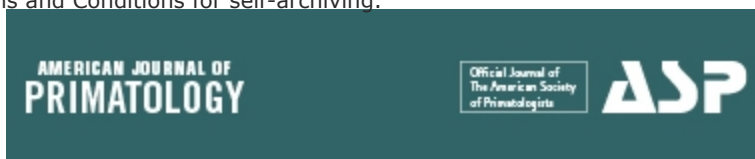


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Changes in Grauer's gorilla (*Gorilla beringei graueri*) and other primate populations in the Kahuzi-Biega National Park and Oku Community Reserve, the heart of Grauer's gorilla global range.

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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.

For Peer Review

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 Grauer's 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

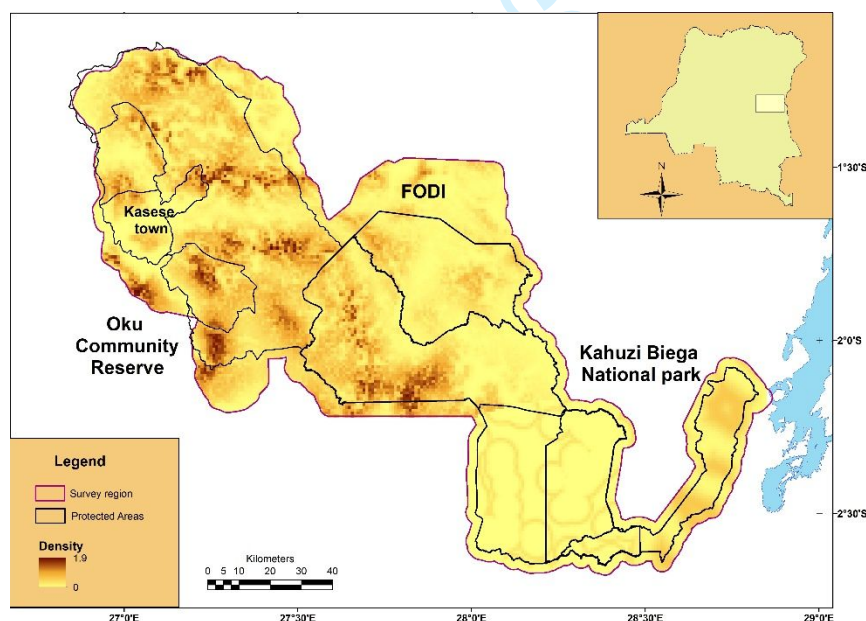
35 results confirm the negative impact of the civil war in the DRC on Grauer's gorilla and other primates
 36 but indicates that the population declines may not be as great as previously feared.

37
 38 **Keywords:** Grauer's gorilla density, eastern chimpanzee, transect survey, population size, red
 39 colobus, primates

41 Research Highlights:

- 42
- 43 • Grauer's gorilla numbers an estimated 4,443 (95% CI: 3,021-6,533) and eastern chimpanzees
- 44 number 4,926 (95%CI: 3,656-6,634) in the Kahuzi Biega National Park (KBNP) and adjacent
- 45 Oku Community Reserve (OCR).
- 46 • Grauer's gorilla is estimated to have declined by 84% in KBNP since the mid 1990s but
- 47 chimpanzees are estimated to have remained stable. Numbers of gorillas in OCR have
- 48 remained stable and chimpanzees have increased.
- 49 • Most other primate species are estimated to have declined significantly due to hunting for
- 50 bushmeat.

52 Graphical Abstract:



54
 55
 56 Modelled density of Grauer's gorillas across the core region of its global range. This model predicts
 57 4,800 (95%CI: 3,310-6,900) gorillas in this part of eastern Democratic Republic of Congo. The map
 58 highlights the importance of the Oku Community Reserve region for the conservation of this ape.

62 Tweetable summary

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

65 INTRODUCTION

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

73 Insecurity during and following the war that occurred in DRC between 1996-2003, and the
74 subsequent proliferation of armed groups in eastern DRC, meant that monitoring populations of this
75 ape, and indeed all wildlife, has been very difficult. A compilation of reconnaissance survey data
76 collected between 2011 and 2015, by rangers and survey teams from the Wildlife Conservation
77 Society (WCS) and Chester Zoo/Zoological Society of London, was used to derive a map of occupancy
78 probability of Grauer's gorillas across their range using several predictor covariables (Plumptre et al.
79 2016a; Plumptre et al. 2015). Threshold occupancy cells were converted to an abundance estimate
80 using an average density obtained from nine sites across the ape's range to estimate a global
81 population of 3,800 (95% confidence interval (CI): 1,280–9,050). Using the same type of conversion
82 to density, eastern chimpanzee numbers were estimated to be 37,740 (95% CI: 14,019–67,196)
83 (Plumptre et al. 2015). These estimates, the best that could be obtained across such a large region,
84 given the insecurity in eastern DRC, indicated a 77-93% decline in the population compared to
85 estimates made in the mid-1990s (Hall et al. 1998a), making the Grauer's gorilla Critically
86 Endangered according to the IUCN Red List criteria (Plumptre et al. 2016b).

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

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2
3 97 was predicted to be present and 56.2% of the estimated gorilla population across its range (A.J.
4 98 Plumptre unpublished data).

5
6 99

100 Survey Area

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

120 The area to the west of Kahuzi-Biega National Park, that was shown to also be important in
121 both Emlen and Schaller's surveys (1960) and by Hall et al. (1998b), did not receive much attention
122 following the 1994-96 surveys because of insecurity. It was envisaged as the Oku Community
123 Reserve (OCR) in 2005 under a USAID-funded program for conservation in the Grauer's gorilla
124 landscape but received little support. In 2011, WCS started a program of support to representatives
125 of the community who were based in Kasese town, and who were able to access the forest and
126 survey for large mammals. During our survey this OCR was divided into a northern (OCR North) and
127 eastern sector (OCR East), but during consultations held since the survey, the local community have
128 opted to create three local community forest concessions (CFCLs) and a reserve in the region. The
129 three CFCLs were legally established in 2018, and further community consultations are currently
130 underway regarding the creation of a faunal reserve in the adjacent forest. The forest in OCR is less

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3 131 rugged than KBNP and drops down to 530 metres a.s.l. with dense canopy and patches of
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5 132 monodominant *Gilbertiodendron dewevrei* forest. The survey area encompassed KBNP and OCR
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7 133 together with FODI and the forest around Kasese town as well as a 3 km buffer region around all
8
9 134 these sites. The total survey area encompassed 15, 372 km² (Figure 1).

10 135 While the focus of the surveys was on the two great apes, there are several other primates
11
12 136 in this region including several threatened species: L'Hoest's monkey (*Allochrocebus lhoesti* = VU),
13
14 137 Owl-faced monkey (*Cercopithecus hamlyni* = VU), Johnstone's Grey-cheeked mangabey (*Lophocebus*
15
16 138 *albigena johnstoni*=NT), Ulindi red river colobus (*Piliocolobus lulindicus* = EN), Schmidt's redbellied
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18 139 monkey (*Cercopithecus ascanius schmidtii* = LC), Stuhlmann's blue monkey (*Cercopithecus mitis*
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20 140 *stuhlmanni* = LC), and Dent's monkey (*Cercopithecus denti* = LC). These were all recorded during the
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22 141 surveys when seen.

23

24 143 METHODS

26 144 Data collection

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29 145 This study complied with guidelines for field research that are used by the Wildlife
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31 146 Conservation Society, adhered to the American Society of Primatologists (ASP) Principles for the
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33 147 Ethical Treatment of Non-Human Primates, and adhered to the research requirements of the Institut
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35 148 Congolais pour la Conservation de la Nature (ICCN).

