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Primates, Apes, and the Study of Chimpanzee Social Behavior

The mammalian order Primates includes roughly 500 species, most of which are found in the tropics.[1] As a group, primates are characterized by a constellation of traits that reflect adaptations to arboreal habitats, dietary flexibility, and extensive parental care. Not every trait is present in every species, and when they are present, most traits are expressed to varying degrees in different groups. Nevertheless, all primates possess most or all of the following:[2]

- Flexible and dexterous hands and feet, with flattened nails and sensitive tactile pads on the tips. All species except humans have opposable big toes, and most have opposable thumbs, permitting enhanced grasping ability with both the feet and hands.
- A generalized dentition, typically with four types of teeth, supporting the ability to process a wide range of foods.
- Excellent vision, including the ability to see color, which is absent in other placental mammals.[3]
- Comparatively large brains for their body size, with a longer period of infant and adolescent development, accompanied by an increased role for learning in acquiring social and technical skills.

The order is divided into two suborders, the Strepsirrhini and the Haplorrhini (Figure 1.1).[4] The strepsirrhines include the more "primitive" species, meaning those that appear to resemble most closely the earliest primate ancestors in body plan and, presumably, behavior.[5] Strepsirrhines have a well-developed sense of smell, eyes that are not completely forward facing and that lack a protective bony socket, and a characteristic form of locomotion called "vertical clinging and leaping."[6] A large percentage of strepsirrhines are small and nocturnal and do not form permanent social groups. Like many other mammals,

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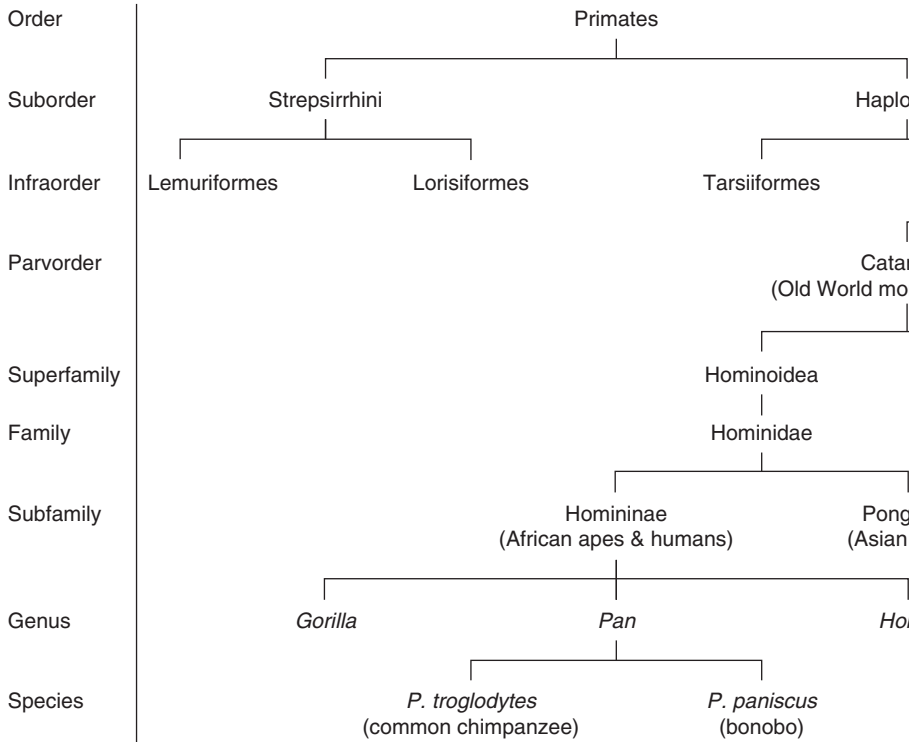

Fig. 1.1 Abbreviated taxonomy of the Primate order, showing the location of chimpanzees wi
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most strepsirrhines are seasonal breeders, with females remaining sexually receptive for narrowly limited periods of time each year.[7]

