

The genus *Gorilla* and gorillas in the wild

A contribution to the EEP Gorilla Husbandry Guidelines

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Taxonomy

The closest relatives of the gorillas (genus *Gorilla*) are chimpanzees (*Pan*) and humans (*Homo*). Both have about the same genetic distance to the gorillas and therefore *Gorilla* and *Pan/Homo* are sister clades. The nuclear DNA differs by 1.2% between humans and chimpanzees, by 1.6% between humans and gorillas and by 1.8% between gorillas and chimpanzees. In mitochondrial DNA, it is 8.8% between humans and chimpanzees, 10.3% between humans and gorillas and 10.6% between chimpanzees and gorillas (Hayasaka et al. 1988; Koop et al. 1989). In Groves (2001) the great apes are classified as the family Hominidae and the African apes + humans into the subfamily Homininae.

The first detailed study on gorilla taxonomy was published by Groves in 1970. He classified all gorillas as one species, *Gorilla gorilla*, with three subspecies (*Gorilla gorilla gorilla*, *Gorilla gorilla beringei* and *Gorilla gorilla graueri*). Genetic studies by Ruvolo et al. (1994) and Garner & Ryder (1996) showed considerable genetic differences between eastern and western gorillas and the authors suggested that they should be separated as two distinct species. A few years ago, experts therefore decided to recognize two gorilla species (Groves 2003): western gorillas (*Gorilla gorilla*) and eastern gorillas (*Gorilla beringei*).

The 2003 IUCN Red List of Endangered Species distinguishes four subspecies. The western lowland gorilla occurs in West Africa (*Gorilla gorilla gorilla*), the Cross River gorilla (*Gorilla gorilla diehli*) at the Nigerian/Cameroonian border; the mountain gorilla (*Gorilla beringei beringei*) lives on the Virunga Volcanoes and in the Bwindi Forest and Grauer's gorilla or the eastern lowland gorilla (*Gorilla beringei graueri*) in the eastern Democratic Republic of Congo.

Externally, the species differ in several characteristics. The nose of the western gorillas is much broader than in the eastern populations. The silvery back of adult males extends to hips and upper thighs in the western gorillas. While the hair of the eastern species is usually deep black (apart from the silvery back of the males), the western gorillas' hair can have a grey or brownish tinge in both males and females. The mountain gorillas of the Virungas have shorter arms than the other populations and very long, silky hair, mainly on the arms.

Morphological features and distinguishing characteristics

Gorillas are the largest living primates. Adult males and females show a very obvious sex difference in size and external features. Upright, gorilla males can reach 1.7 m on average. Western gorillas are the shortest subspecies with an average height of less than 1.7 m; eastern lowland or Grauer's gorillas are the tallest subspecies with a height of 1.75 m or more (Meder 1993).

Male western gorillas have a mean weight of 140–160 kg in the wild, male mountain gorillas 150–160 kg and male Grauer's gorillas 160–180 kg. Free-ranging gorillas weighing more than 200 kg are rare. Females usually weigh between 70 and 110 kg (Meder 1993).

The most striking characteristic of gorilla males is the so-called silverback. The silvery appearance is caused by short, white hairs which cover the males' backs. The silverback develops when the males are fully grown (usually at about 15 years of age in the wild). It is not a sign of old age. Whereas the hair on their backs is shorter than on most other body parts, males have especially long hair on their arms.

Gorillas share many features with the other apes and humans (Gregory 1950; Groves 1986). Their hands and feet resemble those of humans more than the hands and feet of the other apes do. As gorillas spend more time on the ground than all the other apes, their feet are more suited to walking: The distance between the big toe and the others is very short. This is especially true for the mountain gorillas of the Virunga Volcanoes; they climb less on trees than the other populations. Like chimpanzees, gorillas are knuckle-walkers; their fingers are anatomically adapted in many respects to this kind of locomotion (Tuttle & Watts 1985).

The skulls of gorillas show certain characteristics and are clearly sexually dimorphic (O'Higgins et al. 1990). Males and females have nuchal crests, silverback males and a few females have sagittal crests. Males have much larger crests in general. Like all the apes, gorillas have a large laryngeal air sac, especially the silverback males. It intensifies the chest-beating sound.

