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Assessing the Status of Great Apes in the Dja Faunal Reserve Using Distance Sampling and Camera-trapping

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Abstract: Central chimpanzee (*Pan troglodytes troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla)* populations are rapidly declining due to habitat loss, poaching, and disease epidemics. We estimate the abundance and distribution of both species in the 5,260-km² Dja Faunal Reserve, a World Heritage Site in Cameroon. We compare with previous site estimates and with other great ape population estimates from the region. We also document illegal activities in the reserve. A total of 298.2 km of line transects (283) were completed using the standing-crop nest counts method, with a further 1,681.4 km of recces recording human signs. We estimated a chimpanzee nest mean decay rate of 95.4 days (SE = 4.45) and a combined great ape nest mean decay rate of 96.6 days (SE = 2.87). Gorilla population estimates of 0.38 (95% CI = 0.28–0.53) individuals/km² and 2,004 (95% CI = 1,447–2,774) individuals confirmed a significant decline since the 1995 survey in the north-central part of the reserve (a 57% decline for the area) and the reserve-wide survey in 2015 (a 70% decline). The population was also much lower than in most other protected areas in the region. The chimpanzee population with an estimated 0.53 (95% CI = 0.38–0.73) individuals/km² and 2,785 (95% CI = 2,020–3,839) individuals also revealed a marked decline of 34% and 23% compared to the 1995 and 2015 surveys, respectively. Human activity occurred throughout, with the highest levels encountered in the northwest of the reserve. Occupancy estimates from four 40 camera-trap grid surveys showed great apes persisting mainly in the north-eastern part of the reserve where Cameroon's Ministry of Forestry and Wildlife (MINFOF) is considering a community support partnership agreement on sustainable access to forest resources, along with community surveillance networks. The reserve management is also increasing law-enforcement patrols across the reserve. Our findings also inform conservation strategies for great apes across the TRIDOM landscape across Cameroon, Gabon and the Republic of Congo.

Key Words: *Pan troglodytes troglodytes*, *Gorilla gorilla gorilla*, abundance, density, distribution, Dja Biosphere Reserve

Introduction

Central African populations of great apes are in serious decline (IUCN 2014). The central chimpanzee *Pan troglodytes troglodytes* is listed as Endangered on the IUCN Red List (Humle *et al*. 2016) and the western lowland gorilla *Gorilla gorilla gorilla* is classified as Critically Endangered (Maisels *et al*. 2018). The major threats to great apes are the direct and synergystic effects of poaching, habitat loss, and disease (Ebola, in particular) (Strindberg *et al*. 2018).

Reliable estimates of population size, density, and distribution, and trends in these at regional and local scales are required by governments and protected area managers to take informed management action. An adequate understanding of the anthropogenic and ecological factors that influence the distribution of these species within their environment is also vital for adapative mangement strategies (Stokes *et al*. 2010; Strindberg *et al*. 2018). Estimates of the regional great ape population are useful for monitoring overall status and trends (Kühl *et al*. 2008; N'Goran *et al*. 2017). Conservation landscapes (that is, a network of protected areas (PAs) separated and surrounded by alternative land use) provide an effective framework for conservation planning and actions (Gardner *et al*. 2007; Stokes *et al*. 2010). Keeping track of great ape populations in individual PAs is needed to assess their efficacy as source populations and refugia (Stokes *et al*. 2010; N'Goran *et al*. 2017). Regular surveys can provide early warning signs of precipitous declines (Stokes *et al*. 2010). In Minkébé National Park (NP), Gabon, for example, great ape populations declined by about 98% in 1998–2000 compared to pre-1994 estimates, likely due to Ebola outbreaks (Huijbregts *et al*. 2003).

Here we assess the 2018 status of the central chimpanzee and western lowland gorilla (along with forest elephants, Amin *et al*. 2020) in the Dja Faunal Reserve (DFR) in southeast Cameroon, a World Heritage Site (UNESCO 2022; the DFR and its buffer zone constitute the Dja Biosphere Reserve). The DFR's extant megafauna is considered one of the reserve's Outstanding Universal Values (UNESCO 2022). Our main objective was to to assess the status of great apes in the DFR in order to provide baseline data for the adaptive management of the reserve and the TRIDOM landscape (across Cameroon, Gabon and the Republic of Congo).

Methods

Study area

The DFR is the largest protected area (5,260 km²) in Cameroon (3°08'5"N, 13°00'00"E, Fig. 1). Approximately 80% of the DFR is bordered by the Dja River (S, W, and N), which forms a natural barrier and provides some limited protection, although crossing in canoes is common. The biosphere reserve outside the formal DFR largely comprises Forestry Management Units (FMUs), settlements, and community forests. There is also a 450-km² rubber plantation and a hydroelectric dam on the Dja River in the western buffer zone, both adjacent to the DFR boundary (Fig. 1). There are no recent reliable estimates of the human population surrounding the DFR. Estimates suggest 19,500 village inhabitants in the buffer zone and a further 30,000 in the wider area directly surrounding this zone (Fowler 2019; Ngatcha 2019). Expanding settlements and transport corridors to the south and east of the DFR are rapidly clearing natural forest and may soon result in isolation of the DFR (Global Forest Watch 2022).

The DFR is a relatively flat plateau of round-topped hills and ranges at elevations of 600–800 m asl (MINFOF and IUCN 2015). The topography is mainly shallow valleys on either side of a ridgeline that cuts through the DFR east to west (MINFOF and IUCN 2015). Swamp habitat is common on the floor of valleys. Tributaries throughout the DFR flow into the Dja River (UNESCO 2022; MINFOF and IUCN 2015). The three major forest types in the DFR are terra firma mixed-species forest, mono-dominant forest, where *Gilbertiodendron dewevrei* is the most abundant species, and periodically flooded forest (Djuikouo *et al*. 2010). The DFR supports a rich, medium-to-large mammal fauna. In addition to the two species of great apes (central chimpanzee and western lowland gorilla), the biosphere reserve is an important landscape for the Critically Endangered African forest elephant (*Loxodonta cyclotis*). The DFR has a diverse community of forest ungulates and three threatened pangolins, namely the black-bellied pangolin (*Phataginus tetradactyla*): Vulnerable, the white-bellied pangolin (*Phataginus tricuspis*): Endangered, and the giant pangolin (*Smutsia gigantea*): Endangered.

