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Violent encounters between social units hinder the growth of a high-density mountain gorilla population

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Density-dependent processes such as competition for resources, migration, predation, and disease outbreaks limit the growth of natural populations. The analysis of 50 years of mountain gorilla data reveals that social behavior changes observed at high group density may also affect population growth in social species. A sudden increase in social group density observed in 2007 caused a threefold increase in the rate of violent encounters between social units (groups and solitary males). A fivefold increase in the rate of infanticide and seven cases of lethal fights among mature males were subsequently recorded, and the annual subpopulation growth rate declined by half between 2000 and 2017. The increase in infanticide alone explains 57% of this decline. These findings highlight the complex relationship between population density and growth in social species and hold important implications for the management of island populations.

INTRODUCTION

Habitat loss and fragmentation affect a growing number of animal taxa (1). Although most large mammal populations living in shrinking tropical forest islands decline as fast or faster than their habitat and eventually face a risk of extinction, efficient conservation measures have, in rare cases, led to population recovery (2, 3). As protection efforts become more successful, a growing number of endangered populations living in small habitat patches are expected to recover and increase in density (4). Moreover, animal "crowding" may occur when habitat degradation causes animals to move toward remnants of suitable habitat (5). Managing small, isolated, yet high-density populations of endangered mammals will likely become a major challenge in the near future (6).

In open populations, animals can migrate out of high-density areas (2, 7). In isolated populations, food limitation generally reduces the growth of high-density terrestrial and marine mammal populations (6–13). Nutritional stress negatively affects health, decreases female fertility, increases age at first reproduction, and reduces survival rates. Other density-dependent processes such as predation and infectious disease outbreaks may also slow population growth (8–10, 14–16).

The influence of social organization and structure on individual vital rates is well documented at the social group level (17–19). For example, in the African wild dog (Lycaon pictus), an obligate cooperative breeder, per capita fertility and pup survival increase as group size increases (17). In meerkats (Suricata suricatta), adult survival is negatively correlated with group sizes (20). In mountain gorillas (Gorilla beringei beringei), demographic simulations suggest that a low number of adult males compared with females may cause more frequent group disintegration, followed by infanticides by extra-group males (21). Evidence that the social structure of group-living

mammals influences density dependence at the population level is more scarce (17). In species exhibiting agonistic intergroup interactions, the frequency of aggressive behaviors is expected to increase when group density increases, which may have negative consequences for the population growth rate (17). In cooperative breeders, an inverse density dependence of the population growth rate (population-level demographic Allee effect) is theoretically possible but has found very little empirical support (17, 22).

As a result of conservation measures put in place over the last 50 years, mountain gorillas are currently the only great ape taxon whose abundance is steadily increasing (23, 24). They occur in two small, isolated forest islands: the 330-km^2 Bwindi-Sarambwe forest in Uganda and the Democratic Republic of the Congo, and the 455-km^2 Virunga massif at the border between Rwanda, the Democratic Republic of the Congo, and Uganda (Fig. 1). The Virunga population has grown from an estimated 260 to 290 individuals in 1973 to a minimum of 604 individuals in 2016 (23, 25). Local gorilla densities now reach 2 to 10 times the average density of other gorilla populations (26). The population is completely isolated from the Bwindi-Sarambwe population and surrounded by some of the densest human populations in Africa (24). Both individual gorilla density and social group density are, therefore, expected to continue to increase.

The Dian Fossey Gorilla Fund's Karisoke Research Center has been collecting detailed demographic and behavioral data on a subset of the Virunga population since 1967. As of December 2017, the Karisoke database included demographic data on 413 gorillas and 26 social groups (Fig. 1; figs. S1, S2, and S9; and text S1). This study focused on 50 years of data collected between January 1968 and December 2017. During this period, the study subpopulation accounted for 18 to 25% of the overall Virunga population. We investigated how the subpopulation growth rate varied over five decades. We then focused on the 2000–2017 period, during which an exceptional series of social group fission events led to a marked increase in group density. We hypothesized that the number of encounters between social units (i.e., group-group encounters and group-solitary male encounters) would increase during this period and that resulting aggression would affect population growth.