Gorillas feed almost exclusively on plants, which they eat in large quantities. To be able to process these masses of plant material, they have very strong chewing muscles and a large colon and caecum (possibly with symbiotic microorganisms; Collet et al. 1984; Tutin et al. 1991). Their teeth resemble very much those of humans, except for the very long, pointed canines of the adult males. The males do not use those for feeding but for fighting against competing males.

Distribution

Gorillas live in rain forests from the lowland up to the mountains of tropical Africa. Today, the distribution areas of the western and the eastern gorillas are separated by almost 900 km. The reason for this is probably that a formerly uniform area was split at some point, most likely during the ice ages. At that time, climatic changes caused the rain forest to shrink into a few refuge areas. The savannah, which spread between these refuge areas, was not an appropriate habitat for gorillas. Later, when the rain forest spread again over the whole of the African tropics, gorillas could only advance to the Ubangi and Congo Rivers.

The distribution area of western gorillas extends from 8° 50' E to 18° E and from 6° 25' N to about 5° S. Recently, a small population was found within the wide gap that separates the Cross River gorillas from the western lowland gorillas (Morgan et al. 2003). Eastern gorillas live from 26° 30' E to 29° 45' E and from 0° 20' or 1° N to 3° 50' S. The various subspecies/populations are also living in widely separated areas.

Although the borders of the gorillas' distribution area seem to have changed little over the last few decades, the habitat of this ape species has been fragmented and encroached upon considerably as forested areas are increasingly reduced and isolated from each other by cultivation. From some regions gorillas have already disappeared altogether because the forest has been destroyed. Therefore they often are confined to small and isolated forest islands.

Population

Only the numbers of the two mountain gorilla populations are fairly well known. In general, it is not possible to count non-habituated gorillas directly. Their numbers and population densities may be estimated by densities of nest sites or of the nests themselves. Researchers have to resort to the traces they leave, mainly their nests, in order to calculate population numbers. To do this, they walk along pre-determined, straight lines (so-called transects) through the forest and record all gorilla nests visible from the transect (Tutin & Fernandez 1984).

Most recent estimates of gorilla population sizes are given by Harcourt (1996) and Butynski (2001). However, because of new developments and censuses these estimates constantly have to be corrected. The number of western lowland gorillas probably has decreased considerably in the meantime, but no reliable estimate is available. The latest numbers:

Cross River gorillas	280
western lowland gorillas	100,000
Bwindi gorillas	300
mountain gorillas (Virunga Volcanoes)	380
Grauer's gorillas	3,000

The densities of gorillas vary highly across their range (Yamagiwa 1999). The highest population densities (up to more than 2 individuals/km²) of western lowland gorillas are generally recorded in secondary forest; especially high concentrations were found in Dzanga-Sangha at the forest edge and near roads (4.18–10.96/km²; Carroll 1988). But the highest density was reported by Bermejo (1999) in Marantaceae forest: 11.3 gorillas/km². Another highly preferred

habitat is swamp and inundated forest. There, the population density can be as high as 2–4/km² (Carroll 1988; Fay & Agnagna 1992; Fay et al. 1989; Nishihara 1995; Mitani et al. 1993). In *Raphia* forest (a special type of swamp forest), Blake et al. (1995) found 5.88 gorillas/km². If these preferred vegetation types are not available, western lowland gorillas use primary forest (about 0.2 individuals/km²; Carroll 1988; Tutin & Fernandez 1984), but they generally avoid *Gilbertiodendron* forest.

Schaller (1963) estimated the density of the mountain gorillas on the Virunga Volcanoes at 1.13/km². In the distribution area of the eastern lowland or Grauer's gorilla, estimates by various authors showed population densities between 0.27 and 0.83/km². Yamagiwa (1999) found that the population density of gorillas does not vary with altitude.

