Population dynamics of the Bwindi mountain gorillas

Martha M Robbins [a,*], Maryke Gray [b], Edwin Kagoda [c], Andrew M Robbins [a]

[a] Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany
[b] International Gorilla Conservation Program, P.O. Box 48177, Nairobi 00100, Kenya
[c] Uganda Wildlife Authority, P.O. Box 3530, Kampala, Uganda

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ABSTRACT

Mountain gorillas are critically endangered, with just a few hundred animals remaining in each of two populations: in Bwindi Impenetrable National Park in south-western Uganda and the nearby Virunga Volcanoes on the borders of Uganda, Rwanda and the Democratic Republic of Congo. While the life-history and population dynamics of the Virunga gorillas have been studied extensively, comparable information from Bwindi has not been reported. Such studies are difficult to conduct because gorillas are long-lived, have delayed reproduction, and monitoring known individuals requires habituation of social groups. Bwindi has experienced lower levels of human disturbance than the Virungas, yet its gorilla population has shown little or no growth over the past 20 years, while a subpopulation of study groups in the Virungas have grown by 3–4% per year. Here we show that the lower growth rate at Bwindi may arise mainly from lower fertility than the Virunga study groups, rather than higher mortality. This difference may indicate that the more frugivorous Bwindi gorillas have a slower life-history, or that they are closer to the carrying capacity of their habitat. The study groups at Bwindi had a higher growth rate than the broader population, possibly because they receive veterinary care and better protection from poachers, but further analysis is necessary to understand the complex interactions among human disturbance, ecology, and the gorillas' population dynamics. Meanwhile, efforts to increase the Bwindi population should place emphasis on reducing human disturbances, improving our understanding of the impact of habitat quality, and ensuring that the gorillas can expand their home ranges into under-utilized areas of the park.

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1. Introduction

Demographic studies, through either routine censuses of a population or through long-term monitoring of known individuals and social groups, provide crucial information for monitoring change in a population and for predicting population dynamics, which are necessary components in the conservation management of endangered species (e.g., Walpole et al., 2001; Marker et al., 2003; Pusey et al., 2007). Examining how different populations of the same genus or species respond to variability in ecological conditions and the impact of illegal activities can be helpful for developing and monitoring conservation strategies that target specific populations (e.g., Ferguson and Lariviere, 2002; Nawaz et al., 2008; Wich et al., 2008).

Gorillas (genus *Gorilla*) live under different ecological conditions across Africa, which is expected to lead to variability in population dynamics and social structure (Stewart and Harcourt, 1987; Robbins, 2007). The major threats to gorillas include habitat destruction, disease, and poaching for bushmeat and the pet trade,

which currently impact different populations to varying degrees (Caldecott and Miles, 2005). For example, severe declines of western gorilla (*Gorilla gorilla gorilla*) populations have been attributed to Ebola, whereas Grauer's gorillas (*Gorilla beringei graueri*) have primarily been killed during military conflict (Walsh et al., 2003; Mehlman, 2007). The available habitats for Cross River gorillas (*Gorilla gorilla diehli*) and mountain gorillas (*Gorilla beringei beringei*) have been reduced to small areas that are surrounded by dense human populations (Harcourt and Fossey, 1981; Hamilton, 2000; Bergl and Vigilant, 2007). Western gorillas, Cross River gorillas, and mountain gorillas are classified as Critically Endangered, and Grauer's gorillas are classified as Endangered, so an understanding of the population dynamics at each location is important to their conservation (Harcourt and Stewart, 2007; IUCN, 2008).

The majority of information we currently have on the population dynamics of gorillas comes from an ecologically extreme habitat in the Virunga Volcanoes of Rwanda, Uganda, and Democratic Republic of Congo (Weber and Vedder, 1983; Gray et al., in press). The Virunga mountain gorillas live at the highest altitude of any gorilla population, and their habitat has the highest density of herbaceous vegetation but almost no fruit (Watts, 1984; McNeilage, 2001; Ganas et al., 2004). According to seven censuses of the entire

region, the Virunga mountain gorilla population has increased from 274 gorillas in 1971 to 380 gorillas in 2003, which represents an average growth rate of 1% per year (Gray et al., in press). Since 1967, the Karisoke Research Center has collected detailed demographic data on a subpopulation of habituated groups in the Virungas (Harcourt et al., 1981; Gerald, 1995). Age-based matrix modeling and agent based modeling with the Karisoke data have predicted growth rates of 3–4% per year (Miller et al., 1998; Steklis and Gerald-Steklis, 2001; Robbins and Robbins, 2004). Those higher growth rates are consistent with evidence that the Karisoke groups have had higher food density, less severe human disturbances, and a lower proportion of one-male groups than the rest of the Virungas (Kalpers et al., 2003). One-male groups may lead to lower population growth rate than multimale groups because their infants are more vulnerable to infanticide, especially after the dominant male dies (Robbins and Robbins, 2004, Robbins et al., 2007b). These distinctive aspects of the Karisoke groups highlight the need to study the population dynamics of other gorillas in other regions, but such endeavors have been hampered by the difficulty of habituating gorillas and the effort necessary to survey larger areas.

Bwindi Impenetrable National Park, Uganda (331 km^2) is located only 25 km from the Virunga Volcanoes and it contains the only other population of mountain gorillas in the world (Fig. 1a). Despite their relative proximity, the two areas differ in altitude and ecology, most notably because fruit is available at Bwindi (Ganas et al., 2004; Nkurunungi et al., 2004). Bwindi also has a slightly lower density of herbaceous vegetation than the Virungas, but its herb density is higher and its fruit availability is lower than in for-

ests inhabited by Grauer's and western gorillas. Thus Bwindi mountain gorillas can be considered to have an intermediate level of ecological conditions among populations of the genus *Gorilla*. Bwindi previously experienced high levels of human disturbance due to gold-mining, timber extraction, and poaching (Butynski, 1985), which likely are still having long-term impacts on the habitat. Since it was declared a national park in 1991, illegal activities have included poaching (primarily for duiker), firewood collection and pit-sawing, and extraction of other forest resources (Hamilton, 2000; McNeilage et al., 2001, 2006). Gorillas can be killed or maimed by snares set for other wildlife (Fossey, 1983).

