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Changes in Grauer's gorilla (Gorilla beringei graueri) and other primate populations in the Kahuzi-Biega National Park and Oku Community Reserve, the heart of Grauer's gorilla global range.

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Research Highlights:

- Grauer's gorilla numbers an estimated 4,443 (95% CI: 3,021-6,533) and eastern chimpanzees number 4,926 (95%CI: 3,656-6,634) in the Kahuzi Biega National Park (KBNP) and adjacent Oku Community Reserve (OCR).
- Grauer's gorilla is estimated to have declined by 84% in KBNP since the mid 1990s but chimpanzees are estimated to have remained stable. Numbers of gorillas in OCR have remained stable and chimpanzees have increased.
- Most other primate species are estimated to have declined significantly due to hunting for bushmeat.

Title: Changes in Grauer's gorilla (*Gorilla beringei graueri*) and other primate populations in the Kahuzi-Biega National Park and Oku Community Reserve, the heart of Grauer's gorilla global range.

Running title: Changes in Grauer's gorilla distribution and abundance

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Abstract (300 words)

Grauer's gorillas (*Gorilla beringei graueri*) have declined drastically across their range in eastern Democratic Republic of Congo (DRC). A compilation of survey data in different parts of Grauers gorilla range estimated a 77% decline in numbers between the mid- 1990s and 2016 (Plumptre et al. 2016a) and predicted that Kahuzi-Biega National Park (KBNP), and the contiguous Oku Community Reserve (OCR) held much of the global population. An estimate of 3,800 Grauer's gorillas was made across its range (Plumptre et al. 2016a, 2016b). In this paper we publish the most intensive survey of Grauer's gorilla numbers to date, using nest counts from 230 line transects across KBNP and OCR to derive more accurate estimates of both gorilla and chimpanzee numbers. Gorilla numbers were estimated at 1,223 (95% CI: 640-2,338) within KBNP and at 1,967 (95% CI: 1,206-3209) in OCR from line transects. Eastern chimpanzee (*Pan troglodytes schweinfurthii*) numbers were estimated at 2,664 (95% CI: 1,862-3810) in KBNP and 1,170 (95% CI: 686-1,995) in OCR. Estimates of total numbers for the survey area were 4,443 (95% CI: 3,021-6,533) Grauer's gorilla and 4,925 (95% CI: 3,656-6,634) eastern chimpanzees. Chimpanzee numbers were not significantly different to the estimates from the mid-1990s but the gorillas had significantly declined. Most of the estimated decline occurred in KBNP. Modelled densities of these two apes indicated that distances to human presence significantly explained part of the distribution of these apes, with higher densities also found in more rugged and remote sites. Other primates have all declined in this region, likely due to bushmeat hunting, especially the Endangered Ulindi River Red Colobus *Piliocolobus lulindicus*. These

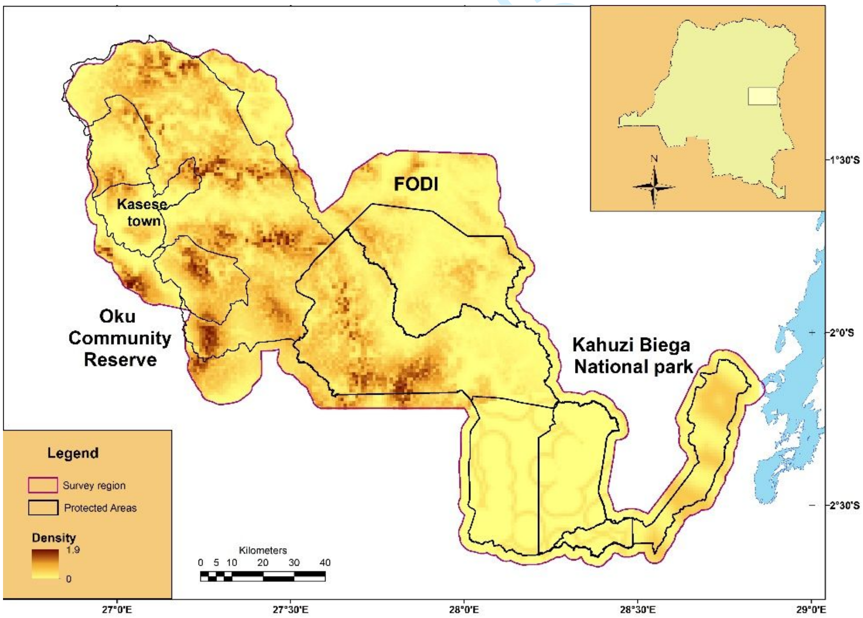
results confirm the negative impact of the civil war in the DRC on Grauer's gorilla and other primates but indicates that the population declines may not be as great as previously feared.

Keywords: Grauer's gorilla density, eastern chimpanzee, transect survey, population size, red colobus, primates

Research Highlights:

- Grauer's gorilla numbers an estimated 4,443 (95% CI: 3,021-6,533) and eastern chimpanzees number 4,926 (95%CI: 3,656-6,634) in the Kahuzi Biega National Park (KBNP) and adjacent Oku Community Reserve (OCR).
- Grauer's gorilla is estimated to have declined by 84% in KBNP since the mid 1990s but chimpanzees are estimated to have remained stable. Numbers of gorillas in OCR have remained stable and chimpanzees have increased.
- Most other primate species are estimated to have declined significantly due to hunting for bushmeat.

Graphical Abstract:



Modelled density of Grauer's gorillas across the core region of its global range. This model predicts 4,800 (95%CI: 3,310-6,900) gorillas in this part of eastern Democratic Republic of Congo. The map highlights the importance of the Oku Community Reserve region for the conservation of this ape.

Tweetable summary

Most comprehensive survey of Grauer's gorilla estimates 4,440 individuals in heart of its range.

INTRODUCTION

Grauer's gorilla (*Gorilla beringei graueri*), a subspecies of the eastern gorilla (*Gorilla beringei*), is endemic to the eastern Democratic Republic of Congo (DRC). In the mid-1990s, the global population was estimated to number about 16,900 individuals across its range based on a compilation of data from several surveys (Hall et al. 1998a). Intensive surveys were made at that time in four areas of the Kahuzi-Biega National Park (KBNP) and three areas in Kasese (named for the nearest town) to the west of KBNP. These surveys estimated a total of 11,000 gorillas and 2,600 eastern chimpanzees (*Pan troglodytes schweinfurthii*) for this survey area (Hall et al. 1998b).

Insecurity during and following the war that occurred in DRC between 1996-2003, and the subsequent proliferation of armed groups in eastern DRC, meant that monitoring populations of this ape, and indeed all wildlife, has been very difficult. A compilation of reconnaissance survey data collected between 2011 and 2015, by rangers and survey teams from the Wildlife Conservation Society (WCS) and Chester Zoo/Zoological Society of London, was used to derive a map of occupancy probability of Grauer's gorillas across their range using several predictor covariables (Plumptre et al. 2016a; Plumptre at al. 2015). Threshold occupancy cells were converted to an abundance estimate using an average density obtained from nine sites across the ape's range to estimate a global population of 3,800 (95% confidence interval (CI): 1,280–9,050). Using the same type of conversion to density, eastern chimpanzee numbers were estimated to be 37,740 (95% CI: 14,019–67,196) (Plumptre et al. 2015). These estimates, the best that could be obtained across such a large region, given the insecurity in eastern DRC, indicated a 77-93% decline in the population compared to estimates made in the mid-1990s (Hall *et al.* 1998a), making the Grauer's gorilla Critically Endangered according to the IUCN Red List criteria (Plumptre *et al.* 2016b).

In 2011, we made a survey plan for Grauer's gorillas and chimpanzees. A line transect design was established (Thomas et al. 2010), and as security in the KBNP-OCR region improved, WCS started distance sampling surveys (Buckland *et al*. 2001) with the Institut Congolais pour la Conservation de la Nature (ICCN). The plan was to survey the whole area as and when security made surveys possible. This paper summarises the results of transect surveys of Grauer's gorilla (*Gorilla beringei graueri*), eastern Chimpanzee (*Pan troglodytes schweinfurthii*) and all monkey species observed in the KBNP and the contiguous proposed Oku Community Reserve (OCR) in eastern DRC. This region forms the heartland of Grauer's gorilla distribution both historically (Emlen & Schaller, 1960; Hall *et al*. 1998a, Omari *et al.* 1999) and more recently as estimated from occupancy mapping (Plumptre *et al.* 2016a). The area was predicted to contain 44.7% of the occupancy cells where Grauer's gorilla was predicted to be present and 56.2% of the estimated gorilla population across its range (A.J. Plumptre unpublished data).

