; in other populations hunting is less frequent. Animal matter can make up 5% or 6% of a chimpanzee's diet. Hunting appears to coincide with times of fruit abundance, suggesting that meat may not be merely a nutritional supplement. *Pan troglodytes* across Africa appear to prefer hunting and eating red colobus monkeys (subfamily Colobinae), but they eat a variety of other mammals as well. Although females hunt in both species, it is an activity performed predominantly by males in *Pan troglodytes.*

Researchers report that populations of *Pan troglodytes* in western Africa hunt in a more coordinated manner than those in eastern Africa (Stanford, 1998). Hunting success rates seem to be related to the size of the subgroup doing the hunting, with larger parties being more successful. When kills are made, the meat is frequently shared among a few individuals, usually the coalition partners and allies of the successful hunter. There is great excitement in the community when kills are made, and many individuals beg for meat, but only a few receive any. Occasionally, if the kill is made by a low-ranking individual, a high-ranking male may steal the kill and not share any with the actual hunter. Interestingly, infanticide (killing of infants) and cannibalism are both reported for *Pan troglodytes.* There are cases in which adult females and males have captured, killed, and eaten infants from their own community and from females of neighboring communities. When an infant is killed and consumed, it is treated very much like a colobus monkey that has been hunted and captured.

Group Aggression

In populations of *Pan troglodytes* (especially Eastern Africa), researchers have reported incidents of intercommunity conflict that resulted in deaths. "Border patrols," or groups of males moving along the communities' geographic boundaries, are reported for most populations of chimpanzees. Researchers hypothesize that these patrols are subgroups of males searching for small subgroups or lone individuals from neighboring communities. Occasionally, when these

subgroups encounter individuals from another community, they attack as a mob. Some researchers have hypothesized that these attacks are an effort to increase the community's access to desired resources and that chimpanzees strategically assess the relative "power" of their neighbors in attempts to increase their ranges (Wilson & Wrangham, 2003).

FIGURE 5.28
Tool use in chimpanzees. At Gombe Stream National Park in Tanzania, chimpanzees use specially prepared twigs to fish for termites from a termite mound.

Tool Use and Social Traditions

Tool use was once thought to be a hallmark of humanity, but we now know that many organisms use *extrasomatic* (outside the body) means to get food. Of all organisms other than humans, chimpanzees appear to exhibit the widest variety of tool use and tool modification. Across their range, chimpanzees use many types of tools, including stone hammers and anvils for cracking nuts, carefully selected sticks and blades of grass for extracting termites from mounds, and forked branches for skimming moss off the top of ponds (Figure 5.28). Although all chimpanzee populations use tools, different groups seem to have different ways of using similar tools, and some don't use certain tools at all. The behavior of tool use is a learned one that, in some cases, takes years to acquire. Both male and female chimpanzees use tools, but it seems that females, at least in *Pan troglodytes*, are the more prolific tool users.

It is not only patterns and styles of tool use that vary across chimpanzee populations; there are also stylized differences in social traditions. *Social traditions* are behaviors that have a learned component and are frequently nonfunctional. For example, in some communities chimpanzees raise their arms above their heads in a hand clasp when they groom each other. In some communities this takes the form of hand holding; in others the chimpanzees simply lean their wrists against one another. Individuals also appear to take their own traditions with them when they move into new groups. At least 39 distinct social traditions have been documented in chimpanzee populations. Some argue that this is evidence for chimpanzee culture (Whiten, et al., 1999). Regardless of what we call it, evidence clearly shows that a substantial component of chimpanzee behavior is passed on through learning and that these behaviors vary regionally and by community. Tool use and possibly some social traditions are excellent examples of Jablonka and Lamb's ideas about behavioral inheritance (remember chapter 4) and are a goal indicator that such patterns are ancestral for at least chimpanzees and humans.

Humans are also primates, and human behavior has an evolutionary history

In this chapter we have reviewed some general, primate-wide behavioral trends and briefly described specific patterns of behavior in two nonhuman primate societies. What can this tell us about humans? As mentioned earlier, the comparative approach asks questions about similarities and differences between us and our close evolutionary relatives with the assumption that some of the patterns we see are the result of natural selection. We know that behavior is complex and that humans have a long and varied evolutionary

history. We can gain some insight into human behavior when we combine our knowledge of human evolution with observations from comparative primatology.