The first attempt to monitor all Bwindi gorilla groups was from 1986 to 1993, and the population was estimated to be stable with 300 gorillas (Butynski and Kalina, 1993; McNeilage et al., 2006). More recently, teams conducted intensive, systematic sweep censuses of the entire park and concluded the population had increased from 300 gorillas in 1997 to 336 in 2006, suggesting a growth rate of 1% per year (McNeilage et al., 2001, 2006). From that perspective, the growth rate at Bwindi seems comparable to the overall population in the Virungas. Yet even that modest growth was called into question by genetic sampling during the census in 2006 at Bwindi, which indicated that the sweep method had double-counted 10% of the gorillas, putting the current population back at 300 individuals (Guschanski et al., 2009). Considering that in any of the censuses some groups could have been double-counted and some groups could have been not counted at all, the apparent 1% annual growth rate from 1997 to 2006 could fall within the precision of the census measurements. Yet despite the limitations of the census measurements, it seems clear that Bwindi
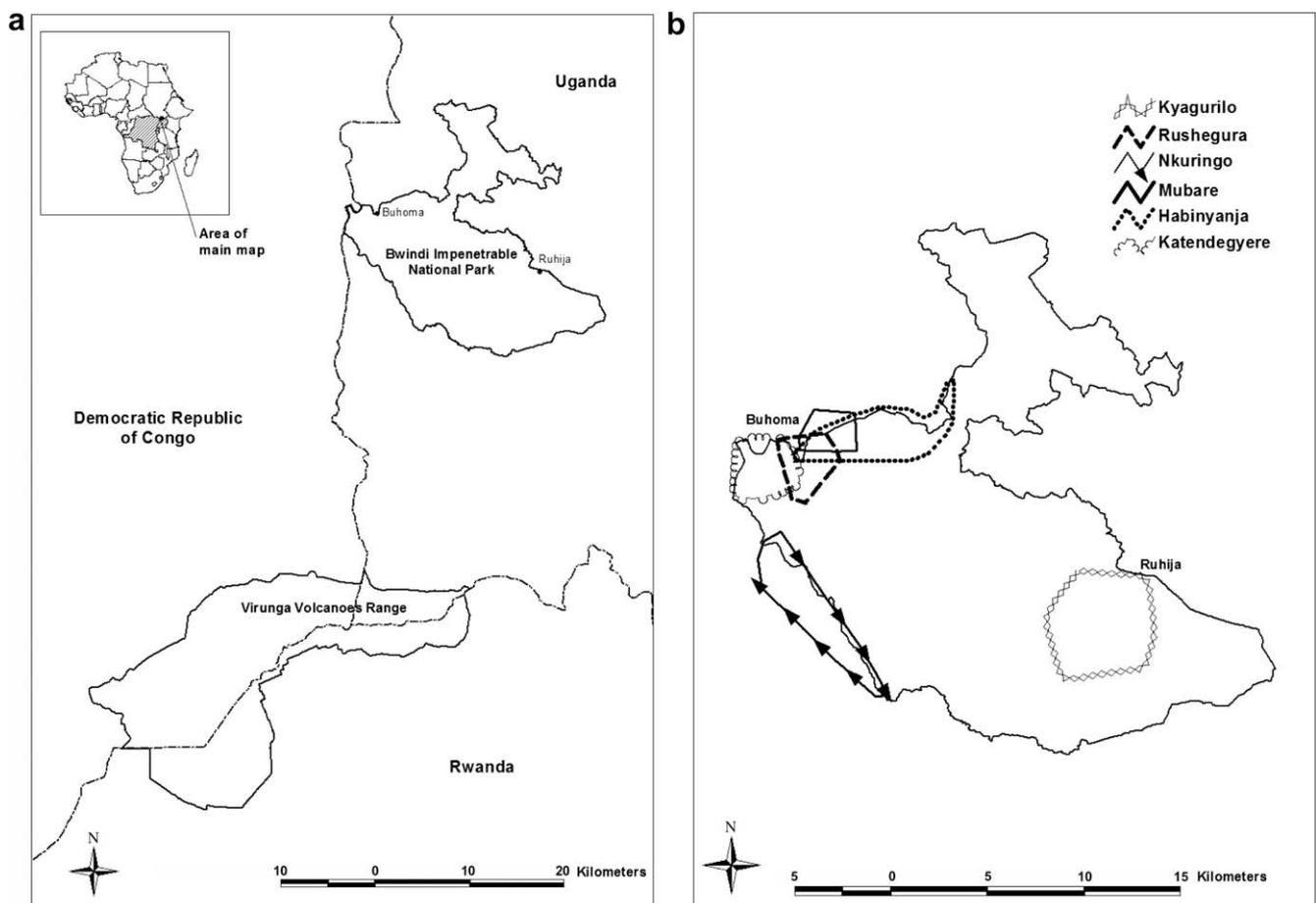
Fig. 1. (a) Map of protected areas containing mountain gorillas: Bwindi Impenetrable National Park and the Virunga Massif and (b) location of the study groups within Bwindi Impenetrable National Park.

has not kept pace with the 3–4% growth of the Karisoke groups. For example, if Bwindi had 300 gorillas in 1986, those growth rates would correspond to a population of 540–660 in 2006, well beyond the inaccuracy of the census sweep method.

