WORLD ATLAS OF GREAT APES AND THEIR CONSERVATION



Martha M. Robbins

CHAPTER 8

Eastern gorilla (Gorilla beringei)

Sarah Ferriss, Martha M. Robbins, and Elizabeth A. Williamson

astern gorillas (*Gorilla beringei* Matschie, 1903), occur in the wild more than 1 000 km from the nearest western gorillas (*G. gorilla* Savage, 1847). They are larger than the western gorilla but otherwise similar, with a broad chest and shoulders, a large head, and a hairless, shiny black face. A full-grown adult male can weigh up to about 220 kg, and a full-grown adult female about half this. 46, 97, 99 Two subspecies of eastern gorilla are currently recognized by the Primate Specialist Group of IUCN–The World Conservation Union: 48 the eastern lowland or Grauer's gorilla (*G. b. graueri* Matschie, 1914); and the mountain gorilla (*G. b. beringei* Matschie, 1903).

A very small population of unusually large eastern lowland gorillas occurs on Mount Tshiaberimu, in the Virunga National Park of the Democratic Republic of the Congo (DRC).82 One population of mountain gorillas, that found in the Bwindi Impenetrable National Park in Uganda, has such distinctive morphology, ecology, and behavior that some have suggested that it should be considered a third subspecies. 73, 123 This is a contentious issue, as it is probable that the mountain gorilla populations have been separated for only the relatively short period during which intensive agriculture has occupied the area between them. The small size of the mountain gorilla populations and the small number of samples available for examination make it more difficult than usual to determine whether the variation between populations is greater than the variation within them. Debate continues on this issue, 14, 47, 48, 92, 135 but here we recognize only two subspecies of the eastern gorilla: the eastern lowland gorilla and the mountain gorilla.

There are few if any absolute physical differences between these two subspecies, although the mountain gorilla tends to have a larger body and longer hair, and is distinguished by its larger cranium and wider facial skeleton, as well as less rounded and more angular nostrils. 47 Genetic divergence of these subspecies was apparently confirmed by comparison of their mitochondrial DNA (mtDNA);76 however, the high frequency of incorporation of mitochondrial into nuclear DNA recently reported in gorillas 146, 166 makes interpretation of the earlier results more difficult. The mtDNA of these two subspecies may turn out to be more similar (or indeed more different) than had previously been thought. It is estimated that the two subspecies diverged some 400 000 years ago. 166

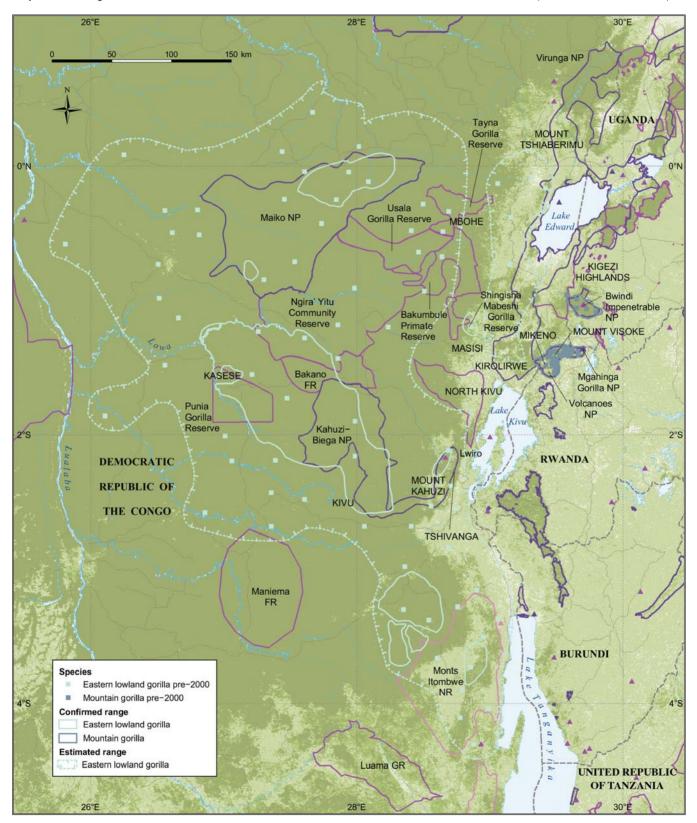
DISTRIBUTION

Mountain gorilla

The mountain gorilla occurs in two known populations within three countries: DRC. Rwanda, and Uganda (Map 8.1). These populations occur almost entirely within national parks. One is found among the extinct volcanoes of the Virunga Massif. These gorillas are officially protected by the Virunga National Park of DRC, the Volcanoes National Park in Rwanda (Parc National des Volcans), and the Mgahinga Gorilla National Park in Uganda; all of these are contiguous and so protect a single area of gorilla habitat (the Virungas). The other population is found mainly in Bwindi Impenetrable National Park in southwest Uganda on the border with DRC. Mountain gorillas occupy about 375 km² in the Virungas and 215 km² in Bwindi, 14 these areas being separated from each other by 25 km of settled farmland. 123

Map 8.1 Eastern gorilla distribution

Data sources are provided at the end of this chapter



The three national parks of the Virungas contain most of the surviving forests in the region, extending to about 440 km². The forested area ranges in elevation from 2 000 m to 4 500 m, and therefore contains a range of ecosystems, including various montane rain forest formations and bamboo stands, as well as areas with little tree cover and abundant herbaceous vegetation. The area has a high rainfall, and complex topography and drainage combine to create lakes, marshes, swamps, and peat bogs at various altitudes. The volcanic history means that there are high eroding peaks and lava plains, and that soil fertility is generally high; this factor is principally responsible for the high density of the surrounding human population.

The Virunga National Park is located in northeastern DRC, is 7 900 km² in area, and has a boundary 650 km in length. It ranges in altitude from almost 800 m to over 5 100 m, so contains nonforested areas at low and high elevation. About 95 percent of the park is in North Kivu (Kivu Nord) Province and the remainder is in Orientale (formerly Haut-Zaire). The park has four sectors, with gorillas found only in the southern sector.

The Volcanoes National Park of Rwanda is about $160~\rm km^2$ in area and ranges in altitude from $2~400~\rm m$ to $4~507~\rm m$. Its boundary is located some $15~\rm km$ northwest of the town of Ruhengeri in the Virunga Massif on the Ugandan and DRC borders.

The Mgahinga Gorilla National Park is 33.7 km² in area, ranges in altitude from around 2 400 m to 4 127 m, and is located in the extreme southwest of Uganda, on the borders with DRC and Rwanda. The park was established specifically for the protection of mountain gorillas in 1991, having been a designated but unprotected reserve prior to that. ^{15, 16, 17, 154}

The second population of mountain gorillas is mainly found in Bwindi National Park, which is located in the Kigezi Highlands of southwest Uganda, on the edge of the Albertine Rift Valley and bordering DRC to the west. ¹⁵¹ Some of these gorillas also occur across the border in DRC itself. Bwindi National Park covers approximately 331 km² and ranges in altitude from 1 160 m to 2 607 m. ⁹⁸

Mountain gorillas occur at a density of 0.85– $1.00/km^2$ in both Bwindi and the Virungas. ^{53, 80, 92, 186, 189}

Eastern lowland gorilla

The eastern lowland gorilla occurs only in eastern DRC, between the Lualaba River and the Burundi-Rwanda-Uganda border. Its distribution encompasses an area of about 90 000 km², within which it is

thought to occupy an estimated 15 000 km² in four broad regions: the Kahuzi-Biega National Park and the adjacent Kasese region; the Maiko National Park and adjacent forest; the Itombwe Forest; and North Kivu.⁴⁹

Kahuzi-Biega covers an area of 6 000 km², ranging in altitude from 600 m to 3 400 m. The park is divided into two parts, a mountain sector (600 km²) and a lowland sector (5 400 km²), connected by a forested corridor. Gorillas occur in both, in the region of Lake Kivu and Mount Kahuzi in the mountain sector, and the Kasese region of the lowland sector. ^{49, 155} Gorilla populations in this park are thought to have been devastated during the DRC civil war during the late 1990s, falling from an estimated 8 000 to an unknown number, perhaps as few as 1 000 individuals. ¹¹³

Maiko National Park and nearby forests are located in the upland region between the central DRC river basin and the mountain ranges of the west side of the Rift Valley. The park has an area of about 10 800 km² and ranges in altitude from 700 m to 1 300 m. ^{83, 156} It is unclear how heavily the war in DRC has impacted Maiko's gorilla population. There are also several developing community reserves around the area of the Maiko, Virunga, and Kahuzi-Biega National Parks; together, these are thought to host between 700 and 1 400 gorillas as well as an unknown number of chimpanzees. ^{78, 93} One of these encompasses the Itombwe Forest, an area of montane, transitional, and lowland tropical forest to the west of Lake Tanganyika, ¹⁰² and includes

Habitat of the eastern lowland gorilla, Tayna Gorilla Reserve, Democratic Republic of the Congo.

Pierre Kakulé Vwirasihikya





Gordon Miller/IRE

Habitat of the mountain gorilla, Bwindi Impenetrable National Park.

protected areas of several different designations. It covers an area of 11 000 km², in which gorillas are found in four separate populations.⁴⁹ A community reserve is also being developed in the Masisi region in the North Kivu area, to the southwest of the Virunga National Park.

BEHAVIOR AND ECOLOGY

Much of the information on the ecology of the eastern gorilla comes from studies on mountain gorillas in the Virunga Massif. 35, 122, 124 Research in the Virungas was initiated by George Schaller in the late 1950s; since 1967, three to four habituated groups have been followed regularly by researchers from the Karisoke Research Center in Rwanda. Less is known about the ecology or demography of mountain gorillas in Bwindi.92 or of the eastern lowland gorilla, but research is ongoing. Most studies of the eastern lowland gorilla have been carried out in Kahuzi-Biega, under the auspices of bodies such as the Congolese Institute for Nature Conservation (ICCN, Kinshasa), the Center of Natural Science Research (CRSN, Lwiro), and Kyoto University. 21, 69, 197, 207 Research findings on the ecological and behavioral differences between and within the eastern gorilla subspecies. and between western and eastern gorillas, are accumulating. 26, 38, 90, 120, 121, 201, 203

Habitat

Mountain gorillas in the Virungas occur at altitudes from 2 000 m to 3 600 m, with occasional excursions

to as high as 4 100 m, while those at Bwindi live between 1 160 m and 2 600 m. Eastern lowland gorillas occur at altitudes between 600 m and 2 900 m. 14, 90, 203, 208 Although the altitudinal ranges of the eastern lowland and mountain gorillas overlap, their populations are geographically separated.