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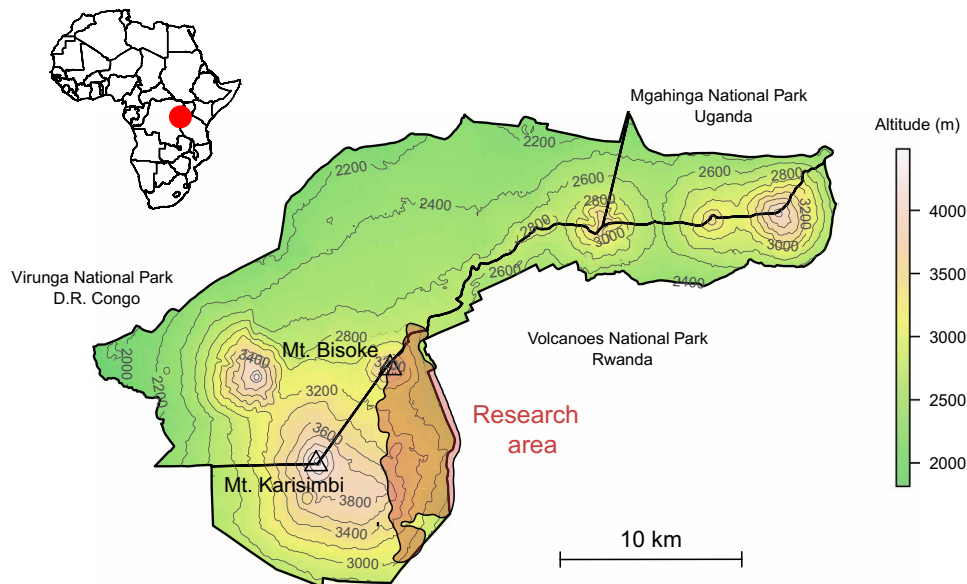[†]These authors contributed equally to this work.

Fig. 1. Location of the research area in the Virunga massif at the border of Uganda, Rwanda, and the Democratic Republic of the Congo. The transparent red area corresponds to the 95% kernel outline of the 2000–2017 study group relocation data. D.R. Congo, Democratic Republic of the Congo.

RESULTS

Population growth

Between 1968 and 2017, the subpopulation studied at Karisoke experienced three distinct demographic periods (Fig. 2). From 1968 to ca. 1980, the overall Virunga population severely declined, and the partially protected study subpopulation remained small, slow-growing, and unstable because of habitat reduction, cattle grazing, and poaching for bushmeat or for sale as trophies and captive specimens (27) (Fig. 2 and figs. S1 and S2). The 1980–2006 period was characterized by a fast growth of the study subpopulation early on [up to 6.2% annually around 1993; 95% confidence interval (CI), 5.8 to 6.6] following a major investment by the Rwandan government in antipoaching and gorilla-focused ecotourism (Fig. 2) (28). Conservation efforts were temporarily reduced between 1994 and 1998 because of the 1994 Rwandan genocide and related insecurity and instability affecting the African Great Lakes region. The study subpopulation growth rate decreased but remained above 3.5% (95% CI, 3.2 to 4.0) between 1994 and 2006 (Fig. 2). By 2006, the study subpopulation was composed of three multimale groups, all reaching well above the 10-individual average group size for Virunga mountain gorillas (29) (observed range, 24 to 65 individuals; Fig. 3A and figs. S1 and S2). The last period started in 2007 and continued beyond the end of our study period in 2017. During that time, a series of group fissions and formations occurred, leading to a threefold increase in the number of social groups (Fig. 3B). New groups kept forming in the following years. These new groups often exhibited short tenure lengths and frequently changed in composition (Fig. 3A). During this period, the number of solitary males sighted every year increased in a similar proportion (fig. S3). Two proximate factors explain this exceptional and sudden change in social organization. First, the three original groups included between six and eight mature males (age > 12 years old) each, among which five to six were less than 20 years of age, an unusually high number for the species (30). Several of these younger males caused social instability in their natal groups and dispersed with some of their natal groups' adult females (26). Sec-

ond, two of the dominant males of the three groups were more than 30 years of age, an advanced age for a male gorilla. One of them was challenged by two of his sons, which resulted in the fission of group BEE (Beetsme) into groups TIT (Titus) and KUY (Kuryama) in 2007 and 2008 (Fig. 3A). The second dominant male died in 2008, which indirectly caused the fission of group SHI (Shinda) into groups NTA (Ntambara), UGE (Ugenda), and URU (Urugamba) (26) (Fig. 3A).

Most of the new groups that formed after 2006 had limited options to move away from the area because of crop fields and human populations on the east side, volcanoes on the north and west side, and other gorilla groups on the south, north, and west sides (29). Between 2000 and 2017, the annual rates of immigration and emigration into and out of the study subpopulation were relatively low, ranging between 0 and 4%, except in 2016 when the emigration rate reached 7% (mean, 2.4%; fig. S4). In comparison, 5.1% (range, 0 to 22.3%) of the individuals from the study subpopulation transferred between study groups every year, on average. Yet, several groups were able to shift their home range to lower-density areas farther south (26). As a result, the total area occupied by the study groups increased by 53% between 2006 and 2017, causing a 30.4% drop in individual gorilla density (Fig. 3B). However, group density for the 2007–2017 period remained between 92 and 199% greater than in that in June 2006 (Fig. 3B). These exceptional circumstances constituted a real-life experiment and an opportunity to investigate the demographic consequences of an increase in the number of social units.

