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Bonobo (*Pan paniscus*) Density and Distribution in Central Africa's Largest Rainforest Reserve: Long-term Survey Data Show Pitfalls in Methodological Approaches and Call for Vigilance

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Abstract

Conservation measures require accurate estimates of density and abundance and population trend assessments. The bonobo (*Pan paniscus*) is considered Endangered in the IUCN Red List. This classification assumes that available population data are representative. However, with only 30% of the bonobo's historic geographical range surveyed, reliable information is needed to assess the species' population status. Here, we use information from 13 surveys conducted between 2002 and 2018 in an area of 42,000 km^2, representing ~27% of bonobo-suitable habitat: Salonga National Park and its corridor, Democratic Republic of the Congo (DRC). Using 8310 km of reconnaissance and transect walks and 27,045 days of camera trapping, we: (1) provide updated estimates of bonobo population density and distribution (42,000 km^2; ~5,000 km^2 of which, to the best of our knowledge, have not been surveyed before by scientists), (2) assess population trends (15,758 km^2; 2002–2008 vs 2012–2018), (3)

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compare estimates obtained with different methods, and (4) assess the factors driving bonobo density and distribution. Although we detected a non-significant population decline, our study suggests that Salonga is a bonobo stronghold, with a population ranging between 8244 and 18,308 mature individuals (density: 0.31 individuals/km^2). Standing crop nest counts returned non-significantly lower density estimates than camera trap distance sampling. Nest count-estimates were higher in areas with *Marantaceae* understorey and those farther away from rivers, while camera trap-estimates were higher in areas with lower human presence. Regardless of the method, bonobos were rarer in proximity to villages. They occurred more often in areas of dense forest cover and in proximity to ranger posts. Our results point towards a declining bonobo population in Salonga, but do not provide sufficient evidence to confirm this statistically. Consequently, the continued monitoring of the bonobo population and preservation of the integrity of Salonga, considering its biological and cultural heritage, will be crucial in the preservation of this stronghold of wild bonobos.

Keywords Camera trap distance sampling · Great apes · Occupancy · Population trend · Salonga National Park · Standing crop nest count

Introduction

The exponential growth of the human population and its activities over the past 200 years have dramatically increased animal extinction rates (Ceballos *et al.*, 2015). An estimated 30% of living terrestrial vertebrates are threatened with extinction (IUCN, 2024). To design effective conservation efforts, national and international conservation organizations require quantitative field data and appropriate analytical methods to estimate population dynamics (Nichols & Williams, 2006). In particular, knowing a species' geographic distribution, population size (i.e., number of individuals), density (i.e., number of individuals per specified area), population trends (i.e., changes in abundance across time), and the challenges threatening the status of populations are pivotal to developing immediate and long-term conservation strategies. Frequently, field data for a particular species are spatially and temporally limited and are often obtained from different sources which entail different levels of standardization and accuracy (Moussy *et al.*, 2021). Although the simultaneous analysis of different dataset generally requires more complicated analytical tools (e.g., Bowler *et al.*, 2019; Farr *et al.*, 2021; Santika *et al.*, 2017; Sollmann *et al.*, 2015; Royle, 2004), if synthesized, these diverse data can provide more comprehensive information that can improve our understanding of the dynamics of the animal populations we aim to preserve (Kühl *et al.*, 2020).

Great apes (orangutans: *Pongo* spp.; gorillas: *Gorilla* spp.; bonobos: *Pan paniscus*; and chimpanzees: *P. troglodytes*) are a taxonomic group of major conservation importance. Today, all great ape species and subspecies are classified as Endangered or Critically Endangered in the Red List of Threatened Species issued by the International Union for the Conservation of Nature (IUCN, 2024). Inhabiting mainly tropical forests, they are rarely observed directly, and surveys traditionally focused on counting indirect signs of great ape presence, namely their sleeping platforms called "nests" (Fruth *et* *al.*, 2018). Each weaned ape usually constructs one nest per night, and mothers share their nest with their infants (Fruth *et al.*, 2018). Great ape nests usually remain visible for days and months, and nests are easier to detect than their constructors.

To obtain information on great ape density and abundance, nests are typically counted along line transects by applying standing crop nest counts (Tutin & Fernandez 1984), a method requiring a single visit and analyses performed in a distance sampling framework (Buckland *et al.*, 2001; Thomas *et al.*, 2010). However, nest counts require conversion factors scaling the number of counted nests to the number of individual apes. Key parameters for the application of standing crop nest counts are: (1) nest production rate, the average daily number of nests built by an individual, (2) nest decay time, the average number of days that it takes until a nest is no longer visible, and (3) the proportion of nest builders, the proportion of weaned individuals (Buckland *et al.*, 2001; Kühl *et al.*, 2008). These values are highly variable across space and time (Bessone *et al.*, 2021; Wessling & Surbeck, 2023), and it is thus recommended to use purposely estimated, survey-specific conversion factors to obtain accurate estimates (Kühl *et al.*, 2008).

