Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Estimating abundance and growth rates in a wild mountain gorilla population

A.-C. Granjon[1], M. M. Robbins[1], J. Arinaitwe[2], M. R. Cranfield[3], W. Eckardt[4], I. Mburanumwe[5], A. Musana[6], A. M. Robbins[1], J. Roy[1], R. Sollmann[7], L. Vigilant[1] & J. R. Hickey[8]

1 Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
2 Bwindi Mgahinga Conservation Area, Uganda Wildlife Authority, Kampala, Uganda
3 Mountain Gorilla Veterinary Project, School of Veterinary Medicine, University of California Davis, Davis, CA, USA
4 The Dian Fossey Gorilla Fund International, Musanze, Rwanda
5 Parc National des Virunga-sud, Institut Congolais pour la Conservation de la Nature, Gisenyi, Rwanda
6 Parc National des Volcans, Rwanda Development Board, Kigali, Rwanda
7 Department of Wildlife, Fish, and Conservation Biology, University of California Davis, Davis, CA, USA
8 International Gorilla Conservation Programme, Kigali, Rwanda

Keywords
capture–mark–recapture; *Gorilla beringei beringei*; monitoring; non-invasive genetic sampling; population growth; population survey.

Correspondence
Anne-Céline Granjon, Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany. Tel: +49 341 3550 206
Email: celine_granjon@eva.mpg.de
Martha M. Robbins, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
Email: robbins@eva.mpg.de

Editor: Res Altwegg
Associate Editor: Philipp Boersch-Supan

Received 24 April 2019; accepted 20 November 2019

doi:10.1111/acv.12559

Abstract

Monitoring population size and growth over time is vital for the conservation of endangered species. Mountain gorillas *Gorilla beringei beringei* remain in two small populations that span the borders of the Democratic Republic of Congo, Rwanda and Uganda. Each population contains two subpopulations that receive differing levels of protection: the monitored groups are visited daily by park staff and researchers and can be counted by sight, whereas the number and growth rate of unmonitored gorillas must be estimated indirectly. Here, we re-analyze published data from a survey in 2010 combined with new results from a survey conducted during two sampling occasions in 2015 and 2016 to estimate mountain gorilla abundance and growth in the Virunga Massif between 2010 and 2016. Using genetic analysis of non-invasively collected samples and two capture–mark–recapture estimates, we estimated that the 186 detected genotypes represented 221 (95% credible interval: 204–243) to 251 (205–340) unmonitored gorillas in 2016. Together with the 418 monitored gorillas, the overall population of the Virunga Massif thus reached 639 (622–661) to 669 (623–758) individuals. We estimated the growth of the entire Virunga Massif population at about 3% per year, but determined that the growth of the monitored gorillas (4.4%) mainly drove that increase. In contrast, the trend of the unmonitored subpopulation could not be determined with confidence because both models provided 95% CI that encompassed zero: 0.5% per year (−0.7% to +1.7%) and 1.1% (−2.7% to +4.4%). While the overall growth rate represents a rare success story for primate conservation, our results highlight the need for greater protection of unmonitored gorillas.

Introduction

Estimating the growth rates of wildlife populations is essential for assessing the effectiveness of conservation measures. Ideally, growth rates should be estimated through long-term studies with time-series data investigating fecundity and survival of marked individuals (Robbins *et al.*, 2011; Gil-Weir *et al.*, 2012; Budy *et al.*, 2017). However, such data are often not available for elusive species or species with long life histories. Alternatively, it is possible to infer growth rates from time series of abundance or density estimates. Although less data intensive, this approach still requires sufficient data to obtain accurate and precise estimates, and necessitates applying the same estimation method across time to make estimates comparable (Dennis, Munholland & Michael Scott, 1991; Gerber, Demaster & Kareiva, 1999; Kühl *et al.*, 2017).

Capture–mark–recapture (CMR) methods are considered the gold standard to obtain estimates of abundance and density (Otis *et al.*, 1978; Begon, 1983; Eggert, Eggert & Woodruff, 2003; Cam, 2009). These require repeated detection/non-detection data of uniquely identifiable individuals to provide estimates of abundance that account for imperfect detection, that is, the problem that we may not detect all individuals in a population of interest. Particularly for rare and elusive species, it is difficult to collect sufficient detection data to obtain precise estimates, which limits the power to detect increases or declines in populations (Nussear & Tracy, 2007; Wanyama *et al.*, 2010; Piel *et al.*, 2015). Species living in social groups present yet another challenge to abundance estimation because most CMR models assume that individuals are detected independently from one another (White & Burnham, 1999; Miller, Joyce & Waits, 2005; Borchers & Efford, 2008). However, for group-living species, the probability of detecting an individual is dependent upon first detecting the group, thereby linking individual detection probabilities to that of the group. Models that do not account for non-independent detections of individuals may not include the true abundance in their confidence interval (e.g. Clement, Converse & Andrew Royle, 2017; Gupta, Joshi & Vidya, 2017; Hickey & Sollmann, 2018).

The endangered mountain gorillas *Gorilla beringei beringei* embody many of the aforementioned challenges for abundance and growth estimation, as they are wide ranging, rare, elusive and group living. These apes are of high conservation interest and live in two isolated populations: the Bwindi–Sarambwe ecosystem that crosses the border of Uganda and the Democratic Republic of Congo (DRC), and the Virunga Massif that spans the borders of the DRC, Rwanda and Uganda. Mountain gorillas have been habituated to human presence for tourism and research and monitored daily for decades, such that more than half have been habituated to human presence since the 1990s (Gray *et al.*, 2013; Roy *et al.*, 2014). These monitored gorilla groups benefit from greater protection against poachers and from veterinary interventions to treat life-threatening diseases or snare wounds, such that monitored gorillas have been reported to experience higher growth and lower mortality rates than unmonitored gorillas (Robbins *et al.*, 2011).

Since the 1970s, regular counts of the unmonitored gorillas have occurred via ‘sweep’ surveys (Weber & Vedder, 1983; Aveling & Harcourt, 1984; Sholley, 1990; McNeilage *et al.*, 2001, 2006; Kalpers *et al.*, 2003; Guschanski *et al.*, 2009; Gray *et al.*, 2010, 2013; Roy *et al.*, 2014). These surveys employed multiple teams simultaneously moving through the entire forest for 2–3 months to search for trails and the nests that gorillas build each evening. In 2006, Guschanski *et al.* (2009) included genetic analysis of fecal samples as part of a population survey in Bwindi, thereby improving the simple field-based nest counts to include non-invasive identification of unique genotypes (Guschanski *et al.*, 2009). Roy *et al.* (2014) further improved the methods to incorporate genetic analyses of samples collected over two sweeps, instead of only one, which allowed the first CMR abundance estimate for that population of mountain gorillas. The CMR analysis revealed that only half of the unmonitored individuals were detected in a given sweep, which meant that detection probability was in fact much lower than the previously assumed near-perfect detection (Guschanski *et al.*, 2009; Gray *et al.*, 2013). In particular, solitary males had extremely low detection probabilities (only one of 16 lone silverbacks was detected in both sweeps).