The goal of this study is to investigate the population dynamics of the Bwindi mountain gorillas, and to determine why their population has not matched the growth of the Karisoke study groups. This study uses detailed demographic data that was collected through a Ranger Based Monitoring program from 1993 to 2007 at Bwindi, in which park staff monitored six gorilla groups that have been habituated for tourism and research. We compare those results with published data from Karisoke. First we examined whether female fecundity is lower at Bwindi than Karisoke, which might arise from their different ecological conditions. (Throughout this paper, we use the term "fecundity" to mean the potential reproductive capacity rather than a birth rate). Next we examined whether one-male groups were more common at Bwindi than Karisoke, and if those differences led to higher infant mortality at Bwindi. We also examined mortality beyond infancy at Bwindi, including the impact of human disturbances. Finally, we incorporated the demographic parameters into Leslie matrix models to evaluate how they would contribute to differences in the growth rates between Bwindi versus Karisoke. The calculations also enabled us to examine whether the Bwindi study groups have grown faster than their surrounding population, just as the Karisoke study groups have grown faster than the rest of the Virungas. We discuss all of those results within the context of findings from other gorilla populations and we discuss the advantages and disadvantages of using data from this type of monitoring program.

2. Methods

2.1. Study population and data collection

This study was conducted in Bwindi Impenetrable National Park, located in the southwest corner of Uganda (0°53′–1°08′N; 29°35′–29°50′E). Bwindi is an afromontane rainforest (altitude 1160–2600 m) characterized by steep-sided hills, peaks, narrow valleys, and extremely dense understory of vegetation (McNeilage, 2001). Data were collected from 1993 to 2007 from five gorilla groups that have been habituated for tourism, one group that was habituated for research, and one solitary male who was monitored for a few months after leaving the research group (Table 1). Four of the tourist groups (Ka, Mu, Ru, and Haa) ranged around Buhoma in the western section of the park, and the fifth (Nk) ranged in the southwest (Fig. 1b). The research group (Ky) ranges near Ruhija in the eastern section of the park. All of the study groups are monitored daily. The research group is observed for four hours per day and its composition is confirmed each day. The tourist groups are observed for one hour per day. Tourism is the top priority of those visits, so changes in group composition may not be noticed immediately.

For this study, we used the same age categories as those used for Karisoke mountain gorillas (Williamson and Gerald-Steklis, 2003). Infants are defined as those gorillas <3 years old (the typical age of weaning), although the census literature uses a cutoff of 3.5 years (the typical age when offspring start to build their own night nest, Kalpers et al., 2003). The age range is 3–5 years for juveniles and 6–7 years for subadults. Females 8+ years old are considered adults. Males between 8–11 years are called blackbacks, and those 12+ years old are called adult males or silverbacks (Williamson and Gerald-Steklis, 2003). Immatures are defined as the sum of infants, juveniles, and subadults (e.g., Kalpers et al., 2003).

The sex of immature gorillas can be difficult to determine due to the long hair covering their genitals (e.g., Fossey, 1983, pp. 103). For example, of the 41 gorillas that were observed to reach age 6 during this study, 23 (56%) are currently assigned to the male category based on suspected or known sex. Another ten gorillas (24%) that reached age 6 are assigned to the female category, and the remaining eight gorillas (20%) are categorized as unsexed individuals. Karisoke has not shown a sex-bias in births or infant survival (Robbins et al., 2007a), so it seems likely that unsexed gorillas at Bwindi are predominantly female, and some immature gorillas that were reported to be males may actually be females. Karisoke results can be more reliable than Bwindi because they come from a longer term study that has tracked a greater proportion of individuals into adulthood. Sex determinations become more straightforward by age 8–10, when females start to give birth, size dimorphism becomes pronounced, and males develop secondary sexual traits such as change in hair coloration. Due to the uncertain sex determinations in this study, we did not make distinctions based on the sex of gorillas below age 6, and we present further evidence of possible errors in the categorization of subadults.

A common problem in demographic analysis of primates is distinguishing between deaths and dispersal when an individual disappears from a study group (e.g., Waser et al., 1994; Alberts and Altmann, 1995). In the absence of evidence to the contrary, death was assumed to be the cause for all disappearances of infants and dominant males. Even when they are usurped by a subordinate, dominant male mountain gorillas typically remain in their group (Robbins, 1995). In this study, one dominant male "left" his group after becoming too disabled to travel, and he died six months later. So even if such incidents could initially be considered dispersal, death is a more realistic categorization of the effective outcome. For the remaining age classes, the demographic records indicate a known or likely cause for some deaths, and a known or likely destination for some dispersal. For 13 other cases, there was no clear indication if the individuals died or dispersed so we regard them as 'unexplained disappearances'. How to treat these individuals is addressed further in the Results and Discussion, including sensitivity tests to show how some results would change if all of the unexplained disappearances were considered deaths instead of dispersal.

Table 1
Summary of study groups. First, last, and total years of observation for each group. The group composition includes the average number of gorillas (total), adult females (AF), silverbacks (SB), and blackbacks (BB); as well as the percentage of observation months in which the group was multimale (mmg %). The birth rates equal the number of births divided by the number of female-years observed.