36 149 A line transect distance sampling design was developed for both the KBNP and OCR
37
38 150 (Buckland *et al.* 2001). The Distance software (version 6.0; Thomas *et al.* 2010), generated 162 three-
39
40 151 km long transects for KBNP, and 68 five-km long transects for the lower altitude OCR (Figure 1).
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42 152 Surveying these transects was very intensive and took time because of the presence of armed rebels
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44 153 operating in parts of the KBNP. Surveys of some sectors, for example the FODI (north of KBNP) and
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46 154 the Kasese sector in KBNP in the far west, were made in 2011/12 and 2013 respectively because of
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48 155 good security at that time, but it was possible to visit some sectors only as recently as 2019. At the
49
50 156 time of the surveys, KBNP was surveyed in four of five sectors (insecurity in Lulingu sector prevented
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52 157 surveys there) and assessments were made of two regions of OCR recognised as OCR north and OCR
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54 158 East (Figure 1). Since that time, several community reserves have started to be designated in OCR
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56 159 and the boundaries have changed as a result.

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58 160 Each team comprised two observers who walked each transect from a base camp, cutting as
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60 161 little as possible of the vegetation to minimise noise. Over the period of 2011-2019 a total of ten
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163 162 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

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3 164 region and were very experienced in undertaking surveys. They would travel with a local guide,
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5 165 usually a hunter, who knew the forest well and was also experienced in identifying species. Before
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7 166 each set of surveys refresher training courses were made to ensure standardised methods were
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9 167 used. Sightings of live animals, tracks, calls, dung, and nests were recorded together with the
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11 168 perpendicular distance to each sighting. In the case of apes (gorillas and chimpanzees), counts were
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13 169 made of nests and the perpendicular distance to the centre of each individual nest was measured in
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15 170 a group of nests (Buckland et al. 2010). In the case of groups of monkeys, the distance to the nearest
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17 171 and farthest animal was measured if all the group were to one side of the transect to estimate the
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19 172 perpendicular distance as: $(\text{Nearest} + \text{Farthest})/2$. If the animal group straddled the transect then
20
21 173 the distance to the farthest individual on the left and right sides of the transect were measured and
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23 174 the perpendicular distance calculated as: $(\text{Farthest}_{\text{left}} - \text{Farthest}_{\text{right}})/2$ (White & Edwards 2000). Once
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25 175 the team completed one transect, they then travelled toward the next transect and established a
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27 176 camp between the two transects.

28
29 177 Nests were determined as gorilla nests if they included any of the following characteristics:
30
31 178 1. ground nest; 2. large size; 3. gorilla faeces; 4. silver hair from large nests; 5. close grouping of
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33 179 nests; 6. most nests in group below 15 metres; 7. feeding sign characteristic of gorillas and 8.
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35 180 presence of ground trails leading to and from nests. Nests of chimpanzees were determined by: 1.
36
37 181 Absence of ground nests; 2. Absence of faeces in nest; 3. Most nests in a group between 10-30+
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39 182 metres; 4. Nests more spread apart in a group. Where a nest could not be assigned to either species,
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41 183 usually when old in age, it was recorded as an ape nest, but as these were few the data were not
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43 184 analysed.

44 185 **Analysis methods**

45 186 *Design-based estimates of ape density*

46
47 187 Standard line transect distance sampling methods (Buckland *et al.* 2001) were applied to the
48
49 188 nest sightings for both chimpanzees and gorillas using. We used Distance software (version 7.0;
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51 189 Thomas *et al.* 2010) to estimate nest density with the perpendicular distance data and then
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53 190 converted nest density to ape density based on nest production and decay rates. (Plumptre &
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55 191 Reynolds, 1996; Buckland et al. 2010).

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57 192 Where the rate of nest construction has been studied, most chimpanzees build about 1.1
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59 193 nests per day (Plumptre & Cox 2005; Plumptre & Reynolds 1997; Sanz 2004; Kouakou, Boesch & Kuhl
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194 2009) and it is usually assumed most gorillas build one nest per day (Hall et al. 1998b), but this has

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3 195 not been measured with habituated groups of eastern gorillas. However, in western gorillas, the
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5 196 value of one nest a day has been widely used (Morgan et al 2006).

6 197 In the 1994-1996 surveys the average nest decay rate was estimated at 106 days for this
7
8 198 region (Hall *et al.* 1998b; Plumptre *et al.* 2016a; 2015) for both gorillas and chimpanzees based on
9
10 199 studies from other sites in the Congo basin. It was not measured in this region at that time. During
11
12 200 the period of this study we monitored the time to decay of gorilla nests built in the highland
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14 201 (Tshivanga) sector of KBNP where habituated groups of gorillas are followed daily for tourism. The
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16 202 provisional results show a faster nest decay rate at that site (average of 61 days (95% CI: 19 – 103
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18 203 days) for 83 nests monitored in this high altitude sector) with few nests surviving for longer than 100
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20 204 days (Plumptre *et al.* 2015). Whether this rate is typical of the whole KBNP-OCR region is unknown
21
22 205 but we believe that the decay of nests is likely to be faster in the highland areas as more nests are
23
24 206 constructed with herbaceous rather than woody plants. Hall *et al.* (1998b –Table VIII) showed that
25
26 207 most nests in the KBNP-OCR region are in woody vegetation with only 2.7% in herbaceous
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28 208 vegetation. Security issues prevented us from monitoring nests in the lower altitude areas. For the
29
30 209 analyses we therefore used 106 days to make estimates comparable between the surveys in 1994-96
31
32 210 but recommend that nest decay measures are obtained across the region when security conditions
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34 211 make this possible.

35
36 212 Design-based density estimates for both gorillas and chimpanzees were made for the whole
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38 213 survey area, KBNP and OCR individually, as well as for the management sectors in KBNP (where line
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40 214 transects had been surveyed), and the eastern and northern parts of the OCR. Density for each
41
42 215 sector was calculated assuming the same detection curve across all sectors but with sector specific
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44 216 cluster size and encounter rate. Lulingu Sector was not surveyed in KBNP because of insecurity but
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46 217 when calculating the total population estimate for the park we used the total area of the park,
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48 218 effectively extrapolating the average density across the other sectors to the Lulingu sector.

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50 219 The 1994-96 surveys estimated the area of KBNP as 6,000 km² at a time when there was not
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52 220 an accurate map of the park or GIS tools readily available. The shapefile we used based on mapping
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54 221 of the park using the legal gazettment document totals an area of 7,257 km², a 21% increase in area.
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56 222 The 1994-96 estimate of the Kasese area was also much larger (6,770 km²) compared with the area
57
58 223 of OCR (4,400 km²). Clearly if different areas are used between studies then extrapolated density
59
60 224 estimates will give different numbers. We therefore compared gorilla and chimpanzee estimates by
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226 225 correcting for area using the densities obtained in 1994-96 and applying them to the more accurate
227
228 226 areas of KBNP and OCR (corrected ape numbers). The 1994-96 surveys also made corrections of nest
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228 227 counts, estimating that they had underestimated gorilla nests and overestimated chimpanzee nests.
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229 228 These same corrections factors, calculated from the data in Hall *et al.* (1998b) were applied to

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3 229 correct the counts so that our estimates were comparable. These two corrections applied are
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5 230 termed 'corrected ape numbers' in the results.

6 231 We also made a comparison of the estimates that would have been obtained from the
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8 232 occupancy estimate (Plumptre et al. 2016) if we had used the densities we obtained for the survey
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10 233 area in this study instead of the 0.19 / km² that was applied in that paper, which was a weighted
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12 234 average density obtained across 15 sites.

13 235 Comparisons between estimates were tested using Z-tests making the following
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15 236 comparisons:

- 16 237 1. Test between densities obtained in 2011-2019 between the design and model-based
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18 238 methods – tested for KBNP and OCR separately as well as the study area as a whole
- 19
20 239 2. Test between corrected ape numbers obtained in 1994-96 with the design-based
21
22 240 estimates from 2011-2019– tested for KBNP and OCR separately as well as the study
23
24 241 area as a whole
- 25 242 3. Test between the occupancy analysis ape numbers from 2016 and the design-based
26
27 243 results presented here for 2011-2019

28 29 244 ***Design-based estimates of monkey density***

30 245 Densities of other primate species were also estimated from sightings of monkeys along
31
32 246 transects using Distance software and using group size observed as the cluster size. If perpendicular
33
34 247 distance and cluster size are correlated, then average cluster size is potentially biased. Corrections
35
36 248 were made to the cluster size if the correlation was significant ($p < 0.05$) using the default method in
37
38 249 Distance which regresses log cluster size on the density function (Thomas et al. 2010). Sightings of
39
40 250 monkeys were rare and as a result we also estimated a total density of monkey species assuming the
41
42 251 same detection curve across all species, although we recognise that in reality detection will likely
43
44 252 vary between monkey species.