The estimation of growth rates must be approached differently for the monitored and unmonitored subpopulations. For the monitored groups, growth can be calculated based on daily demographic records, including births, deaths, immigrations and emigrations of uniquely identified and habituated individuals. Because both the Bwindi–Sarambwe ecosystem and the Virunga Massif are surrounded by human settlements and represent geographically closed populations, immigration and emigration are only possible internally between the monitored and unmonitored subpopulations, but not between the two spatially distinct populations. Therefore, the records of immigrations and emigrations in the monitored groups are informative with regard to the unmonitored subpopulation, and mountain gorillas represent a rare case in which intrinsic growth (due to births and deaths) of both subpopulations may be disentangled from net changes in population size due to migrations between the subpopulations. However, for the unmonitored subpopulation, the changes in sampling effort over successive surveys prevented any direct estimation of growth rates because researchers could not distinguish between a higher number of observed individuals derived through improved detection probability versus a true increase in abundance (Guschanski *et al.*, 2009; Gray *et al.*, 2013; Roy *et al.*, 2014).

Here, we estimate population size and growth of the Virunga Massif mountain gorilla population using data collected during a single sweep in 2010 (Gray *et al.*, 2013) and during two sweeps in 2015 and 2016. First, we compare the minimum population abundances in 2010 and 2016, based on the count of unique genotypes detected from unmonitored gorillas combined with the count of monitored individuals. Second, we (re-)estimate the abundance of the unmonitored subpopulation in 2010 and 2016 using two Bayesian closed-population CMR methods. We first used a standard null model, which uses the detection histories of individuals across the 2015 and 2016 sweeps and assumes equal detection probability across individuals (henceforth referred to as the one-step model). We also used a two-step model (Hickey & Sollmann, 2018), which uses the detection histories of groups and solitary individuals across sweeps, as well as of individuals within groups, assuming equal detection probabilities within each of these categories. The two-step model may overestimate the abundance more than the one-step model, but its broader confidence intervals are more likely to encompass the true abundance (Hickey & Sollmann, 2018). Finally, we estimate growth rates from 2010 to 2016 for the entire Virunga Massif population and for the monitored and unmonitored subpopulations separately, and discuss the implications for mountain gorilla conservation.

Materials and methods

Sweeps and sample collection

For the 2010 survey, we used the detection and genotype data described in Gray *et al.* (2013). The field survey in 2015–2016 followed previously detailed methods (Gray *et al.*, 2013; Roy *et al.*, 2014). In brief, field teams of four to five members conducted two ‘sweeps’ of the Virunga Massif, from October to December 2015 (57 days) and again from March to May 2016 (59 days). Teams moved through the forest on foot without the aid of paths, following approximate compass bearings and cutting narrow reconnaissance trails (recces) spaced about 500 m apart.

From the recces, teams followed detected gorilla trails estimated to be <5 days old. Gorillas construct nests each night in which they typically defecate prior to departing. Upon finding a nesting site, teams assigned the gorilla group a unique identity and collected fecal samples from every nest that contained dung. Teams followed the gorilla trails and aimed to sample all nests from three consecutive nesting sites per group, ideally including a fresh nesting site from the previous night. All samples collected were associated with GPS locations entered into handheld electronic devices (Toughpad FZX1, Panasonic™, Japan) equipped with Cybertracker software (http://www.cybertracker.org) that was customized for this survey. Groups were described in the field with the terms ‘putatively monitored’ or ‘putatively unmonitored’.

All fecal samples were collected for genetic analysis following the two-step procedure (Nsubuga *et al.*, 2004). In brief, we submerged approximately 4 g of feces in a tube containing 96% ethanol. After 24–30 h, we transferred the fecal matter into tubes filled with silica beads to complete desiccation. Silica tubes were then stored at room temperature until exportation to Germany where they were stored at room temperature until extraction, then at +4°C for long-term storage.

We selected a subset of the collected samples for genetic analysis. To estimate the number of unmonitored gorillas, we extracted and attempted to amplify DNA from all samples of solitary males and all groups identified as ‘putatively unmonitored’. We also genotyped selected samples from nesting sites of groups identified as ‘putatively monitored’ to confirm that teams had correctly identified them in the field. The genetic analysis revealed that some putatively unmonitored groups were, in fact, monitored. Therefore, we refer to the confirmed monitored and unmonitored groups (after genetic analysis) as ‘monitored’ and ‘unmonitored’ respectively.

Genotyping of gorilla feces

We extracted all selected samples using the Stool DNA Kit (Roboklon, Berlin, Germany) according to the manufacturer’s instructions with the following modifications: we used 20–60 mg of desiccated stool sample and after cell lysis we incubated samples in the bead tube for 12–48 h before continuing the extraction procedure. We attempted to amplify each extract at one sex-specific microsatellite locus (amelogenin) and 13 autosomal microsatellite loci (D1s550, D2s1326, D4s1627, D5s1457, D5s1470, D6s1056, D7s2204, D7s817, D8s1106, D10s1432, D14s306, D16s2624 and vWf) used in previous studies of gorillas (Arandjelovic *et al.*, 2009).

We amplified each extract in two to six replicates on 96-well plates including three to five negative controls and a positive control, using a modified two-step multiplexing PCR approach (Arandjelovic *et al.*, 2009, Supporting Information Appendix S1). We electrophoresed each PCR product on an ABI PRISM 3130 Genetic Analyser and visualized and manually scored the results with GeneMapper Software version 3.7 (Applied Biosystems, Foster City, CA, USA).

Genetic data analysis

To compare genotypes from each extract and identify unique genotypes in the dataset, we used both the R package AlleleMatch (Galpern *et al.*, 2012) in R version 3.4.2 and the program Cervus (Kalinowski, Taper & Marshall, 2007). We first created consensus genotypes with clusters of genotypes matching at eight or more loci. We compared the consensus genotypes with the remaining genotypes allowing for six matching loci and up to three mismatches, all of which we examined for genotyping errors and determined whether they represented unique individuals. We used allele frequencies of the entire population of genotypes to determine the non-exclusion probability of siblings (P_{IDsib}, Waits, Luikart & Taberlet, 2001) for two genotypes. We considered two genotypes to belong to the same individual when $P_{IDsib} < 0.01$. When two genotypes matched with a $P_{IDsib} > 0.01$, we excluded the least complete genotype from further analyses. Finally, we checked whether genotypes typed at five or less loci were unique. All but one matched consensus genotypes with a $P_{IDsib} > 0.01$ and were excluded from further analyses.

Minimum counts

We used the number of unique consensus genotypes from the unmonitored gorillas to obtain a minimum count of unmonitored gorillas: the 106 genotypes from Gray *et al.* (2013) for 2010, and all the unique genotypes detected across 2015–2016 for the 2016 minimum count. Due to long-term monitoring on a near-daily basis, the total number and age–sex composition of monitored groups was known independently (e.g. Robbins *et al.*, 2011; Gray *et al.*, 2013) from the sweeps described herein and was obtained based on group membership on 1 June 2016.