While nest counts may bias calculations of population size due to inaccurate conversion factors (Aebischer *et al.*, 2017), obtaining these factors is time- and resource-demanding and not always feasible (Kühl *et al.*, 2008). Therefore, density estimates obtained by classical nest counts in the past are now sometimes replaced by other methods. Some studies have replaced human observers with drones (Wich *et al.*, 2015; Bonnin *et al.*, 2018) and camera traps (Spehar *et al.*, 2015; Cappelle *et al.*, 2019), while others estimated density from ape genetic material (Arandjelovic and Vigilant, 2018). While nest counts provide data on nesting sites only, camera traps and genetic methods also provide information on diurnal spatial use, including travelling and foraging.

Camera traps and genetic surveys can provide great ape density using capture–recapture frameworks (Borchers & Efford, 2008) based on the requisite that ape feces and images are assigned to individual apes. Although this requirement can be fulfilled in genetic capture–recapture, the broad application of this method has been hindered by the costs required for sample analyses (Piel *et al.*, 2022). Camera trap images have been long been used to estimate population density in capture–recapture analysis (Karanth & Nichols, 1998). However, applicability to great apes has been limited by the difficulties in individually recognizing great apes (but see Després-Einspenner *et al.*, 2017). Although the recent development of camera trap-based methods (not requiring individual recognition: Rowcliffe *et al.*, 2008; Howe *et al.*, 2017; Nakashima *et al.*, 2018) has made camera trap studies highly successful in recent years, these methods are still under development; they make strong assumptions and present caveats specific to the habitat or the species being investigated (Spehar *et al.*, 2015; Gilbert *et al.*, 2021). Finally, another method suggested as a promising alternative is acoustic capture–recapture, using either humans (Kidney *et al.*, 2016) or passive acoustic monitoring devices (Crunchant, 2020) recording ape-calls. However, acoustic methods have suffered the same issue of camera trap capture–recapture: it is difficult to assign recorded calls to individual apes. Consequently, traditional nest counts remain a highly relevant monitoring tool.

The bonobo is an endangered great ape endemic to the lowland rainforest south of the Congo River in the Democratic Republic of the Congo (DRC). So far, population size estimations have been suggestive only (15,000–20,000 individuals) given the survey coverage was too small and patchy to allow thorough estimations (Fruth *et al.*, 2016). As accessibility to areas occupied by bonobos has been historically limited by the lack of infrastructure and DRC's civil and political unrest, there are proportionally fewer bonobo field studies compared to those of other more widespread African apes, gorillas, and chimpanzees. In addition, although some studies covered larger areas (Kano, 1984; Grossmann *et al.*, 2008; Inogwabini *et al.*, 2008; Hart, 2009), most studies focused on a few bonobo groups over relatively small areas of less than 200 km^2 (Furuichi *et al.*, 1998; Eriksson, 1999; Dupain *et al.*, 2000; Van Krunkelsven *et al.*, 2001; Hohmann & Fruth, 2003; Reinartz *et al.*, 2006; Serckx 2014; Surbeck *et al.*, 2017). As a result, despite the species' high conservation value, bonobo density and distribution are unknown in 70% of its estimated geographic range. The remaining 30% of the range has been only sparsely surveyed (Fruth *et al.*, 2016).

At the heart of the species' range lies Salonga National Park, a World Heritage Site (UNESCO World Heritage Committee, 2021). Together with its human-inhabited corridor, Salonga includes approximately 27% of bonobo-suitable habitat (Hickey *et al.*, 2013). It is, therefore, considered a bonobo stronghold (Fruth *et al.*, 2016). Salonga is one of the few sites which has been surveyed twice over large areas (~24,000 km^2), providing both bonobo detection/non-detection and count data (Appendix 1). Between 2002 and 2008 we obtained survey data using a combination of 'reconnaissance walks' (recces) and nest counts. A second round of surveys took place between 2012 and 2018 using a combination of recces, nest counts, and camera trap distance sampling (Bessone *et al.*, 2020), a method to estimate density by extending point transect distance sampling to the use of camera traps (Howe *et al.*, 2017).

Here, we use this database to: (1) provide updated estimates of bonobo population density and abundance in Salonga and corridor (42,000 km^2), 2) assess population trends in an area of 15,758 km^2 comparing data between 2002–2008 and 2012–2018, (3) compare estimates obtained in (1) and (2) by using (i) different nest decay values and (ii) camera traps over 17,141 km^2 between 2016 and 2018 (Bessone *et al.*, 2020), and (4) investigate how bonobo density and distribution are affected by ecological predictors, anthropogenic threats, and proxies for conservation measures considering area-specific socio-cultural factors.

