

# Distribution, abundance and conservation status of Grauer's gorilla

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*This report updates the distribution and provides abundance estimates for Grauer's gorilla *Gorilla gorilla graueri* across its 90,000-sq-km range. The authors divide the range of Grauer's gorilla into four regions within which they identify 11 populations and estimate a total of c. 16,900 individuals. Gorillas found in the Kahuzi-Biega lowland–Kasese region represent 86 per cent of the subspecies's total population. Further, approximately 67 per cent of known Grauer's gorillas inhabit Kahuzi-Biega, Maiko and Virunga National Parks. The eastern region of the Democratic Republic of Congo (formerly Zaire) has an extremely high human population growth rate indicating that deforestation and wildlife use trends will continue to increase. Thus, in spite of the encouraging results of surveys to identify populations and characterize abundance, no Grauer's gorilla population should be considered safe from extirpation.*

## Introduction

In 1959 John Emlen and George Schaller undertook the first range-wide assessment of eastern gorillas (Emlen and Schaller, 1960), including the first in-depth study of gorilla ecology (Schaller, 1963). Since this pioneering work, several surveys and censuses have been undertaken to determine the abundance of western gorillas *Gorilla gorilla gorilla* (e.g. Tutin and Fernandez, 1984; Carroll, 1988; Fay, 1989; Fay and Agnagna, 1992) and mountain gorillas *G. g. beringei* (e.g. Harcourt *et al.*, 1981; Weber and Vedder, 1983). However, until 1990, few attempts were made to characterize populations of eastern lowland or Grauer's gorilla *Gorilla gorilla graueri*, partly due to the remoteness and inaccessibility of many of these populations.

In 1991, the Wildlife Conservation Society, in partnership with the Institut Zairois pour la Conservation de la Nature (now Institut Congolais pour la Conservation de la Nature), began a systematic effort to identify all populations of *G. g. graueri* and evaluate their status (Hall and Wathaut, 1992). This paper summarizes this effort and presents the first range-

wide assessment of Grauer's gorilla to be based on field data since Emlen and Schaller (1960) first travelled through what is now eastern Democratic Republic of Congo (hereafter referred to as Congo). We identify and provide abundance estimates for all confirmed populations of this gorilla subspecies, and discuss prospects for survival of discrete populations in terms of threats.

## Distribution and abundance

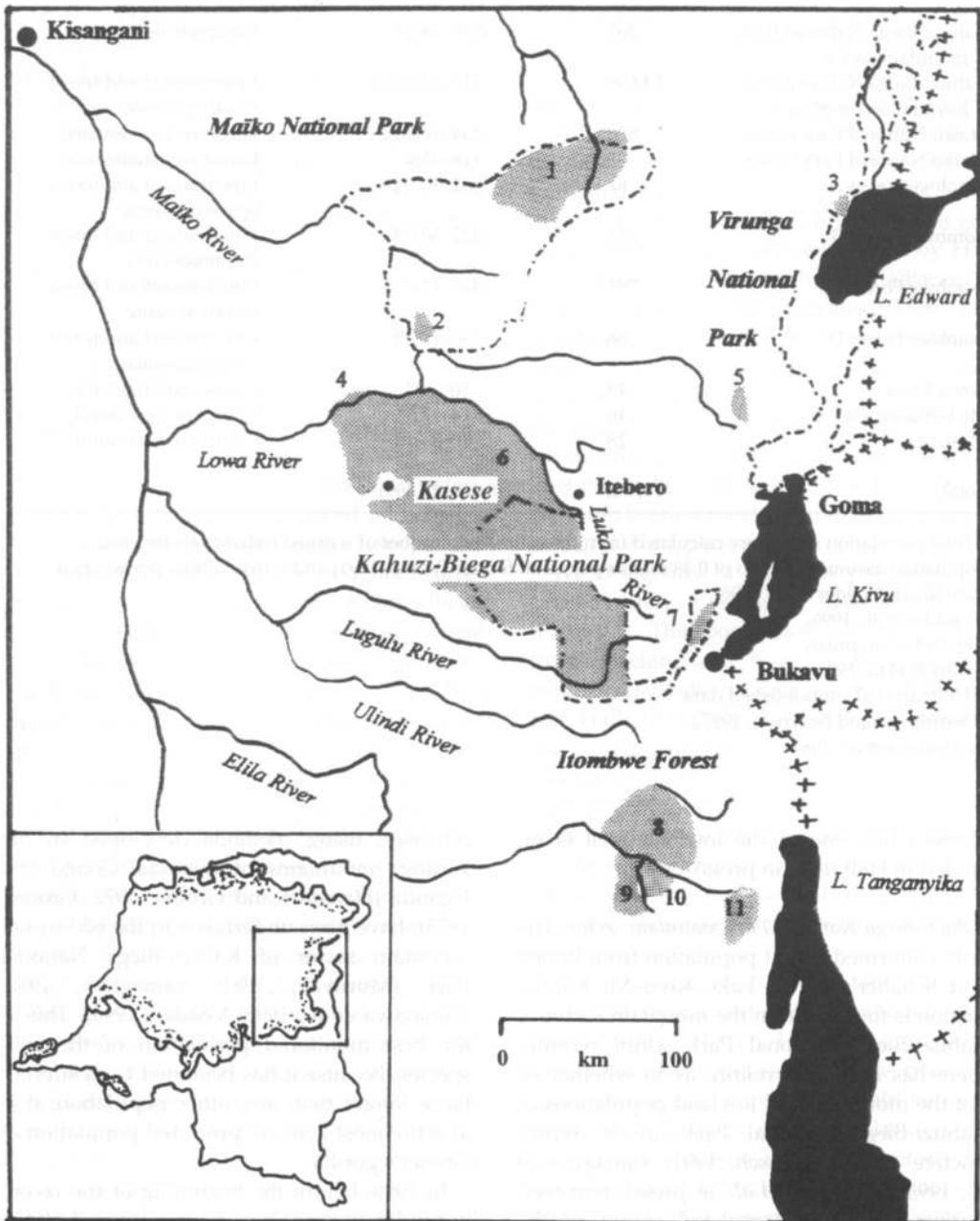
Using geographic and human barriers to movement, here we identify 11 populations within four general regions across the 90,000-sq-km range of Grauer's gorilla (Figure 1). We estimate the total population of *G. g. graueri* to be approximately 16,900 gorillas (Table 1).

