
The Evolving Female

A Life-History Perspective

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8 Natural History of Apes: Life-History Features in Females and Males

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LIFE HISTORY, as defined broadly in this volume, offers a comparative, functional, and evolutionary framework that reflects the complexities of individual female and male lives. I first recognized the mosaic nature of sex differences in the 1960s while studying fossil bones of our probable ancestors (the human family, hominids who lived 2 to 5 million years ago). Sex differences involve many biological levels: from the genetic base to the anatomy and physiology of the brain, bones, and teeth, body size, shape and composition, external features, and expressed behaviors. What does it "mean" to be a female? What does it "mean" to be a male? Sex differences are life-history features that reflect species-defined variation in the pattern and timing of growth, development, reproduction, and aging.

The study of sex differences has been a major focus in my research. How can we understand sex differences in humans, fossil hominids, and nonhuman primates? When I first asked this question in the 1960s, I was doing research on fossil hominids. I was attempting to sort and explain species variation from variation between males and females. I thought this would be an easy task, but as my research progressed, it became apparent that defining and explaining sex differences in fossil populations and, in addition, determining whether these differences increased or decreased during the course of human evolution, are problematic. Furthermore, explaining sex differences in living species is also difficult; most explanations generally are overly simplistic and rely too heavily on one or two traits. I now recognize that a life-history framework more accurately

clarifies female-male similarities and differences and how females as well as males survive and reproduce within the wider context of the species' adaptation.

I will briefly review the steps I took in coming to my current framework. The hominid fossil record is fragmentary, and it is difficult at best to distinguish variation that results from species differences from variation attributed to sex differences. The distinctions used by other researchers largely rest on canine size and estimates of body weight (e.g., Wolpoff 1975). With few complete bones of individuals and no way to draw a population sample (Morbeck chap. 9), it is not possible to establish body-weight ranges for presumed females and males within, or even between, species (Zihlman 1976, 1982, 1985). Even with sophisticated statistical techniques, most researchers accept that smaller teeth and bones are female, and larger, more robust ones, male. Other skeletal features are assumed to follow a similar size pattern.

Research on monkeys, apes, and humans also led me to conclude that sex differences are expressed as a mosaic and are species-specific. For example, body weights differ between female and male of both pygmy chimpanzees (*Pan paniscus*) and common chimpanzees (*P. troglodytes*). Yet, *P. paniscus* individuals show no sex differences in cranial capacity, limb bone length, or joint size, whereas *P. troglodytes* do (Cramer and Zihlman 1978; Zihlman and Cramer 1978). Because of the variation in differences within each species, I concluded that, even in closely related species, species-defined sex differences consist of a mosaic of features.

Body weight alone (or, for fossils, estimates of weight) cannot predict the *degree* of sex difference in other features *within* or *between* species.

Finally, my research led me to conclude that traditional explanations for sex differences in body size have little bearing on other differences between females and males (Zihlman 1981). Larger body size was first proposed by Darwin (1871) to give males an advantage in competing with other males for access to females. He proposed the mechanism of sexual selection to account for increases in male body size associated with the presumed variation among males in successful mating. Thus, sexual dimorphism in body size, often based on a single measurement (e.g., Alexander et al. 1979), usually is interpreted in terms of male-male competition, sexual selection, and mating patterns. In other words, in many species where males are twice the body size and weight of females (i.e., extremely sexually dimorphic for this feature), the males establish and maintain territories through fighting and breed with many females (e.g., see Reiter chap. 4). In species with little size difference, males may breed with only one female.

The functional meaning of body weight differs between species, among age classes, and between females and males. It is not a uniform feature (Grand 1977a,b, 1983, 1990). Linking body weight only to male-male competition (for which there are few direct measures [Fedigan 1992]) focuses exclusively on the mating behavior of males. This ignores female body weight as related to her behavior and, especially, reproduction. Consequently, sexual selection cannot account fully for variation in body-size differences within and between species (Ralls 1976, 1977). Finally, sexual dimorphism is not one invariant entity on which selection operates uniformly (Fedigan 1992).

My recent research continues to explore the mosaic nature of sex differences in human and nonhuman primates. Dozens of anatomical dissections of apes and intensive study of the skeletons of known chimpanzees combined with new observational data on free-ranging groups

allow me to begin to answer my original questions, What does it mean to be female, or to be male? (e.g., Morbeck and Zihlman 1988; Zihlman et al. 1990).

Humans are primates. Primates are mammals. Large-brained, long-lived animals like humans and other primates respond throughout their lifetimes by altering behavior. There is no simple or direct relationship between biological sex differences and differences in survival and lifetime reproductive outcomes. Long-term observations of free-ranging primates document reproductive outcomes of females (e.g., Fedigan et al. 1986; Altmann et al. 1988; Fedigan 1991), and time-allocation methods illuminate how females and males spend their time and energy over their lifetimes.¹ Whether females are ovulating, pregnant, or lactating influences the frequency of activities. Social group variables such as rank and social network, as well as environmental variables such as food availability, predators, and group size also affect behavior and, consequently, survival and reproductive outcome of females and males, each with their own life story.

To explore several dimensions of sex differences, this chapter incorporates case studies of gibbons and great apes, our closest living relatives, into a life-history perspective. Each "profile" looks at the species adaptation and female and male variation within it. A life-history framework means considering individual as well as species histories (Morbeck chap. 1) and helps to clarify and quantify female-male variations on a species theme. Because humans also are hominoids and have shared a long evolutionary history with the great apes, this framework also provides a way to broaden understanding of what it means to be women and men.

FEMALES AND MALES: PROFILES OF THE APES

Old World monkeys, apes, and humans share catarrhine primate features (Morbeck chap. 9) and are characterized by long, socially

complicated lives (Smuts chap. 5; Fedigan chap. 2; Hiraiwa-Hasegawa chap. 6; Pavelka chap. 7). Apes and humans, together referred to as hominoids, are variations on the catarrhine theme. In this chapter, I highlight gibbons (lesser apes) and orangutans, gorillas, and chimpanzees (great apes). Humans, in many ways, are another kind of ape, a large-brained, talking, two-legged ape. Lifeways and life cycles and some of the biological foundations of these life-history features of humans are emphasized in the following chapters (Parts IV, V).

In the following ape profiles, I describe for each species (1) a mosaic of anatomical and behavioral features; (2) the range of survival life-history features, that is, the daily (and seasonal) activities for each sex, such as locomotion and foraging, other social-maintenance behaviors, and mating and rearing offspring during their lifetimes. These case studies illustrate similarities and differences among the genera and between species, and female and male variation within species. The shared features of hominoid life history underlie the adaptations of apes as expressed in body weight, group composition, and ecology.

Shared Phylogeny

The evolutionary history of the apes and humans goes back some 20–25 million years when the hominoids diverged from the Old World monkeys (cercopithecoids) (Sarich and Cronin 1976). Hominoids have similarities in dentition, limb and body proportions, timing of growth and development, and most notably, trunk and upper limb specialization. Hominoids share a vertical orientation of the trunk; enhanced shoulder mobility through positioning of the large, well-developed clavicle on a broad chest; a stable elbow joint but with forearm rotation; wrist flexibility; and “finely tuned” grasping hands (Washburn 1951, 1968; Schultz 1968, 1969a). Human beings, compared to other hominoids, have relatively larger brains and longer life stages, as well as an

emphasis on hindlimbs related to bipedal locomotion (see Morbeck chap. 9; Zihlman chap. 13).

