Spatio-temporal variation in the distribution of great apes in the Dja-Ngoyla Complex in Cameroon, and implications for conservation

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Abstract Central African great ape populations are in serious decline as a result of poaching, habitat loss and disease. Reliable estimates of population size are urgently needed for informed management action. We estimate the abundance and distribution of central chimpanzee *Pan troglodytes troglodytes* and western lowland gorilla *Gorilla gorilla gorilla* populations in the c. 11,000 km² Dja-Ngoyla Complex in Cameroon, a critical component of the Tri National Dja-Odzala-Minkébé (TRIDOM) transboundary landscape, which covers 178,000 km². We compare our results with previous site estimates and with other population estimates from the region. We completed 1,096.64 km of line transects ($n = 559$) in 2021 using the standing-crop nest counts method. The Dja-Ngoyla Complex supported c. 11,787 great apes. Chimpanzee abundance was significantly higher in Dja, and Ngoyla-Mintom supported 71% of the gorilla population. Thirty-seven per cent of the gorilla population and 17% of the chimpanzee population occurred in logging concessions. There was no significant change in the species' abundance in Dja Faunal Reserve compared to our 2018 estimate using the same methodology. The chimpanzee population density was much higher in Dja and Ngoyla Faunal Reserves compared to other protected areas in the region. There was large variation in great ape densities across logging concessions, and those with implemented management certification schemes supported higher densities. This study also highlights the high risk of Dja's great ape population becoming isolated. Promoting forest management certification to strengthen wildlife and habitat protection in all logging concessions in the Complex is urgently needed and will also allow local communities to benefit from these forests.

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Introduction

Western lowland gorillas *Gorilla gorilla gorilla* and central chimpanzees *Pan troglodytes troglodytes* live in sympatry across much of the remaining tropical rainforests of western equatorial Africa. Populations of both species are rapidly declining because of habitat degradation and loss, poaching and disease epidemics (Ebola, in particular; Strindberg et al., 2018). The central chimpanzee (hereafter chimpanzee) is categorized as Endangered on the IUCN Red List (Maisels et al., 2016) and the western lowland gorilla (hereafter gorilla) is categorized as Critically Endangered (Maisels et al., 2018). They are keystone species in their forest habitat, and their protection is essential to the long-term management of the Congo Basin.

In Cameroon, the chimpanzee and gorilla are mainly distributed in the south-east, with strongholds in Lobeke, Boumba-Bek and Nki National Parks, and the Dja and Ngoyla Faunal Reserves. The Dja-Ngoyla Complex covers c. 11,000 km² of moist lowland forest, encompassing the Dja and Ngoyla Faunal Reserves and their surrounding areas comprising a mosaic of forestry and hunting concessions, agricultural land, mining areas, communal and community forests. The Complex is a key component of the Tri National Dja-Odzala-Minkébé (TRIDOM) transboundary conservation landscape and is a priority site for the conservation of great apes (IUCN, 2014). Here, we assess the population status of the chimpanzee and gorilla in the Dja-Ngoyla Complex following a baseline study in the Dja Faunal Reserve in 2018 (Amin et al., 2022). A key recommendation of the 2018 study was to obtain great ape population estimates for the Complex and to identify key areas and their connectivity within the TRIDOM landscape.

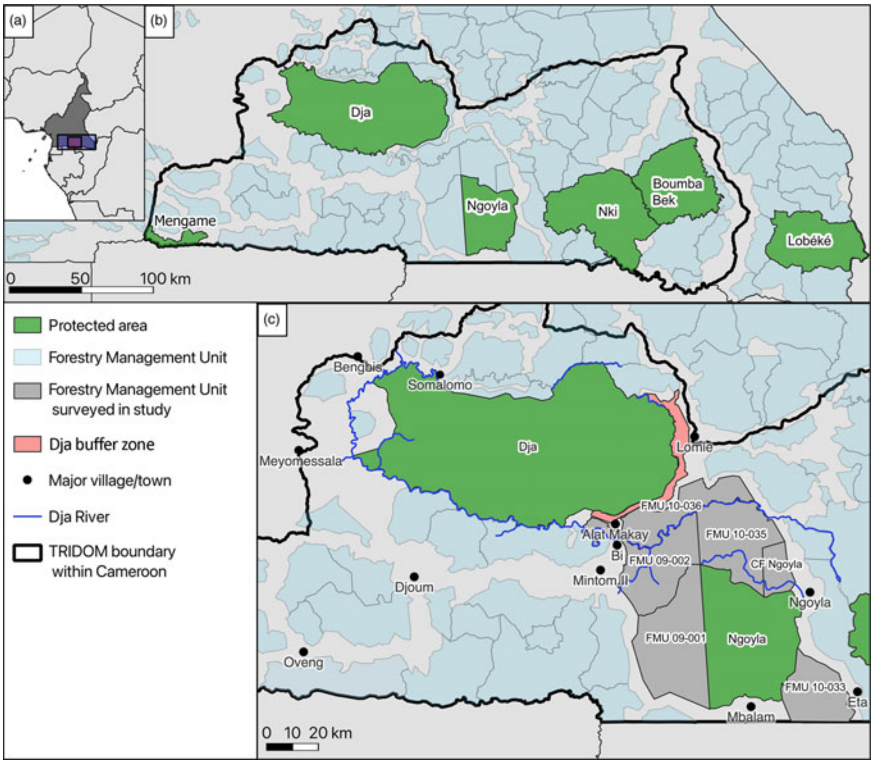

Fig. 1 (a) Location of the Dja-Ngoyla Complex, Cameroon. (b) Overview of the protected areas, Forest Management Units (FMUs) and the boundary of the Tri National Dja-Odzala-Minkébé (TRIDOM) transboundary landscape falling within Cameroon. (c) A detailed overview of the Dja-Ngoyla Complex, showing the buffer zone of the Dja Faunal Reserve, the surveyed FMUs identified by the number listed by the Cameroon forest administration, major towns and villages, and the Dja River around the Dja Faunal Reserve and through the FMUs.

