

# EXPLORATIONS: AN OPEN INVITATION TO BIOLOGICAL ANTHROPOLOGY, 2ND EDITION

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# Chapter 6: Primate Ecology and Behavior

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*This chapter is a revision from “Chapter 6: Primate Ecology and Behavior” by Karin Enstam Jaffe. In Explorations: An Open Invitation to Biological Anthropology, first edition, edited by Beth Shook, Katie Nelson, Kelsie Aguilera, and Lara Braff, which is licensed under CC BY-NC 4.0.*

## Learning Objectives

- Describe the variables that affect primate diets.
- Explain how primates interact with other organisms in their environment.
- Discuss why primates live in groups, types of primate groups, and components of their social systems.
- Describe the reproductive strategies of males and females.
- Explain the ways in which primates communicate.
- Discuss the evidence for primate cultural traditions.

I remember the summer after my first year of graduate school vividly. There I was, in Kenya, following wild monkeys through the bush. Finally! It was a dream come true for me. I have loved monkeys for as long as I can remember. As a child, I played with monkey stuffed animals instead of dolls. In high school, my AP history teacher gave me an introductory textbook about anthropology and I was overjoyed to learn that I could study my favorite animals in college and beyond. Now, roughly five years later, I was intently observing a group of about 50 patas monkeys (*Erythrocebus patas*) as they searched for food, played, and groomed one another. Suddenly, one of the monkeys gave a loud, staccato vocalization that sounded like “Nyow!” Soon, other individuals joined in. There I was, in the middle of the group, taking it all in and loving every second of it. That is until my advisor slowly approached me and pointed to the grass on the edge of the group. “Look,” she said, “we need to go back to the car.” I looked closely in the direction she was pointing and saw, crouching in the grass, a large lion. We slowly backed away and walked to our car. Looking back, I should have been scared, but I wasn’t, I was thrilled. I would return a year later to study the same group’s response to predators for two years.

Nonhuman primates (hereafter, “primates”) are a fascinating group of animals, whose similarity to humans can be striking. Because of this similarity, studying primates helps anthropologists to gain insight into how our human ancestors may have behaved. It also allows us to better understand our own behavior through **comparison** (examining similarities and differences) with other primates as well as by comparing different species of primates to one another. In this way, studying primates helps anthropologists comprehend humanity from a biological perspective, which contributes to anthropology’s commitment to **holism**, the idea that the parts of a system interconnect and interact to make up the whole.

**Ethology** is the study of animal behavior, while **primatology** is the study of primate behavior. People who study primates are called **primatologists**. Research on primates can be conducted in the field (i.e., on wild primates) or in captivity (i.e., zoos) and may or may not involve experiments, such as playing recorded alarm calls to see how individuals react. Unlike some other Science, Technology, Engineering, and Math (STEM) fields, primatology has a long history of research conducted by women (see “Special Topic: Women in Primatology”). Primatologists come from many different disciplines, have diverse backgrounds, and study primates for different reasons. Biologists study primates as examples of evolutionary theories like natural selection, and to understand behaviors as **adaptations**, or traits with a function that increases **fitness**, i.e. an individual’s survival and/or reproduction. Primate intelligence is of interest to psychologists who want to learn more about deception or cooperation and to linguists interested in the principles of communication and language. Ecologists consider how primates interact with the habitats they occupy, and conservationists examine how primates are affected by deforestation, poaching, or illegal animal trade (see Appendix B: Primate Conservation for more information on these topics). Biological anthropologists, like myself (Figure 6.1), who study primates are interested

in learning about their social complexity, and ecological and behavioral variation, to better understand the biological basis of human behavior. And, similar to biologists, we also explore how primate behavior is adaptive and contributes to individual fitness. Like other sciences, primatology is only as strong as its researchers, methods, and theories, and the field has benefitted recently from efforts to increase diversity and reckon with its colonialist past, as discussed below in “Special Topic: Women in Primatology.”



Figure 6.1: The author observing patas monkeys from a distance in Laikipia, Kenya. Credit: Karin Enstam Jaffe observing patas monkeys in Laikipia, Kenya (Figure 6.5) by Rebecca Chancellor is under a CC BY-NC 4.0 License.

Humans share many traits in common with primates. As you learned in Chapter 5, some of these traits are similar due to **homology**, traits both species inherited from a common primate ancestor. For example, like most other primates, humans are social animals who live in groups. Group living did not evolve independently in humans and other primates. Rather, group living is a trait that evolved in a primate ancestor, and because it benefited survival, it was retained in the species’ **descendants** (or the species that come after the ancestor species). In contrast, humans and other primates can have similar traits that evolved independently, which is called **analogy**. For example, both humans and Japanese macaques (*Macaca fuscata*) use natural hot springs (Figures 6.2a-b). Research on these monkeys indicates that sitting in hot springs reduces stress and helps keep them warm, much as it does for humans (Takeshita et al. 2018). But this behavior is not the result of humans and Japanese macaques having a shared ancestor who used hot springs. Rather, the behavior arose independently in two species that both occupy northerly environments and adapted to cold climates using a similar behavior. Studying the homologous traits we share with other primates, like living in groups, helps us develop hypotheses about human behaviors as adaptations, which in turn helps us develop models for the behavior of our human ancestors. Studying analogous traits, like hot springs use, allows us to better understand the effects of ecological variables on morphology and behavior of both primates and humans, living and extinct.



Figure 6.2a-b: Both humans (left) and Japanese macaques (right) use natural hot springs to reduce stress and relax. This similar trait arose independently in the two species, making it a good example of analogy. Credit: a. Hot Spring Landscape by Pexels has been modified (cropped) and has been designated to the public domain (CC0) under a Pixabay License. b. Jigokudani hot spring in Nagano Japan 001 by Yosemite is under a CC BY-SA 3.0 License.

## Special Topic: Women in Primatology

While many STEM fields have traditionally been, and continue to be, dominated by men, primatology has a long history of significant research conducted by women. This is due, in part, to the fact that three of the most well-known primatologists are women. In the early 1960s, British paleoanthropologist Louis Leakey (discussed in Chapters 9 and 10) was looking for students to study the great apes in hopes of shedding light on the behaviors of our early ancestors. He chose Jane Goodall (Figure 6.3a) to study chimpanzees (*Pan troglodytes*), Birute Galdikas (Figure 6.3b) to study Bornean orangutans (*Pongo pygmaeus*), and Dian Fossey (Figure 6.3c) to study mountain gorillas (*Gorilla beringei beringei*). The work of these three women, sometimes referred to as Leakey's "Trimates," has transformed our understanding of ape (and primate) behavior.



Figure 6.3a-c: Louis Leakey's "Trimates" (left to right): a. Jane Goodall's research on the Gombe chimpanzees spans over half a century; b. Birute Galdikas's research and rescue work on behalf of orangutans spans 40 years; c. Dian Fossey studied mountain gorillas in Rwanda for almost 20 years, until her murder in 1985. Credit: a. Jane Goodall HK by Jeekc has been modified (cropped) and is under a CC BY-SA 3.0 License. b. Dr Birute Galdikas by Simon Fraser University – University Communications has been modified (cropped) and is under a CC BY 2.0 License. c. US-223658 Dian Fossey by Mary-Lynn has been modified (cropped) and is under a CC BY 2.0 License.

Arriving at the Gombe Stream Reserve in Tanzania in 1960, Jane Goodall was one of the first scientists to conduct a long-term study of wild nonhuman primates. Before then, most studies lasted less than a year and were often zoo-based. By 1961, she had made two astounding observations that forced us to reconsider what differentiates humans from the rest of the primate order. She observed chimpanzees eating a colobus monkey, the first reported evidence of meat eating in our closest relatives (she later observed them hunting and sharing meat). And she discovered that chimpanzees make and use tools by stripping leaves off twigs to "fish" for termites. Her work, spanning several decades, has produced long-term data on chimpanzee mating strategies, mother-infant bonds, and aggression. In the mid-1980s, Goodall transitioned from field researcher to conservationist and activist, advocating for the humane use of nonhuman animals (Stanford 2017).

Birute Galdikas began her study of orangutans in Kalimantan, Borneo, in 1971. Hers was the first long-term study conducted on the Bornean orangutan. Galdikas and her colleagues have collected over 150,000 hours of observational data, focusing on the life histories of individual orangutans. While conducting behavioral research, Galdikas discovered that the pet trade and habitat loss were adversely affecting the orangutan population. Eventually, Galdikas's conservation efforts began to extend beyond advocacy and into rehabilitation and forest preservation (Bell 2017). If you would like to learn more about primate conservation efforts, please see Appendix B: Primate Conservation.

In 1967, Dian Fossey began her long-term study of mountain gorillas and founded the Karisoke Research Center in Rwanda. Her and her colleagues' research, over several decades, revealed much about gorilla social behavior, ecology, and life history. Her efforts also led to the development of mountain gorilla conservation programs. However, she was a controversial figure, as discussed below. Fossey was murdered in December 1985; the case remains unsolved (Stewart 2017).

## Decolonizing Primatology

Recently, the movement to **decolonize** primatology, by understanding and highlighting the theories and research of non-Western individuals and perspectives, has gathered steam. This movement draws attention to the maltreatment of local people by Western primatologists. For example, Michelle Rodrigues (2019) argues that it's time we stop focusing on the scientific and conservation contributions of Dian Fossey and acknowledge that her "active conservation" techniques included kidnapping and torturing local Rwandans who were known as, or suspected to be, gorilla poachers. Rodrigues (2019) argues:

The image of Fossey, a white American woman, whipping and torturing black African poachers is evocative of the behavior of white slaveholders in the American South. It is appalling enough to think of that behavior occurring in the 1850s; there is no way we can explain Fossey's behavior in the 1970s as the product of "a different time." Yet, almost three decades later, the romantic notion of a noble martyr who died for her devotion to gorillas prevails, and these terrifying actions are often described as simply unorthodox methods. Perhaps these truths are softened due to fears that the reality of this legacy would harm gorilla conservation efforts. But memorializing her as a martyr and patron saint of gorilla conservation demands that we forget the cruel acts she advocated for and performed.

Further, Louis Leakey's installment of Goodall, Galdikas, and Fossey to study chimpanzees, orangutans, and mountain gorillas, respectively, is itself viewed as recapitulating the colonial legacy in Africa and Asia. Given that Leakey was the offspring of British missionaries, Rodrigues (2019) argues, it is no accident that he was willing to mentor British and American women, while overlooking women from Africa and Asia as potential researchers. This leads us to another level of the decolonizing movement, which aims to highlight the research of non-Western primatologists, particularly those living in what primatologists refer to as "habitat countries" that are home to living primates. As you will see in this chapter, scientists from diverse backgrounds are active contributors to exciting research on primates around the world.