Life History Features

Time-based reproductive life-history characters for five species of hominoids (table 8.1) are more similar than one might predict given the wide variation in body size of lesser versus great apes. These similarities reflect the common evolutionary history of the hominoids. Gibbons are among the smallest catarrhine primates, and gorillas are the largest; they also show considerable variability in diet and habitat and in social organization. However, female body weights that range from 5 kg in gibbons to 85 kg in gorillas are not paralleled in gestation lengths (210 vs. 256 days). Among free-ranging populations, the small-bodied gibbons take 6 to 8 years to reach sexual maturity (Geissmann 1991), and age at first reproduction is about 9 years, close to the average for mountain gorillas (Watts 1990a). In contrast, a 7-kg monkey (*Macaca nemestrina*) has a gestation of 170 days and age at first reproduction at 4 years. The similarities in gestation lengths, ages at weaning, sexual maturity, and age at first reproduction reflect the shared evolutionary history of complex social and survival behavior and of anatomical features (such as a large brain) of the hominoids, despite extremes in body weight.

Each example reviews the main features of anatomy and behavior of free-ranging populations and integrates anatomical, functional, and behavioral features. This approach does not preferentially treat one anatomical feature, such as body weight, or one behavioral pattern, such as male-male competition or female care-taking of infants. Female-male differences are part of a total pattern that contributes to the reproductive success of each species and are more than the sum of single or unrelated characteristics. The mosaic of anatomical and behavioral differences illustrates, not only the shared way of life of females and males, but also

TABLE 8.1. Ape Life History

Species	Female Weight (kg)	Female/Male Weight (%)	Birth Weight (kg)	Female's Age at First Reproduction (years)	Gestation Length (days)	Age at Weaning (years)	Birth Interval (years)	Life Span (years)
Lar Gibbon <i>Hylobates lar</i>	6-7	92	0.4	9	210	3	3+	30+
Orangutan <i>Pongo pygmaeus</i>	40-50	45	1.5 (1.3-1.6)	12 (9-13)	260	6	8	40+
Gorilla <i>Gorilla gorilla</i>	80-90	51-55	2.0 (1.6-2.3)	10 (9-13)	256	4-5	4+	40+
Common chimpanzee <i>Pan troglodytes</i>	30-40	75-85	1.8 (1.4-2.4)	15 (11-23)	228	4-5	5+	40+
Pygmy chimpanzee <i>Pan paniscus</i>	30-35	75-80	1.3	13-15	230+	4-5	5+	40+

SOURCES: Data were compiled from information on free-ranging populations whenever possible: Schultz 1956; Willoughby 1978; Harcourt et al. 1980; Goodall 1986; Harvey et al. 1987; Kuroda 1989; Morbeck and Zihlman 1989; Galdikas and Wood 1990; Nishida et al. 1990; Geissman 1991; Kano 1992; Tutin 1994; Palombit 1995.

NOTE: The values given are the means. Numbers in parentheses are the reported ranges.

their divergence from each other, to a greater or lesser degree, into distinctive and separate lives.

Gibbons

The gibbons (*Hylobates*), including siamangs (sometimes designated as a separate genus *Symphalangus syndactylus*), comprise nine species (Marshall and Sujardito 1986) inhabiting the rain forests of Malaysia, islands of Malaysia, Indonesia, and the Indo-China mainland. The hylobatids diverged from other hominoids about 15-18 million years ago (Cronin et al. 1984). The species within the genus *Hylobates* share similarities in locomotion, feeding, and social life (Preuschoft et al. 1984). These highly arboreal apes, renowned for their spectacular "brachiating" abilities, rely on fruit as a major dietary item and feed effectively on terminal branches (Grand 1972). Their social groups, unusual among catarrhine primates, consist of one adult female, one adult male,

and several offspring. Females and males are similar in body size. Each group physically and vocally defends the boundaries of its small home range.

Anatomy

Most species of lesser apes weigh about 5 kg, although *H. hoolock* weigh slightly more (6-8 kg), and siamangs are twice as heavy (10-12 kg) (Schultz 1973; Willoughby 1978; Leighton 1987). Among wild shot lar gibbons, males tend to be slightly heavier than females (5.7 vs. 5.3 kg) so that females are 92% of male body weight. In trunk length, females are slightly longer, although the difference may not be significant (271 mm-269 mm) (Schultz 1944). In some species of gibbon, pelage differs in color between females and males.

Cranial capacity averages are similar within each sex (101 cc vs. 104 cc), although there is a considerable range (Schultz 1944). There is little sex difference in jaw morphology (Lucas 1981) or canine size and shape, though male

canines apparently are slightly longer than females in lar gibbons (Schultz 1944; Frisch 1973). In all hylobatids, both females and males have *pronounced* canine teeth. Among siamangs, both sexes have laryngeal sacs and vocally announce their presence and defend their territory.

In the limbs and trunk, a mosaic of differences is apparent. In lengths and proportions of limb bones, female gibbons are 99% of males, whereas female siamangs are 96% of males (Schultz 1973). However, in body proportions, male siamangs, and to a lesser extent male gibbons, have somewhat larger chest girth and shoulder breadth relative to females, but there is little difference in relative hip breadth (Schultz 1956, 1973).

The bones and teeth, although similar in size and shape, may nonetheless "record" relative proportion of trauma experienced by each sex. For example, in adult dentition, 41% of males compared to 20% of females had lost, severely damaged, or broken canines (Frisch 1973). Similarly, in a collection of 233 gibbon skeletons (*H. lar*), 37% of adult males, but only 28% of females showed healed fractures of the long bones (Schultz 1944). These differences in trauma apparently mirror differences in behavior of females and males during life.

Behavior

Young individuals, females without young, and males can be difficult to distinguish from anatomical features alone unless the observer manages a close look at the genitals. Sex differences in feeding and travel are not marked, although some do exist. In all species, females carry the young exclusively for at least the first year of life. In some species, adult females travel first in group progressions, which may give them first access to fruit. Among lar gibbons, a female in late pregnancy and in the early postpartum period becomes dominant to the male during feeding (Ellefson 1974). Among the larger-bodied and more folivorous siamangs, females feed faster than adult males and for about 30 minutes longer each day (Chivers 1977). Males participate very little in

direct infant care although male siamangs may carry the young in its second year (Chivers 1974), apparently as a result of the infant's initiative (Alberts 1987).