Group	Study-years		Group-years	Group composition					Birth rate	Births	Female years
	First	Last		Total	AF	SB	BB	mmg (%)			
Haa	2002	2007	5.5	20.2	6.4	2.3	2.1	55	0.284	10	35.3
Ka	1993	1998	4.8	6.0	1.4	2.0	1.7	63	0.296	2	6.8
Ky	1998	2007	9.6	14.1	5.6	1.9	2.5	72	0.131	7	53.6
Mu	1993	2007	14.3	12.8	5.0	1.0	1.1	0	0.224	16	71.4
Nk	1997	2007	10.1	18.6	4.7	2.4	4.6	100	0.212	10	47.3
Ru	2002	2007	5.5	12.0	5.0	1.0	1.0	0	0.218	6	27.5
Overall	1993	2007	49.8	14.3	4.9	1.7	2.2	46	0.211	51	241.8

2.2. Calculations for birth rates and interbirth intervals

To examine whether differences in female fecundity have contributed to a lower population growth rate at Bwindi than Karisoke, we compared the birth rates and interbirth intervals at each site. The overall birth rate at Bwindi was calculated as the total number of births observed during the study, divided by the total number of female-years observed (e.g., Singh et al., 2006; Wich et al., 2007; see also Watts, 1990 for similar calculations at each group size). We also calculated a separate birth rate for each group, which equaled the number of births observed in the group, divided by its number of female-years observed (Table 1). We performed an ANOVA to compare those birth rates for each group with published values from eleven groups at Karisoke (Robbins et al., 2006). The ANOVA determined whether the difference between the two sites was statistically significant in comparison with the variance among groups within each site. To reduce the potential impact of demographic stochasticity in that analysis, the birth rate of each group was weighted according to its number of female-years observed (for further discussion of weighted data points see Chatterjee and Price, 1991; Sokal and Rohlf, 1995; Kendall, 1998; Robbins et al., 2007b).

We report the average, mean, median, and ranges for interbirth intervals when the offspring survived to age three (IBIS), and when the offspring died before age 3 (IBID). When the offspring died before age 3, we also show the interval from that death until the mother gave birth again. We used a log-rank test to examine differences between IBIS at Bwindi versus Karisoke, and between IBIS versus IBID at Bwindi. Those tests included birth intervals that were censored by the end of observations (e.g., see Galdikas and Wood, 1990; Fedigan and Rose, 1995; Wich et al., 2004). All analyses were limited to intervals in which the beginning and end dates were both known to within 15 days.

2.3. Calculations for the potential influences of social structure

To examine whether differences in social structure could contribute to a lower population growth rate at Bwindi than Karisoke, we used Fisher exact tests to compare the proportion of births in one-male versus multimale groups at each site, as well as the proportion of offspring that survived to reach age 3. The latter comparison excluded offspring that were born after August 2004 at Bwindi, because this study ended before we could fully determine whether those infants would survive to reach age 3. A similar approach was used for the published data from Karisoke (Robbins et al., 2007b). We used a log-rank test to compare the survivorship of infants that were born in one-male versus multimale groups at Bwindi, including censoring for gorillas that were still infants at the end of the study (e.g., Ha et al., 2000; Sterck et al., 2005; Delgiudice et al., 2006).

2.4. Calculations for deaths and dispersal

We calculated mortality rates by tallying the number of deaths within a specified age category throughout the study, and dividing by the number of gorilla-years observed for that category (e.g., Alberts and Altmann, 2000, pp. 79). We calculated one mortality rate based on the assumption that unexplained disappearances were due to dispersal, and another mortality rate based on the assumption that they were deaths. For example, the deaths of three silverbacks were reported during the 85 silverback-years that were observed during the study, which represents a mortality rate of 0.035 deaths per silverback-year (three divided by 85). One unexplained disappearance of a silverback was also reported, so if that disappearance was due to death, the mortality rate would be 4/85 = 0.047 deaths per silverback-

year. Sample sizes of mortality rates were too small for meaningful statistical comparisons with Karisoke, so we merely present a graph of the results to illustrate the qualitative patterns across the age classes.

The female immigration rate was calculated as the number of immigrations into the study groups, divided by the number of group-years observed. We used a rate-based chi-square test to compare that immigration rate with published results from Karisoke (Altmann and Altmann, 1977; Robbins et al., 2009b). The rate-based chi-square test was done in an Excel spreadsheet. All other statistical analyses were performed using Systat 11 (2004, SYSTAT Software Inc., Richmond, CA).

2.5. Growth rate calculations

The habituated groups at Bwindi are not a closed population, but because all of the individuals are known, it is possible to calculate a growth rate that adjusts for exchanges with the broader population. The growth rate of the study groups was determined by starting with the initial habituated population (24 gorillas), and using Eq. (1) to calculate the number of gorillas in each subsequent month:

$$N_i = [N_{i-1} * (1 + r_m)] + A_i \tag{1}$$

In this equation, N_i represents the number of gorillas in month "i", N_{i-1} is the number of gorillas in the previous month, r_m is the monthly growth rate. The adjustment factor "A_i" equaled the number of gorillas that joined the study population through immigration or additional habituation during each month, minus the number of gorillas that left the study population through emigration. We used manual iterations to find the value of r_m that enabled us to match the observed size of the habituated population at the end of the study period (82 gorillas). The monthly growth rate was converted into an annual growth rate (r_a) using Eq. (2), to account for monthly compounding.

$$(1 + r_a) = (1 + r_m)^{12} \tag{2}$$

Published data are not available to perform the same growth rate calculations for the Karisoke study groups, so instead we used a basic Leslie matrix model (e.g., Caswell, 2001, pp. 23–25). The Karisoke matrix model uses published data for the birth rate and mortality of females only (Gerald, 1995; Robbins and Robbins, 2004; Robbins et al., 2006). Mountain gorillas are not seasonal breeders, so we used birth flow calculations. Each year of age was a separate stage in the models, even though the same birth rate was used for all adult females (reference "a" in Table 2), and the same mortality estimate was used throughout some age ranges (Table 3). A balanced birth sex-ratio was assumed in the models (based on Robbins et al., 2007a).

The growth rate for the Bwindi population is based on a scalar model (time series equation), which can be biased when used for species with long generation times such as gorillas, because it does not account for demographic stochasticity due to an unstable age structure (e.g., see Morris and Doak, 2002; Dunham et al., 2006). Conversely, sensitivity analyses with the matrix model can be biased because it does not account for potential covariance among the vital rates (Morris and Doak, 2002; Dunham et al., 2006). Unfortunately, the samples sizes from Bwindi are still too small for Leslie matrix modeling, so we could not compare the two populations using the same methodology. Although both types of calculations can produce similar results, the conclusions based their comparisons should be considered tentative (see also Doak and Morris, 1999; Sibly and Hone, 2003; Largo et al., 2008).