Methods

Study Area

The Salonga National Park, DRC, covers 33,346 km^2. It is divided into two blocks, north and south, separated by a human-inhabited corridor (8570 km^2). From an elevation of 350 m increasing southwards to 500 m, Salonga is composed of more than 90% primary mixed lowland rain forest. The remaining 10% include water bodies, marshes,

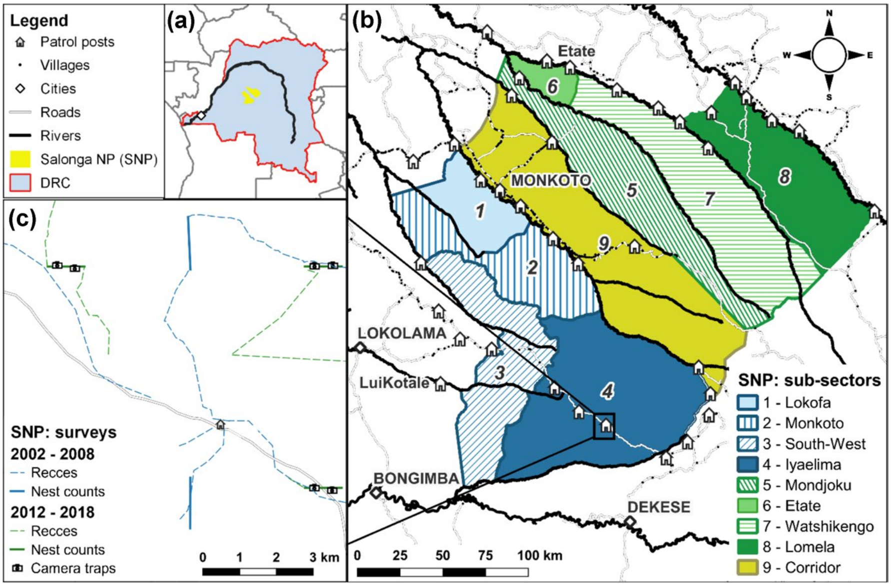

Fig. 1 Salonga National Park (SNP) in (**a**) the Democratic Republic of the Congo (DRC), (**b**) sub-sectors surveyed, and (**c**) survey methods applied. We surveyed sub-sectors 1, 4, 6 and 8 (*solid colors*) in 2002–2008 and 2012–2018; we surveyed sub-sectors 2, 3, 5, and 7 (*hashed colors*) in 2012–2018 only. We surveyed the corridor (9; *solid yellow*) with recces only in 2002–2008 and with nest counts in 2012–2018. In 2012–2018 we also surveyed the South block (sub-sector 1, 2, 3 and 4) with camera-traps.

regenerating forest, intercalary savannahs, and cultivation. Salonga consists of six sectors or administrative units. It has been managed by the national conservation authority, the *Institut Congolais pour la Conservation de la Nature* (ICCN), since its creation in 1970, and more recently co-managed with WWF since 2016 (Fig. 1). Historically and presently, the forest of Salonga and corridor is basically unaffected by logging and mining activities, although deforestation is expanding in the buffer zone around the park due to slash and burn practices driven by an increasing human population (Soliday *et al.*, 2023). As a result, around Salonga the bonobo is primarily threatened by illegal hunting, mostly by professional hunters coming from other areas of DRC and to a lesser extent by local hunters. Approximately 600,000 people with different cultures, languages, and traditions live in Salonga's buffer zone. Although in some areas people hunt bonobos, in other areas bonobo killing and consumption are considered taboo (Thompson *et al.*, 2008; Yokotsuka 2023).

Bonobo Data

Our analyses incorporate data on bonobo density (counts) and distribution (detection/non-detection) from 13 different surveys (Appendix 1). We obtained ten of these from the IUCN SSC A.P.E.S. database (Heinicke *et al.*, 2019; https://www.iucngreatapes.org/apes-platform). The data are based on surveys conducted between 2002 and 2018 in nine survey areas, i.e., “sub-sectors” (Corridor, Etate, Iyaelima, Lokofa, Lomela, Mondjoku, Monkoto, South-West, Watshikengo — Fig. 1b), and within two 7-year periods: 2002–2008, and 2012–2018. Overall, we considered data from 4352 km of recces, 3958 km of line transects (nest counts), and 27,045 days of camera trap footage (Appendix 1). In 2002–2008, we surveyed 2617 km of recces (observing 2950 nests) and 362 km of line transects (749 nests) in five sub-sectors (i.e., Etate, Iyaelima, Lokofa, Lomela, and the Corridor) and calculated density estimates for four sub-sectors (i.e., Etate, Iyaelima, Lokofa, and Lomela). In 2012–2018, we surveyed all nine sub-sectors using 1735 km of recces (325 nests) and 3596 km of line transects (3555 nests) and adding ~5,000 km^2 to the area previously surveyed. The data collected in 2012–2018 allowed us to compare bonobo density estimates for the four sub-sectors already surveyed in 2002–2008 (i.e., Etate, Iyaelima, Lokofa, and Lomela; Table I). We only applied camera trap distance sampling in four sub-sectors in the South block of Salonga (i.e. Iyealima, Lokofa, Monkoto, and South-West — Fig. 1b) following the method described by Howe *et al.*, 2017. These data were the subject of a previous publication providing camera-trap estimates of bonobos and other species (Bessone *et al.*, 2020). We only consider them here to compare methods and to analyse factors affecting estimates from camera traps (Table I).