The Virungas mountain gorilla habitat

The Virungas are a forested, mountainous volcanic region that contains a number of vegetation zones. The most widespread type is a *Hagenia abyssinica* (Rosaceae) and *Hypericum revolutum* (Clusiaceae) woodland, with a relatively open canopy and extremely dense herbaceous or, less frequently, grassy understory. 90, 180, 181 Other areas frequented by mountain gorillas in the Virungas include open herbaceous areas, often dominated by *Mimulopsis excellens* (Acanthaceae), in the flat saddle between Mounts Visoke and Sabinyo; monospecific stands of bamboo; dense ridge vegetation with abundant *Hypericum revolutum* and shrubby growth of *Senecio mariettae* (Asteraceae); and high-altitude vegetation with a stature of 4–5 m. 90

Bwindi mountain gorilla habitat

Bwindi gorillas live at lower elevations, and are more arboreal than gorillas of the Virungas. They occur in a range of vegetation types which include open forest with a discontinuous canopy, sometimes dominated by *Mimulopsis arborescens* (Acanthaceae); mixed forest dominated by understory and canopy trees and shrubs, usually interspersed with lianas and woody vines, especially *Mimulopsis* spp.; riverine forest, along permanent or temporary rivers or streams, with an open or continuous canopy; and regenerating forest that has been disturbed previously, for example by logging. There is a greater density of fruit-bearing trees in the gorilla habitats of Bwindi National Park than in the Virungas. 38, 98

Eastern gorilla habitat

The eastern lowland gorilla has the widest altitudinal and geographical range of any of the eastern gorillas, living in montane, transitional, and lowland tropical forests. They have been reported at a range of densities: 0.25/km² in Maiko National Park, 0.55/km² at Mount Tshiaberimu, and 1.03–1.26/km² in Kahuzi-Biega. ^{50, 53, 111, 207} One of the best-studied populations of eastern lowland gorilla occupies the mountain region of Kahuzi-Biega. Here habitats vary from dense primary forest intermixed with bamboo, to mesophytic (moderately moist) wood-

land, to areas of *Cyperus* (Cyperaceae) swamp and peat bog, with alpine and subalpine grassland at higher altitudes; patches of open vegetation also occur at lower elevations. 155

Diet

Mountain gorillas

Mountain gorillas are large-bodied herbivores; in the Virungas, they feed almost exclusively on the leaves and stems of herbs, vines, and shrubs harvested in the dense herbaceous understory, supplementing this with bark and roots. 90, 168 In contrast, the Bwindi mountain gorillas live in a more fruit-rich habitat, and take advantage of this. Around the Karisoke Research Center in the Volcanoes National Park, a study recorded mountain gorillas eating 38 plant species from 18 families. 168, 170 These included the stems and roots of Peucedanum linderi (celery, Umbelliferae); the stems and roots of Laportea alatipes (nettle, Urticaceae); and the stems and roots of Urtica massaica (stinging nettle. Urticaceae): as well as the leaves of L. alatipes, Carduus nyassanus (thistle, Asteraceae), and the leaves of Galium ruwenzoriense (galium vine, Rubiaceae). Mountain gorillas have a preference for:

- the leaves of G. ruwenzoriense, Arundinaria alpina (bamboo, Poaceae), and Rubus spp. (berry, Rosaceae);
- the stems of *P. linderi*; and
- (especially) bamboo shoots. 106, 163

Bamboo is high in protein. Its availability fluctuates seasonally and it is consumed heavily by mountain gorillas when it is abundant. A number of feeding techniques have been observed; these are interpreted as measures to avoid injury from leaves bearing stings or sharp hooks. As a result of the low quality and poor digestibility of much of their diet, mountain gorillas in the Virungas spend at least half of their daylight hours feeding, and much of the remainder resting.

The gorillas of the Virungas and of Bwindi both require abundant quantities of easily harvestable plant material. The gorilla habitat around the Karisoke Research Center contains little edible fruit, sa is reflected in gorilla diets there, while in Bwindi fruit is an important component of gorilla diet. The most important fibrous foods consumed by the Bwindi gorillas also differ from those consumed in the Virungas, and include

species of Basella (Basellaceae), Brillantaisia (Acanthaceae), Clitandra (Apocynaceae), Ipomea (Convolvulaceae), Laportea (Urticaceae), Mimulopsis (Acanthaceae), Mormodica (Curcurbitaceae), Myrianthus (Moraceae), Palisota (Commelinaceae), Triumfetta (Tiliaceae), and Urera (Urticaceae).³⁸

Occasional items that mountain gorillas have been seen eating, all of which are speculated to have a nutritional function, include insects (ants and cocoons of unspecified origin);^{37, 168, 172} at Karisoke Research Center, subsoil sediments five to six times per year, possibly as a source of sodium or iron;⁸⁸ dung;^{40, 57, 168} and rotting wood.^{36, 136}

Mountain gorillas show dietary flexibility; within both the Virungas and Bwindi their diet has been shown to vary according to the distribution and abundance of food resources that, in turn, vary according to altitudinal and climatic factors. 38, 90 For example, at Bwindi, groups of gorillas living at lower altitudes consumed more species of fibrous food (140 versus 62) and fruit (36 versus 11) than those living at higher altitudes. There is little seasonal variation in the diet of the mountain gorilla in parts of the Virungas, probably because most of their food is available throughout the year, 168 while the fruit component of the diet of the Bwindi gorilla varies over the course of a year.³⁸ The total number of species eaten and the degree of frugivory are more similar between eastern lowland gorillas at Kahuzi-Biega and mountain gorillas at Bwindi than between the populations of mountain gorillas at Bwindi and the Virungas.38

A silverback male eating Myrianthus fruit.







Martha M. I

A gorilla infant, Bwindi Impenetrable National Park, Uganda.

Mountain gorillas appear to visit feeding areas that have received little recent use and those that produce nutritious food. ¹⁸⁰ Foraging areas with less abundant high-quality food, or where renewal rates are lowest, are visited less frequently than other areas. When bamboo shoots are available in large quantities, mountain gorillas feed almost exclusively on bamboo. As bamboo declines in abundance, the gorillas move away from the bamboo areas and consume other herbaceous foods. When all preferred foods are scarce, the gorillas alter their diet and expand the foraging area covered each day. ¹⁶³, ¹⁹⁶

Nutrient supply does not appear to be a limiting factor for mountain gorillas in the Volcanoes National Park. 106 While food abundance varies over the range, no areas are so productive that it would be advantageous for gorilla groups to establish and defend exclusive foraging zones.168 Instead, home ranges may overlap by up to 100 percent, 170, 180 with the groups tending to avoid one another.32 The availability of abundant, evenly distributed food resources means that overall feeding competition within groups is also rather low, and so the costs of social foraging are also likely to be low, 169, 182 although some competitive disputes do occur, especially in larger groups. 169 Silverbacks have priority access to food, and there are weak dominance hierarchies among females. 51, 169, 176, 178 Hence, group living may carry some costs for lower-status blackbacks, females, and juveniles. 182

Eastern lowland gorillas

The varied diet of the eastern lowland gorilla includes a wide range of plants, their fruit, seeds, leaves, stems, and bark as well as ants, termites, and other insects.²⁰⁸ Seasonality in diet and habitat use is greater for eastern lowland gorillas in lowaltitude forests than for mountain gorillas. 182 Eastern lowland gorillas eat more fruit than do Bwindi mountain gorillas, but not as much as western gorillas. 38, 182, 203, 208 When fruits are scarce, eastern lowland gorillas travel less and increase their consumption of herbaceous vegetation. 206, 208 Large quantities of bamboo shoots, as well as several types of fruit, are eaten seasonally by eastern lowland gorillas of the upper altitudinal reaches of Kahuzi-Biega.^{21, 39} These gorillas also occasionally feed on ants, but have not been observed eating insects as often as have eastern gorillas in lowland forests. Insects are never more than a minor part of the diet for any gorillas. 208 The ant-feeding sites have all been found in primary or ancient secondary forests on ridges or slopes. Most plant parts are eaten on the ground, although leaves, bark, and fruit are sometimes eaten in trees. Signs of feeding activity have often been observed along gorilla trails in valleys and swamps.²⁰⁸

Ranging behavior

In the Virungas, the typical annual home range of a mountain gorilla group is about 5.5-11.1 km². 163, 170, 175 Bwindi gorillas may use 20-40 km² in a year. 121 The ranging behavior of gorilla groups is mainly determined by the distribution and abundance of fruit and herbaceous vegetation in the environment, 121 but may also be influenced by social factors such as competition for mates or the mate-quarding tactics of silverbacks. 175 These complex and changing factors are reflected in diverse ranging behavior, with groups generally spending more time in foodrich areas. 90, 163 Solitary males in the Virungas have larger home ranges than would be expected for a single individual; 175, 194 there are no equivalent published data for Bwindi gorillas. Food is an important influence on the movement patterns of lone males, and other gorillas are not always avoided.^{20, 175, 194, 204}

Eastern lowland gorilla groups in montane forest have home ranges of 13–17 km^{2,203} Although the size of their home range in lowland tropical forest is unknown, they are known to have shorter average day journeys in montane forest than in lowland forests.

Ecological role

Not only is gorilla behavior adapted to the ecosystems in which they live, but gorillas also help to shape these ecosystems. As large, heavy, and dexterous animals that consume a lot of foliage, they also change the structure of vegetation by trampling it. This can stimulate regrowth and productivity; stem densities of some herbaceous foods increase in the aftermath of gorilla feeding. ¹⁷⁰ It is not certain whether there is a positive-feedback mechanism through which gorilla activity leads to a more edible plant community. ^{105, 180}

In many forest communities, primates act both as seed predators and as seed dispersers; they are likely to have an important impact on patterns of forest regeneration and on the diversity of tree species⁸⁶ (see also Boxes 4.4 and 5.1). Western gorillas have been reported to disperse seeds, ¹⁵⁰ and the consumption of fruit by eastern lowland and Bwindi mountain gorillas suggests that they may also play this role.