Interunit encounters and lethal aggressions

The two- to threefold increase in social unit density (i.e., groups and solitary males) observed after 2006 had a marked cascading effect on gorilla behavior and demography. First, the median overlap between social group home ranges was multiplied by 11.4 (Fig. 4). As a consequence, the number of encounters observed between social groups tripled (×3.3, N = 538 encounters; Fig. 4 and fig. S5). Second,
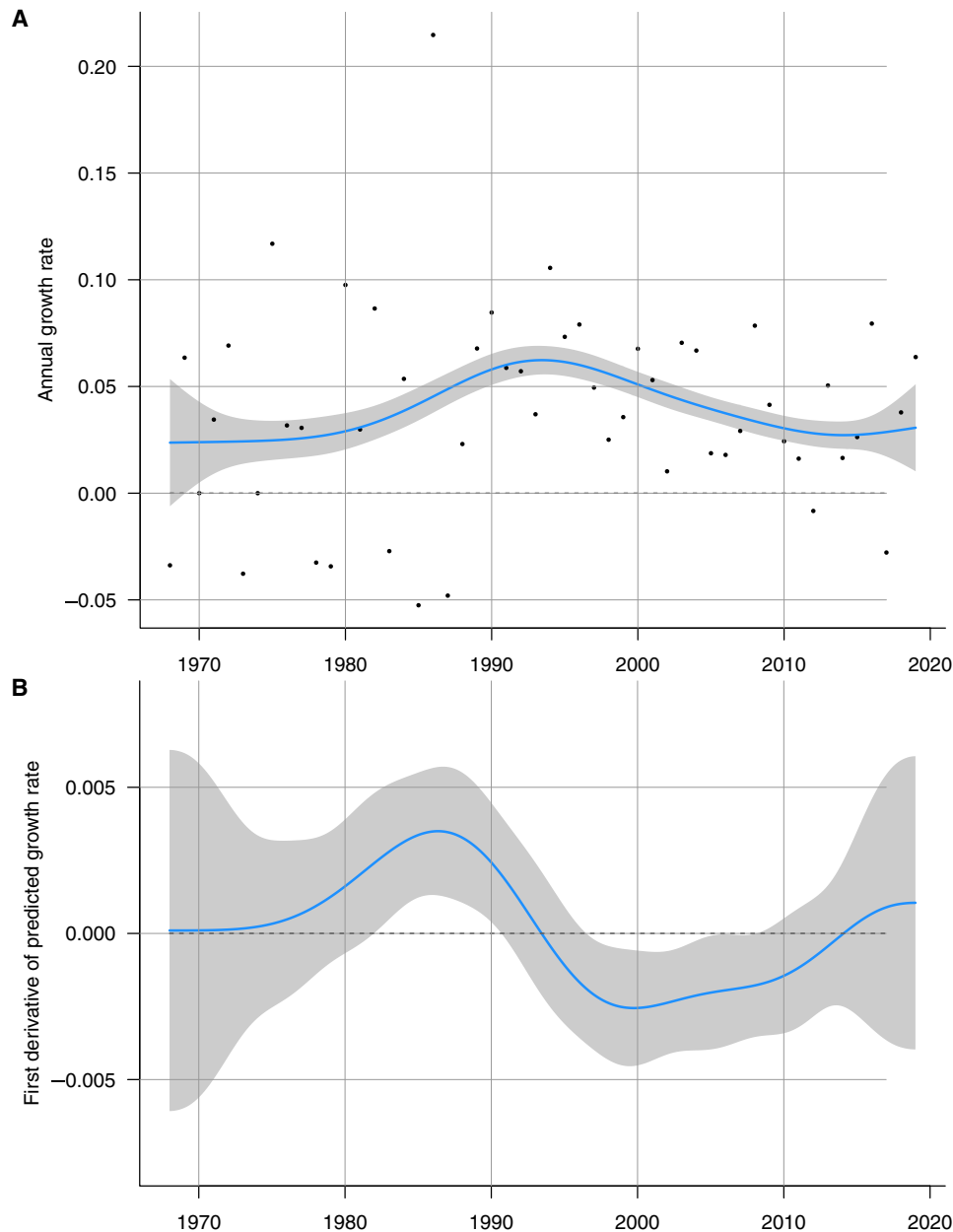
Fig. 2. Growth of the study subpopulation. (**A**) Fluctuation of the annual growth rate of the study subpopulation between 1968 and 2017. Black dots: Independent estimations for each of the 50 years of the study. Blue line: Fitted values of a generalized additive model with moving average temporal autocorrelation structure of order 1. Gray band: Simultaneous 95% CIs. The statistical significance of the fitted slope can be assessed on (B). (**B**) First derivative of the slope of the growth rate curve derived from the generalized additive model and shown on (A). The gray band corresponds to the simultaneous 95% CIs of the estimates of the slope. Areas where the gray band does not overlap with the $y = 0$ line indicate periods when the growth rate varies significantly. After a period of increasing growth in the mid and late 1980s, the growth rate started declining significantly in the late 1990s. CIs for more recent slope estimates (2008–2017) become larger because of the absence of data from the future.

as immature and adult female gorillas generally disperse during encounters (*31*), the annual rate of female transfers between social units (calculated after excluding group fission events) increased from 0.0137 (95% CI, 0.0053 to 0.0349) to 0.139 (95% CI, 0.113 to 0.170) transfers per adult female per year between 2000–2006 and 2007–2017, a 10-fold increase (total: 82 cases in 850 female·years; chi-square test, $df = 1$, $P < 10^{-6}$; fig. S6).