We collected recce data independently or on the path between transects. As a result, there was no overlap between recce and line transect data. In all but one survey, we deployed evenly spaced line transects (mean transect length = 1,221 m; SD = 425; range = 211–8111) systematically from a random origin following standing crop nest count best practices (Appendix 1). We provide a detailed description of the survey design, spatial extent and location of recces, transects and camera traps in both periods in Appendix 1. We georeferenced the location of bonobo signs (e.g., nests, feeding remains, footprints, vocalisations and direct observations) using tracklogs of the paths walked and waypoints recorded by the survey teams (Kühl *et al.*, 2008). We collected nest counts data following distance sampling best practices (Buckland *et al.*, 2001; Kühl *et al.*, 2008). In contrast to distance sampling data, recce data did not include information on the observed object’s perpendicular distance from the path, preventing an accurate estimate of the surveyed area. Therefore, for the analysis of detection/non-detection data (which included recce observations), we superimposed a fine scale grid (cell size = 1 km^2; number of cells = 44,898) on Salonga and the corridor. We thus coded each cell with either "1" (bonobo detected, with any method), "0" (not detected), or a missing code (not surveyed) and calculated method-specific survey effort as the length of the path (transect or recce), or sampling duration (camera traps) in each cell.

Data Analysis

Estimates of Bonobo Population Density and Distribution

Density

We fitted method- and survey-specific detection functions in Distance 7.3 (Thomas *et al.*, 2010) to obtain estimates of bonobo nest density using nest counts for a) the entire Salonga and corridor (i.e., all nine sub-sectors) between 2012 and 2018, and b)

Table I Analyses and methods used for the different bonobo survey data collected in Salonga National Park, Democratic Republic of the Congo, between 2002 and 2018, and data availability by period and sub-sector

Data	Analysis	Method	Sub-sector	Data availability	
				2002–2008	2012–2018
Reconnaissance walks	✓ Estimates of bonobo distribution ✓ Population trend (distribution) ✓ Drivers of bonobo distribution	→ Occupancy model → Comparison between periods → Occupancy model	Corridor	X	-
			Lokofa	X	X
			Lomela	X	-
			Iyaelima	X	X
			Monkoto	-	X
			South-West	-	X
Nest counts	✓ Estimates of bonobo density ✓ Population trend (density; distribution) ✓ Methods comparison (nest decay) ✓ Drivers of bonobo density	→ Distance sampling analysis → Comparison between periods (Z test; contrast of posterior distributions) → Comparison between periods (Z test) → Zero-inflated gamma regression model	Corridor	-	x
			Etate	X	X
			Lokofa	X	X
			Lomela	X	X
			Iyaelima	X	X
			Mondjoku	-	X
			Monkoto	-	X
			South-West	-	X
			Watshikengo	-	X
Camera traps	✓ Methods comparison (nest counts vs camera traps) ✓ Drivers of bonobo density	→ Comparison between estimates (Z test) → Zero-inflated gamma regression model	Lokofa	-	X
			Iyaelima	-	X
			Monkoto	-	X
			South-West	-	X

Data availability: X = available; - = unavailable.

four sub-sectors (i.e., Etate, Iyaelima, Lokofa, and Lomela) between 2002 and 2008. For each period (2002–2008 and 2012–2018) we first estimated bonobo density in the entire surveyed area by modelling a single detection function for all surveys conducted during the specific period. By including all available data for each period, we aimed to obtain the most accurate and precise estimate possible of bonobo mean density. Similarly, we obtained bonobo density estimates for each subsector (for both periods) by fitting survey-specific detection functions (including specific truncation distances). We then calculated bonobo abundance for each sub-sector by multiplying the obtained densities by their respective areas. We obtained bonobo abundance for the Salonga and corridor by summing up abundances estimated for each sub-sector. This stratified approach allowed us to provide more conservative estimates of the variation in overall abundance in the Salonga and corridor.

Distribution

We investigated bonobo distribution by estimating bonobo occurrence probability using a Bayesian occupancy model integrating detection/non-detection data from recces and nest counts collected in Salonga and its corridor in two periods (2002–2008 and 2012–2018). The model estimates the period-specific 'latent bonobo occupancy' (*O)* and explicitly accounts for method-specific detection probability π, i.e. the probability of detecting bonobo signs if bonobos were present in the area. In this analysis, as we included recce data, we used our 1-km^2 cell size grid to define sites of bonobo detection/non-detection. Estimating π requires multiple visits to the same site, but we surveyed only 1.8% ($N = 805$) with recces and nest counts simultaneously (2002–2008: $N = 266$; 2012–2018: $N = 539$). Therefore, we estimated bonobo detection probability π and occurrence probability ψ from cells where we applied both methods. If a cell was not visited, we used Bayesian imputation, a method independent of the percentage of missing values and known to improve the precision of the estimates (McElreath 2021). In this way, we assigned a prior distribution to the missing values, (i.e. the unsurveyed cells) and estimated the parameters within the same Bayesian model.