CMR analyses of unmonitored gorillas in 2010 and 2016

For both the one-step and two-step methods, we used the hierarchical modeling approach with data augmentation published in Hickey & Sollmann (2018) to estimate the unmonitored 2016 abundance based on the 2015–2016 two-sweep survey data (Supporting Information Appendices S2 and S3). The one-step model uses individual detection data across both sweeps to estimate a unique detection probability (p). The observed individual detection data are augmented with a large number of unobserved hypothetical individuals, and the model estimates which of these are part of the population but went unobserved (Royle & Dorazio, 2012). The two-step model accounts for individual detection as conditional on group detection. It uses group-level detection/non-detection data across the two sweeps to estimate detection probability for groups (p_g); total number of groups is estimated using data augmentation. To account for the fact that solitary individuals have much lower detection probability than groups (Roy *et al.*, 2014; Hickey & Sollmann, 2018), the model uses detection data for these individuals across sweeps to estimate a separate detection probability (p_s); the number of solitary individuals is estimated by data augmentation. For observed groups, the model further uses individual-level detection data across nesting sites to estimate detection probability of individuals within groups (p_i), as well as group size, which is assumed to follow a zero and one-truncated Poisson distribution (because a group has to have at least 2 individuals) with constant mean.

We obtained the total unmonitored abundance estimate by summing the estimated sizes of observed groups, the number of unobserved groups times mean group size and the estimated number of solitary individuals. We documented six cases of individuals who dispersed from monitored groups after the start of the sweep conducted in 2015 and that were detected in the unmonitored subpopulation during the 2016 sweep. We excluded these individuals from the CMR analyses because by definition, they could not be sampled within the unmonitored subpopulation in 2015 and therefore violated the assumption of population closure. Despite these nuances, we still considered the unmonitored subpopulation as essentially closed during the 2015–2016 sampling period. We added these six individuals to both the one-step and two-step 2016 abundance estimates to obtain two complete estimates of unmonitored gorilla abundance. All unmonitored abundance estimates for 2016 included these six individuals.

Because the 2010 unmonitored abundance estimate published by Gray *et al.* (2013) was based on a single-sweep minimum count and various correction factors (e.g. correction for undetected infants), it was not directly comparable to the 2016 CMR estimate presented here. Therefore, we re-estimated the 2010 abundance within the above-described CMR models. Specifically, we assumed that detection probabilities were comparable in the sampling occasions 2010, 2015 and 2016, and therefore modified both the one-step and the two-step models to apply the estimated detection probabilities of individuals and groups derived from the 2015–2016 survey to the 2010 detection data. For the one-step model, we estimated 2010 abundance by dividing the number of observed individuals (minimum count) by p. For the two-step model, we estimated number of groups in 2010 by dividing the number of observed groups by p_g; we estimated the size of each observed group as the number of observed individuals in that group, divided by the total probability of being detected $[1 - (1 - p_i)^K$, where K is the number of nests found for that group]; and we estimated the number of solitary individuals by dividing the number of observed solitaries by p_s. We obtained total unmonitored abundance in 2010 by summing the estimated sizes of all observed groups and adding the number of unobserved groups times average group size, as well as the estimated number of solitary individuals (Supporting Information Appendices S1 and S2).

We ran the one-step and two-step models in JAGS (version 4.3.0) through the software R (version 3.4.2) using the packages rjags (version 4.8) and jagsUI (version 1.5.0). We used uniform (0, 1) priors for all detection probabilities (p, p_g, p_i, p_s), as well as for all the augmentation parameters. For average group size, we used a uniform (0, 30) prior. Average group size in mountain gorillas is 8–17 individuals (Gray *et al.*, 2013; Roy *et al.*, 2014), and 30 is therefore a reasonable upper bound that should not truncate estimates of average group size. We ran three parallel chains of 50 000 iterations and discarded the first 20 000 iterations as burn-in, resulting in 90 000 posterior samples. We achieved convergence for all parameters (Gelman-Rubin statistic $\widehat{r} < 1.01$). We extracted the posterior means and 95% Bayesian credible intervals (CI: 2.5th and 97.5th percentiles of the posterior distribution) from the posterior distributions of each parameter. We used estimates of 2010 and 2016 abundances of unmonitored gorillas to calculate total population size, as well as growth rates of the unmonitored and the total population (detailed below). We calculated these quantities for all 90 000 posterior samples to obtain their posterior distributions and we present their posterior means and 95% Bayesian CI.

Total minimum counts and population abundances

To obtain the total minimum counts of the entire population of the Virunga Massif in 2010 and 2016, we added the minimum count of unmonitored individuals to the known count of monitored gorillas (Gray *et al.*, 2013 and as of 1 June 2016 respectively). We estimated total abundance of the entire Virunga Massif population for each survey by adding the count of monitored gorillas to the estimated number of unmonitored gorillas obtained with each CMR approach respectively.

Growth rates between 2010 and 2016

To control for the unequal sampling effort of the unmonitored subpopulation in 2010 and 2016 and to propagate the uncertainty in detection probability to the abundance estimates for both surveys, we calculated the growth rate of the entire Virunga population from 2010 to 2016 for each posterior sample, with the equation (1):

$$(P_x/P_0)^{(1/x)}-1 \tag{1}$$

where P_0 is the total abundance estimate for 2010, P_x is the total abundance estimate for 2016 (both obtained as described above) and x is the number of years between the two estimates (Kalpers *et al.*, 2003).

To estimate the growth rates of the two subpopulations while controlling for migrations between them, we used a time-series calculation in R (Robbins *et al.*, 2011; Gray *et al.*, 2013). Starting with the size of the subpopulation in 2010, and adjusting for the exchanges with the other subpopulation (Supporting Information Appendix S1), the time-series calculations determined the intrinsic growth rate that produced the estimated subpopulation abundance in 2016 (see Supporting Information Appendix S1). This was performed for each posterior sample of the unmonitored subpopulation abundance estimates. All migrations in the 2010–2016 period were documented on a daily basis through the long-term monitoring program (see definitions of emigrations and immigrations in Supporting Information Appendix S1). Because the population is closed, by definition migrations could only occur between the monitored and unmonitored subpopulations, such that any emigration from a monitored group was considered to be an immigration into the unmonitored population, and any immigration into a monitored group equated to an emigration out of the unmonitored subpopulation.

Results

Survey effort

Survey effort was similar in each sweep, with 1069 and 1063 km walked and 1102 and 1131 fecal samples collected in 2015 and 2016 respectively. Of these, 740 and 1493 samples were from putative unmonitored and monitored gorillas respectively. A single sweep in 2015–2016 comprised comparable effort as the 2010 survey (1143 km walked and 307 samples collected from unmonitored gorillas in one sweep, Gray *et al.*, 2013).

Genotyping success and individual identification

We attempted to genotype 739 samples from putative unmonitored gorillas and 384 samples from putative monitored gorillas to confirm group identities at each nesting site found in 2015 and 2016. Of these 1123 extracts, 305 yielded genotypes that could not be confidently attributed to unique individuals, including 206 that amplified five or fewer autosomal loci. Using data from all genotyped extracts, there were on average 5.46 alleles per locus and a mean observed heterozygosity value of 0.558. The allele frequency analysis indicated that even if two genotypes could be compared only at the eight least informative loci, the probability of identity for siblings was very low ($P_{IDsib} = 0.0072$, Waits *et al.*, 2001).