Eastern gorillas share their habitat with other large mammalian herbivores, and so might be expected to compete with them for food. Mammalian herbivores in the Virungas include buffalo (Syncerus caffer) and bushbuck (Tragelaphus scriptus), but these are not thought to have a significant impact on the mountain gorilla population. 106, 107, 110 Other herbivores, such as black-fronted duiker (Cephalophus nigrifrons) and the African forest elephant (Loxodonta cyclotis), show little dietary overlap with the mountain gorilla. 106 Elephants have considerable potential to impact the food supply of the mountain gorilla, but their numbers are so low as to have little real effect. 107 Mountain and eastern lowland gorillas are sympatric (occur together) with chimpanzees in some areas, and their diets are known to overlap. 136, 205 Although one competitive encounter between chimpanzees and the Bwindi mountain gorillas has been observed, different foraging strategies are employed by these species and there is little evidence of feeding competition between them. 136 It has been suggested that sympatry with chimpanzees may have promoted a leafeating strategy in gorillas, moving their feeding niche away from that occupied by chimpanzees²⁰³ (see Box 8.1).

The only known predators of gorillas are humans and leopards (*Panthera pardus*). ¹²⁴ Evidence of attacks by leopards on western gorillas is outlined in Chapter 7, but these cats no longer

occur in the Virungas, and may also have been lost from Bwindi.

Social behavior

More than 30 years of research at the Karisoke Research Center established by Dian Fossey has made mountain gorillas one of the best-studied primate species. 122 Much is known about their social behavior, feeding ecology, life history patterns, and demography. 115, 118, 134, 140, 178, 183 Given the ecological variability between gorillas in different habitats, one important question is the extent to which the information available from Karisoke applies to other gorilla populations.

Groups of eastern gorillas may contain only one mature male, several mature males (in a 'multimale' group), or may consist of males only. 116, 195 Most comprise a single dominant adult male or silverback, typically with three or four females and four or five offspring.53, 186 Over the past three decades in the Virungas, between 10 percent and 50 percent of mountain gorilla groups have been multimale,80 while at Bwindi about 50 percent of groups are multimale.92 About 10 percent of eastern lowland gorilla groups are multimale.203 If the dominant male mountain gorilla dies in a one-male group, the group may disintegrate; should this happen in a multimale group, however, one of the subordinate males can take over leadership and the group may then stay

A male silverback eastern lowland gorilla, Democratic Republic of the Congo.

Elizabeth A. Williamson



intact.¹¹⁵ This pattern is in marked contrast to that seen in western gorillas, among which multimale groups are extremely rare.¹²⁰

Group size is variable among eastern gorillas; groups ranging from two to 53 individuals have been observed. 80, 189, 196 In general, median group size is similar for both eastern and western gorillas. across various habitat types and the different diets associated with them. 103, 120, 200, 203 In the Virungas. median and mean group size are eight and 11 individuals respectively (see Table 8.2).80 At Bwindi, a mean group size of about 10 has been reported.92 In the area surrounding Tshivanga in Kahuzi-Biega, the mean group size of eastern lowland gorillas (excluding solitary males) is almost 10.69 Mean group size in the highland sector of Kahuzi-Biega decreased from about 16 per group in 1978, to 11 in 1990, to 10 in 1996.²⁰¹ Other studies indicate a mean group size of seven animals in Kahuzi-Biega but only three in the adjacent Kasese region. 50

The sex ratio at birth in both the Virungas and Kahuzi-Biega is approximately 1:1.174, 201 Upon reaching maturity, most males and females leave the group in which they were born (their natal group). Males that emigrate usually remain solitary until they can attract females and establish their own groups; occasionally, males form all-male groups. After emigration from the natal group, some males spend a large proportion of their time alone, although in the home range of their natal group. 20,53 It is very unusual for fully adult males to migrate into other groups. 53, 115, 118, 195 Young males may also stay within the natal group and eventually inherit its leadership. 58, 115, 118 Most multimale groups, but not all, may be the result of males maturing and remaining in their natal groups, 115 and are therefore believed to contain several related adult males. Genetic studies confirm that this is often, but not always, the case. 100

Whether a young male remains in his natal group or emigrates could be determined by a range of factors including changes in social relationships and demographic structure, such as the availability of mating opportunities within the group, the death of a parent, or disintegration of the natal group. ^{28, 115, 118} Males that develop strong affiliative (friendly) relationships with the dominant silverback while they are infants are more likely to be close to the leading male during adolescence, and are therefore more likely to remain in their natal group. ⁵⁸ Male eastern lowland gorillas in Kahuzi-Biega rarely stay with their putative fathers but

instead form their own groups, sometimes taking females with them from the natal group.²⁰¹

Both natal dispersal (leaving the natal group and transferring to a new group), and secondary dispersal (subsequent transfer to yet another group), occur among female eastern gorillas. Females have also been known to remain and reproduce within their natal group. 61, 134, 169, 183 Female mountain gorillas of the Virungas usually transfer from their natal group alone, while female eastern lowland gorillas sometimes transfer with another female and their offspring. 201 If a female is pregnant or has an infant when she transfers to a new group, there is a risk that the new silverback will kill the infant. 173 Infanticide has been observed occasionally in eastern gorillas, 173, 202 although not in every instance of transfer with an infant 133 (see Box 8.2).

Female transfer could offer a number of possible advantages, such as the opportunity of higher social rank, ³⁵ especially following migration into a small or new group; avoidance of inbreeding; increased choice of mates; improved reproductive success; reduced feeding competition; or improved protection against infanticide. ¹³⁴

Females may have preferences with regard to mates, and this choice may be influenced by male behavior. 134 From the male point of view, good relationships with females are important to mating access and breeding success, as a female is free to leave the group. Although gorilla groups are essentially controlled harems, males cannot therefore afford to make them unduly oppressive ones.

Both aggressive and affiliative interactions between males and females have been observed. Males have been seen to direct aggressive displays toward females, and females to appease those males (see Box 8.3), although the reasons for these displays and their impact on female mate choice remain unclear.¹³⁴ Males may also vocalize and engage in nonaggressive behaviors toward females, possibly to maintain proximity with females.¹³⁴ Females may sometimes intervene in an attempt to end aggressive interactions between adult males.¹³²

Silverback males in mixed-sex groups do not interact much with each other but, when they do, the behavior tends to be more competitive and aggressive than affiliative, presumably as a result of competition over access to mates. ¹¹⁸ Affiliative interactions are rarely seen, ¹¹⁶ but occasional cooperation by males within the same group has been observed, apparently to prevent females from leaving the group. ¹³¹ Relations between silverbacks

Box 8.1 COEXISTENCE OF GORILLAS AND **CHIMPANZEES**

Gorillas and chimpanzees live together in the same forests in many parts of equatorial Africa, a coexistence known as sympatry. As they are so similar to one another, how do they manage to coexist without one species displacing the other? Earlier studies 77, 124 suggested that their different diets and ranging behaviors reduced competition through 'niche differentiation'. Fruit-eating (frugivorous) chimpanzees tended to range in primary forests and stay on the dry ridges, while leaf-eating (folivorous) gorillas tended to range in secondary regenerating forests and stay in the wet valleys. These ecological differences were thought to affect their societies, and to determine their densities in different types of habitat. The dynamic 'fission-fusion' social structure of chimpanzees was therefore thought to be caused by their frugivory, while the more cohesive groups of gorillas were associated with their folivory.

More recent studies, however, have shown that there is actually extensive overlap of gorillas and chimpanzees in both diet and ranging. Western and eastern lowland gorillas include fruits and insects in their diet, and range in primary forests in close proximity to chimpanzees. ^{25, 85, 114, 148, 149, 195, 205, 208} Western lowland gorillas consume plant foods as diverse as those eaten by sympatric chimpanzees. Of the fruit species eaten by western lowland gorillas at Lopé National Park, Gabon, 79 percent are also consumed by chimpanzees in the same forest. 149 All fruit species eaten by eastern lowland gorillas at Kahuzi-Biega are also eaten by sympatric chimpanzees. 205 However, analysis of fecal samples at Kahuzi-Biega and Bwindi shows that there are marked differences between the two species in their reliance on particular fruit species, such as Ficus spp. (Moraceae), Syzygium sp. (Myrtaceae), Bridelia sp. and *Drypetes* sp. (both Euphorbiaceae). 136, 205

The presence of gorillas is thought to influence the choice of nesting trees by chimpanzees. In secondary forests at Kahuzi-Biega, eastern chimp-

anzees (Pan troglodytes schweinfurthii) tend to avoid nesting in those trees with ripe fruits of the type preferred by gorillas.8 Eastern lowland gorillas tend to extend their day-journey length during the fruiting season in both lowland and montane forests, while sympatric chimpanzees tend to stay in a small area, continually revisiting particular fruiting trees. 9, 205, 206 Such differences in diet, ranging patterns, and nesting-site choice may limit competition between sympatric gorillas and chimpanzees. Gorillas and chimpanzees occasionally encounter each other in the same fruiting trees at Kahuzi-Biega and Bwindi, with most encounters being tense but peaceful. 136, 205 At Ndoki, in Congo, typical encounters between western lowland gorillas and chimpanzees are even more peaceful. 144

Many aspects of foraging behavior seen among gorillas and chimpanzees may vary with environmental conditions, and the true extent of this variability is still unknown. This is likely to be important in predicting how gorillas and chimpanzees will react to habitat change wrought by humans, which is fundamental to wise conservation planning. 187, 196 Continuing research on eastern lowland gorillas and sympatric chimpanzees at Kahuzi-Biega and Bwindi will help to clarify the scope for improving the survival of sympatric great ape populations.