The haplorrhines include the monkeys, the apes, and humans. With the exception of the several owl monkey species (genus *Aotus*) in Central and South America, haplorrhines are diurnal. They rely greatly on sight, which is reflected in several morphological traits: Their eyes are more forward facing, enhancing depth perception (stereopsis), and are housed in bony sockets.[8] Additionally, their retinas are more sensitive, and they have a comparatively large area of brain cortex associated with visual processing.[9] Consistent with their greater reliance on sight, visual signaling plays an important role in haplorrhine social interactions. The majority of haplorrhines form permanent social groups with multiple adult females and at least one permanent male member. They also have relatively larger brains than strepsirrhines, associated in general with more complex social behavior.

THE APES (SUPERFAMILY HOMINOIDEA)

At the peak of their ecological success, during the Miocene epoch, scores of ape species existed throughout Asia, Europe, and Africa.[10] As a consequence of the gradual reduction in tropical forest cover caused by cooler temperatures and changing rainfall patterns worldwide, most of these apes went extinct by the end of the Miocene. Today only a handful of species remain, confined to dwindling tropical forests in southeast Asia and Africa. The Asian apes include twelve to fourteen species of gibbons (family Hylobatidae, the small-bodied "lesser apes") and two species of orangutans (*Pongo pygmaeus* and *P. abelii*, members of the "great apes," restricted to the islands of Borneo and Sumatra, respectively).[11] Four species of African great apes also survive: two species of gorillas (*Gorilla gorilla*, western gorillas, and *G. beringei*, eastern gorillas) and two species of chimpanzees (*Pan troglodytes*, the common chimpanzee, and *P. paniscus*, the bonobo).[12]

Current fossil and genetic evidence indicates that the last common ancestor of gibbons and the great apes lived roughly 16 to 18 million years ago (mya).[13] Among the great apes, the orangutans shared a common ancestor with the African apes 12 to 16 mya. The gorilla and chimpanzee lineages appear to have split 9 to 12 mya, while the last common ancestor of humans and the two chimpanzee species lived 6 to 9 mya. Common chimpanzees (hereafter referred to simply as "chimpanzees") and bonobos diverged after the split from the human lineage, around 1 mya.[14] The fossil record for the African

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apes is poor, and consequently it is unclear how much their lineages changed in appearance and behavior since these branching points. By contrast, many bipedal species evolved and disappeared over the past 5 million years, first in Africa and subsequently in Europe and Asia. Some fraction of these bipedal taxa were direct ancestors of modern humans.[15]

A number of general features distinguish the apes (and humans) from other primates. They lack tails as well as facial hair, the latter enhancing facial expressiveness and visual communication. Ape shoulder joints allow full rotation of the arms, an adaptation that enables them to hang or swing efficiently under branches – whereas monkeys primarily walk along the top surfaces of canopy branches to travel, apes frequently hang beneath branches and move arm over arm in a form of locomotion referred to as "brachiation" or "suspensory locomotion" (humans can employ a form of suspensory locomotion on "monkey bars," the horizontal ladder that is a standard feature on playground equipment). Apes have comparatively large brains and extended periods of development during which infants and juveniles acquire social and technical skills. In addition, their larger comparative brain size, and more specifically their enlarged frontal cortex, is associated with enhanced cognitive complexity compared with monkeys.[16]

The different ape genera also exhibit distinctive locomotor specializations. Gibbons are quintessential brachiators. They have comparatively long arms and fingers, short legs, and reduced thumbs, and with their small body size can swing exceptionally fast and acrobatically through the forest canopy. They commonly walk bipedally when they are on the ground. The large-bodied apes usually move more slowly through the canopy and generally walk quadrupedally on the ground to travel. Orangutans walk on the soles of their feet and on the backs of their hands, which are balled into fists (called "fist-walking"). The African apes also walk on the soles of their feet, but on the knuckles of their partly flexed hands ("knuckle-walking"; specifically, on the back surface of the middle phalanges or finger bones). Humans, of course, walk and run bipedally. Although with significant training we can become competent at climbing trees, our lack of an opposable big toe makes it impossible to attain the skill of an ape.[17]