### *Kahuzi-Biega National Park–Kasese region*

The entire Kahuzi-Biega National Park–Kasese region (1°8'–2°29'S, 26°51'–28°51'E) was once continuous forest (Figure 1). The habitat within this region spans an environmental gradient ranging from montane (Mt Kahuzi,

3308 m) through mountain transition to low-land tropical forest (Kasese, 600 m). An

overview of the vegetation of the mountain sector was given by Steinhauer-Burkhart *et al.*



**Figure 1.** Distribution of Grauer's gorilla (*Gorilla gorilla graueri*) populations. 1, Maiko National Park, north; 2, Maiko National Park, south; 3, Mt Tshiaberimu; 4, Lowa River; 5, Masisi; 6, Kahuzi-Biega lowland sector—Kasese; 7, Kahuzi-Biega mountain sector; 8, Itombwe Forest C; 9, Itombwe Forest A; 10, Itombwe Forest B; 11, Itombwe Forest D; national parks designated by dot-dashed lines.

**Table 1.** Population sizes for 11 subpopulations of Grauer's gorilla

Geographic region	Population size		Survey method
	Estimate*	Range	
Kahuzi-Biega National Park mountain sector	262	(245–288)†	Complete nest count
Kahuzi-Biega National Park lowland sector–Kasese	14,659	(7,410–22,203)‡	Line transect and forest reconnaissance
Maiko National Park north	826	(444–1090)§	Forest reconnaissance
Maiko National Park south	33	(18–45)§	Forest reconnaissance
Itombwe Forest A	67	(32–103)¶	Line transect and forest reconnaissance
Itombwe Forest B	211	(122–301)¶	Line transect and forest reconnaissance
Itombwe Forest C	791	(316–1267)¶	Line transect and forest reconnaissance
Itombwe Forest D	86	(46–125)¶	Line transect and forest reconnaissance
Lowa River	13	(0–26)‡	Forest reconnaissance
Mt Tshiaberimu	16	(14–17)**	Complete nest count
Masisi	28	(0–33)††	Complete nest count
Total	16,902	(8,660–25,499)	

\* Total population sizes were calculated from the estimated number of weaned individuals for each population assuming a ratio of 0.33 infants per adult female (Watts, 1991) and 0.16 juveniles per weaned individual (Vedder *et al.*, 1996).