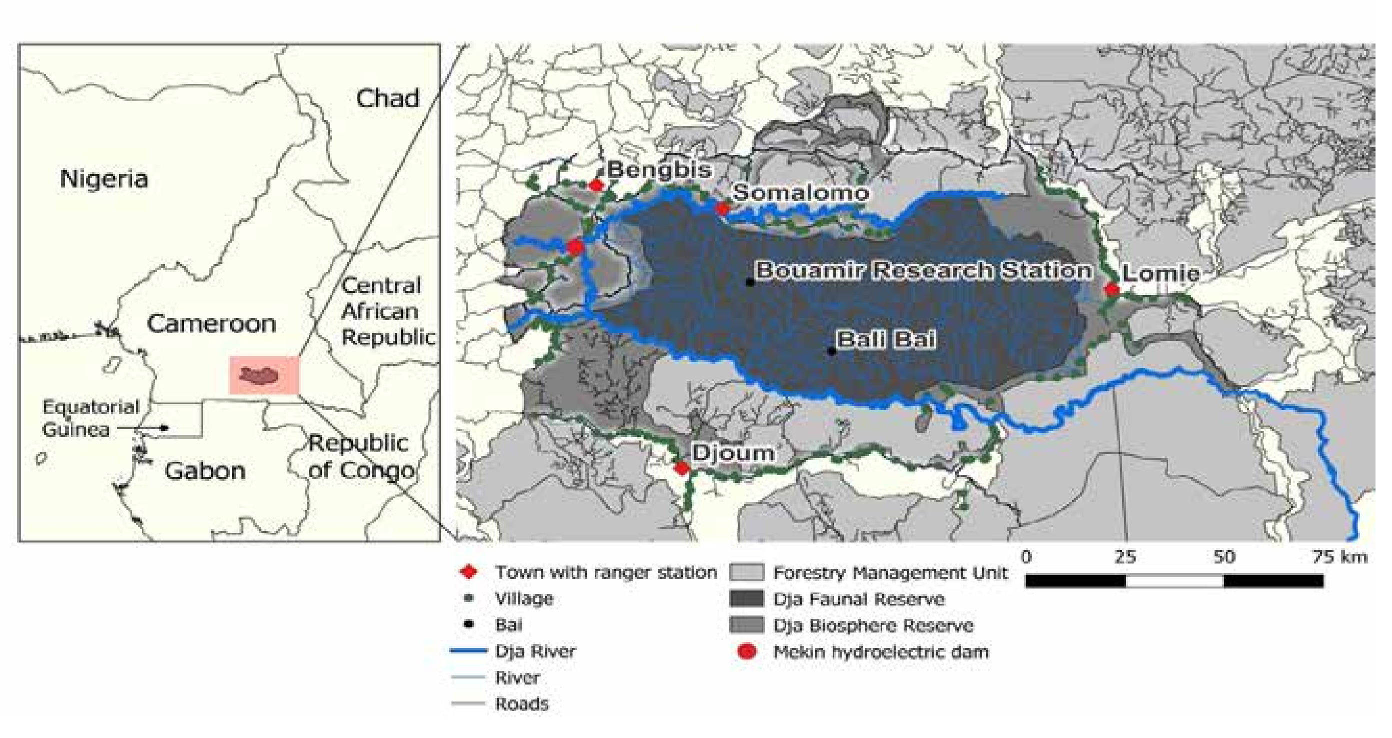

Figure 1. Location of the Dja Faunal Reserve, Cameroon.

There are four main seasons: the long rains (August–November); the longer dry season (November–March); the short rains (March–May); and a shorter dry season (June–July) (MINFOF and IUCN 2015). In the dry season there is, on average, <100 mm of rainfall out of the mean annual rainfall of approximately 1,570 mm (UNESCO 2022). The mean annual temperature is 23.5°C–24.5°C. The maximum temperature is reached in February and the minimum in July (MINFOF and IUCN 2015).

Poaching in and around the DFR is largely through non-traditional means, such as guns and wire snares. Much of the poaching supplies the commercial and illegal wildlife trade (UNESCO 2022). Other significant threats to biodiversity around the DFR include logging, agricultural clearance for subsistence crops and commercial crops such as pineapple, loss of the last remaining large forested corridor to the Ngoyla-Mintom forest block if the south-eastern road is developed, rubber plantations (for example, Sud-Cameroun Hévéa) and the associated demands for bushmeat, and the ecological impacts of existing (the Hydro Mekin) and planned hydroelectric dams (MINFOF and IUCN 2015; UNESCO 2022).

Cameroon's Ministry of Forestry and Wildlife (MINFOF) is responsible for the management of the DFR and the Dja Biosphere Reserve. The DFR has been divided into four management sectors with a base responsible for each sector in the nearest town: Lomié (East Sector), Djoum (South Sector), Meyomessala (West Sector), and Somalomo (North Sector).

Estimating great ape population densities and abundance

Central chimpanzee and western lowland gorilla population densities and abundances were estimated with distance sampling carried out through nest-based transect surveys (White and Edwards 2000), as part of a megafauna inventory. We used a standardized survey protocol to provide robust estimates for monitoring changes in the populations over the long-term (Kühl *et al*. 2008).

Line transect surveys

We first estimated the total length of transect we would need to achieve a desired precision in the density estimates for the great apes. We used the following equation (Buckland *et al.* 2001) and data from a previous transect survey (MINFOF and IUCN 2015).

$$L = (b \div \{cv_t(\hat{D})\}^2).(L_o \div n_o),$$

where L = estimate of total transect-line length to be surveyed to achieve target coefficient of variation; b = dispersion factor (set to a default value of 3 as per Buckland *et al*. 2011); cv_t = target coefficient of variation of density estimate $\hat{D}$; L_o = total length of all transects (from previous survey); and n_o = total number of observations on all transects (from previous survey). We estimated that 286 km of transects were needed to achieve a 10% coefficient of variation (based on the 2015 survey comprising 612 km of transects; MINFOF and IUCN 2015).