Therefore, we modelled O in each cell I in period t as

$$\begin{gathered} O_{i,t} \sim Bernoulli\left(\psi_{i,t}\right) \\ o_{i,j,t}\big|O_{i,t}\sim Bernoulli\left(O_{i,t}\pi_j\right) \end{gathered} \tag{1}$$

where $O_{i,t}$ is the latent occupancy (i.e. , the real occupancy) and $\psi_{i,t}$ the occurrence probability at site i in period t (i.e. the probability a site is occupied by bonobos)*;* $o_{i,j,t}$ is the observed occupancy array for site i, method j and period t (i.e., whether bonobo signs were observed or not); π_j is the average detection probability for method j estimated above. We modelled π by accounting for method-specific survey effort L (i.e., line length), thus controlling for differences in survey protocols and design, specific to each investigating organisation (Appendix 1) as:

$$\operatorname{logit}\left(\pi i_{,j}\right) = \alpha_{j,t} + \eta_{j,t} \times L_{i,j,t} \tag{2}$$

where α is the intercept for method *j* and period *t* and η is a parameter controlling for the effort offset in the logistic regression. In this way, we also accounted for the fact that higher effort typically results in higher detection probability. Although some environmental features might have a negative effect on π, we did not model any covariate except for the effort. For example, the proportion of *Marantaceae* cover could have reduced the visibility of bonobo signs on the ground, but it was not available for the entire dataset. Similarly, forest type could have influenced π on recces, with lower probability of detection in swampy areas where attention is constrained by challenges moving through difficult terrain. However, we did not expect the same to apply to line transects, where attention was required to be high regardless of the habitat. In addition, the habitat-related variable we used (forest cover) did not provide information about factors like canopy openness, yet it included savannahs and open areas, where detection probability was expected to be high due to good visibility.

Conversely, we modelled the occurrence probability $\psi_{i,t}$ as a function of covariates:

$$\operatorname{logit}\left(\psi_{i,s,t}\right) = \alpha 1_{i,s,t} + \beta 1_{i,s,t} \times \mathrm{V}_{w,j} + \cdots + \delta n_{i,s,t} \times \mathrm{V} n_{i,s,t} \tag{3}$$

where α3 is the intercept varying by sub-sector s and period *t*; δ1 to δ*n* are parameters specific to each variable *V* included in the model and potentially affecting bonobo occurrence probability, i.e., slopes for continuous variables or factors for categorical variables. Finally, we predicted bonobo occurrence probability in the Salonga and corridor using our 44,898 (1 km^2) cells. However, as bonobos live in communities of 20 to 120 individuals (Fruth *et al.*, 1999) and have large home ranges, in order to provide biologically meaningful predictions of bonobo occurrence, we calculated the mean of the occurrence probability values obtained for the 1-km^2 cells over 42-km^2 cells (Appendix 2), thereby approximating bonobo home-range sizes in the area (Fruth & Hohmann, 2018). In doing so, our predictions were directly interpretable as the probability of a bonobo community being present in each cell. As we assumed no false positives in our observations, we improved the accuracy of our estimates by considering a cell to be occupied if we recorded at least one bonobo sign (i.e., occurrence probability was assumed to be equal to 1).

To provide some limited information on the estimated parameters without affecting the posterior distribution, we set weakly informative priors (Lemoine, 2019 — Appendix 3). We developed our Bayesian model in Stan (Carpenter *et al.*, 2017) using Rstan (Stan Development Team, 2020) in R 4.0.4 (R Core Team, 2020) to test and fit the final model [four chains of 2000 iterations each (warmup = 1000)].

Population Trend

We compared bonobo density across the two time periods (2002–2008 and 2012–2018) using a Z test (Buckland *et al.*, 2001), and compared bonobo distribution by contrasting the posterior distribution of bonobo occurrence probability predicted for the two periods.

Methods Comparison

We compared density estimates obtained by using (i) different nest decay values and (ii) camera traps.

We investigated the influence of variation in nest decay by scaling estimated nest density to bonobo density using two approaches. In the first approach, we calculated a period-specific nest decay time value, using nests constructed from 3 months before the beginning of each of the two periods until their end [2002–2008 = 90.5 (SD = 2.53) days; 2012–2018 = 103.7 (SD = 3.27) days]. Here, we estimated nest decay following 1511 bonobo nests constructed between 2004 and 2018 at the LuiKotale research site located in Salonga's buffer zone (Fig. 1) from construction to decomposition (Bessone *et al.*, 2021). In the second approach, we applied a fixed nest decay time of 95.5 days (SD = 1.93) obtained from the analysis of all nests included in the dataset, regardless of the period (Bessone *et al.*, 2021). To account for the fact that a bonobo may build more than one nest/day, we applied a nest construction rate of 1.37 (Mohneke & Fruth, 2008). However, we did not correct for the proportion of nest builders. In this way, all density estimates provided here refer to weaned bonobos only and do not include young, non-weaned, bonobos who do not build nests. We then compared the obtained estimates using a Z test (Buckland *et al.*, 2001).