Juichi Yamagiwa

Juichi Yamaniwa

A female gorilla and infant, Kahuzi-Biega National Park.

and blackbacks tend to be weak. 116, 118 Blackbacks are subordinate to silverbacks, and generally spend a lot of time on the periphery of the group. 118

Young, unrelated males that form all-male groups are thought to do so to develop social skills. and perhaps to increase safety from predators. 116, 118

Relations between males in all-male groups tend to be more affiliative than among males in mixed-sex groups, as measured by the occurrence of playing, grooming, and time spent in close proximity. 116, 118 Homosexual behavior has also been observed. 195 Aggression is more frequent in all-male groups, but

Box 8.2 INFANTICIDE IN GORILLAS

Few behaviors observed in the animal kingdom have led to more heated debate concerning its function than infanticide (the killing of young from the same species). Why would the killing of dependent young evolve as an adaptive strategy? The prevailing view is that infanticide by males is related to competition over access to females, in line with the sexual-selection hypothesis.66 Specifically, if a male kills unweaned offspring of other males, and thus shortens the time that he must wait to impregnate their mothers, he will increase his own reproductive success compared to that of other males who do not follow this strategy. Given the cost to females in lost reproductive effort, infanticide results in a conflict between the sexes. Infanticide occurs rarely, but over the past four decades has been suspected or observed in more than 40 species of primates, including gorillas.

Known or probable infanticide and attempted infanticide in mountain gorillas were recorded 13 times at Karisoke between 1967 and 1988; these comprised three observed cases, nine inferred cases, and one unsuccessful attack inferred from wounds.¹⁷³ If all were indeed cases of infanticide, this would have accounted for at least 37 percent of infant mortality during this period.¹⁷³ The majority of these cases occurred when the mothers of the infants were not accompanied by the group's silverback, typically because he had died. This suggests that an important motivation for females to form long-term associations with males is to obtain protection against infanticide.

Is infanticide universal among gorillas? Interestingly, in Kahuzi-Biega, female eastern lowland gorillas with dependent young have been observed unaccompanied by silverbacks for many months. Females have also transferred between social units with unweaned infants that were not killed, but three cases of infanticide have been observed at Kahuzi-Biega.²⁰¹ On the other hand, two

cases of infanticide have been inferred in western gorillas following group disintegrations. 143

The risk of infanticide is thought to have played a large role in shaping the social behavior and group structures observed in many primate species. 162 Where there is only one male per group. females can exert mate choice by transferring between social units: because of the risk of infanticide, the opportunity for a female to transfer without risk is limited to the brief time window when she does not have a dependent offspring. 134 A multimale group structure is advantageous because, in the event of the death of the leading silverback, another (often related) adult male is likely to take over the leadership of the group; this prevents group disintegration and infanticide by an outsider male. 115, 118 Since the late 1980s, while the gorilla groups studied at Karisoke have been almost exclusively multimale, no group disintegrations have occurred, and neither have any infanticides by males been observed or suspected. 80 Infanticide has rarely been observed during encounters between groups, and male eviction and group takeovers by extragroup males have not been observed in gorillas. 118, 134, 173 Recently, at Kahuzi-Biega, following the simultaneous transfer of several females, the new silverback killed one unrelated infant at the time of transfer, and (despite the efforts of the females in the group to intervene) killed two other infants shortly after their births, which occurred only a few months after the transfers. 202

In addition to its impact on sociality, infanticide has implications for population dynamics. The death of a silverback represents initially the loss of only one individual in a population. If, however, he was the leader of a one-male group, his death is likely to lead to the deaths of all his unweaned offspring. This impacts overall infant mortality, future births, group age structure, and the rate of population growth, which can be critical for small populations such as those of the mountain gorilla.

Martha M. Robbins

disputes between males in mixed-sex groups (when they occur) are more serious and more likely to result in wounds. This difference is probably a result of competition between males over mating, an issue that does not arise in all-male groups.

Apart from those between mothers and their offspring, social bonds between females tend not to

be well developed. Females commonly leave their natal group, so complex social networks between females do not occur. The female coalitions that do emerge, allowing common defense against aggressors, are thought to be more common among related than unrelated individuals. ^{179, 183} Males frequently intervene in conflicts between females, thus

limiting the effectiveness of female coalitions. Such interventions involve only moderate aggression, pose little risk to social relationships with females, and may help males to retain mates by maintaining their own status and control over the group. 179

Immature gorillas often receive defensive support from their mothers, but rarely from unrelated adult females. Juveniles rarely receive consistent support even from their mothers, however, if they behave aggressively toward larger opponents. 179 During infancy, gorillas often develop an attraction to the leading male of the group, who may buffer the young animals against aggression from others, serve as a spatial focus for young animals, and provide an attachment figure as the maternal bonds weaken. 139 The behavior of the male toward infants and juveniles is paternalistic, though no great effort is put into this. 139 Adult males may protect immature gorillas against larger opponents but provide little support to immature individuals who behave aggressively, intervening mostly in conflicts between immature peers only to maintain control. 179

Reproduction

Successful gorilla males typically mate with more than one female (are polygynous). Generalizing from the Virunga gorillas, it seems that female mountain gorillas reach sexual maturity around the age of six and a half years (5.8–7.1 years). Between the first bout of estrus-like behavior and the first conception there is a phase of adolescent sterility that lasts two years. 53, 174 Although less regular among young females, the menstrual cycle among adults has a median length of 28 days; females are most receptive and attractive to males at around mid-cycle, for one to four days.²⁴ The gestation period lasts about eight and a half months. 23, 34, 54, 147 Mating or mating attempts occur at times during both the menstrual cycle and pregnancy when estrogen concentrations are highest. 24, 54, 174

Mountain gorillas do not have a birth season, presumably because of the lack of seasonality in food availability. Infant mortality rates at Karisoke are highest during the wettest months (April and May), when the animals are colder and more susceptible to respiratory infections. 182 The interbirth interval lasts approximately four years, as gorillas are not fertile while still suckling young (lactational amenorrhea). The recorded interbirth interval for the eastern lowland gorilla is slightly longer than that of mountain gorillas of the



Gordon Miller/IRF

Virungas (4.6 versus 3.9 years). 174, 201 Should an infant die, this interval is shortened, allowing its mother to conceive again within three to six months. Infants are typically weaned at three or four years, 33, 138 but there is variation in both directions. 30

Social rank and group composition may change during an individual's lifetime. Assuming a different relative position within the group can be expected to change that individual's reproductive strategies. Although mountain gorillas are considered to have a one-male mating system, many multimale groups exist. In one-male groups, the only male present does all the mating. In multimale groups, subordinate males do mate, including at times when conception is likely to occur, although dominant males tend to participate in more matings with adult females, and subordinate males with subadult females. 117 Genetic studies reveal that subordinate males do sire a proportion of offspring. 12, 100, 101 Mating with individuals from other groups is exceptionally rare in mountain gorillas. 134

In multimale groups, males often try to remain in proximity to females at mid-cycle. 134 Females sometimes mate with more than one male, sometimes even in the same mid-cycle period. This may be voluntary or the result of male coercion. 119 Harassment of copulating males can occur, and is often but not always practiced by dominant males. 117

Eastern lowland gorillas share many reproductive characteristics with mountain gorillas, including a sterile subadult period in females, the Part of the Mapuwa group of mountain gorillas, Virunga National Park.

	Table 8.1 Eastern	lowland and	mountain	gorilla	populations
--	-------------------	-------------	----------	---------	-------------

Subspecies	Approximate population size	Approximate area of occupancy (km²) ¹⁴
Mountain gorilla (Virungas)ª	380 ^{44, 80}	375
Mountain gorilla (Bwindi)	320 ^{91, 92}	215
Eastern lowland gorilla ^b	? ^c 17 000 ± 8 000 ^d	15 000

a See also Table 8.2.

Table 8.2 Mountain gorilla populations of the Virungas (1971-2003)

Census years	Total gorillas counted	Estimated population size	Number of social groups	Mean group size	Number of solitary males	Multimale groups (percent)	Immature individuals (percent)
1971-1973 ^{45, 5}	⁵ 261	274	31	7.9	15	42.0	39.8
1976-1978 ¹⁸⁶	252	268	28	8.8	6	39.0	35.8
1981 ⁵	242	254	28	8.5	5	40.0	39.7
1986 ¹⁶⁵	279	293	29	9.2	11	8.0	48.2
1989 ¹²⁹	309	324	32	9.2	6	28.0	45.5
200080	359	359-395	32	10.9	10	52.9	44.7
2003 ⁶⁸	380	-	-	-	-	_	-

Adapted from Kalpers, J., et al. (2003).

Geographic region	Estimated population size (2001–2004)	Estimated population size (1994–2000)
Kahuzi-Biega National Park and adjoining Kasese region	present (2005)	15 703 (7 655-22 491) (1994-1995) ^{49, 164}
Tayna and other proposed community reserves	1 050 (700–1 400) (2004) ⁹³	?ª
Maiko National Park	assumed present (2005)	859 (462-1 135) (1996) ⁶⁴
Itombwe Forest	present (2005)	1 155 (516–1 796) (1999) ¹⁰²
Northern bank of Lowa River (north of Kasese region)	?	13 (0–26) (1998) ⁴⁹
Mount Tshiaberimu, Virunga National Park	20 (2004) ¹³	?
Masisi (including Shingisha Mabeshi)	present ¹⁹⁹	28 (0-33) (1988-1998) ⁹⁶
Mbohe, North Kivu	?	small ⁴⁹

a '?' indicates that no data are available.

Adapted from Hall, J.S., et al. (1998) and later sources, as cited in the table.

b See also Table 8.3.

c No data; fieldwork was being undertaken in 2005 to estimate the extent of the decline.

d Estimate based on 1998 survey data, obtained prior to outbreak of war in the area. 49

age at first parturition (giving birth), interbirth interval, and infant mortality rates. 201, 203

Nest building

Adults and weaned immature gorillas build nests each night, in which they sleep. Unweaned offspring share the nests of their mothers: otherwise. gorillas sleep alone. The gorilla defecates either in or next to the nest, and the size of the dung is directly proportional to the age of the gorilla.53, 124 Counting and measuring nests and dung can therefore provide information on the number of gorillas in a group and the age class of the individual using each nest, so it is a commonly used census method. In the Virungas, mountain gorillas almost always make nests on the ground, while about half of the nests of eastern lowland gorillas in the lowland tropical forest of Kahuzi-Biega are constructed in trees.²⁰⁸ In the montane forest of Kahuzi-Biega, most nests are made on the ground but, even here, immature gorillas tend to make nests in trees more frequently than do adults: more immature and female gorillas tend to nest in trees if the group's silverback has died. This is thought to be a result of their vulnerability to large terrestrial predators. 197

POPULATION

Status and trends

The population of mountain gorillas of the Virungas has been monitored since the 1970s. Fewer data are available on the status and trends of mountain gorillas at Bwindi, or of eastern lowland gorillas. Recent estimates of overall numbers of eastern gorillas are given in Table 8.1.