† Vedder *et al.*, 1996.

‡ Hall *et al.*, in press.

§ Hart & Hall, 1996.

¶ I. Omari *et al.*, unpublished data.

\*\* Sarmiento and Butynski, 1997a.

†† Mwanza *et al.*, 1988.

(1995) while one of the lowland area is included in Hall *et al.* (in press).

*Kahuzi-Biega National Park mountain sector.* The only confirmed extant population from Emlen and Schaller's (1960) Lake Kivu–Mt Kahuzi Region is found within the mountain sector of Kahuzi-Biega National Park. Until recently there has been uncertainty as to whether or not the mountain and lowland populations of Kahuzi-Biega National Park are in reproductive contact (Refisch, 1991; Yamagiwa *et al.*, 1993; Saltonstall *et al.*, in press); however, during a recently completed census of the mountain population the corridor was found to be effectively severed (B. Inogwabini *et al.*, unpublished data).

Since the late 1970s several 'complete count'

censuses, using methods developed in the Virunga mountains of Rwanda, Congo and Uganda (Harcourt and Groom, 1972; Groom, 1973), have been undertaken in the 600-sq-km mountain sector of Kahuzi-Biega National Park (Murnyak, 1981; Yamagiwa, 1983; Yamagiwa *et al.*, 1993; Vedder, 1996). This is the best monitored population of the subspecies. Because it has benefited from surveillance longer than any other population, it is also the most actively protected population of Grauer's gorilla.

In 1990, before the beginning of the recent instability in the region, Yamagiwa *et al.* (1993) conducted a census and found the gorilla population to have increased slightly since the previous census. However, gorillas were no longer present in some of the regions noted by

Emlen and Schaller (1960) and Schaller (1963). In May–July 1996, a census was undertaken to assess how the mountain population had fared during the previous 6 years of political turmoil. Preliminary results reported in Vedder (1996) suggest a stable population, because there is little difference between their minimum number (245) and the one reported in Yamagiwa *et al.* ( $n = 258$ ; 1993). However, Vedder (1996) found 40 fewer nest-building individuals than Yamagiwa *et al.* (1993), which raises concerns about the actual status of the population. The fact that at least one individual in each of the tourist habituated groups has lost a hand to snares (J. S. Hall *et al.*, unpublished data) underscores the precarious status of these gorillas. More recently, there have been reports that many of these gorillas were killed in the chaos after the civil war.

*Kahuzi-Biega National Park lowland sector–Kasese.* The Utu region, described by Schaller (1963) and by Emlen and Schaller (1960) as the Walikale–Shabunda region, roughly corresponds with the area of Kahuzi-Biega National Park lowland and adjacent forest (hereafter referred to as the Kasese region) between the Lowa, Luka and Lugulu rivers. In a recent survey using line transect sampling techniques, Hall *et al.* (in press) found that Grauer's gorillas are no longer as widely distributed as they were during the time of Emlen and Schaller (1960; Figure 1). In contrast to Emlen and Schaller (1960), who reported areas of gorilla concentration with lower background densities throughout the Kahuzi-Biega-lowland–Kasesi area, Hall *et al.* (in press) found the highest densities to be within their Kahuzi-Biega lowland survey region and lower densities within their Kasese sampling zones. The authors documented anecdotal reports of heavy hunting of gorillas within the Kasese region, and attributed the combination of significantly lower group sizes and nest site densities in the Kasese survey area, coupled with a marked reduction in gorilla range, to be a result of poaching. In contrast, they concluded that the gorillas within the park's lowland sector have been relatively well protected from poaching.

#### *Maiko National Park and adjacent forest*

The Maiko National Park (1°N–1°S, 27°–28°30'E) consists predominantly of lowland tropical forest (Hart and Sikubwabo, 1994). The first biological exploration of Maiko National Park was recently completed by Hart and Sikubwabo (1994). Although they were unable to estimate gorilla densities based on their data set alone, Hart and Hall (1996) re-evaluated the original presence/absence data to provide an abundance estimate. Seven gorilla subpopulations were designated by Hart and Sikubwabo (1994) within and adjacent to Maiko National Park. Because Hart and Sikubwabo (1994) indicate a continuum of gorilla signs in map quadrants adjacent to and between many of their subpopulations, they are probably in reproductive contact. Thus, we initially consolidated them into three distinct populations. However, based on a recent visit, the westernmost population is believed extinct (J. Hart, pers. comm.).