The remaining 818 extracts (549 from unmonitored and 269 from monitored groups) were on average 80% complete (range: 5–13 loci) and we determined the sex for 96% of them. We found that 62 of the 740 samples from putative unmonitored groups were misidentified in the field and actually represented monitored groups, but no putative monitored groups were misidentified as unmonitored.

After identity analyses, we found that the 818 genotyped extracts represented 353 unique consensus genotypes with a $P_{IDsib} < 0.01$. These included 184 unique genotypes from unmonitored gorillas [average 95% complete (range: 7–13 loci)]. We added two solitary males (Ra1 because it was found in an area where no other sample was collected within a 3-km radius in either sweep, and the previously monitored adult male Mukunda because he was identified by sight during the 2016 sweep) that could not be genotyped to obtain a minimum count of 186 unmonitored gorillas in 2016.

Minimum population counts

The minimum population count in 2010 was 458 (106 genotypes of unmonitored gorillas and 352 monitored gorillas, Gray *et al.*, 2013). In 2016, we counted 186 unmonitored gorillas, in 13 groups of average size 13 (range 2–30) and 14 solitary males (Table 1; Fig. 1). As of 1 June 2016, there were 418 monitored gorillas, in 28 groups of average size 15 (range 5–33) (Table 1; Fig. 1). The minimum population count for the Virunga Massif in 2016 was therefore 604 individuals.

CMR abundance estimates of unmonitored gorillas

In the unmonitored subpopulation, we found 52 of the 186 unique individuals in the 2015 sweep only, 56 in the 2016 sweep only and 78 in both sweeps. Overall, five groups went undetected in one of the sweeps: two and three groups in 2015 and 2016 respectively. The one-step model estimated an individual detection probability per sweep (p) of 0.60 (CI: 0.53–0.67). The two-step model estimated a detection probability per sweep of 0.72 (CI: 0.48–0.89) for groups (p_g) and 0.25 (CI: 0.07–0.53) for solitary males (p_s). Conditional on detection of a group, individuals had an estimated 0.54 (CI: 0.50–0.58) probability (p_i) of being detected at each nesting site.

For each year, 2010 and 2016, we obtained two CMR estimates of the abundance of unmonitored gorillas: a traditional one-step approach and the two-step approach that accounts for the social structure of the gorillas. The one-step model estimates were 177 (CI: 158–200) and 221 (CI: 204–243) unmonitored individuals in 2010 and 2016 respectively (Table 2; Fig. 2). The two-step model estimated 200 (CI: 147–299) and 251 (CI: 205–340) unmonitored gorillas in 2010 and 2016, respectively, including 44 (CI: 15–120) solitary males, 16 (CI: 12–22) groups of average size 10 (CI: 9.6–10.2) in 2010, and 40 (CI: 15–107) solitary males and 15 (CI: 13–20) groups with average group size 14 (CI: 12–16) in 2016 (Table 2; Fig. 2).

Total population abundance

The sum of the count of monitored gorillas and the one-step CMR estimate of the unmonitored subpopulation yielded 529 (CI: 510–552) and 639 (CI: 622–661) total individuals in 2010 and 2016 respectively. Summing the count of monitored gorillas and the two-step estimate of unmonitored subpopulation, we estimated that there were a total of 552 (CI: 499–650) and 669 (CI: 623–759) mountain gorillas in 2010 and 2016 respectively (Table 2; Fig. 2).

Growth rates between 2010 and 2016

Between 2010 and 2016, the monitored groups experienced 188 births, 83 deaths, 2 unexplained disappearances, 39 emigrations to and 2 immigrations from the

Table 1. Mountain gorilla groups and solitary males detected in the Virunga Massif during the 2015–2016 census. I: unmonitored groups; II: unmonitored solitary males; III: monitored groups

					Number individuals		
	Social unit	Status	Country	Times found	2015	2016	Total
I[a]	A2-A1-A2	Unmonitored	DRC	3	22	27	30
	B1-Ga2	Unmonitored	DRC	2	14	17	17
	D2-D1	Unmonitored	DRC	2	8	13	13
	Ga1-D3b	Unmonitored	DRC	2	10	11	12
	K1-K2	Unmonitored	DRC	2	9	18	19
	K4-K3-K4a	Unmonitored	DRC	3	8	10	10
	K6-K4b	Unmonitored	DRC	2	15	9	15
	Na2-Na1	Unmonitored	DRC	2	13	1	13
	D3a-D5	Unmonitored	DRC	2	16	Not found	16
	V2	Unmonitored	Rwanda	1	2	Not found	2
	V4	Unmonitored	Rwanda	1	4	Not found	4
	D2b	Unmonitored	DRC	1	Not found	13	13
	Ja1	Unmonitored	DRC	1	Not found	8	8
II	Irakoze	Unmonitored	Rwanda	3	1	1	1
	Kubona	Unmonitored	Rwanda	4	1	1	1
	A1a	Unmonitored	DRC	1	1	Not found	1
	E2	Unmonitored	DRC	1	1	Not found	1
	Gb5	Unmonitored	Rwanda	1	1	Not found	1
	J1	Unmonitored	DRC	1	1	Not found	1
	J2	Unmonitored	DRC	1	1	Not found	1
	Ra1	Unmonitored	Uganda	1	1	Not found	1
	Shirimpumu	Unmonitored	Rwanda	1	1	Not found	1
	Himbara	Unmonitored	Rwanda	2	Not found	1	1
	K1b	Unmonitored	DRC	1	Not found	1	1
	Mukunda	Unmonitored	DRC	1	Not found	1	1
	Na2b	Unmonitored	DRC	1	Not found	1	1
	Urugwiro	Unmonitored	Rwanda	1	Not found	1	1
III	Agashya	Monitored	Rwanda				19
	Amahoro	Monitored	Rwanda + DRC				19
	Bageni	Monitored	DRC				24
	Giraneza	Monitored	Rwanda				6
	Hirwa	Monitored	Rwanda				19
	Humba	Monitored	DRC				9
	Igisha	Monitored	Rwanda				26
	Isabukuru	Monitored	Rwanda				19
	Isimbi	Monitored	Rwanda				15
	Iyambere	Monitored	Rwanda				5
	Kabirizi	Monitored	DRC				19
	Karisimbi	Monitored	Rwanda + DRC				12
	Kurira	Monitored	Rwanda				17
	Kuryama	Monitored	Rwanda + DRC				10
	Kwitonda	Monitored	Rwanda				28
	Lulengo	Monitored	DRC				10
	Mafunzo	Monitored	Rwanda				11
	Mapuwa	Monitored	DRC				22
	Munyaga	Monitored	DRC				9
	Musilikale	Monitored	Rwanda				13
	Ntambara	Monitored	Rwanda				8
	Nyakagezi	Monitored	Uganda				10
	Nyakamwe	Monitored	DRC				11
	Pablo	Monitored	Rwanda				33
	Rugendo	Monitored	DRC				9
	Sabyinyo	Monitored	Rwanda				16

Table 1. Continued.