Survey Area

Emlen and Schaller in 1959 documented that Grauer's gorillas occurred at low overall density with a highly fragmented and patchy distribution. High densities were found only in small, localised subpopulations, while large areas of contiguous and seemingly suitable habitats were unoccupied (Emlen & Schaller, 1960). They concluded that gorillas were rare and likely undergoing a rapid population decline due to habitat conversion in the highland regions and widespread hunting. At the time they estimated the existence of between 5,000 and 15,000 individuals across their range based on limited survey data (Emlen & Schaller, 1960; Schaller, 1963). They indicated that the KBNP region and the area to the west of KBNP contained the largest concentration of gorillas. KBNP was established in 1970 and inscribed as a World Heritage Site in 1980. It is managed by ICCN. It was then inscribed on the 'In Danger' list of World Heritage sites in 1997 due to continuing habitat loss and poaching due to the ongoing civil unrest in the area. Between 1994 and 1996 more intensive surveys were made in various sites across Grauer's gorilla range (Hall et al. 1998a). These estimated a global population of 16,900. The highland sector (Tshivanga) of KBNP in the east has open montane forest with a dense herbaceous vegetation below the canopy and open marshes with dense reeds. This sector reaches over 3,000 metres a.s.l. on the mountains Kahuzi and Biega. To the west, the park transitions to closed canopy montane forest and a rugged topography in the Nzovu, eastern Lulingu and Itebero sectors (Figure 1), dropping down to lower altitude and flatter terrain with lowland forest and patches of monodominant *Gilbertiodendron dewevrei* forest from 600-1000 metres a.s.l. (Hall et al. 1998b).

The area to the west of Kahuzi-Biega National Park, that was shown to also be important in both Emlen and Schaller's surveys (1960) and by Hall et al. (1998b), did not receive much attention following the 1994-96 surveys because of insecurity. It was envisaged as the Oku Community Reserve (OCR) in 2005 under a USAID-funded program for conservation in the Grauer's gorilla landscape but received little support. In 2011, WCS started a program of support to representatives of the community who were based in Kasese town, and who were able to access the forest and survey for large mammals. During our survey this OCR was divided into a northern (OCR North) and eastern sector (OCR East), but during consultations held since the survey, the local community have opted to create three local community forest concessions (CFCLs) and a reserve in the region. The three CFCLs were legally established in 2018, and further community consultations are currently underway regarding the creation of a faunal reserve in the adjacent forest. The forest in OCR is less rugged than KBNP and drops down to 530 metres a.s.l. with dense canopy and patches of monodominant *Gilbertiodendron dewevrei* forest. The survey area encompassed KBNP and OCR together with FODI and the forest around Kasese town as well as a 3 km buffer region around all these sites. The total survey area encompassed 15, 372 km^2 (Figure 1).

While the focus of the surveys was on the two great apes, there are several other primates in this region including several threatened species: L'Hoest's monkey (*Allochrocebus lhoesti* = VU), Owl-faced monkey (*Cercopithecus hamlyni* = VU), Johnstone's Grey-cheeked mangabey (*Lophocebus albigena johnstoni*=NT), Ulindi red river colobus (*Piliocolobus lulindicus* = EN), Schmidt's redtail monkey (*Cercopithecus ascanius schmidti* = LC), Stuhlmann's blue monkey (*Cercopithecus mitis stuhlmanni* = LC), and Dent's monkey (*Cercopithecus denti* = LC). These were all recorded during the surveys when seen.

METHODS

Data collection

This study complied with guidelines for field research that are used by the Wildlife Conservation Society, adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates, and adhered to the research requirements of the Institut Congolais pour la Conservation de la Nature (ICCN).

A line transect distance sampling design was developed for both the KBNP and OCR (Buckland *et al*. 2001). The Distance software (version 6.0; Thomas *et al*. 2010), generated 162 three-km long transects for KBNP, and 68 five-km long transects for the lower altitude OCR (Figure 1). Surveying these transects was very intensive and took time because of the presence of armed rebels operating in parts of the KBNP. Surveys of some sectors, for example the FODI (north of KBNP) and the Kasese sector in KBNP in the far west, were made in 2011/12 and 2013 respectively because of good security at that time, but it was possible to visit some sectors only as recently as 2019. At the time of the surveys, KBNP was surveyed in four of five sectors (insecurity in Lulingu sector prevented surveys there) and assessments were made of two regions of OCR recognised as OCR north and OCR East (Figure 1). Since that time, several community reserves have started to be designated in OCR and the boundaries have changed as a result.

Each team comprised two observers who walked each transect from a base camp, cutting as little as possible of the vegetation to minimise noise. Over the period of 2011-2019 a total of ten Congolese field assistants acted as observers coming from the WCS, ICCN and a local community environmental group in OCR. These people had been involved in multiple transect surveys in the region and were very experienced in undertaking surveys. They would travel with a local guide, usually a hunter, who knew the forest well and was also experienced in identifying species. Before each set of surveys refresher training courses were made to ensure standardised methods were used. Sightings of live animals, tracks, calls, dung, and nests were recorded together with the perpendicular distance to each sighting. In the case of apes (gorillas and chimpanzees), counts were made of nests and the perpendicular distance to the centre of each individual nest was measured in a group of nests (Buckland et al. 2010). In the case of groups of monkeys, the distance to the nearest and farthest animal was measured if all the group were to one side of the transect to estimate the perpendicular distance as: (Nearest + Farthest)/2. If the animal group straddled the transect then the distance to the farthest individual on the left and right sides of the transect were measured and the perpendicular distance calculated as: ($Farthest_{left}$ – $Farthest_{Right}$)/2 (White & Edwards 2000). Once the team completed one transect, they then travelled toward the next transect and established a camp between the two transects.

Nests were determined as gorilla nests if they included any of the following characteristics: 1. ground nest; 2. large size; 3. gorilla faeces; 4. silver hair from large nests; 5. close grouping of nests; 6. most nests in group below 15 metres; 7. feeding sign characteristic of gorillas and 8. presence of ground trails leading to and from nests. Nests of chimpanzees were determined by: 1. Absence of ground nests; 2. Absence of faeces in nest; 3. Most nests in a group between 10-30+ metres; 4. Nests more spread apart in a group. Where a nest could not be assigned to either species, usually when old in age, it was recorded as an ape nest, but as these were few the data were not analysed.

Analysis methods

Design-based estimates of ape density

Standard line transect distance sampling methods (Buckland *et al.* 2001) were applied to the nest sightings for both chimpanzees and gorillas using. We used Distance software (version 7.0; Thomas *et al.* 2010) to estimate nest density with the perpendicular distance data and then converted nest density to ape density based on nest production and decay rates. (Plumptre & Reynolds, 1996; Buckland et al. 2010).

Where the rate of nest construction has been studied, most chimpanzees build about 1.1 nests per day (Plumptre & Cox 2005; Plumptre & Reynolds 1997; Sanz 2004; Kouakou, Boesch & Kuhl 2009) and it is usually assumed most gorillas build one nest per day (Hall et al. 1998b), but this has not been measured with habituated groups of eastern gorillas. However, in western gorillas, the value of one nest a day has been widely used (Morgan et al 2006).

In the 1994-1996 surveys the average nest decay rate was estimated at 106 days for this region (Hall *et al.* 1998b; Plumptre *et al.* 2016a; 2015) for both gorillas and chimpanzees based on studies from other sites in the Congo basin. It was not measured in this region at that time. During the period of this study we monitored the time to decay of gorilla nests built in the highland (Tshivanga) sector of KBNP where habituated groups of gorillas are followed daily for tourism. The provisional results show a faster nest decay rate at that site (average of 61 days (95% CI: 19 – 103 days) for 83 nests monitored in this high altitude sector) with few nests surviving for longer than 100 days (Plumptre et al. 2015). Whether this rate is typical of the whole KBNP-OCR region is unknown but we believe that the decay of nests is likely to be faster in the highland areas as more nests are constructed with herbaceous rather than woody plants. Hall et al. (1998b –Table VIII) showed that most nests in the KBNP-OCR region are in woody vegetation with only 2.7% in herbaceous vegetation. Security issues prevented us from monitoring nests in the lower altitude areas. For the analyses we therefore used 106 days to make estimates comparable between the surveys in 1994-96 but recommend that nest decay measures are obtained across the region when security conditions make this possible.

Design-based density estimates for both gorillas and chimpanzees were made for the whole survey area, KBNP and OCR individually, as well as for the management sectors in KBNP (where line transects had been surveyed), and the eastern and northern parts of the OCR. Density for each sector was calculated assuming the same detection curve across all sectors but with sector specific cluster size and encounter rate. Lulingu Sector was not surveyed in KBNP because of insecurity but when calculating the total population estimate for the park we used the total area of the park, effectively extrapolating the average density across the other sectors to the Lulingu sector.