45 253 ***Model-based estimates of density and distribution***

46
47 254 We used generalized additive models (GAMs) that are flexible and able to capture nonlinear
48
49 255 responses (Wood 2017). The models were fit in R (version 4.0.1; R Core Team 2020) using the *mgcv*
50
51 256 package (version 1.8-31; Wood 2011) with the restricted maximum likelihood (REML) to optimize
52
53 257 smoothing parameter estimation (Marra & Wood 2011). We used a Tweedie distribution (Jørgensen
54
55 258 1987) and estimated the value of its power parameter with an iterative search (Miller *et al.* 2013) to
56
57 259 deal with the zero-inflation (Peel *et al.* 2012) evident in these data (Suppl. Fig S1) due to the many
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59 260 transects where no great ape nests were found. Models were built using thin plate regression splines
60
261 for each of the explanatory variables and the basis dimension was restricted ($k=5$) to avoid

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2
3 262 overfitting. Generally explanatory variables were removed from a model when their approximate p-
4
5 263 values were greater than 0.05. Gorilla or chimpanzee nest density was modelled by including area
6
7 264 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
8
9 265 segment i) as an offset term in the model. Transects were split into smaller segments of 1km where
10
11 266 possible to reduce variability in effort and ensure that explanatory variables were at a sufficiently
12
13 267 fine resolution to capture the conditions at the location of the nest counts.

14
15 268 To identify the important predictors of Grauer's gorilla and eastern chimpanzee density and
16
17 269 distribution, we considered human-related variables, such as distance to road, distance to villages,
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19 270 distance to mines, distance to forest loss, and distance to steep slopes (as a proxy for the ease, or
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21 271 otherwise, of human access), management-related variables such as the number of days or
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23 272 aggregate distance covered by rangers or community ecoguards, and a landscape variable reflecting
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25 273 regional distinctions (Nzovu (a sector with villages within the park), the highland sector (Tshivanga),
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27 274 and the Lowlands, which included Punia Gorilla Reserve (RGPU) as well as Lulingu and Itebero
28
29 275 sectors in KBNP). We also considered ecological variables such as the degree of tree cover, tree
30
31 276 height, and altitude. The potential drivers of great ape density and distribution were the same as
32
33 277 those used by Plumptre et al. (2016) and are summarised in the Supplementary materials (Table S1).
34
35 278 We considered the correlation between all variables to ensure that highly correlated variables were
36
37 279 not included in the same model. The final models were used to predict density of Grauer's gorillas
38
39 280 and eastern chimpanzee in each cell of a 1 km by 1 km grid overlaid across the survey area. This
40
41 281 permitted model-based estimation of overall density and abundance, as well as survey sector-
42
43 282 specific results.

44
45 283 A total of 999 bootstraps were conducted to estimate variance and percentile confidence
46
47 284 intervals (CIs) of gorilla or chimpanzee density and abundance by resampling transect segments at
48
49 285 random, and with replacement. To account for the original hierarchical structure of the data set,
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51 286 during each bootstrap resample, the same number of sampling units was selected as in the original
52
53 287 data set for each of the surveys, with their corresponding number of transects segments. Nest
54
55 288 density and abundance estimates were obtained from these resampled data, conditioned on the
56
57 289 original model fit. Nest density and abundance estimates were converted to gorilla or chimpanzee
58
59 290 abundance by applying the conversion factors (described above: nest creation and decay rates) with
60
291 the associated total variance obtained by incorporating the variance associated with the conversion
292 factors. During each bootstrap iteration, conversion factor values were generated from a normal
293 distribution with a mean equal to the estimated value of the conversion factor and a variance equal
294 to the squared value of the associated standard error. Gorilla or chimpanzee density estimates were
295 ordered from smallest to largest, and the 25th and 975th values were used to define the percentile CI.

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5 **RESULTS**6
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8 298 **Design-based density estimates of apes**9
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11 299 *Estimated numbers in KBNP and OCR*

12 300 A total of 194 gorilla nests were counted along 689 km of transects with 328 km walked in
13 301 KBNP, 289 km walked in OCR and 72 km outside these two sites in FODI or near Kasese town west of
14 302 OCR (see transects surveyed in Figure 1). Altogether, 319 chimpanzee nests were counted along
15 303 these transects. The detection curves for gorilla and chimpanzee nests were reasonable with most
16 304 observations within 20 metres (Figure S2); data were right truncated to this distance from the
17 305 transect line. We estimated 1,223 (95% CI:640-2,338) Grauer's gorillas in KBNP and 1,967 (95%
18 306 CI:1,206-3,209) in OCR, with a total of 4,443 (95% CI:3,021-6,533) for the survey area (including
19 307 FODI, Kasese town and buffer regions). Similarly, we estimated 2,664 (95% CI:1,862-3,810)
20 308 chimpanzees in KBNP and 1,170 (95% CI:686-1995) in OCR, with a total of 4,925 (95% CI:3,656-6,634)
21 309 chimpanzees for the survey area.

22
23 310 *Estimated numbers in sectors of the survey area*

24 311 Gorilla densities were quite variable with highest densities in the Highland Sector of KBNP
25 312 and in the eastern region of OCR (Table 1). The eastern part of the Nzovu sector in KBNP has likely
26 313 lost all of the gorillas that once occurred there (Hall et al. 1998b) as no sign of gorillas was found in
27 314 our surveys.

28 315 Results for chimpanzees in the different sectors show that densities are higher in KBNP than
29 316 in OCR and that this species tends to be at higher densities in the more rugged sectors with forest at
30 317 higher altitude (Table 2). The highest densities were in the Highland Sector of KBNP together with
31 318 the western part of Nzovu sector.

32
33 319 **Design-based density estimates of other primates**

34 320 Sightings of monkeys were few, with only 150 sightings of monkey groups from six species:
35 321 redtail monkey, owl-faced monkey, L'hoest's monkey, blue monkey, Dent's monkey, and grey-
36 322 cheeked mangabey. Ulindi red colobus monkeys were heard in OCR once and not detected
37 323 anywhere else.

38 324 With such rare sightings, the density of only four species were estimated with any
39 325 confidence, assuming the same detection curve for each species across sectors (Table 3). Total
40 326 monkey densities were highest in OCR with about 36 individuals/km² (95% CI: 26-51) while in KBNP,

327 FODI and outside the OCR (south west of OCR) densities varied between 7-15 individuals/km² (range
328 of 95% CI:1-46).

329 **Model-based estimates of great ape density distribution and abundances**

330 The final models used to predict Grauer's gorilla density estimated 4,797 (95% CI: 3,313-
331 6,906) weaned individuals (Table 4) with mapped density surfaces showing their distribution in
332 Figure 2. Of these total estimates 1,476 (95% CI: 710-2,719) gorillas were estimated to occur in KBNP
333 and 2,233 (95% CI: 1,440-3,136) gorillas in OCR. Covariables that were important predictors were
334 those that reflected distance from people, such as distance to road, distance to villages, and distance
335 to mines, and distance to steep slopes (as a proxy for the ease or difficulty of human access). Which
336 variables were important varied by region in the landscape, with gorilla density and distribution in
337 the Lowlands particularly influenced by distance to roads, distance to mines, and distance to steep
338 slopes, in the Nzovu sector by distance to villages, and in the highland sector by distance to roads
339 (although the approximate p-value > 0 .05, this term was retained in the model, because the lack of
340 significance was due to the large amount of variation associated with the estimate caused by the
341 small sample size (33) for the highland sector).