Social Organization and Behavior in Humans

Like macaques and chimpanzees, humans can be characterized as living in primate societies. For most of our evolutionary history, humans lived in small foraging groups consisting of some related and some unrelated individuals. All individuals cooperated in food collection, defense, and possibly, to some extent, rearing of young. By 2 million years ago or so, our ancestors were moving around and out of Africa, encountering new environments and new organisms. Humans appear to have met these challenges in groups, both by developing increasingly complex tools and other extrasomatic techniques and by forming social coalitions and alliances with other individuals and groups.

These small bands of humans most likely did not exceed a few hundred individuals and probably were much smaller than that until the appearance of our species, *Homo sapiens.* Bands would have moved about within home ranges and met other such bands, sometimes interacting peacefully, maybe exchanging members, other times fighting, and probably frequently just avoiding one another. After the initial spurt of movement 2 million years ago, humans probably moved fairly frequently. This means that over time, individuals lived in semisedentary groups, periodically encountered new groups and occasionally joined them, and sometimes moved far away from other groups.

With the appearance of anatomically modern *Homo sapiens sapiens* (discussed in detail in chapter 9), we begin to see substantial changes in the fossilized evidence of social behavior. Groups appear to get larger, more sedentary, and probably more diversified in terms of roles and divisions of labor within the group. By 20,000 to 40,000 years ago, there is evidence of larger aggregates of groups and, soon thereafter, relatively permanent settlements. By the time agriculture began to flourish, population sizes were dramatically greater, manipulation of the environment was substantially different, and the ways in which humans interacted in groups were probably more diversified. Additionally, disease may have become a more important selective force as population densities increased and became more settled.

Given our evolutionary history, what can we conclude about the basic characteristics of human behavior? We live in multifemale/multimale groups with varied subgroup patterns. We have both male and female philopatry depending on the culture and demography. We have an omnivorous diet, much of which we now grow or raise as domestic animals and plants. We form very strong social bonds both heterosexually and homosexually with both kin and nonkin. Sometimes these bonds are related to mating behavior, and sometimes they are not. Human females do not appear to have a visible signal of estrus. Mating patterns vary a great deal, but humans appear to mate with multiple individuals and exert both male and female choice. Although many of these behaviors may be common to other primates, there is one behavior that humans display that no other primate (as far as we can tell) does: We use symbol and language to interact with one another.

Comparisons with Macaques

Humans and macaques share some general characteristics, such as the existence of multifemale/multimale groups, the importance of biological kin in social interactions, and the ability to coexist in a wide variety of habitats. We

also overlap in the general sense of having dominance hierarchies and having many ways in which dominance is attained and maintained. There are critical differences in our morphologies, however, especially locomotion patterns, relative and absolute brain size, and the size and complexity of our social organization. Another difference is that adult male and adult female macaques have life trajectories that are very different from each other, and such an extreme difference is not characteristic of human societies (at least not many).

It is interesting that macaques and humans can (and do) coexist in many areas, perhaps because both species have great flexibility in the face of environmental challenges. Both spread across much of the planet during about the same time periods, and perhaps the two species' shared ways of foraging and behaving became increasingly flexible, and overlapping, to meet the environmental challenges they encountered.

Comparisons with Chimpanzees

Although humans have some things in common with macaques, we have more in common with chimpanzees. One commonality is the type of community living we practice. Modern human communities are larger and much more complex than those of chimpanzees, but the patterns of subgrouping and the types of relationships between individuals in communities, especially among those who know one another but do not interact or see one another on a daily basis, may be a common element between our two genera.

The use of sex in a social context and the male–male bonding related to aggression may also be patterns of behavior that we share with our close relatives. The active acquisition of meat and subsequent sharing among selected group members in both species of chimpanzee, and the similar behavior with large fruit sources in bonobos, bear a resemblance to the acquisition and social distribution of prestige goods in human societies.

What about sexual aggression, mate guarding, and intercommunity aggression in chimpanzees? Could they be related to rape, marriage laws, and war in humans? Although such behaviors may bear a superficial resemblance across species, there is currently a great deal of debate over whether human patterns and chimpanzee patterns are analogous, homologous, or not comparable as the same types of behavior.