The 1994-96 surveys estimated the area of KBNP as 6,000 km^2 at a time when there was not an accurate map of the park or GIS tools readily available. The shapefile we used based on mapping of the park using the legal gazettment document totals an area of 7,257 km^2, a 21% increase in area. The 1994-96 estimate of the Kasese area was also much larger (6,770 km^2) compared with the area of OCR (4,400 km^2). Clearly if different areas are used between studies then extrapolated density estimates will give different numbers. We therefore compared gorilla and chimpanzee estimates by correcting for area using the densities obtained in 1994-96 and applying them to the more accurate areas of KBNP and OCR (corrected ape numbers). The 1994-96 surveys also made corrections of nest counts, estimating that they had underestimated gorilla nests and overestimated chimpanzee nests. These same corrections factors, calculated from the data in Hall et al. (1998b) were applied to correct the counts so that our estimates were comparable. These two corrections applied are termed 'corrected ape numbers' in the results.

We also made a comparison of the estimates that would have been obtained from the occupancy estimate (Plumptre et al. 2016) if we had used the densities we obtained for the survey area in this study instead of the 0.19 / km^2 that was applied in that paper, which was a weighted average density obtained across 15 sites.

Comparisons between estimates were tested using Z-tests making the following comparisons:

1. Test between densities obtained in 2011-2019 between the design and model-based methods – tested for KBNP and OCR separately as well as the study area as a whole
2. Test between corrected ape numbers obtained in 1994-96 with the design-based estimates from 2011-2019– tested for KBNP and OCR separately as well as the study area as a whole
3. Test between the occupancy analysis ape numbers from 2016 and the design-based results presented here for 2011-2019

Design-based estimates of monkey density

Densities of other primate species were also estimated from sightings of monkeys along transects using Distance software and using group size observed as the cluster size. If perpendicular distance and cluster size are correlated, then average cluster size is potentially biased. Corrections were made to the cluster size if the correlation was significant ($p<0.05$) using the default method in Distance which regresses log cluster size on the density function (Thomas et al. 2010). Sightings of monkeys were rare and as a result we also estimated a total density of monkey species assuming the same detection curve across all species, although we recognise that in reality detection will likely vary between monkey species.

Model-based estimates of density and distribution

We used generalized additive models (GAMs) that are flexible and able to capture nonlinear responses (Wood 2017). The models were fit in R (version 4.0.1; R Core Team 2020) using the *mgcv* package (version1.8-31; Wood 2011) with the restricted maximum likelihood (REML) to optimize smoothing parameter estimation (Marra & Wood 2011). We used a Tweedie distribution (Jørgensen 1987) and estimated the value of its power parameter with an iterative search (Miller *et al*. 2013) to deal with the zero-inflation (Peel *et al.* 2012) evident in these data (Suppl. Fig S1) due to the many transects where no great ape nests were found. Models were built using thin plate regression splines for each of the explanatory variables and the basis dimension was restricted (k=5) to avoid overfitting. Generally explanatory variables were removed from a model when their approximate p-values were greater than 0.05. Gorilla or chimpanzee nest density was modelled by including area surveyed ($2\hat{\mu}l_i$, where $\hat{\mu}$ is the survey-specific effective strip half-width and l_i is the length of transect segment *i*) as an offset term in the model. Transects were split into smaller segments of 1km where possible to reduce variability in effort and ensure that explanatory variables were at a sufficiently fine resolution to capture the conditions at the location of the nest counts.

To identify the important predictors of Grauer's gorilla and eastern chimpanzee density and distribution, we considered human-related variables, such as distance to road, distance to villages, distance to mines, distance to forest loss, and distance to steep slopes (as a proxy for the ease, or otherwise, of human access), management-related variables such as the number of days or aggregate distance covered by rangers or community ecoguards, and a landscape variable reflecting regional distinctions (Nzovu (a sector with villages within the park), the highland sector (Tshivanga), and the Lowlands, which included Punia Gorilla Reserve (RGPU) as well as Lulingu and Itebero sectors in KBNP). We also considered ecological variables such as the degree of tree cover, tree height, and altitude. The potential drivers of great ape density and distribution were the same as those used by Plumptre et al. (2016) and are summarised in the Supplementary materials (Table S1). We considered the correlation between all variables to ensure that highly correlated variables were not included in the same model. The final models were used to predict density of Grauer's gorillas and eastern chimpanzee in each cell of a 1 km by 1 km grid overlaid across the survey area. This permitted model-based estimation of overall density and abundance, as well as survey sector-specific results.

A total of 999 bootstraps were conducted to estimate variance and percentile confidence intervals (CIs) of gorilla or chimpanzee density and abundance by resampling transect segments at random, and with replacement. To account for the original hierarchical structure of the data set, during each bootstrap resample, the same number of sampling units was selected as in the original data set for each of the surveys, with their corresponding number of transects segments. Nest density and abundance estimates were obtained from these resampled data, conditioned on the original model fit. Nest density and abundance estimates were converted to gorilla or chimpanzee abundance by applying the conversion factors (described above: nest creation and decay rates) with the associated total variance obtained by incorporating the variance associated with the conversion factors. During each bootstrap iteration, conversion factor values were generated from a normal distribution with a mean equal to the estimated value of the conversion factor and a variance equal to the squared value of the associated standard error. Gorilla or chimpanzee density estimates were ordered from smallest to largest, and the 25th and 975th values were used to define the percentile CI.

RESULTS

Design-based density estimates of apes

Estimated numbers in KBNP and OCR

A total of 194 gorilla nests were counted along 689 km of transects with 328 km walked in KBNP, 289 km walked in OCR and 72 km outside these two sites in FODI or near Kasese town west of OCR (see transects surveyed in Figure 1). Altogether, 319 chimpanzee nests were counted along these transects. The detection curves for gorilla and chimpanzee nests were reasonable with most observations within 20 metres (Figure S2); data were right truncated to this distance from the transect line. We estimated 1,223 (95% CI:640-2,338) Grauer's gorillas in KBNP and 1,967 (95% CI:1,206-3,209) in OCR, with a total of 4,443 (95% CI:3,021-6,533) for the survey area (including FODI, Kasese town and buffer regions). Similarly, we estimated 2,664 (95% CI:1,862-3,810) chimpanzees in KBNP and 1,170 (95% CI:686-1995) in OCR, with a total of 4,925 (95% CI:3,656-6,634) chimpanzees for the survey area.

Estimated numbers in sectors of the survey area

Gorilla densities were quite variable with highest densities in the Highland Sector of KBNP and in the eastern region of OCR (Table 1). The eastern part of the Nzovu sector in KBNP has likely lost all of the gorillas that once occurred there (Hall et al. 1998b) as no sign of gorillas was found in our surveys.

Results for chimpanzees in the different sectors show that densities are higher in KBNP than in OCR and that this species tends to be at higher densities in the more rugged sectors with forest at higher altitude (Table 2). The highest densities were in the Highland Sector of KBNP together with the western part of Nzovu sector.

Design-based density estimates of other primates

Sightings of monkeys were few, with only 150 sightings of monkey groups from six species: redtail monkey, owl-faced monkey, L'hoest's monkey, blue monkey, Dent's monkey, and grey-cheeked mangabey. Ulindi red colobus monkeys were heard in OCR once and not detected anywhere else.

With such rare sightings, the density of only four species were estimated with any confidence, assuming the same detection curve for each species across sectors (Table 3). Total monkey densities were highest in OCR with about 36 individuals/km^2 (95% CI: 26-51) while in KBNP, FODI and outside the OCR (south west of OCR) densities varied between 7-15 individuals/km^2 (range of 95% CI:1-46).

Model-based estimates of great ape density distribution and abundances

The final models used to predict Grauer's gorilla density estimated 4,797 (95% CI: 3,313-6,906) weaned individuals (Table 4) with mapped density surfaces showing their distribution in Figure 2. Of these total estimates 1,476 (95% CI: 710-2,719) gorillas were estimated to occur in KBNP and 2,233 (95% CI: 1,440-3,136) gorillas in OCR. Covariables that were important predictors were those that reflected distance from people, such as distance to road, distance to villages, and distance to mines, and distance to steep slopes (as a proxy for the ease or difficulty of human access). Which variables were important varied by region in the landscape, with gorilla density and distribution in the Lowlands particularly influenced by distance to roads, distance to mines, and distance to steep slopes, in the Nzovu sector by distance to villages, and in the highland sector by distance to roads (although the approximate p-value > 0 .05, this term was retained in the model, because the lack of significance was due to the large amount of variation associated with the estimate caused by the small sample size (33) for the highland sector).