The survey, therefore, consisted of 286 one-km transects systematically positioned with orientation east to west to align transects along potential great ape density gradients, as the majority of watercourses in the DFR run north–south (Fig. 2). We conducted the survey at the end of the dry

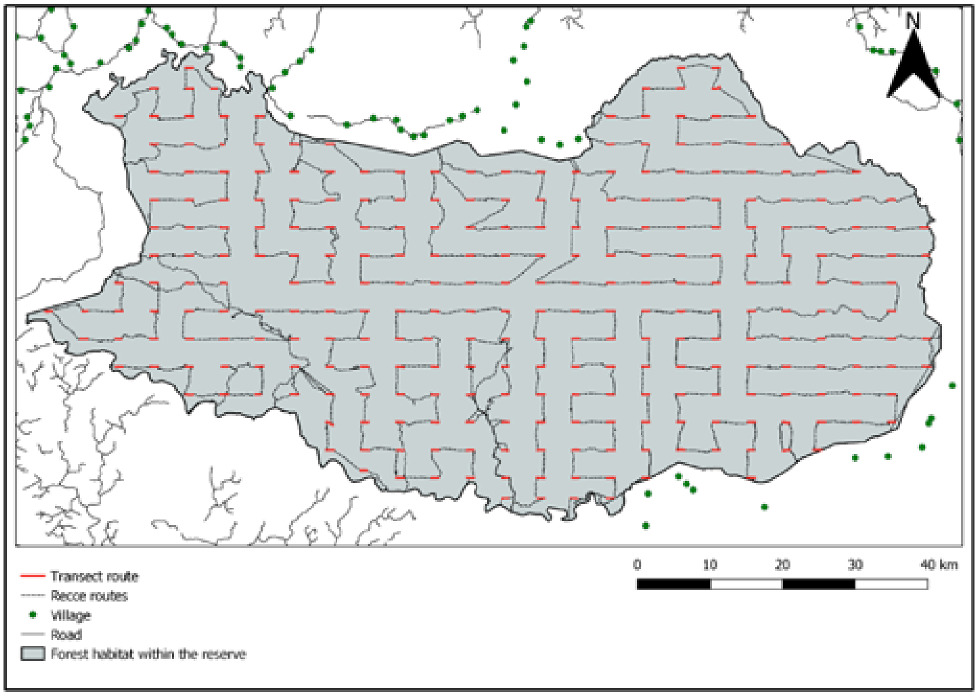

Figure 2. Locations of line transects and the associated routes between them (recces), systematically covering the entire Dja Faunal Reserve, Cameroon.

season between 4 April 2018 and 3 June 2018 using eight teams. Each team had two observers, one looking up for great ape nests, while the other looking at ground level for great ape nests, as well as human sign and other signs on the ground, such as elephant dung. Each team had two data recorders as well as four porters who walked at a distance behind the team and were responsible for carrying supplies and camping equipment.

The observers were trained in identifying and aging great ape nests. Nest-aging categories were based on the system proposed by Tutin and Fernandez (1984) and Kühl *et al.* (2008), namely: New: <24 hours old, with fresh faeces or urine under the nest; Fresh: vegetation green or not wilted (up to a week old); Recent: vegetation dry and changing colour (up to two weeks old); Old: vegetation dead, but nest still intact (>2 weeks); Decayed: nest beginning to disintegrate, holes visible in structure.

We used the approach of Kühl *et al.* (2008) to record nests. Great apes tend to build nests in groups. Once a great ape nest was detected from the transect, an area with a radius of 50 m was searched around the nest for other nests of the same age class. If another nest of the same age was found within 50 m, the search would begin again from that point. When no more nests within 50 m were found, the search was ended and perpendicular distances to each individual nest from the transect line were measured to the nearest cm and recorded along with the nest age category. Gorilla and chimpanzee nests were distinguished based on nest characteristics, shed hair, feces, odor and tracks. However, there is always a possibility that some of the tree nests were misassigned to the nest-builder.

Estimation of great ape nest decay rates

The standing-crop nest-count method used in this study, where all nests encountered were recorded in a distance-sampling framework, requires a nest production rate and a nest decay rate to convert nest density to population density of weaned apes (Kühl *et al*. 2008). Between April 2018 and September 2018, 119 fresh great ape nests were located and carefully marked across the study area. At the end of the study, the marked nests were checked to see which had disappeared and which were still visible. The data on state of the nests and time since nest construction were analyzed using logistic regression, with distribution left-truncated at $x = 0$ and rescaled, in R software package (R Development Core Team 2019; Laing *et al*. 2003) to estimate central chimpanzee and western lowland gorilla nest mean decay rates and their variance. For the production rate, we used 1.09 great ape nests per day (Morgan *et al*. 2006).

Recording human activity

The survey also recorded sign of human activity, both along line transects and during the approximately 3.8 km walk (hereafter, recce) between transects. Types of human sign recorded were trails, snares, signs of passage, machete cuts, shelters and camps, firearms and ammunition, timber exploitation, direct encounters with people, and gunshots heard. Camps were defined as any structure used for sleeping within the forest evident from cleared ground and the presence of a fire pit or structures. However, as a caveat, it is impossible to differentiate poacher's trails and cuts from those of ecoguards and NGO work within the DFR.

When combined with the information on the distribution of a species, human activity data can provide insights into the role of hunting pressure and human disturbance in diminishing wildlife populations. This also provides baseline data against which the effectiveness of management activities can be measured.

Transect and recce data management

All data were recorded using the Spatial Monitoring and Reporting Tool – Ecological Records (SMART-ER https://smartconservationtools.org) on Cedar Personal Digital Assistants (PDAs) and also in notebooks so as to have duplicate copies of the data. A Global Positioning System (GPS) point with date and time was also taken for each observation and recorded in the notebook.

The data were exported from the PDA units into a SMART desktop application. We checked all data entries in SMART against their paper counterparts to ensure that they were consistent with each other. We then exported the clean data in SMART into Excel and converted the data into a suitable format for analysis in *Distance 7.2* (Thomas *et al*. 2010; http://distancesampling.org/distance). We did not group nests so as to avoid potential bias in group size estimates due to the possibility of not all nests in a group being found and with ground nests likely to decay faster. This, however, may lead to some underestimate of variance. We considered models of the detection function with the half-normal, hazard-rate, and uniform key functions with cosine, simple polynomial, and Hermite polynomial adjustment terms for each species and for the combined great ape line-transect data. Adjustment terms were constrained, where necessary, to ensure the detection function was monotonically decreasing. We selected among candidate models by comparing AIC (Akaike Information Criterion) values. We also checked for model fit to the data using the Kolmogorov-Smirnov test provided by *Distance*. All maps were produced using the Quantum Geographic Information System (QGIS Development Team 2019).