Study area

The Dja-Ngoyla Complex is located in south-eastern Cameroon between latitudes 2°12'–3°23'N and longitudes 12°25'–14°00'E. It consists of the Dja Faunal Reserve and its buffer (Dja), and the Ngoyla-Mintom Technical Operational Unit (Ngoyla-Mintom) comprising Ngoyla Faunal Reserve, Ngoyla Council Forest and Forest Management Units (FMUs; Fig. 1). The Dja-Ngoyla Complex, especially Ngoyla-Mintom, is important as it maintains connectivity between forests and enables genetic flow between great ape populations across the 178,000 km^2 greater TRIDOM landscape. The Dja Faunal Reserve is designated a World Heritage Site, with its extant megafauna considered an Outstanding Universal Value (UNESCO, 2021).

The Dja-Ngoyla Complex is relatively flat, with round-topped hills and ranges at elevations of 600–800 m (MINFOF & IUCN, 2015) in Dja and 500–850 m (Laclavère, 1979) in Ngoyla-Mintom. The Complex has a dense hydrographic network because of its topography and sub-equatorial climate with relatively consistent rainfall throughout the year. The largest river is the Dja River, originating north of Lomié, and surrounding 80% of the Dja Faunal Reserve, except part of the eastern sector of the Reserve (Fig. 1). The Dja River crosses Ngoyla-Mintom in the north before joining the Boumba River to form the Ngoko River near the border of Cameroon and the Republic of Congo.

Dja has three main forest types: terra firma mixed species forest, monodominant forest where the evergreen *Gilbertiodendron dewevrei* is the most abundant species, and periodically flooded forest (Djuikouo et al., 2010). The vegetation of Ngoyla-Mintom is characterized by dense evergreen rainforest, swamp forest complexes, a mosaic of secondary forests, agricultural plantations and inhabited areas, and forest clearings (Ngalla, 2007). These vegetation formations are associated with significant biodiversity. The Dja-Ngoyla Complex supports a rich variety of medium-sized and large mammals. In addition to the two species of great apes, the Complex is an important landscape for the Critically Endangered African forest elephant *Loxodonta cyclotis*. The Complex has a diverse community of forest ungulates and three threatened pangolins, namely the black-bellied pangolin *Phataginus tetradactyla* (categorized as Vulnerable), white-bellied pangolin *Phataginus tricuspis* and giant ground pangolin *Smutsia gigantea* (both categorized as Endangered; IUCN, 2025).

Based on the literature and studies conducted in the area, the human population of the Dja-Ngoyla Complex is estimated to be c. 62,000. Around Dja, the human population is estimated to be 19,500 in the villages in the buffer zone and 30,000 in the wider area directly surrounding Dja (Fowler, 2019; Ngatcha, 2019). The Ngoyla-Mintom forest massif is inhabited by an estimated 12,300 people spread over c. 60 villages and hamlets (Defo, 2012).

The Dja-Ngoyla Complex faces many pressures. Poaching is among the most significant threats and is mainly carried out by non-traditional means, such as firearms and wire traps. Much of the poaching fuels the illegal wildlife trade (UNESCO, 2021). Other significant threats to biodiversity in the area include logging, clearing the landscape for commercial and cash crops such as cocoa and pineapple, and the ecological ramifications of constructing railways, roads and dams in the Complex. For example, the Kribi-Mbalam railway connects an iron production site in Mbalam (located south of Ngoyla Faunal Reserve) to the deep-sea port in Kribi on the west coast of Cameroon, and the Hydro Mekin hydroelectric dam was built to the west of the Dja Faunal Reserve (MINFOF & IUCN, 2015; UNESCO, 2021). These threats directly lead to the reduction of suitable habitats and resources for wildlife and cause edge effects such as increased human access and changing environmental conditions (Laurance et al., 2009). Furthermore, they cause indirect impacts, such as increasing the demand for bushmeat, driven by the growing human populations linked to infrastructure development (Poulson et al., 2009). Future threats include the loss of the last remaining large, forested corridor linking the Dja Faunal Reserve to the Ngoyla-Mintom forest block if the south-eastern road from Bi to Lomié town is developed further and planned hydroelectric dams are constructed.

Several stakeholders manage the Dja-Ngoyla Complex. The Dja Faunal Reserve and Ngoyla Faunal Reserve are managed by the Ministry of Forestry and Wildlife (MINFOF), the FMUs by concessionaires, and the Ngoyla Council Forest by the Council of Ngoyla and Lomié. The FMUs within and around the Dja-Ngoyla Complex are managed for 30 years following a MINFOF-validated management plan that is assessed every 5 years, except for FMUs 09-001 and 09-002, which until 2022 were not allocated and therefore not managed. The plan specifies zonation and overall strategy within the concessions to ensure that logging is carried out sustainably, and stipulates regular anti-poaching patrols, wildlife inventories and habitat assessments.