In the Lowland region the greatest distance from a mine or to areas of steep slope is approximately 28 km and 39 km, respectively. Grauer's gorilla nest density increased with increasing distance from mining up to a distance of about 7 km before declining back down again with increasing distance. In the Lowlands, proximity to steep areas were associated with higher gorilla nest density as well. In Nzovu the greatest distance from a village is less than 9 km and Grauer's gorilla density increased with increasing distance to villages up to a distance of about 5 km. In the Lowlands and in the highland sector the greatest distance from a road is approximately 28 km and less than 10 km, respectively, and Grauer's gorilla density increased with increasing distance to roads up to a distance of about 10 km and 7 km, respectively, before tapering off (Figure 3).

The models for eastern chimpanzee estimated 5,454 (95% CI:3,742-13,900) weaned individuals with 2,901 (95% CI: 1,259-7,315) chimpanzees estimated to occur in KBNP and 1,069 (95% CI: 732-1,468) chimpanzees in OCR. Covariables that were important predictors were also those that reflected distance from people, such as distance to road, distance to villages, and distance to mines, and distance to steep slopes. Chimpanzee density and distribution in the Lowlands was particularly influenced by distance to villages, distance to mines, distance to steep slopes, and distance to rugged areas, and in the Nzovu sector by distance to villages and distance to mines (only the distance to villages in the Nzovu sector and the ruggedness score in the Lowland region had associated approximate p-values < 0 .05, however, the remaining terms were retained in the model, because the lack of significance was due to the large amount of variation associated with the estimate, as for gorillas).

Eastern chimpanzee nest density increased with increasing distance to mining, up to a distance of about 13 km in the Lowlands before tapering off, whereas there was a continuous increase in nest density in Nzovu with increasing distance from a mine with the largest distance of 17 km from any mine in this sector. In the Lowlands proximity to steep areas were associated with higher chimpanzee nest density as well. Chimpanzee density increased with increasing distance to villages in both the Lowlands and Nzovu up to a distance of about 10 km and 5 km, respectively. In the Lowlands chimpanzee density increased with increasing ruggedness score (Figure 4).

Survey area ape population comparisons

Table 5 summarises the estimates for gorillas and chimpanzees, comparing population estimates for KBNP, OCR and the survey area mapped in Figure 1. The original numbers from Hall et al. (1998b) are provided together with the revised estimate that we calculated using the density data from the paper, the GIS-calculated areas of each of the three sites, and the proportional correction provided by the revised nest counts in that paper (p226 – where gorilla nest numbers were revised upwards by 18% because of suspected misidentification). These estimates are compared with those from the transect data and the model estimates in Table 5.

Testing differences between design and model-based estimates

A Z-test was used to compare the model- and design-based estimates for gorilla density in KBNP (Z= 0.727, P=0.23), OCR (Z=0.420, P=0.38) and the survey area (Z=0.220, P=0.41) and for chimpanzee density in KBNP (Z= 0.502, P=0.31), OCR (Z=0.307, P=0.38) and the survey area (Z=0.257, p=0.40). Given that there was no statistically significant difference or strong effect between the model- and design-based estimates, we use the design-based estimates as our estimate for each site in subsequent comparisons.

Testing differences between corrected 1994-96 ape numbers and 2011-2019 design-based estimates

In order to compare the 1994-96 estimates with the 2011-2019 estimated numbers we needed to use the corrected estimates of density based on correct areas for the region and using uncorrected nest classifications – see methods. We estimated corrected numbers of gorillas (Table 5) in the survey area (12,390; 95% CI: 7,501-18,679) and chimpanzee (3,795; 95% CI: 2,374-5,589). Design-based estimates of gorilla numbers were significantly lower for the study area in 2011-2019 (Z=2.56; P=0.005) and higher for chimpanzees but not significantly different (Z=1.030; P=0.15).

Corrected gorilla numbers for KBNP (Table 5) were significantly lower than the design-based estimates in 2011-2019 than in 1994-1996 (Z=3.591; P=<0.001) but not significantly different in OCR (Z=0.362; P=0.36). Corrected chimpanzee numbers were not significantly different in KBNP (Z=0.325; P=0.37) but were significantly higher in 2011-2019 for OCR (Z=3.344; P<0.001).

Testing differences for the study area between design-based estimates and occupancy estimates

Comparison between the great ape numbers estimated for the survey area from the design-based estimates and the occupancy model (Plumptre et al. 2016) showed that the occupancy model estimate for gorillas was significantly smaller (Z=1.75, P=0.04), but the estimates of chimpanzees were not significantly different (Z=0.653, p=0.26).

DISCUSSION

Changes in estimated density and numbers of primates

Changes in ape numbers in KBNP, OCR and study area

Estimates were made of the populations of chimpanzees and gorillas in sectors of KBNP and OCR between 1994-1996 (Hall et al. 1998b; Inogwabini et al. 2000). Comparison of these results with the recent survey estimates a large decline in gorilla numbers over the study area but stable chimpanzee numbers (Table 5). Both the 1994-96 and 2011-2019 surveys were based on nest counts and it is possible to confuse chimpanzee and gorilla nests (Tutin et al. 1995). We were fairly confident that the observers we used were able to identify nests accurately, but acknowledge that old nests can be difficult to identify accurately. Hall et al. (1998b) corrected their nest counts, because they perceived there may have been misidentification of gorilla nests, and therefore revised their gorilla nest counts and hence density upward and their chimpanzee density downward. We therefore re-analysed the data for the survey area as a whole using the densities from Hall et al. (1998), ensuring the area of each site was the same and that the methods were comparable, removing the correction they made for the misclassification of nests. It should also be recognised that the surveys in 1994-96 were made in seven regions of the survey area (Figure 1) and transects were not located as systematically across the region as in this study, which would likely have led to some differences in numbers but probably not enough to explain the estimated decline in gorilla numbers. The 2011-2019 gorilla population estimate from the design-based transect data indicates a significant decline in numbers of 86% in KBNP. In OCR gorilla numbers have remained relatively stable (Table 5). Chimpanzee numbers appear to have remained stable across the study region as a whole but have actually significantly increased in OCR while remained stable in KBNP (Table 5).

The highland sector (Tshivanga) is where the KBNP headquarters and gorilla tourism occurs. Surveys in this sector have made total counts of gorillas in the past with an estimate of 245 individuals in 1996 (Inogwabini et al. 2000) and more recent estimates in 2000, 2004, 2010 with the most recent indicating 213 gorillas in 2015 (Spira et al. 2016; Plumptre et al. 2016c). This recent number compares favourably with the estimate of 199 individuals (Table 4) from the model-based estimates for this sector but not very well with the 321 from the design-based estimate (Table 1). While the recent total counts have not been able to access the very north of the sector because of insecurity there the transect surveys did not find sign of gorillas there.

Bushmeat hunting is likely responsible for the decline in gorillas (Plumptre et al. 2016a); the clear positive relationship between density and increasing distance from mining, roads, and villages supports this (Figure 3). Gorillas are valued by hunters because they provide a very large amount of meat for a single cartridge or bullet, compared to the much smaller-bodied duikers or monkeys in the area. In addition, gorillas move in groups that are relatively easy to track and find. Chimpanzees, which have a fission-fusion social organisation, do not move in groups all the time and hence are harder to track. Chimpanzees will also flee, often silently and stealthily, when confronted as opposed to the typical response of gorillas, where the silverback faces up to and threatens the attacker, thus risking being shot. These behavioural differences have likely contributed to the better survival of chimpanzees in the region compared to gorillas (Table 5).

Monkey densities were very low in comparison with those in western Uganda or Rwanda, indicating that hunting is also having a major impact on these species. Apart from within OCR, monkey densities tended to be lower than those estimated for the Itebero sector by Hall et al. (2003). This author estimated monkey densities between 10-36 individuals/km^2 for all primate species, apart from owl-faced monkey which occurred at around 5-7 individuals/km^2 (Table 6). Hall et al. (2003) cut transects and then re-walked them to estimate monkey densities. Our study only counted monkeys seen while walking the transects once. While every effort was made to minimise noise and cutting of transects it is likely monkeys may have fled from observers in our surveys. However, the varying field implementation is unlikely to explain the large differences observed between 1994-96 and 2011-2019. Red colobus *Piliocolobus lulindicus* monkeys were relatively abundant at the time of Hall et al.'s (2003) survey, but apart from one call in OCR this species was not detected in this region during our surveys. The range of this red colobus, which extends from the Lualaba River eastwards to the edge of the highlands, is more than 95,000 km^2 (Red Colobus Action Plan –Linder et al 2020). The sharp drop in their population across the species range (estimated as at least 50% by IUCN) in the last 30 years or three generations, combined with about 15% habitat loss, has resulted in *P. lulindicus* having recently been assessed as Endangered by Hart et al. (2020). This is supported by the major declines observed for this species in these current results. Red colobus are often the first monkey species hunted out in an area when people move in, partly because they occur in large groups and tend to remain above the hunters or observers, or try to hide rather than flee, and partly because their large body size relative to other monkeys renders them one of the more profitable taxa to shoot in terms of cost of a shotgun cartridge vs the amount of meat gained per shot.