Both females and males are aggressive and intolerant of other adults of the same sex encountered in neighboring groups. As the young mature, they become peripheral in the family unit, then leave the natal group and establish their own territory. Both sexes play a role in defending their territory and in maintaining the integrity of the pair (Raemakers and Raemakers 1985). In intergroup interactions, however, males engage more often and for longer in calling and chasing than do females. For example, in encounters at territorial boundaries, lar gibbon males threaten and chase neighbors (Ellefson 1968). In conflicts between siamang groups, females hide while males chase each other (Chivers 1974). Males of *Hylobates agilis* spend 13% of their activity in territorial behavior and are the protagonists in territorial disputes 76% of the time, compared to the females' 10% (Gittins 1980). Female (*H. agilis*) gibbons apparently take a less active role than do males in territorial behavior when carrying a small infant. Moloch gibbon (*Hylobates moloch*) females engage in indirect aggression through vocalizations toward neighboring groups, but the males engage in direct aggression toward intruders that have entered the territory (Kappeler 1984).

Vocalizations

Field data document the importance of vocalizations in the overall adaptation of all gibbon species, both in their species-specificity and in sex differences (Marshall and Marshall 1976; Mitani 1992). As a social activity within and between groups, calling takes up about 4% of the activity period (Leighton 1987). Among gibbons and siamangs, as in other primate species, individual calls are recognizable to neighboring groups and thus provide information on age, sex, and number of individuals in the group. These calls also function to attract mates, to reinforce the group's female-male bond, to identify the caller's sex to neighbor-

ing groups, and to locate, define, and maintain territorial boundaries.

In most species, females and males vocalize together in duets and, except for hoolock gibbons, there are sex differences or sexual "divocalism" (Haimoff 1984). The "great call" produced by the females of all species is the most easily identified part of gibbon songs and appears to be neurologically programmed and strongly determined by inheritance (Brockelman and Schilling 1984). The frequency of calling differs among species, and within species differences may exist between females and males. For example, among Kloss's gibbons, males sing once every 2.5 days, whereas females sing once every 5 days (Tenaza 1976).

Orangutans

Today orangutans (*Pongo pygmaeus*) are found in rain forests that vary from hilly or mountainous areas to swampy lowlands of Borneo and Sumatra (Galdikas 1988) but remains from Pleistocene and Holocene times have been discovered in southern China, Vietnam, and Java (Groves 1986). Orangutans diverged from the African group some 9–11 million years ago (Cronin et al. 1984). They inhabit the forest canopy, rely on fruit as a main dietary item, and exploit these resources through their climbing, hanging, and reaching skills (Chevalier-Skolnikoff et al. 1982). Their prehensile hands and feet and extreme fore- and hindlimb joint mobility allow orangutans to be both large bodied and highly arboreal. In fact, they are the largest arboreal mammal, although orangutans have pronounced sex differences in body weight and proportions. Socially, they are unusual in their low level of association (except between mother and offspring) and lack of formal group organization (Galdikas 1979).

Anatomy

The features that distinguish females and males clearly demonstrate the mosaic nature of morphological variation (Morbeck and Zihlman 1988). In body weight, females average about 37 kg (range 31–45 kg), and males 80–

85 kg, although they may weigh more than 90 kg (Rodman 1984). Females are about 45% of male body weight, or stated another way, males weigh 223% of females. I use a ratio of male-female values to express differences. (Males can be interpreted as "built-on" the species plan [McCown 1982].) Orangutans differ in features other than adult body weight and canine tooth size, but until recently these features have not been emphasized in assessing sex differences (Morbeck and Zihlman 1988).

Substantial sex differences occur in skull dimensions (Schultz 1962), and brain and tooth size differ, but to a lesser degree than does their body weight. Brain weight in females, for example, is 84% of males (119% male/female, calculated from Willoughby 1978); consequently, females have a larger brain to body index compared to males (94.2 vs. 88.5). Canine length and breadth in males are 135% of females', whereas molar teeth are less than 10% larger, demonstrating a mosaic within the dentition itself (Schultz 1973; Oxnard et al. 1985; Morbeck and Zihlman 1988). In males, chewing muscles are twice as large relative to body weight as those in females (Morbeck and Zihlman 1988).

There are differences between females and males in several linear and volume dimensions of the trunk and limbs. In relative chest girth (chest circumference relative to trunk length), for example, males are 118% of females, but both sexes have similar hip breadth (Schultz 1956). Long bone lengths of males average 116% of females, and bone weights 210% of females. Females, on the other hand, have larger acetabular and femoral head joint surface areas relative to body weight than do males (Morbeck and Zihlman 1988).

Based on dissections of two animals, proportions of muscle, bone, and fat also differ between females and males. The female has less muscle tissue relative to body weight and more body fat than the male. Relative limb weights also differ. Forelimbs are similar (female: 16%; male 17% of total body weight) whereas hindlimbs differ (female 18%; male 12%) (Morbeck and Zihlman 1988).

Growth and Development

Sex differences are apparent in patterns and timing of growth and maturation. Among immature orangutans, significant sex differences appear in skull length, breadth, and height (Schultz 1941; Winkler 1987). Females achieve adult body weight about 10 years, males at 15 years (Fooden and Izor 1983). Females complete skeletal growth at 8 to 9 years but males continue until age 15. Similarly, the distinctive adult features of males—inflatable throat sac, prominent fatty cheek pads, and a fatty neck region (Schultz 1941; Rodman and Mitani 1987; Morbeck and Zihlman 1988)—are not completely developed until about 15 years of age. These features distinguish adult males visually and vocally from other age/sex classes (MacKinnon 1974; Galdikas 1979; Schurmann and van Hooff 1986). By about 10 years of age, female and male orangutans also have diverged behaviorally in daily and seasonal activities.

Behavior

Field observations suggest that sex differences in locomotion, feeding, and social behavior exist, although research at different study sites is not consistent in the extent or in the direction of the differences (e.g., Rodman 1977, 1988; Galdikas 1988). Some differences might be predicted based on body weight, whereas others are not.

To some extent, body weight correlates with mode of locomotion, use of the trees, and feeding postures. Adult females use “quadrumanous scrambling” as their most frequent mode of locomotion and hang more and sit less than do males (Sujardito 1982; Sujardito and van Hooff 1986; Cant 1987a, 1987b). Females and adolescents generally sleep and travel in the higher levels of the forest than do the males. Males engage more than twice as often in tree swaying to travel across branches to new trees and less travel by quadrumanous scrambling. In some areas, males, but not females, travel or feed on the forest floor, where leopards and pigs present a threat.

When females are carrying young, they travel more frequently in the lower canopy than do the adult males, apparently in response to the additional weight of the young that requires caution during locomotion. Females with infants have, no doubt, honed their arboreal skills to compensate for a changed center of mass. Although females with offspring travel in lower levels, they return to higher zones to rest and sleep, whereas males do not. The additional weight of offspring could account for females' relatively larger hip-joint surfaces.

During feeding, females hang under branches more frequently and use smaller branches, whereas males sit and stand on larger branches (Cant 1987b). Females pluck the food from branches, whereas males more often pull in branches to detach food using their long and strong arms and hands.

A 4-year study from Tanjung Puting, Central Borneo, documents diet, range, and activity with comparisons between females and males (Galdikas 1988). Here orangutans consume an estimated 400 food types, almost all found in the canopy. Fruit (mostly ripe) accounts for 61% of observed foraging time; other items include flowers, leaves, vines, and insects, and bark and sap of various trees. Diet varies with time of year. For example, in Galdikas's study, orangutans eat 51 species of bark. During 6 months of year they eat none, whereas in 1 month they feed on it 47% of the time.