Table 2
Comparisons of demographic data between the Bwindi and Karisoke study groups. IBIS are interbirth intervals with offspring that survive to reach age 3.

Test	Variable	Bwindi	Karisoke	Statistics
2.1	Birth rate per group	0.211	0.257[a]	ANOVA: $R^2 = 0.33$; $F_{15,1} = 7.5$; $p = 0.015$
2.2	IBIS average (months)	56.4	47.8[a]	Log-rank test: chi-sq = 5.3; df = 1; $p = 0.022$
2.3	% of births in one-male groups	57%	23%[c]	Fisher test: $p < 0.001$
2.4	Offspring mortality before age 3	26%	27%[a]	Fisher test: $p = 1.0$
2.5	Female immigration/group-year	0.040	0.35[b]	Rate-based chi-sq = 13.3; df = 1; $p < 0.001$
2.6	Males disappear:become dominant	4:6	5:8[de]	Fisher test: $p = 1.0$

[a] Robbins et al. (2006).
[b] Robbins et al. (2009b).
[c] Robbins et al. (2007a).
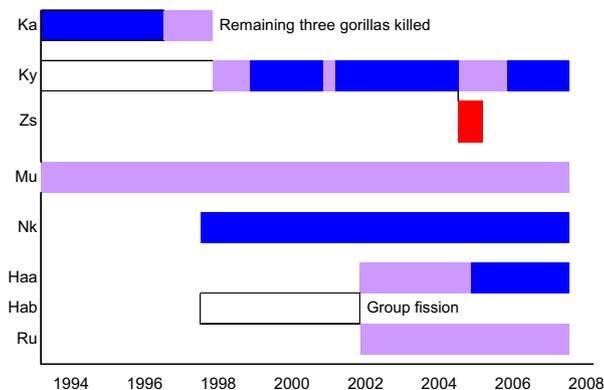[d] Robbins (1995).
[e] Bradley et al. (2005).

Table 3
Karisoke mortality parameters used in the Leslie matrix calculations. When a female reaches each year of age, "Q(x)" represents the probability that she would die before reaching the next year of age. Each year of age was a separate stage in the models, even though the same birth rate was used for all adult females (reference "a" in Table 2), and the same mortality estimate was used throughout some age ranges. Parameter values are taken directly from (Gerald, 1995) for ages 0–7, and from (Robbins and Robbins, 2004) for all subsequent ages.

Age	Q(x)
0	0.230
1	0.115
2	0.000
3	0.074
4	0.029
5	0.000
6	0.000
7	0.038
8–11	0.014
12–17	0.017
18–23	0.018
24–29	0.029
30–39	0.083
40–43	0.400
44	1.000

3. Results

3.1. Group transitions

Demographic data for the Ka and Mu tourist groups began in 1993 (Fig. 2). The Mu group has remained a one-male group with the same silverback throughout the 14.3 years of this study (Table 1). All three gorillas remaining in the Ka group were reportedly killed by villagers in late 1997 after traveling into DRC and raiding crops. The Nk tourist group was habituated in July 1997 and has remained multimale throughout the study. Four gorillas in the research group (Ky) were killed in a poaching incident in 1995, but overall demographic data are not available for the group until 1998. Zs was the dominant male of the Ky group until he became too injured to travel with the group, and died as a solitary male. The Hab tourist group was habituated in 1997, but overall demographic data are not available until it fissioned in 2002 (into the Haa and Ru Groups).

3.2. Potential influences of female fecundity

To examine whether differences in female fecundity have contributed to a lower population growth rate at Bwindi than Karisoke, we first compared the birth rate of each population. During the 242 adult female-years observed through August 2007 at Bwindi, 51 births were reported, which represents an average rate of 0.211 births/adult-female/year (51 divided by 242). The birth rates of Bwindi groups are 18% lower than published values for Karisoke, which is statistically significant in comparison to the variance among groups within each site (Test 2.1 in Table 2). These results suggest that lower female fecundity at Bwindi may contribute to a lower population growth rate than Karisoke.

A lower birth rate at Bwindi would not necessarily lead to lower population growth, however, if it arises from lower infant mortality. To examine the potential for such correlations between birth rates and infant mortality at Bwindi, we compared the interbirth intervals with offspring that died during infancy versus those that survived to reach age 3 (Fig. 3). When offspring survived to age 3 at
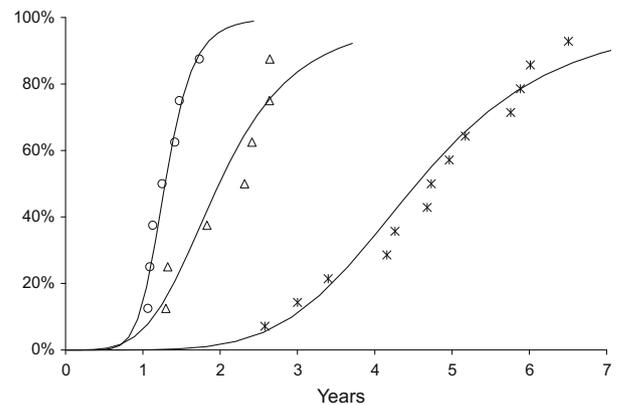
Fig. 2. Timelines for the study groups. Multimale groups are shown in dark blue, one-male groups are lavender, and a solitary male is shown in red. The white bars indicate habituated groups before overall demographic data are available.