Methods

Estimating great ape population densities and abundance

We estimated chimpanzee and gorilla population densities and abundances for the Dja-Ngoyla Complex based on distance sampling through nest-based transect surveys (White & Edwards, 2000; Kühl et al., 2008) as part of a megafauna inventory. We used the standardized survey protocol for great apes (Kühl et al., 2008; Amin et al., 2022) to allow our estimates to be comparable to the survey conducted in 2018, in order to monitor changes in great ape populations over time. Other surveys in the region conducted in 1995, 2010 and 2015 used differing methodologies that rendered direct comparisons challenging.

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 the previous transect survey in the Dja Faunal Reserve in 2018 (Amin et al., 2022):

$$L = (b/\{cv_t(\widehat{D})\}^2).(Lo/no),$$

where L is the estimate of total transect-line length to be surveyed to achieve the target Coefficient of Variation (CV); b the dispersion factor (set to a default value of 3 as per Buckland et al., 2001); cv_t the target CV of the density estimate $\widehat{D}$; L_o the total length of all transects (298.2 km from 2018 survey); and n_o the total number of observations on all transects (minimum 127 observations of gorillas from 2018 survey).

Given 16% CV was achieved for the gorilla estimate in 2018, we estimated that 1,120 km of transects would be needed to achieve a 10% CV. Starting at a random point, we systematically positioned 2 km length transects with 3 km spacing in the Complex. In Dja transects were oriented east to west and in Ngoyla-Mintom north-east to south-west to align them perpendicular to the watercourses, which represent the most likely ecological gradient within the Dja-Ngoyla Complex. We established 289 transects (578 km) in Dja and 300 transects (600 km) in Ngoyla-Mintom across the five FMUs, Ngoyla Faunal Reserve and Ngoyla Council Forest (Fig. 2).

We conducted the surveys at the end of the dry season during 22 April 2021–6 July 2021 using 14 teams, both in Dja and Ngoyla-Mintom. Each team had two observers; one observer visually searched for great ape nests in trees, using binoculars to identify features when they were located, while the other observer looked at ground level for great ape nests, signs of human disturbance, and other wildlife droppings and tracks. Each team had two data recorders and four porters who walked at a distance behind the team and were responsible for carrying supplies and camping equipment.

We trained the observers to identify and age great ape nests. Nest-age categories were based on the system proposed by Tutin & 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 1 week old); recent: vegetation dry and changing colour (up to 2 weeks old); old: vegetation dead, but nest still intact ($>$ 2 weeks); decayed: nest beginning to disintegrate, holes visible in structure.

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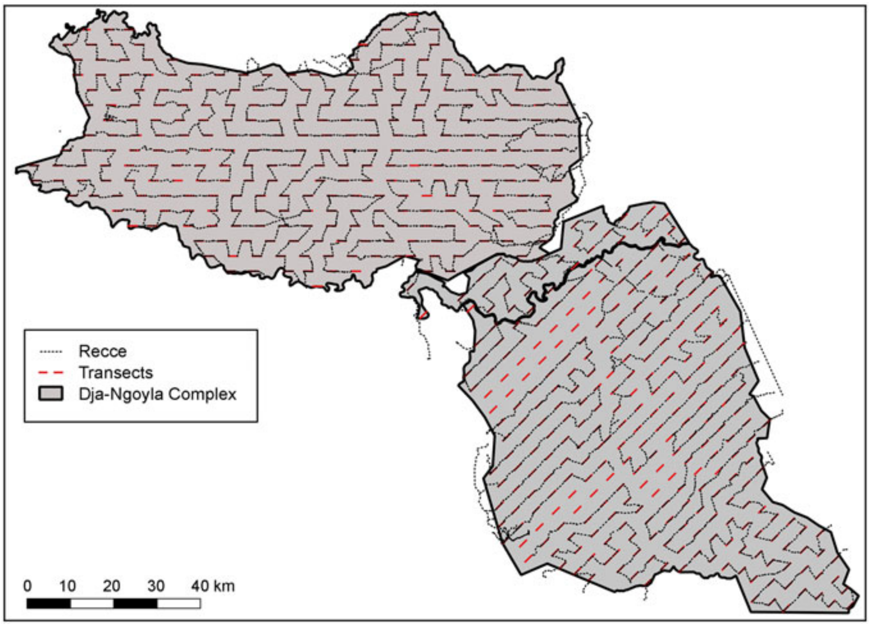

Fig. 2 Locations of line transects systematically covering the entire Dja-Ngoyla Complex, Cameroon. Paths walked between transects (referred to as recces) are also shown and transects without a recce connecting them were not accessible.

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 along the transect, the observers searched within a 50 m radius 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 the observers found no more nests within 50 m, the search was ended, and the perpendicular distance from the transect line to each individual nest was measured to the nearest cm and recorded together with the nest-age category. We also recorded the geographical location (with a GPS), date and time for each observation. The observers looked for shed hair, faeces, tracks and odour in and around the nest, as well as recording the construction type of the nest, and its height above ground according to the following categories: 0 m, 1–5 m, 6–10 m, 11–15 m, 16–20 m and > 20 m, to distinguish which species had constructed the nest. If no definitive signs were observed following Tutin & Fernandez (1984), we used the following definitions to identify the nest builder: (1) all ground nests were attributed to gorillas; (2) all nests in trees that were of the same age as nearby ground nests were attributed to gorillas; (3) all nests that were > 2 m above ground in a tree and with no associated ground nests in that cluster were assigned to chimpanzees.