Implications of results for global estimates of Grauer's gorilla

The gorilla estimates for the survey area totalled 4,430 individuals from the design-based transect estimates, which is higher than the total global population estimate of 3,800 individuals obtained from the occupancy analysis across Grauer's range (Plumptre et al. 2016a). The 2016 global population assessment used the results of an occupancy analysis to estimate gorilla numbers converting occupied cells to numbers using an average density estimate of 0.19 gorillas per km^2, a value that was obtained from density estimates across this ape's range. We used our more accurate estimates of density from this survey to test whether the occupancy method was underestimating the ape numbers for this region. The results showed that gorilla numbers were significantly underestimated but that chimpanzee numbers were not significantly different using both methods. Given gorillas also occur in Itombwe Forest Reserve, Tayna Community Reserve, and areas north of KBNP-OCR up to Maiko National Park the total global population will be higher still than our estimated 4,430. At the time the occupancy analyses were made not much of the OCR region had been surveyed, and it is possible that a recalculation using updated data including this region might increase the overall estimate of numbers of gorillas, given that it is likely one of the last strongholds for this ape. Grauer's gorilla was classified as critically endangered based upon the 2016 occupancy estimate because there had been a 77% decline in about one generation based on that estimate (Plumptre et al. 2016b). Our estimate of 4,443 for this study area is 26% of the 1994-96 range wide estimate of 17,000 (Hall et al. 1998a). It is unlikely that all other sites across its range combined would exceed an additional 1,500 gorillas given crude estimates from surveys. This gives about a 65% decline in a single generation (1995-2014), as the annual rate of decline was 5.4% 1994-2019. If this continued at the same rate for another generation (until 2033), 88% of the population would have been lost since 1994, so it would still qualify as Critically Endangered.

Conservation value of the KBNP-OCR region

It is clear that the Oku Community Reserve is of great importance for gorilla conservation, as well as for the conservation of several other primates. It has an estimated 1,967 Grauer's gorillas, 1,170 chimpanzees, as well as higher monkey densities than KBNP. Grauer's gorilla has not declined significantly in this region and chimpanzee numbers are estimated to have increased here. Parts of OCR also contain the few remaining elephants in the region, together with large ungulates such as bongo (*Tragelaphus eurycerus*), forest buffalo (*Syncerus caffer nanus*), and sitatunga (*Tragelaphus spekii*). It probably has more Grauer's gorillas than any other site across this ape's range, and together with the Kahuzi-Biega National Park is the last stronghold for this ape. Hall *et al*. (1998b) made a call for 'significant and sustained efforts for conservation' in their paper to conserve the primates in this region. The civil war in DRC and continued presence of armed rebel groups has made this exceedingly difficult. The focus of conservation efforts is now on the local community that are able to live and operate in this region, because they are tolerated by the rebel groups. Since 2012, efforts have been made to work with the community (including one of the authors - EN) to protect this area of forest. In 2018, three local community forest concessions comprising a total area of 1,465 km^2 were created with the consent of the local community. WCS and ICCN are currently working with community-led NGO Reserve des Gorilles de Punia (RGPu), to conduct consultations with the local community to obtain Free Prior and Informed Consent (FPIC) to create a faunal reserve adjacent to the three CFCLs. The creation of a faunal reserve could secure up to 3,000 km^2 of forest for gorillas and the diversity of flora and fauna in this area. If this initiative is successful, there will be a need to secure further funding to support the development of the governance structures for the reserve and CFCLs, and to support the local community through implementation of community conservation projects.

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Data availability

The data used to make the analyses have been provided to the APEs database to be stored with other ape survey data.

Conflict of Interest Statement

There are no conflicts of interest.

Author contributions

AP conceived of the survey, designed the survey with JK and CS, supervised the surveys, analysed the data with FM and SS and wrote the paper with all authors. AK, CS, RN, SB, LO and DK oversaw the field teams and organised logistics to keep them safe and supplied. JK, GM, and EN, led teams in the field and also coordinated the logistics in the field, engaging local chiefs and community leaders to obtain permissions for the surveys and support when in the field.

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Table 1. Estimated density ($\hat{D}$; $/\mathrm{km}^2$) and abundance ($\hat{N}$) of gorillas with 95% confidence interval (95% CI) for sectors of KBNP and OCR from design-based line transect sampling surveys. Total numbers for KBNP is estimated for the total park area including the unsurveyed Lulingu sector, applying a weighted average density across all sectors to the whole park area.

Sector	**$\hat{D}$ No/km²**	**$\hat{N}$**	**95% CI Lower limit**	**Upper limit**
Kahuzi-Biega National Park				
Itebero	0.19	270	99	733
Kasese	0.17	125	38	405
Lulingu	Unsurveyed			
Nzovu east	0.00	0	0	0
Nzovu west	0.11	117	30	450
Highland Sector	0.41	321	63	1,645
KBNP (all park)	**0.17**	**1,223**	**640**	**2,338**
Oku Community Reserve				
OCR East	0.64	1,165	757	1,793
OCR North	0.34	872	366	2,075
OCR (all reserve)	**0.45**	**1,967**	**1,206**	**3,209**
Survey Area	**0.29**	**4,443**	**3,021**	**6,533**

Table 2. Estimated density ($\hat{D}$; /km²) and abundance of chimpanzees ($\hat{N}$) with 95% confidence interval (95% CI) for sectors of KBNP and OCR from design-based line transect distance sampling surveys. Total numbers for KBNP is estimated for the total park area including the un-surveyed Lulingu sector, applying a weighted average density across all sectors to the whole park area.

Sector	$\hat{D}$ No/km²	$\hat{N}$	95% CI Lower limit	95% CI Upper limit
Kahuzi-Biega National Park				
Itebero	0.37	518	328	817
Kasese	0.08	56	17	181
Lulingu	Un-surveyed			
Nzovu east	0.30	261	60	1,128
Nzovu west	0.62	653	364	1,173
Highland Sector	0.57	449	167	1,205
KBNP (all park)	**0.37**	**2,664**	**1,862**	**3,810**
Oku Community Reserve				
OCR East	0.27	489	263	911
OCR North	0.27	681	321	1,445
OCR (all reserve)	**0.27**	**1,170**	**686**	**1,995**
Survey area	**0.32**	**4,925**	**3,656**	**6,634**

656 Table 3. Monkey densities of individuals ($\hat{D}$; /km²) from design-based line transect surveys with 95%
657 confidence intervals (95% CI).

Sector	$\hat{D}$ No/km²	95% CI Lower limit	95% CI Upper limit
Kahuzi-Biega National Park			
Cercopithecus ascanius	5.7	3.1	10.6
Cercopithecus hamlyni	0.2	0.0	1.3
Cercopithecus mitis	5.8	3.2	10.4
Cercopithecus denti	4.2	1.5	11.5
All Monkeys combined	**15.6**	**10.6**	**22.8**
Oku Community Reserve			
Cercopithecus ascanius	9.1	5.1	16.5
Cercopithecus hamlyni	2.2	0.8	6.1
Cercopithecus mitis	12.5	7.3	21.5
Cercopithecus denti	13.5	5.7	31.9
All Monkeys combined	**36.1**	**25.6**	**50.7**
All Monkeys combined Outside KBNP-OCR			
Kasese town	14.9	4.9	46.0
FODI	7.2	1.2	43.8

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Table 4. Overall and sector-specific model-based density ($\hat{D}$; /km²) and abundance ($\hat{N}$) estimates for Grauer's gorilla and eastern chimpanzee with 95% confidence intervals in brackets, plus the associated surface areas.