Sex differences exist in proportions of resources in the diet and in ranging patterns. Females consume more food types per day than males (mean for females 9.6 food types; for males, 7.1) and spend more time eating bark and young leaves, whereas males spent more time eating termites mostly from the ground. In terms of activity pattern, adult females spend from 57%–68% each day foraging; males forage for 41%–65%.

Adult females with their dependent offspring occupy smaller (5–6 km²) and more stable home ranges than those of adult males. At Tanjung Puting, exact figures for adult male

ranges are not available because no adult male remained in the study area throughout the 4 years. Their movements indicate that male ranges encompass several adult females' home ranges (Galdikas 1979). Daily distance traveled is smaller for prime adult females than for prime adult males (females, 710 m; males 850 m). However, there are no differences in mean daily travel time because males travel faster than females.

Orangutan social life is shaped by a combination of a predominantly arboreal, frugivorous, and opportunistic diet, which entails large body size and monitoring and using seasonal foods from trees. Sociality is expressed as sustained proximity during traveling or resting and by mutual tolerance during feeding (Galdikas and Vasey 1992). Focal adult females spent 13.5 % of their time in social groups. They associate with all age and sex classes, with other adult females more often than with adolescent females and, depending on reproductive condition, with males (Galdikas 1984, 1985a). Day ranges increased considerably when adult females traveled together or contacted other units. The use of permanent resources such as bark enhanced the occurrence of social groupings among adult females; when sharing preferred foods, adult females ate fruits faster than when alone. During consortships, adult females had larger day ranges than usual, and males had shorter ones, suggesting each sex compromises to remain in consort (Galdikas 1988). Focal adolescent females were in groups 40.8% of the time over and above the time spent with their mothers.

Immature males are gregarious and participate in groups about 41% of time when observed as focal animals. Their sociality centers around females; they associate with them 86% of the time, versus 3% exclusively with other males (Galdikas 1985b).

Adult males are the most solitary of any age or sex class. They spend less than 2% of their time in contact with other individuals and only associate with females; nonconsorting adult males are, almost without exception, solitary

(Galdikas 1984, 1985ab). Their loud calls, which carry over long distances, distinguish them from other age and sex classes (Galdikas 1983). Playback experiments demonstrate that these long calls do not function in attracting mates but seem to regulate spacing between males through avoidance (Mitani 1985).

Adult males avoid each other, and males seem to be avoided by others (Galdikas 1979, 1981). Healed wounds on males indicate overt fighting occurs between them, and aggression can be severe in the presence of an adult female. Galdikas (1985b) suggested that direct aggression between males may be more prevalent than indicated by the violent incidents observed.

Male anatomy may enhance their presence and visibility: their inflatable throat sac emphasizes resonating vocalizations; the facial configuration of prominent fatty cheek pads serves as a visual signal denoting age and status. These features may serve to attract females, to repel other males, or to enable animals to choose whether to associate. Their large body size and canine size enable them to inflict serious wounds on other individuals.

Gorillas

Gorillas (*Gorilla gorilla*) inhabit the mature lowland tropical forests and swamps of West and Central Africa and the montane forests of Rwanda, Uganda, and eastern Zaire (Schaller 1963; Casimir 1975; Tutin and Fernandez 1985; Fay et al. 1989). Evolutionarily, after orangutans split off, gorillas shared a common ancestor with chimpanzees and humans before branching off some 6–8 million years ago (Miyamoto et al. 1988). Gorillas comprise three distinct populations or subspecies: *Gorilla gorilla beringei* (mountain), *G. g. graueri* (eastern lowland), and *G. g. gorilla* (western lowland) (Groves 1986). These large-bodied apes are generalized opportunists and feed on a diversity of foliage, fruits, and insects (Schaller 1963; Goodall 1977; Tutin and Fernandez 1988). Gorillas live and forage in cohesive

groups with several adult males, females, and young. Using their hominoid ability for climbing and reaching, they feed and sleep in the trees but also travel, feed, and sleep on the ground. When moving quadrupedally they knuckle-walk and bear weight on the mid-dorsum of flexed fingers.

Information differs according to subspecies, which is an added difficulty for assessing sex differences and life-history characters. On the one hand, information on anatomy and physiology (such as birth weights) and social behavior of captive animals derives almost exclusively from lowland gorillas (e.g., Willoughby 1978; Dixon 1981; Maple and Hoff 1982). On the other hand, knowledge about individual lives, social behavior, and organization among free-ranging populations comes almost exclusively from long-term studies on the mountain gorillas (*G. g. beringei*) in the Virunga Volcanos (e.g., Schaller 1963; Fossey 1983; Harcourt 1979; Stewart 1987; D. Watts 1990a; Tutin et al. 1991). Ongoing studies at Lopé, Gabon have yielded information on foraging profiles of free-ranging lowland gorillas (*G. g. gorilla*) and the sympatric chimpanzees (*Pan troglodytes*) (see, Tutin et al. 1991).

In contrast to the foraging profile of mountain gorillas, lowland gorillas frequently eat almost 100 species of fruit and regularly search for and consume several species of insects. Even silverback males climb trees up to 30 meters high in order to feed on fruit (Tutin and Fernandez 1985, 1992; Williamson et al. 1990). That gorillas eat so many species of insects and fruits came as somewhat of a surprise, because gorillas—based on the mountain gorilla data—were traditionally characterized as “folivorous.” These findings highlight the influence of the environment on diet, since gorillas seem to prefer fruit if it is available.

Anatomy

Adult females are half the body weight of adult males (Willoughby 1978; Groves 1986). In mountain gorillas, males average 190 kg; whereas females weigh an average of 100 kg and are 53% of male body weight (190% male/

female). Lowland gorilla males are 156 kg and females at 85 kg are 54% (calculated from Willoughby 1978).

A number of other features differ between the sexes, though to a lesser degree than does body weight, and serve once again to illustrate a mosaic pattern. For example, among western lowland gorillas, cranial capacity in females is 85% that of males (117% male/female), and brain/body weight index is 92 in females and 90 in males (Willoughby 1978). In dentition, degree of sex difference varies among tooth types. Male canine teeth are 60% larger than those of females, whereas molar teeth are only 6% larger than those of females (McCown 1982). Adult males are significantly larger than females in cranial dimensions and have more prominent sagittal and nuchal crests. On these crests, attach large temporal and nuchal muscles that move the large jaws and canine teeth.

The length of each of the long bones (humerus, radius, femur, tibia) in lowland females is 85% that of males (117% male/female). The greatest sex difference lies in the upper body, in chest, arm, and forearm girths (80% female/male). The least difference is in wrist and ankle girth (88% female/male), and 82% ratio in hips, thigh, and knee girths (calculated from dimensions on live lowland animals reported in Willoughby [1978]).

Fully mature males, called “silverbacks” because of the silver pelage on the dorsal part of their trunk, also possess a prominent “axillary organ” that is more well developed than in females. Large and numerous apocrine sweat glands are concentrated in the armpit and are responsible for the pungent odor of silverbacks (Ellis and Montagna 1962; Dixon 1981) that has been noted by field researchers (e.g., Fossey 1983).