Habitat and Ecology

Gorillas live in a huge variety of habitats: primary lowland rainforest, secondary forest, swamp forest, marshy clearings (bais), and montane forest. The vegetation types are described by many authors, e. g. Jones & Sabater Pí (1971) for Río Muni, Fay et al. (1989) for the swamp forests of the Likouala, Carroll (1988) for the Dzanga-Sangha region, Casimir (1975) and Goodall (1977) for the highland of Kahuzi-Biega, Schaller (1963) and Fossey (1983) for the Virunga Volcanoes.

Primary forest, i. e. forest largely untouched by humans, is very rich in species. Secondary forest develops in areas that have been cleared of primary forest and is characterized by a few fast growing plant species; many of them are the gorillas' preferred food plants. Gorillas sometimes also visit cultivated land and raid fields at the edge of the forest.

Although gorillas live in the forest, they leave it occasionally when looking for food in the open grassland, especially for certain trees they regularly visit when they are in fruit (Williamson et al. 1988). Mountain gorillas occasionally climb beyond the tree line: their tracks have been found at 4,000 m altitude (Schaller 1963).

Gorillas live primarily on the ground. They spend only 5–20% of the day in trees, whereas chimpanzees spend about 50% of the day above the ground and orang-utans almost 100%. But gorillas do like to climb in order to play or to harvest fruit. Almost always they climb quadrupedally; only very rarely they brachiate or jump from branch to branch. Silverback males do not often leave the ground because of their great weight. But even they will climb high into fruiting trees if the branches can carry their weight (Remis 1999; Tutin 1996; Williamson et al. 1990).

Gorillas do not occupy discrete territories and do not defend areas against conspecifics. Instead, they roam in so-called home ranges. Where food sources are widely dispersed, the home ranges are larger. If especially nutritious and high quality food plants are abundant, the distance between feeding sites becomes shorter. In general, the home ranges comprise several vegetation zones which are seasonally exploited. The annual home range covers about 8 km² in the Virunga Volcanoes, but over the years it may be much larger (Watts 1998, 2000b). Areas of 20–30 km² were recorded in western lowland rain forest (Tutin 1996; Remis 1997a) and 30–40 km² in Kahuzi-Biega (Casimir 1975; Goodall 1977). The home range size depends on food availability and group size; the more members a group has, the further the group has to roam and the larger is the home range (Watts 1990a, 1991c, 2000b; McNeilage 2001). Usually, the home ranges of several groups overlap; sometimes the range of one group even lies completely inside the area of another one (Tutin et al. 1992; Watts 1998; Yamagiwa et al. 1996).

In general, gorilla groups move an average of 0.5–2 km a day to forage, depending on habitat and food availability. However, they can move over great distances to visit trees with particularly favoured food (Goldsmith 1999). In western lowland gorillas, day ranges of more than 5 km have been observed (Doran & McNeilage 2001).

Gorillas sleep on bare earth or in nests, which they build on the ground or in trees, depending on various factors, such as the vegetation, rainfall and temperature. Silverbacks sleep on the ground more often than the other group members (Brugiere & Sakom 2001; Mehlman & Doran 2002; Tutin et al. 1995; Yamagiwa 2001). Every evening they construct a new nest, even if it is only a few metres from the nest they used the night before. Each animal builds its own nest; only infants sleep in the same nest as their mothers. About half an hour before it gets dark

the gorillas settle in the nest. Occasionally, they also build nests for the midday rest (Schaller 1963).

To build a ground nest, the animals pull the branches of bushes and other plants into the centre, layer them and anchor them to each other. Other plants are bent in to form the nest rim. Tree nests are built mainly in forks of branches or similar structures. Females and young animals prefer to sleep in trees, whereas silverback males hardly ever do.

Gorillas forage in early morning, they rest during the late morning and around midday, in the afternoon they forage again before resting at night. They leave their sleeping sites when the sun rises at around 6 am, except when it is cold and overcast; then they often stay longer in their nests (Schaller 1963; Jones & Sabater Pí 1971; Watts 1988).

Mountain gorillas spend about half of the day eating. Rest periods take up approximately a third of the day. They spend about 6.5% of their time moving from one location to another and they are engaged in social behaviour for 3.6% of their time. Social contacts occur mainly during rest periods. Therefore, the midday rest period is very important for the social life of the group.