		Gorilla		Chimpanzee	
Sector	**Area (km²)**	$\hat{D}$ **No/km²**	$\hat{N}$	$\hat{D}$ **No/km²**	$\hat{N}$
Itebero	1,407	0.19 (0.096-0.305)	270 (134-430)	0.35 (0.25-0.504)	497 (352-710)
Lulingu	2,420	0.38 (0.233- 0.518)	910 (565-1,254)	0.20 (0.133-0.278)	476 (322-672)
Nzovu	1,913	0.05 (0.019-0.136)	97 (2-270)	0.84 (0.238-2.806)	1,597 (455-5,369)
Highland	791	0.25 (0.012-0.967)	199 (9-765)	0.42 (0.164-0.714)	331 (130-564)
KBNP Total	**6,531**	**0.23** (0.109-0.416)	**1,476** (710-2,719)	**0.44** (0.193-1.12)	**2,901** (1,259-7,315)
OCR North	2,569	0.44 (0.278-0.607)	1,136 (715-1,560)	0.22 (0.146-0.297)	553 (376-764)
OCR East	1,828	0.60 (0.397-0.862)	1,097 (725-1,576)	0.28 (0.195-0.385)	516 (356-704)
OCR Total	**4,397**	**0.51** (0.328-0.713)	**2,233** (1,440-3,136)	**0.24** (0.166-0.333)	**1,069** (732-1,468)
Remaining region	4,444	0.25 (0.167-0.375)	1,087 (741-1,665)	0.33 (0.241-0.733)	1,485 (1071-3,256)
Survey area	**15,372**	**0.31** (0.216-0.449)	**4,797** (3,313-6,906)	**0.36** (0.244-0.904)	**5,454** (3,742-13,900)

666 Table 5. Great ape population estimates $(\hat{N})$ and 95% confidence intervals (95% CI) in the survey
667 area for data from 1994-1996 (Hall *et al*. 1998), 1994-1996 densities recalculated using the same
668 surface areas for KBNP and OCR, and 2011-2019 for the design- and model-based results. We also
669 estimate the numbers that would have been obtained from the occupancy model (Plumptre et al.
670 2016) applying the average density for each ape for the survey area (Tables 1 and 2).

	Gorilla		**Chimpanzee**	
	$\hat{N}$	**95% CI**	$\hat{N}$	**95% CI**
Kahuzi-Biega National Park				
1994-1996 Original	7,670	4,180-10,830	2,000	1,290-3,290
1994-1996 corrected ape numbers	9,143	5,878-12,197	2,902	1,886-4,209
2011-2019 design-based	1,223	640-2,338	2,664	1,862-3,810
2011-2019 model-based	1,476	710-2,719	2,901	1,259-7,315
Oku Primate Reserve				
1994-1996 Original	3,350	1,420-5,950	600	330-1,210
1994-1996 corrected ape numbers	1,759	879-3,122	484	263-747
2011-2019 design-based	1,967	1,206-3,209	1,170	686-1,995
2011-2019 model-based	2,233	1,440-3,136	1,069	732-1,468
Survey area				
1994-1996 Original	11,020	5,699-16,780	2,600	1,620-4,500
1994-1996 corrected ape numbers	12,390	7,501-18,679	3,795	2,374-5,589
2011-2019 design-based	4,443	3,021-6,533	4,925	3,656-6,334
2011-2019 model-based	4,797	3,313-6,906	5,454	3,742-13,900
Occupancy model 2016	2,603	1,456-3,229	4,144	3,584-4,352

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674 Table 6. Monkey density estimates (/km^2) for KBNP (Itebero sector) in 1994 (Hall et al 2003) and
675 between 2011-2019 (Itebero, Nzovu, and Kasese sectors).

Species	**Density 1994 No/km^2**	**Density 2011-2019 No/km^2**
Cercopithecus ascanius	30.4	5.7
Cercopithecus hamlyni	5.3	1.3
Cercopithecus mitis	36.0	10.4
Cercopithecus denti	17.3	11.5
Cercopithecus lhoesti	Too few to estimate	Too few to estimate
Lophocebus albigena	15.9	Too few to estimate
Piliocolobus lulindicus	20.6	Too few to estimate

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FIGURE LEGENDS

Figure 1. Map of the survey area showing transect points in KBNP and OCR and the sectors, which were analysed separately using the transect data. Model-based predictions of Grauer's gorilla and eastern chimpanzee densities were made across the area designated as the 'Survey region'. Stippled areas are those that were surveyed in 1994 by Hall et al. (1998b).

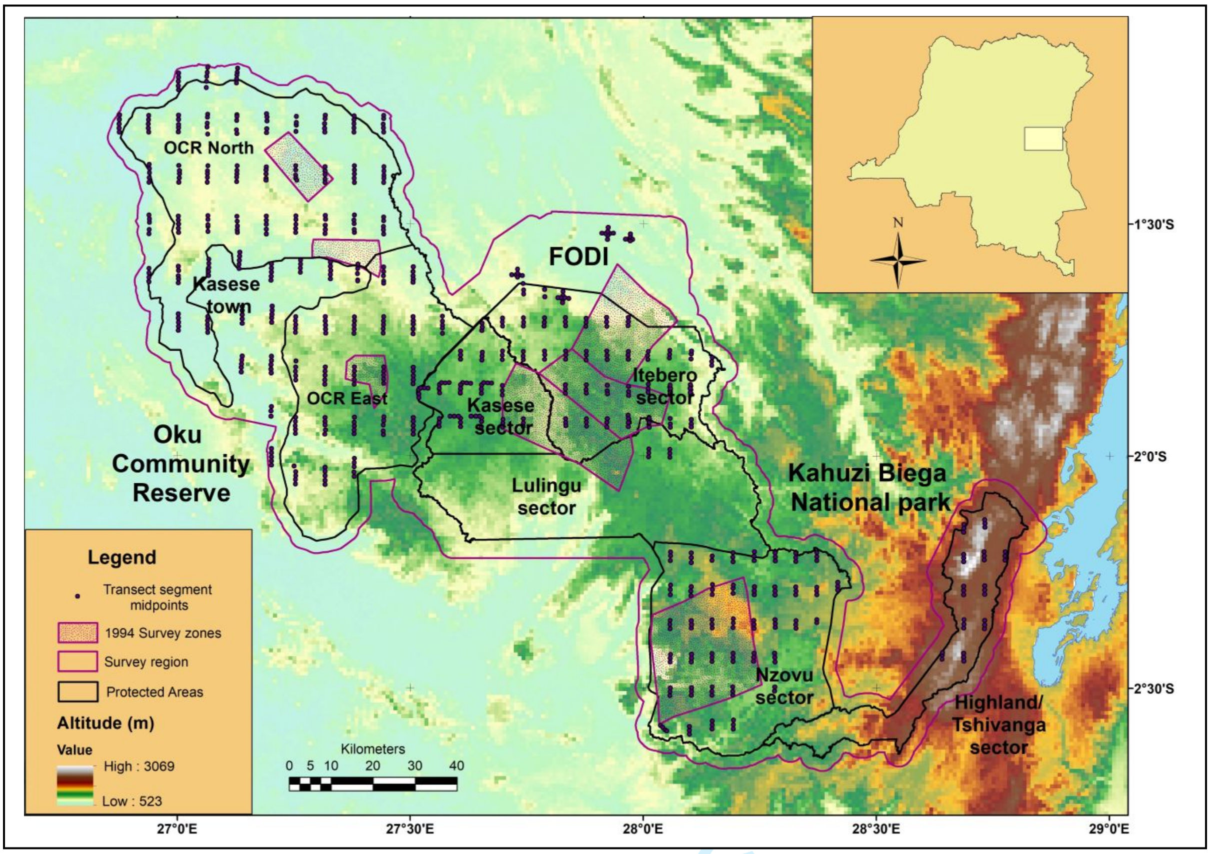
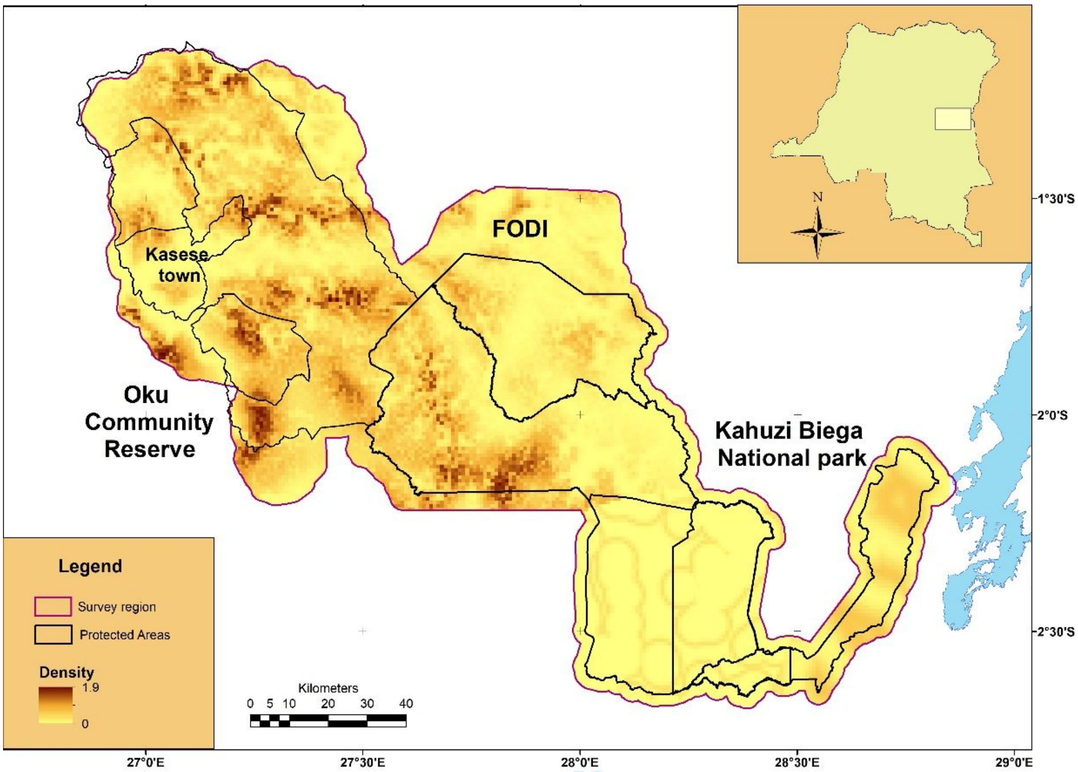