Mountain gorillas in the Virungas

The mountain gorillas of the Virungas have been studied for over 40 years. A summary of selected population estimates can be seen in Table 8.2. These data show a decline through the 1970s and into the early 1980s, with most reduction occurring in the DRC section. 70, 186 The population was estimated to contain about 450 gorillas in the late 1950s, 124 275 in 1973, 53 and 254 in 1981. 5, 70 The 1989 census of mountain gorillas in the Virungas counted 309 animals and estimated 324 to be present. 129 A population estimate in 2000, based on repeated observation of 17 habituated groups and information on 15 unhabituated groups, suggested that the Virunga population of the mountain gorilla had further increased to between 359 and 395.80 In the

DRC parts of the Virunga Massif, seven habituated gorilla groups had declined from a total number of 103 individuals to 66 between 1995 and 1998, but showed an overall increase from 66 to 86 between 1998 and 2002.¹¹ The most recent census of the Virunga gorillas recorded 380 animals.⁶⁸

The increased numbers of mountain gorillas revealed by these censuses should be viewed with some caution because nearly all of the population growth can be attributed to the Research/Susa section of the Volcanoes National Park, an area that is relatively well protected, and which is believed to be a particularly good gorilla habitat. Other sectors are known to have experienced a decline in the number of gorillas, ⁸⁰ so there is still conservation work to do.

Mountain gorillas in Bwindi

The small Bwindi mountain gorilla population also appears to be stable. A survey in the early 1990s found about 300 animals, ^{15, 16} which was confirmed by a complete census of the entire park in the late 1990s, ⁹² and raised to about 315 by another census in 2002. ⁹¹

Eastern lowland gorillas

The total area known to be occupied by eastern lowland gorillas declined from about 21 000 km² in 1963 to 15 000 km² by the early 1990s. The overall geographic range, calculated by Butynski from historical locality data, was 112 000 km². This illustrates the degree of fragmentation of populations at that time. By the mid-1990s, there were estimated to be about 17 000 (± 8 000) eastern lowland gorillas in at least 11 subpopulations, with 86 percent living in Kahuzi-Biega and the adjacent Kasese region of DRC. 49, 111

More recent events in Kahuzi-Biega and the surrounding region, however, indicate that the species has undergone a substantial decline in numbers 104, 113 (see Table 8.3). Access to much of the gorilla range has been difficult in recent years, and is only just becoming possible again. The available information is very limited, but there is consensus among field workers that a drastic decline in total population has occurred. This is attributed to the combined effects of the rise in demand for 'coltan' ore (discussed in more detail below) and the warfare that engulfed the whole of the eastern lowland gorilla range from the late 1990s onwards; armies, rebels, refugees, and miners all lived off the land and consumed bushmeat. 113

Box 8.3 THE VOCAL BEHAVIOR OF MOUNTAIN GORILLAS

Mountain gorillas use a variety of vocalizations to communicate, both within and beyond their social group. Calls aimed outside the group are given primarily by adult males in response to potential danger, such as a human hunter or a rival silverback. These calls convey alarm/threat and include various types of 'barks', more intimidating roars, and screams; they are sometimes accompanied by a charge. When encountering another group or a lone male, adult males also give a form of 'long call', which is a series of loud, resonant hoots, usually combined with displays such as chestbeating or ground thumping.^{31, 124}

Intragroup vocalizations are quieter and less energetic, but far more frequent and varied. Some of these signals occur in specific contexts and often evoke specific responses. To human observers, the meaning of the calls is often quite clear, as for the mildly aggressive 'cough-grunt', the whimpering of an infant that has lost its mother, the breathy 'chuckles' given only during play, or the staccato whimpers that accompany copulation.³¹

Far more mysterious are the frequent, quiet, 'close calls' that gorillas give throughout the day in various nonspecific contexts. The most common of these signals are atonal, belch-like grunts, usually of one or two syllables, that sound much like a human male clearing his throat. Other 'close calls' include syllable-free grumbles, and higher-pitched tonal calls, similar to human humming and singing. 62, 127

If vocal communication is viewed as a form of social behavior, then 'close calls' are the most frequent social interaction between gorillas. In two

study groups at Karisoke, adult gorillas vocalized about once every eight minutes. Over half of these calls occurred as part of an exchange, in which a vocalization was 'answered' by a call from another individual. A key feature of this vocal behavior is that gorillas usually give and exchange calls when other individuals are nearby, within 2–5 m.⁶⁰

The vocal habits of gorillas correlate with other aspects of their social behavior. For example, the nature and frequency of 'close calls' are related to age and dominance status. Adult males, who dominate other group members, vocalize more frequently than do adult females, who are in turn more vocal than younger and more subordinate immature animals. The adult vocal repertoire consists mainly of syllabled grunts, whereas younger gorillas do more humming and singing. 59, 62, 127 One obvious, but not exclusive, context in which adult females grumble or hum intensely is when they are near an adult male who has just displayed. In this case, the vocalizations seem to signify subordinance and act as appeasement signals. 62, 134, 177 Most of the time, however, it is not clear what prompts an animal to vocalize, or what purpose the signal might serve. The syllabled grunts are particularly enigmatic. The animals grunt most frequently during feeding, while traveling, or resting. Calls evoke either no discernible response or, at most, a vocal answer from another animal. 31,62

While acoustical analyses indicate that many grunts are individually distinctive (suggesting that gorillas can recognize each other from their grunts), few features of the sounds relate to behavior. ¹²⁷ As far as we can tell, grunts given during feeding are the same, acoustically, as those given during resting. It is possible that these signals convey a

The best-documented example of this decline in population is in the mountain sector of Kahuzi-Biega; here only 130 eastern lowland gorillas remained in 1999, down from 245 in the same location in 1996. 112, 184, 198 The eastern lowland gorilla population in the lowland sector of Kahuzi-Biega is believed by the park wardens to have suffered even greater casualties; a crash in all populations of large mammals is inferred from the reported lack of meat of these formerly abundant species in bushmeat supplies sold by hunters to coltan miners. 113 At the beginning of the coltan rush, the miners in the lowland sector of Kahuzi-Biega

mostly ate large mammals; toward the end, they relied upon small mammals, birds, and turtles. The conflict situation has prevented field surveys, but the Wildlife Conservation Society was coordinating a gorilla survey in 2004–2005; it is hoped this will offer a more solid estimate of remaining numbers.

In summary, about 700 mountain gorillas and thousands of eastern lowland gorillas still survive. Both subspecies have declined significantly in numbers. This process is ongoing (perhaps catastrophically so) for eastern lowland gorillas, while the mountain gorillas have been slowly increasing since the early 1980s (Table 8.2). Both the Virunga

general message such as "I am about to change activity", or simply, "I am here". The function of this communication will then depend on the context. For example, during feeding periods, vocalizations might be important in interindividual spacing and the avoidance of feeding competition.⁵⁹ In other situations, 'close calls' seem to play a role in coordinating group movement and activity. Toward the end of a midday rest period, resting gorillas increase the frequency of their grunting, as if to indicate that they are ready to end the siesta. They seem to be signaling their 'intent' to move on, but wait to do so until they have heard from the rest of the group. Even when the animals are doing nothing but lying still, an observer can often tell when the rest period is about to end, just from the increase in 'conversation'. 141

All our data on vocal communication in the wild comes from the mountain gorillas of the Virunga Volcanoes. Studies of western gorillas in captivity and preliminary observations in the wild suggest that the vocal repertoires of other populations of gorillas are generally similar. We still have much more to learn, however, about gorilla vocal communication.

Kelly J. Stewart

Above: A young silverback hooting during a chestbeating display. Below: An adult female and silverback playing; they have just sat back from some gentle wrestling. The female is beating her chest. They both have the open-mouthed 'play face' that accompanies the breathy pants known as play chuckles. These vocalizations are characteristic of, and very specific to, play. They are given by young infants upwards.



A.H. Harcourt/Anthrophoto



and Bwindi populations of mountain gorillas were classified (separately, because of the uncertainty over their taxonomic status) by IUCN as Critically Endangered, on the basis of their small population sizes, with fewer than 250 adults in each case; eastern lowland gorillas were classified as Endangered, albeit on the basis of the 1998 estimate of population numbers.⁷³

Threats

Hunting

Gorillas are hunted for their meat, as specimens (particularly infants) for collections, and as trophies.

The hunting of gorillas for sale as trophies (skins, heads, skulls, feet, and hands – sold, for example, as ash-trays) emerged in the mid-1970s, and continued until quite recently. 112, 142 Occasionally individual gorillas that raid the crops of local people are killed. 49 For example, a young mountain gorilla was stoned to death in January 2003 when his group damaged fields near the border of the Virunga National Park; 84 Rugendo, the previous silverback of this habituated group, had been killed in 2001 in crossfire. 11

Infant gorillas have been captured for sale, or attempted sale, to public or private collections,



A plaque in Bwindi National Park commemorates seven of those who died at the hands of militia in March 1999.

and many adults have been killed while trying to protect their infants from this fate. The capture of infant mountain gorillas in the Virungas was a serious problem in the 1970s, although it declined greatly through the 1980s and into the 1990s. In 1995, however, four adult gorillas were killed in Bwindi, and there have been reports of infant gorillas being taken for sale to private collectors. Foaching leading to the deaths of at least seven gorillas occurred in 2002 in the Virungas; in 2003, nine Rwandan poachers were fined and imprisoned for two to four years each for stealing a baby gorilla in Volcanoes National Park, and for killing two adult gorillas that had been protecting it. Hunting remains a threat in the Virungas.