Ape Diets and Daily Activity Patterns

Ripe fruits predominate in the diets of all apes, with the exception of mountain gorillas, for whom fruits are less readily available (Plate 1).[18]

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Leaves, flowers, seeds, pith, and even bark from a multitude of trees, shrubs, and herbaceous plants are also utilized – some populations of chimpanzees feed on more than 200 different plant species, although they rely on some types more than others.[19] Variability between populations within ape species in the percentage of the overall diet represented by fruits and other plant parts is linked to botanical diversity and productivity in different forest areas.[20] All apes consume insects to varying degrees, especially ants and termites. Meat eating is generally rare, except in chimpanzees, who are avid hunters and prey on a wide variety of mammal species (Chapter 9).

The timing of fruit production in tropical forests is variable, both within and between tree species.[21] Apes must therefore search continuously for ripe fruits, covering distances each day ranging from a few hundred meters to many kilometers (Chapter 4).[22] The area utilized by individuals over the course of a year, their "home range," varies widely depending on their nutritional requirements, habitat characteristics, and competition with group members and neighbors. Home ranges vary from as little as 0.2 km^2 in some gibbon groups to 50.0 km^2 for chimpanzees living in arid habitats. In gibbons and chimpanzees, a portion of the home range, referred to as a group's "territory," is aggressively defended (Chapter 8).

Bouts of travel and feeding that begin early in the morning are interspersed with periods of resting and, in group contexts, socializing on the ground or in the canopy. Members of all species end the day by choosing a new sleeping site. Gibbons, orangutans, and chimpanzees sleep high in trees, whereas gorillas sleep either low in trees or on the ground.[23] Adolescent and adult great apes build a new sleeping "nest" each evening prior to nightfall by bending and weaving branches together into a rough platform that can support their weight. Occasionally individuals also construct more makeshift nests to rest in during the day. Nests are rarely reused, and individuals do not share them to sleep together, with the exception of dependents and their mothers.[24] Individuals may wake and produce vocalizations from their nests but they rarely travel to new locations during the night.[25]

Ape Social Systems and the Mother–Infant Bond

The "social system" of a primate species has three quantifiable components.[26] First, "social organization" refers to the size, sexual composition, and cohesion of the groups in which individuals regularly associate. Second, patterns of individual social relationships, both

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within and between the sexes, represent the "social structure" of the group. Finally, the "mating system" refers to how many members of the opposite sex individuals typically copulate with. Four basic mating systems are recognized in primates: monogamy (one male and one female mate only with each other over the course of many years), polygyny (one male mates with many females, while the females only mate with that male), promiscuity (both males and females mate with multiple members of the opposite sex), and polyandry (one female mates with more than one male and the males only mate with that female).

The apes exhibit a range of social systems, and as with other primates, typical patterns can vary within species. Gibbons usually live in groups with one adult male, one adult female, and younger individuals, but some groups may temporarily include additional adults of either sex.[27] Although historically classified as monogamous, both male and female gibbons may seek matings with individuals in other groups, and both polygynous and polyandrous groups are occasionally observed. Orangutan social organization is referred to as "solitary," since adults do not associate in cohesive social groups, although a form of dispersed group structure may exist in some populations.[28] Dominant males mate polygynously, attempting to defend exclusive sexual access to several females whose home ranges lie within their own, while subordinate males roam widely. Gorilla groups contain several females and one or, less often, multiple males; temporary all-male groups also form, comprised of individuals who have not succeeded in forming a group with females.[29] Like dominant orangutan males, dominant gorilla males mate polygynously as a rule. Finally, chimpanzees and bonobos live in multi-female, multi-male groups ranging in size from 20 to roughly 200 individuals, and their mating system is promiscuous (Chapter 7).