As noted earlier, the two species of chimpanzee appear to use aggression and social sex quite differently. In fact, *P. troglodytes* groups in different parts of Africa differ in these behaviors as well. Are some groups more similar to humans than others? Probably not. Humans and chimpanzees have spent more than 6 million years evolving separately from one another, so all chimpanzee species and subspecies are more evolutionarily similar to one another than any are to humans. Humans have encountered many more environments and, at least for the last 2 million years, have relied much more heavily on extrasomatic adaptations, and they have a substantially larger relative and absolute brain size than chimpanzees.

It is not surprising that there is considerable overlap in the kinds of behavior exhibited by the genus *Pan* and the genus *Homo*, considering our evolutionary proximity and a shared range of underlying potential variation in behavior. It appears that behavioral flexibility in social traditions and the ability to use and manipulate extrasomatic elements are important adaptations of both chimpanzees and humans. Because humans are more widespread and are theoretically more flexible in their behavior (due to their larger brain and use of symbols and language), we should expect to see in humans more behavioral complexity than

we see in chimpanzees and bonobos. It might just be that our potential expression of behavior is much broader than that of our closest relatives.

What is Uniquely Human?

Making direct comparisons between human behavior and the behavior of other organisms is difficult because we interact with our environment through a substantial interface that affects both behavior and morphology: human culture. Culture structures all aspects of our lives. This is not to say that culture overrides or negates any biological facets of our existence. Rather, just as the social traditions of chimpanzees affect the way individuals from different groups behave, human culture interacts with our biology and the varying environments in which we live to create a myriad of behavioral results.

For example, language enables us to communicate content not accessible to other organisms and, combined with our use of symbolic representation (including writing), allows us to acquire, manipulate, and broadcast knowledge more quickly and thoroughly than other organisms. Language and the ability to use symbolic representation, which have been around for at least 60,000 years, have dramatically changed our species' environment in the recent past (recent, that is, in evolutionary terms). Our population sizes have grown by thousands-fold in just the last millennium; our ability to grow and manipulate our own food has changed the types and patterns of foraging we can exhibit; and our ability to alter the face of the planet is so dramatic that we are one of the driving forces in ecological change on the earth. In short, humans are able to undertake more dramatic and far-reaching niche construction than any other primate. Such complexity in everything we do makes it quite difficult, but not impossible, to use comparative primatology to attempt to understand the evolution of human behavior. If done carefully and systematically, comparative primatology can give us insight into those patterns of behavior that have arisen through natural selection and other mechanisms of evolution.

It is also worth emphasizing that the evolutionary changes that make us human arose over time and continue to arise. For example, the lower body anatomy that allows us to be bipedal emerged several million years ago. The dramatic

CONNECTIONS

Why We Never Shut Up

Language makes a difference. It separates humans from other animals on this planet; even from our closest relatives, the primates. Language allows humans to construct real and imagined niches and scenarios and gives us the power to do things that nothing else can do. Language gives us the ability to share information about the past and the future as well as to lie, to create fantasies, to explain thoughts and emotions—all things that are not possible for other animals. You are reading this right now and I am transferring ideas and information to you without my even being there. We see that the other primates have complex social lives, but that they do it without languages. They do have many ways to communicate, but none of them are as information-rich and temporally complex as language. Even humans who cannot speak can still use language (sign language or writing). To understand how important this is, try to go a few hours using words that represent only things in your immediate line of sight, that refer only to the present moment, and that contain no adjectives or representations of your inner thoughts. It will not be easy. We take the importance of language for granted because we are so totally reliant on it. That is why we never shut up.

What We Know

Questions That Remain

What We Know
Much behavior is the result of evolutionary adaptation over the history of our species. Examining our closest relatives can give us insight into primate-wide behavior, anthropoid-wide behavior, and even hominoid-wide behavior.

Questions That Remain
Although it is relatively easy to identify general patterns as adaptations, it is not so easy to sort out the evolutionary aspects of specific behaviors in humans. What parts of behaviors like our choice of sexual partner, our decision to stay or leave home, or the kinds of relationships we have with members of the other sex can be traced to specific adaptations? Human culture makes it very difficult to answer these questions. However, the comparative approach offers careful and methodical ways of investigating these issues.

What We Know
There are five aspects of a behavior that we can investigate scientifically: phylogeny, ontogeny, proximate stimulus, the behavior itself, and the function of the behavior. A behavioral ecological approach can assist in understanding the pressures that affect a behavior and the outcomes of the behavior.