Most female and male differences develop postnatally (Watts and Pusey 1993). At birth, body weight and girth are similar; at about 5 years of age, differences appear in body weight (80% female/male). Arm and leg length, which are less different in adults, diverge somewhat later, at about 7 years of age (based on measurements from captive lowland gorillas re-

ported in Willoughby [1978]). The size differences in the skull remain insignificant until the last stages of growth, when the canine teeth and third molars are fully developed (Schmid and Stratil 1986). Males acquire their silver pelage after age 12, about the time they reach adult size and weight.

Behavior

There is some information from field studies regarding sex differences in locomotion, foraging, and feeding among mountain gorillas at Karisoke, Rwanda. For free-ranging lowland gorillas in Gabon, there are fewer observations.

Sex differences in locomotion do exist, but they are not marked. For example, except for juveniles, females with or without infants climbed more frequently than other age and sex classes, and silverback males climbed the least (Schaller 1963). Females may travel more slowly in the final stages of pregnancy, and the group may slow down to accommodate them (Fossey 1983). Only adult females are reported to travel tripodally (Tuttle and Watts 1985); during an infant's first month of life, the female tightly supports it with one arm while using the other for locomotion (Schaller 1963; Fossey 1979). Silverbacks have the highest frequency of bipedal behavior because they beat their chests in displays (Tuttle and Watts 1985).

Observations on captive lowland gorillas tend to support the field data that females alter locomotor and social behavior during reproduction. During the first three months of pregnancy, these activities declined, remained low throughout pregnancy, and were more reliable indicators of pregnancy than physical appearance (Meder 1986).

In feeding and foraging, sex differences among Karisoke mountain gorillas are slight and less pronounced than those found in orangutans with a similar degree of difference in body weight. Absolute distance traveled per day tends to be short for mountain gorillas (D. Watts 1991b). Silverback males feed longer and spend less time moving than do females (Harcourt and Stewart 1984; Watts 1988). Between silverback males and adult fe-

males the difference in feeding time varies among females at different reproductive stages. Nonpregnant and nonlactating females fed for less time on average (53.2%) than pregnant or lactating females (55.8%) (D. Watts 1988). Although this difference among females is small, the direction of the difference is consistent across all vegetation zones. According to Watts (1988), this supports the interpretation that nutritional demands of reproduction may account for the small disparity in feeding behavior between females and males. Among lowland gorillas at Lopé, there is no indication of significant differences in locomotion or foraging profile, except that silverbacks eat insects at a slightly lower, but not significant, rate than other age-sex classes (Tutin and Fernandez 1992).

Gorillas live in relatively cohesive social groups of variable size, from about 6 to over 20 individuals; each group consists of at least 1 and up to 4 silverback males, 1 or 2 blackback males, several adult females, juveniles, and infants (Schaller 1963; Fossey 1972; Casimir 1975; Stewart 1981; Yamagiwa 1987; Tutin et al. 1992). Both female and males leave the natal group to form new groups and male silverbacks may be solitary (Stewart and Harcourt 1987; D. Watts 1990b, 1991b). Adult females in a group are usually not related. The cohesion of mountain gorilla groups seems to depend primarily on the relationship between the dominant silverback and the adult females rather than on the relationships among the females. Females and young animals tend to spend more time near the silverback than to any other adult (Harcourt 1979; Stewart and Harcourt 1987).

Among mountain gorillas, adult males have been observed to confront other male gorillas and females and infants in other groups, even injuring and killing them (Fossey 1983; D. Watts 1989). At the same time, adult males seem to contribute a great deal to group stability and cohesion. The use of bipedal display combined with vocalizations makes males effective sentries, watchful of movements of other gorilla groups, possibly predators, and

also humans. Leopards do attack gorillas (Schaller 1963; Tutin and Benirschke 1991; M. Remis pers. comm.), and males attempt to defend the group against perceived threats, whether other male gorillas, carnivores, or humans who seek to capture the young (Fossey 1983; Tutin and Fernandez 1988). Adult females and other group members also act to protect the young, though males seem to be first to confront danger.

Although mountain gorillas are generally silent, there are sex differences in types and frequency of vocalizations. The screaming roar, the clear hooting preceding the chest beat, and the staccato copulation call seem to be unique to adult male gorillas (Schaller 1963; Fossey 1972; Harcourt cited by Marler 1976). Female mountain gorillas apparently emit the largest variety of sounds of all age/sex classes, and the pant ho-ho-ho produced during displays may be peculiar to them alone (Schaller 1963). Male gorillas dominate in vocal output (Marler 1976). Whether similar differences hold for western lowland gorillas is not yet known.

Chimpanzees

Chimpanzees (*Pan*) are most relevant to humans because the two lineages shared a common ancestor after gorillas split about 6 million years. The chimpanzee-human divergence took place about 5 million years ago (Sibley and Ahlquist 1984; Miyamoto et al. 1988; Ueda et al. 1988; Hasegawa 1992). Chimpanzees comprise two species, *Pan paniscus* and *Pan troglodytes*; the two separated at 2 and 2.5 million years ago (Cronin et al. 1984).

Chimpanzees inhabit a wide range of habitats in Africa, from Senegal on the West African coast, across the northern part of the equatorial rainforest to the eastern part of Lake Tanganyika, a range that stretches some 6000 km (McGrew et al. 1981; Collins and McGrew 1988; Kano 1992). Chimpanzees are opportunistic omnivores and feed on numerous species of fruit, herbs, leaves, insects, and vertebrates (including other primates and mammals); they forage in the trees and on the ground, and like

gorillas, bear weight on their knuckles when walking quadrupedally. Chimpanzees live in communities of about 50 individuals with remarkable tolerance among males compared to other hominoids (Nishida and Hiraiwa-Hasegawa 1987). Within the community, daily group size consists of "parties" that vary in size and composition. Their social system is described as "fission-fusion" and contrasts with the more stable and relatively cohesive gorilla groups.

Prominent genitals distinguish adult male chimpanzees, unlike gibbons and gorillas. Females have pink sex skin that swells during estrus. Although the two species overlap in overall body weight, surprisingly, they differ in the degree of sex difference in other features. For this reason, each species will be treated separately.

Pan troglodytes

Pan troglodytes comprises three subspecies: *P. t. schweinfurthii* in the easternmost part of the range in Tanzania, *P. t. verus* in central Africa, and *P. t. troglodytes* in the western range. The habitats are diverse, ranging in altitude up to 3000 meters, and in climate from high humidity and annual rainfall to more arid habitats. Long-term studies of free-ranging populations continue at several localities including (1) Gombe since 1960 by Goodall and colleagues (Goodall 1986); (2) Mahale Mountains in Tanzania since 1965 by Nishida and colleagues (Nishida 1990); and (3) the Tai Forest, Ivory Coast since 1980 by C. Boesch and H. Boesch (1989). These studies document variation between populations in habitat, diet, group size, social behavior, and tool using (Collins and McGrew 1988; Boesch and Boesch 1990; Nishida 1990; McGrew 1992), as well as the variation that occurs within populations between females and males and is emphasized here.