## Ecology

The more than 600 species and subspecies of living primates are highly diverse in their dietary preferences and the habitats they occupy. In this section we'll briefly discuss aspects of **ecology**, or the relationship between organisms and their physical surroundings, that impact a primate's life, the foods they eat, and the other species with whom they interact.

## Primate Diets

Diet may be the most important variable influencing variation in primate morphology, behavior, and ecology. Most primates are **omnivores** who ingest a variety of foods in order to obtain appropriate levels of protein, carbohydrates, fats, and fluids, but one type of food often makes up the majority of each species' diet. You learned about the dental and digestive adaptations of **frugivores** (who feed primarily on fruit), **folivores** (whose diet consists mostly of leaves), and **insectivores** (who eat mainly insects) in Chapter 5, so we will not discuss them again here.

## Body Size and Diet



Figure 6.4a-b: Primates eat different types of food. Small primates, like the spectral tarsier (left), eat mostly insects while large primates, like the mountain gorilla (right), eat mostly leaves. Credit: a. Spectral Tarsier *Tarsius tarsier* (7911549768) by Bernard DUPONT has been modified (cropped) and is under a CC BY-SA 2.0 License. b. Mountain gorilla (*Gorilla beringei beringei*) eating by Charles J Sharp (creator QS:P170,Q54800218) has been modified (cropped) and is under a CC BY-SA 4.0 License.

Insects are a high-quality food, full of easily digestible protein and high in calories that meet most of a primate's dietary needs. Although all primates will eat insects if they come upon them, those species that rely most heavily on insects tend to be the smallest. Why? Because larger primates simply cannot capture and consume enough insects every day to survive. Because of their small size (less than 150 g), spectral tarsiers (*Tarsius spectrum*) have a fast **metabolism**, which means they turn food to energy quickly, but they do not need to consume large amounts of food each day. It does not matter to a spectral tarsier that a grasshopper only weighs 300 mg, because the tarsier (*Tarsius*) itself is so small that one grasshopper is a good-size meal (Figure 6.4a). That same grasshopper is not even a snack for an adult male mountain gorilla (*Gorilla beringei beringei*), who may weigh up to 200 kg. Fortunately for gorillas (*Gorilla*), their large body size means they have a slow metabolism, converting food into energy much more slowly, so they can eat lower quality food that takes longer to digest, provided there is a lot of it. For gorillas, leaves, which are hard to digest but plentiful, fit the bill (Figure 6.4b). Most medium-sized primates are highly frugivorous, and supplement their fruit based diet in ways that correspond with their size: Smaller frugivores tend to supplement with insects, while larger frugivores tend to supplement with leaves.

## Food Abundance and Distribution

Nutrients are not the only dietary considerations primates must make. They must also ensure that they consume more calories than they use. The abundance and distribution of food affect energy expenditure and calorie intake because they determine how far animals must travel in search of food and how much they must compete to obtain it. **Abundance** refers to how much food is available in a given area while **distribution** refers to how food is spread out. In terms of abundance, food is either plentiful or scarce (Figure 6.5a–b). Food is distributed in one of three ways: uniformly (Figure 6.6a), in clumps (Figure 6.6b), or randomly (Figure 6.6c). In general, higher-quality foods, like fruit and insects, are less abundant and have patchier distributions than lower-quality foods, like leaves. Primates who eat fruit or insects usually have to travel farther to find food and burn more calories in the process. Abundance and distribution of food is another reason why larger primates tend to rely more heavily on leaves than either fruit or insects.

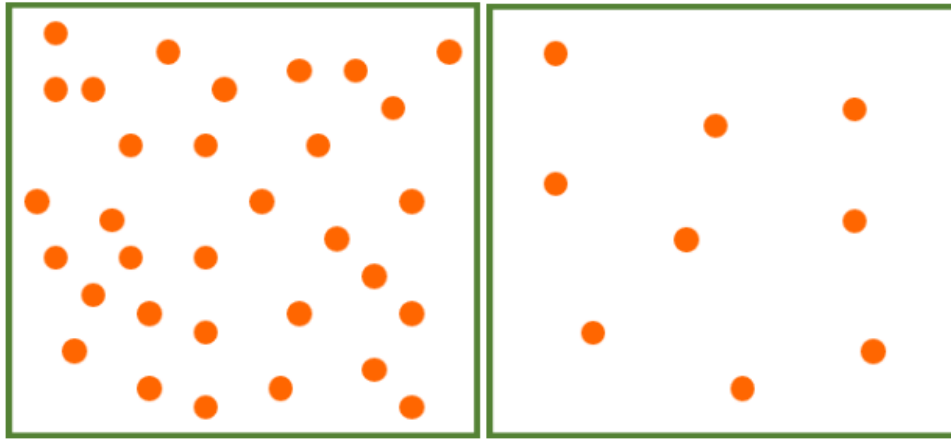


Figure 6.5a-b: Two types of food abundance. Food is plentiful when there is a lot of it in a given area (left). Food is scarce when there is not very much of it in a given area (right). Credit: Food abundance and food scarcity (Figure 6.7) by Karin Enstam Jaffe original to Explorations: An Open Invitation to Biological Anthropology is under a CC BY-NC 4.0 License.

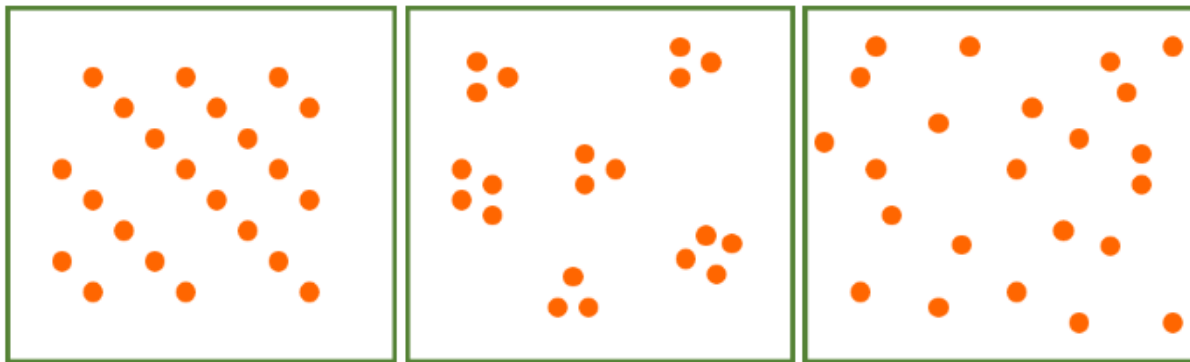


Figure 6.6a-c: Three types of food distribution. a. Food has a uniform distribution when it is spread out evenly in the environment. b. Food has a clumped distribution when it is found in patches. c. Food is randomly distributed when it has neither uniform nor clumped distribution. Credit: Food distribution patterns (Figure 6.8) by Karin Enstam Jaffe original to Explorations: An Open Invitation to Biological Anthropology is under a CC BY-NC 4.0 License.

## Community Ecology

Primates are members of broader ecological communities composed of other species, including other primates, predators, parasites, and even humans. **Community ecology** deals with the relationships and interactions between different organisms that occupy the same habitat. Interactions with **conspecifics** (members of the same species) and **heterospecifics** (members of different species) are critical aspects of ecological communities. Some habitats support highly diverse **primate communities** consisting of 10 or more primate species. How can so many primate species occupy the same area and avoid competition? In most cases, the primate species that live together occupy different **niches**, which means they do not meet their needs for food and shelter in the exact same way. Two species can avoid competition by eating different kinds of food, living at different levels of a forest, or even searching for food at different times of day. Because tropical rainforests, like Manu National Park in Peru, are highly variable, with many habitats and many sources of food and shelter, there are many different niches for multiple species to exploit, and large primate communities can result (Figure 6.7).





Figure 6.7: Eight of the 14 primate species in Manu National Park, Peru. Top row, left to right: Goeldi's marmoset (*Callimico goeldi*), Rio Tapajós saki (*Pithecia irrorata*), tufted capuchin (*Sapajus apella*); middle row, left to right: emperor tamarin (*Saguinus imperator*), black-headed night monkey (*Aotus nigriceps*), Bolivian red howler (*Alouatta sara*); bottom row, left to right: black-capped squirrel monkey (*Saimiri boliviensis*), Peruvian spider monkey (*Ateles chamek*). Credit: Primate species in Manu National Park original to Explorations: An Open Invitation to Biological Anthropology (2nd ed.) by Karin Jaffe is a collective work under a CC BY-NC-SA 4.0 License. [Includes: Tamarin Baby/Goeldi's Monkey by stefan\_fotos, CC BY 2.0 License; *Pithecia irrorata* -Brazil-8b by Ana\_Cotta, modified (cropped), CC BY 2.0 License; Tufted Capuchin on a Branch in Singapor by Basile\_Morin, modified (cropped), CC BY-SA 4.0 License; Tamarin Portrait by Brocken Inaglor, modified (cropped), CC BY-SA 3.0 License; *Aotus nigriceps* 1 by DuSantos, modified (cropped), CC BY 2.0 License; *Alouatta sara* (Bolivian Red Howler) by Raul Ignacio, modified (cropped), CC BY-SA 2.0 License; Black-Capped Squirrel Monkey (Chalalan) by Rodrigo Mariaca, modified (cropped), CC BY-SA 4.0 License; Maquisapa (Spider Monkey) by Ivan Mlinaric, modified (cropped), CC BY 2.0 License].

### Competitive Interactions

Although species living in the same location often occupy different niches to avoid competition, when a resource that is important for survival or reproduction is scarce, individuals will compete to obtain that resource. This is a central tenet of Charles Darwin's theory of evolution by natural selection (see Chapter 2). Competition between primates takes two forms: Individuals engage in **direct competition**, which involves physical interaction between individuals (such as fighting), over resources that are large and worth defending (fruit is a good example of a food resource over which primates will fight). Individuals engage in **indirect competition**, in which there is no physical interaction between individuals, when a resource is small. Primates often engage in indirect competition for insects, like grasshoppers, that are eaten quickly, often before another individual arrives on the scene. Primates may engage in direct and/or indirect competition with members of their own group, with members of other groups of conspecifics, or with heterospecifics.