Questions That Remain
For each behavior, which of the factors impacting it is more important? Not all behaviors have equal input from the five factors, and it is not always clear what the most important questions to ask in a given context might be. If not all behavior is functional, and if we do not know all of the possible constraints on, or life experience of, an individual, our examinations can sometimes be misdirected. For this reason, investigations into the behavior of human evolution need to proceed very cautiously.

What We Know
Kin selection has been proposed to explain many apparently altruistic (selfless) acts. We can hypothesize that altruism should be rare because of its potential costs to the individual.

Questions That Remain
Does true altruism exist? Without a way of measuring actual costs to individuals, this question is hard to answer accurately. It is possible that in social organisms, such as primates, the costs and benefits of many behaviors are deeply imbedded in long-term complex social relationships between individuals. These relationships, coalitions, and alliances may be a very important arena for continued primatological research.

What We Know
Members of the genus *Pan* are among our closest evolutionary relatives on this planet. Some behavior of both species in this genus appears to be similar to human behavior and may offer insight into shared adaptive histories.

Questions That Remain
Because the two species of *Pan* differ in some key behavioral patterns, which one is a better model for humans? It is possible that neither are good models or that all three of our species (*Pan troglodytes, Pan paniscus,* and *Homo sapiens*) have some commonalities in behavioral potentials. It is also possible that differing ecologies, evolutionary histories, and morphologies have resulted in a patchwork of behavioral similarities and differences across the three species. Future study, especially long-term studies on all three species, may help to disentangle these relationships.

increase in brain size that distinguishes us from other primates occurred over a period of about 1 million years and then leveled off in our archaic ancestors. The chin, unique to humans, began to appear in the fossil record about 200,000 years ago. These and innumerable other characteristics of our species arose over time as pieces in a larger system. It is inaccurate to think of humans as big-brained geniuses trapped in bodies adapted to evolutionary pressures that existed hundreds of thousands of years ago or, put another way, that we are caught in a completely new realm of cultural complexity such that our biology is being outpaced and rapidly rendered irrelevant. Rather, humans are organisms whose main adaptation is a biocultural one and who exist in a dynamic interconnection of biology, behavior, history, and culture—and who have done so for a very long time. In chapters 9 and 11 we will go into more detail about current ways researchers investigate the evolution of human behavior.

Conserving the Nonhuman Primates Is a Critical Challenge

This chapter ends with a cautionary note. We gain valuable insight into human nature by studying our primate relatives, but comparative primatology may not be a viable field of research for much longer. All of the African apes, the orangutan, and many monkey and prosimian species are severely threatened with habitat loss and possible extinction. As of 2009, more then 30% of primate species and subspecies were considered to be threatened or endangered. Modification of the planet for human use is currently driving many of our closest evolutionary relatives to the brink of extinction. To ensure that 60 million years of shared evolutionary history does not come to an end in our lifetime, we need to seriously consider how best to reduce and manage these threats.

SUMMARY

- The study of the nonhuman primates can provide information from which we can attempt to reconstruct aspects of human evolution, especially the evolution of our behavior.
- Behavior may be defined as all the actions and inactions of an organism.
- Both quantitative and qualitative research methods enrich our study of behavior.
- A behavior may be viewed from five different perspectives: phylogeny, ontogeny, proximate stimulus, the behavior itself, and the function of the behavior.
- Behavior that is widespread in a taxonomic group is frequently considered to be an adaptation.
- Behavioral ecology is the study of behavior from ecological and evolutionary perspectives.
- Basic ecological stresses on organisms fall into the following five general areas: nutrition, locomotion, predation, intraspecific competition, and interspecific competition.
- We measure the success of behavioral adaptation generally in terms of estimated energy costs and benefits in the sense of how these could potentially impact lifetime fitness (reproductive success).
- Kin selection, the favoring of close genetic relatives, has been proposed to explain apparent altruistic acts in organisms.