In response to the situation in DRC from the late 1990s onwards, the United Nations Security Council established an expert panel on the illegal exploitation of natural resources in DRC. It concluded that the various armies active in DRC were systematically exploiting five natural resources either to finance themselves or to exchange for weapons; these were diamonds, copper, cobalt, gold, and coltan. Coltan is an alluvial ore of niobium (columbium) and tantalum, metals that are used in the manufacture of mobile telephones and computer equipment. The ore has a ready market, and its high value has attracted miners to

locations where it is abundant, including rivers in Kahuzi-Biega. ^{6,72,128} Professional hunters joined the miners to provide meat for them, and the eastern lowland gorillas of Kahuzi-Biega were severely affected. ^{111,113} More information on the decline of eastern lowland gorillas can be found in the DRC country profile in Chapter 16.

Traditionally, gorillas were rarely eaten in the eastern Congo Basin, which has given the eastern gorilla a certain amount of protection. These traditions are weakest in areas inhabited by the eastern lowland gorilla and, as seen in Kahuzi-Biega, are fast becoming a thing of the past. They were and remain strongest, however, around the Virungas and Bwindi, providing continued protection to the mountain gorillas there. 112

War and political unrest

Wars kill gorillas as well as people, and death can disrupt gorilla groups as effectively as it does human communities. Gorilla groups may disintegrate in response to losses, particularly of the dominant silverback, which can result in additional mortality and declining populations. Armed conflict and political unrest have taken their toll on both the eastern lowland gorilla and on the mountain gorilla populations, with a series of conflicts and wars which have affected the people, landscapes, and wildlife of DRC, Rwanda, and Uganda.

The early 1990s saw the outbreak of fighting in Rwanda, including within the Virungas; by April 1994, this had expanded into DRC and resulted in a stream of refugees pouring into the gorilla habitat and its surrounds. About half of Rwanda's civilian population was displaced during this conflict, with 860 000 refugees being concentrated in the vicinity of the Virunga National Park, and a further 332 000 having fled into DRC near Kahuzi-Biega. Soon after the 1994–1995 influx of Rwandan refugees into DRC came the 1996 war in DRC; fighting broke out again in 1998.

Refugees can put massive pressure on gorillas and their habitats through uncontrolled harvesting of wood for fuel, increased hunting, and disruption of migration patterns. During the war in Rwanda, three of the four refugee camps in North Kivu were located in or near to the Virunga National Park buffer zone; much of the park has been affected by wood harvesting or poaching. Subsequent conflict in DRC led to looting and destruction of the park's infrastructure, and the deaths of about 5 percent of the mountain gorilla population in the

Virungas.⁸⁰ These factors led to the Virunga National Park being placed on the 'World Heritage in Danger' list in 1994.¹⁵⁷ As described above, hunting for gorilla meat in Kahuzi-Biega has increased as a result of war and displacement.^{111, 113}

In addition to the influx of refugees, the forests that are home to gorillas have served as hiding places and retreats for rebel forces, leading to disturbance and hunting. This is a common phenomenon at times of war in forests that straddle international borders. 112

The long-term impacts of the recent wars in Central Africa are unclear, and the civil wars in Rwanda and DRC have made it difficult to assess how the mountain gorillas have fared. 111 although some censuses have been carried out.68,80 One hopeful sign relates to the mountain gorillas in the eastern Virungas. This small and somewhat isolated subpopulation numbered about 57 in 1989 and, despite intense military activity in the early 1990s, there appeared to be at least 57 gorillas remaining in 2000.80 The lowland protected areas of DRC, where most of the eastern lowland gorillas occurred during the 1990s, remain inaccessible to researchers so it is difficult to assess their status. 111 The population in the area around Tshivanga in Kahuzi-Biega was relatively stable between 1990 and 199669 but, since then, two rebellions have occurred, with large numbers of eastern lowland gorillas being killed. 113, 201 Over just four years, the highland sector of Kahuzi-Biega lost more than 95 percent of its elephant population and about 50 percent of its gorilla population. Local resentment toward the park and its authorities may have contributed to this illegal exploitation of wildlife resources. 198

Conflict can also deter international conservation organizations, aid agencies, and governments from investing in affected areas, leading to frozen budgets, withdrawal of staff, reduction in antipoaching efforts, and the closure of projects. Nevertheless, some organizations continued to support park authorities in the Virungas throughout the war,80 even though research programs were interrupted. Protection of the gorillas in many areas has proved extremely difficult and often hazardous in recent years, and many national conservationists take tremendous risks in the course of their work, sometimes with fatal consequences. Ten staff and assistants of ICCN, for example, were murdered, apparently by militiamen who had been hiding in DRC since the genocide in Rwanda, while surveying

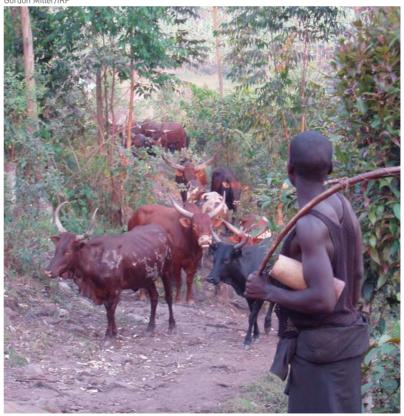
Kahuzi-Biega boundaries to reestablish the park limits.^{22, 63} These were not the first or the only park-service employees to be kidnapped or killed while they were attempting to protect the area and its wildlife.^{69, 74, 75, 125, 126} In all, 92 Congolese park staff are reported to have been killed between 1996 and 2004.⁶⁷ During the conflicts in Rwanda, several workers from Karisoke lost their lives, others were imprisoned, and the center itself was destroyed;^{142, 191, 192} much more international attention was drawn by the killing of eight tourists and four guides at Bwindi by Interahamwe militia in March 1999.¹⁰ Without the determination and commitment of park rangers, it would be impossible to imagine the long-term survival of the eastern gorilla.

Habitat loss or modification

The mountain and eastern lowland gorillas live surrounded by some of the densest rural human populations in Africa, with up to 300–600 people per square kilometer, and a correspondingly high demand for land and food. 112, 145 As a result, gorillas are increasingly confined to smaller and more isolated forest fragments as human populations increase. 14

Cattle herding in Uganda.





Habitat loss, specifically forest clearance for agriculture, was one of the main causes of population decline among mountain gorillas during the 1970s. 14, 142 In 1968, more than one third of the Rwandan Volcanoes National Park was excised for an agricultural project. 112 Little forest cover now remains in Rwanda, and virtually no forest habitable by gorillas remains outside protected areas.83 The boundaries of protected areas are generally respected by planners and farmers, so there has been very little further habitat loss in Rwanda, although disturbance from increased human presence, social instability, genocide, and war has occurred. 111, 112 The forest has also been used as a source of wood for building and fuel, and is accessed both for water and to graze cattle. 112

In Mgahinga Gorilla National Park, Uganda, agricultural and pastoral activities and hunting were major pressures; incursions by local people and their livestock used to be common. 70 The park has a complex history of designation changes, having originally been defined both as a game reserve and a forest reserve, established in 1930 and 1939 respectively. The boundaries for each reserve were defined by the contour line running at 2 425 m, on the lower slopes of the three volcanoes in what is now Mgahinga Gorilla National Park. In 1951, the forest reserve boundary was raised to 2 730 m, thereby significantly reducing its area and removing some important gorilla habitats. 1, 154 After the Mgahinga Gorilla National Park was designated in 1991, people living in this area were evicted. Meanwhile, the game reserve boundary was lowered to the 2280 m contour in 1964, significantly increasing its area and including land that was already settled. The designated national park encompasses part of this additional game reserve area,81 which means that a large community with a tradition of extractive use of park resources occurs both within and adjacent to the park. A community-based conservation program is now attempting to balance the needs of the people and the wildlife.

In DRC, demand for fuelwood by Rwandan refugees affected 105 km² (1.3 percent) of Virunga National Park by 1997, of which 35 km² had been completely cleared. Since 2001, much of the Kirolirwe sector has been cleared by refugees returning to DRC from Rwanda, who were settled there by the Rassemblement Congolais pour la Democratie, an armed opposition movement. Short 15 km² of land was cleared by Rwandan

farmers in May 2004 in the Mikeno sector, also on the DRC side of the park.⁶⁷ After international protest, Rwandan soldiers removed the 6 000 loggers and farmers, killing two,⁴ and the park's drystone boundary wall was rebuilt. As DRC becomes more stable, it is likely that commercial logging companies will quickly move into its forests.¹¹¹ This could well impact eastern lowland gorillas, but it is unlikely that large-scale logging would occur in the high-altitude forests of the Virungas. Gorillas often favor areas of secondary vegetation, and so might be able to coexist with logging, if it were not for the associated hunting.¹¹¹

The Bwindi population of mountain gorillas is relatively well protected. Prior to the 1980s, manual felling and head-load extraction (i.e. the removal of no more than the quantity of wood, usually branches, that can be carried on one's head) of timber was permitted throughout the area, which was then a forest reserve. 70 These nonmechanical techniques made for very selective and environmentally benign logging. Nevertheless, only about 10 percent of the forest in Bwindi is entirely free of past human disturbance. 151 No data are available on the intensity and distribution of habitat disturbance since Bwindi was declared a national park, since when antipoaching and other enforcement efforts are thought to have led to much reduced levels of disturbance.92

Eastern lowland gorillas and their habitats face similar problems of habitat loss, which add to the impacts of hunting that have been noted above. The increasing human population and the corresponding need for land is a serious and ongoing pressure.49 The boundaries of Kahuzi-Biega were altered in 1974, resulting in the loss of an important area of gorilla habitat. 49 It has been suggested that the rate of loss of habitat for the eastern lowland gorillas is probably the highest for any gorilla subspecies, but the lack of clarity about the situation in DRC means that no absolute figures are available. 111 The fuelwood reserves outside Kahuzi-Biega have been severely depleted by refugees, so fuelwood collection within the park is an ongoing threat. 111, 113

Disease transmission from humans

Gorillas are susceptible to many human diseases, as detailed in Chapter 7; increased exposure of gorillas to humans or to human feces is occurring as more people live in or around the forests, or enter them more often because they are displaced

by conflict.¹⁹⁰ Disease may be carried by park guards, researchers, tourists, tour guides, loggers, hunters, or by local people using nearby roads. Data on the impacts of disease among eastern gorillas, particularly outside the Virungas,¹¹¹ are limited, but the Ebola virus has not affected eastern gorilla populations.