We also used a Z-test to investigate differences between density estimates obtained in the sub-sectors composing Salonga South block (i.e. Iyaelima, Lokofa, Monkoto and South-West — Fig. 1 and Appendix 1) and those obtained in the same area using camera traps (Bessone *et al.*, 2020).

Drivers of Bonobo Density and Distribution

Bonobo nesting sites are found in specific locations characterized by environmental factors, such as fruit availability (Serckx *et al.*, 2016) or *Marantaceae* understorey (Reinartz *et al.*, 2006). Therefore, to maximise the relevance of the factors associated with observed patterns of bonobo density and distribution, our assessment focussed on the smallest area possible around bonobo observations. Providing perpendicular distances to observed objects, distance sampling data from nest counts and camera traps allowed us to define with relative precision the extent of the sampled area. Therefore, we calculated covariate values within buffer areas around the transects. In the case of nest count data, the buffer area was a strip of width equal to the truncation distance used in the DS analysis and specific to each survey, on each side of the transect (width = truncation distance x 2). For camera trap data, the buffer area was a circle, with a radius equal to the truncation distance of the distance-sampling analysis (Bessone *et al.*, 2020). In this way, we were able to assign covariate values specific to each sampling unit. However, for the occupancy analysis, we also calculated covariate values in each 1-km^2 cell of the fine-scale grid superimposed over the study area. In doing so, we assigned detailed covariate values to all occurrence data, including recces for which the area surveyed could not be accurately defined.

We extracted five remotely derived variables from the analysis of spatial data and Landsat-8 satellite imagery (courtesy of the U.S. Geological Survey) in QGis 3.2.0 (QGis Development Team, 2020), ArcMap 10.7 (ESRI, 2019) and ENVI 5.5.3 (Exelis Visual Information Solutions, 2020). These data were available for the entire park and corridor.

Proportion of Forest Cover (F) Bonobos typically inhabit mature primary mixed rainforest on *terra firma*, a habitat providing high tree diversity and food availability (Fruth *et al.*, 2016; Hickey *et al.*, 2013; Reinartz *et al.*, 2006). However, they also use secondary and seasonally inundated forests (Hashimoto *et al.*, 1998) and forest–savannah mosaic habitats (Pennec *et al.*, 2020; Serckx, 2014) depending on fruit availability (Mulavwa *et al.*, 2008; Serckx *et al.*, 2014; Terada *et al.*, 2015). Therefore, we predicted a positive correlation between F and both bonobo occurrence probability and bonobo density. To calculate the proportion of forest cover, we first extracted habitat types in Salonga and corridor from Landsat 8 satellite imagery in ENVI 5.5.3 (Exelis Visual Information Solutions, 2020), creating a raster distinguishing five habitat types: (1) forest (including seasonally inundated lowland and secondary forest), (2) swamp and permanently inundated forest along main rivers, (3) savannah, (4) human settlement (including villages and cultivations), and (5) roads and rivers. Second, we created a binary raster of forest cover by discriminating forest (1) from all other habitats (2) to (5). Then we calculated the proportion of forest within each buffer area around transects (density analysis) and each 1-km^2 cell (occurrence analysis). As forest cover in Salonga was found to be unchanged between 2002 and 2016 (Bessone *et al.*, 2019), we used fixed values for both periods considered in the analysis.

Distance to Cities (C) In Central Africa, cities and towns are hubs of the commercial bushmeat trade that affects great ape abundance even more than local hunting (Kühl *et al.*, 2009). Salonga has a long history of intensive hunting mainly driven by the high demand of cities such as Kinshasa, Mbandaka, and Ilebo (Hart *et al.*, 2008), and commercial hunting continues (IUCN 2020). Consequently, we expected a positive correlation between C and bonobo density and distribution. Given the high population growth and urbanisation rates across DRC between the two periods in study (WorldPop, 2024), we expected this correlation to increase between periods; we used period-specific values of C in our analyses.

Distance to Village (V) The proximity to human settlements is reported to be among the most negative drivers of bonobo density and distribution, and villages (population $<$ 5,000) are no exception (Hickey *et al.*, 2013). As Salonga has villages within its borders, where high bonobo densities were found in the past (Grossmann *et al.*, 2008; Thompson *et al.*, 2008), we expected the effect of V to vary geographically and also temporally due to the ongoing human population growth (Ezeh *et al.*, 2020) and relaxation of traditional taboos (Yokotsuka 2023) in the area.