Like the other apes and humans, gorillas cannot swim naturally, therefore they usually avoid large bodies of water and rivers. However, often young and adult animals like to play with water or use it for various purposes, such as display. In search of food they sometimes wade through swamps on two legs with the water reaching up to their waist.

If gorillas are surprised by a rain shower, they simply stay motionless and wait for the rain to finish. If there is a cave or a similar shelter close by, they will sit underneath, but they will never use large leaves or branches to cover themselves, which is what bonobos and orang-utans occasionally do.

Apart from humans, gorillas do not really have enemies. The only predator to prey on gorillas is the leopard. Walter Baumgärtel found the remains of several gorillas after they had been killed by leopards in the Virunga Volcanoes. Other hints were found in Gabon and the Central African Republic (Tutin & Fernandez 1991; Fay et al. 1995).

When a group of gorillas feels threatened, the group members behave in a special way. Silverback males give off a particularly intense smell and emit characteristic vocalisations. The other animals gather together and hug each other or gather around the male. It is one of the tasks of adult males to defend their group against attacks and to position themselves between the attacker and the group. Frequently, younger males take on this duty. They drive the group away from the source of danger and attack the enemy at the same time (Fossey 1983; Tutin & Fernandez 1991).

Diet

What gorillas eat depends on what their habitat provides and on the time of the year. Mountain gorillas mainly feed on green plant parts – leaves, pith, stems, shoots –, whereas lowland gorillas eat a lot of fruit. However, in the dry season only a few juicy fruits are available and so the apes have to eat more seeds and tree bark instead (Rogers et al. 1988; Tutin et al. 1997). Other less important (sometimes highly favoured) food items are flowers, rotting wood, seeds, roots, tubers and mushrooms.

Usually, fruits grow on trees; gorillas of all ages climb these trees to harvest them. Although western gorillas eat a higher percentage of fruit than of leaves, stems, pith and shoots, they still eat markedly less fruit than do chimpanzees and orang-utans (Tutin & Fernandez 1993; Tutin et al. 1991).

The food range of western lowland gorillas is very broad: in Gabon, they eat parts from 221 plant species, among them 97 fruit species (Tutin & Fernandez 1993). About the same variety was found in the Central African Republic; the diversity is very high in primary and secondary forest, but much lower in montane or disturbed areas (Remis et al. 2001). They particularly like plants belonging to the ginger and arrowroot families and mainly eat the pith. In contrast, the mountain gorillas in the Virunga Volcanoes eat only 62 different plant species, mainly *Galium*, thistles, celery and nettles (Watts 1984, 1996).

The composition of gorilla diet depends on the availability of certain plants. Fruit is a favourite dietary item in lowland areas, and leaves and the shoots/pith/stem/bark category (mainly from

herbaceous vegetation) predominate at higher altitudes. Even where fruit is the main food item, herbaceous vegetation is still highly utilized. Utilisation of fruit and of herbaceous vegetation varies seasonally among western gorillas (Doran et al. 2002). In the dry season in Gabon only 30% of the diet is fruit, but for the rest of the year the percentage is 68% (Tutin et al. 1991), in the Central African Republic fruit consumption is 0% in the dry season, in the rainy season 65% for males and 41% for females (Remis 1997b), and at Nouabalé-Ndoki, Congo Republic, fruit consumption varies from 20% to over 80% (Nishihara 1995). Much the same seasonal variation is true for Grauer's gorilla (Yamagiwa et al. 1994, 1996).

On the mountains of the Central African Rift, bamboo forests are visited by gorillas when young shoots are growing, and bamboo is their main food item during that season. Western lowland gorillas also eat a special diet in swamps; Blake et al. (1995) found that in the Likouala swamps the *Raphia* palm was their main food. In general, gorillas also eat field crops, especially the pith of banana trees.