Figure 2: Predicted densities (/km^2) of (A) Grauer's gorillas and (B) eastern chimpanzee across the survey area. These maps show the outline of the proposed revised boundaries of community reserves in OCR.

A.



B.

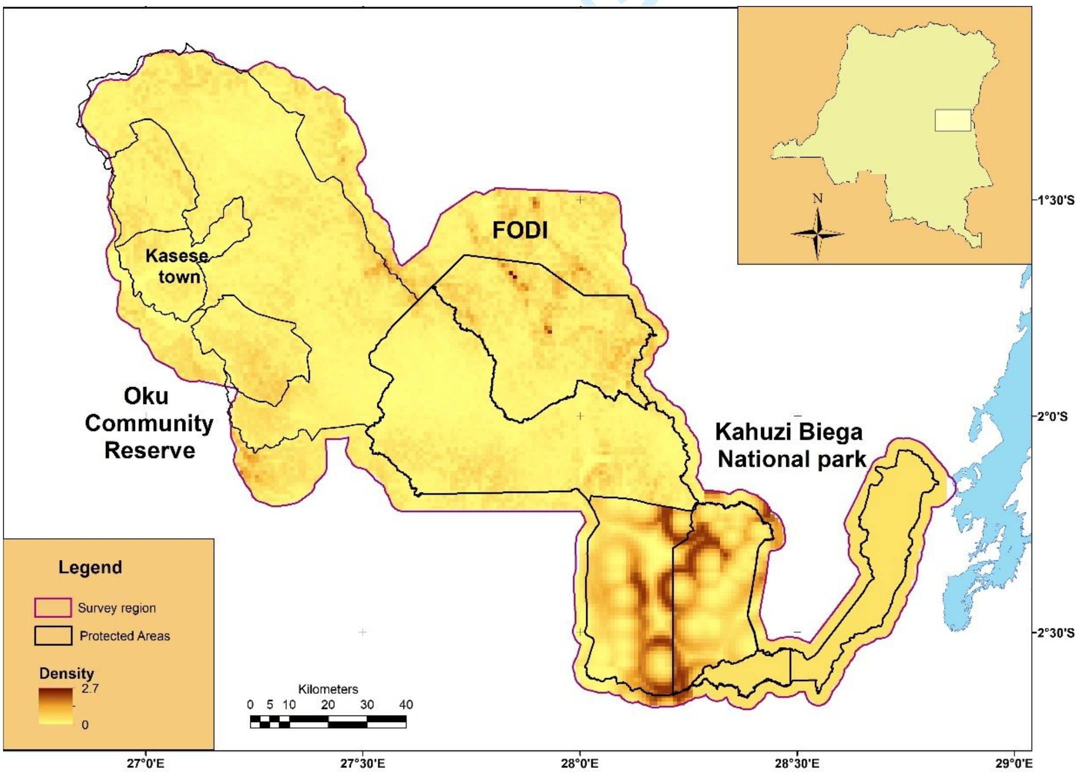


Figure 3. Estimated conditional dependence of Grauer's gorilla nest density on (A) distance to mining, (B) steep areas, and (C) roads all in the Lowland region, and (D) distance to villages in the Nzovu sector and (E) distance to roads in the Tshivanga sector (with (F) the relationship detailed by zooming in to the curve shown in (E)). The y axis (nest density) is on the scale of the linear predictor. Estimates (solid lines) with confidence intervals (grey shading) are shown together with a rugplot.