Estimating occupancy

We used camera-trap data from standardized grids deployed across the management sectors of DFR to assess the distribution of central chimpanzees and western lowland gorillas. The camera-trap surveys were conducted to provide replicable baseline information on medium-to-large mammal species, including great apes, that occur in the DFR.

Camera-trap surveys

Four camera-trap grids were setup in the North (management) Sector between January 2018 and May 2018 (38 camera-traps); East Sector between January 2018 and May 2018 (39 camera-traps); South Sector between August 2018 and December 2018 (39 camera-traps); and West Sector between October 2019 and February 2020 (35 camera-traps) (Fig. 3). The West Sector grid was deployed in 2019 due to limited resources in difficult conditions. Bushnell Trophy Aggressor Low Glow camera-traps (Bushnell Outdoor Products, Kansas, USA) were placed at each locality with a two-km spacing between each camera-trap (Ahumada *et al*. 2011). Each grid operated long enough to achieve at least 1,000 camera-trap days of sampling effort (O'Brien *et al*. 2003). Global Positioning System receivers were used to locate the grid points. A single camera was placed at a height of about 30 cm, as close to the grid sampling point as possible, with a consistent and unobstructed field of view to capture lateral full-body images of small to medium-sized mammals. The cameras were programmed to take three images per trigger.

We modeled the effect of 'management sector' on central chimpanzee and western lowland gorilla occurrence. We did not have complete and up-to-date datasets on potential indicators of hunting pressure or disturbance such as distance to villages to investigate in this study. We assumed detection probability was constant across the four camera-trap grids, which were deployed using a standardized protocol. We constructed a detection / non-detection history, using a five-day period as the sampling occasion, for each camera-trap site. We performed Bayesian occupancy analysis implemented in *JAGS 4.3.0* (Plummer 2003), accessed through *R 3.6.0* (R Code Development Team 2019), using the package *RJAGS 3-10* (Plummer 2014). We ran three Markov Chain Monte Carlo (MCMC) chains with 110,000 iterations, a burn-in of 10,000 and a thinning rate of 10. This combination of values ensured an adequate number of iterations to characterize the posterior distribution of the modeled occupancy estimate. We checked for chain convergence with trace plots and the Gelman-Rubin statistic (Gelman *et al*. 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman and Hill 2006). We assessed model fit using Freeman-Tukey discrepancy (Kery and Schaub 2012). We calculated the P value, i.e., the probability of obtaining a discrepancy at least as large as the observed discrepancy if the model fits the data. Values near 0.5 indicate a good fit; values above 0.9 or below 0.1, a poor fit.

Results

We traversed 283 transects, totaling 298.2 km. Two transects had to be abandoned due to flooding. One was abandoned as part of it was in a settlement. Recces covered a distance of 1,681.4 km (Fig. 2). We recorded 276 central chimpanzee nests and 138 western lowland gorilla nests suitable for distance analysis. However, as noted in

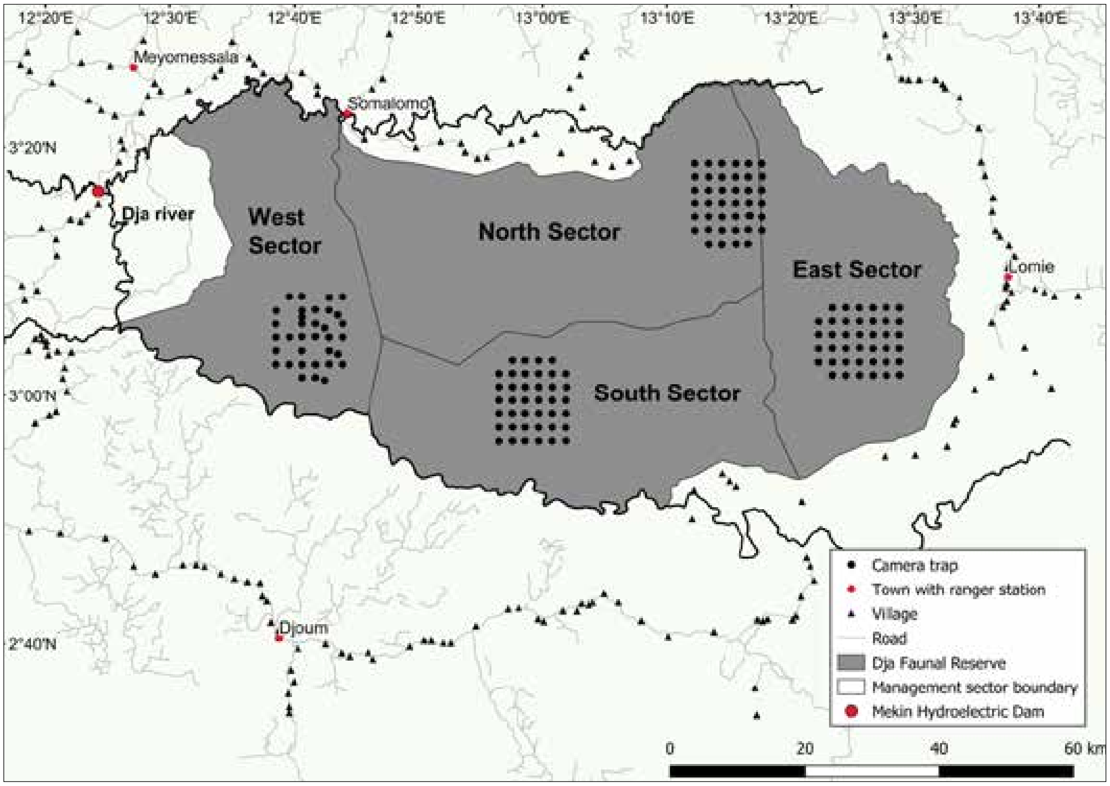

Figure 3. Location of camera-trap grids in the North, East, South and West Management Sectors in the Dja Faunal Reserve, Cameroon.

the methods, there is a possibility that some of the tree nests were misassigned to the nest-builder.