Among herbaceous vegetation, gorillas select more proteinaceous, less fibrous leaves; in general, the herbaceous vegetation eaten by gorillas has fewer digestion inhibitors than forest trees' foliage. Calvert (1985) found that leaves eaten by western lowland gorillas contain more tannin than in the Virungas. Possibly this tannin binds excess dietary iron or helps to maintain a healthy population of gut microbes (Remis et al. 2001). Rogers et al. (1990) found that gorillas select fruit with lower fat content than chimpanzees.

An adult Grauer's gorilla male is estimated to eat 30 kg of plants every day, an adult female about 18 kg (Goodall 1977). For western lowland gorillas, no estimates are available. The processing of plants is very complicated sometimes, e.g. stinging or indigestible plant parts have to be removed. This was studied in detail by Richard Byrne for mountain gorillas (e. g. Byrne 2001; Byrne & Byrne 1993; Byrne et al. 2001).

Although gorillas do not kill big animals, they regularly eat small animals, mainly insects. Often they actively open ant and termite nests. Many authors observed gorillas feeding on invertebrates and found local traditions (Deblauwe et al. 2003). However, animals constitute less than 0.1% of their food. In chimpanzees, up to 6% of the food may be animal matter (Tutin & Fernandez 1992).

Gorillas ingest soil occasionally. Perhaps it contains minerals that are missing in their normal diet, or the minerals neutralize poisonous substances in their food (Williamson et al. 1990; Mahaney et al 1995). It is not unusual for mountain gorillas to eat their own faeces, but it is observed rarely (Harcourt & Stewart 1978).

Life history

Gorillas grow faster and breed more rapidly than do other hominids. Adults have a relatively short life expectancy; silverback males, in particular, seem to have a hard life and to die young (Groves & Meder 2001).

Newborn gorillas are quite helpless: they cannot coordinate their movements and see very little, just as humans. The facial skin is relatively pale, whereas palms and soles usually show irregular, pale patterns on a dark skin. In many places the body hair is very sparse; the longest and densest hair is on the head.

Young gorillas show the same reflexes as newborn human babies. Among them are the instinctive searching for the nipple and the clinging reflex. The latter is much better developed in gorillas because the babies have to be able to cling to the mother's body without help.

Infant development in mountain gorillas is described by Fossey (1979) and Fletcher (2001). As a rule, gorillas „mother“ their infants very little. Experienced females in particular do not concern themselves much with their offspring apart from carrying, nursing, grooming and protecting them. During the first few months, a young gorilla is constantly in physical contact with its mother. At first the mother supports the baby with one hand, but even on its first day it can cling to her fur without help for a certain length of time. Physical contact with the mother starts to decrease at the latest in the baby's fourth or fifth month, when it starts to walk quadrupedally.

In general, gorilla infants are nursed for at least 2 years. At four to six months they start to put plant parts into their mouth and to bite on them. At eight months they regularly ingest solid

food (Watts 1985). At about three years they start to become independent and their mother may give birth to the next baby. In spite of this, mother and older offspring maintain a strong relationship.

During the first three years gorillas are usually called infants, ages three to six are juveniles, and the subadult category begins thereafter. At eight years of age, females are adult. Males who are apparently sexually mature but have not yet achieved full size are called blackbacks, and fully grown males, whose backs have acquired the silvery "saddle" of maturity, are called silverbacks (Groves & Meder 2001).

From its first day of life, a gorilla is part of the group. Under the protection and control of the mother it slowly grows into the community. As soon as the mother permits the others to approach, they will look at the newborn baby, smell and touch it. At latest when the young gorilla starts moving away from its mother, the other animals seize the opportunity to make contact with it. Usually, adult gorillas will hold, carry and groom the infants, while young gorillas will try to play with them (Fossey 1983).

Reaching adulthood, female gorillas usually leave the group they were born in and join a new partner. In their choice of males, gorilla females can be quite particular: Usually they transfer to a new group several times before they settle down with a certain silverback male (Watts 1990a). This decision is probably determined at least in part by the quality of the male's home range and by reproductive success.

If a mountain gorilla mother transfers between groups while she has a baby, if a dominant male dies or if another silverback male takes over the group, the baby is frequently killed by the new male (Fossey 1984; Watts 1989). Infanticide causes 37% of infant deaths. So far infanticide has been observed only in the mountain gorillas of the Virunga Volcanoes.