Given that using these definitions could ascribe some of the nests to the incorrect species, to be conservative, we also collectively calculated the density of great apes by combining both species. These aggregated results are comparable between the different survey strata, and with the 2018 survey in the Dja Faunal Reserve.

Transect data management

We recorded all data using the Spatial Monitoring and Reporting Tool – Survey Module (SMART, 2022) on personal digital assistants (PDAs) and in paper notebooks so as to have duplicate copies of the data, which we then checked for consistency during data processing. We converted the data into a suitable format for analysis in *Distance 7.2* (Thomas et al., 2010). We did not group nests to avoid potential bias in group size estimates as a result of the possibility that not all nests in a group were found and because ground nests are likely to decay faster. However, this may lead to underestimation 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 site and species line-transect data (Buckland et al., 2001). We assessed the detection distances to ensure that our models conformed to the critical assumption that all nests on the transect had a detection probability of 1. When this was not the case, we used left truncation to transform the data to meet the assumption (Buckland et al., 2001; Amin et al., 2022). We also used right truncation to prevent a small number of observations at the furthest distances from overly influencing our model selection process and potentially introducing inaccuracy in our estimates (Buckland et al., 2001). Adjustment terms were constrained, where necessary, to ensure the detection function was monotonically decreasing. We selected among candidate models by comparing Akaike information criterion (AIC) values (Akaike, 1973).

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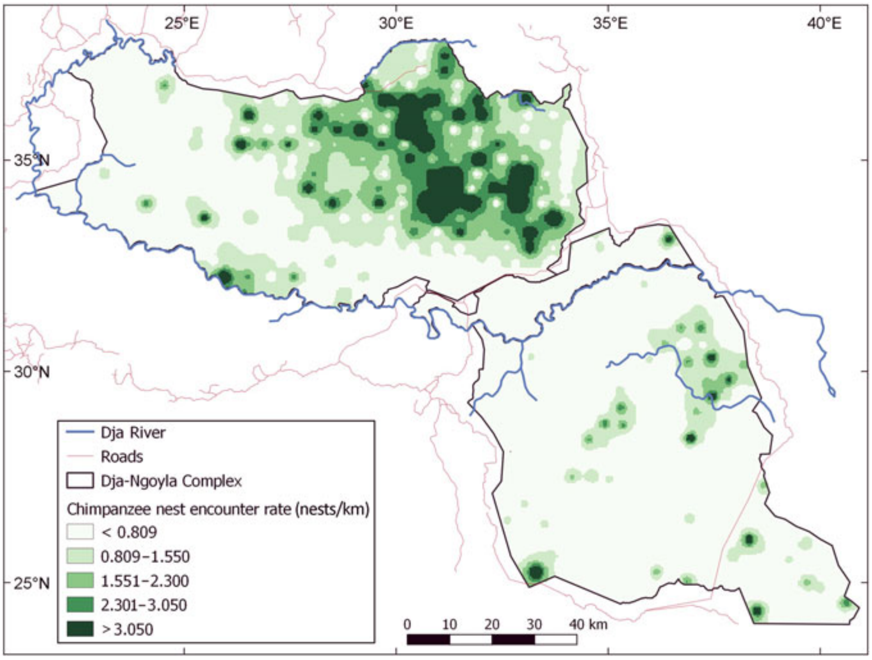

FIG. 3 Distribution of central chimpanzee *Pan troglodytes troglodytes* nests within the Dja-Ngoyla Complex, Cameroon in 2021. Darker shades represent higher nest encounter rates.

We also checked for model fit to the data using the Kolmogorov-Smirnov and χ^2 tests provided by *Distance*. We used a chimpanzee nest mean decay rate of 95.40 ± SE 4.45 days and a combined great ape nest mean decay rate of 96.60 ± SE 2.87 days for the gorilla (Amin et al., 2022). For the production rate, we used 1.09 great ape nests per day (Morgan et al., 2006).

We obtained overall chimpanzee and gorilla population estimates for the Dja-Ngoyla Complex by summing the Dja and Ngoyla-Mintom estimates. We summed the individual estimate variances to obtain the variance of the combined estimate (Buckland et al., 2001). The distribution of the population estimate is positively skewed, and we assumed a log-normal distribution to calculate the 95% confidence interval (Burnham et al., 1987): $\hat{N} \div C$, $\hat{N} \times C$, where $C = \exp\left(z_{\propto} \times \sqrt{\widehat{var}(log_e\widehat{D})}\right)$ and $\widehat{var}\left(log_e\widehat{D}\right) = log_e\left[1 + \left(\widehat{var}\left(\widehat{D}\right) \div \widehat{D}^2\right)\right]$

We also calculated combined great ape population estimates for Dja and Ngoyla-Mintom. We used the Wald test to assess for significant differences between great ape population estimates for Dja and Ngoyla-Mintom and to test for temporal changes in the Dja Faunal Reserve's great ape populations by comparing estimates from 2018 and 2021. All maps were produced using *QGIS 3.36* (QGIS Development Team, 2019).