- Genetic, morphological, and phylogenetic characteristics set the basic potential for any given behavior; the particular expression of that behavior (called performance) is elicited by a myriad of factors including ontogeny, health, and type of proximate stimulus.
- Not all behavior is functional.
- Primate-wide trends in behavior include strong mother-offspring bonds, certain primary grouping patterns, an important role for use of space and grooming, the establishment of dominance hierarchies, an important role for life history and dispersal patterns, and an important role for coalitions and alliances in both conflict and cooperation.
- Macaques live in multifemale/multimale societies with male dominance, distinct male and female hierarchies, matrifocal clusters, female philopatry, and flexible male strategies for attaining dominance.
- Chimpanzees live in multifemale/multimale communities characterized by a fission-fusion social pattern. The species *Pan troglodytes* exhibits clear male dominance and more serious intercommunity aggression and conflict than does the species *Pan paniscus,* which is characterized by female dominance and a higher frequency of sociosexual behavior, with both aggressive and affiliative intercommunity interactions. All chimpanzees have complex social lives characterized by female dispersal, sharing of favored food sources (including hunted meat), tool use, and the passing of learned social traditions within different communities.
- No other primate is a perfect model for human evolution; even the members of the genus *Pan* have millions of years of separate evolution from us. However, both *Macaca* and *Pan* can provide some insight into aspects of human behavior and evolution.
- Humans are similar to other primates in a number of ways, yet specific aspects of our evolutionary history have resulted in a distinct trajectory of biocultural adaptation. The complexity of culture can make it difficult, but not impossible, to untangle the evolutionary history of human behavior.
- Many primate species are currently endangered, in large part due to human alteration of the environment. We are responsible for ensuring that our relatives continue to exist on this planet.

CRITICAL THINKING

1. What kinds of different information are gathered by qualitative versus quantitative methods? Why is this difference important, and how can each approach contribute to a better overall understanding of behavior?
2. How can a behavior not have a function? Doesn't everything "cost" energy? How could behaviors that do not have a cost or a benefit arise?
3. Is altruism incompatible with natural selection? Is it feasible to measure all reciprocal altruism? Considering that not all of our cultural kin are biological kin, how might kin selection impact humans?
4. Why are chimpanzees frequently held up as a good model for understanding human evolution? What morphological and behavioral similarities might they have with early humans? If we see extreme male aggression such as lethal fighting, sexual coercion, and group attacks in both chimpanzees and humans, is it not reasonable to explain it as a common adaptation in both species? Why or why not?

5. What does it mean to say "culture is biological"? How can something be abstract and symbolic and yet be impacted by biology? Think about each of the following human behaviors: language use, mate choice, eating habits, and sleeping patterns. How is each one impacted by both morphology and evolutionary history, on the one hand, and cultural patterns, on the other?

RESOURCES

PRIMATOLOGY BOOKS

Campbell, C., Fuentes, A., Mackinnon, K. C., Bearder, S. K. & Stumpf, R. M. (Eds.). (2010). *Primates in perspective 2nd Ed.* New York: Oxford University Press.
The first in-depth overview of the field of primatology in nearly 20 years, this volume provides extensive coverage of all the major primate groups and a review of current issues in theory and methodology in primatology.

de Waal, F. B. M. (Ed.). (2001). *Tree of origin: What nonhuman primate behavior can tell us about human social evolution.* Cambridge: Harvard University Press.
This edited volume contains essays focusing specifically on understanding human social evolution by examining the nonhuman primates.

Dolhinow, P., & Fuentes, A. (Eds.). (1999). *The nonhuman primates.* New York: McGraw-Hill.
This collection of short essays deals with the behavioral and evolutionary diversity in nonhuman primate behavior and ecology.

Rowe, N. (1996). *The pictorial guide to the living primates.* East Hampton, NY: Pogonias Press.
An overview of all the living primates, this guide contains stellar photos and brief summaries of their behavior, ecology, distribution, and conservation status.

Strier, K. B. (2006). *Primate behavioral ecology* (3rd ed.). Boston: Allyn & Bacon.
This textbook is a rich source of information about the nonhuman primates and the evolution of primate behavior.

Sussman, R. W. (1999, 2000, 2003). *Primate ecology and social structure,* Vols. 1–3. Needham Heights, MA: Pearson Custom Publishing.
These three books provide in-depth coverage of the behavior and ecology of the prosimians (Vol. 1), the neotropical primates (Vol. 2), and the Old World forms, the monkeys and apes (Vol. 3).

PRIMATES ON THE WEB

www.asp.org The home page of the American Society of Primatologists has a variety of educational links on the study and conservation of primates.

pin.primate.wisc.edu/ The home page of the Primate Information Network hosted by the Wisconsin Primate Research Center and the National Primate Research Centers Program at the University of Wisconsin-Madison is the gateway to hundreds of links exploring the diversity of primates, the field of primatology, and all things primate.

www.internationalprimatologicalsociety.org This is the home page of the International Primatological Society.

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