## Predator-Prey Interactions

The plants and animals that primates eat are an important part of their ecological community. In addition to insects, many primates incorporate some **vertebrate** (animals with an internal spinal column or backbone) prey into their diet. Often, predation by primates is opportunistic, occurring because the prey happens to be in the right place at the right time. I've observed vervets (*Chlorocebus pygerythrus*) opportunistically killing lizards by smashing them against a rock or tree trunk and eating them. More rarely, hunting is deliberate and cooperative. In some chimpanzee (*Pan troglodytes*) populations, hunts involve multiple individuals, each of whom plays a specific role and is rewarded afterward with a share of the prey that has been captured (Samuni et al. 2018).

All primates are susceptible to predation by mammalian **carnivores** (animals whose diet consists primarily of animal tissue (e.g., Figure 6.8a), reptiles (e.g., Figure 6.8b), or birds of prey (e.g., Figure 6.8c). Although the specific predators found in an ecological community differ based on geography, smaller primates always fall prey to a wider range of predators. Because predators are diverse in their hunting tactics, primates have evolved a wide range of tactics to avoid or escape them. We will discuss some of these behavioral adaptations later in this chapter in the section titled “Why Do Primates Live in Groups?.”



Figure 6.8a-c: Examples of primate predators: the Indian leopard (*Panthera fusca*) is an example of a mammalian carnivore (top left), the South African python (*Python natalensis*) is an example of a reptilian predator (bottom left), and the harpy eagle (*Harpia harpyja*) of Central and South America is an example of a bird of prey (right). Credit: a. Leopard by Srikanth Sekar has been modified (cropped) and is under a CC BY-SA 2.0 License. b. Python natalensis G. J. Alexander by Graham J. Alexander, University of the Witwatersrand, USGS, is in the public domain. c. Harpy Eagle clutching captured bird – Itirapina Reserve by Jonathan Wilkins has been modified (cropped) and is under a CC BY-SA 3.0 License.

## Mutualistic Interactions

So far, we've discussed competitive and predator-prey interactions in primate communities. But there are some interactions (between different primate species and between primates and other species) that are **mutualistic**, which is when organisms of different species work together, each benefiting from the interaction or relationship. One example is **seed dispersal**, which is the process by which seeds move away from the plant that produced them in preparation for germination and becoming a new plant. When seeds are dispersed by animals, like primates, it is an example of mutualism. The primate eats the fruit of a plant, which provides nutrients for its body, and in the process ingests the plant's seeds. Later, it deposits the seeds at another location as a pile of fertilizer.

Another example of mutualism is **polyspecific associations**, which are associations between two or more different species that are maintained by behavioral changes by at least one of the species. While some associations are short in duration, others are semi-permanent. The mutualistic benefits of polyspecific associations include one species gaining access to food that would otherwise have been inaccessible or being alerted to the presence of predators that they would not have known were present otherwise. In some cases, individuals seem to recognize and seek out specific members of another species. Twenty years of observations on chimpanzees and Western lowland gorillas (*Gorilla gorilla gorilla*) in the Republic of Congo has revealed social ties (some might call them friendships) between individual chimpanzees and gorillas that last for years and occur in a variety of social contexts, including play (Sanz et al. 2022).

## Parasite-Host Interactions

Primates are hosts for a variety of **parasites**, which are organisms that live in or on another organism (the host). Parasites come in many forms and pose varying levels of danger to the host. Blood parasites cause diseases like yellow fever and malaria. Skin parasites include fleas and ticks, which feed on the host's blood, and botflies, which lay eggs in the host's flesh. Bot fly larvae feed on the host's flesh as they develop and eventually (if not removed) break through the skin at maturity. Gut parasites, like tapeworms, get into the intestines and feed off of the food that is being digested by the host. Because most primates live in groups (see the "Primate Societies" section of this chapter), the tendency for **social transmission** of parasites, or the transfer of parasites from one individual to another, is high. Primates have evolved mechanisms to avoid parasite infection, including switching sleeping and feeding sites so as to avoid parasites. Mandrills (*Mandrillus sphinx*) have been shown to avoid grooming infected conspecifics as well as to avoid their feces, which smell different than the feces of individuals who are not infected with parasites (Poirotte et al. 2017). Other primates, including chimpanzees, appear to self-medicate when infected with parasites by ingesting plants that have antiparasitic properties (Krief et al. 2005).

## Human-Primate Interactions

Humans are part of many primate communities and our relationship with our closest relatives is often complicated. In some areas, humans hunt primates for their meat or as trophies, or so they can sell the infants as pets. As the human population increases in size, our demand for natural resources, like wood to build houses or land on which to grow food, also increases, often at the expense of pristine primate (and other animal) habitat. As their natural habitat shrinks, primates search for food in areas occupied by humans and may be shot as crop-raiding pests. While deforestation, hunting, and the pet trade are examples of ways in which humans negatively affect the lives of primates, some human-primate interactions are beneficial. In some parts of the world primates are central to **ecotourism**, which focuses on nature-based attractions to educate tourists and uses economically and ecologically sustainable practices. Perhaps one of the greatest success stories of ecotourism involves the mountain gorillas of Rwanda (see Figure 6.4b). After internal conflict plagued Rwanda during the 1990s, the Virunga Mountains area developed gorilla-based tourism to aid in socioeconomic development and to bring stability to the region. This process not only helped to increase mountain gorilla populations but was also able to generate enough income to cover the operation costs of three national parks and provide income and other benefits to people living in the area (Maekawa et al. 2013). You can learn more about human-primate interactions in Appendix B: Primate Conservation.

## Primate Societies

Unlike many other animals, primates are highly social and many live in stable groups consisting of adult males and females, even outside the **breeding season**, when females are **receptive** and available for mating because they are not pregnant or nursing. Indeed, **sociality**, or the tendency to form social groups, is a key behavioral adaptation of the order primates (see Chapter 5). This has led primatologists to ask two questions: "Why do primates live in groups?" and "What types of groups do primates live in?"

## Why Do Primates Live in Groups?

Primates live in groups when the benefits of doing so exceed the costs. Although there are many potential benefits to group living, enhanced feeding competition and predator avoidance are important benefits for many group living primates. When primates feed on high-quality, scarce food (like fruit), larger groups are more successful in competition with other groups. For example, in a long-term study of vervets in Kenya's Amboseli National Park, larger vervet groups had larger and better **home ranges**, which is the area in which a group regularly moves around as it performs its daily activities, including searching for food and water. Females in larger groups had higher average infant and female survival rates than the smallest group. Because pregnancy and nursing are energetically expensive for females, female **reproductive success**, or genetic contribution to future generations (measured by the number of offspring produced), is limited by access to food. Although living in a group means females compete with members of their own group for food, the benefits of being a member of a larger vervet group outweigh the costs (Cheney and Seyfarth 1987).

However, because they contain more individuals, larger groups are more likely to attract the attention of predators compared to smaller groups. This is one of the reasons that primates who rely on **crypsis**, or the ability to avoid detection by others, including predators, are often **solitary** (the term used to describe individuals who do not live together with other members of their species) and **nocturnal**, or active at night. If an animal is already hard to see because it is active at night, then moving quietly in small groups is a good strategy to avoid detection by predators.

The slow loris (*Nycticebus coucang*) of Southeast Asia is a good example of this strategy (Figure 6.9a). Nocturnal and solitary, the slow loris moves slowly and quietly as its primary strategy to avoid detection (Wiens and Zitzmann 2003). In contrast, primates who live in large groups and are **diurnal**, or active during the day (like gelada baboons [*Theropithecus gelada*]; Figure 6.9b) cannot avoid detection by predators. Instead, group-living primates rely on behaviors that alert others to the presence of danger and/or deter predators, including shared **vigilance** (watchful behavior to detect potential danger), **mobbing** (the act of cooperatively attacking or harassing a predator), and **alarm calling** (vocalizations emitted by social animals in response to danger). We will discuss alarm calls in the Communication section.

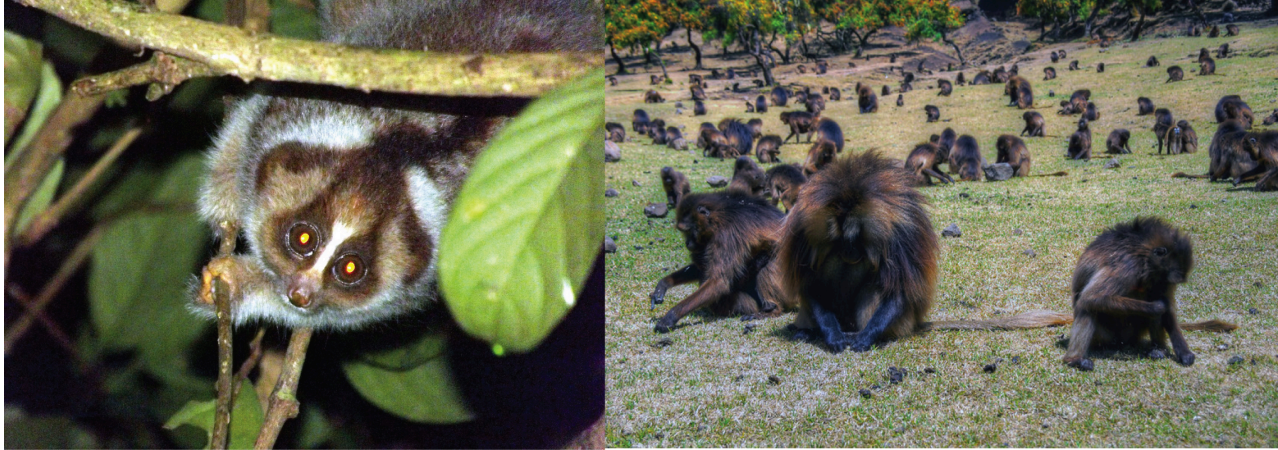


Figure 6.9a-b: Some primates, like the slow loris (left), are solitary and spend most of their time alone. However, most primates, like the gelada baboon (right), live in groups of varying sizes. Credit: a. Slow Loris by JmiksaneK is under a CC BY-SA 3.0 License. b. Field of baboons by mariusz kluzniak is under a CC BY-NC-ND 2.0 License.