Density and abundance

We estimated a central chimpanzee nest mean decay rate of 95.4 days (SE = 4.45, 95% CI = 86.67–104.13). There were insufficient western lowland gorilla samples to estimate a nest decay rate, so we estimated the combined great ape nest mean decay rate at 96.6 days (SE = 2.87, 95% CI = 90.97–102.23).

Exploratory analyses revealed fewer detections close to the line (0–3m) than expected for the central chimpanzee. This was most likely due to observers missing nests on trees above their heads. We, therefore, analyzed this data using left truncation at 3 m with rescaling. The hazard-rate model with no adjustments minimized AIC for the rescaled central chimpanzee data right truncated to 10 m (172 observations). The Kolmogorov-Smirnov goodness of fit P value (0.63) indicated a good fit. The central chimpanzee nest density estimate was 55.04 (95% CI = 40.44–74.91) nests/km^2 and the average detection probability was 0.52 (95% CI = 0.43–0.63) (Fig. 4). Effective strip width was 5.24 (95% CI = 4.34–6.33) m. The central chimpanzee density was estimated as 0.53 (CV = 16.45%; 95% CI = 0.38–0.73) individuals/km^2 with a population estimate of 2,785 (95% CI = 2,020–3,839) individuals.

The half-normal model minimized AIC for the western lowland gorilla line transect data truncated to 12 m (127 observations). The Kolmogorov-Smirnov goodness of fit P value was 0.58. Western lowland gorilla nest density estimate was 40.1 (95% CI = 29.1–55.23) nests/km^2 and detection probability was 0.44 (95% CI = 0.39–0.5) (Fig. 5). Effective strip width was 5.31 (95% CI = 4.69–6.01) m. Western lowland gorilla density was estimated as 0.38 (CV = 16.66%; 95% CI = 0.28–0.53) individuals/km^2 with a population estimate of 2,004 (95% CI = 1,447–2,774) individuals.

The hazard model minimized AIC for the combined great ape line transect data truncated to 10 m (297 observations). The Kolmogorov-Smirnov goodness of fit P value was 0.15. Combined great ape nest density estimate was 96.57 (95% CI = 75.81–123.01) nests/km^2 and detection probability was 0.52 (95% CI = 0.45–0.6). Effective strip width was 5.16 (95% CI = 4.47–5.95) m. Great ape density was estimated as 0.92 (CV = 12.72%; 95% CI = 0.72–1.18) individuals/km^2 with a population estimate of 4,825 (95% CI = 3,672–6,188) individuals.

Occupancy

The total sampling effort was 14,082 camera-trap days: 3,647 trap days in the North Sector; 3,787 trap days in the East Sector; 3,689 trap days in the South Sector; and 2,959 trap days in the West Sector. Thirteen camera-traps failed to function (<30 days). Western lowland gorilla occupancy (ψ) was significantly higher in the North Sector (Fig. 6, posterior probability: ψ North Sector > ψ East Sector = 1; ψ North Sector > ψ South Sector = 1; ψ North Sector > ψ West Sector = 1). The estimated detection probability was 0.06 (95% CI = 0.04-0.08). Central chimpanzee occupancy was also significantly higher in the North Sector (posterior probability: ψ North Sector > ψ East Sector = 1; ψ North Sector > ψ South Sector = 0.95; ψ North Sector > yWest Sector = 0.83). The estimated detection probability for the central chimpanzee was 0.09 (95% CI = 0.08-0.11).

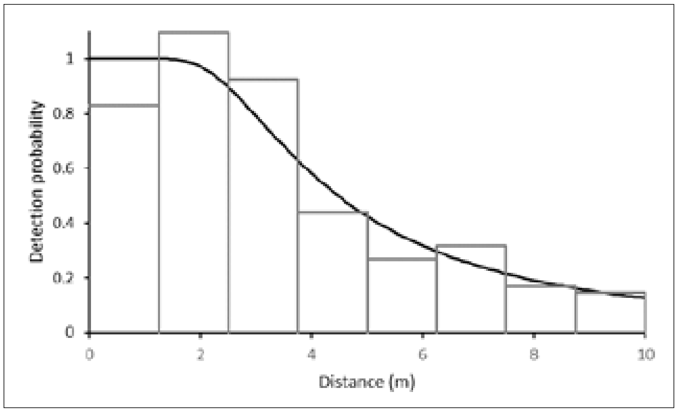

Figure 4. Hazard-rate detection function fit to the perpendicular distances of central chimpanzee nests from the line transect in the Dja Faunal Reserve, Cameroon (2018). The histograms of the observed distances are also shown.

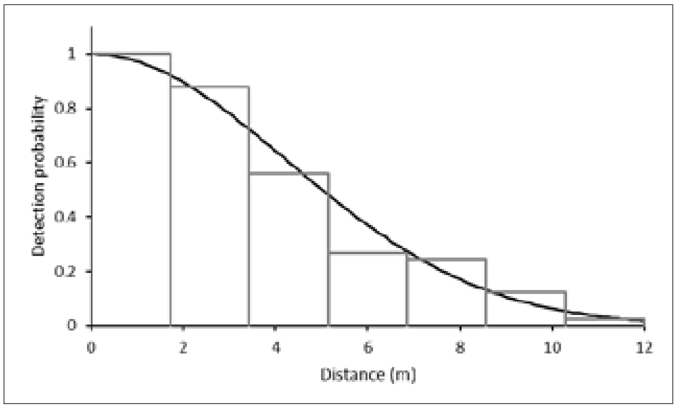

Figure 5. Half-normal detection function fit to the perpendicular distances of western lowland gorilla nests from the line transect in the Dja Faunal Reserve, Cameroon (2018). The histograms of the observed distances are also shown.