Anatomy

Overall, sex differences vary from moderate to slight. In body weight, females are similar to

female orangutans and range from 25 to 45 kg; males range from 40 kg to considerably more than 50 kg. The Gombe population is the lightest, where females average 30 kg, and males, 40 kg (Morbeck and Zihlman 1989). In other populations, individuals are, on average, heavier (e.g., Mahale: females, 42 kg; males, 48 kg; Uehara and Nishida 1987). In body weight then, female weight is usually between 75% and 85% of male body weight (or 133–134% male/female).

In a Zaire skeletal series, male cranial capacity averages 404 cc, and females 375 cc (males 108% of females), and some skull dimensions are larger in males (Cramer 1977). Male canines are larger, but there is little difference in postcanine tooth area (Kinzey 1984; Oxnard et al. 1985).

Details of the postcranial skeleton also differ, but only minimally. For example, in the Gombe population, long bone lengths of females and males are relatively similar, whereas in aggregated populations, males have longer limb lengths, on average and larger joint diameters (Schultz 1969b; Zihlman 1976; Zihlman and Cramer 1978). Females have a wider pelvic outlet than males and a wider pelvis relative to thigh length (Kerley 1966). The pubis is longer, on average in females (Morbeck et al. 1992). Males have a larger average chest circumference and longer clavicles (Schultz 1956; Zihlman and Cramer 1978).

Females and males in captivity exhibit an adolescent growth period with the female spurt occurring earlier (E. Watts 1985a). Behavioral differences are not marked before adulthood, but some sex differences are observed in ant-eating behavior, daytime bed-making behavior, and greeting (Hiraiwa-Hasegawa 1989; chap. 6).

Behavior

Sex differences exist in daily travel and range. Females have shorter daily ranges than males at Mahale (Hasegawa 1990), in the Tai Forest (Doran 1989), and at Gombe (Wrangham and Smuts 1980). Females in estrus have longer daily ranges than females in late stages

of pregnancy, and for a few weeks after giving birth; females with young have smaller ranges than do cycling females (Goodall 1986; Hasegawa 1990). These sex differences in travel suggest that females' energy budgets vary during their reproductive cycle. The greater amount of solitary foraging by females at Gombe has been interpreted as a strategy to reduce competition for food but could also relate to reducing time (and energy) spent in social interaction with other than immediate family members (e.g., Altmann 1980; Dunbar and Dunbar 1988).

Among Tai chimpanzees, average daily range differs between adult females and males, although they do not differ in frequencies of overall locomotor activities (Doran 1989). During feeding, however, females are more quadrupedal, whereas males climb and scramble more and are more bipedal than females (Doran 1989).

Sex differences have not been reported for locomotor mode as for orangutans and, to a small degree, for gorillas. However, the contribution of effective locomotion to raising offspring is illustrated by two adult Gombe females afflicted with poliomyelitis that partially immobilized muscles of the wrist or arm. This affliction inhibited the mothers' ability to move tripedally in order to give added support to newborns, to forage and feed effectively, and to protect offspring adequately. No offspring of these mothers survived beyond a few months or a year, and their mothers' locomotor disabilities must have been a contributing factor (Zihlman et al. 1990; Morbeck et al. 1991).

In composition of diet, food processing, tool using, and predatory behavior, some differences between females and males have been documented from long-term studies. For example, females are more insectivorous at Mahale (Uehara 1986). At Gombe, chimpanzee females engage more frequently and for longer periods in using implements to extract termites hidden in mounds throughout the year (McGrew 1979; McGrew et al. 1981; Goodall 1986). Among Tai Forest chimpanzees,

females use stone and wooden hammers to crack open nuts with more efficiency and with greater frequency than do males (Boesch and Boesch 1981, 1984). Females are active in catching prey; at Mahale, females engage in predation more frequently than do females at Gombe and take different prey (e.g., Takahata et al. 1984; Goodall 1986). But in both populations as well as in the Tai Forest (Boesch and Boesch 1989; Uehara et al. 1992), males engage in predatory activity more frequently than do females.

Social relationships between females and males differ to varying degrees among populations. Adolescent or cycling females change communities, whereas females with young tend to be more solitary and associate less with each other than do males (e.g., Wrangham and Smuts 1980; Wrangham et al. 1992; Nishida 1989). However, among Tai Forest chimpanzees, unrelated females form alliances and share food to a greater extent than do females in other populations. Boesch (1991a) attributed the more cohesive and mixed associations of the Tai chimpanzee social system to ecology and to the demonstrated predator pressure from leopards.

Males engage in aggressive displays (Kuroda 1980; Nishida and Hiraiwa-Hasegawa 1987; Kano 1992). Sex differences are apparent in affiliation; males associate closely and travel together to patrol the territorial boundaries of the community.

In vocal communication, there are no sex differences comparable to those of other hominoids; the basic categories of all chimpanzee vocalizations are uttered by both sexes (Marler 1976). However, gestural communication involving greeting behavior does differ between females and males (Goodall 1986; de Waal 1989). At Mahale, sex differences in greeting behavior appear early in development (Hiraiwa-Hasegawa 1989; chap. 6). Males attack more than females and consequently have more ways to deal with aggression. Attacks by males are more often followed by reassurance toward the victim than are attacks by females (Goodall 1986; de Waal 1989).

Pan paniscus

Pygmy chimpanzees (*Pan paniscus*) inhabit the rain forest in a small region of Central Africa in the Zaire River Basin and have been studied at four localities (Uehara 1990; Kano 1992). Two field sites have sustained studies since the 1970s, at Wamba (e.g., Kuroda 1980; Furuichi 1989; Kano 1992) and at Lomako (Susman 1984; Thompson-Handler et al. 1984). Some differences may exist in social organization between the two sites. Nonetheless, because of their fewer numbers and their more limited geographical distribution, *P. paniscus* is less well known in behavior and anatomy than *P. troglodytes*.

The term "pygmy" was initially applied to the small cranial, facial, and dental features of *P. paniscus* before research on its postcranial anatomy and body weight (e.g., Coolidge 1933). Later studies demonstrated that *P. paniscus* and *P. troglodytes* are distinguished by body proportions (e.g., humerus/femur and intermembral indices) but not body weight, which overlaps a great deal in the two species (e.g., Zihlman and Cramer 1978; Morbeck and Zihlman 1989). Species distinction has been demonstrated in DNA and proteins with estimated divergence time of 2–2.5 million years (Cronin and Sarich 1976). Distinguishing species' features in social behavior of *P. paniscus* include the strong relationships that develop between unrelated females, the low level of agonistic and intimidation behavior of males, more elaborate sexual behavior, and distinct vocalizations (e.g., Mori 1984; Furuichi 1989; Idani 1991; White and Wrangham 1988; de Waal 1989)

Anatomy

Based on small samples, body weight ranges from 27 to 38.5 kg for females and 38 to 61 kg for males; females average 33 kg and males 45 kg (reviewed in Morbeck and Zihlman 1989). Females are 73% of male body weight, close to that of Gombe chimps. Canine teeth are relatively small in both sexes, though canine lengths and breadths show some discern-

ible sex difference. No significant difference occurs in postcanine dentition (Johanson 1974; Kinzey 1984). In spite of a fairly significant sex difference in body weight, there is no difference in cranial capacity, cranio-facial dimensions, limb bone lengths, and joint sizes (Cramer 1977; Cramer and Zihlman 1978).