## What Types of Groups Do Primates Live In?

Primates vary with regard to the types of groups in which they live. A **social system** describes a set of social interactions and behaviors that is typical for a species. The components that make up a species' social system include:

- Group size, which refers to the number of individuals that typically live together. Primate group size can be highly variable, ranging from one or a few individuals, to a few dozen, upward to several hundred individuals.
- Group composition describes group membership in terms of age class (e.g., adult, juvenile, infant) and sex. In some primates, groups consist of a mother and her dependent offspring while in others, one adult male lives long-term with one adult female and their dependent offspring. In other species, one or more adult males live with multiple females and their offspring.
- A species' **mating system** refers to which male(s) and female(s) mate. The terms that describe a mating system (e.g., **polygyny**, in which one male mates with multiple females) are sometimes used to describe a primate species' social system, but a mating system is one component of the species' social system. For example, two species might both have polygynous mating systems, but in one species, the group is composed of one male and multiple females, while members of the other species live as solitary individuals.
- **Ranging behavior** refers to the way in which animals move about their environment. Most primate species have a home range, where they perform their daily activities. Some primates defend a **territory** which is the part of the home range that the group actively guards in an attempt to keep out conspecifics.
- **Dispersal** patterns describe which sex moves to a new group to reproduce. In most primate species, males disperse because the benefits of dispersal, including increased access to mates and reduced competition from other males, outweigh the costs of migrating into a new group, which often comes with aggression from current group members. For many female primates, the opposite is true: females usually benefit from remaining **philopatric**, or in the group of their birth. This allows them to maintain strong alliances with female relatives, which helps them compete successfully against other groups for food. In solitary species, offspring of both sexes leave their mother's home range and become solitary. If this did not happen, the species would not be solitary. Even though both sexes disperse in solitary species, males usually disperse farther than females.
- Social interactions describe the ways in which individuals interact with members of their own and other groups of conspecifics. **Affiliative** (i.e., friendly or nonaggressive) behaviors include **grooming** (picking through the fur of another individual), playing, or **coalitions**

(temporary alliances between individuals). **Agonistic** (i.e., aggressive) behaviors include fighting over food or fighting over access to mates. In groups that contain multiple adult individuals of the same sex, it is common to have a **dominance hierarchy**, or a group of individuals that can be ranked according to their relative amount of power over others in the hierarchy. Initially, dominance hierarchies are established through the outcome of conflicts. Individuals who lose conflicts with others are **subordinate** (or low rank) to those who win them. Those who win conflicts are **dominant** (or high rank). Dominant individuals gain access to resources, like food or mates, before subordinates. Once a hierarchy is established, agonism decreases because everyone “knows their place.”

The main types of primate social systems are as follows: solitary; single-male, single-female; single-male, multi-female; multi-male, multi-female; fission-fusion; and multi-male, single-female. These types are discussed below.

## Solitary

Recall that the term *solitary* is used to describe species in which individuals do not live or travel together with other members of the same species, except for mothers and unweaned offspring. Males typically occupy a large home range or territory that overlaps the home ranges of multiple females, with whom they mate (Figure 6.10a). Because one male mates with multiple females, the mating system of solitary primates is polygyny. Social interactions between adults are limited but because some males do not get to mate, competition between males is intense. When males compete physically, they benefit from large body size and weaponry. The result is **sexual dimorphism**, when males and females look different from one another. Both males and females disperse, although males move farther from their mother than females. The nocturnal West African potto (*Perodicticus potto*; Figure 6.10b) is solitary. Bornean orangutans, which are diurnal, are also solitary.

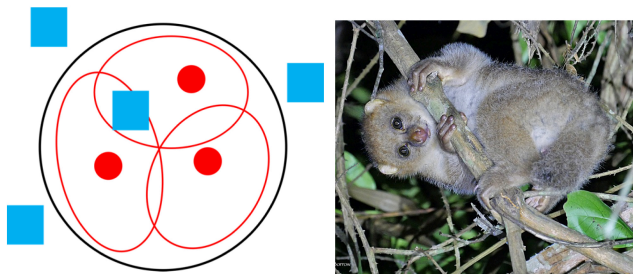


Figure 6.10a-b: Illustration of a solitary species' grouping pattern is shown on the left. Key: square = adult male; dot = adult female; open circle represents the outline of the male's home range; open oval represents individual female home ranges. The West African potto is a solitary primate (right). A full text description of this image is available. Credit: a. Polygyny in a Solitary Social System original to Explorations: An Open Invitation to Biological Anthropology (2nd ed.) by Karin Enstam Jaffe is under a CC BY-NC 4.0 License. b. West African Potto *Perodicticus potto* Kakum National Park, Ghana by Nik Barrow has been modified (cropped) and is under a CC BY-NC 2.0 License.

infant when it is not nursing. Once offspring are sexually mature, both males and females disperse. As with solitary species, males disperse farther from their parents than females. Bolivian Gray titi monkeys (*Plecturocebus donacophilus*) are an example of a species that has a single-male, single-female social system. One of their signature behaviors is tail twining, when two individuals sit with their tails wrapped around each other (Figure 6.11b). This behavior reinforces the social bond among family members and is especially common between the adult male and female. Gibbons (*Hylobates*) and owl monkeys (*Aotus*) also live in single-male, single-female groups.

## Single-Male, Multi-Female

**Single-male, multi-female** groups consist of one adult male living with multiple adult females and their dependent offspring (Figure 6.12a). These groups can range from as few as five or ten individuals to as many as 50. Female social relationships are governed by the female dominance hierarchy. Females are usually philopatric and males disperse. Males who are unable to join a group of females may join a bachelor group with other males. Because a single male mates with multiple females, the mating system is polygyny. Species that form single-male, multi-female groups may or may not defend a territory, but the **resident male**, who lives with a group of females, is aggressive toward other males, who may try to take over the

## Single-Male, Single-Female

Primate species in which an adult male and adult female live together with their dependent offspring have a **single-male, single-female** social system, sometimes referred to as a “family,” with group sizes between two and five individuals. The adult male and adult female engage in behaviors that strengthen their social relationship, or **pair bond**, including mutual grooming and resting together. The pair defend a territory (Figure 6.11a) and keep same-sex individuals away from their mate. The adult male and adult female mate with each other, so the mating system is **monogamy**, although mating outside the pair bond may occur. Species with monogamous mating systems are usually **sexually monomorphic** (males and females look similar) because competition for mates is relaxed since most males are able to obtain a mate. Males are usually confident that they are the father of their mate's infant, so they help with offspring care by carrying the

group and become the new resident male. Competition between males to be the resident male of a group is intense, and these species usually display sexual dimorphism, with males being larger than females and possessing large canines. Hanuman langurs (*Semnopithecus entellus*) of India form single-male, multi-female groups (Figure 6.12b). When a new male takes over a group of females and ousts the former resident male, he may commit **infanticide**, or kill the unweaned infants. This is especially likely if the new resident male has not yet mated with any of the females and thus cannot be the infants' father. This causes the females, who were nursing, to become sexually receptive sooner, increasing the new resident male's chances of producing offspring (Sharma, Ram, and Raipurohit 2010). Gorillas, patas monkeys, and golden snub-nosed monkeys (*Rhinopithecus roxellana*) also live in single-male, multi-female groups.



Figure 6.12a-b: An illustration of the one-male, multi-female grouping pattern is shown on the left. Key: square = adult male; dot = adult female; open circle represents the outline of the group's home range (or territory). The Hanuman langur (right) is an example of a species with a one-male, multi-female social system. Credit: a. Single-Male, Multi-Female Social System original to Explorations: An Open Invitation to Biological Anthropology (2nd ed.) by Karin Enstam Jaffe is under a CC BY-NC 4.0 License. b. Close-up of Two Grey Langurs by Amit Rai has been modified (cropped) and is free to use via Pexels.

determines a female's access to food. Because their place in the hierarchy can affect their reproductive success, males compete with each other, but because it is rare for males to be excluded from mating altogether, the level of competition and degree of sexual dimorphism are less extreme than what we see in polygynous species. Usually, females are philopatric and males disperse. Vervet monkeys (Figure 6.13b), ring-tailed lemurs (*Lemur catta*), white-faced capuchins (*Cebus capucinus*), and black-capped squirrel monkeys (*Saimiri boliviensis*) live in multi-male, multi-female groups.

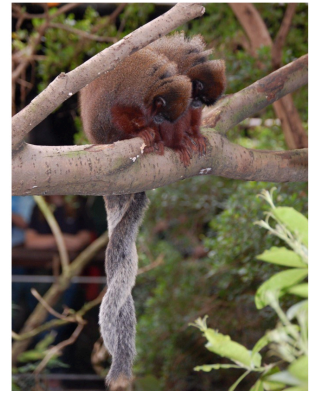
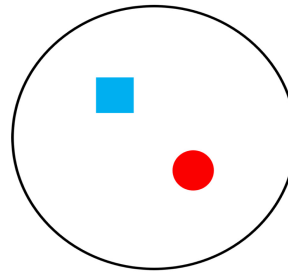


Figure 6.11a-b: Illustration of a single-male, single-female grouping pattern is shown on the left. Key: square = adult male; dot = adult female; open circle represents the outline of the group's territory, which the bonded pair defend against conspecifics. The titi monkey (right) is an example of a primate species with a single-male, single-female social system. Credit: a. Single-Male, Single-Female Social System original to Explorations: An Open Invitation to Biological Anthropology (2nd ed.) by Karin Enstam Jaffe is under a CC BY-NC 4.0 License. b. Two Red Titi Monkeys (*Callicebus cupreus*) sitting together with their tails intertwined at the London Zoo by Steven G. Johnson has been modified (cropped) and is under a CC BY-SA 3.0 License.

### Multi-Male, Multi-Female

**Multi-male, multi-female** groups consist of multiple adult males living with multiple adult females and their dependent offspring. Although there is more than one adult male, there are more adult females than adult males in the group (Figure 6.13a). Multi-male, multi-female groups can range in size from about ten to as many as 500 individuals. They occupy a home range but may or may not defend a territory. In groups that contain multiple males and multiple females, it is not possible for one male to monopolize all the matings, so the mating system is **polygamy**, in which multiple males mate with multiple females. However, this does not mean that all males have an equal opportunity to mate with all females. In multi-male, multi-female groups, both males and females form a dominance hierarchy. The male dominance hierarchy determines their access to females for mating in much the same way that a female dominance hierarchy

## Fission-Fusion

**Fission-fusion** is a fluid social system in which the size and composition of the social group changes, with groups splitting (fission) or merging (fusion) depending on food availability (Pinacho-Guendulain and Ramos-Fernández 2017). When key resources are scarce, individuals spread out (fission) and move and feed individually or in small subgroups (Figure 6.14a). When key food resources are plentiful, individuals come together (fusion) and individuals travel and feed as a more cohesive group (Figure 6.14a). Fission-fusion social structure is believed to reduce feeding competition when resources are scarce. Because group composition changes over time, species with fission-fusion social systems are referred to as a community. Communities consist of multiple adult males, multiple adult females, and offspring, and group size varies but typically ranges from ten to a few dozen individuals. Females typically disperse and males are philopatric. Thus, community males are related and display unusual forms of cooperation. The mating system associated with fission-fusion is polygamy. Because males are not excluded from mating, competition for mates is relaxed and sexual dimorphism is moderate (males are slightly larger than females). Geoffroy's spider monkeys (*Ateles geoffroyi*) (Figure 6.14b) and chimpanzees both have fission-fusion social system.