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

351 The models for eastern chimpanzee estimated 5,454 (95% CI:3,742-13,900) weaned
352 individuals with 2,901 (95% CI: 1,259-7,315) chimpanzees estimated to occur in KBNP and 1,069
353 (95% CI: 732-1,468) chimpanzees in OCR. Covariables that were important predictors were also
354 those that reflected distance from people, such as distance to road, distance to villages, and distance
355 to mines, and distance to steep slopes. Chimpanzee density and distribution in the Lowlands was
356 particularly influenced by distance to villages, distance to mines, distance to steep slopes, and
357 distance to rugged areas, and in the Nzovu sector by distance to villages and distance to mines (only
358 the distance to villages in the Nzovu sector and the ruggedness score in the Lowland region had
359 associated approximate p-values < 0 .05, however, the remaining terms were retained in the model,

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3 360 because the lack of significance was due to the large amount of variation associated with the
4
5 361 estimate, as for gorillas).

6 362 Eastern chimpanzee nest density increased with increasing distance to mining, up to a
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8 363 distance of about 13 km in the Lowlands before tapering off, whereas there was a continuous
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10 364 increase in nest density in Nzovu with increasing distance from a mine with the largest distance of 17
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12 365 km from any mine in this sector. In the Lowlands proximity to steep areas were associated with
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14 366 higher chimpanzee nest density as well. Chimpanzee density increased with increasing distance to
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16 367 villages in both the Lowlands and Nzovu up to a distance of about 10 km and 5 km, respectively. In
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18 368 the Lowlands chimpanzee density increased with increasing ruggedness score (Figure 4).

19 369 **Survey area ape population comparisons**

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21 370 Table 5 summarises the estimates for gorillas and chimpanzees, comparing population
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23 371 estimates for KBNP, OCR and the survey area mapped in Figure 1. The original numbers from Hall et
24
25 372 al. (1998b) are provided together with the revised estimate that we calculated using the density data
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27 373 from the paper, the GIS-calculated areas of each of the three sites, and the proportional correction
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29 374 provided by the revised nest counts in that paper (p226 – where gorilla nest numbers were revised
30
31 375 upwards by 18% because of suspected misidentification). These estimates are compared with those
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33 376 from the transect data and the model estimates in Table 5.

34 377 ***Testing differences between design and model-based estimates***

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36 378 A Z-test was used to compare the model- and design-based estimates for gorilla density in
37
38 379 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
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40 380 chimpanzee density in KBNP ($Z=0.502$, $P=0.31$), OCR ($Z=0.307$, $P=0.38$) and the survey area ($Z=0.257$,
41
42 381 $p=0.40$). Given that there was no statistically significant difference or strong effect between the
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44 382 model- and design-based estimates, we use the design-based estimates as our estimate for each site
45
46 383 in subsequent comparisons.

46 384 ***Testing differences between corrected 1994-96 ape numbers and 2011-2019 design-based*** 47 48 385 ***estimates***

49
50 386 In order to compare the 1994-96 estimates with the 2011-2019 estimated numbers we
51
52 387 needed to use the corrected estimates of density based on correct areas for the region and using
53
54 388 uncorrected nest classifications – see methods. We estimated corrected numbers of gorillas (Table
55
56 389 5) in the survey area (12,390; 95% CI: 7,501-18,679) and chimpanzee (3,795; 95% CI: 2,374-5,589).
57
58 390 Design-based estimates of gorilla numbers were significantly lower for the study area in 2011-2019
59
60 391 ($Z=2.56$; $P=0.005$) and higher for chimpanzees but not significantly different ($Z=1.030$; $P=0.15$).

392 Corrected gorilla numbers for KBNP (Table 5) were significantly lower than the design-based
393 estimates in 2011-2019 than in 1994-1996 ($Z=3.591$; $P<0.001$) but not significantly different in OCR
394 ($Z=0.362$; $P=0.36$). Corrected chimpanzee numbers were not significantly different in KBNP ($Z=0.325$;
395 $P=0.37$) but were significantly higher in 2011-2019 for OCR ($Z=3.344$; $P<0.001$).

396 *Testing differences for the study area between design-based estimates and occupancy* 397 *estimates*

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

403 **DISCUSSION**

404 **Changes in estimated density and numbers of primates**

405 *Changes in ape numbers in KBNP, OCR and study area*

406 Estimates were made of the populations of chimpanzees and gorillas in sectors of KBNP and
407 OCR between 1994-1996 (Hall et al. 1998b; Inogwabini et al. 2000). Comparison of these results with
408 the recent survey estimates a large decline in gorilla numbers over the study area but stable
409 chimpanzee numbers (Table 5). Both the 1994-96 and 2011-2019 surveys were based on nest counts
410 and it is possible to confuse chimpanzee and gorilla nests (Tutin et al. 1995). We were fairly
411 confident that the observers we used were able to identify nests accurately, but acknowledge that
412 old nests can be difficult to identify accurately. Hall et al. (1998b) corrected their nest counts,
413 because they perceived there may have been misidentification of gorilla nests, and therefore revised
414 their gorilla nest counts and hence density upward and their chimpanzee density downward. We
415 therefore re-analysed the data for the survey area as a whole using the densities from Hall et al.
416 (1998), ensuring the area of each site was the same and that the methods were comparable,
417 removing the correction they made for the misclassification of nests. It should also be recognised
418 that the surveys in 1994-96 were made in seven regions of the survey area (Figure 1) and transects
419 were not located as systematically across the region as in this study, which would likely have led to
420 some differences in numbers but probably not enough to explain the estimated decline in gorilla
421 numbers. The 2011-2019 gorilla population estimate from the design-based transect data indicates a
422 significant decline in numbers of 86% in KBNP. In OCR gorilla numbers have remained relatively

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3 423 stable (Table 5). Chimpanzee numbers appear to have remained stable across the study region as a
4 whole but have actually significantly increased in OCR while remained stable in KBNP (Table 5).

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6 425 The highland sector (Tshivanga) is where the KBNP headquarters and gorilla tourism occurs.
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8 426 Surveys in this sector have made total counts of gorillas in the past with an estimate of 245
9
10 427 individuals in 1996 (Inogwabini et al. 2000) and more recent estimates in 2000, 2004, 2010 with the
11
12 428 most recent indicating 213 gorillas in 2015 (Spira et al. 2016; Plumptre et al. 2016c). This recent
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14 429 number compares favourably with the estimate of 199 individuals (Table 4) from the model-based
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16 430 estimates for this sector but not very well with the 321 from the design-based estimate (Table 1).
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18 431 While the recent total counts have not been able to access the very north of the sector because of
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20 432 insecurity there the transect surveys did not find sign of gorillas there.

21 433 Bushmeat hunting is likely responsible for the decline in gorillas (Plumptre et al. 2016a); the
22
23 434 clear positive relationship between density and increasing distance from mining, roads, and villages
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25 435 supports this (Figure 3). Gorillas are valued by hunters because they provide a very large amount of
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27 436 meat for a single cartridge or bullet, compared to the much smaller-bodied duikers or monkeys in
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29 437 the area. In addition, gorillas move in groups that are relatively easy to track and find. Chimpanzees,
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31 438 which have a fission-fusion social organisation, do not move in groups all the time and hence are
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33 439 harder to track. Chimpanzees will also flee, often silently and stealthily, when confronted as opposed
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35 440 to the typical response of gorillas, where the silverback faces up to and threatens the attacker, thus
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37 441 risking being shot. These behavioural differences have likely contributed to the better survival of
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39 442 chimpanzees in the region compared to gorillas (Table 5).