Distance to Rivers (R) In Central Africa, roads facilitate access to areas of great ape distribution, and their proximity has been shown to negatively affect ape abundance (Strindberg *et al.*, 2018). As in Salonga rivers replace roads, connecting the park to both cities and villages, we expected the distance to rivers *R* to have a positive effect on bonobos.

To test the influence of the proximity to cities, villages and navigable rivers, we created period-specific cost distance raster to cities, villages and rivers around Salonga (grain size = 1 ha) in ArcMap 10.7 (ESRI 2019), using the "Cost distance" algorithm provided in the "Spatial analyst" license. Therefore, these variables were available for each period in the study. We accounted for differences in travelling speed according to habitat type; we weighed costs according to field observations (M.Be, P.A., P.B.D.C., E.D.B.F., B.B.I., M.D.I., M.A.K., D.B.M., M.L.K.W.: *personal observation*), with the least costly valued at 1 and the costliest, at 10. We allocated values as follows: (1) forest (cost value = 5), (2) swamp and permanently inundated forest (cost value = 10), (3) savannah (cost value = 2), (4) human settlement (cost value = 2), and (5) road and river (cost value = 1). Finally, we calculated the mean of the cost distance raster values obtained for each 1-km^2 cell (occupancy analysis) and each transect-buffer (count analysis) to obtain site- and period-specific cost distances to cities, villages, and rivers.

Proximity of a Ranger Patrol Post The conservation status of Salonga is still of serious concern due to ongoing hunting (IUCN 2020). During the time of this study, 31 ranger patrol posts with usually less than ten rangers each were permanently based near or within a village. From patrol posts, rangers operate anti-hunting patrols and monitor the bushmeat trade (Ilambu 2006). We expected bonobos to benefit from the proximity of a patrol post. Therefore, we designated a buffer of 15 km radius around each patrol post. This radius has been reported being the furthest distance invested for subsistence hunting in other sites in sub-Saharan Africa (Fa *et al.*, 2015). Then we dummy coded each buffered transect and each 1-km^2 cell and as "1" when intersecting the 15 km buffer, and "0" if not. By that we obtained a binary, categorical variable for proximity of a patrol post.

Additionally, we collected field-data to obtain a set of anthropogenic and ecological variables potentially affecting bonobo occurrence and density. These variables were available only for count data (nest counts and camera traps) collected in 2012–2018 in Salonga South block. Because the variables were only available for 1.8% of our prediction grid (N = 810 cells) and represented only between 0.3 and 3.2% of the cell area, we only used them for the analysis of count data.

Human Signs Encounter Rate Human activities such as hunting and logging have been reported as the most important drivers of great ape population decline worldwide (Kühl *et al.*, 2017; Plumptre *et al.*, 2016; Walsh *et al.*, 2003; Wich *et al.*, 2016). Historically, higher encounter rates of human signs were negatively correlated with bonobo density in Salonga (Maisels *et al.*, 2009, 2010; Reinartz *et al.*, 2006). Therefore, we predicted that human encounter rates, expressed as number of signs / 100 m would negatively affect bonobo populations. We recorded the number of human signs (direct observations of humans, hunting and fishing camps, snares, gun shells, paths, machete cuts, and felled trees — see N'Goran *et al.*, 2016) along line transects to obtain transect-specific values of human signs per 100 m of transect. As such, our values did not account for potential habitat–human interactions, e.g., higher number of signs (e.g., machete cuts) in closer habitat or closer to fishing camps. Nevertheless, due to the size of the study area, we expected these interactions to be restricted to a few transects and, thus, to have a negligible effect on the model estimates.

Proportion of Bonobo Feeding Trees and Marantaceae Food availability including fruit, leaves, and terrestrial herbaceous vegetation (THV), particularly species of the family *Marantaceae* (Malenky *et al.*, 1996; Serckx *et al.*, 2016; Terada *et al.*, 2015), is a critical factor driving spatial distribution and abundance of bonobos (Hohmann *et al.*, 2012; Mulavwa *et al.*, 2008; Serckx *et al.*, 2014; Reinartz *et al.*, 2008; White 1998). Consequently, we expected the density of bonobo feeding trees and of *Marantaceae* to positively affect bonobo occurrence and density. To assign the proportion of bonobo feeding trees in each transect, we first identified all tree species with a diameter at breast height (DBH) ≥ 20 cm along 500 m of each transect and within 1.5 m of each side of the transect (Bessone *et al.*, 2019). Then, we dummy coded each tree as "1" if at least one part (leaf, flower, fruit) of the tree species was known to be consumed by bonobos (Beaune *et al.*, 2013) and "0" if no parts were known to be consumed. Finally, we divided the number of feeding trees by the total number of trees found along the transect in order to obtain transect-specific proportion of bonobo feeding trees. Similarly, we recorded the understorey beneath each tree visited in the 500 x 3 m strip described above; we recorded four understorey types (Reinartz et al, 2006): 1) "open" (i.e., no vegetation); 2) "lianas"; 3) "*Marantaceae*"; and 4) "woody" (i.e., tree saplings). Then, we dummy coded each sampling area as "1" if the understorey was recorded as *Marantaceae* (type 3) and "0" in all other cases (1, 2, and 4). In this way, we calculated transect-specific proportion of *Marantaceae* vegetation.