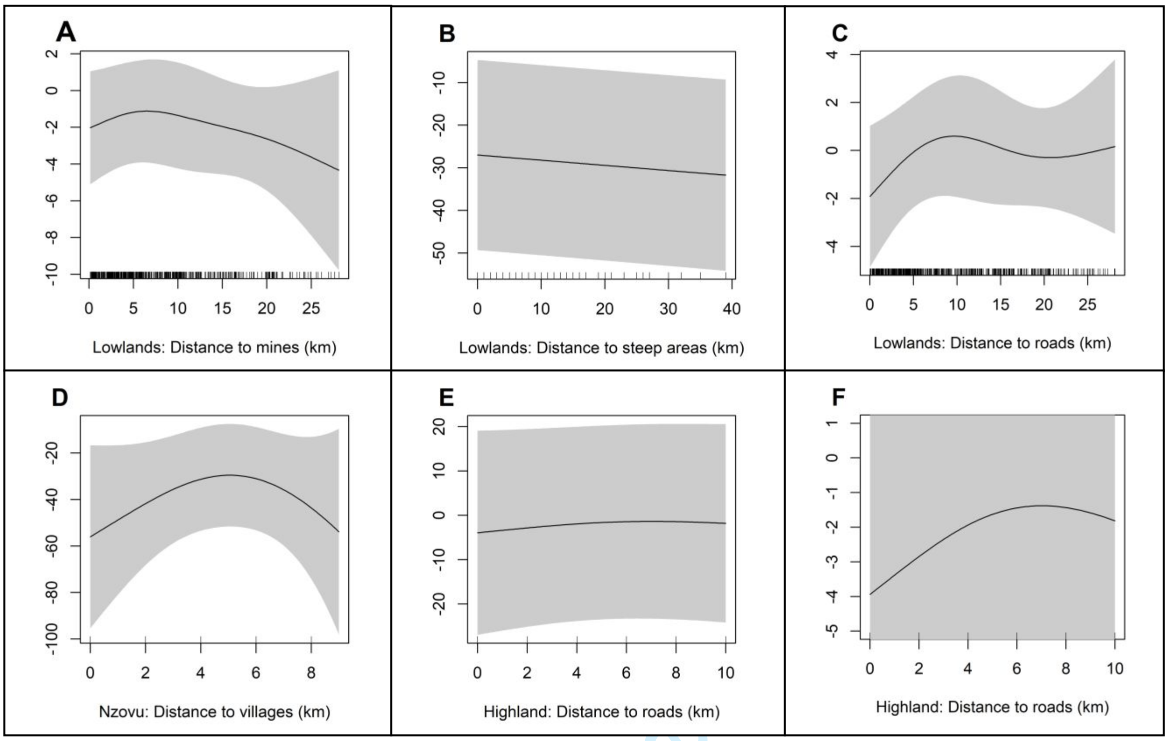
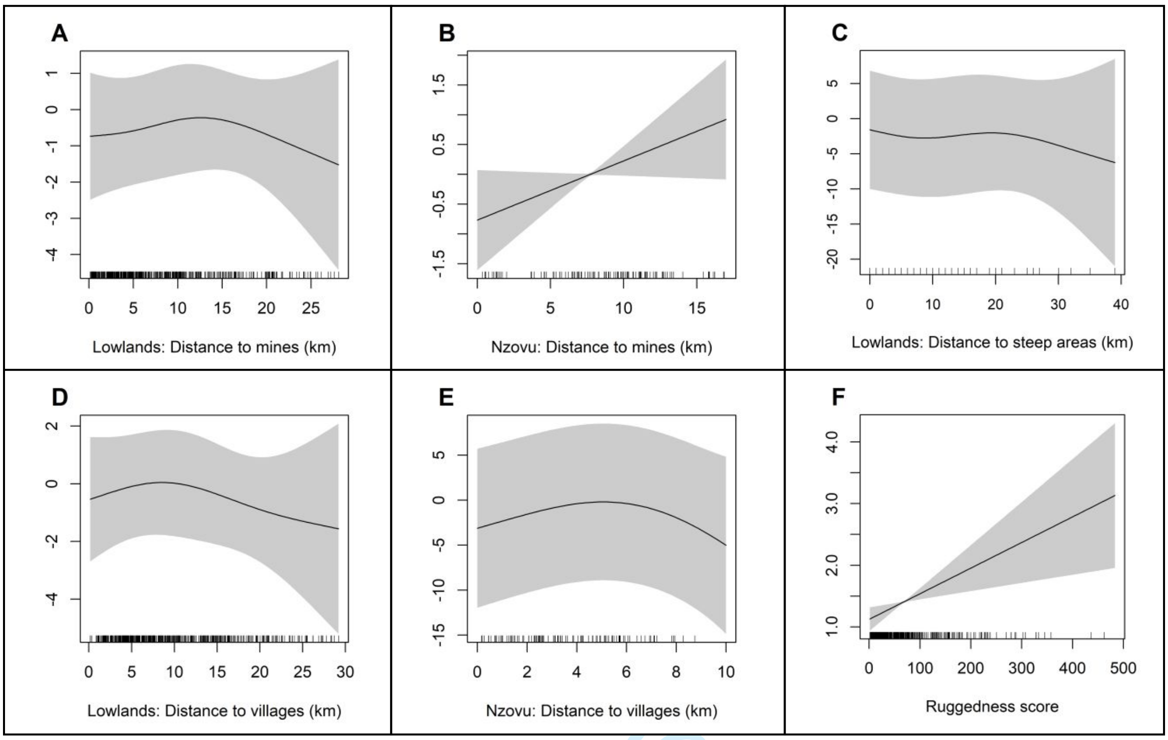
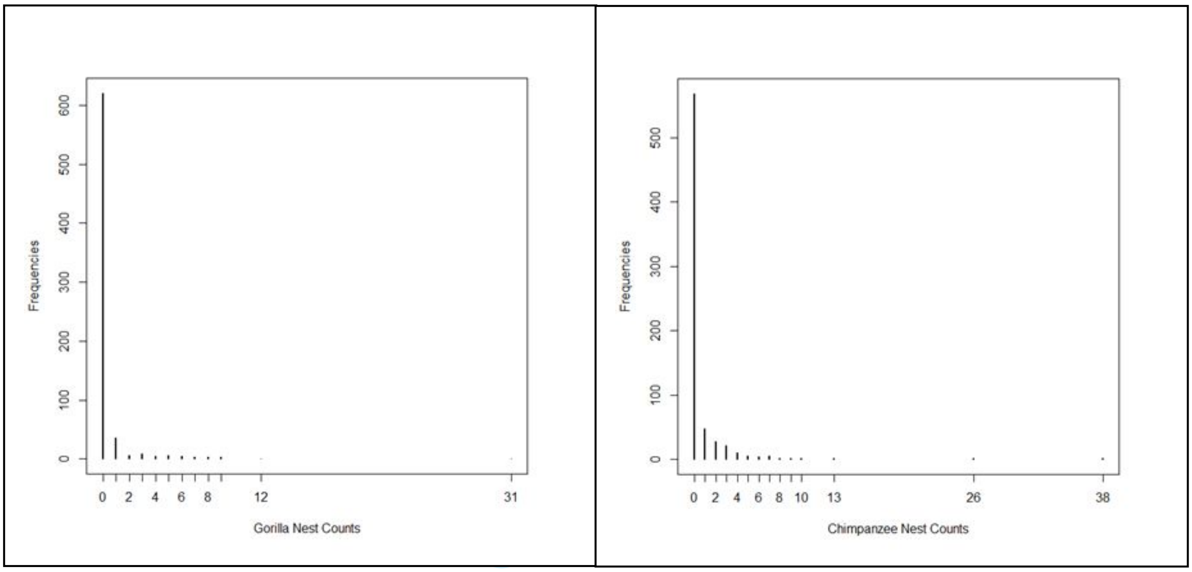


Figure 4. Estimated conditional dependence of eastern chimpanzee nest density on distance to mining in the (A) Lowland region and (B) Nzovu sector, (C) distance to steep areas in the Lowland region, distance to villages in the (D) Lowland region and (E) Nzovu sector, and (F) ruggedness score in the Lowland region. The y axis (nest density) is on the scale of the linear predictor. Estimates (solid lines) with confidence intervals (grey shading) are shown together with a rugplot.



SUPPLEMENTARY MATERIAL

Figure S1: The frequency of Grauer’s gorilla (left) and eastern chimpanzee (right) nest counts along 1 km transect segments.



704 **Table S1.** Covariables used to predict ape density across the survey area.

Covariable Name	Measures	Source
Topographic and forest variables		
dem	Elevation above sea level	SRTM data at University of Maryland http://glcf.umd.edu/data/srtm/
rugged	Ruggedness of topography	Available at http://diegopuga.org/data/rugged/#grid
slope	Slope – calculated from DEM layer	SRTM data at University of Maryland http://glcf.umd.edu/data/srtm/
stslopdis	Distance to steep slopes	Calculated by Lilian Pintea at Jane Goodall Institute from SRTM data
treecov	Percentage tree cover	Calculated by Lilian Pintea at Jane Goodall Institute from Hansen *et al* (2103)*
Treeht	Average tree height	Calculated by Lilian Pintea at Jane Goodall Institute from Hansen *et al* (2103)*
Human impact variables		
disforlos	Distance to forest that has been recently lost	Calculated by Lilian Pintea at Jane Goodall Institute from Hansen *et al* (2103)*
minedist	Distance to artisanal mines	Data from International Peace Information Service and mine location data from SMART
rivdis	Distance to rivers	Calculated from UNOCHA data in eastern DRC
roaddis	Distance to roads	Calculated from UNOCHA data in eastern DRC
villdis	Distance to villages	Calculated from UNOCHA data in eastern DRC
Patrol_day	Number of days of patrols by rangers/community ecoguards	Calculated from SMART data for each 1x1 km
Patrol_km	Number of km walked by rangers/community ecoguards	Calculated from SMART data for each 1x1 km

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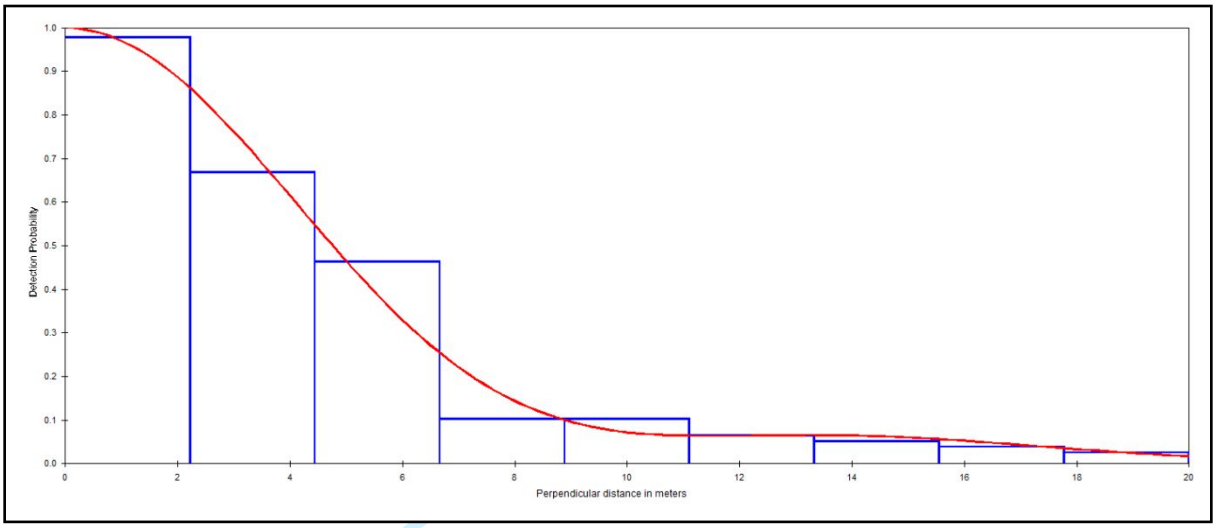
706 *M.C. Hansen et al, High-resolution global maps of 21st-century forest cover change.
707 Science 342**:** 850–53 (2013). Data available on-line from:
708 http://earthenginepartners.appspot.com/science-2013-global-forest.

709

Figure S2. The frequency of perpendicular distances (blue bars) and the detection function (red line) fitted to these data for Grauer's gorillas (a) and eastern chimpanzees (b).

a.



b.