We designated a northern population located within a roughly 2500-sq-km area (Figure 1). This population has not suffered from poaching and is believed to have remained relatively stable in recent years (Hart and Hall, 1996). The southern population is the Uvia population designated by Hart and Sikubwabo (1994) and has probably suffered from poaching and habitat pressure. Because both the northern and southern Maiko populations exist within a continuous forest block, much of which has not yet been surveyed, these two populations may well exchange individuals.

An additional gorilla population has recently been confirmed on the northern bank of the Lowa River (Figure 1; Hall *et al.*, in press). Given the width and depth of the river it is doubtful that this population could be in reproductive contact with gorillas on the southern bank (Kasese region). Therefore, they are more likely to exchange individuals with the southern Maiko population. However, recent human settlement along the road as well as the likelihood of increased forest conversion will probably impede future contact between these populations.



Female Grauer's gorilla with baby from mountain sector of Kahuzi-Biega National Park (Kristin Saltonstall).

#### *Itombwe Forest*

The Itombwe Forest (2°50'–4°S, 28°15'–29°4'E) consists of 11,000 sq km of montane, mountain transition and lowland tropical forest west of Lake Tanganyika (Figure 1). Until recently, only short-term assessments had been made of gorilla populations within this region (Emlen and Schaller, 1960; Wilson and Catsis, 1990; Hall and Wathaut, 1992; Sikubwabo, 1993). In 1996, I. Omari *et al.* (unpublished data) completed a 4-month survey using transect and forest reconnaissance methodologies. The nine subpopulations they identified can be pooled into four populations that are reproductively isolated from one another by large rivers (J. Hart, pers. comm.).

There has been extreme human pressure on the habitat of the eastern populations within this region. Hall and Wathaut (1992) and I. Omari *et al.* (unpublished data) documented the disappearance of gorillas recorded by Emlen and Schaller (1960) as a result of forest conversion to pasture. However, further west the forest is less accessible and therefore relatively well protected from conversion pressures. Moderate hunting pressure also has an impact on all populations within this forest (Hall and Wathaut, 1992; I. Omari *et al.*, unpublished data).

#### *North Kivu*

Many reports suggest several small and isolated populations in the North Kivu region of Congo (Figure 1). E. Sarmiento and T. Butynski (unpublished data) reported 14 individuals on Mt Tshiaberimu (0°5.8'–0°9.7'S, 29°24.4'–29°27.2'E) in Virunga National Park. Mwanza *et al.* (1988) reported 23–25 individuals in what they refer to as the Shingisha Mabeshi gorilla reserve (1°12'S, 28°51'E) in the Masisi zone. These are the best known populations in North Kivu.

Hall and Wathaut (1992) reported anecdotal accounts of other gorilla populations in the administrative zone of Masisi. In addition, W. M. Wathaut (pers. comm.) and J. A. Hart (unpublished data) have received reports of the presence of gorillas east of the Maiko National Park, and E. Sarmiento and T. Butynski (unpublished data) report gorilla presence at Mbohe. Thus there are potentially several small populations within this region. Until a more complete investigation can be undertaken, the number and location of different populations within North Kivu will remain unknown.

#### **Threats**

Recent studies have attempted to gauge the extent and effects of forest disappearance on both elephant and gorilla populations across central Africa (Barnes, 1990; Harcourt, 1996; Oates, 1996). In all cases, high rates of human

population growth and intensive use of forested areas have had severe impacts on wildlife populations. The Kivu region of eastern Congo has one of the highest human population densities in central Africa. Much of the region supports densities of over 300 individuals/sq km (Mbake, 1995) and, overall, it experienced a 4 per cent rate of growth between 1950 and 1984 (Wils *et al.*, 1976; Institut National de la Statistique, 1984). In recent years, human population pressures on forest environments have been exacerbated by the stay of nearly one million refugees from neighbouring Rwanda and Burundi.

A series of reports has documented the threats to Grauer's gorilla posed by hunting and forest conversion (Emlen and Schaller, 1960; Schaller, 1963; Goodall, 1980; Gaeverts and Colyn, 1988; Mwanza *et al.*, 1988; Hall and Wathaut, 1992; Hart and Sikubwabo, 1994; Hart and Hall, 1996). Today the most significant threat is the burgeoning human population's increasing need for land. Outside protected areas, people clear forest and eliminate gorilla populations with little regard for their protected status (Goodall, 1980; Hall and Wathaut, 1992; Hall *et al.*, in press). Yet forest conversion is not the only threat facing gorillas. In areas of low human population density, gorillas are often considered pests and are killed in retaliation for crop raiding and for meat (Emlen and Schaller, 1960; Schaller, 1963; Goodall, 1980; Hall and Wathaut, 1992; Hart and Hall, 1996; Hall *et al.*, in press).