40 443 Monkey densities were very low in comparison with those in western Uganda or Rwanda,
41
42 444 indicating that hunting is also having a major impact on these species. Apart from within OCR,
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44 445 monkey densities tended to be lower than those estimated for the Itebero sector by Hall et al.
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46 446 (2003). This author estimated monkey densities between 10-36 individuals/km² for all primate
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48 447 species, apart from owl-faced monkey which occurred at around 5-7 individuals/km² (Table 6). Hall
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50 448 et al. (2003) cut transects and then re-walked them to estimate monkey densities. Our study only
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52 449 counted monkeys seen while walking the transects once. While every effort was made to minimise
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54 450 noise and cutting of transects it is likely monkeys may have fled from observers in our surveys.
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56 451 However, the varying field implementation is unlikely to explain the large differences observed
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58 452 between 1994-96 and 2011-2019. Red colobus *Piliocolobus lulindicus* monkeys were relatively
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60 453 abundant at the time of Hall et al.'s (2003) survey, but apart from one call in OCR this species was
454 not detected in this region during our surveys. The range of this red colobus, which extends from the
455 Lualaba River eastwards to the edge of the highlands, is more than 95,000 km² (Red Colobus Action
456 Plan –Linder et al 2020). The sharp drop in their population across the species range (estimated as at

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3 457 least 50% by IUCN) in the last 30 years or three generations, combined with about 15% habitat loss,
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5 458 has resulted in *P. lulindicus* having recently been assessed as Endangered by Hart et al. (2020). This is
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7 459 supported by the major declines observed for this species in these current results. Red colobus are
8
9 460 often the first monkey species hunted out in an area when people move in, partly because they
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11 461 occur in large groups and tend to remain above the hunters or observers, or try to hide rather than
12
13 462 flee, and partly because their large body size relative to other monkeys renders them one of the
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15 463 more profitable taxa to shoot in terms of cost of a shotgun cartridge vs the amount of meat gained
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17 464 per shot.
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19 465

466 ***Implications of results for global estimates of Grauer's gorilla***

21 467 The gorilla estimates for the survey area totalled 4,430 individuals from the design-based
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23 468 transect estimates, which is higher than the total global population estimate of 3,800 individuals
24
25 469 obtained from the occupancy analysis across Grauer's range (Plumptre et al. 2016a). The 2016 global
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27 470 population assessment used the results of an occupancy analysis to estimate gorilla numbers
28
29 471 converting occupied cells to numbers using an average density estimate of 0.19 gorillas per km², a
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31 472 value that was obtained from density estimates across this ape's range. We used our more accurate
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33 473 estimates of density from this survey to test whether the occupancy method was underestimating
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35 474 the ape numbers for this region. The results showed that gorilla numbers were significantly
36
37 475 underestimated but that chimpanzee numbers were not significantly different using both methods.
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39 476 Given gorillas also occur in Itombwe Forest Reserve, Tayna Community Reserve, and areas north of
40
41 477 KBNP-OCR up to Maiko National Park the total global population will be higher still than our
42
43 478 estimated 4,430. At the time the occupancy analyses were made not much of the OCR region had
44
45 479 been surveyed, and it is possible that a recalculation using updated data including this region might
46
47 480 increase the overall estimate of numbers of gorillas, given that it is likely one of the last strongholds
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49 481 for this ape. Grauer's gorilla was classified as critically endangered based upon the 2016 occupancy
50
51 482 estimate because there had been a 77% decline in about one generation based on that estimate
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53 483 (Plumptre et al. 2016b). Our estimate of 4,443 for this study area is 26% of the 1994-96 range wide
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55 484 estimate of 17,000 (Hall et al. 1998a). It is unlikely that all other sites across its range combined
56
57 485 would exceed an additional 1,500 gorillas given crude estimates from surveys. This gives about a
58
59 486 65% decline in a single generation (1995-2014), as the annual rate of decline was 5.4% 1994-2019. If
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487 this continued at the same rate for another generation (until 2033), 88% of the population would
488 have been lost since 1994, so it would still qualify as Critically Endangered.

489 Conservation value of the KBNP-OCR region

490 It is clear that the Oku Community Reserve is of great importance for gorilla conservation, as
491 well as for the conservation of several other primates. It has an estimated 1,967 Grauer's gorillas,
492 1,170 chimpanzees, as well as higher monkey densities than KBNP. Grauer's gorilla has not declined
493 significantly in this region and chimpanzee numbers are estimated to have increased here. Parts of
494 OCR also contain the few remaining elephants in the region, together with large ungulates such as
495 bongo (*Tragelaphus eurycerus*), forest buffalo (*Syncerus caffer nanus*), and sitatunga (*Tragelaphus*
496 *spekii*). It probably has more Grauer's gorillas than any other site across this ape's range, and
497 together with the Kahuzi-Biega National Park is the last stronghold for this ape. Hall *et al.* (1998b)
498 made a call for 'significant and sustained efforts for conservation' in their paper to conserve the
499 primates in this region. The civil war in DRC and continued presence of armed rebel groups has made
500 this exceedingly difficult. The focus of conservation efforts is now on the local community that are
501 able to live and operate in this region, because they are tolerated by the rebel groups. Since 2012,
502 efforts have been made to work with the community (including one of the authors - EN) to protect
503 this area of forest. In 2018, three local community forest concessions comprising a total area of
504 1,465 km² were created with the consent of the local community. WCS and ICCN are currently
505 working with community-led NGO Reserve des Gorilles de Punia (RGPu), to conduct consultations
506 with the local community to obtain Free Prior and Informed Consent (FPIC) to create a faunal
507 reserve adjacent to the three CFCLs. The creation of a faunal reserve could secure up to 3,000 km² of
508 forest for gorillas and the diversity of flora and fauna in this area. If this initiative is successful, there
509 will be a need to secure further funding to support the development of the governance structures
510 for the reserve and CFCLs, and to support the local community through implementation of
511 community conservation projects.

512

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518 working in the Community Reserves who have been involved in the collection of data presented in
519 this study, sometimes collected in very insecure situations, having to flee from armed groups. We
520 are grateful to the traditional chiefs in the region who helped us negotiate access to the forest from
521 the various armed groups to make these surveys.

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3 523 **Data availability**

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5 524 The data used to make the analyses have been provided to the APEs database to be stored with
6 525 other ape survey data.

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10 527 **Conflict of Interest Statement**

11 528 There are no conflicts of interest.

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15 530 **Author contributions**

16 531 AP conceived of the survey, designed the survey with JK and CS, supervised the surveys, analysed the
17 532 data with FM and SS and wrote the paper with all authors. AK, CS, RN, SB, LO and DK oversaw the
18 533 field teams and organised logistics to keep them safe and supplied. JK, GM, and EN, led teams in the
19 534 field and also coordinated the logistics in the field, engaging local chiefs and community leaders to
20 535 obtain permissions for the surveys and support when in the field.

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643 Table 1. Estimated density (\hat{D} ; /km²) and abundance (\hat{N}) of gorillas with 95% confidence interval
 644 (95% CI) for sectors of KBNP and OCR from design-based line transect sampling surveys. Total
 645 numbers for KBNP is estimated for the total park area including the unsurveyed Lulingu sector,
 646 applying a weighted average density across all sectors to the whole park area.
 647

Sector	\hat{D} No/km ²	\hat{N}	95% CI	
			Lower limit	Upper limit
<i>Kahuzi-Biega National Park</i>				
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
<i>Oku Community Reserve</i>				
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

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649

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

Sector	\hat{D} No/km ²	\hat{N}	95% CI	
			Lower limit	Upper limit
<i>Kahuzi-Biega National Park</i>				
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
<i>Oku Community Reserve</i>				
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

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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/km ²	95% CI	
		Lower limit	Upper limit
Kahuzi-Biega National Park			
<i>Cercopithecus ascanius</i>	5.7	3.1	10.6
<i>Cercopithecus hamlyni</i>	0.2	0.0	1.3
<i>Cercopithecus mitis</i>	5.8	3.2	10.4
<i>Cercopithecus denti</i>	4.2	1.5	11.5
All Monkeys combined	15.6	10.6	22.8
Oku Community Reserve			
<i>Cercopithecus ascanius</i>	9.1	5.1	16.5
<i>Cercopithecus hamlyni</i>	2.2	0.8	6.1
<i>Cercopithecus mitis</i>	12.5	7.3	21.5
<i>Cercopithecus denti</i>	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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660 Table 4. Overall and sector-specific model-based density (\hat{D} ; /km²) and abundance (\hat{N}) estimates for
 661 Grauer's gorilla and eastern chimpanzee with 95% confidence intervals in brackets, plus the
 662 associated surface areas.