Fig. 3. Quantile plots for the intervals between two births by the same female when the first offspring survived (asterisks) and when the first offspring died (triangles). For cases when the first offspring died, the circles show the interval from the death of that offspring until the mother gave birth again. Each point represents an observed interval, and smoothed curves are from regressions of logit (quantile) versus ln (time).

Bwindi, the interbirth intervals have averaged 56.4 + 14.4 SD months (*N* = 13, median = 56.8, range = 31–78), which is significantly longer than the 24.8 + 7.0 months when the offspring dies (*N* = 7, median = 27.8, range = 16–32, log-rank test: chi-square = 13.9, d*f* = 1, *p* < 0.001). Similar differences have been reported for Karisoke, and they show that lower birth rates can arise from lower infant mortality (e.g., Gerald, 1995).

To compensate for this confounding influence of infant mortality upon birth rates, we performed an additional comparison of female fecundity at Bwindi versus Karisoke, by examining the interbirth intervals with surviving offspring at each site. When offspring survived to reach age 3, the average interbirth interval at Bwindi has been 17% longer than published data from Karisoke. After accounting for censored birth intervals in both populations, that difference is statistically significant (Test 2.2). Thus we again found evidence of lower female fecundity at Bwindi than Karisoke, even after compensating for the potentially confounding influences of infant mortality.

3.3. Potential influences of social structure

To examine whether differences in social structure could contribute to a lower population growth rate at Bwindi than Karisoke, we first compared the proportion of births in one-male versus multimale groups at each site. At Bwindi, 57% of all births occurred in one-male groups, which is significantly higher than published value of 23% for the proportion of births in one-male groups at Karisoke (Test 2.3). This difference reflects the proportion of female-years that were observed in one-male groups at each site (54% at Bwindi versus 24% for Karisoke). Higher infant mortality has been reported in one-male groups than multimale groups at Karisoke (Robbins et al., 2007b), so we next examined whether the prevalence of one-male groups at Bwindi led to higher infant mortality than Karisoke. Of the 31 infants born before August 2004 at Bwindi, eight died before reaching age 3 (26%), which is not significantly different from the 27% mortality reported for Karisoke (Test 2.4). So although Bwindi had a greater proportion of births in one-male groups, it did not have higher infant mortality than Karisoke.

The lack of higher infant mortality at Bwindi may arise partially because this study did not overlap with the death of any silverbacks with infants in one-male groups (see below), a situation that typically leads to infanticide at Karisoke (Fossey, 1984; Watts, 1989). As a result, survivorship to age 3 was not significantly different for infants born in one-male versus multimale groups at Bwindi: 0.73 + 0.10 SE for the 24 infants born in one-male groups versus 0.71 + 0.09 SE for the 27 infants born in multimale groups (log-rank test: chi-square < 0.01, d*f* = 1, *p* = 0.98). Thus we did not find any benefit for Bwindi females to reproduce in multimale groups.

3.4. Deaths and dispersal

Preliminary mortality data for Bwindi resemble the U-shaped pattern reported for Karisoke, with higher rates for the youngest and oldest age classes (Fig. 4). The biggest potential discrepancy between the Bwindi and Karisoke mortality data is with the subadults, but only if the seven unexplained disappearances at Bwindi were due to deaths. Three of the seven missing gorillas were categorized as males, two as females, and the sex of the other two was unknown. Female dispersal has been the main reason for Karisoke groups to lose subadults (Gerald, 1995; Robbins, 1995; Robbins et al., 2009a), which might suggest that the missing subadults at Bwindi were emigrating females, even though some of them had been categorized as males (see Methods for difficulties with sex determinations). However, we cannot exclude the possibility of subadult male emigration at Bwindi, because one subadult male
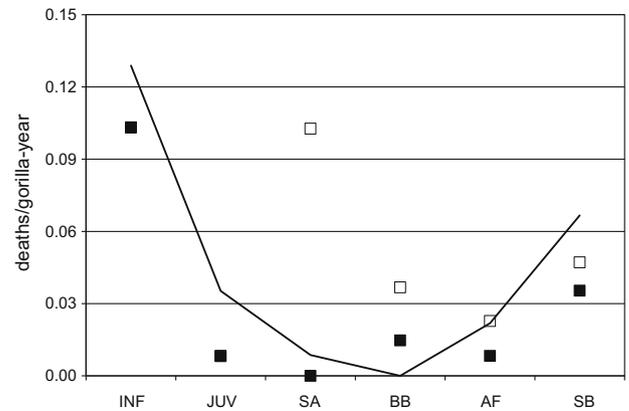

Fig. 4. Mortality rates per gorilla-year for infants (INF), juveniles (JUV), subadults (SA), blackbacks (BB), adult females (AF), and silverbacks (SB) at Bwindi (squares) versus Karisoke (solid line). The filled squares are based on the assumption that unexplained disappearances were dispersal, and the open squares show the rate if those disappearances were deaths. Karisoke data are estimated from (Gerald, 1995) for the first four age classes, and are taken from (Robbins et al., 2007b) for adult females, and (Robbins, 1995; Robbins et al., 2004) for silverbacks.

has immigrated (from an unhabituated group) and stayed long enough to eliminate any uncertainty about his sex.

Only two females have immigrated into the study groups during 49.8 group-years at Bwindi (one subadult and one adult), for an annual rate that is barely 10% of the corresponding value from Karisoke (Test 2.5). In addition to two deaths, there have been five emigrations and three unexplained disappearances by adult females. None of the ten adult females were reported to be ill or old when they were last observed.

In addition to the immigration of a subadult male (above), one subordinate silverback emigrated from the Ky group to become solitary, then returned to the group four months later and eventually became dominant. One year after the fission of the Haa group, a blackback transferred from one of the resulting groups to the other one, and then transferred back nine months later. Of the eighteen gorillas that have been observed as subordinate silverbacks, four have become dominant within a habituated group (22%), six have emigrated or disappeared without becoming dominant (33%), and the remaining eight are still subordinate (44%). Karisoke reportedly has had a similar proportion of subordinates who die or disperse versus become dominant (Test 2.6). All three deceased silverbacks had been dominant, but two had been in multimale groups, and the third did not have any infants at the time of his death.