Social unit	Status	Country	Times found	Number individuals 2015	 2016	 Total
Titus	Monitored	Rwanda				7
Umubano	Monitored	Rwanda				12
Total				130	134	604

DRC, Democratic Republic of Congo.

[a] Names of unmonitored groups are based on the sector in which they were found.

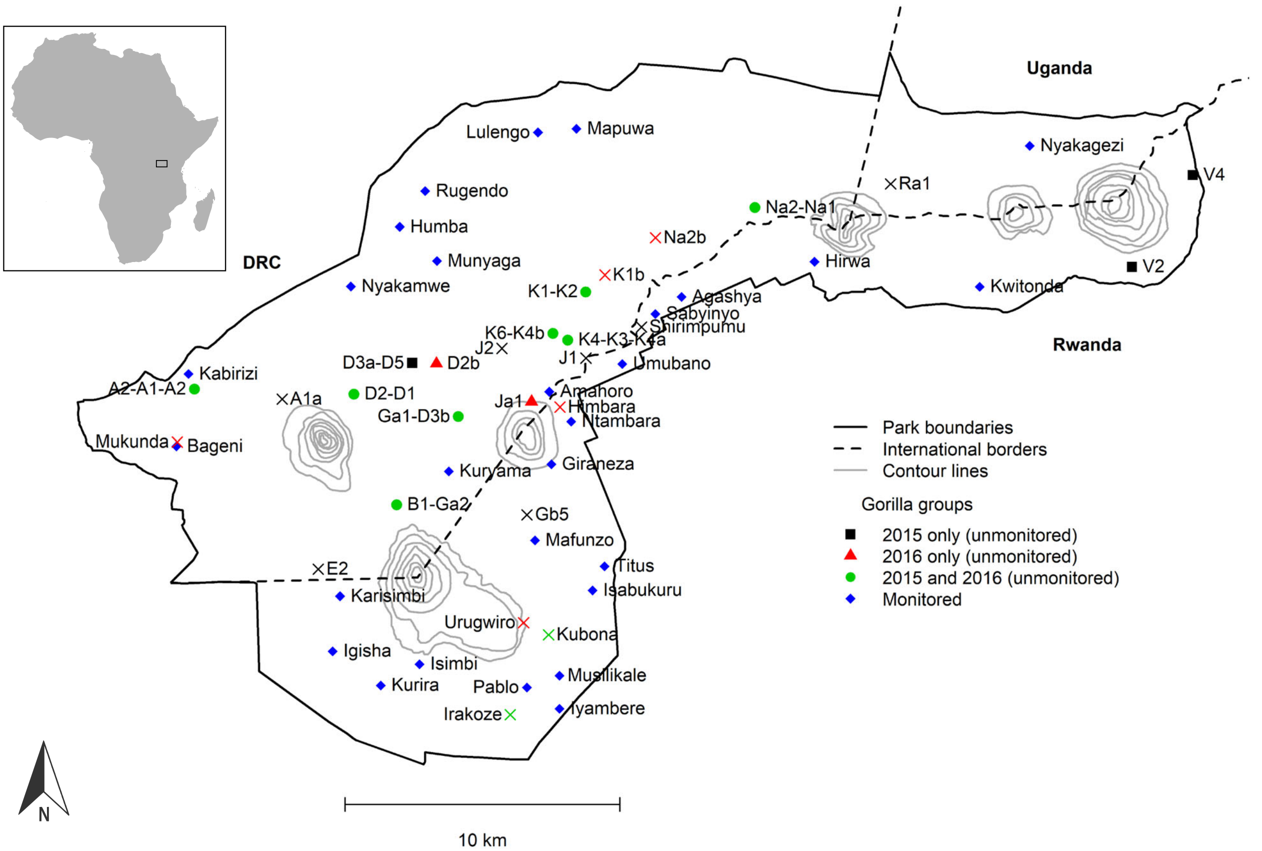

Figure 1 Average locations of mountain gorilla groups and solitary males in the Virunga Massif during the 2015–2016 survey. Xs denote unmonitored solitary males following the same color code as the unmonitored groups. DRC, Democratic Republic of Congo. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

unmonitored subpopulation. The intrinsic growth rate of the monitored gorillas was 4.4% per year. From the posterior distributions of CMR abundance estimates of the two approaches, we estimated the intrinsic growth of the unmonitored gorillas from 2010 to 2016 as either 0.5% per year (−0.7% to +1.7%) or 1.1% per year (−2.7% to +4.4%) based on the one-step and two-step model posterior distributions respectively (Table 2). Similarly, we estimated the intrinsic growth of the entire population of the Virunga Massif as either 3.0% (CI: 2.5–3.4%) or 3.1% (CI: 1.4–4.3%) per year with the one-step and two-step posterior distributions respectively (Table 2).

Discussion

The 2015–2016 population survey of the Virunga Massif revealed more mountain gorillas than ever recorded in this area since surveys began in 1960. By adding the estimated 400 individuals from the 2011 survey of Bwindi Impenetrable National Park (Roy *et al.*, 2014) to each of the CMR estimates in the Virunga Massif, we estimated the global abundance of mountain gorillas as 1039 (CI: 1022–1061) or 1069 (CI: 1023–1158) using the one-step and two-step models respectively. At a minimum, the subspecies reached 1004 individuals (Hickey *et al.*, 2019). The growth of the entire Virunga Massif population was 3.0% (CI: 2.5–3.4%)

Table 2. Abundance estimates (with 95% credible intervals, CI), dispersal events to and from monitored and unmonitored subpopulations, and intrinsic growth rates between 2010 and 2016 estimated for the Virunga mountain gorilla population and each subpopulation

		Unmonitored (CI)		Virunga total (CI)	
	Monitored	One-step	Two-step	One-step	Two-step
2010	352[a]	177 (158–200)	200 (147–298)	529 (510–552)	552 (499–650)
# of groups	24	–	16 (12–22)	–	40 (36–46)
# of solitaries	3	–	44 (15–120)	–	47 (18–123)
Avg. group size	15	–	10 (9.6–10.2)	–	
2016	418	221 (204–243)	251 (205–340)	639 (622–661)	669 (623–758)
# of groups	28	–	15 (13–20)	–	43 (41–48)
# of solitaries	0	–	40 (15–107)	–	40 (15–107)
Avg. group size	15	–	14 (12–16)	–	
Emigrations[b]	39	2 (+2[c])		0	
Immigrations[b]	2 (+2[c])	39		0	
Intrinsic growth per year	4.4%	0.5% (−0.7 to +1.7%)	1.1% (−2.7 to +4.4%)	3.0% (2.5 to 3.4%)	3.1% (1.4 to 4.3%)

[a] From Gray *et al.*, 2013.

[b] See Supporting Information Appendix S1 for definitions of migrations.

[c] Two gorillas disappeared from monitored groups, and were considered equally likely to arise from either death or dispersal in estimating the growth rates (Supporting Information Appendix S1).