Human activity

A total of 359 human signs were encountered on the transects and 1,309 signs on recces resulting in an overall encounter rate of 0.84 sign/km. The most prevalent signs encountered were established trails (0.27/km), machete cuts (0.17/km), and signs of passage, such as marked trees and bent sticks (0.15/km). Among the signs directly attributable only to poaching, the most prevalent was spent firearm ammunition (0.11/km), followed by snares (0.06/km). The distribution of human signs encountered on recces and transects is shown as an encounter rate (signs/km) density contour map (Fig. 7).

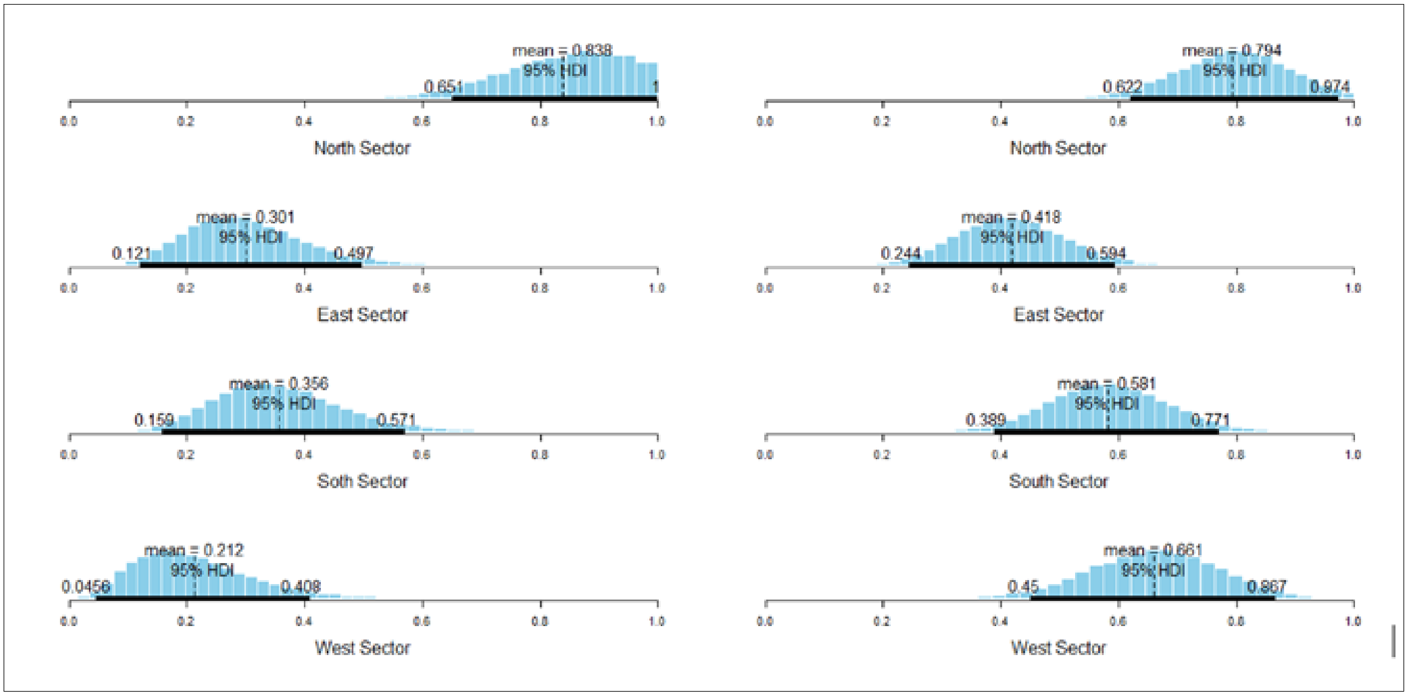

Figure 6. Western lowland gorilla (left) and central chimpanzee (right) occupancy posterior distributions for North, East, South, West management sectors, Dja Faunal Reserve, Cameroon. The 95% highest posterior density "credible" interval (HDI), the Bayesian equivalent to 95% confidence interval, are also shown.