Free-ranging mountain gorilla males are fully grown at approximately 15 years of age. Like the females, most of them leave the group on reaching adulthood. After leaving, they often stay on their own until they are joined by females. In western gorillas, they may form a dispersed male network (Bradley et al. 2004). Watts (2000a) discusses male mating strategies. He describes two types of males: „followers“ stay in the group as subordinates and „bachelors“ leave the group before they become fully mature to live without females for some time.

At an age of 35 or more, gorillas show distinct signs of age. Old mountain gorillas often suffer from arthritis, which mainly damages the bones in their hands and feet. They also suffer from the loss of teeth as a consequence of periodontitis, so that they have a problem with feeding. It takes them longer to feed and to travel than the other group members. Gorilla groups adjust their activities accordingly and look after the aged members, in a similar way as they treat sick individuals. Only when death is imminent, the old animals are sometimes abandoned or they retreat on their own accord.

To date, no exact data on the maximum age of free-ranging gorillas are available, as animals in the wild have only been observed since 1967. Some researchers assume that they can reach 60 years, but on average they probably reach 40–45 years.

Reproductive parameters

Gorillas have no mating season. Mating and births occur throughout the year. When females reach sexual maturity, they develop a hormone cycle (similar to that of humans) which is usually 26–32 days long. Female mountain gorillas can ovulate for the first time when they are about eight years old, but usually the first ovulation happens in their tenth year. Captive gorillas usually reach sexual maturity earlier, sometimes in their sixth year (Meder 1993).

The female comes into estrus in mid-cycle. This can last up to four days, but usually it lasts only one day. During this phase she shows a labial swelling which generally is not very obvious. The female's behaviour and the relations with the other group members change. She approaches adult males (and occasionally females) to initiate mating, while other animals seek more contact with her.

If the egg is not fertilised, the mucous membrane of the uterus is flushed out of the body with menstrual bleeding, just as in humans. Bleeding lasts for two to three days and is considerably weaker than in humans.

In male gorillas, puberty extends over several years. This is when a blackback male turns into a silverback – the silvery back, the huge canines and the other secondary sexual characteristics develop. When exactly males in the wild reach sexual maturity has not yet been determined. In captivity, occasionally individuals just under 7 years old turn out to be fertile. Czekala & Robbins (2001) found that the testosterone level increased dramatically during maturation.

Compared to their body mass, gorilla testes and penises are small: Gorilla testes weigh 30–35 g, those of a chimpanzee about 120 g. As a rule, an erect gorilla penis is only 3 cm long, whereas a chimpanzee penis reaches about 8 cm (Harcourt et al. 1981).

After a pregnancy that lasts on average 257 days (humans: 265 days), gorillas usually give birth in less than half an hour and the mother doesn't seem to feel any great pain. However, difficult births do occur and can take up to three days. Twin births occur approximately as often as in humans, but no free-ranging mother has been observed to raise both twins. Newborn western gorillas weigh between 1,396 and 3,058 g (2,200 g on average), compared to 3,300 g in humans (Meder 1991). This means that while adult females and males weigh approximately twice and three times as much as average humans, their newborn babies are only two thirds the weight of newborn humans.

Once they have reached an age of approximately 10 years, female mountain gorillas give birth to one baby every four years. 26% of mountain gorilla infants die in their first year (Watts 1991b). In Kahuzi-Biega, 19.6% of the infants die in the first year (Yamagiwa & Kahekwa 2001). Inter-birth intervals are at least 3 years long (Stewart 1988). As most gorilla mothers have only a few offspring who survive to adulthood, gorilla numbers increase only very slowly. One mountain gorilla mother holds the record with six surviving offspring (Watts 1991b). Another female gave birth to eight babies, but only two of them reached sexual maturity. The fertility of free ranging mountain gorilla females has not been observed to decrease with old age.