3.5. Growth rate calculations

The number of monitored gorillas increased from 24 when the study began in May 1993, to 82 when the study ended in August 2007. The increase includes the addition of 55 gorillas that were habituated in four groups, so the final population contained only three more gorillas than were habituated (82 − 55 − 24 = 3 gorillas). However, the study groups also had a net emigration of 15–28 gorillas, depending on whether the unexplained disappearances were deaths or dispersal. To deal with the uncertainty of those unexplained disappearances, we calculated one growth rate that assumed they were deaths, and another growth rate that assumed they were dispersal. After adjusting for habituation of additional groups during the study period, and the net emigration from the study groups (Eq. (1)), the growth rate was 2.5% per year if we assume that unexplained disappearances were deaths, and 4.4% if we assume that they were dispersal. Those rates are higher than the 0–

1% annual growth that has been estimated for the overall population at Bwindi. From this perspective, it seems remarkable that the broader population would have lower growth despite receiving a net gain of 15–28 gorillas from the study groups.

Published data are not available to perform the same growth rate calculations for the Karisoke study groups, but when the published data for birth rates and mortality at Karisoke are entered into a Leslie matrix model, they predict a growth rate of 3.0% per year. Thus the predicted growth rate for Karisoke falls within the range of 2.5–4.4% for the estimated growth rates at Bwindi. From that perspective, the growth rates of the Bwindi study groups seem more similar to study groups in the Virungas than to the broader population at either site.

If the Bwindi study groups have had a similar growth rate to Karisoke, then presumably the lower birth rate at Bwindi has been offset by lower mortality than Karisoke. However, it is unclear whether any apparent difference in mortality would merely reflect demographic stochasticity, or differences in the methods for calculating growth rates, or if there are inherent differences between the two populations. Unfortunately, samples sizes are still too small for demographic modeling of the mortality rates at Bwindi. If we insert the Bwindi birth rate into the Leslie matrix for Karisoke (while still using the Karisoke mortality data) it predicts a growth rate of 2.0% per year. So even if Bwindi has the same mortality as Karisoke, the lower birth rate would not be enough to explain a growth rate of only 0–1% for its overall population.

4. Discussion

4.1. Birth intervals and birth rates

This initial study of the Bwindi mountain gorillas has shown some notable differences with the demography of their Karisoke counterparts. Interbirth intervals with surviving offspring were 17% longer at Bwindi than Karisoke, and birth rates were 18% lower (Tests 2.1 and 2.2). The lower reproductive rate at Bwindi could indicate that the population is closer to its carrying capacity (Dobson and Lyles, 1989). As a population approaches its carrying capacity, resource limitations are predicted to affect demographic parameters in the following sequence: higher offspring mortality, followed by a later age of first reproduction, lower female fertility, and ultimately higher adult mortality (Eberhardt, 1977; Gaillard et al., 2000; Eberhardt, 2002; Gough and Kerley, 2006; Grange et al., 2009). The Bwindi study groups did not have higher offspring mortality than Karisoke (Test 2.4), so our results are not consistent with the predicted sequence. However, that sequence may be more appropriate for seasonal breeders than for mountain gorillas. If a female has a narrow seasonal window of opportunity for reproduction, then her optimal strategy might be to attempt reproduction even when resource limitations create a high risk that the offspring will die (because even if the offspring dies, her fitness may not be lower than if she had not reproduced at all). In contrast, mountain gorillas are not seasonal breeders (Gerald, 1995), and their interbirth intervals span several years. If resources become limited, it would seem better for the female to insure the survival of an offspring by extending the interbirth interval by a few months, rather than wasting years of maternal investment to resume reproduction prematurely.

The lower reproductive rate at Bwindi could also indicate that its population has a slower life-history. Gorillas are more frugivorous at Bwindi than in the Virungas (Ganas et al., 2004; Robbins, 2008), so their diet may be more seasonal. Seasonality of food availability has been reportedly led to slower life histories in other primates, because the risks of starvation are reduced when the metabolic needs for maturation are spread over a longer period

of time (Janson and van Schaik, 1993; Wich et al., 2004; Brockman and van Schaik, 2005). Preliminary data suggest that western gorillas and Grauer's gorillas also have slower reproductive rates than Karisoke, and they are also more frugivorous (Yamagiwa and Kahekwa, 2001; Robbins et al., 2004; Masi et al., 2009; Breuer et al., 2009). Further study is needed to determine whether the more frugivorous gorillas have longer lifespans than at Karisoke, which would represent further evidence of a slower life-history (Charnov, 1993), but would not be expected for populations that are closer to their carrying capacity (Eberhardt, 1977).

4.2. Deaths and dispersal

There were few indications of differences in mortality between Bwindi and the Karisoke gorillas, although the dataset from Bwindi is relatively small. Mortality was highest for infants and adults, following a similar pattern to what has been found in other great apes (Hill et al., 2001; Nishida et al., 2003; Wich et al., 2004). In particular, there was no difference in infant mortality among Bwindi and Karisoke, the age class containing the most data, but this may be impacted by the occurrence or absence of infanticide.

The Bwindi study groups had a net emigration of 15–28 gorillas, depending on whether the unexplained disappearances were deaths or dispersal. If gorillas transferred only among established groups, then we might expect study groups to have an even balance of immigrations and emigrations (e.g., Waser et al., 1994; Alberts and Altmann, 1995). However, dispersing males almost always become solitary, and females can join solitary males instead of established groups, so some net emigration is expected (Harcourt, 1978; Robbins, 1995; Robbins et al., 2009b). Overall, because many animals have dispersed out and very few have immigrated into the study groups, the overall net increase in the number of gorillas in the habituated groups has been rather low, group sizes have been relatively constant, and the study groups have been acting as 'sources' not 'sinks' for the overall population.