Behavior

At present there is little indication of notable sex differences in travel, foraging, and ranging at Lomako or Wamba. During travel, males climb, scramble, and leap more frequently than females, and females use more quadrupedalism than males (Doran 1989). Tool use has not been documented from any population, and there are only a few reports of predation, mostly on flying squirrels (Inhobe 1992). Because social groups are most frequently mixed age-sex classes (Kano 1980, 1982; Kuroda 1980), sex differences in foraging or ranging would therefore not be expected.

In social behavior as in anatomical features, few sex differences stand out. Rates of aggression are low for both sexes, and males do not engage in the types of aggressive displays characteristic of *Pan troglodytes*. The small canine teeth of both sexes and especially those of males, and the associated musculature, are consistent with the behavioral findings. Food sharing is widespread, and both sexes share (Kuroda 1984). A distinctive feature of this species is that females tolerate feeding close together. They actively bond and interact in grooming and food sharing and engage in genital-genital rubbing, an expression of greeting and friendly behavior (Thompson-Handler et al. 1984; Furuchi 1989; Idani 1991). High levels of affiliation also exist between females and males but not among males.

The Apes in Review

Hylobatids, comprising gibbons and siamangs, are small-bodied, fruit-eating apes living in groups of one male, one female, and their young. Few if any significant sex differences exist within each species in anatomical

features such as weight, proportions, and skeletal, and dental dimensions. However, field observations indicate slight sex differences in activities including (1) calling, (2) relative engagement in territorial behavior, (3) duration of feeding time at different reproductive stages, and (4) engagement in aggression as reflected in behavioral accounts and supported by findings on damaged canine teeth and broken bones. The slight differences in trunk proportions noted by Schultz may relate to the female's role in carrying additional weight during pregnancy and while carrying a nursing infant.

These minor differences in anatomy and behavior emerge by adulthood. They are important in the lives of the animals and suggest that females adjust their activities to accommodate pregnancy, lactation, and carrying offspring in addition to self-maintenance. At the same time, females also contribute to defense of the territory and its resources. They do so while expending less energy than the males. Male care of infants is rarely direct. However, a continuous male presence in the group indirectly contributes to the survival of the young through territorial defense and promotion of group integrity.

In the large-bodied, fruit-eating, opportunistic, highly arboreal orangutans, the sexes diverge considerably in a number of anatomical features, such as body weight and proportions, skull dimensions, canine tooth size, facial cheek pads, and to a lesser degree, molar tooth size, limb length, and joint sizes. Because their diet depends a great deal on fruit that is dispersed throughout the forest canopy, adults must forage independently. Females and their young associate with each other, though other social interactions are infrequent. Adult females interact more frequently than do adult males. Females and males become less social as they pass adolescence. Consequently, adult females and males live most of their lives independent from each other.

Compared to other species of apes, orangutan females and males differ to the greatest extent from each other anatomically and in their individual life histories. Anatomical differences

relate in both general and specific ways to everyday survival behaviors (e.g., locomotion and feeding), to social interaction including mating, and to females' caretaking of offspring.

The large-bodied gorillas consume foliage, fruit, and insects, feed and sleep in trees or on the ground, and travel exclusively on the ground. Gorillas live in relatively cohesive groups, usually with several adult males, adult females, and young. Sex differences in body weight are marked; differences in cranial capacity, limb bone lengths and girths are less pronounced. There are not marked differences in foraging profile and locomotion. The main sex differences in displays and vocalizations (and canine teeth) seem to relate to the aggressive protective function of the males toward other group members, a pattern distinctive in anatomy and behavior from orangutans.

Pan troglodytes is a moderate-sized omnivore that forages on a wide range of plant and animal species, using tools to exploit them, in communities of changing party size. Sex differences in anatomy are moderate in some features (body weight, canine size) and slight in others (cranial capacity, postcanine dentition, limb length, joint size). Overall, the mosaic of anatomical features is distinctive in *P. troglodytes* compared to other living hominoids and to *P. paniscus*.

The society is hierarchical, where adult males are generally dominant over adult females, and are aggressive to females and young and to each other, but the aggression is mitigated through communication. Females may travel to neighboring communities to mate and return or to stay; they tend to be less social than males and, with their offspring, range less widely. Females are more insectivorous, and males engage more often in predatory behavior. Females and males in all populations use implements of organic materials or stone to exploit a range of insect species and kinds of nuts. Sex differences are observed in frequency and skill level. These behaviors no doubt reflect possible dietary differences and emerge during adolescence. These differences seem to have

little to do with anatomical features per se and instead seem to be influenced by resource availability, predator pressure, learning and practice, social patterns, and individual bioenergetics.

Pan paniscus, like *P. troglodytes*, forages on a wide range of plant and animal species and lives in communities of changing party size. Tool use among free-ranging animals is rare, and predatory behavior infrequent. The society is nonhierarchical, and males do not dominate females. The most obvious sex differences observed are in social behavior, in the close bonding of nonrelated females, and in the close bonding of adult males with their mothers and not with other males. Ongoing research on this species offers future possibilities for delineating in more detail possible sex differences in anatomy and behavior.

LESSONS FROM THE APES

Taken together, the apes illustrate several points. Sex differences within species comprise a mosaic of features in anatomy, growth and development, and behavior. The study of whole animals and whole lives in a social and environmental context more clearly highlights the ways the two sexes diverge or converge in order to survive and reproduce, than if a single trait (body size or canine size) or a single behavior (mating or fighting) is used. There is no simple correlation between anatomy and behavioral expression, within or between species. In comparing sex differences (e.g., body weight difference) across species, the ecological setting and adaptation of the species are important variables.

Of the apes, female and male gibbons diverge least in their life pathways. Although they differ little in body size and proportions, the sexes differ in frequency of damaged or broken canines. Except for distinct vocalizations, only direct study of the animals' lives reveals that behavioral variation is not pronounced.

Both species of chimpanzees exhibit moderate sex differences in body weight; however,

the two species express different patterns of female and male features of canine teeth, cranial capacity, and limb bone lengths.

In *Pan paniscus*, sex differences are most pronounced in social interactions. Females apparently take priority during feeding, and even unrelated females bond with each other. Bonds between females and males are strong. Males maintain strong bonds with their mothers into adulthood, but bonds between males, even brothers, are very weak. The small canine teeth of both females and males may reflect the overall sociable relationships among various age/sex classes.

Female and male *P. troglodytes* diverge more than do female and male *P. paniscus* in canine size, cranial capacity, and limb bone length and joint size. Some of the species differences, such as canine size, may be due to the greater habitat variability of *P. troglodytes*, and more time spent on the ground, with the consequently greater risk of predation. It is also possible that *P. troglodytes* males must guard the territory and resources (food and females) from other community males. This could account for the pronounced aggression as well as the affiliation between males, and somewhat less intense bonds among females whose travel and foraging patterns differ from those of males. Females and males differ in tool-using behaviors that would not have been predicted on the basis of anatomy nor discovered without long-term field studies.