Aggressive behaviors between mature males were reported during 22% of directly observed encounters ($N = 625$) between 2002 and

2017. Among mountain gorillas, infants are frequently targeted by mature males of the opponent social unit during aggressive encounters (*32*). In the study subpopulation, the average number of encounters each infant was exposed to, per year, more than tripled from 2006 to 2007 and remained higher compared with pre-2007 values until 2017 (fig. S7), so we expected to observe an increase in the number of infanticides. The infanticide rate increased significantly from 0.020 (95% CI, 0.007 to 0.058) to 0.090 (95% CI, 0.060 to 0.132) infanticide per infant per year between 2000–2006 and 2007–2017,
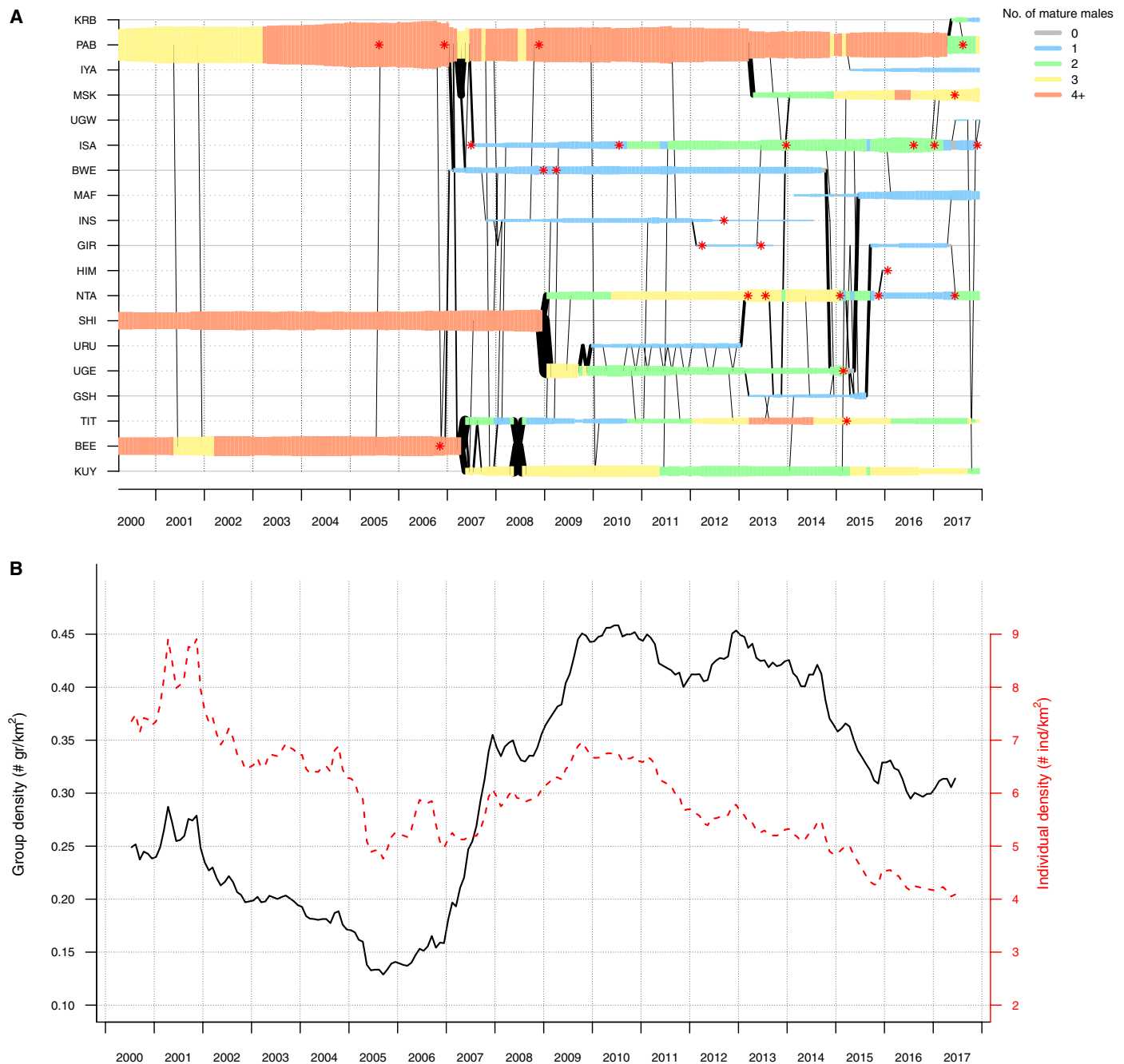
Fig. 3. Change in social dynamics and local density between 2000 and 2017. (**A**) Variation in study group composition between 2000 and 2017. Each horizontal colored band corresponds to a gorilla group, with color indicating the number of mature males (>12 years old) in the group, and thickness indicating the number of individuals in the group. Black lines indicate individual transfers between study groups, between consecutive months. Black line thickness is proportional to the number of individuals transferring. Red asterisks: Infanticide events. Time step: 1 month. (**B**) Monthly variation in gorilla group and individual density in the study area. The total areas used to calculate density values were the 95% kernel densities of all relocation data available for the 12-month periods centered around each month of the timeline. gr, group; ind, individual.