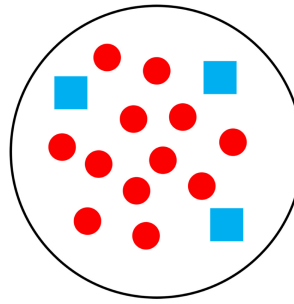


Figure 6.13a-b: An illustration of the multi-male, multi-female grouping pattern is shown on the left. Key: square = adult male; dot = adult female; open circle represents the outline of the group's home range (or territory). Vervet monkeys (right) are an example of a species that lives in multi-male, multi-female groups. Credit: a. Multi-Male, Multi-Female Social System original to Explorations: An Open Invitation to Biological Anthropology (2nd ed.) by Karin Enstam Jaffe is under a CC BY-NC 4.0 License. b. Vervet Monkeys (*Chlorocebus pygerythrus*) by Bernard DUPONT has been modified (cropped) and is under a CC BY-SA 2.0 License.

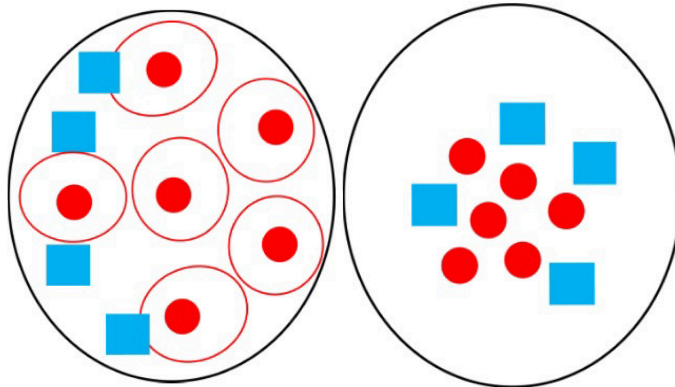


Figure 6.14a-b: An illustration of the fission-fusion grouping pattern appears on the left. The left illustration represents fission, when females travel and feed independently in individual home ranges within the community boundary. The right illustration represents fusion, when community members form a cohesive group. A full text description of this image is available. Key: square = adult male; dot = adult female; open circle represents the outline of the community boundary. Open ovals represent individual female home ranges when the group fissions. Credits: a. Fission-Fusion Social System original to Explorations: An Open Invitation to Biological Anthropology (2nd ed.) by Karin Enstam Jaffe is under a CC BY-NC 4.0 License. b. Geoffroy's Spider Monkeys (*Ateles geoffroyi*) by Bernard DUPONT has been modified (cropped) and is under a CC BY-SA 2.0 License.

## Multi-Male, Single-Female

In **multi-male, single-female** groups, two or more males live with one breeding female, her dependent offspring, and non-breeding females (Figure 6.15a). This type of social system is found in the **callitrichids**, the primate family that includes marmosets (*Callithrix*; Figure 6.15b) and tamarins (*Saguinus*) of Central and South America. Their groups rarely exceed 15 individuals, and each group actively defends their territory from conspecifics. Although more than one adult female may live in the group, the mating system is **polyandry** because there is only one breeding female who mates with all of the adult males. This is achieved through **reproductive suppression**, which involves the breeding female preventing other females from reproducing through physiological and/or behavioral means (Digby, Ferrari, and Salzman 2011). This limits the opportunities for other females in the group to become pregnant. Instead, these females, and the males in the group, help raise the breeding female's offspring. This is

referred to as **cooperative breeding** and usually takes the form of carrying infants, grooming them, and protecting them from danger (de Oliveira Terceiro and Burkart 2019). Because reproductive opportunities for female tamarins and marmosets are limited, they are very competitive, and females are slightly larger than males, which helps them compete for the breeding spot in a group.

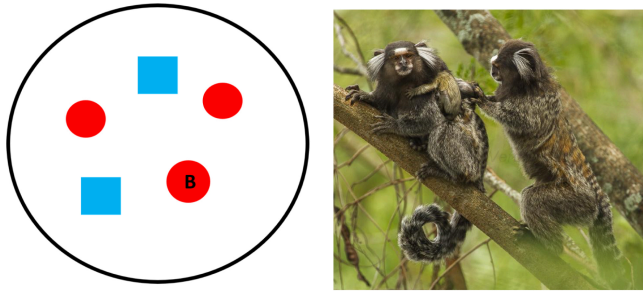


Figure 6.15a-b: An illustration of multi-male, single-female grouping pattern appears on the left. Key: square = adult male; B dot = breeding female; unmarked dot = non-breeding female; open circle represents the outline of the group's territory, which is defended against conspecifics. The common marmoset (*Callithrix jacchus*) is an example of a primate species that has this type of social system (right). Credit: a. Multi-Male, Single-Female Social System original to Explorations: An Open Invitation to Biological Anthropology (2nd ed.) by Karin Enstam Jaffe is under a CC BY-NC 4.0 License. b. Family of Common Marmoset – REGUA – Brazil MG 9480 (12930855765) by Francesco Veronesi has been modified (cropped) and is under a CC BY-SA 2.0 License.

Biologically speaking, **parental investment** is any time or energy a parent devotes to the current offspring that enhances its survival (and eventual reproductive success) at the expense of the parent's ability to invest in the next offspring (Trivers 1972). Female primates invest more heavily in offspring than males. Even before conception, females produce energy-containing eggs, and they will be responsible for sustaining a fertilized egg until it implants in the uterus. After that, they invest in pregnancy and lactation (Figure 6.16). Because all of this investment requires a lot of energy, female primates can only produce one offspring (or litter) at a time. A species' **interbirth interval**, or the typical length of time between one birth and the next, is determined by the length of time necessary to maximize each offspring's survival without jeopardizing the female's ability to produce the greatest number of offspring possible. If a female invests too little (i.e., weans an offspring too early), she may give birth to many offspring, but very few (if any) of them will survive. If she invests too much (i.e., nurses an offspring even after it could be weaned), she ensures the survival of that individual offspring but will not be able to produce very many during her lifetime. To maximize her reproductive success, a female must invest *just* long enough to ensure the greatest number of offspring survive to reproduce. We often think of maternal care as an **innate** (or natural), instinctive behavior. Yet this is not the case. The "Special Topic: Is Maternal Behavior Innate?" dispels the myth that maternal behavior is solely instinctual and explains how female primates learn to be good mothers.

## Sexual Selection

**Sexual selection**, or selection for traits that maximize mating success, comes in two forms. **Intrasexual selection** is selection for traits that enhance the ability of members of one sex to compete amongst themselves ("intrasexual" = within one sex). **Intersexual selection** is selection for traits that enhance the ability of one sex to attract the other ("intersexual" = between the sexes).

Intrasexual selection most often operates on males. In the wild, adult females are either pregnant or lactating for most of their adult lives. So, in a given population, there are usually more males available and willing to mate than there are females. The result? Females are a scarce resource over which males compete. Intrasexual selection favors traits that help a male win fights with other males. In primates, these traits include large body size

## Reproductive Strategies

Reproductive strategies have evolved to maximize individual reproductive success. These strategies can be divided into those that deal with offspring production and care (parental investment) and those that maximize mating success (sexual selection). Because the reproductive physiology of male and female primates differs, males and females differ with regard to parental investment and sexual selection strategies. Female strategies focus on obtaining the food necessary to sustain a pregnancy and choosing the best male(s) to father offspring. Male strategies focus on gaining access to receptive females.

## Parental Investment



Figure 6.16: A female Japanese macaque nursing her infant. Credit: Snow monkey baby milk time by Daisuke Tashiro is under a CC BY-SA 2.0 License.



(Figure 6.17a) and large canines (Figure 6.17b). Because females don't possess these same traits, males and females of some species look different; that is, they are sexually dimorphic (Figure 6.17a).



Figure 6.17a-b: a. Hamadryas baboons (*Papio hamadryas*) are sexually dimorphic. The male (left) is much bigger than the female (center) and also has different colored fur. b. Adult males, like this gelada baboon, also have larger canines than females. Credit: a. Dierenpark Emmen baboon (2679944324) by robin bos has been modified (cropped) and is under a CC BY 2.0 License. b. Olive Baboon *Papio anubis*, Picture Taken in Tanzania by Nevit Dilmen has been modified (cropped) and is under a CC BY-SA 3.0 License.

Intersexual selection also tends to operate on males, selecting traits that make a male more attractive to females. Females, in turn, choose among potential fathers. Because female primates invest more in offspring production and care than males (see the “Parental Investment” section, above), it is more costly for them if the offspring dies before maturity or reaches maturity but does not reproduce. Thus, it benefits a female primate to be choosy and try to pick the healthiest male as a mate. Males must display traits that tell a female why she should choose *him*, and not another male, as her mate.

What traits are female primates looking for? In humans, women may look for a mate who can provide important resources, such as food, paternal care, or protection. This is rare in other primates, though, since most females do not need males to provide resources. More commonly, female primates obtain genetic benefits for their offspring from choosing one male over another. Often the specific criteria by which females select mates is unknown. However, if a female chooses a healthy (as indicated by traits like a plush coat, bright coloration, or large body size) or older male, she may obtain genes for her offspring that code for health or long life. If a male's rank is determined by competitive ability that has a genetic component, females who choose males who win fights may acquire these genes (and qualities) for their offspring. Females in some species appear to prefer new immigrants, sometimes even “sneaking” copulations with males who are not established members of their groups. Such a preference may provide their offspring with novel genes and increase genetic variation (for more about the importance of genetic variation, see Chapter 4). Female choice is often more subtle than male-male competition, so it can be more difficult to study. However, as more research is conducted, we continue to improve our understanding of the ways that female primates exert their choice.

### Special Topic: Is Maternal Behavior Innate?

Zoos almost always have nurseries where infants are cared for by zookeepers if their mothers will not care for them (Figure 6.18). These exhibits are among the most popular because the babies are so cute and so much fun to watch. And the caretaking positions

in zoo nurseries are often among the most coveted by zoo personnel for the same reasons. But if maternal behavior is instinctive, why do zoo nurseries even exist? The answer is that in many species, including primates, maternal behavior is not purely instinctual; it is dependent on **social learning** (behavior learned by observing and imitating others), as well.