Results

We traversed 565.04 km of line transects (286) in Dja and 531.60 km (273 transects) in Ngoyla-Mintom. Three transects in Dja and 27 transects in Ngoyla were not accessible (Fig. 2). We recorded 892 chimpanzee nests and 250 gorilla nests in Dja, and 252 chimpanzee nests and 452 gorilla nests in Ngoyla-Mintom. We mapped the distribution of nest observations as encounter rate (nests/km) density contour maps (Figs 3, 4). The great ape distributions were similar to the distributions based on new, fresh and recent nest observations, which was a subset of all nests found and recorded (Supplementary Figs 1, 2).

Dja

Our exploratory analyses revealed fewer detections of nests directly on the transect or nearby (0–2.5 m) than expected for the chimpanzee in Dja. This was most probably a result of observers missing nests in trees directly overhead. Therefore, we analysed these data using left truncation at 2.5 m with rescaling. The hazard-rate model with no adjustments minimized the AIC value for the rescaled chimpanzee data right truncated to 20 m (713 observations). The Kolmogorov-Smirnov goodness of fit P value (0.99) indicated a good fit. The chimpanzee nest density estimate was 51.76 (95% CI = 41.81–64.08) nests/km² and the mean detection probability was 0.61 (95% CI = 0.56–0.67; Fig. 5a). Effective strip width was 12.19 (95% CI = 11.16–13.32) m. The chimpanzee density was estimated to be 0.50 (CV = 11.85%; 95% CI = 0.40–0.63) individuals/km², with a population estimate of 2,756 (95% CI = 2,186–3,475) individuals in Dja.

The half-normal model with no adjustment terms, with a fixed distance interval of 1 m, minimized AIC for the gorilla line-transect data right truncated to 8 m (230 observations). The χ^2 goodness of fit P value for the 1 m

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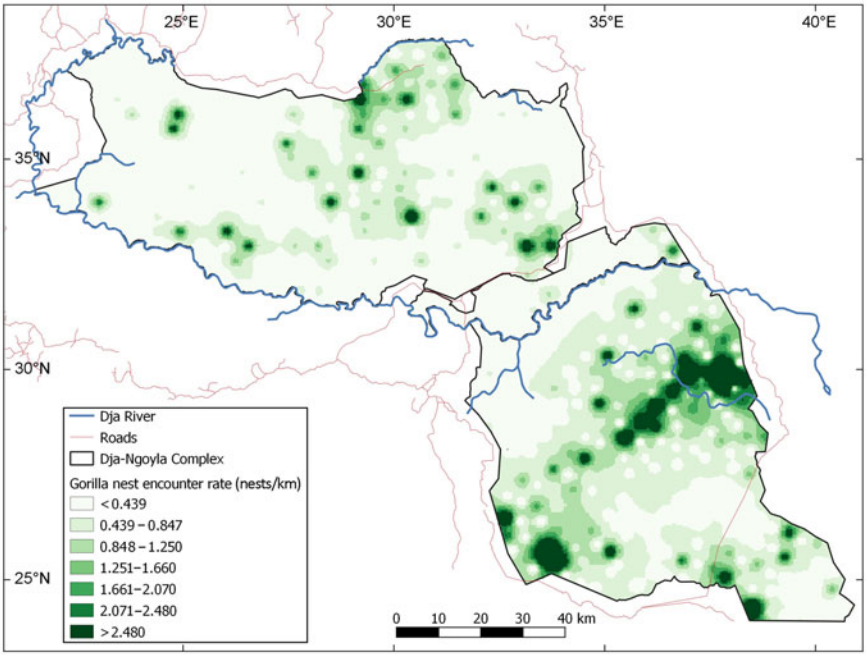

FIG. 4 Distribution of western lowland gorilla *Gorilla gorilla gorilla* nests within the Dja-Ngoyla Complex, Cameroon in 2021. Darker shades represent higher nest encounter rates.

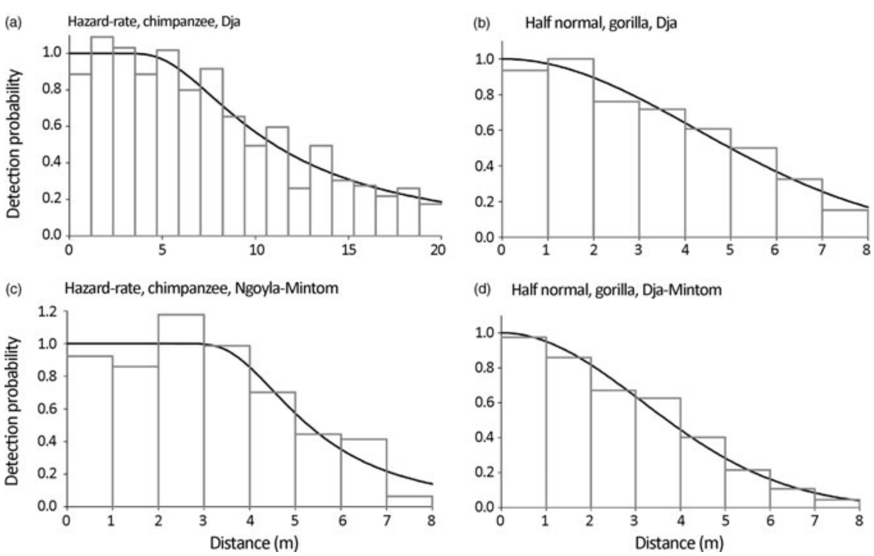

FIG. 5 Fit of detection functions to the perpendicular distances of chimpanzee and gorilla nests from the line transects in Dja-Ngoyla Complex, Cameroon (2021). The histograms of the observed distances are also shown. (a) Hazard-rate detection function for chimpanzee nests in Dja. (b) Half-normal detection function for gorilla nests in Dja. (c) Hazard-rate detection function for chimpanzee nests in Ngoyla-Mintom. (d) Half-normal detection function for gorilla nests in Dja-Mintom.