While some gorillas are hunted within protected areas, the presence of the National Park Service has served as a significant deterrent (Butynski and Sarmiento, 1995; Hall *et al.*, in press). Nevertheless, setting wire snares to capture medium- and small-bodied terrestrial mammals has proved a difficult problem to combat. Even the best protected Grauer's gorillas, those habituated for tourists in the Kahuzi-Biega mountain sector, are threatened by wire snares. Killing of adult gorillas as a result of the capture of infants for illegal trade in international markets has also increased in recent years and probably occurs in national parks as well as unprotected forests.

## Discussion

The population of the Kahuzi-Biega National Park lowland sector and adjacent Kasese region represents 86 per cent of the overall *G. g. graueri* population. In the recent past these two gorilla subpopulations have been subject to different human pressures because of the non-protected status of the Kasese region. Heavy hunting in the past has probably been the cause of population decline in the region (Hall *et al.*, in press). However, today this large continuous population forms the core of Grauer's gorilla populations as a whole and should remain a focus of conservation efforts for the subspecies.

One additional threat to the gorillas of the Kahuzi-Biega National Park lowland sector stems from the recent delineation of the park boundaries in the Itebero area. Prior to the delineation, the Luka River was considered as the park boundary. A substantial area that previously had been treated as park has now been zoned outside the park. This area was found by Hall *et al.* (in press) to have the second highest densities of gorillas within the population. Because gorillas outside the park have clearly not fared as well as those within the park, efforts must be made to ensure that the gorillas are not adversely affected by the increased human use.

The gorillas of the Itombwe Forest region have been subject to varying degrees of human pressures but have persisted throughout the region (I. Omari *et al.*, unpublished data). These populations may also represent an important component of Grauer's gorilla genetic diversity because of their geographic isolation from other populations (Figure 1). Recent initiatives to work with local people in the area to protect gorillas (Schilter and Doumenge, 1993) were encouraging but have ceased with the political instability in the region. The rapidly increasing human population coupled with this instability could foreshadow the doom of otherwise viable populations of gorillas. Therefore it is imperative that the Itombwe gorillas become a more visible focus of gorilla conservation.

The gorilla population inhabiting the north-

ern portion of Maiko National Park is apparently little threatened and its conservation prospects look very good. Nevertheless, given projected human immigration and deforestation trends (Barnes, 1990), these gorillas could soon experience threats similar to those of the southern Maiko National Park and the Kahuzi-Biega National Park lowland sector-Kasese region. The park is understaffed, and training and infrastructure are poor (Hart and Sikubwabo, 1994; Hart and Hall, 1996). Efforts here should be proactive so that staff are able to deal with the complexities of human conflict.

The fate of the remaining three Grauer's gorilla populations described here is more problematic. The environmental legacy of increased land conversion and fuel-wood shortages left by the recent stay of approximately one million Rwandan refugees in the region is yet to be seen. Regardless of the refugees, these gorilla populations are surrounded by a dense human population that requires land and forest resources (e.g. fuel wood, building materials). Even if the Park Service's enforcement capacity is buttressed in the Mt Tshiaberimu area of Virunga National Park, serious questions remain about the population's long-term survival because of intense land use, isolation and its small size. Similarly, without extraordinary efforts within a tremendously volatile region, we predict that the Masisi population may also disappear in the very near future. In fact, unconfirmed reports indicate that this population has recently been eliminated. The population near the Lowa River is also at risk because of its small size and isolation.

The successful conservation of Grauer's gorilla populations will necessitate a multi-disciplinary approach. The combined results from recent surveys indicate that 67 per cent of the extant population of Grauer's gorillas is found within national park boundaries. The apparent success of the Park Service in maintaining these populations suggests that they serve as a core for conservation of the subspecies.