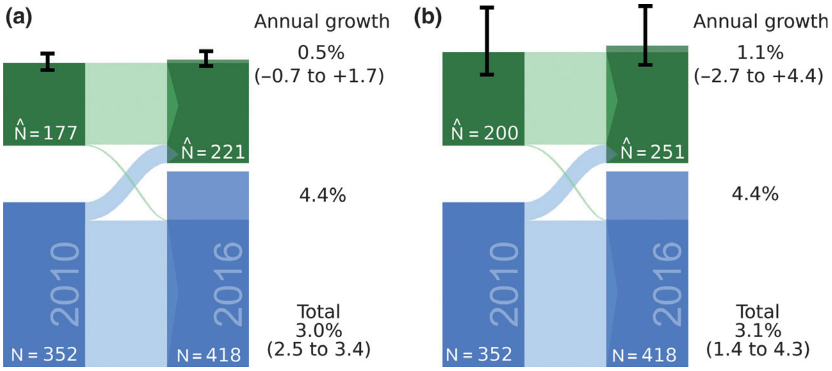

Figure 2 Abundance and growth estimates of the Virunga mountain gorilla population from 2010 to 2016 using (a) the one-step and (b) the two-step method. Monitored abundance (blue): direct count. Unmonitored abundance (green): CMR estimates. Vertical bars: 95% credible intervals of CMR abundance estimates. CMR, Capture–mark–recapture. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

or 3.1% (1.4–4.3%) per year between 2010 and 2016 (Table 2). This rate was slightly lower than the estimated rate from 2003 to 2010 of 3.7% per year, but higher than the overall rate from 1989 to 2010 of 2% per year (Robbins *et al.*, 2011), although differences in methods across time make absolute comparisons uncertain. Currently, what is certain is that while all other subspecies of great apes are declining (Plumptre *et al.*, 2016; Kühl *et al.*, 2017; Santika *et al.*, 2017; Strindberg *et al.*, 2018), the mountain gorilla is the only subspecies that is not. However, our data suggest that monitored groups, which represent over 60% of all gorillas in the Virunga Massif, mainly drove that population growth.

The monitored subpopulation, which continues to benefit from intense conservation interventions (Robbins *et al.*, 2011), grew by 4.4% per year from 2010 to 2016 (Table 2). This rate is within the range of the growth observed since 1967 (4.1% per year) and from 2003 to 2010 (4.7% per year, Robbins *et al.*, 2011). The monitored subpopulation represents the majority of gorillas in the Virunga Massif and their growth is higher than that of the entire population. Furthermore, there were proportionally more movements from the monitored to the unmonitored subpopulations between 2010 and 2016 compared to the period 1967–2010 (Robbins *et al.*, 2011), which reduced the absolute increase in individuals in the monitored subpopulation, and in turn increased the number of unmonitored gorillas. The potential impact on growth rate estimates of individual movements between subpopulations emphasizes the need to associate abundance trends with records of transfers among subpopulations to better interpret trends and make informed conservation decisions (Weegman *et al.*, 2016).

Two processes, observational and biological, contributed to the higher number of unmonitored gorillas detected from 2010 to 2016: first, increased sampling effort led to a higher detection probability. Second, net immigration from monitored to unmonitored groups, and probably some intrinsic growth, contributed to a higher abundance in 2016 than in

2010. After controlling for the net flux of gorillas transferring from monitored to unmonitored groups and for the lower sampling effort in 2010 compared to 2016, it remains unclear how much intrinsic growth really contributed to the higher abundance because of the uncertainty around the abundance estimates themselves (204–243 for the one-step and 205–340 for the two-step model). Although the upper bound of the two-step model-based growth estimate was as high as that of the monitored subpopulation (4.4%, Table 2), the uncertainty around the estimated growth was wide and largely encompassed zero, such that we cannot confidently conclude the direction of change (growth, stability or decline) of the unmonitored gorillas.

Both subpopulations are of high conservation interest, but the unmonitored gorillas receive less protection. The density of illegal activities detected throughout the Virunga Massif was unchanged since 2010 (Hickey *et al.*, 2019), and is likely to have a higher impact on the unmonitored gorillas because they do not receive veterinary interventions when snared. Previous findings have suggested that differences in mortality, largely due to gorillas suffering from wounds caused by snares that target duikers, may explain the difference in growth rates between the monitored and unmonitored mountain gorillas, rather than variation in natural habitat quality in the Virunga Massif (Robbins *et al.*, 2011). Furthermore, modeling suggested that more than half of gorilla mortality might be attributed to poaching when veterinarians cannot intervene (Robbins *et al.*, 2011). Our results support calls for an increase in intensive law enforcement patrols, such as snare removal teams and targeted anti-poaching patrols in the areas where unmonitored groups are primarily found, as well as community-based programs to reduce illegal activities in the parks (Rowcliffe, de Merode & Cowlishaw, 2004; Gray *et al.*, 2010; Robbins *et al.*, 2011).

Population abundance and growth rate are key measures to evaluate targeted conservation activities. The very cost-intensive two-sweep method used with the 2015–2016 survey allowed us to provide the first CMR abundance estimates for the Virunga Massif population. As expected, by not accounting for the social structure of mountain gorillas (Hickey & Sollmann, 2018), the one-step model provided a narrower interval around the abundance estimate than did the two-step model, although its CI may be too narrow to include the true abundance (Hickey & Sollmann, 2018; Woodruff, Lukacs & Waits, 2018). The increased complexity of the two-step model that is necessary to account for group living and non-independent individual detection resulted in low precision of abundance estimates, and simulations show they tend to overestimate true abundance more than the one-step model (Hickey & Sollmann, 2018). The annual growth rates inferred from these abundance estimates also featured large uncertainty (ranging from −2.7% to +4.4%) which precluded us from determining a population trend of the unmonitored subpopulation. Therefore, methods to survey the mountain gorillas should be further improved in order to obtain accurate and precise abundance and growth estimates at manageable costs.

Improving detection of groups, more than detection of individuals within groups, would improve both accuracy and precision of abundance estimates, regardless of the model used (Hickey & Sollmann, 2018). Within the framework of surveying wild mountain gorillas, this could be achieved either by increasing the number of sweeps (Roy *et al.*, 2014) or by reducing distance between recces, both of which would further increase the already high costs and logistical challenges. Alternatively, Roy *et al.* (2014) used a 'slow sweep', accomplished by fewer teams over a longer timeframe (8 months) and a short sweep (2 months), which seemed to yield comparable results. Slow sweeps may be performed with less effort in a more continuous manner and repeated for 2–3 years, until enough detections could be collected to allow efficient CMR analyses (K. E. Langergraber and L. Vigilant, unpubl. data). Although the impact of potentially violating the assumptions of demographic closure must be considered, such sampling periods might be acceptable with species with slow life histories (Granjon *et al.*, 2017).