a 4.5-fold increase (total: 25 cases in 398 infant·years; exact Wilcoxon-Mann-Whitney test, $P = 0.029$; Fig. 5).

The proportion of infanticide committed by group silverbacks (68%) and solitary males (32%) was consistent with the proportions of group-group encounters (60%, 538 of 893 encounters) and group-solitary male encounters (40%, 355 of 893 encounters), revealing that

solitary males were not more likely to engage in infanticide than group males (chi-square test, $df = 1$, $P = 0.56$; fig. S5).

Because infants represented 22% of the study subpopulation on average between 2000 and 2006, the increase in infanticide was responsible for an estimated $(0.090 - 0.020) \times 22\% = 1.54\%$ decrease in the growth rate of the study subpopulation. The annual growth
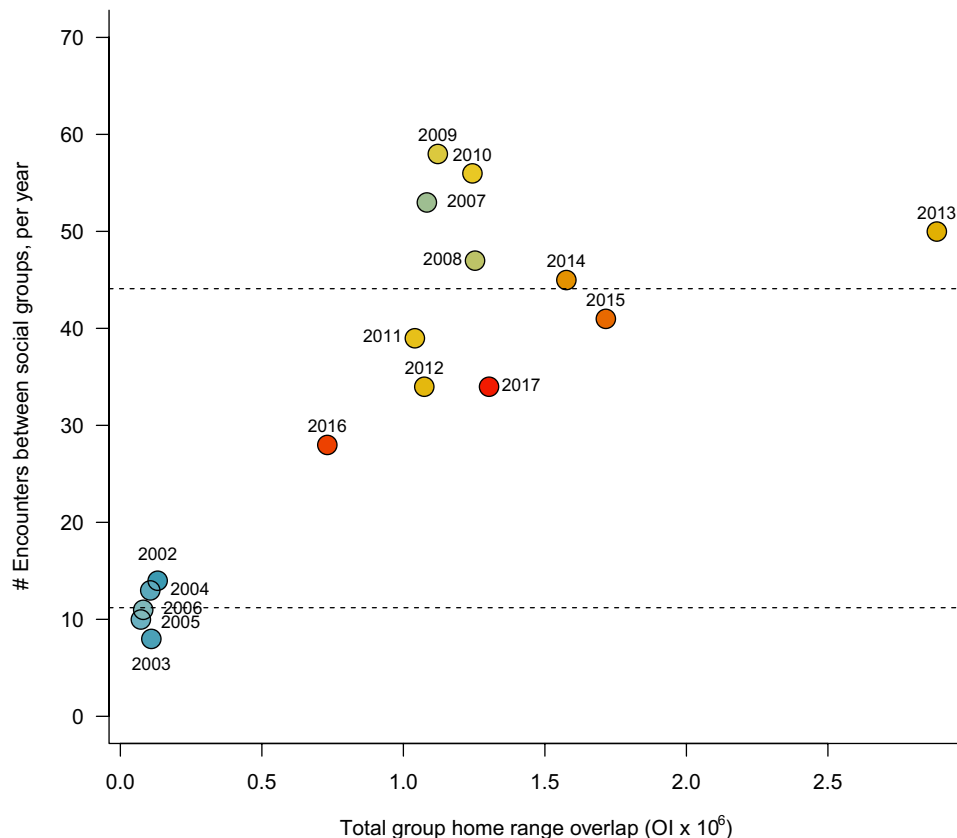
Fig. 4. Relationship between the group home range overlap and the number of encounters observed between social units from 2002 to 2017. Horizontal dashed lines indicate the average annual number of encounters for the 2002–2006 period (before group density increase) and the 2007–2017 period (after group density increase).
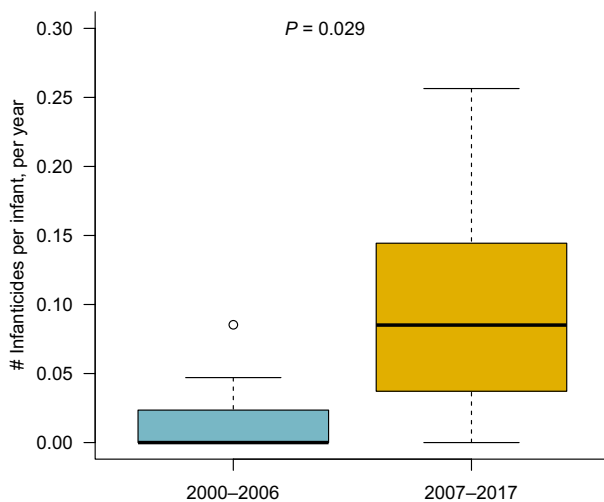