Although 17 per cent of forested land in eastern Congo is currently within protected areas (Hart and Hall, 1996), creative alternatives to protect other forested lands must be

explored. Due to extensive public opposition, designation of additional parks and expansion of current protected areas is not feasible. However, community-based efforts to conserve forest resources through education and sustainable uses are possible and therefore can complement conservation efforts within the parks. Efforts are also needed to control the conditions that have forced humans to compete with gorillas and other species for land. With a growing human population, demand for land and other natural resources will continue to increase.

While the total number of Grauer's gorillas is a positive indicator of long-term survival of the subspecies, we recognize that the negative effects of habitat clearance and fragmentation, as well as hunting pressures, will increase for all Grauer's gorilla populations. Thus, the optimism offered by our population size estimates should not be accompanied by complacency. Unconfirmed reports of gorillas having been killed within the mountain sector of Kahuzi-Biega National Park and of rebel activity within the lowlands highlights the urgent need to buttress conservation efforts for these gorillas. This analysis suggests that a unique opportunity remains to ensure the conservation of the subspecies well into the next millennium. However, without significant and sustained conservation efforts, the opportunity will be lost.

#### *Acknowledgments*

The Kahuzi-Biega National Park (KBNP) lowland sector and adjacent forest, Maiko National Park (MNP), Itombwe Forest surveys and the KBNP mountain sector census were financed by the Wildlife Conservation Society (WCS) in collaboration with the Zairean National Park Service. The Walt Disney Corporation provided additional support for the survey of the Kasese region and the census of the mountain sector of KBNP, while Berggorilla und Regenwald Direkthilfe provided additional support for the KBNP, MNP and Itombwe Forest surveys. The Deutsche Gesellschaft für Zusammenarbeit (GTZ) provided logistical assistance for the work in KBNP, and Zoo Atlanta collaborated in the Itombwe Forest Survey. The project could not have been undertaken without the support of A. Vedder and Mankoto ma Mbaelele. We

would like to thank all those who participated on different aspects of the surveys summarized herein. D. Skelly, T. Butynski and an anonymous referee reviewed the manuscript. G. Schaller generously shared information from previous surveys. Finally, we owe an enormous debt of gratitude to our guides, porters and field staff without whom this work could not have been carried out.