Figure 6.18: Newborn orangutan at Audubon Zoo being bottle-fed. Credit: Newborn orangutan born at Audubon Zoo being bottle fed (2022) by Audubon Nature Institute is used by permission.

Captive female primates, including gorillas and chimpanzees, who have not had the opportunity to observe their mother or other females care for infants do not know how to care for their own offspring. Although it is preferred that the primate mother care for her own infant, there are cases when she will not and humans must step in to ensure the offspring survives. When hand-rearing by humans is necessary, the infant is returned to the group as soon as possible in the hopes that it will learn species-typical behavior from its mother and other conspecifics. Observations such as these indicate that maternal behavior is learned, not innate, and that maternal care is critically important to the social and psychological development of young primates.

## Communication

In its most basic form, communication occurs when one individual (the sender) emits a signal that conveys information, which is detected by another individual (the receiver). We have discussed several aspects of primate sociality in this chapter, all of which require the communication of information between individuals. But exactly *how* does a female chimpanzee communicate her sexual availability? *How* does a vervet monkey communicate the approach of a leopard or that a python is nearby? *How* do solitary, nocturnal primates, like the slow loris, communicate information about themselves to conspecifics? Primate communication comes in four forms: vocal, visual, olfactory, and tactile. Species vary in their reliance on each.

### Vocal Communication

Primates use sound to communicate danger or threats, to claim and maintain a territory, or make contact with other group members. Alarm calls are given in response to predators. In some cases, alarm calls are used to alert members of the group to the presence of a predator so they can take

evasive action. In other cases, they are directed at the predator itself, signaling that it has been detected. You can learn more about alarm calls as forms of vocal communication in the highlight box in this chapter entitled “Dig Deeper: Alarm Calls: Signals to Friends or Foes?”

Loud calls are designed to travel great distances and are used in territorial defense by many primate species including indris (*Indri indri*), orangutans, gibbons, and howler monkeys (*Alouatta*). In dense forest, where visual communication can be difficult, loud calls can be useful in signaling to conspecifics that a group or individual occupies a specific area. Howler monkeys are named for their loud calls, or “roars,” which can be heard one kilometer or more away (Schön Ybarra 1986). Howler monkey roars may act to maintain distance between neighboring groups or keep extragroup males from entering the home range (Schön Ybarra 1986).

Other vocalizations are intended to communicate with individuals in one’s own group. These include vocalizations given as part of threat displays or dominance interactions, as well as contact calls that provide information about one’s location to other group members. Chacma baboons (*Papio ursinus*) have a rich repertoire of vocalizations for communicating with other group members (Fischer et al. 2008). Adult males give specific vocalizations during threat displays and physical confrontations. Subordinates “screech” when retreating from a dominant individual, signaling submission. Since baboons rely on membership in their group for finding food and detecting predators, a baboon separated from his group will vocalize in an attempt to regain contact. Young baboons emit their own contact calls when separated from their mothers.

## Visual Communication



Figure 6.19a-b: Two female hamadryas baboons. The female on the left has a sexual swelling while the female on the right (in foreground, with infant clinging to her belly) does not. An adult male is behind her. Credit: a. Sexual swelling in female Hamadryas baboon by Mamoritai has been modified (cropped) and is under a CC BY-SA 2.0 License. b. Hamadryas baboon at Giza Zoo by Hatem Moushir 36 by Hatem Moushir has been modified (cropped) and is under a CC BY-SA 3.0 License.

**Visual communication**, which involves signals that can be seen, is an important component of nonhuman primate behavior, alone or in combination with other forms of communication. **Piloerection**, or raising one’s hair or fur, is used in aggressive interactions to make an individual appear larger than it actually is. Female macaques (*Macaca*), baboons (*Papio*), and chimpanzees, signal sexual receptivity through changes in the size, shape, and, often, color of their hindquarters, called a **sexual swelling** (Figure 6.19a). The sexual swelling reaches its maximum size at ovulation. When females are not receptive, either because they are pregnant or are nursing, they do not display a sexual swelling (Figure 6.19b). Thus, the presence or absence of a sexual swelling signals a female’s reproductive state.

Monkeys and apes use diverse facial expressions in visual communication. Showing your teeth in a “smile” sends a signal of friendship in humans. Displaying teeth in this way is a sign of anxiety or fear in primates. That male mandrill you see “yawning” at your local zoo is actually displaying his teeth to signal tension or to threaten a rival (Figure 6.20a). In addition to showing their canines, male gelada baboons use “lip flips,” in which the gums and teeth are exposed by flipping the upper lip up over the nostrils (Figure 6.20b), and “raised eyelids,” in which the pale eyelids are exposed

by pulling the scalp back as threatening gestures (Aich, Moos-Heilen, and Zimmerman 1990). Submissive males respond by fleeing or presenting their hindquarters.



Figure 6.20a-b: Males use visual displays to communicate with other males. The male mandrill (left) is yawning to display his canines, and the male gelada baboon (right) enhances the yawn by flipping his upper lip back and raising his eyelids. Credit: a. Mandrill by Mathias Appel has been modified (cropped) and designated to the public domain (CC0). b. BabouinGeladaAuReveil by BluesyPete has been modified (cropped) and is under a CC BY-SA 3.0 License.



Figure 6.22a-b: Many monkey species have colorful faces, including the bald uakari (*Cacajao calvus*; left) and the white-bellied spider monkey (*Ateles belzebuth*) (right). Credit: a. Uakari by Coadra dragos has been modified (cropped) and is under a CC BY-SA 4.0 License. 6.22b *Ateles belzebuth* (White-bellied spider monkey) 2 by Ewa (username: Ewcek65) has been modified (cropped) and is under a CC BY 2.0 License.

Primates also communicate through color. In female and male mandrills, facial coloration provides information about an individual's health, competitive ability, and reproductive state to conspecifics (Figure 6.21; Setchell et al. 2008; Setchell, Wickings, and Knapp 2006). Variation in facial coloration among monkeys of Central and South America ranges from very simple (Figure 6.22a) to complex (Figure 6.22b). Species living with larger numbers of other primate species have evolved more complex facial coloration patterns, suggesting that this trait evolved as a form of **species recognition**, or the ability to differentiate conspecifics from members of other species (Santana, Lynch Alfaro, and Alfaro 2012).

### Olfactory Communication

All primates use scent to communicate. Females secrete chemicals from their **anogenital** region (the area of the anus and genitals) that provide males with information about their reproductive state. In some species, like macaques and chimpanzees, this olfactory signal is enhanced by a sexual swelling, as discussed above.

**Olfactory communication**, or communicating through scent, is particularly important for monkeys of Central and South America, lemurs, and lorises. Male and female common squirrel monkeys (*Saimiri sciureus*) (Figure 6.23a) engage in “urine washing,” in which an individual urinates on its hands and feet and then uses them to spread urine all over its body. Urine washing may be used to mark trails for others to follow, to control body temperature, as part of dominance displays, or to communicate reproductive state (Boinski 1992). During aggressive interactions with other males, male ring-tailed lemurs rub their tails with scent from glands on their wrists and chests. They use their “perfumed” tails in aggressive interactions with other males, who may respond by waiving their own scented tail, with physical aggression, or by fleeing (Jolly 1966). Males also waive their tails, saturated in scent, to attract females (Shirasu et al. 2020). Males use scent glands in their wrists to mark territorial boundaries (Figure 6.23b; Mertl-Millhollen 1988).



Figure 6.21: The colorful face of the male mandrill provides information about health and fitness to other mandrills. Credit: Mandrill by Mathias Appel has been modified (cropped) and designated to the public domain (CC0).



Figure 6.23a-b: Some primates, like the common squirrel monkey (left) and the ring-tailed lemur (right), communicate using scent. Credit: a. *Saimiri sciureus* by Ruben Undheim is under a CC BY-SA 2.0 License. b. *Lemur catta* 004 by Maky has been modified (cropped) and is under a CC BY-SA 3.0 License.

### Tactile Communication

**Tactile communication**, or communicating through touch, is very important in all primate species. Physical contact is used to comfort and reassure, is part of courtship and mating, and is used to establish dominance and alliances. Grooming is an important and clearly enjoyable form of

tactile communication for all primates (Figure 6.24). Not only does grooming serve to clean the skin and fur, removing parasites and debris, but it is an important affiliative behavior that helps reinforce social bonds, repair relationships, and cement alliances.



Figure 6.24: Examples of grooming in Japanese macaques (upper left), tufted capuchins (*Sapajus apella*) (upper right), gelada baboons (lower left), and black-and-white ruffed lemurs (*Varecia variegata*; lower right). Credit: Examples of grooming original to *Explorations: An Open Invitation to Biological Anthropology* (2nd ed.) by Karin Jaffe is a collective work under a CC BY-NC-SA 4.0 License. [Includes Yakushima macaques grooming each other by Grendelkhan, CC BY-SA 4.0 License; Tufted capuchin monkeys grooming session III by Adrian Soldati, CC BY-SA 4.0 License; Baboons Wunania 012018 by Kim Toogood, CC BY-SA 4.0 License; Black-and-white ruffed lemur 03 by Mattis2412, public domain (CC0 1.0)].

### Dig Deeper: Alarm Calls: Signals to Friends or Foes?

Alarm calls are common among group-living primates. They often serve to notify conspecifics of potential danger, as is the case with vervet monkeys. Research has shown that: (1) vervets classify predators based on hunting style; (2) alarm calls convey information to other vervets about that hunting style; and (3) other vervets respond in ways appropriate for evading that type of predator (Seyfarth, Cheney, and Marler 1980a). When a vervet gives a “leopard” alarm call (directed at mammalian carnivores like leopards, Figure 6.25a), monkeys on the ground climb the nearest tree, while monkeys already in trees stay there or climb higher. Since most mammalian carnivores hunt on the ground, getting into, and staying in, a tree is the best option for escape. When the “snake” alarm call is given, vervets stand on their hind legs and look down at the ground (Figure 6.25b). Since snakes are not pursuit predators, locating them quickly so as to avoid them is the best strategy. Lastly, when an “eagle” alarm call is given, vervets look up or run into bushes, both of which are useful responses for avoiding hawks and eagles, which attack from above (Figure 6.25c).

Vervets clearly understand the meaning of each type of alarm call, as they respond appropriately even when they do not see the actual predator (Seyfarth, Cheney, and Marler 1980b). Such **semantic communication**, which involves the systematic use of signals to refer to objects in the environment, was once believed to be unique to humans. It may be a precursor to the symbolic capacities of human language.