Social structure

Gorillas generally live in groups, only adult males may stay solitary for some time. Usually these groups consist of one adult male, several females and their offspring. However, in mountain gorillas about 40% of all groups include more than one adult male (they are usually related to each other); in the other gorilla subspecies, this seems to be rare (Magliocca et al. 1999; Robbins 2001; Yamagiwa et al. 2003). The dominant male has a higher testosterone level than the subordinate (Czekala & Robbins 2001, Stokes et al. 2003). In multi-male groups, the subordinate males often sire offspring too and females often copulate with more than one male during estrus (Sicotte 2001). Adult females usually prefer the leading male and subadult females are more likely to mate with subordinate males (Robbins 1999; Watts 1990b).

As groups contain more females than males, many males are „left over“. They roam the forests as loners that make up 5–10% of the gorilla population (e. g. Magliocca et al. 1999). Virunga gorilla males occasionally form all-male groups that usually contain one mature male and a few younger males (Harcourt 1988; Yamagiwa 1987a). In these groups, males stay closer together than males in heterosexual groups; they show more affiliative, homosexual and aggressive behaviour but their aggression is less serious (Robbins 1996).

Gorilla groups can have very different histories (Robbins 2001). If the dominant male dies, the group may disperse if no subordinate silverback is there to take over the leadership; if there are two younger silverbacks, the group may split. Stable groups without a silverback male that were led by adult females for up to 29 months have been observed only in Grauer's gorilla so far (Yamagiwa et al. 2003).

One way a new one-male group starts is by a female transferring from her natal group to a lone male. This seems to be even more common in western lowland gorillas than in mountain gorillas (Parnell 2002; Stokes et al. 2003). Growing offspring of either sex usually leave their natal group. Females always join another group or a lone male, whereas male gorillas usually turn into loners. In mountain gorillas, 72% of the females leave their natal group, usually as young adults; some transfer several times between different groups (Sicotte 2001; Watts 1996). Western lowland gorillas behave very similarly (Stokes et al. 2003).

Most of the males leave their natal group, also usually as young adults. The separation proc-

ess is slow: they spend more and more time on the edge of the group until they leave altogether. In contrast, a female leaves her group only if she encounters another male. The home ranges of various gorilla groups and of lone silverback males overlap, so encounters are frequent. Lone males often make a special effort to seek out harem groups, as this is their only chance to gain females. The leaders of stable groups avoid contact with other adult males in order to avoid losing females. If they detect a competitor, they try to drive him away by displaying or attacking (Yamagiwa 1987b; Watts 1991b).

In a gorilla group there is a clear hierarchy (Watts 1996). The leading silverback has the highest rank, and adult females are dominant over young animals. Among the females, rank depends on factors such as how long they have been in the group, for example (Watts 1991a, 1994, 2001). Among the young animals, rank usually depends on age. Social bonds in unrelated group members are strongest between females and silverbacks.

A gorilla male achieves his high-ranking position not only because of his strength, which he proves when fighting against competitors, but also because of his experience and abilities. For instance, he has to know the area very well in order to lead his group to the right feeding sites at the right time of the year. These days, it is also very important that he knows how to deal with humans. Experienced gorilla males can, for example, remove poachers' snares from the hands or feet of their group members (Fossey 1983). As young males lack the necessary experience, they will find it difficult to lead a group. If the females notice that their silverback male is too inexperienced, they will transfer to another one. In the Virunga gorillas, the mean length of tenure of a dominant silverback in a group is 4.7 years (Robbins 1995).

The size of gorilla groups is very variable. An average gorilla group contains about 9–10 members (Parnell 2002; Yamagiwa et al. 2003).

Young animals always search out the group leader who usually is their father as well (Stewart 2001). They frequently stay close to him, they lean on him and include him in their games. For them a close relationship with their father can be vital. He protects the infants and his care increases their chances of survival if their mother dies or if she leaves the group. In such a case the silverback male is usually the only one who looks after them intensively. He even allows them to sleep in his nest.