Significant differences as well as similarities exist between the apes in patterns of social relationships within groups. The closest adult relationships in gibbons and gorillas, taxa in which both sexes typically disperse to breed, occur between males and females. In gibbon groups that contain an additional adult male or female, individuals of the same sex may be mutually tolerant and somewhat affiliative.[30] The adult females in gorilla groups are usually unrelated and are generally tolerant but indifferent to each other, focusing their social attention instead on the dominant male. This male provides protection from outsider males and predators, and intervenes in conflicts between females competing for resources. In multi-male gorilla groups, which often include

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sons that have not dispersed, male relationships are generally tense.[31] By contrast, the strongest adult bonds are formed among males in chimpanzees (Chapter 6) and among females in bonobos. In both of these species, it is females that disperse to breed in neighboring groups (Chapter 3).[32]

Yet despite these differences in adult patterns, the most consistently strong relationships in all ape species are between mother and offspring. Periods of infant and juvenile dependency lasting many years are characterized by high levels of physical proximity and contact, grooming, protection, and play (Chapter 5 and later in this chapter). The intensity and importance of the mother–offspring bond in chimpanzees, for example, is revealed when one of them dies: Mothers may carry a dead infant for weeks before finally relinquishing it, while even weaned juveniles may fail to thrive after the death of their mother.[33] Among chimpanzees and bonobos, species in which males remain for life in their natal group, enduring relationships between mothers and sons are common.[34] Analogous father–son relationships do not exist, since females mate with many males and fathers apparently cannot recognize their offspring (Chapter 7).

Triadic Awareness

The ability to maintain a variety of social relationships with known individuals within stable groups is characteristic of, but not unique to, group-living primates.[35] What is perhaps especially well developed among primates, however, is the ability to recognize the varied relationships of other individuals, and to interact with those individuals accordingly. For example, immediately following aggressive encounters with group mates, fight participants sometimes direct aggression at a third, uninvolved individual, a behavior known as "redirected aggression." In many monkey species in which females remain in the groups they are born into and form close, lifelong relationships with their female relatives, redirected aggression is often targeted at relatives of the aggressor's original opponent.[36] Male mountain gorillas intervene in conflicts between females without taking sides, perhaps in effect maintaining a protective role toward all and discouraging females from transferring out of their breeding groups.[37] And male chimpanzees are keenly aware of the relative dominance ranks of other males as they vie for coalition partners during dominance conflicts (Chapter 6).

In at least some monkey species, this so-called "triadic awareness"[38] appears to involve the ability to simultaneously classify group members

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according to both rank and membership in matrilines. It also includes classifying and tracking important temporary associations, such as between a male and an estrous female.[39] Whether chimpanzees and other social species characterized by "fission–fusion" social organization (see later) may have an even richer capacity for triadic awareness is unknown.[40] In any case, observations both in the wild and under experimental conditions suggest that increased comparative brain size and, by extension, intelligence in primates evolved because of the advantages individuals gained by being better able to navigate complex social landscapes.[41]

QUANTIFYING CHIMPANZEE SOCIAL BEHAVIOR TO ASSESS INDIVIDUAL RELATIONSHIPS

Social relationships are formed through the accumulation over time of behavioral interactions.[42] Researchers characterize social relationships by quantifying the relative frequency, duration, and intensity of "affiliative," "cooperative," and "agonistic" behaviors that individuals direct toward each other (roughly speaking, behaviors that are friendly, supportive, or associated with aggression and submission).[43] Individuals that interact peacefully with each other at especially high rates are described as being "socially bonded."[44] Socially bonded individuals, in turn, are often more likely to engage in mutually supportive behaviors. By contrast, agonistic interactions reflect conflicts of interest between individuals. Agonistic encounters form the basis of dominance relationships, which in turn generally determine access to contested resources. As described previously, patterns of individual social relationships then constitute the social structure of a species, which together with social organization and mating system comprise the species' social system (or "society").