Among orangutans and gorillas, the feature that has received the most attention is the much larger body size and weight of adult males. To explain large male body size, the mechanism of sexual selection, which presumes male-male competition and differential mating success of males, is most frequently invoked (e.g., Rodman and Mitani 1987). The problem here is that sexual selection overemphasizes the significance of male body size and underemphasizes female body size. The significant body-weight difference between the sexes in orangutans and gorillas must be considered from two points of view: (1) constraints on female body

weight, and (2) advantages for larger-bodied males.

Orangutan females and males live most of their adult lives separate from each other and are distinct in anatomy, as well as in foraging, locomotion, and social behavior. For mountain gorillas, on the other hand, in spite of the large difference in body weight, females and males do not diverge as much in diet and foraging, travel, and range size as do the chimpanzees and diverge considerably less than do orangutan females and males.

In orangutans, female body size (within the chimpanzee range) is probably constrained by the demands of gestation and lactation in a highly arboreal habitat and in associating with juvenile offspring. Females forage for seasonal foods and travel with infant and juvenile offspring through the forest canopy, which requires locomotor skill, time, and energy. Maintaining small body size might help reduce energy requirements and minimize potential feeding competition between females and juveniles. Furthermore, most of the time, adult females forage independently from other adult females and males.

The larger body size of orangutan males may have fewer constraints and may be advantageous in several ways. In spite of their large body size, adult males retain arboreal skills and do so because of their extreme hominoid features—large, heavy, and well-muscled hands and feet, long upper limbs, and mobile limb joints (Zihlman 1992). Larger body size permits greater fat storage in the cheek and neck regions that may cushion against seasonally reduced food abundance or variable quality. (In turn, these features combined with vocalizations distinguish adult males from other age/sex classes). Their large size also permits relative safety during occasional terrestrial travel and makes possible a larger seasonal home range that provides increased resources and greater opportunities for finding and mating with females. Finally, large size may be advantageous for aggressive encounters with other males.

Thus, the variation between adult female and male orangutans is an expression of *both sexes'* living within the constraints of being a highly arboreal, frugivorous, large-brained, large-bodied hominoid, with a long period of infant dependency.

In contrast, among mountain gorillas, terrestrial travel and foraging combined with a somewhat folivorous diet allow females to become large. From the point of view of females, it may be desirable to have at least one and preferably more adult males available in the group for mating, for promoting group stability, and for protecting resources and infants from other males and from outside threats. Unlike adult male orangutans, adult male gorillas can live together in the presence of adult females in spite of their large body size and potentially lethal aggression. Therefore, the presence of several males may increase reproductive outcome for both females and males, as it does for cebus monkeys, which live in groups larger than 15 (Robinson 1988a).

This comparison between orangutans and gorillas highlights the overriding *species' adaptation*, within which the pattern of sex differences is expressed. Given the larger absolute body weights of female and male gorillas versus those of orangutans, one might expect an even greater degree of difference between the sexes in gorillas than in orangutans. Perhaps there is less difference than expected because of social interactions, divergent environments, and the distribution of resources.

Two factors relate to species' adaptation and may influence sex differences. The first is terrestriality. Female gorillas travel primarily on the ground, which imposes fewer constraints on gorilla body size, in contrast to female orangutans who, with dependent offspring, travel exclusively through the forest canopy. Furthermore, given the terrestriality of gorillas and the potential danger of dwelling on the ground, large size may be advantageous for both sexes.

Second, female and male gorillas of both species have a somewhat more folivorous diet than orangutans or chimpanzees. Gorillas forage on or near the ground on herbaceous and

leafy foods that are more available and more evenly distributed than fruit and require less travel between food patches. Even when eating fruit, lowland gorillas (Tutin et al. 1991) do not travel through the forest canopy, but on the ground, ascending and then descending trees. This feeding and foraging pattern allows several gorilla females and their juvenile offspring and mature males to remain together with minimal competition.

Male gorillas also experience few constraints on body size. In fact, large size may be a distinct advantage. Males, the first to meet danger, provide formidable threat vocalizations and displays to protect other group members from aggression by other male gorillas or attacks by predators. Fighting abilities of male gorillas may be enhanced by their large size, but it does not necessarily follow that sexual selection alone can account for large body size of male and female gorillas.

For both orangutans and gorillas, the mechanism of sexual selection and emphasis on male-male competition and differential mating success of males, although perhaps one element, offers only a limited way of looking at body size and other features. Explaining female body size is also a consideration. Within the life-history perspective, it is apparent that body size and weight may be more or less constrained depending on the species' way of life and how each sex accommodates to it. For instance, because of exclusively arboreal travel, the necessity of carrying dependent offspring, and a diet of mainly ripe fruits, female orangutans must be constrained in body size. Female gorillas, in contrast, given their more terrestrial traveling and foraging over short daily ranges and a relatively folivorous diet, are less constrained. Male gorillas appear even less constrained in body size than females—or male orangutans—and for similar reasons. For male orangutans, perhaps their adaptation *is* a large body size that gives them greater flexibility in dietary composition and foraging, larger home-range size, and body proportions that contribute to their locomotor abilities for arboreal travel.

SUMMARY

Hominoid sex differences in anatomy and behavior range from minimal to extreme. Too often sex differences have been dealt with simplistically (only body weight, body size, or canine size) with the male as the standard; too much attention has been focused on mating and too little on the entire life.

Behavioral studies on free-ranging apes significantly document the relationship between anatomical and behavioral features. To underscore this point, note that female and male gorillas are more similar to each other in how they live their lives than might be expected given the large body-size difference. Conversely, among chimpanzees (*Pan troglodytes*), behavioral variation between females and males (e.g., tool use, predatory behavior) perhaps is greater than would be expected given the moderate or minimal differences in anatomical features.

A life-history framework takes into account the species (or genus) adaptation and therefore goes beyond body weight or canine tooth size, and beyond form and function, to consider sex differences in the context of what each sex has to do to survive and reproduce throughout the life course. The integration of survival with reproductive life-history characters gives a more complete picture of adaptation and possible mechanisms of evolutionary change. It offers a wider framework for interpreting sex differences during early and recent hominid evolution (Zihlman 1993; chap. 13; Morbeck chap. 1; Borgognini Tarli and Repetto chap. 14).

In reproductive life-history features, as illustrated in table 8.1, the hominoids share more

similarities than is expected given their divergent body weights. Consequently, the function or evolutionary significance of body size between females and males and between species do not lend themselves to simplistic explanations because body weight can account for only part of the variation.

The perspective presented here highlights the behavioral flexibility that is part of the life-history profile of catarrhine primates and its contribution to survival in each species. This flexibility, especially as expressed in females, emerges during an individual's life. The long period of development and late sexual maturity is beneficial to both females and males. At the same time, this long period of individual experience before sexual maturity allows for the variation expressed during adult lives, and finding simple correlations or causal relationships between anatomy and behavior is more difficult.

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Note

1. Time-allocation studies assist in indirectly assessing energy budgets and recognize that energetic output cannot be accurately measured directly (e.g., Coehlo 1974, 1986; Altmann 1980; Bernstein and Williams 1986; also see Panter-Brick chap. 17).