All indications are that the Bwindi population has suffered less human-induced mortality than the Virunga population. For example, we are aware of seven gorilla killings in the past 13 years in Bwindi (three in the Ka Group and four in the Ky Group), compared to the nearly 40 deaths in the past 18 years in the Virungas, largely due to the political instability in the region (Kalpers et al., 2003; Jenkins, 2008). While the increasing number of confiscated gorillas in Rwanda and DRC emphasize the severity of the threat in the region (four Virunga gorillas as of 2008, Spelman, 2007), we are aware of only one incident of poachers being arrested in Bwindi following an unsuccessful attempt on the Nk Group in 2002 (Stephen Asuma, personal communication). While it is possible that killings go unreported, given the high density of people that live surrounding both protected areas and the local knowledge of the value of the gorillas via ecotourism, it is unlikely that park staff would not hear of news of gorilla poaching. Approximately 75% of the Bwindi gorilla population is unhabituated versus only 29% in the Virunga Volcano Massif. Given that the unhabituated gorillas are not monitored regularly, it is possible that they have suffered higher mortality due to humans or some other cause such as disease.

4.3. Growth rates

After adjusting for net emigration and additional habituation during the study, the estimated growth rate of the Bwindi study groups was 2.5–4.4% per year, depending on whether the unexplained disappearances were deaths or dispersal. Thus the growth rate of the Bwindi study groups seems higher than the overall population (0–1%), just as the Karisoke study groups have shown higher growth (3–4%) than the overall population in the Virungas (1%).

The Karisoke study groups reportedly have better habitat than the rest of the Virungas, which could hypothetically contribute to higher birth rates (McNeilage, 1995). However, computer simulations suggested that the higher growth at Karisoke was due to lower mortality, because higher birth rates would have led to a greater proportion of immature gorillas than has been observed (Robbins and Robbins, 2004).

In contrast with Karisoke, the Bwindi study groups are more broadly distributed throughout their park, so their habitat quality is less likely to differ from their unhabituated counterparts (Fig. 1b). Thus it seems more plausible that the Bwindi study groups have lower mortality than the broader population, which might be expected because monitored groups receive veterinary care and better protection from poachers. Demographic stochasticity could also contribute to lower mortality in the Bwindi study groups, because they have not yet had group disintegrations that would lead to infanticide. Our findings lead to the question of whether habituated groups are representative of the population as a whole and draws attention to the difficulties of drawing conclusions about population dynamics of a long-lived species with low reproductive rates from individuals in few social groups that likely receive better protection than the population as a whole (Robbins and Robbins, 2004).

4.4. Conservation implications

Another park-wide census with genetic sampling is needed to more accurately determine growth of the entire Bwindi population, but our results indicate that a growth rate greater than 1% per annum should be possible. If the population is experiencing little or no growth under the current ecological conditions and management schemes, then what could be done to improve the situation? Even if the gorillas are near the carrying capacity of their current habitat, further growth could be possible by expanding into areas of the park that are not utilized. The eastern region of the park appears to have suitable habitat (Caillaud et al., unpublished data), yet it has been devoid of gorillas during the three most recent censuses (McNeilage et al., 2001, 2006; Guschanski et al., 2009). Local people claim that gorillas were hunted out of the area in the 1970s and 1980s, and it still contains some of the highest signs of human disturbance (McNeilage et al., 2001, 2006; Guschanski et al., 2009). Similarly, the gorillas have rarely used the northern sector of the park, where access may be limited due to the small 'neck' connecting it to the main part of the park (Fig. 1). Ongoing analysis of habitat utilization by the habituated groups will help us understand their 'natural' tendency to expand their home range into new areas, but meanwhile such expansion could be facilitated by management strategies to reduce human disturbances in those areas. The gorillas already receive better protection than most primate populations (Gray and Kalpers, 2005), but further improvements might reduce mortality in the currently utilized areas, especially for the unhabituated groups. More detailed demographic information about the unhabituated groups may become available if genetic sampling during future censuses will allow us to track the births, deaths, and dispersal of most individuals (Guschanski et al., 2009). Future studies could incorporate such data into models of population dynamics, along with information about temporal and spatial variability in illegal activities and habitat quality (Harcourt, 1995).

One noteworthy aspect of this study is that most of the demographic data was collected through a Ranger Based Monitoring Program. This shows that data can be collected concurrently with the other activities of the park staff, such as taking tourists to see the gorillas (Gray and Kalpers, 2005). Given the large investment necessary to habituate and monitor gorillas, it is important to maximize the benefits obtained from those efforts. Routine (re)training, supervision, and feedback to the field staff can help them to appreciate the value of accurate data collection, and it might reduce potential difficulties such as the mis-sexing of immature individuals. Another potential improvement would be to have teams on standby to search for missing gorillas to determine if they died or dispersed. Nonetheless, we recognize the limitations faced by the rangers as they need to balance the priorities of tourism and data collection. We also recognize the vital role that tourism plays in supporting mountain gorilla conservation, by providing funding for the park staff, and by giving the surrounding communities an economic incentive to preserve the species (Hamilton, 2000; Kiss, 2004; Kruger, 2005).

Developing effective conservation strategies for optimizing environmental conditions of a critically endangered species with a slow life-history requires integrating knowledge of its population dynamics with an understanding of the past and present human-induced threats. This study exemplifies how such a task is complex and challenging. The results of this study can be incorporated with information on habitat quality and illegal activities to create a multifaceted approach to conserving this population, as well as contribute to gorilla conservation elsewhere.

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