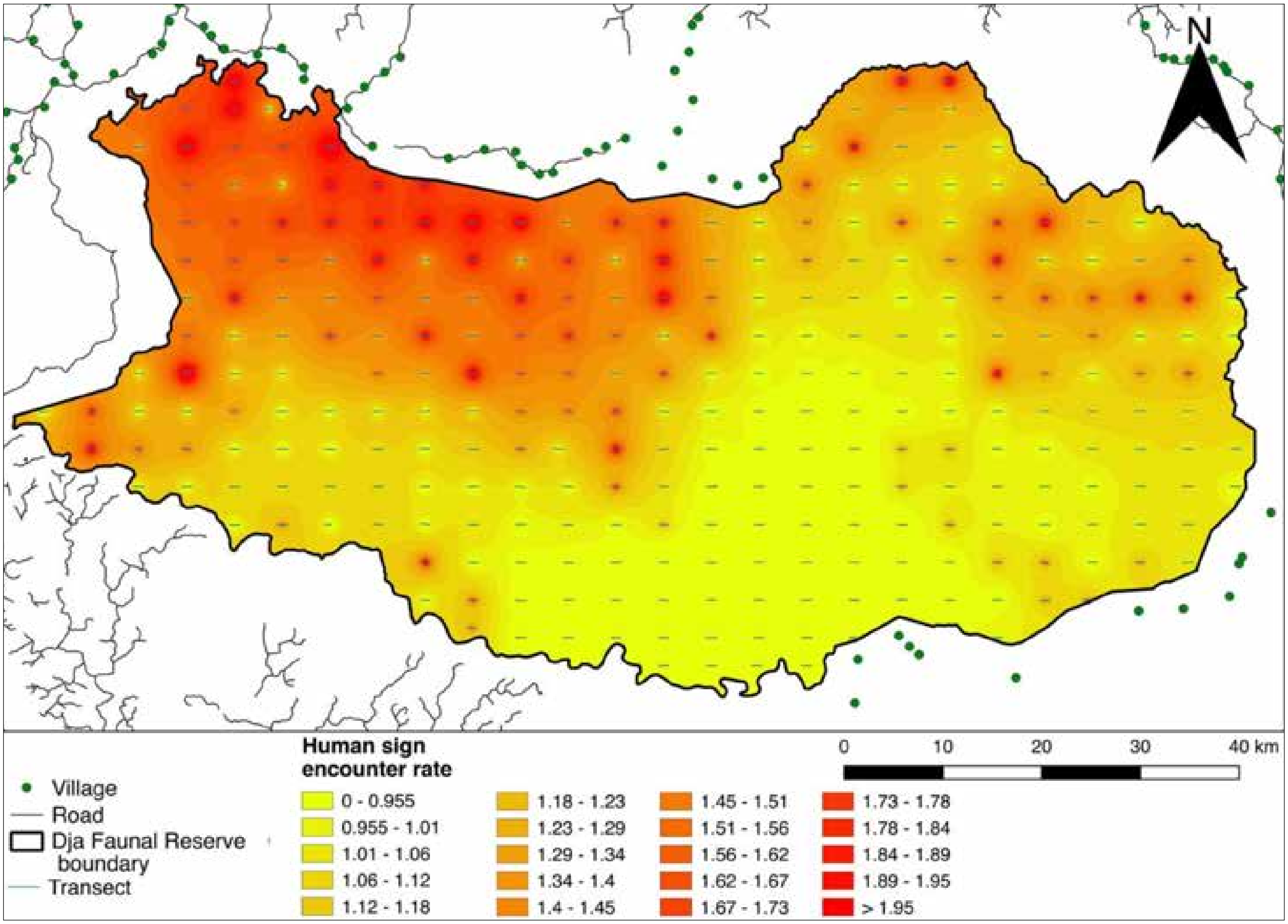

Figure 7. Distribution of signs of human activity (signs/km) within the Dja Faunal Reserve, Cameroon.

Discussion

This reserve-wide survey confirms that great ape populations within the DFR have diminished markedly over recent years in comparison to two earlier surveys by Williamson and Usongo (1995) and MINFOF and IUCN (2015) (Table 1). The Williamson and Usongo (1995) survey was conducted mainly in the north-central part of the reserve. For comparison, we analyzed our study transects that were located in the 1995 survey area. Central chimpanzees in the sampled area have declined by ~34%, and the western lowland gorillas by ~57% (Table 1). Compared to the 2015 inventory, the western lowland gorilla also showed the greater decline in estimated density, with more than a threefold decrease (Table 1). Survey methodology differences could, however, be magnifying the apparently sharp decline. Gorillas are thought to be less susceptible to anthropogenic impacts than chimpanzees when appropriate management is applied (Strindberg *et al*. 2018). An Ebola outbreak causing the major decline in western lowland gorillas in the DFR is not supported, as there have been no reports of rangers finding large numbers of dead animals and the impact of the disease would be expected to cause a similar decline in the central chimpanzee population. Western lowland gorilla numbers in the DFR are low compared to those in other protected areas of the region. The density of western lowland gorillas reported in Noubalé-Ndoki National Park, for example, is approximately three times higher (Table 1), and densities as high as 5.4 individuals/km² have been reported in Odzala National Park in the Republic of Congo (Bermejo 1999). More recent surveys in the nearby Mengame Gorilla Sanctuary (Kom-Mengame Wildlife Complex) and the Goualougo Triangle reported densities of 2.53 individuals/km² (Halford *et al.* 2003) and 1.28 individuals/km² (Sanz *et al*. 2007), respectively. Densities of 1.61 and 0.95 have also been reported from Boumba Bek National Park and Nki National Park in Cameroon, respectively (Nzooh *et al*. 2016b).

The DFR has the second highest reported density of central chimpanzees in Cameroon (Table 1), yet this is approximately half the density reported in Noubalé-Ndoki National Park, Republic of the Congo (Stokes *et al*. 2010). We are not able to conclude whether this difference represents ecological differences in forest composition or historic and current human activities such as hunting and other forest-based resource use between the two sites.

Drivers of declines

Human activity within the DFR remains pervasive (MINFOF and IUCN 2015). Human signs were found throughout the DFR in this survey with the highest frequency of human signs encountered in the northwest of the DFR. When compared to the 2015 inventory (MINFOF and IUCN 2015), the pattern is broadly similar with the northwest of the reserve experiencing the highest intensity of human activity. The main difference between the 2015 and 2018

Table 1. Central chimpanzee and western lowland gorilla population density estimates from recent surveys in protected areas of Cameroon and northwest Central Africa.

Country	Site and survey	Central chimpanzee density estimate (individuals/km²)	Western lowland gorilla density estimate (individuals/km²)
Cameroon	DFR 2018 (this study)	0.53 (95% CI = 0.38–0.73)	0.38 (95% CI = 0.28–0.53)
Cameroon	DFR 2015 (MINFOF and IUCN 2015)	0.69 (95% CI = 0.52–0.91)	1.26 (95% CI = 0.95–1.67)
Cameroon	DFR – north-central area 1995 (Williamson and Usongo 1995)	0.79 (95% CI = 0.6–1.14)	1.71 (95% CI = 1.02–2.86)
Cameroon	DFR – north-central area only (this study with area corresponding to Williamson and Usongo 1995)	0.52 (95% CI = 0.3–0.89)	0.74 (95% CI = 0.4–1.38)
Cameroon	Lobéké NP (Nzooh *et al*. 2016a)	0.29 (95% CI = 0.18–0.46)	1 (95% CI = 0.64–1.56)
Cameroon	Nki NP (Nzooh *et al*. 2016b)	0.16 (95% CI = 0.09–0.26)	0.95 (95% CI = 0.62–1.44)
Cameroon	Boumba Bek NP (Nzooh *et al*. 2016b)	0.24 (95% CI = 0.15–0.39)	1.61 (95% CI = 1.41–2.27)
Cameroon	Campo Ma'an NP (Nzooh *et al*. 2016c)	0.26 (95% CI = 0.20–0.35)	0.22 (95% CI = 0.14–0.33)
Cameroon	Korup NP (Kupsch *et al*. 2014)	0.13 (95% CI = 0.07–0.24) **Pan troglodytes ellioti*	Not detected
Cameroon	Mount Cameroon NP (Eno-Nku *et al*. 2013)	0.67 (95% CI = 0.41–1.11)	Not detected
Republic of Congo	Noubalé-Ndoki NP (Stokes *et al*. 2010)	1.03 (95% CI = 0.61–1.71)	1.02 (95% CI = 0.59–1.77)

surveys is what appears to be a reduction in human signs in the South Sector. This is most likely due to the establishment of a permanent river ecoguard post in proximity to Bali Bai (see Fig. 1). There also appears to be increased human signs around the research station at Bouamir, which is most likely due to an increase in station activities. While not all the signs of human activity are directly attributable to hunting or poaching, for example, machete marks and forest camps are also made by ranger patrols and researchers, we presume that areas that contain generally higher encounter rates of human sign are likely to be experiencing greater hunting or poaching pressure than areas with lower encounter rates of all measured human sign. The frequent presence of humans across a large proportion of the DFR may also be pushing great apes away from key resources, such as swamps and bais (forest clearings), with associated stress on the population.