Some eastern gorillas carry parasites including protozoans (e.g. Cryptosporidium spp.)⁴² and nematodes (e.g. Capillaria hepatica),43 but these parasite loads might be unrelated to human presence.95 Mountain gorillas are also susceptible to the skin mites that cause scabies or mange (Sarcoptes spp.), an outbreak of which, in a habituated group in Bwindi in 1996, led to the death of an infant male, probably from secondary infection of scratch abrasions. 41,79 The source of this disease is unknown, but is suspected to have originated among the people and livestock living around the park, where it is prevalent. 79 Another outbreak of mites occurred in Bwindi in 2000, but did not result in any deaths. 94 Much more seriously, an outbreak of pneumonia in Rwanda's Volcanoes National Park in 1988, possibly with an acute viral infection such as measles as the primary infection, claimed the lives of six gorillas, but 27 others were treated successfully. 130, 193 The high rate of infection (81 percent) suggested that the disease was new to these gorillas. 14 Vaccination against measles was subsequently given to 65 habituated gorillas from this population. 130, 167, 193

While tourism can make a vital contribution to conservation by generating funds and through education, it does represent a potential source of disease^{14, 16} that could threaten small populations.⁹⁵ In addition, disturbance through contact with humans may increase stress and thereby susceptibility to disease.89 The expansion of gorilla tourism exposes more gorillas to diseases that they may never have encountered before and against which they may have no natural immunity, while encouraging protection of the gorillas from habitat loss and hunting. Healthy, fee-paying tourists who contribute strongly to financing conservation and to building political support, deter poachers by their mere presence, so in most circumstances these tourists are likely to be on balance beneficial to gorillas. A survey in 1981 compared reproductive success in 'quarded' gorilla groups exposed to tourism with that of unquarded groups. The latter were found to have a smaller proportion of immature animals.56 Infants are not only often



Alastair McNeilage

direct targets of hunting but, as discussed above, are likely to suffer disproportionately when groups are broken up.

In the Virungas and Bwindi, strict rules regulating tourism are in place (though not necessarily always obeyed). These limit tourist visits to one hour per day, set a maximum group size of eight tourists, and require tourists to maintain a minimum distance from gorillas of 7 m. 112 Other disease prevention measures include burying human excrement deeper than 30 cm and chasing gorillas away from private lands that surround the parks. 65, 79 Veterinary assistance is also available at these mountain gorilla centers. In Uganda, veterinary intervention is limited to diseases caused by human beings and to life-threatening conditions that could affect a substantial number of gorillas in a group. 79 The Mountain Gorilla Veterinary Project in Rwanda has a similar nonintervention policy, with restrictions on emergency treatment to illnesses that could threaten the group or population.95

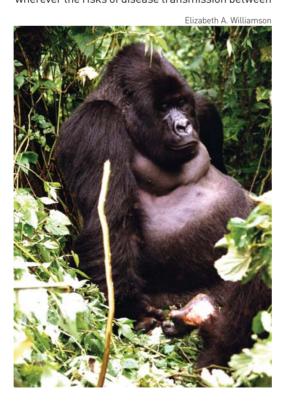
Tourists at Mgahinga Gorilla National Park, Uganda.

Other threats

Gorillas can easily be caught in wire snares set for ungulates; this can result in the loss of a hand or foot. 95, 112 The three research groups in Volcanoes National Park reported 50 snare injuries to gorillas between 1971 and 1998, four of which had fatal consequences. Snares set for medium-sized mammals such as antelopes also wounded many eastern lowland gorillas in Kahuzi-Biega. 49, 207 Of the groups habituated for tourism in the montane sector of the park, at least one individual per group had lost a hand in a snare. 49 Snares are therefore considered an important threat to eastern gorillas in the Volcanoes National Park and elsewhere. 109

The isolation and small size of mountain gorilla populations has given rise to concerns about inbreeding. However, two studies have suggested that the Virunga population, which is of much the same size and composition as the Bwindi population, is likely to be safe from genetic problems for 400 years or more. ^{2, 29} A comparison of a sample of Bwindi gorillas and western lowland gorillas shows only minimal reduction of genetic variability (heterozygosity) in the Bwindi gorillas, despite their small population size. ⁸⁷ Nevertheless, every effort should be made to maintain or restore habitat connectivity and gene flow between gorilla populations, wherever the risks of disease transmission between

A silverback sits with a young female, whose foot (just visible) was injured by a snare, Virunga National Park, Democratic Republic of the Congo.



the reconnected populations are exceeded by the benefits of expanding the gene pool.

CONSERVATION AND RESEARCH

Conservation activities and research focused on eastern gorillas have been underway for many years. These prolonged efforts have met with much success although many problems persist. Despite the significant threats associated with warfare in the region, mountain gorilla population numbers – although small – appear to be stable and, in some cases, increasing. Eastern lowland gorilla populations are, however, declining – possibly very quickly. Increased numbers of mountain gorillas in the Virungas are probably a direct result of protection efforts, and are concentrated in one or two areas. 80, 137 These findings indicate that, with local commitment and sufficient investment, it is possible to protect gorilla populations.

The eastern gorilla is protected by national legislation in all three of its range states, and most known populations live in protected areas that are not all, or not only, 'paper parks' (areas protected in law, but not in practice). Where park rangers are present and local residents supportive, gorilla populations have a good chance of survival. A park ranger's work may include monitoring gorilla populations, patrolling for poachers, law enforcement, and community development work. That gorilla parks can make a real difference to local attitudes is illustrated by the commitment of staff members, who have been known to risk their lives in defense of their parks, even when pay has not always been forthcoming. Cooperation and coordinated efforts in park management involving the governments of Rwanda, Uganda, and DRC, supported by researchers and national and international nongovernmental organizations, have contributed to the conservation of the mountain gorilla throughout its range, and will continue to do so.

Conservation and research activities

Our growing understanding of gorilla biology (including such features as group structure and dynamics, ranging behavior, habitat requirements, and population densities), has contributed in many ways to the selection of protected areas and the design of conservation action. It has also contributed indirectly to the raising of global public and political awareness, and of much-needed funds. Population monitoring reports are particularly helpful in management, because they provide

feedback on what is working and what is not, as well as early warning of new kinds of threat. This allows gorilla conservation to adapt over time, to become increasingly effective.

The Karisoke Research Center, managed by the Dian Fossey Gorilla Fund International, has sustained studies of mountain gorillas since 1967. These have included long- and short-term census work, as well as studies on social structures. group dynamics, feeding behavior, habitat use, and reproduction. 122 Because of Karisoke, the only period without regular monitoring of mountain gorillas was 15 months during 1997-1998, a time when armed conflict prevented personnel from entering the park. 142 In addition, the Mountain Gorilla Veterinary Program established a veterinary center to monitor the health of the gorillas and act in emergency situations, including the removal of snares from gorillas and dealing with disease outbreaks. Eastern gorilla studies have more recently been extended to the Bwindi mountain gorillas and the eastern lowland gorillas of Kahuzi-Biega and elsewhere. 38, 121, 200

The Impenetrable Forest Conservation Project led to the establishment of the Bwindi Impenetrable National Park and a buffer zone in 1992.71 The Institute of Tropical Forest Conservation, part of Uganda's Mbarara University, is the successor institution of this project. It has an active ecological monitoring program that is studying water quality, the impact of forest fires, and forest-gap dynamics. Other research includes work on barriers to cropraiding by gorillas and a long-term project on the ecology, behavior, and population dynamics of the Bwindi mountain gorillas. This research supported the preparation of a management plan for the park, which was updated in 2001 to guide actions for tourism development, biological inventories, and other measures that are now in place.

In Kahuzi-Biega, a long-term community-based conservation project was established in 1985 with the support of the German overseas development agency GTZ, with community-focused economic development as one of its primary objectives. 15, 69 Managers at Kahuzi-Biega and GTZ developed an emergency plan for, among other things, collecting and distributing fuelwood in response to the refugee crisis of the late 1990s. GTZ has also helped to fund gorilla population censuses, including one in Kahuzi-Biega that was also supported by the Wildlife Conservation Society and others. 184 In the same region, local people,

including park guards and guides, established a nongovernmental organization that helped to spread conservation knowledge and reduce conflict among local people.¹⁹⁸

The revenues created by gorilla tourism have channeled significant resources into the protection of gorillas and parts of their habitat (see Box 8.4 and Chapter 14). In Uganda, the money so generated is distributed throughout the system of national parks, not just among the gorilla parks, making a broad contribution to national needs and building political support for gorilla conservation, albeit at the cost of diluting the funds available for managing gorilla populations and habitats. Conflicts deter tourists, but during those of the 1990s, the authorities of gorilla range states (the Uganda Wildlife Authority, the Office Rwandais du Tourisme et des Parcs Nationaux, and the ICCN) did what they could to maintain conservation efforts. The decrease in revenues from tourism led, however, to huge enforcement problems. This was partially offset in the Virungas by the contribution of additional funds and other resources by outside organizations. Some of the extensive educational and outreach programs developed prior to the conflict also continued.80 The continuity of these efforts was made possible largely by international nongovernmental organizations such as the

Firewood collection in the region of the Kahuzi-Biega National Park, Democratic Republic of the Congo.





Box 8.4 EASTERN GORILLA TOURISM

In Rwanda, Uganda, and DRC, gorilla tourism generates significant revenue, increases public awareness, and has undoubtedly been a motivator in securing government commitments to the protection of gorillas and their habitats. It should not, however, be seen as an ideal solution to the very specific problem of gorilla conservation, as gorillas are exposed to considerable risk through the consequent increased contact with humans.

The first project to develop gorilla tourism began in Kahuzi-Biega in the 1970s. Far better known, though, is the program established in Rwanda a decade later in response to plans to clear a large area of the Volcanoes National Park for cattle grazing. Habitat loss was viewed as the greatest threat to the survival of the gorillas, so a carefully planned and well controlled tourism program began as a means of making the gorillas 'pay for themselves', and further conversion of park land was averted.