Sector	Area (km ²)	Gorilla		Chimpanzee	
		\hat{D} No/km ²	\hat{N}	\hat{D} No/km ²	\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)

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665

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
<i>Kahuzi-Biega National Park</i>				
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
<i>Oku Primate Reserve</i>				
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
<i>Survey area</i>				
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 (/km²) for KBNP (Itebero sector) in 1994 (Hall *et al.* 2003) and
 675 between 2011-2019 (Itebero, Nzovu, and Kasese sectors).

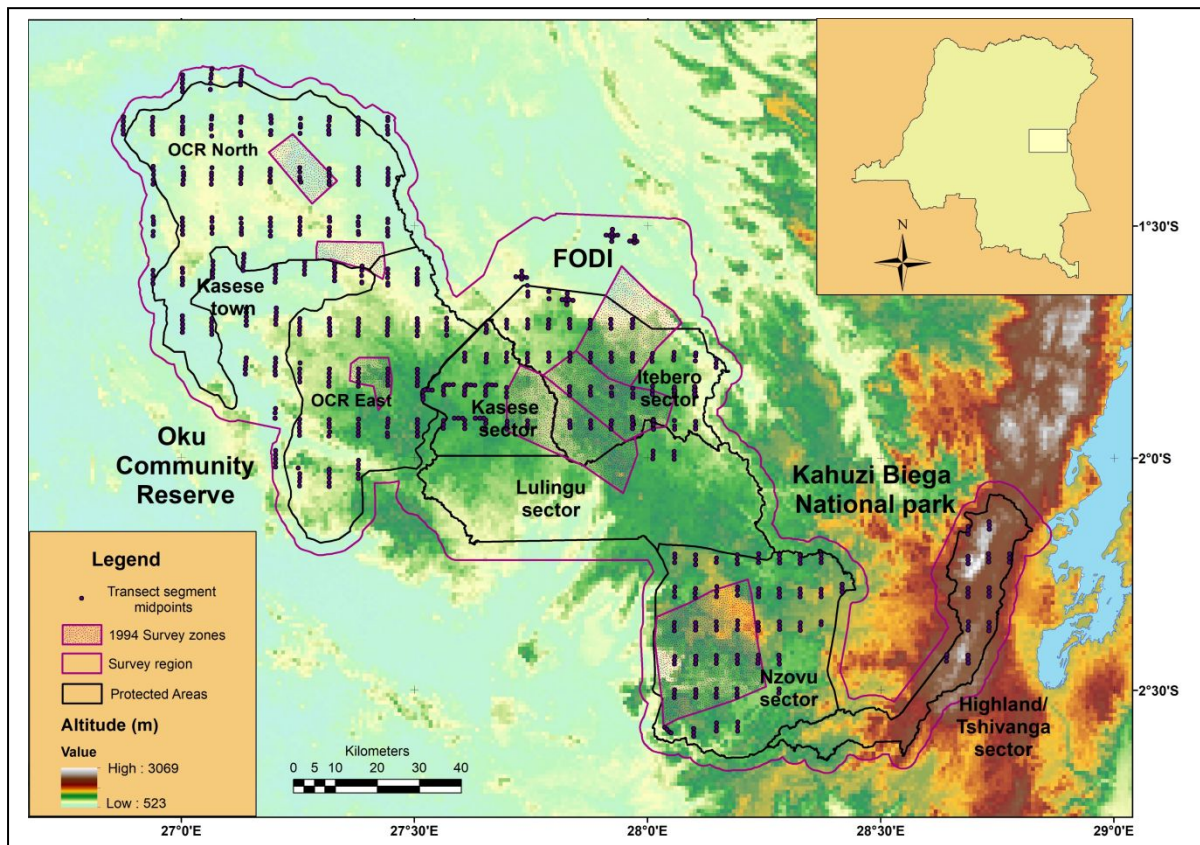
Species	Density 1994 No/km ²	Density 2011-2019 No/km ²
<i>Cercopithecus ascanius</i>	30.4	5.7
<i>Cercopithecus hamlyni</i>	5.3	1.3
<i>Cercopithecus mitis</i>	36.0	10.4
<i>Cercopithecus denti</i>	17.3	11.5
<i>Cercopithecus lhoesti</i>	Too few to estimate	Too few to estimate
<i>Lophocebus albigena</i>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

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677

678 **FIGURE LEGENDS**

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

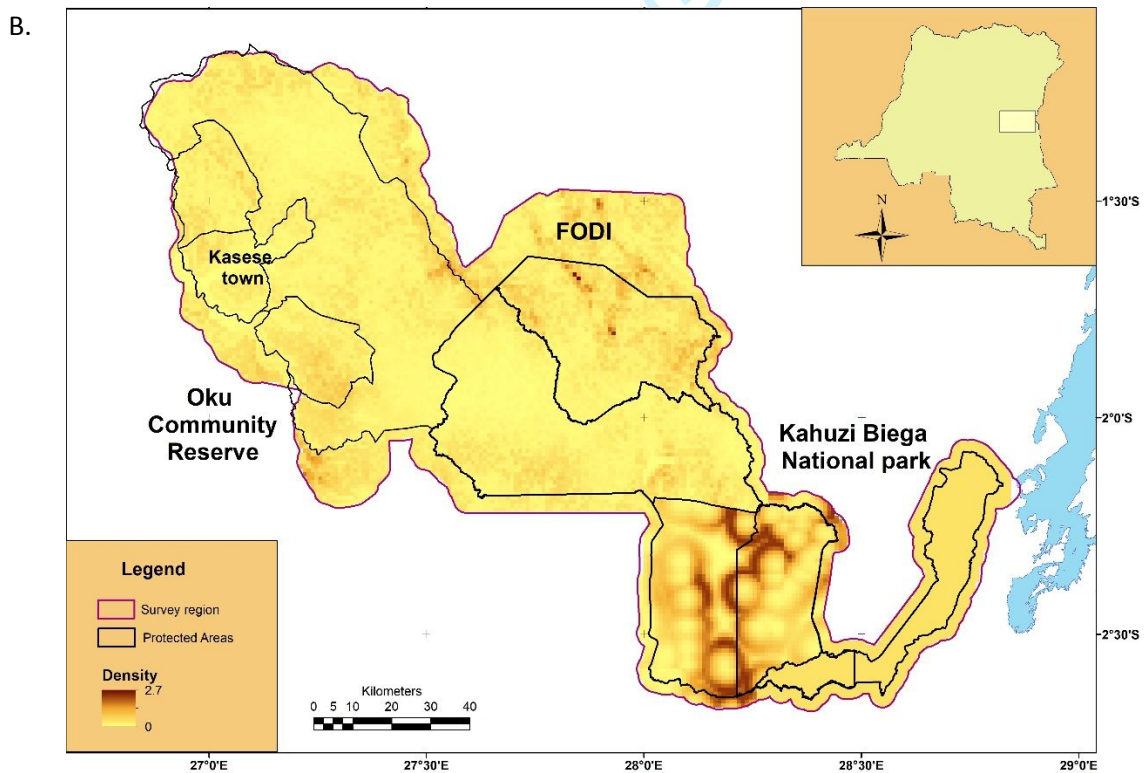
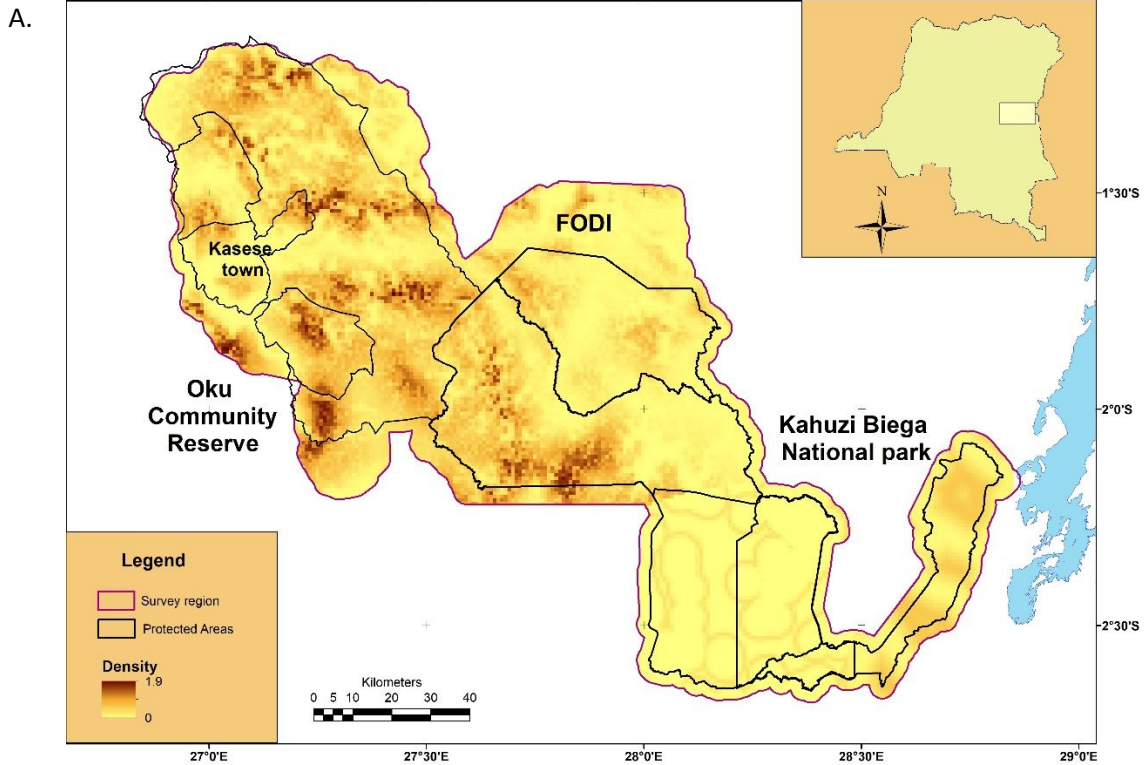