Confidently assessing population trends of wild or elusive animals remains very challenging (Nussear & Tracy, 2007; Wanyama *et al.*, 2010; Brooks *et al.*, 2017). This study confirmed that the mountain gorilla population of the Virunga Massif continued growing, reaching a minimum of 604 gorillas, and more likely reaching an estimated 639–669 total individuals as of June 2016. Conservation measures thus seem to be effective overall, but population growth appears to be dependent on human interventions. In spite of the immense effort invested in surveying the unmonitored gorillas of the Virunga Massif, estimates of population trends still exhibit low precision, which is a general problem for populations of high conservation concern. Researchers and conservationists should emphasize developing methods (both field and analytical) that improve accuracy and precision of population trend estimates. To this end, new analytical methods may be developed (Clement *et al.*, 2017; Hickey & Sollmann, 2018) and simulation studies may help to investigate the sampling design needed to reach the desired precision (Roy *et al.*, 2014; Gupta *et al.*, 2017).

Acknowledgements

We thank Méthode Bahizi, Charles Kayijamahe, Gaspard Nzayisenga and Eustrate Uzabaho, for organizing supplies and samples; Anette Nicklisch and Veronika Städele for laboratory assistance; Roger Mundry for statistical support; Florian Böhnhardt and Cristina Zickert for help with the figures; Anna Behm Masozera and Christophe Boesch for helpful discussion; the associate editor and two anonymous reviewers for helpful comments on the manuscript; and all partner organizations for their support and providing field staff, including the authors' organizations, the Greater Virunga Transboundary Collaboration, the Institute of Tropical Forest Conservation and the North Carolina Zoo. This work was funded by the World Wildlife Fund for Nature, Fauna & Flora International (Laura J. Niles Foundation), Partners in Conservation/Columbus Zoo & Aquarium, Berggorilla & Regenwald Direkthilfe and The Max Planck Society, who

did not contribute to the design, interpretation or the writing of this study.

References

Arandjelovic, M., Guschanski, K., Schubert, G., Harris, T.R., Thalmann, O., Siedel, H. & Vigilant, L. (2009). Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. *Mol. Ecol. Resour.* **9**, 28–36. https://doi.org/10.1111/j.1755-0998.2008.02387.x.

Aveling, C. & Harcourt, A.H. (1984). A census of the Virunga gorillas. *Oryx* **18**, 8–13. https://doi.org/10.1017/S0030605300018524.

Begon, M. (1983). Abuses of mathematical techniques in ecology: applications of Jolly's capture-recapture method. *Oikos* **40**, 155. https://doi.org/10.2307/3544213.

Borchers, D.L. & Efford, M.G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* **64**, 377–385.

Brooks, L., Palmer, C., Griffiths, A.D. & Pollock, K.H. (2017). Monitoring variation in small coastal dolphin populations: an example from Darwin, Northern Territory, Australia. *Front. Mar. Sci.* **4**. https://doi.org/10.3389/fmars.2017.00094.

Budy, P.E., Bowerman, T., Al-Chokhachy, R., Conner, M. & Schaller, H. (2017). Quantifying long-term population growth rates of threatened bull trout: challenges, lessons learned, and opportunities. *Can. J. Fish. Aquat. Sci.* **74**, 2131–2143. https://doi.org/10.1139/cjfas-2016-0336.

Cam, E. (2009). Contribution of capture-mark-recapture modeling to studies of evolution by natural selection. In *Modeling demographic processes in marked populations. Environmental and ecological statistics*: 83–129. Thomson, D.L., Cooch, E.G. & Conroy, M.J. (Eds). Boston: Springer. https://doi.org/10.1007/978-0-387-78151-8_5.

Clement, M.J., Converse, S.J. & Andrew Royle, J. (2017). Accounting for imperfect detection of groups and individuals when estimating abundance. *Ecol. Evol.* **7**, 7304–7310. https://doi.org/10.1002/ece3.3284.

Dennis, B., Munholland, P.L. & Michael Scott, J. (1991). Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.* **61**, 115–143. https://doi.org/10.2307/1943004.

Eggert, L.S., Eggert, J.A. & Woodruff, D.S. (2003). Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. *Mol. Ecol.* **12**, 1389–1402.

Galpern, P., Manseau, M., Hettinga, P., Smith, K. & Wilson, P. (2012). Allelematch: an R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. *Mol. Ecol. Resour.* **12**, 771–778. https://doi.org/10.1111/j.1755-0998.2012.03137.x.

Gerber, L.R., Demaster, D.P. & Kareiva, P.M. (1999). Gray whales and the value of monitoring data in implementing the U.S. Endangered Species Act. *Conserv. Biol.* **1**, 1215–1219. https://doi.org/10.1046/j.1523-1739.1999.98466.x.

Gil-Weir, K.C., Grant, W.E., Douglas Slack, R., Wang, H.-H. & Fujiwara, M. (2012). Demography and population trends of whooping cranes. *J. Field. Ornithol.* **83**, 1–10. https://doi.org/10.1111/j.1557-9263.2011.00349.x.

Granjon, A.-C., Rowney, C., Vigilant, L. & Langergraber, K.E. (2017). Evaluating genetic capture-recapture using a chimpanzee population of known size. *J. Wildl. Mgmt.* **81**, 279–288. https://doi.org/10.1002/jwmg.21190.

Gray, M., McNeilage, A., Fawcett, K., Robbins, M.M., Ssebide, B., Mbula, D. & Uwingeli, P. (2010). Censusing the mountain gorillas in the Virunga volcanoes: complete sweep method versus monitoring. *Afr. J. Ecol.* **48**, 588–599. https://doi.org/10.1111/j.1365-2028.2009.01142.x.

Gray, M., Roy, J., Vigilant, L., Fawcett, K., Basabose, A., Cranfield, M., Uwingeli, P., Mburanumwe, I., Kagoda, E. & Robbins, M.M. (2013). Genetic census reveals increased but uneven growth of a critically endangered mountain gorilla population. *Biol. Conserv.* **158**, 230–238. https://doi.org/10.1016/j.biocon.2012.09.018.

Gupta, M., Joshi, A. & Vidya, T.N.C. (2017). Effects of social organization, trap arrangement and density, sampling scale, and population density on bias in population size estimation using some common mark-recapture estimators. *PLoS ONE* **12**, e0173609. https://doi.org/10.1371/journal.pone.0173609.

Guschanski, K., Vigilant, L., McNeilage, A., Gray, M., Kagoda, E. & Robbins, M.M. (2009). Counting elusive animals: comparing field and genetic census of the entire mountain gorilla population of Bwindi Impenetrable National Park, Uganda. *Biol. Conserv.* **142**, 290–300. https://doi.org/10.1016/j.biocon.2008.10.024.

Hickey, J.R. & Sollmann, R. (2018). A new mark-recapture approach for abundance estimation of social species. *PLoS ONE* **13**, e0208726. https://doi.org/10.1371/journal.pone.0208726.

Hickey, J.R., Granjon, A.C., Vigilant, L., Eckardt, W., Gilardi, K.V., Babaasa, D., Ruzigandekwe, F., Leendertz, F.H. & Robbins, M.M. (2019). *Virunga 2015–2016 surveys monitoring mountain gorillas, other select mammals, and illegal activities*. Kigali: GVTC, IGCP & Partners.