The conservation benefits of this program include increased surveillance of gorilla groups habituated for tourism, and more antipoaching patrols. Daily monitoring also facilitates rapid intervention by veterinarians when necessary, for example, to remove snares from injured gorillas. With increased protection from poachers, the mountain gorilla population began to recover. International awareness and concern for the plight of gorillas has generated funds for conservation activities and research, at the same time enhancing the profiles of the gorilla range states. The gorilla was adopted as a national symbol in both Rwanda and Zaire (now DRC), and is depicted on bank notes, stamps, postcards, carvings, and murals. Today both the Rwandese passport and visas for foreigners feature mountain gorillas.

International publicity and the advent of organized tourism have attracted many visitors and made tourism an important earner of foreign currency. Tourism stimulates the economy, not only via park fees, but also through expenditure on car hire, hotel accommodation, and restaurant meals. People from communities around the parks may gain employment as guides or porters, while in Uganda, a fixed proportion of the revenue from Mgahinga Gorilla and Bwindi Impenetrable National Parks is contributed to local schools and health centers through a trust fund.

Research has begun only recently on the impact on gorilla behavior of tourist visits, and on the risk of disease transmission between humans and gorillas. Prior to these studies, conservationists relied on speculation, extrapolation, and common sense to evaluate these. Studies of captive gorillas show them to have a definite susceptibility to human diseases, leading Homsy to warn of "the catastrophic consequences of unconscious gorilla tourism."65 Illnesses to which the gorillas have never previously been exposed are potentially the most dangerous and international tourists may carry viruses new to the region, such as novel strains of influenza. To minimize stress and risks to both gorillas and humans, there are very important regulations regarding minimum distances to be maintained between gorillas and people, the maximum number of tourists, and the duration of their visits, as well as guidelines for appropriate visitor behavior. A tourist should never attempt to get closer than the regulation 7 meters or, worse still, to touch a gorilla.

Tourism is a lucrative business, which puts pressures on the gorillas and on park authorities, leading some people to question the continued justification for gorilla viewing. The cost of gorillaviewing permits must be set at a level that limits demand, while maintaining the revenue that needs to be accrued by the governing authorities. Despite the dangers inherent in tourism, it provides a mechanism for ensuring that national parks and the gorillas are valued for many reasons, and has certainly contributed to their survival.

Elizabeth A. Williamson

A tourist and ranger enjoy the antics of a young gorilla in Virunga National Park.



International Gorilla Conservation Programme (IGCP) of the African Wildlife Foundation, Fauna and Flora International, and WWF-The Global Conservation Organization. IGCP has run a number of projects, is involved in population censuses, and works with national institutions and agencies to support conservation efforts, strengthen resources, and build capacity.

Other international organizations are also involved in eastern gorilla conservation, often in collaboration with local organizations. For example, the Wildlife Conservation Society has projects in all of the eastern gorilla range states:

- in DRC, it is involved in gorilla monitoring, reestablishment of park infrastructure, habitat mapping, and exploration of the lowland sector in Kahuzi-Biega;
- in Uganda, it is undertaking a biological survey of Bwindi, a census of the gorilla population, and studies on the impacts of tourism on gorilla behavior; and
- in Rwanda, it provides guard support in the Virungas and is undertaking a study of cropraiding patterns around the Volcanoes National Park.

Habitat monitoring is complementary to population monitoring, providing early warning of potential threats to gorilla ecology, and measuring the success of conservation management. The United Nations Educational, Scientific and Cultural Organization (UNESCO) and all the international space agencies established the 'Open Initiative' project, which aims to help countries to monitor World Heritage Sites via the use of satellite images. ¹⁵⁸ In April 2003, the European Space Agency provided significant funding and technical support for a joint project with UNESCO called Build Environment for Gorillas (BEGo). A series of maps

of national parks in inaccessible mountain areas (up to 5 000 m) that are home to the mountain gorilla is being produced for Uganda, Rwanda, and DRC. Comparisons with 1992 satellite images will allow the assessment of changes in gorilla habitats in World Heritage Sites. ¹⁵⁸ In a separate exercise, a computer simulation of the Virungas was developed for the Dian Fossey Gorilla Fund International. It aims to plot the movements of gorillas through a virtual reserve, to show habitat preferences, deduce the carrying capacity of the reserve, monitor human activities (including poaching), and to assist in the management of the national parks. ¹⁸⁸

In conclusion, mountain gorillas survive in small but apparently stable populations in several national parks in the Virungas, and in Bwindi. These parks are managed and otherwise supported by the governments of DRC, Rwanda and Uganda, and by conservation and research groups, with gorillabased tourism programs yielding significant funding. These gorilla populations are potentially vulnerable to disease and hunting but, by the global standards of great ape conservation, they are relatively secure at present.

Nothing similar can be said about the eastern lowland gorilla, however, the population status of which is largely unknown following the recent spread of warfare throughout its range. Many may have been killed to provide bushmeat for armed factions, displaced people, and miners, and the entire population may have collapsed as a result. As the military and political situation remains highly unstable, it is very difficult for conservationists to undertake the fieldwork required to clarify the circumstances of these gorillas, much less to support local people in their efforts to achieve sustainable development. The fates of humans and their needs for good governance, prosperity, and peace - are intertwined with the fate of the wildlife with which they share their environments.

FURTHER READING

Butynski, T.M., Kalina, J. (1998) Gorilla tourism: a critical look. In: Milner-Gulland, E.J., Mace, R., eds, *Conservation of Biological Resources*. Blackwell Science, Oxford. pp. 280–300.

Fossey, D. (1972) Vocalisations of the mountain gorilla (Gorilla gorilla beringei). Animal Behaviour 20: 36–53.

Hall, J.S., Saltonstall, K., Inogwabini, B.I., Omari, I. (1998) Distribution, abundance and conservation status of Grauer's gorilla. *Oryx* 32 (2): 122–130.

Harcourt, A.H. (1986) Gorilla conservation: anatomy of a campaign. In: Benirschke, K., ed., *Primates: The Road to Self-Sustaining Populations*. Springer-Verlag, New York. pp. 31–46.

Harcourt, A.H., Stewart, K.J., Hauser, M. (1993) Functions of wild gorilla 'close' calls I. Repertoire, context, and interspecific comparison. *Behaviour* 124: 89–122.

- Hart, J., Hart, T. (2003) Rules of engagement for conservation: lessons from the Democratic Republic of the Congo. Conservation in Practice 4 (1). http://conbio.org/inpractice/article41RUL.cfm. Accessed July 13 2004.
- Homsy, J. (1999) Ape Tourism and Human Diseases: How Close Should We Get? Report to the International Gorilla Conservation Programme. http://www.mountaingorillas.org/files/ourwork/Homsy_rev.pdf. Accessed February 10 2005.
- Hrdy, S.B. (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology & Sociobiology* 1: 13–40.
- Kalpers, J., Williamson, E.A., Robbins, M.M., McNeilage, A., Nzamurambaho, A., Lola, N., Mugiri, G. (2003) Gorillas in the crossfire: population dynamics of the Virunga mountain gorillas over the past three decades. *Oryx* 37 (3): 326–337
- Robbins, M.M., Sicotte, P., Stewart, K.J., eds (2001) Mountain Gorillas: Three Decades of Research at Karisoke. Cambridge University Press, Cambridge, UK.
- Schaller, G.B. (1963) The Mountain Gorilla: Ecology and Behavior. University of Chicago Press, Chicago.
- Seyfarth, R.M., Cheney, D.L., Harcourt, A.H., Stewart, K.J. (1994) The acoustic features of gorilla double-grunts and their relation to behaviour. *American Journal of Primatology* 30: 31–50.
- Stanford, C.B., Nkurunungi, J.B. (2003) Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: diet. *International Journal of Primatology* 24 (4): 901–918.
- Taylor, A.B., Goldsmith, M.L., eds (2002) Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, UK.
- van Schaik, C.P., Janson, C.H. (2000) Infanticide by Males. Cambridge University Press, Cambridge, UK.
- Watts, D.P. (1995) Post-conflict social events in wild mountain gorillas (Mammalia, Hominoidea) I. Social interactions between opponents. *Ethology* 100: 139–157.
- Weber, A.W. (1993) Primate conservation and ecotourism in Africa. In: Potter, C.S., Cohen, J.I., Janczewski, D., eds, Perspectives on Biodiversity: Case Studies of Genetic Resource Conservation and Development. AAAS Press, Washington, DC. pp. 129–150.
- Yamagiwa, J., Kahekwa, J., Basabose, A.K. (2003) Intra-specific variation in social organization of gorillas: implications for their social evolution. *Primates* 44: 359–369.
- Yamagiwa, J., Mwanza, N., Yumoto, Y., Maruhashi, T. (1994) Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates* 35: 1–14.

MAP SOURCES

Map 8.1 Eastern gorilla data are based on the following source, with updates as cited in the relevant country profiles in Chapter 16:

Butynski, T.M. (2001) Africa's great apes. In: Beck, B.B., Stoinski, T.S., Hutchins, M., Maple, T.L., Norton, B., Rowan, A., Stevens, E.F., Arluke, A., eds, *Great Apes and Humans: The Ethics of Coexistence*. Smithsonian Institution Press, Washington, DC. pp. 3–56.

For protected area and other data, see 'Using the maps'.

ACKNOWLEDGMENTS

Many thanks to Dan Bucknell (Dian Fossey Gorilla Fund), Thomas Butynski (Conservation International), Colin Groves (Australian National University), Alexander Harcourt (University of California, Davis), José Kalpers (International Gorilla Conservation Programme), Michael Wilson (Gombe Stream Research Center), and Juichi Yamagiwa (Kyoto University) for their valuable comments on the draft of this chapter.

AUTHORS

Sarah Ferriss, UNEP World Conservation Monitoring Centre

Martha M. Robbins, Max Planck Institute for Evolutionary Anthropology

Elizabeth A. Williamson, University of Stirling

Box 8.1 Juichi Yamagiwa, Kyoto University

Box 8.2 Martha M. Robbins, Max Planck Institute for Evolutionary Anthropology

Box 8.3 Kelly J. Stewart, University of California, Davis

Box 8.4 Elizabeth A. Williamson, University of Stirling