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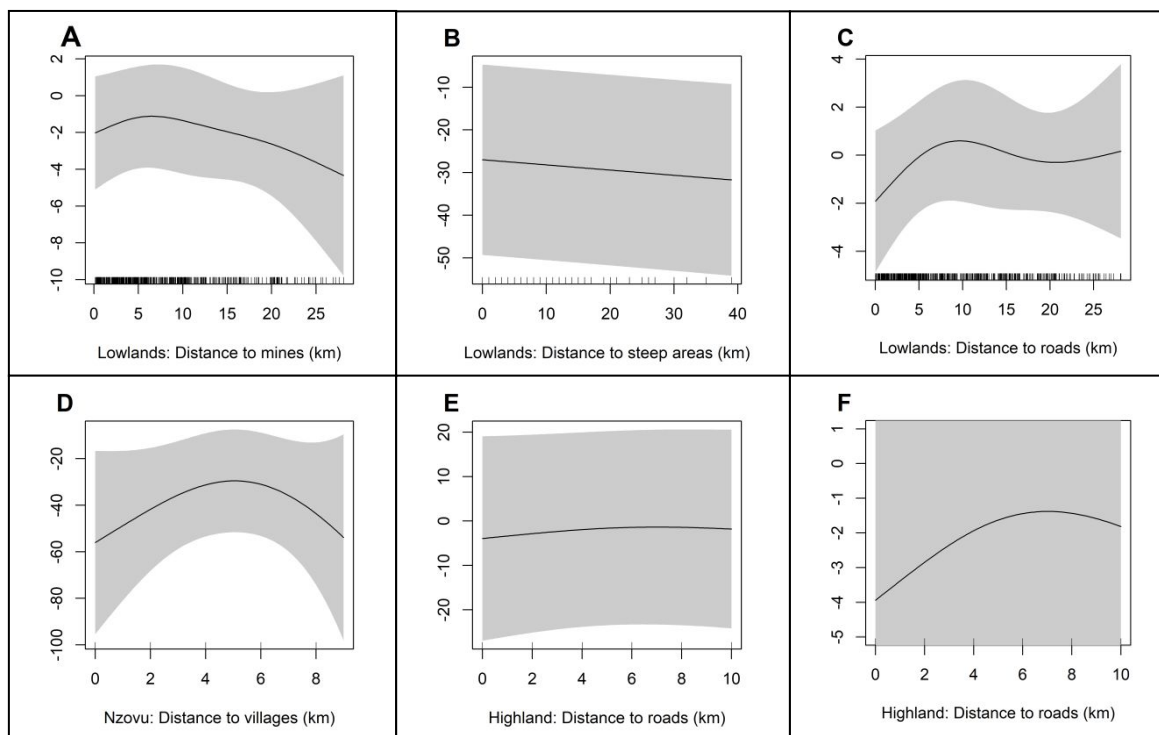
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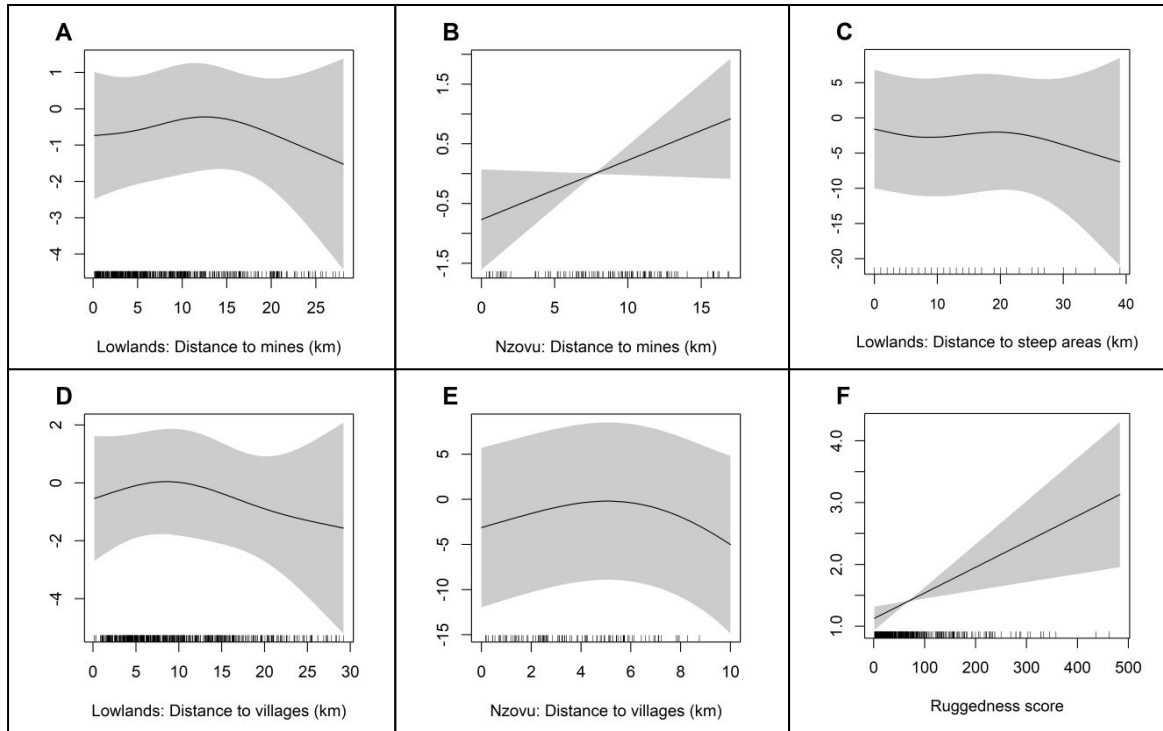
Figure 2: Predicted densities (/km²) of (A) Grauer's gorillas and (B) eastern chimpanzee across the survey area. These maps show the outline of the proposed revised boundaries of community reserves in OCR.