Interaction between human impacts and wildlife distributions has been modeled at a variety of scales in the Congo Basin. In general, the distance to roads and human densities provides a reliable predictor of great ape distributions, with increasing densities of the species with distance from anthropogenic infrastructure and settlements (Strindberg *et al*. 2018). The same general pattern was found in this survey. The area containing the most human activity/signs of activity was closer to significant infrastructure, such as the Hydromekin Dam and the Sud-Cameroun Hévéa rubber plantation and associated human settlements. These areas had the lowest encounter rates of great ape nests.

A proposed standard monitoring protocol for great apes of the DFR

Protected area managers should continue to adhere to best practice methods for distance sampling surveys (Kühl *et al*. 2008). The distance sampling analysis used here, with data collected through systematic line transects designed to achieve a desired coefficient of variation, are recommended to periodically assess great ape population size and trends. Estimated survey effort to achieve a desired precision in the population estimates should also account for the uncertainty in the nest production and decay rate estimates, one of the reasons for the slightly higher CV compared to the desired CV in this study. The use of individual nests instead of nest groups, as used in this study, is also recommended to avoid potential bias in density estimates. If species detections become few then the central chimpanzee and western lowland gorilla observations can be combined and analyzed using multiple covariate distance sampling with species as a covariate to estimate density of each species. The DFR survey is planned to be repeated in 2021. If populations continue to decline, then the survey effort (in transect length) required to achieve a set coefficient of variation would make transect sampling prohibitively inefficient within the DFR. Camera-trap surveys provide an alternative approach to assessing population trends (discussed below).

Indirect nest surveys should yield unbiased estimates of density and abundance for monitoring trends in population status if implemented carefully to address sources of sampling error, such as variation in skills among those doing the surveys and differential detectability of nests in different habitats. The largest source of error when calculating density estimates, however, is the estimate of nest decay rate. Nest decay rate can vary substantially both within and between areas due to several factors, including rainfall, altitude, nest height, exposure, soil pH, and nest tree species (Kühl *et al*. 2008), and now due to climate change (Bessone *et al*. 2021). This means that survey specific nest decay rate estimates are necesssary.

Occupancy model estimates derived from camera-trap data offer an alternative rigorous measure for monitoring trends in great ape status as they are corrected by detection probability (i.e., the likelihood that a species was detected when present) (MacKenzie *et al*. 2006). Heterogeneity in site use and detection can be incorporated into the modeling. Occupancy data also has the advantage of being relatively easy to collect in a standardized format, and the use of camera-traps is particularly suited to this approach as they can be set up to operate constantly over the survey period. The use of modeled occupancy for monitoring the status of wildlife populations has become popular for a range of taxa (O'Connell *et al*. 2011). The use of distance sampling with camera-traps for estimating population densities of medium-to-large terrestrial mammals is also being developed and implemented (Howe *et al*. 2017; Amin *et al*. 2022). Whilst this approach has been tested for chimpanzees with camera-traps placed intentionally within the home range of one fully known group (Cappelle *et al*. 2019), further validation of the method needs to be carried out in populations of both chimpanzees and gorillas where group structures and home ranges are less well understood to enable effective monitoring of trends in great ape populations.

The documented decline in the great ape population (and forest elephants, Amin *et al*. 2020) is a contributory factor to UNESCO's possible downgrading of the World Heritage status of the DFR (https://whc.unesco.org/en/decisions/7889). The Cameroon Government is strengthening conservation measures as outlined in the 2020–2025 Dja Faunal Reserve Management Plan, which addresses many of the concerns raised by UNESCO concerning the management of the reserve. Great apes are currently most abundant in the north-eastern part of the DFR where local communities have exerted their traditional rights to collect non-timber forest products and to undertake small-scale subsistence hunting. The DFR Conservation Service is considering a community partnership agreement on sustainable access to forest resources and, to date, these great ape refugia have also been receiving greater management attention, both in terms of routine patrol coverage and rapid ranger response following alerts from local communities. The southern part of the DFR is much more vulnerable to organized wildlife crime gangs (OCGs), especially from the southern wildlife trafficking hub around the town of Djoum, which does not fall within traditional community areas (Poulsen *et al.* 2017). The presence of traditional subsistence hunters in the northern part of the DFR may provide a disincentive to OCGs to operate there compared to the more remote south where they can poach with relative impunity. The DFR management is implementing a community surveillance network and increasing law-enforcement patrols, especially along the southern boundary of the DFR with its many exit routes.

With improved security and appropriate engagement with local communities and the private sector in the region, it is hoped that the remaining great ape population will start to expand across the biosphere reserve and numbers gradually increase. The Dja Biosphere Reserve is an integral component of the TRIDOM transborder landscape which covers 178,000 km², roughly 10% of the Central African forest. It offers one of the last remaining opportunities for the long-term conservation of great apes, forest elephant, and other threatened species in the region. To prevent the increasing isolation of populations of large mammals, it is recommended that management plans for protected areas such as the Dja Biosphere Reserve in the TRIDOM landscape, incorporate zones outside and between the protected areas, such as private sector logging concessions and commercial plantations. Landscape level, transboundary planning is required to maintain existing wildlife corridors. Existing and future survey results, based on line-transects and camera-traps, should be used to identify areas used by great apes and other large mammals for travel within the landscape. These results should be incorporated into wildlife management plans and land-use plans for the region, such as the existing TRIDOM landscape agreement between Cameroon, Gabon and the Republic of Congo. Law enforcement strategies and community engagement activities in the landscape should be developed and strengthened.

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