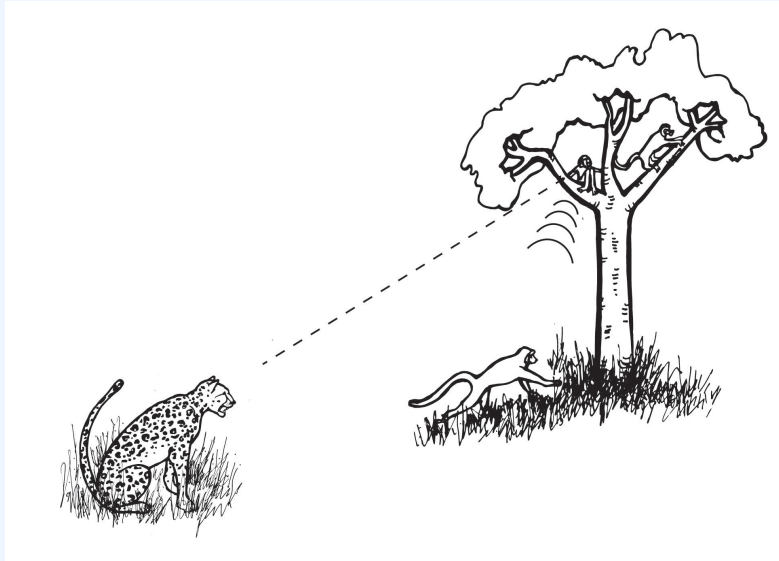


Figure 6.25a

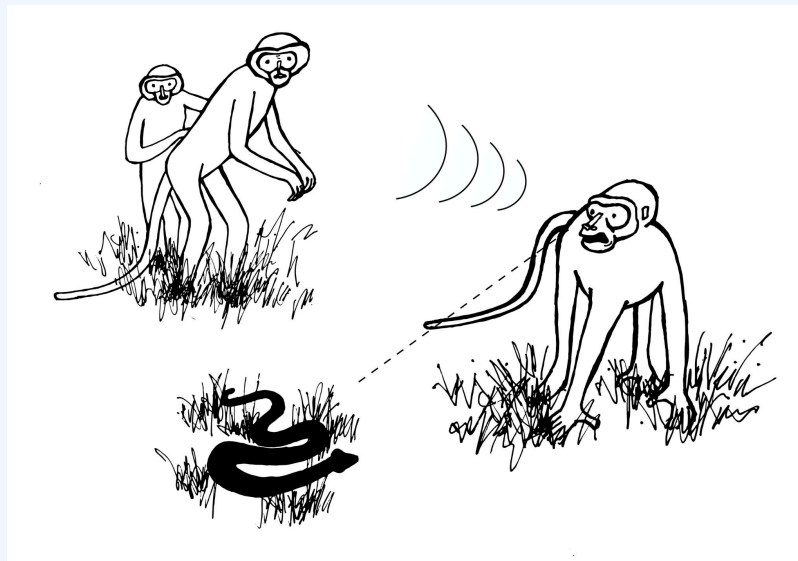


Figure 6.25b

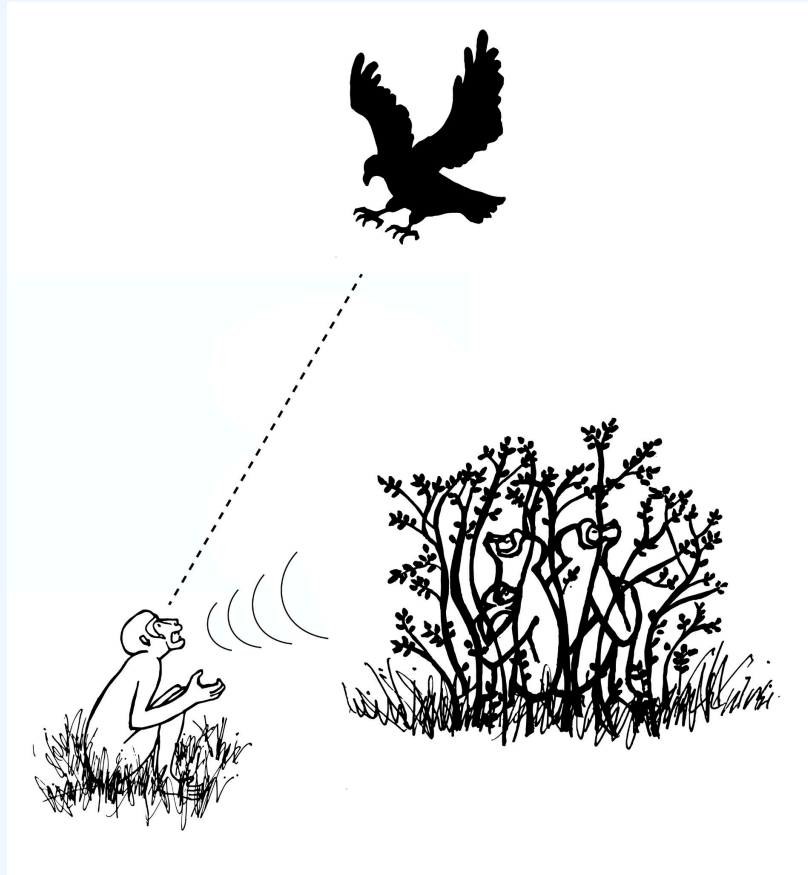


Figure 6.25a-c: Vervet monkeys respond in different ways to alarm calls for each of their three main predators (leopards, snakes, and eagles) which are appropriate to predator hunting strategies. Credit: Vervet Monkey Alarm Calls by Mary Nelson, original to *Explorations: An Open Invitation to Biological Anthropology*, 2nd edition, is under a CC BY-NC 4.0 License.

Research on other African monkeys indicates that some species use alarm calls to signal to the predator that it has been detected. Diana monkeys (*Cercopithecus diana*) give alarm calls to leopards (*Panthera pardus*) but not chimpanzees (Zuberbühler, Noë, and Seyfarth 1997). Because leopards are stealth predators, they rely on the element of surprise to sneak up on their prey (Figure 6.26a). Alarm calling at leopards appears to tell the leopard that it has been seen and therefore its chance of success will be low. Research shows leopards are more likely to stop hunting after an alarm call has been emitted. Unlike leopards, chimpanzees are pursuit predators and may even use alarm calls to locate potential prey (Figure 6.26b). With such a predator, prey are better off remaining as silent as possible so as not to alert the predator to their location (Zuberbühler et al. 1999).





Figure 6.26a-b: Because leopards (left) and chimpanzees (right) hunt differently, Diana monkeys react differently to them. Credit: a. Crouching Leopard by Thimindu Goonatillake is under a CC BY-SA 2.0 License. b. Chimpanzee in the wild by D.G. Kulakov is under a CC BY-SA 4.0 License.

## The Question of Culture

It may be surprising in a chapter on nonhuman primates to see a discussion of culture. After all, culture is considered by many, including cultural anthropologists, to be a distinguishing characteristic of humans. Indeed, some anthropologists question claims of culture in primates and other animals. Definitions of animal culture focus on specific behaviors that are unique to one population. Anthropological definitions of human culture emphasize shared ideology (e.g., values, morals, beliefs) and symbols, not just behavior. Using this definition, some cultural anthropologists view primates as lacking culture because of the absence of symbolic life (e.g., religion). However, the longer we study primate groups and populations, the more insight we gain into primate behavioral variation. If we define **culture** as the transmission of behavior from one generation to the next through social learning, then we must view at least some of the behavioral variation we see in primates as forms of **cultural tradition**, or a distinctive pattern of behavior shared by multiple individuals in a social group that persists over time (Whiten 2001).

## Chimpanzee Culture

Due to both their high level of intelligence and the large number of long-term studies on several different populations, chimpanzees provide the best example of cultural tradition in primates. Chimpanzees express cultural variation in multiple behavioral patterns, ranging from population-specific prey preferences and hunting strategies to tool-use techniques and social behaviors. For example, in Tanzania, chimpanzees fish for termites by stripping twigs and then poking the twigs into termite mounds. The termites react to the “invasion” by attacking the twig. The chimpanzee pulls the twig out, termites attached, and eats them. In Gambia, they use modified twigs to extract honey from holes in trees. In Fongoli, Sénégal, chimpanzees use sticks as “spears” that they stab into tree cavities to hunt for galagos (Figure 6.27). Multiple chimpanzee populations use a “hammer and anvil” to crack open nuts, but the specific techniques differ. Because the cultural traditions are so diverse and unique, if a researcher can observe enough of a chimpanzee’s behavior, it is possible to assign that individual to a specific community, much in the same way a human being can be associated with a specific culture based on his or her behavior (Whiten 2011).



Figure 6.27a-d: Tool-assisted hunting by a chimpanzee at Fongoli, Sénégal. An adult male chimpanzee uses a tree branch with a modified end to (a–c) stab into a cavity within a hollow tree branch that houses a galago. He ultimately captures the galago as (d) his adolescent brother looks on. Credit: Pan troglodytes, tool use in Senegal by J. D. Pruetz, P. Bertolani, K. Boyer Ontl, S. Lindshield, M. Shelley, and E. G. Wessling is under a CC BY 4.0 License.

How do chimpanzee cultures develop, and how does cultural transmission occur? Although we do not know for sure how chimpanzee cultural traditions develop initially, it is possible that different groups invent, either accidentally or deliberately, certain behaviors that other individuals copy. **Immigration**, or movement of an individual into a new group or community, is an important avenue of cultural transmission in chimpanzees, much as it is between human cultures. Immigrants (typically females) may bring cultural traditions to their new community, which residents observe and learn. Conversely, immigrants may observe and learn a cultural tradition practiced in their new community (Whiten 2011).

## Cultural Transmission in Macaques

Two monkey species are well-known for behavioral variation that has been called “pre-cultural” by some primatologists: Japanese macaques and tufted capuchins (*Sapajus apella*). The transmission of unique **foraging** (the act of searching for food) behaviors through the members of a provisioned group of Japanese macaques on Koshima Island is well known (Matsuzawa 2015). In an effort to keep the monkeys nearby, researchers provided them with piles of sweet potatoes. A juvenile female named Imo spontaneously washed a muddy sweet potato in a stream. This new food-processing technique first spread among other juveniles and then gradually to older individuals. Within 30 years, it had spread across generations, and 46 of 57 monkeys in the group engaged in the behavior. Another example comes from a group living far to the north, in Shiga-Heights, Nagano Prefecture. Researchers used apples to entice Japanese macaques to the area. Within a few years, monkeys visited the area regularly and were observed playing with the water in the hot springs. Soon, they climbed into the hot springs and learned to immerse themselves to keep warm and reduce stress when not foraging (Figure 6.28; Matsuzawa 2018; Takeshita et al. 2018; recall also our discussion of hot spring use as an example of analogous traits at the beginning of this chapter). These examples share several characteristics with human culture, including invention or modification of behavior, transmission of behavior between individuals, and the persistence of the behavior across generations (McGrew 1998).