Fig. 5. Rate of infanticide before and after the increase in group density. The significance of the difference between the two distributions was tested using the exact Wilcoxon-Mann-Whitney test.

rate dropped from an estimated 5.05% (CI, 4.45 to 5.65) in 2000 to 2.37% in 2017 (95% CI, 0.38 to 4.35), corresponding to a 2.68% decline (Fig. 2A). The increase in infanticide alone, therefore, explained $100 \times 1.54/2.68 = 57\%$ of the overall change in the growth rate since 2000.

Violent encounters between social units also increased mature male mortality. During the 2007–2017 period, seven mature males died after being wounded during an encounter with another social unit, compared with one in the 2000–2006 period. These deaths will likely not have the same direct long-term demographic consequences as infant mortality because female fertility does not depend on the number of males. However, dominant males protect their group's infants against extra-group males, and their death is often followed by a rise in infanticide (32).

Variation in female fertility

Lethal aggressions between social units accounted for 57% of the decrease in growth rate between 2000 and 2017. We tested whether part of the remaining variation in the growth rate could be explained by a decrease in female fertility. As a proxy for fertility, we calculated interbirth intervals (IBIs) following surviving births and tested whether IBI varied significantly between 1976 and 2017. The analysis of a generalized additive model fitted to the time series indicated no significant variation in IBI ($P = 0.10$; fig. S8).

DISCUSSION

Fifty years of mountain gorilla demographic and behavioral data reveal important fluctuations in the growth rate of the subpopulation monitored by the Karisoke Research Center in Rwanda. The growth rate increased between 1968 and the mid-1990s and, while still positive, has been declining ever since. Our main finding was that behavioral

factors (ranging behavior and aggressive social interactions) rather than ecological factors (e.g., feeding competition, infectious diseases, and predation) were the primary drivers of the decline in the growth rate observed between 2000 and 2017. To our knowledge, few empirical or modeling studies have demonstrated the effect of social behavior on the regulation of high-density natural populations. Silk (*33*) showed that in a captive population of bonnet macaques (*Macaca radiata*), female fertility and infant survival were inversely correlated with the number of females per adult male. In the absence of nutritional constraints, unidentified behavioral or physiological factors may have played a role. A simulation work from Robbins and Robbins (*21*) also suggests that in mountain gorillas, an increase in the number of females per males due to higher male mortality may lead to more frequent group disintegration and, consequently, cause an increase in infanticide. In a key study of the long-term demography of endangered northern muriquis from Brazil (*Brachyteles hypoxanthus*), Strier and Ives (*6*) found that while the population was increasing fivefold, prime-male mortality and female fertility increased in conjunction with a major behavioral change. The animals became more terrestrial and were able to access previously underused food resources, which likely caused the increase in female fertility. Males became even more terrestrial than females and experienced increased mortality, possibly because of increased exposure to predators and pathogens. In a long-term study of Serengeti lions, Packer (*19*) found that the existence of a threshold minimum viable pride size because of an intense between-pride territorial competition, combined with a higher mortality of cubs born in large prides suffering from feeding competition, explained the presence of "saltatory equilibria" in the population growth curve.

We found that infanticides occurring during aggressive encounters between social units explained 57% of the recent decline in the subpopulation growth rate. Secondary factors, such as feeding competition, male-male aggressions, stress, and infectious diseases, may explain most of the remaining 43%. The relative importance of these factors remains to be investigated. It is unlikely that an increase in feeding competition played a major role, as feeding competition is low overall, and there was no evidence of an overall decline in food availability in the study area between the 1980s and 2010 (*34*). In a study focusing on five key food plant species accounting for 70% of the gorilla diet, Grueter *et al.* (*34*) found that the biomass of three species increased between 1988–1989 and 2009–2010, while the biomass of the remaining two species declined. Furthermore, Caillaud *et al.* (*26*) observed that group home range sizes remained stable between 2000 and 2012 and that group size had little impact on group home range sizes, which indicates that feeding competition was likely low during this period. Last, no significant increase in IBIs was observed during the study period, as one would expect if feeding competition had increased significantly and reduced female fertility. Yet, we cannot exclude that feeding competition had small, undetected, negative effects on female fertility and individual survival. Other factors that may have contributed to the decrease in the growth rate include stress and disease. Physiological studies revealed intergroup encounters to be a significant source of stress, increasing cortisol levels by as much as 8.8 times (*35*, *36*). Increased stress, high home range overlap, intergroup contact rates, and frequent female transfers may also increase individual susceptibility to pathogens, increase pathogen transmission, and thus contribute to the observed growth rate decline.