686 **Figure 3.** Estimated conditional dependence of Grauer’s gorilla nest density on (A) distance to
 687 mining, (B) steep areas, and (C) roads all in the Lowland region, and (D) distance to villages in the
 688 Nzovu sector and (E) distance to roads in the Tshivanga sector (with (F) the relationship detailed by
 689 zooming in to the curve shown in (E)). The y axis (nest density) is on the scale of the linear predictor.
 690 Estimates (solid lines) with confidence intervals (grey shading) are shown together with a rugplot.
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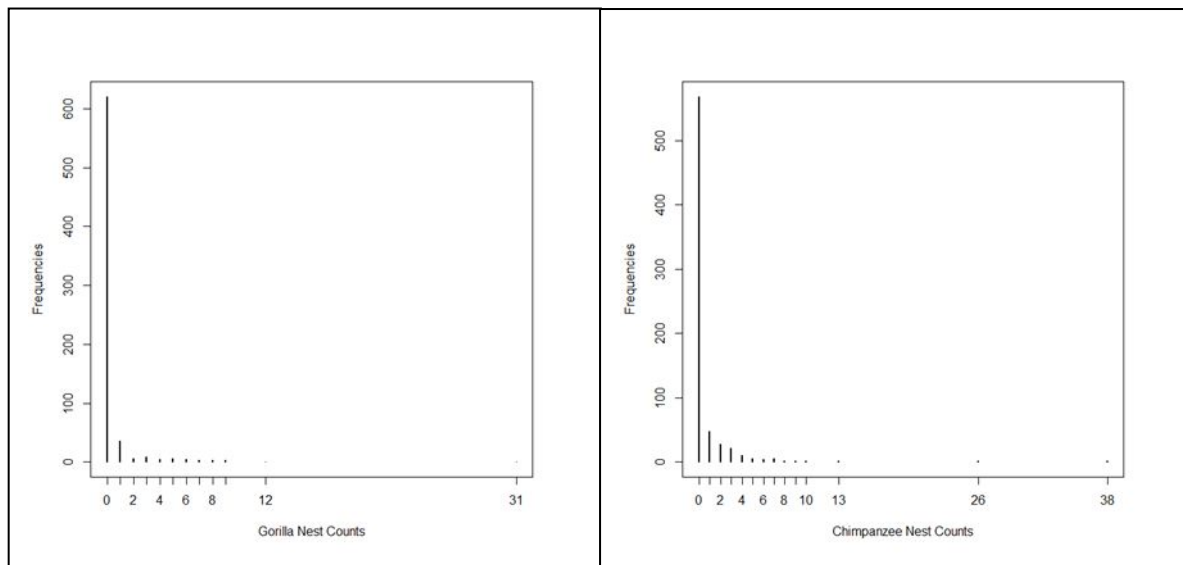
692 Figure 4. Estimated conditional dependence of eastern chimpanzee nest density on distance to
 693 mining in the (A) Lowland region and (B) Nzovu sector, (C) distance to steep areas in the Lowland
 694 region, distance to villages in the (D) Lowland region and (E) Nzovu sector, and (F) ruggedness score
 695 in the Lowland region. The y axis (nest density) is on the scale of the linear predictor. Estimates (solid
 696 lines) with confidence intervals (grey shading) are shown together with a rugplot.



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699 **SUPPLEMENTARY MATERIAL**

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



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Peer Review

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

Covariable Name	Measures	Source
<i>Topographic and forest variables</i>		
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 <i>et al</i> (2103)*
Treeht	Average tree height	Calculated by Lilian Pintea at Jane Goodall Institute from Hansen <i>et al</i> (2103)*
<i>Human impact variables</i>		
disforlos	Distance to forest that has been recently lost	Calculated by Lilian Pintea at Jane Goodall Institute from Hansen <i>et al</i> (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

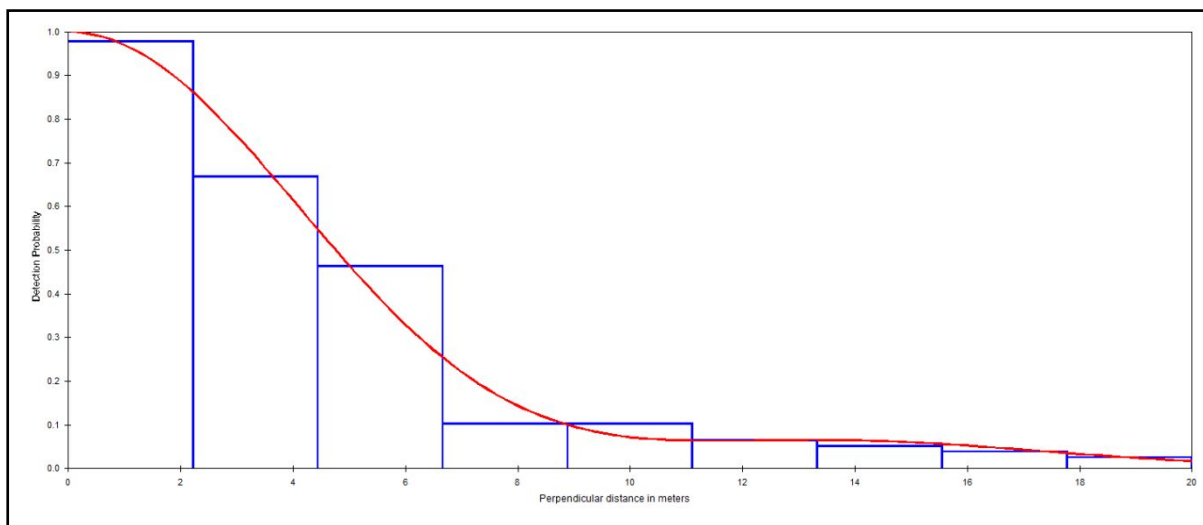
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706 *M.C. Hansen et al, High-resolution global maps of 21st-century forest cover change.
 707 Science 342: 850–53 (2013). Data available on-line from:
 708 <http://earthenginepartners.appspot.com/science-2013-global-forest>.

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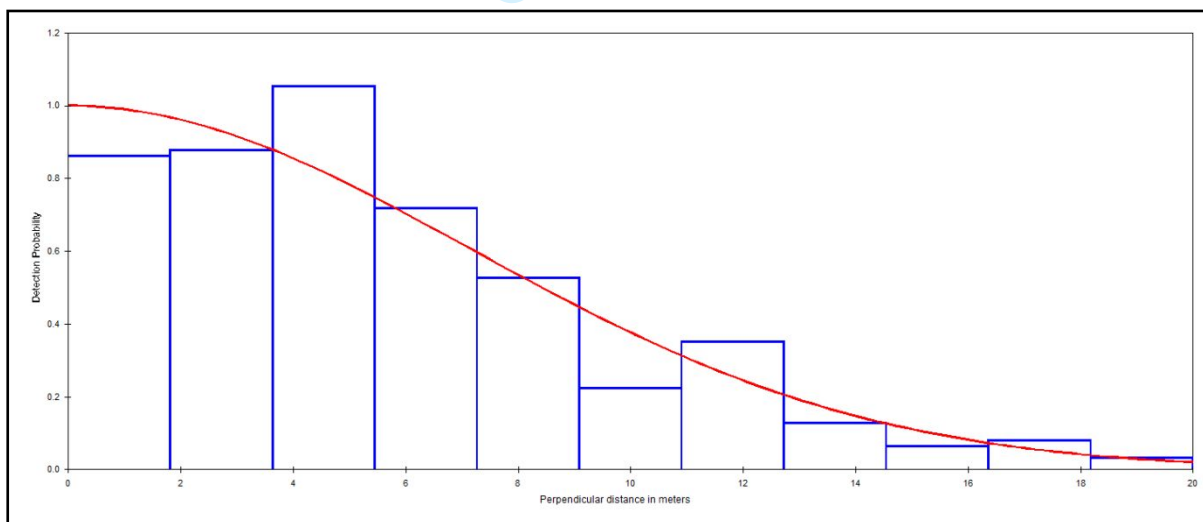
710 **Figure S2.** The frequency of perpendicular distances (blue bars) and the detection function
 711 (red line) fitted to these data for Grauer's gorillas (a) and eastern chimpanzees (b).

712 a.



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714 b.



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