Figure 6.28: Hot spring use by Japanese macaques is a culturally transmitted behavior. Credit: Oooh, This Feels Sooo Good! by Peter Theony – Quality HD Photography is under a CC BY-NC-SA 2.0 License.

## Conclusion

Primates are socially complex, extremely intelligent, and highly adaptable. In this chapter we discussed aspects of primate ecology, including how body size and characteristics of food affect what primates eat and how primates interact with other species in their environment. We examined why primates live in groups, the types of groups in which they are found, and the reproductive strategies used by males and females to maximize reproductive success. Like other aspects of their behavior, primate communication is varied and complex, and we discussed how primates communicate using vocal, visual, olfactory, and tactile signals. Finally, we explored the question of culture among nonhuman primates and learned that some species have cultural traditions, distinctive patterns of behavior shared by multiple individuals in a social group that persist over time. Humans and other

primates are similar in many ways. Learning about principles of primate ecology and behavior can help us better understand our own behavior and the behaviors of our extinct relatives.

## Review Questions

- If anthropology is the study of humans, why do some anthropologists study primates?
- How does a primate's ecology affect their diet and interactions with other organisms?
- Why do primates live in groups and in what types of groups do they live?
- What is parental investment and sexual selection?
- What are some examples of primate communication?
- What is the evidence for cultural traditions in primates and how do primatologists think cultural transmission occurs in primates?

## Key Terms

**Abundance:** How much food is available in a given area.

**Adaptation:** A trait with a function.

**Affiliative:** Nonaggressive social interactions and associations between individuals.

**Agonistic:** Conflict; aggressive interactions between individuals.

**Alarm calling:** Vocalizations emitted by social animals in response to danger.

**Analogy:** A similar trait found in different species that arose independently.

**Anogenital:** Relating to the anus and genitals.

**Breeding season:** The time of year when females are receptive to mating.

**Callitrichids:** The primate family that includes marmosets and tamarins.

**Carnivores:** Organisms whose diet consists primarily of animal tissue.

**Coalition:** A temporary alliance between individuals.

**Community ecology:** The branch of ecology that deals with the relationships and interactions between different organisms that occupy the same habitat.

**Comparison:** An examination of the similarities and differences between two things, such as two primate species.

**Conspecifics:** Members of the same species.

**Cooperative breeding:** When individuals other than the mother and father help raise the offspring.

**Crypsis:** The ability to avoid detection by other organisms, such as predators.

**Cultural tradition:** A distinctive pattern of behavior shared by multiple individuals in a social group, which persists over time and is acquired through social learning.

**Culture:** The transmission of behavior from one generation to the next through observation and imitation.

**Decolonize:** Understanding and highlighting the theory and research of non-Western individuals and perspectives.

**Descendant:** A species that comes after the ancestor species.

**Direct competition:** Competition that involves physical interaction between individuals, such as fighting.

**Dispersal:** To leave one's group or area. This may or may not involve joining another group.

**Distribution:** How food is spread out.

**Diurnal:** Active during the day.

**Dominance hierarchy:** The ranked organization of individuals established by the outcome of aggressive-submissive interactions.

**Dominant:** Being of high rank.

**Ecology:** The relationship between organisms and their physical surroundings.

**Ecotourism:** A form of tourism that focuses on nature-based attractions to provide learning opportunities and that uses economically and ecologically sustainable practices.

**Ethology:** The study of animal behavior.

**Fission-fusion:** Societies in which group composition is flexible, such as chimpanzee and spider monkey societies. Individuals may break up into smaller feeding groups (fission) and combine into larger groups (fusion).

**Fitness:** An individual's ability to survive and reproduce relative to other members of the same species.

**Folivores:** Organisms whose diet consists primarily of leaves.

**Foraging:** The act of searching for food.

**Frugivores:** Organisms whose diet consists primarily of fruit.

**Grooming:** Picking through the fur of another individual for cleaning or bonding purposes.

**Heterospecifics:** Members of different species.

**Holism:** The idea that the parts of a system interconnect and interact to make up the whole.

**Home range:** The area that a group or individual uses over a given period of time (often over a year).

**Homology:** A similar trait found in different species because it was inherited from a common ancestor.

**Immigration:** Movement of an individual into a new group or community.

**Indirect competition:** Competition that does not involve physical interaction between individuals, such as eating food before another individual arrives at the food site.

**Infanticide:** The killing of infants of one's own species.

**Innate:** Natural; as in behavior that comes naturally.

**Insectivores:** Organisms whose diets consist primarily of insects.

**Interbirth interval:** The typical length of time between one birth and the next for a species.

**Intersexual selection:** The selection for traits that enhance the ability of the members of one sex to attract the attention of the other.

**Intrasexual selection:** Selection for traits that enhance the ability of members of one sex to compete amongst themselves.

**Mating system:** A way of describing which male(s) and female(s) mate.

**Metabolism:** The chemical changes that take place in an organism that turn nutrients into energy.

**Mobbing:** Cooperatively attacking or harassing a predator.

**Monogamy:** A mating system in which one male mates with one female.

**Multi-male, multi-female:** A group that consists of multiple adult males, multiple adult females, and their dependent offspring.

**Multi-male, single-female:** A group that consists of two or more adult males, one breeding female, their dependent offspring, and non-breeding females.

**Mutualistic/mutualism:** When different species work together, with each benefiting from the interaction.

**Niche:** The role of a species in its environment; how it meets its needs for food, shelter, etc.

**Nocturnal:** Active at night.

**Olfactory communication:** Conveying information through scent.

**Omnivores:** Organisms whose diet consists of plant and animal matter.

**Pair bond:** A strong, long-term relationship between two individuals.

**Parasite:** An organism that lives in or on another organism.

**Parental investment:** Any time or energy a parent devotes to the current offspring that enhances its survival (and eventual reproductive success) at the expense of the parent's ability to invest in the next offspring.

**Philopatric:** Remaining in the group of one's birth.

**Piloerection:** Raising one's hair or fur in an effort to look bigger.

**Polyandry:** A mating system in which multiple males mate with a single breeding female.

**Polygamy:** A mating system in which multiple males mate with multiple females.

**Polygyny:** A mating system in which one male mates with multiple females.

**Polyspecific association:** An association between two or more different species that involves behavioral changes in at least one of them to maintain the association.

**Primate community:** All primate species that occur in an area.

**Primatologist:** A scientist who studies primate behavior and/or ecology.

**Primateology:** The scientific field that studies primate behavior and/or ecology.

**Ranging behavior:** Refers to the way in which animals move about their environment.

**Receptive:** A term used to describe females who are ready for sexual reproduction (i.e., not pregnant or nursing).

**Reproductive success:** An individual's genetic contribution to future generations, often measured through the number of offspring produced.

**Reproductive suppression:** The prevention or inhibition of reproduction of healthy adults.

**Resident male:** Term that describes the male who lives with a group of females.

**Seed dispersal:** The process by which seeds move away from the plant that produced them in preparation for germination and becoming a new plant.

**Semantic communication:** The systematic use of signals to refer to objects in the environment.

**Sexual dimorphism:** When males and females of a species have different morphological traits.

**Sexual selection:** The selection for traits that increase mating success. This occurs via intersexual selection and intrasexual selection.

**Sexual swelling:** Area of the hindquarters that change in size, shape, and often color over the course of a female's reproductive cycle, reaching maximum size at ovulation. Occurs in many primate species that live in Africa and Asia.

**Sexually monomorphic:** When males and females of a species have similar morphological traits.

**Single-male, multi-female:** A group that consists of one adult male, multiple adult female, and their dependent offspring.

**Single-male, single-female:** A group that consists of one adult male, one adult female, and their dependent offspring.

**Social learning:** The idea that new behaviors can be acquired by observing and imitating others.

**Social system:** A way of describing the typical number of males and females of all age classes that live together.

**Social transmission:** Transfer of something from one individual to another; this can include parasites, information, or cultural traditions.

**Sociality:** The tendency to form social groups.

**Solitary:** Living alone.

**Species recognition:** The ability to differentiate conspecifics from members of other species.

**Subordinate:** Being of low rank.

**Tactile communication:** Conveying information through touch.

**Territory:** A home range whose boundary is defended from intrusion by conspecifics.

**Vertebrates:** The group of animals characterized by an internal spinal column or backbone. This includes fish, amphibians, reptiles, birds, and mammals.

**Vigilance:** Watchful behavior used to detect potential danger, usually in the form of predators or potential competitors.

**Visual communication:** Conveying information through signals that can be seen.

**Vocal communication:** Conveying information through signals that can be heard.

## About the Author



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Dr. Karin Enstam Jaffe has loved primates since she was five years old. As an undergraduate at U.C. San Diego, she participated in projects studying orangutans, langurs, and Mona monkeys. She earned her Ph.D. in Anthropology from U.C. Davis studying vervet and patas monkey antipredator behavior in Kenya. She has been a faculty member in the Anthropology Department at Sonoma State University since August 2002. A dedicated teacher-scholar, Dr. Jaffe has won several teaching, scholarship, and mentoring awards, including SSU's Excellence in Teaching Award, Educational Experience Enhancement Award, and the President's Excellence in Scholarship Award. In addition to teaching, she has led student research projects on behavioral enrichment involving ring-tailed lemurs, chimpanzees, and sun bears, as well as a study of the social network of hamadryas baboons at Oakland Zoo.

## For Further Exploration

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Primate Info Net is an information service of the National Primate Research Center at the University of Wisconsin, Madison. It includes Primate Factsheets, primate news and publications, a list of primate-related jobs, and an international directory of primatology, among other information.

Primate Specialist Group is a collection of scientists and conservationists who work in dozens of African, Asian, and Latin American nations to promote research on primate conservation.

Short videos of some primate behaviors discussed in this chapter:

- Watch vervet monkeys respond to different types of predators: BBC One. n.d. "Vervet Monkey's Escape Plans – Talk to the Animals: Episode 2 Preview." Accessed December 16, 2022. <https://www.youtube.com/watch?v=q8ZG8Dpc8mM>.
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- Watch (and listen to!) howler monkeys "roar": Science News. N.d. "Hear a Male Howler Monkey Roar." Accessed November 21, 2022. <https://www.youtube.com/watch?v=PYar0dkZ6v8>.
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