fixed interval data was 0.91. The gorilla nest density estimate was 40.71 (95% CI = 30.69–54.01) nests/km² and detection probability was 0.63 (95% CI = 0.56–0.70; Fig. 5b). Effective strip width was 5.00 (95% CI = 4.46–5.61) m. The gorilla density was estimated to be 0.39 (CV = 14.76%; 95% CI = 0.29–0.52) individuals/km², giving a population estimate of 2,141 (95% CI = 1,604–2,857) individuals in Dja.

Ngoyla-Mintom

Our exploratory analyses for the chimpanzee also showed fewer detections of nests close to the transect (0–2.5 m) for Ngoyla-Mintom. Therefore, data were left truncated to 2.5 m and rescaled. The hazard-rate model with no adjustments minimized AIC for the rescaled data right truncated to 8 m (175 observations). The Kolmogorov-Smirnov goodness of fit P value (0.6) indicated a good fit. The chimpanzee nest density estimate was 29.56 (95% CI = 21.39–40.84) nests/km² and the mean detection probability was 0.70 (95% CI = 0.62–0.79; Fig. 5c). Effective strip width was 5.57 (95% CI = 4.94–6.28) m. The chimpanzee density was estimated to be 0.28 (CV = 17.20%; 95% CI = 0.20–0.40) individuals/km², giving a population estimate of 1,526 (95% CI = 1,091–2,135)

TABLE 1 Central chimpanzee *Pan troglodytes troglodytes* population density and abundance estimates for the Dja and Ngoyla faunal reserves and Forest Management Units (FMUs). CV, coefficient of variation; CI, confidence interval.

Management unit	Density (CV, 95% CI) (individuals/km²)	Abundance (95% CI)	Transect length (km)	Number of transects
Dja (faunal reserve plus buffer)	0.50 (11.85%, 0.40–0.63)	2,756 (2,186–3,475)	565.04	286
Dja Faunal Reserve	0.52 (11.93%, 0.41–0.65)	2,724 (2,157–3,441)	541.54	274
Ngoyla Faunal Reserve	0.45 (24.70%, 0.28–0.72)	699 (431–1,132)	155.95	81
Ngoyla Council Forest	0.32 (37.06%, 0.14–0.70)	62 (28–137)	19.25	10
FMU 10-035	0.51 (30.07%, 0.28–0.93)	402 (223–727)	84.53	43
FMU 09-001	0.20 (33.49%, 0.11–0.39)	213 (111–410)	106.90	55
FMU 10-033	0.14 (78.88%, 0.03-0.56)	71 (17–295)	57.75	29
FMU 09-002	0.04 (100.21%, 0.01–0.20)	26 (5–143)	48.67	25
FMU 10-036	0.03 (69.81%, 0.01–0.11)	17 (5–61)	58.54	30

TABLE 2 Western lowland gorilla *Gorilla gorilla gorilla* population density and abundance estimates for the Dja and Ngoyla faunal reserves and Forest Management Units (FMUs). CV, coefficient of variation; CI, confidence interval.

Management unit	Density (CV, 95% CI) (individuals/km²)	Abundance (95% CI)	Transect length (km)	Number of transects
Dja (faunal reserve plus buffer)	0.39 (14.76%, 0.29–0.52)	2,141 (1,604–2,857)	565.04	286
Dja Faunal Reserve	0.39 (14.98%, 0.29–0.52)	2,050 (1,530–2,748)	541.54	274
Ngoyla Faunal Reserve	1.18 (43.37%, 0.52–2.69)	1847 (809–4,219)	155.95	81
Ngoyla Council Forest	3.10 (61.84%, 0.86–11.21)	604 (167–2,185)	19.25	10
FMU 10-035	1.34 (27.63%, 0.78–2.31)	1049 (607–1,811)	84.53	43
FMU 09-001	1.07 (27.44%, 0.62–1.84)	1124 (656–1,928)	106.90	55
FMU 10-033	0.82 (40.39%, 0.37–1.82)	431 (195–954)	57.75	29
FMU 09-002	0.18 (43.87%, 0.07–0.42)	125 (53–298)	48.67	25
FMU 10-036	0.06 (73.56%, 0.02–0.24)	35 (9–136)	58.54	30

individuals in Ngoyla-Mintom. Chimpanzee densities were highest in the eastern part of Ngoyla-Mintom and lowest in the two management units connecting to Dja (Table 1).

The half-normal model with no adjustment terms minimized AIC for the Ngoyla-Mintom gorilla line-transect data right truncated to 8 m (436 observations). The χ^2 goodness of fit P value for the 1 m fixed interval data was 0.77. The gorilla nest density estimate was 105.19 (95% CI = 72.23–153.19) nests/km² and detection probability was 0.49 (95% CI = 0.45–0.53; Fig. 5d). Effective strip width was 3.90 (95% CI = 3.62–4.20) m. The gorilla density was estimated to be 1.00 (CV = 19.5%; 95% CI = 0.68–1.46) individuals/km², giving a population estimate of 5,364 (95% CI = 3,668–7,846) individuals. Densities of the gorilla were highest in the eastern part of Ngoyla-Mintom and very low in the management units closest to Dja (Table 2).