References

- Barnes, R.F.W. 1990. Deforestation trends in tropical Africa. *African Journal of Ecology*, **28**, 161–173.
- Butynski, T. and Sarmiento, E. 1995. Gorilla census on Mt Tshiaberimu: preliminary report. *Gorilla Journal*, **1**, 11.
- Carroll, R.W. 1988. Relative density, range extension, and conservation potential of lowland gorilla (*Gorilla gorilla gorilla*) in the Dzanga-Sangha region of southwestern Central African Republic. *Mammalia*, **52**, 309–323.
- Emlen, J.T. and Schaller, G.B. 1960. Distribution and status of the mountain gorilla (*Gorilla gorilla beringei*) – 1959. *Zoologica*, **45**, 41–52.
- Fay, J.M. 1989. Partial completion of a census of the lowland gorilla (*Gorilla g. gorilla* (Savage and Wayman)) in southwestern Central African Republic. *Mammalia*, **53**, 203–215.
- Fay, J.M., and Agnagna, M. 1992. Census of gorillas in northern Republic of Congo. *American Journal of Primatology*, **27**, 275–284.
- Gaeverys, H. and Colyn, M. 1986. Analyse craniométrique des populations de *Gorilla gorilla graueri* (Primates) de la rivière Lowa et comparaison avec d'autres populations du bloc forestier centre-africaine. *Annales de la Faculté des Sciences, Université de Kisangani*, 27–30.
- Goodall, A.G. 1980. *Pilot survey for conservation management of eastern gorillas in Zaire*. Final Report. IUCN/WWF Project 1731.
- Groom, A.F. 1973. Squeezing out the mountain gorilla. *Oryx*, **12**, 207–215.
- Hall, J. and Wathaut, W.M. 1992. *A preliminary survey of the eastern lowland gorilla*. Wildlife Conservation Society, New York.
- Hall, J.S., White, L.J.T., Inogwabini, B.I. et al. In press. A survey of Grauer's gorillas (*Gorilla gorilla graueri*) and chimpanzees (*Pan troglodytes schweinfurthi*) in the Kahuzi-Biega National Park lowland sector and adjacent forest in eastern Zaire. *International Journal of Primatology*.
- Harcourt, A.H. 1996. Is the gorilla a threatened species? How should we judge? *Biological Conservation*, **75**, 165–176.
- Harcourt, A.H. and Groom, A.F.G. 1972. Gorilla census. *Oryx*, **28**, 59–70.
- Harcourt, A.H., Fossey, D. and Sabater-Pi, J. 1981. Demography of *Gorilla gorilla*. *Journal of Zoological Society of London*, **195**, 215–233.
- Hart, J.A. and Hall, J.S. 1996. Status of eastern Zaire's forest parks and reserves. *Conservation Biology*, **10**, 316–324.
- Hart, J.A. and Sikubwabo, C. 1994. *Exploration of the Maiko National Park of Zaire 1989–1992: History, environment and the distribution and status of large mammals*. Wildlife Conservation Society, New York.
- Institut National de la Statistique. 1984. *Recensement scientifique de la population 1984: projections démographiques Zaire et régions, 1984–2000*. Ministère du Plan et Aménagement du Territoire, Kinshasa.
- Mbake, S. 1995. The Kahuzi-Biega National Park and the IZCN/GTZ project. *Gorilla Journal*, **1**, 12–13.
- Murnyak, D.F. 1981. Censusing the gorillas in Kahuzi-Biega National Park. *Biological Conservation*, **21**, 163–176.
- Mwanza, N., Maruhashi, T., Yumoto, T. and Yamagiwa, J. 1988. Conservation of eastern lowland gorillas in the Masisi region, Zaire. *Primate Conservation*, **9**, 111–114.
- Oates, J. 1996. Habitat alteration, hunting and the conservation of folivorous primates in Africa. *Australian Journal of Ecology*, **21**, 1–9.
- Refisch, J. 1991. *Presence des grands mammifères dans le Parc National de Kahuzi-Biega et l'influence humaine sur les populations des animaux*. Rapport dans le cadre du Projet IZCN/GTZ – Conservation de la Nature Intégrée, l'Est Zaire.
- Saltonstall, K., Amato, G. and Powell, J. In press. Mitochondrial DNA variability in Grauer's gorillas of Kahuzi-Biega National Park. *Journal of Heredity*.
- Schaller, G.B. 1963. *The Mountain Gorilla, Ecology and Behavior*. The University of Chicago Press, Chicago.
- Schilter, C. and Doumenge, C. 1993. *Programme Itombwe: rapport de mission, 19 juillet au 19 aout 1993*. IZCN/IUCN, Zaire.
- Sikubwabo, C.K. 1993. *Rapport de mission enquête faune-chasse: programme Itombwe*. IZCN/IUCN, Bukavu.
- Steinhauer-Burkhart, B., Muhlenberg, M. and Slowik, J. 1995. *Kahuzi-Biega National Park*. IZCN/GTZ Project, Zaire.
- Tutin, C. and Fernandez, M. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *American Journal of Primatology*, **6**, 313–336.
- Vedder, A. 1996. *Projet inventaire des gorilles et d'autres grands mammifères de l'est du Zaire: secteur original du Parc National de Kahuzi-Biega*. Institut Zairois pour la Conservation de la Nature/



- Wildlife Conservation Society.
- Watts, D.P. 1991. Mountain gorilla reproduction and sexual behavior. *American Journal of Primatology*, **24**, 211–225.
- Weber, A.W. and Vedder, A. 1983. Population dynamics of the Virunga gorillas 1959–1978. *Biological Conservation*, **26**, 341–366.
- Wils, W., Carael, M. and Tondeur, G. 1976. *Le Kivu montagneux: surpopulation – sous nutrition – érosion du sol. Etude prospective par simulations mathématiques*. CEMUBAC/IRS, Zaire.
- Wilson, J.R. and Catsis, M. 1990. *A preliminary survey of the forests of the 'Itombwe' mountains and the Kahuzi-Biega National Park extension, east Zaire, July–September 1989*. Project Report for WWF Project 3902.
- Yamagiwa, J. 1983. Diachronic changes in two eastern lowland gorilla groups (*Gorilla gorilla graueri*) in the Mt Kahuzi region, Zaire. *Primates*, **24**, 174–183.
- Yamagiwa, J., Mwanza, N., Spangenberg et al. 1993. A census of the eastern lowland gorillas *Gorilla gorilla graueri* in Kahuzi-Biega National Park with reference to mountain gorillas *G. g. beringei* in the Virunga Region, Zaire. *Biological Conservation*, **64**, 83–89.
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Received 24 July 1997

Accepted 5 January 1998