Our study also suggests that in social mammals, group density may play a larger role than individual density in regulating population growth. This may apply especially to species exhibiting aggressive intergroup encounters, such as social carnivores [e.g., (*20*, *37*)] or some primate species [e.g., (*38*)]. This has considerable implications for conservation because it suggests that the amount of space a species may require will vary depending on its social organization at any one moment in time. For example, in gorillas, three groups each containing 20 animals may require less space than six groups containing 10 animals. This is of particular relevance for the mountain gorillas in the near future.

Population surveys conducted between 2003 and 2017 in the entire Virunga massif have revealed that population growth and gorilla spatial distribution are not homogeneous across the Virunga massif. Between 1989 and 2010, the area where the Karisoke study subpopulation ranged had the highest group density in the massif, and the density grew at a higher rate than the overall population (*29*, *39*). However, the last population census (2015–2016) indicated that the rest of the Virunga population is currently experiencing growth rates that are similar to the growth rate of the Karisoke subpopulation from 1989 to 2010 (*23*). In addition, these groups are becoming larger and include an increasing number of mature males (*23*), as did the Karisoke study subpopulation 20 years ago. If these groups fission and the rate of interunit encounters increase, we expect the regulatory processes described in this study to affect the broad population.

Even if the growth rate is currently declining in at least one area of the Virunga massif, it remains positive. The Virunga gorilla population is still growing at a high, 3% annual rate (*23*), and we can expect group density to keep increasing in the future. As a consequence, aggressive encounters between social units will likely become more frequent. Protected-area managers should expect infanticides, injuries, and overall stress to increase. The decrease in animal welfare will have ethical implications that will affect conservation policies in place in Rwanda, Uganda, and the Democratic Republic of the Congo.

MATERIALS AND METHODS
Study site
The Virunga massif is a 455-km^2 afromontane forest divided into three national parks: Virunga National Park in the Democratic Republic of the Congo, Volcanoes National Park (VNP) in Rwanda, and Mgahinga Gorilla National Park in Uganda. Initiated in 1967, the long-term research and conservation project led by the Dian Fossey Gorilla Funds Karisoke Research Center (Karisoke) focuses on gorilla groups ranging predominantly in the central and southeast region of VNP over a surface area of 50 km^2 and at an elevation ranging between 2400 and 3800 (Fig. 1).

Demographic data
The current study is based on 50 years of demographic data collected at Karisoke between 1 January 1968 and 31 December 2017 and includes 413 individuals and 26 social groups in total. Dian Fossey founded Karisoke in September 1967, when she began the habituation and monitoring of three mountain gorilla groups ranging on the slopes of Mt. Bisoke and Mt. Karisimbi in VNP (*40*). All gorilla groups included in this 50-year-long study originate from these groups (fig. S2). New groups formed when individuals (generally adult females) joined a solitary male or when an established multimale group split into two groups (*41*). Individual gorillas were reliably

identified using nose prints and other morphological characteristics. Birth and death events were recorded, as well as individual dispersal between, into, and out of the study groups. Missing individuals were considered dead if they showed signs of severe illness or injury before their disappearance or were old (>30 years for males and >35 years for females). The occurrence of encounters between social units at the time of disappearance was also considered. For example, subadult or adult females that went missing after an encounter with an unknown group likely transferred to that group and were not considered dead.

Cases of infanticide were either observed directly or established during postmortem examinations. In addition, the disappearance of healthy infants aged ≤3.5 years during aggressive encounters with solitary males or other groups were considered cases of infanticide (*32*). A total of 35 infanticides were recorded over the 50-year study period.

Between 1993 and 1998, monitoring efforts were periodically reduced or interrupted because of civil unrests in Rwanda and the Democratic Republic of the Congo (table S1). Between 1999 and 2017, the monitoring of the study groups was continuous, for up to 4 hours a day. However, data collection was interrupted when groups crossed the Democratic Republic of the Congo border (Table S1).

Population growth rates

Analyses presented here focus on social groups that persisted for at least 30 days and included at least one male above 12 years of age, referred to as "mature male" or "silverback." Groups composed of only adult females and/or young individuals were excluded from the analyses as they rarely occur and are unstable. The number of births (*Nbirths*) and deaths (*Ndeaths*) observed every year and the total number of individuals (*Nind*) present in the study groups every month (on the 15th day of the month) were used to calculate the population growth rate for each of the 50 years of the study

$$R_i = \frac{Nbirths_i - Ndeaths_i}{\sum_{j=1}^{12} Nind_{i,j}/12}$$

with *i* and *j* denoting the year and the month, respectively. Reduced monitoring efforts during the 1993–1998 period likely resulted in some birth and death events being missed. In particular, it is possible that individuals born during an observation gap died before observations resumed and, therefore, could not be included in the database. However, such cases did not affect the numerator of the above formula and only had a negligible impact on the denominator. R_i is, therefore, robust to observation gaps.