As gorillas live in dense rain forest where group members often cannot see each other, they use mainly vocalisations for communication. In accordance with their role as group leaders, silverback males are the ones to vocalize most frequently (Harcourt & Stewart 2001). Sounds called „grunts“ and „barks“ in many variations are the gorillas' most important vocalisations (Harcourt et al. 1993). They indicate the whereabouts of individual group members and can accompany social interactions. On average, adults make eight such vocalisations per hour, most often during travelling. Group members probably recognise each other from these sounds.

However, body postures and facial expressions also indicate the gorillas' mood. Certain behaviour patterns involve certain body postures and often require another animal to do something. Postures signalling mood or intention to the partner are sometimes even used for communication over greater distances; this is particularly true for display behaviour.

Silverback males are famous for their display behaviour culminating in the chest beating and loud hooting (Schaller 1963). The chestbeat sounds especially impressive in silverback males. Because of their sharp canines and great strength, they are very dangerous opponents. Severe aggression is rare in stable gorilla groups, but when two mountain gorilla groups meet, the leading silverbacks can sometimes engage in a fight to the death, mainly using their canines to cause deep, gaping injuries (Fossey 1983; Sicotte 1993). In western lowland gorillas, however, groups often intermingle peacefully (Bradley et al. 2004).

Conservation

In their natural habitat, gorillas are threatened by many different factors, such as

- * isolation of gorilla populations in small forest islands,
- * destruction of the forest through deforestation, fire or mining of mineral resources,
- * hunting for their meat,

- * hunting for fetishes and trophies,
- * hunting in revenge for crop-raiding,
- * injuries through snares set for other animals,
- * war and its consequences,
- * stress caused by the constant presence of people,
- * diseases transferred by people or domestic animals.

Eastern gorillas are threatened by extinction if no effective measures are taken to protect them; western lowland gorillas are considered less threatened.

Many national parks have been established to protect the gorillas and deploy rangers hired by the respective country's authorities. However, enforcing the protected status of large areas is not sufficient: the forests and their occupants can only be protected if local authorities and people support these efforts. Activities to ensure the conservation of gorillas have been summarized by Oates (1996).

In some areas, authorities have been trying to set up controlled tourism as a means to conserve the gorillas. In the Virunga Volcanoes, this has probably helped to save the mountain gorillas from extinction, but tourism may cause severe problems too (Butynski & Kalina 1998; McNeilage 1996).

As gorillas are very sensitive to changes in their environment, the mere presence of humans can be a threat. Even in the Virunga Volcanoes, gorillas are continually disturbed: cattle herds, loggers, collectors of grass and honey, smugglers and poachers are active in the national parks in spite of strict laws. In many areas, the exploitation of mineral resources is an additional disturbance.

Poachers set traps, in particular wire snares, in order to catch duikers (forest antelopes). However, gorillas get into the snares too and often they don't succeed in removing the wire. In such a case they can lose a hand or a foot, or even die from gangrene. Vets are sometimes able to remove the snares in those groups habituated to people.

The hunting pressure on Grauer's and western gorillas is very high. They are still killed for their meat by the local human population, although this is illegal. In addition, local hunters and farmers often kill gorillas because they raid the fields. One gorilla group can destroy the whole harvest.

Another problem is the increasing destruction of the gorillas' habitat. The deforestation of the rain forests leads to the isolation of small forest islands, to which the animals are now confined because there is no adequate habitat close-by. In 1959, Emlen and Schaller (1960) considered this problem critical for the survival of the eastern gorillas. In the meantime, the wars, refugees, political turmoil and the looting of natural resources are more immediate threats in the eastern gorillas' distribution area, and have led to a mass slaughter of Grauer's gorillas. This slaughter is still going on. Gorilla orphans are also traded in this area.

In the Congo basin, forests still are disturbed through timber harvest by logging companies and cleared to make way for cultivation. Roads, initially built to transport the timber, subsequently facilitate the settlement of the forest. In its turn, this leads to increased hunting to provide the workers with food and slash-and-burn cultivation. Bushmeat (including gorilla meat) is frequently transported into the cities with the timber transports (Ammann 2001; Bowen-Jones & Pendry 1999; Remis 2000). This trade has developed considerably during the last few decades. At the moment it is the most imminent danger for all gorilla populations except for the mountain gorillas.

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