Researchers typically begin field studies by observing, describing, and classifying social and other behaviors exhibited by their study animals. The resultant behavioral catalog is known as an "ethogram." Because primate social behaviors frequently seem familiar to us, the risk of attributing human motivations and intentions to them is high. Ethogram entries thus tend to be rather sterile descriptions of physical movements, in an effort to avoid anthropomorphic bias and improve consistency in data collection within and between study sites. For socially complex species such as chimpanzees, ethograms grow over time as new behaviors are observed, resulting ultimately in extensive behavioral records.[45] A relatively narrow group of behaviors within the

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ethogram are used to build a statistical picture of social relationships. Some of the key behaviors used to characterize chimpanzee relationships are described in the following sections.

Affiliative Behaviors

Spending Time Together

Chimpanzees forage, socialize, and rest in small, spatially separate subgroups within their community throughout the day. Membership in these subgroups changes over time, so that individuals may be in the company of different community members on different days or even at different times on the same day, a grouping pattern referred to as fission–fusion social organization (Chapter 3).[46] The amount of time two individuals spend near each other consequently represents an initial indicator of social bonding between them, on the premise that friendly individuals seek out each other's company. The Dyadic Association Index (DAI), which quantifies the proportion of total observation time that pairs of individuals are seen together, characterizes this aspect of relationships (Chapter 4, endnote 15). Additionally, DAIs are used to compare patterns of social attraction between different classes of individuals within chimpanzee communities.[47]

Measures of association, however, are only suggestive of social affinity, since mutual attraction to food sources or other community members can also bring individuals into proximity. To develop a more accurate picture of social relationships, researchers therefore rely on analyses of the frequency and duration of social grooming and the incidence of cooperative behaviors. These behaviors are overtly directed at particular individuals and can involve a significant commitment of time and energy, therefore implying a higher degree of social bonding.

Social Grooming

Social grooming is a tactile and highly visual behavior in which one individual closely scrutinizes and meticulously picks through the hair of another, removing debris and insects with their hands and/or mouth.[48] It is a pervasive feature of chimpanzee life and occurs in a wide range of contexts. The subjective impression reported by human observers is that grooming is pleasurable to chimpanzees, insofar as individuals being groomed appear relaxed and may allow

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groomers to manipulate their body parts in the process. Grooming sessions can last anywhere from a few minutes to two hours or more, representing a significant commitment of time that might otherwise be spent on feeding or resting.[49] Two isolated individuals may take turns grooming each other or groom each other simultaneously (referred to as "mutual grooming"). Groups of chimpanzees, sometimes ten or more, may groom in close proximity, often with several individuals grooming in a chain (A grooms B while B grooms C, etc.) or pairs of individuals grooming a third.

Results from studies in a variety of primate species, including chimpanzees, indicate that grooming is important socially. Individuals spend more time grooming in species that form larger groups, suggesting that it helps them navigate more complex social landscapes.[50] In contrast, individuals in large-bodied species do not groom more than those in small-bodied species, which would be expected if grooming merely served a hygienic function.[51] In some species, the likelihood of grooming increases when social relationships are unstable and after agonistic interactions, apparently helping to alleviate stress. This conclusion is supported by analyses showing that grooming reduces heart rates, circulating levels of glucocorticoid hormones, and behavioral indicators of stress (e.g., self-scratching).[52] Finally, grooming appears to play a key role in the formation and maintenance of social bonds, whether by simply promoting tolerance around more dominant and potentially aggressive individuals, or by strengthening cooperative relationships by reinforcing familiarity, trust, and predictability between partners.[53] The bond-maintenance effect of grooming is additionally supported by evidence that circulating levels of oxytocin, a hormone that elevates affiliative behavior in mammals, increase in socially bonded chimpanzees after they groom together.[54]

Social Play

Chimpanzees of all ages and both sexes play, although it is most common among juveniles and adolescents. Social play can take the form of a seemingly infinite variety of both vigorous and gentle behaviors, including chasing, grappling, tickling, "finger wrestling," sexual play, and play mothering.[55] Like social play in other animals, it is widely assumed to provide important opportunities to develop physical and social skills. However, since social play is rarely the focus of long-term research, no doubt in part because it is difficult to assess its

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