A generalized additive model was fit to the R_i time series using R 3.6.0 and package mgcv (*42*, *43*), following methods described by Simpson (*44*). The model included a thin plate regression spline as a smoothing basis and a moving-average (MA) temporal autocorrelation structure of the order 1. Attempts to use autoregressive (AR) correlation structures or a combination of MA and AR resulted in higher Akaike information criterion (AIC) values. Annual growth rates calculated during periods when the study subpopulation was small were expected to be more variable. To account for heteroskedasticity in growth rate estimates across years, we included variance weights in the model, with each weight being calculated as the mean population size for that year divided by the overall mean population size across the entire study period. This resulted in the AIC decreasing by 26 points. R_i values and 95% CIs predicted by

the fitted model are shown in Fig. 2A. Estimates of the first derivative of the growth rate were also calculated, along with the associated 95% CIs, following Simpson (*44*) (Fig. 2B). This first derivative corresponds to the slope of the growth rate in relation to time. A positive derivative indicates an increase in the growth rate, and a negative derivative indicates a decrease in the growth rate. The CI of the first derivative indicates whether the growth rate variation was statistically significant. If the 95% CI of the first derivative did not include "zero," we could conclude that the growth rate variation was statistically significant at that particular time.

Interunit encounter data

All occurrences of auditory and visual encounters between study groups, as well as between study groups and solitary males, were recorded between 2002 and 2017 (N = 893 encounters). During an auditory encounter, either the involved social units exchanged chest-beats and calls or only one unit engaged in chest-beats and/or calls without receiving an acoustic response from the other unit. Encounters occurring outside of the 4-hour daily data collection period were inferred from tracking data. Encounter sites were identified when the trails of two social units crossed each other and the vegetation was significantly trampled as a result of male charges and displays, which may also be performed by other group members. Traces of blood, hair, or diarrhea were often found at encounter sites. When the vegetation was trampled, blood and diarrhea were observed, and a solitary male was observed in the area on the same day, the day before, or the day after; the encounter was classified as an encounter between a group and a solitary male. The presence of fresh wounds in a gorilla group or an unusually long daily travel distance was also considered as a cue that, in conjunction with the signs mentioned above, could indicate a recent encounter. Encounters that involved the same social units and occurred on the same day were pooled and were considered as a single encounter (*45*).

Home range analysis

From September 1999 to December 2017, Global Navigation Satellite System coordinates were recorded at the nest site of monitored groups, as well as at the groups' locations at 12:00. Nest site time stamps were set to 0:00. For each group and for each year between 2002 and 2017, home range utilization distributions were estimated using the biased random bridge (BRB) approach (*46*). This approach explicitly considered the correlation between successive relocations by assuming that each movement step followed the biased random walk model and could be represented by a "bridge" bivariate density distribution. The estimated utilization distribution (UD) of a gorilla group was the combination of the bridges estimated for all the steps. BRB-based utilization distributions were calculated using the "adehabitatHR" R package (*47*). BRB estimation was restricted to steps of less than 72 hours and more than 50 m. Grid cell size was set to 200 m by 200 m. The smoothing parameter was set to 100 m, and the diffusion coefficient was estimated using maximum likelihood. The home range overlap index (*OI*) was calculated for each year and each pair (*i*, *j*) of gorilla groups, following Caillaud *et al.* (*26*)

$$OI_{i,j} = \iint UD_j \cdot UD_j \, dx \, dy$$

Each year's total home range overlap was also calculated by summing all the $OI_{i,j}$ for that year.

Female fertility

As a proxy for female fertility, we calculated IBIs for all instances when two consecutive births were observed in a female that was continuously monitored between these births. IBIs corresponding to cases when the first infant died before the second birth were excluded from the analysis. The longest observed surviving IBI was almost 8 years. As no IBI equal or greater than 8 years could be observed during the first 8 years of the study, all the IBIs that ended before 1976 were excluded from the analysis. In some cases, the birth date of infants was not accurately known. When the uncertainty of the date of birth was greater than 30 days, the corresponding IBI was also excluded from the analysis.

A generalized additive model was fit to the IBI data. The model included a thin plate regression spline as a smoothing basis for the date of the second birth. We also added the identity of the female as a random effect variable. We calculated 95% CIs for the IBIs (fig. S8). The overlap between the CIs estimated throughout the 1976–2017 period was very high. We concluded that the IBIs did not vary significantly during this period, and we did not proceed in calculating first derivatives and associated 95% CIs.

Migration rates

We calculated the annual immigration and emigration rates into and out of the study subpopulation for adult females and mature males. Adult individuals that disappeared after showing signs of severe illness or injury before their disappearance were added to the number of death events and excluded from the migration rate calculation, along with individuals who disappeared at an age >30 years for males and >35 years for females (see section on "Demographic data"). Adult males that emigrated from the study groups, became solitary, and were not sighted for two consecutive years were considered as emigrants.

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