Dja-Ngoyla Complex

The chimpanzee population estimate for the Dja-Ngoyla Complex was 4,282 (95% CI = 3,536–5,185) individuals. Dja had a significantly higher population than Ngoyla-Mintom (P = 0.003). Dja Faunal Reserve (i.e. Dja without the buffer) had a population density estimate of 0.52 (CV = 11.93%, 95% CI = 0.41–0.65) individuals/km², giving a population estimate of 2,724 (95% CI = 2,157–3,441) individuals. There was no significant difference with the 2018 population of 2,785 (95% CI = 2,020–3,839) individuals (P = 0.91).

The gorilla population estimate for the Dja-Ngoyla Complex was 7,505 (95% CI = 5,650–9,969) individuals. Ngoyla-Mintom had a significantly higher population than Dja (P = 0.003). Dja Faunal Reserve had a population density estimate of 0.39 (CV = 14.98%, 95% CI = 0.29–0.52) individuals/km², giving a population estimate of 2,050 (95% CI = 1,530–2,748) individuals. There was no significant difference from the 2018 population estimate of 2,004 (95% CI = 1,447–2,774) individuals (P = 0.92).

Combined great ape estimate

We also estimated the size of the combined great ape population for both Dja and Ngoyla-Mintom, given the possibility that the nest builder of some tree nests could have been misassigned, and for future comparisons. The great ape density estimate for Dja was 0.84 (CV = 10.17%, 95% CI = 0.69–1.03) individuals/km², with a population estimate

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Table 3 Great ape density and abundance estimates for Dja, Ngoyla-Mintom and the Dja-Ngoyla Complex. CI, confidence interval.

Species (by site)	Density (95% CI) (individuals/km^2)	Abundance (95% CI)
Dja		
Chimpanzee	0.50 (0.40–0.63)	2,756 (2,186–3,475)
Gorilla	0.39 (0.29–0.52)	2,141 (1,604–2,857)
Combined great ape	0.84 (0.69–1.03)	4654 (3,813–5,680)
Ngoyla-Mintom		
Chimpanzee	0.28 (0.20–0.40)	1,526 (1,091–2,135)
Gorilla	1.00 (0.68–1.46)	5,364 (3,668–7,846)
Combined great ape	1.18 (0.85–1.64)	6327 (4,544–8,809)
Dja-Ngoyla Complex		
Chimpanzee	0.39 (0.32–0.48)	4,282 (3,536–5,185)
Gorilla	0.69 (0.52–0.91)	7,505 (5,650–9,969)
Combined great ape	1.01 (0.82–1.24)	10,981 (8,913–13,529)

of 4,654 (95% CI = 3,813–5,680). The great ape population density estimate for Ngoyla-Mintom was 1.18 (CV = 16.96%, 95% CI = 0.85–1.64) individuals/km^2, with a population estimate of 6,327 (95% CI = 4,544–8,809) individuals.

The population estimates from the nest analysis for great apes combined were slightly lower (< 8%) than the sum of the population estimates for chimpanzees and gorillas calculated separately for each of Dja and Ngoyla-Mintom (Table 3).

Discussion

The TRIDOM transboundary landscape is crucial for conserving great apes in Central Africa, and the Dja-Ngoyla Complex is a critical component of this landscape (Amin et al., 2022). We conducted the first standardized great ape survey of the Dja-Ngoyla Complex, providing an overall estimate of 10,981 (95% CI = 8,913–13,529) adult great apes, with Dja supporting 4,654 (95% CI = 3,813–5,680) individuals and Ngoyla-Mintom supporting 6,327 (95% CI = 4,544–8,809) great apes. Although the population density and size for all great apes combined did not differ significantly between Dja and Ngoyla-Mintom, discernible patterns became apparent when we considered the two species separately. Chimpanzee abundance was highest in Dja (64%), while Ngoyla-Mintom supported 71% of the gorilla population. Thirty-seven percent of the gorilla population and 17% of the chimpanzee population occurred in logging concessions. The lower density of the chimpanzee compared to the gorilla in the Dja-Ngoyla Complex follows a similar pattern to other major protected areas in Cameroon (Nzooh et al., 2016). Further, the much higher density of chimpanzees in the protected areas of Dja-Ngoyla compared to other protected areas in the region (Nki National Park 0.16/km^2, Boumba Bek National Park 0.24/km^2) also suggests that the Complex has a vital role in conserving the species in the wider TRIDOM landscape.

Population trends

Long-term population data from Dja Faunal Reserve show a significant decline in gorillas, as opposed to chimpanzees, over time, although our standardized surveys indicate that the population has been stable in recent years (2018–2021) compared to the decline recorded from 2015–2018. However, methodological differences between our surveys (2018–2021) and previous surveys could account for some of these differences. For example, previous surveys were carried out in a subsection of the reserve and were then extrapolated to the whole area; the orientation of transects varied within the same survey; and the decay rate of great ape nests was not measured and instead documented estimates from other sites were used. The stability in the gorilla population seen in recent years suggests that there have not been any disease outbreaks and that law enforcement efforts have been effective. To continue monitoring great ape trends, we recommend that future surveys maintain a standardized approach while updating the nest decay rate estimate to account for climate change. Climate change models predict more varied and overall decreased precipitation in the Congo Basin. A dryer climate is likely to increase nest decomposition time and during seasonal events like storms, great apes tend to construct more durable nests (Bessone et al., 2021).