Kalinowski, S.T., Taper, M.L. & Marshall, T.C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**, 1099–1106. https://doi.org/10.1111/j.1365-294X.2007.03089.x.

Kalpers, J., Williamson, E.A., Robbins, M.M., McNeilage, A., Nzamurambaho, A., Lola, N. & Mugiri, G. (2003). Gorillas in the crossfire: population dynamics of the Virunga mountain gorillas over the past three decades. *Oryx* **37**, 326–337. https://doi.org/10.1017/S0030605303000589.

Kühl, H.S., Sop, T., Williamson, E.A., Mundry, R., Brugiere, D., Campbell, G., Cohen, H., Danquah, E., Ginn, L., Herbinger, I., Jones, S., Junker, J., Kormos, R., Kouakou, C.Y., N'Goran, P.K., Normand, E., Shutt-Phillips, K., Tickle, A., Vendras, E., Welsh, A., Wessling, E.G. &

Boesch, C. (2017). The critically endangered western chimpanzee declines by 80%. *Am. J. Primatol.* **79**, e22681. https://doi.org/10.1002/ajp.22681.

McNeilage, A., Plumptre, A.J., Brock-Doyle, A. & Vedder, A. (2001). Bwindi Impenetrable National Park, Uganda: Gorilla Census 1997. *Oryx* **35**, 39–47. https://doi.org/10.1046/j.1365-3008.2001.00154.x.

McNeilage, A., Robbins, M.M., Gray, M., Olupot, W., Babaasa, D., Bitariho, R., Kasangaki, A., Rainer, H., Asuma, S., Mugiri, G. & Baker, J. (2006). Census of the mountain Gorilla *Gorilla beringei beringei* population in Bwindi Impenetrable National Park, Uganda. *Oryx* **40**, 419–427. https://doi.org/10.1017/S0030605306001311.

Miller, C.R., Joyce, P. & Waits, L.P. (2005). A new method for estimating the size of small populations from genetic mark-recapture data. *Mol. Ecol.* **14**, 1991–2005. https://doi.org/10.1111/j.1365-294X.2005.02577.x.

Nsubuga, A.M, Robbins, M.M, Roeder, A.D, Morin, P.A., Boesch, C. & Vigilant, L. (2004). Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. *Mol. Ecol.* **13**, 2089–2094. https://doi.org/10.1111/j.1365-294X.2004.02207.x.

Nussear, K.E. & Tracy, C.R. (2007). Can modeling improve estimation of desert tortoise population densities? *Ecol. Appl.* **17**, 579–586. https://doi.org/10.1890/05-1970.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* **62**, 3–135.

Piel, A.K., Cohen, N., Kamenya, S., Ndimuligo, S.A., Pintea, L. & Stewart, F.A. (2015). Population status of chimpanzees in the Masito-Ugalla Ecosystem, Tanzania. *Am. J. Primatol.* **77**, 1027–1035. https://doi.org/10.1002/ajp.22438.

Plumptre, A.J., Nixon, S., Kujirakwinja, D.K., Vieilledent, G., Critchlow, R., Williamson, E.A., Nishuli, R., Kirkby, A.E. & Hall, J.S. (2016). Catastrophic decline of world's largest primate: 80% loss of Grauer's gorilla (*Gorilla beringei graueri*) population justifies critically endangered status. *PLoS ONE* **11**, e0162697. https://doi.org/10.1371/journal.pone.0162697.

Robbins, M.M., Gray, M., Fawcett, K.A., Nutter, F.B., Uwingeli, P., Mburanumwe, I., Kagoda, E., Basabose, A., Stoinski, T.S., Cranfield, M.R., Byamukama, J., Spelman, L.H. & Robbins, A.M. (2011). Extreme conservation leads to recovery of the Virunga mountain gorillas. *PLoS ONE* **6**, e19788. https://doi.org/10.1371/journal.pone.0019788.

Rowcliffe, J.M., de Merode, E. & Cowlishaw, G. (2004). Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proc. R. Soc. B* **271**, 2631–2636. https://doi.org/10.1098/rspb.2004.2915.

Roy, J., Vigilant, L., Gray, M., Wright, E., Kato, R., Kabano, P., Basabose, A., Tibenda, E., Kühl, H.S. & Robbins, M.M. (2014). Challenges in the use of genetic mark-recapture to estimate the population size of Bwindi mountain gorillas (*Gorilla beringei beringei*). *Biol. Conserv.* **180**, 249–261. https://doi.org/10.1016/j.biocon.2014.10.011.

Royle, J.A. & Dorazio, R.M. (2012). Parameter-expanded data augmentation for bayesian analysis of capture-recapture models. *J. Ornithol.* **152**, 521–537. https://doi.org/10.1007/s10336-010-0619-4.

Santika, T., Ancrenaz, M., Wilson, K.A., Spehar, S., Abram, N., Banes, G.L., Campbell-Smith, G. et al (2017). First Integrative trend analysis for a great ape species in Borneo. *Sci. Rep.* **7**, 4839. https://doi.org/10.1038/s41598-017-04435-9.

Sholley, C. (1990). *Census of the Virunga gorilla population, 1989*. Washington: African Wildlife Foundation.

Strindberg, S., Maisels, F., Williamson, E.A., Blake, S., Stokes, E.J., Aba'a, R., Abitsi, G. et al (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Sci. Adv.* **4**, eaar2964. https://doi.org/10.1126/sciadv.aar2964.

Waits, L.P., Luikart, G. & Taberlet, P. (2001). Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Mol. Ecol.* **10**, 249–256. https://doi.org/10.1046/j.1365-294X.2001.01185.x.

Wanyama, F., Muhabwe, R., Plumptre, A.J., Chapman, C.A. & Rothman, J.M. (2010). Censusing large mammals in Kibale National Park: evaluation of the intensity of sampling required to determine change. *Afr. J. Ecol.* **48**, 953–961. https://doi.org/10.1111/j.1365-2028.2009.01197.x.

Weber, A.W. & Vedder, A. (1983). Population dynamics of the Virunga gorillas: 1959–1978. *Biol. Conserv.* **26**, 341–366. https://doi.org/10.1016/0006-3207(83)90096-4.

Weegman, M.D., Bearhop, S., Fox, A.D., Hilton, G.M., Walsh, A.J., McDonald, J.L. & Hodgson, D.J. (2016). Integrated population modelling reveals a perceived source to be a cryptic sink. *J. Anim. Ecol.* **85**, 467–475. https://doi.org/10.1111/1365-2656.12481.

White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**(Suppl. 1), S120–S139. https://doi.org/10.1080/00063659909477239.

Woodruff, S.P., Lukacs, P.M. & Waits, L.P. (2018). Comparing performance of multiple non-invasive genetic capture-recapture methods for abundance estimation: a case study with the Sonoran pronghorn *Antilocapra americana sonoriensis*. *Oryx* 1–9. https://doi.org/10.1017/S003060531800011X.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Methods for amplification of microsattelite loci and methods for estimating growth rates while accounting for movements between the subpopulations.

Appendix S2. JAGS code to fit conventional (One-Step) closed capture-recapture model.

Appendix S3. JAGS code to fit Two-Step closed capture-recapture model.