Great ape status in logging concessions

The establishment of logging concessions can increase human infrastructure, bushmeat demand, and disease transmission risk to great apes (Poulson et al., 2009). Intensive logging can directly reduce the environment's carrying capacity by removing key trees that serve as sources of food or nesting materials (Morgan et al., 2013, 2018, 2019). However, appropriately managed logging concessions can increase great ape densities in the longer term by maintaining variation in age, size and species of trees, and ensuring protection (Clark et al., 2009; Bortolamiol et al., 2014; Haurez et al., 2016; Tchakoudeu Kehou et al., 2021). Gorillas are posited to reach higher densities than chimpanzees in forest concessions and fragmented habitats because of their flexible social structure and preference for successional vegetation promoted by forest gaps (Clark et al., 2009; Haurez et al., 2013; Morgan et al., 2018; Tagg et al., 2018; Ginath Yuh et al., 2020). Our results suggest this could be the case in the Dja-Ngoyla Complex, with gorillas attaining higher densities in three FMUs and their highest overall density in the Ngoyla Council Forest, almost 10 times higher than in the Dja Faunal Reserve.

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None of the forest concessions we surveyed in the Complex are part of the Forest Stewardship Council (FSC) or Programme for the Endorsement of Forest Certification (PEFC) sustainable management certification scheme, which ensures minimum standards that have been shown to benefit great ape populations (Morgan et al., 2013). The duration and level of management also differ between the concessions. FMUs 09-001 and 09-002, until recently, had not been allocated and were, therefore, vulnerable to poaching and other illegal activities as access restrictions were not enforced. Despite this, gorillas attained relatively high densities within the FMU 09-001 concession. In contrast, the other three main concessions in the Complex (FMU 10-033, FMU 10-035 and FMU 10-036) have operated with management plans over the last decade. FMU 10-035 had the highest gorilla density outside a protected area, and FIPCAM (Fabrique Camerounaise de Parquet), who manages the concession, has put in place a system and procedures audited by a third party through the Origine et Légalité des Bois (OLB) certification scheme to show compliance with the country's forest legislation. However, FMU 10-033 and FMU 10-036 have not yet moved towards a certification scheme, and they are potentially vulnerable to increased bushmeat hunting pressure because of their locations: FMU 10-033 is closer to Souanké in northern Republic of Congo and FMU 10-036 is closer to the Cameroon town of Lomié. FMU 10-036 also lies adjacent to Dja and this situation could lead to the isolation of Dja's great ape population. The lack of gene flow between populations can increase the risk of localized extinctions because of stochastic events, susceptibility to disease, and an inability to adapt to environmental changes (Bergl and Vigilant, 2007; Baas et al., 2018).

Land use planning and management

Proper land-use planning is crucial to protect important habitats and promote connectivity among isolated populations of great apes. Identifying and protecting High Conservation Value (HCV) areas, which is an FSC approach that considers biological values and environmental service, is essential for preserving remnant habitats that great apes use to traverse across the landscape (Morgan et al., 2013). A track that runs from Bi to Lomié in the southeast sector of the Dja Faunal Reserve is increasingly being settled and used for transport and, if this development continues, has the potential to create an expanded and increasingly damaging hunting and disturbance corridor between the Dja and Ngoyla forest blocks.

The logging forest blocks have the potential to contribute to improving wildlife protection in the Dja-Ngoyla Complex through sustainable forest management certification schemes. For example, FSC or PEFC certification requires implementation of Reduced Impact Logging (RIL) practices. From a habitat perspective, this includes establishing narrower roads, a planned skid-trail network, directional felling and closure of old logging roads. From a wildlife perspective, this includes prohibition of bushmeat and hunting material, provision or access to alternative meat sources for workers and their families, and surveillance by rangers. In addition, FSC certification is valid for 5 years and logging companies undergo a compliance audit through third-party annual assessments (Zwerts et al., 2024). All these measures have been found to significantly support great ape survival within the Congo Basin (Medjibe et al., 2013; Haurez et al., 2014; Strindberg et al., 2018).

It is expected that simultaneous and coordinated implementation of best practices for forest and wildlife management in the Complex and the neighbouring logging concessions will stabilize and increase populations of great apes, and enable them to act as a source for other areas of the TRIDOM landscape.

In conclusion, the Dja-Ngoyla Complex is crucial for the conservation of great apes in the TRIDOM landscape. This is attributed to the relative stability in great ape populations within the Dja Faunal Reserve from 2018 to 2022, suggesting that protection measures are effective. Chimpanzees also exhibited high densities compared to other protected areas in the TRIDOM with documented population estimates. As logging concessions were found to be an important habitat for gorillas, it is imperative that the efficacy of FSC practices and the response of great apes to them are monitored within an adaptive management framework. Promoting the adoption of best forest and wildlife management practices throughout the Dja-Ngoyla Complex can help maintain habitat connectivity and ensure the preservation of great ape source populations within the broader TRIDOM landscape.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. No specific ethics approval was required to conduct this study, which is a routine activity within the Dja Wildlife Management Plan.

Data availability The data supporting the findings of this study are available from the corresponding author on request and with the permission of the Ministry of Forestry and Wildlife of Cameroon.

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