Primate and Black Mangabey Density Aside from the bonobo, at least eight diurnal primate species are present in Salonga (Bessone *et al.*, 2023): Tshuapa red colobus (*Piliocolobus tholloni*), Angola colobus (*Colobus angolensis*), Allen's swamp monkey (*Allenopithecus nigroviridis*), black mangabey (*Lophocebus aterrimus*), golden-bellied mangabey (*Cercocebus chrysogaster*), de Brazza's monkey (*Cercopithecus neglectus*), Wolf's monkey (*Cercopithecus wolfi*), and red-tailed monkey (*Cercopithecus ascanius*). Field observations from LuiKotale (BF) also indicate that high primate densities may impact bonobos due to inter-specific competition over food. Of all these primate species mentioned above, the two mangabey species were the most likely food competitors of bonobos, given their overlapping repertoire (Kingdon *et al.*, 2013; McLester 2022) and their abundance in Salonga (Bessone *et al.*, 2023). However, as we did not have enough observations to estimate the density of *C. chrysogaster* (Bessone *et al.*, 2023), we concentrated on *L. aterrimus*, expecting a negative effect of black mangabey density on bonobos. We investigated the effect by recording perpendicular distance to the center of each black mangabey group observed along the line transects used for bonobo nest counts. From these data, we calculated transect specific mangabey density in Distance 7.3 (Thomas *et al.*, 2010) based on group size (Plumptre and Cox 2006).

Prior to running the analyses, we standardized all continuous variables to a mean = 0 and SD = 1.

Model Selection Procedure

As our study aimed to evaluate the influence of different factors on bonobo density and distribution over a large area, we expected geographical differences in the effects of our explanatory variables. Similarly, while nest counts provided data on bonobo nocturnal behaviour only, camera traps also provided information on diurnal behaviours. Therefore, we estimated sub-sector- and method-specific parameters. We first wrote a set of candidate linear models addressing our research questions based on 1) available covariates and 2) biological meaning. For the latter, we used our expert knowledge of bonobo ecology and behaviour and our experience in the Salonga National Park. Furthermore, to reduce the risk of detecting false effects we included different combinations of varying intercepts and slopes (Oberauer, 2022) for three main parameters: 1) probability of a transect having bonobo signs (φ), 2) bonobo mean density (μ), and 3) occurrence probability (ψ). Then, we evaluated potential collinearity between variables by examining pair plots of the posterior distribution of the parameters (Gabry *et al.*, 2019), and we re-ran the models by excluding one variable from each collinear pair based on our research questions. We used data from the South block of Salonga in 2012–2018, where a larger number of covariates was available. We separately analysed detection/non-detection data from three methods to evaluate (1), and count data from two methods for evaluating (2) and (3). We also fitted intercept-only models, assessing whether our predictors were meaningful.

For each main parameter and each sampling method, we ran one chain of 2000 iterations (warmup = 1000) for all candidate models using RStan (Stan Development Team, 2020) and compared their predictive power by evaluating the expected log predictive density (ELPD) using the R package “loo” (Vehtari *et al.*, 2017). The model with the lowest ELPD provided the best fit to the data; the lowest ELPD value was set as the reference for comparing other models by using the difference in ELPD (Δ-Elpd) from the best fitting model. If a model was the best fit for one method (e.g., camera traps) but fitted poorly another (e.g., nest counts), we summed up the differences in ELPD for each method and selected the one returning the highest value. If Δ-Elpd was smaller than its standard error (SE) we considered the model equivalent to the best fitting (i.e., Δ-Elpd = 0.0). Finally, if the best fitting model was no better than the null model, we used an intercept-only model.

Density

In this analysis, our main objective was to assess the drivers of bonobo density. As we wanted to account for imperfect detection in our observations and knowing that the correlation between counts (i.e., observed) and density (estimated) was very high (0.78, $p < 0.001$), we used distance sampling density estimates for each transect, rather than using counts. We investigated the factors affecting bonobo density using a gamma regression analysis. We accounted for the fact that both nest counts, and camera trap data are typically zero-inflated by first estimating φ, the probability of finding bonobo signs on transect *w*, in the same way as a zero inflated model. We modelled φ for each method *j* as

$$z_{w,j} \sim Bernoulli\left(\varphi_j\right) \tag{4}$$

where $z_{w,i}$ is a matrix where each transect was dummy coded as 0 if no bonobo signs were found on the transect *w* (observed density "*d*" = 0) and 1 if bonobo signs were recorded ($d > 0$).

We modelled μ as a function of covariates as

$$\mathrm{logit}\left(\varphi_{w,j}\right) = \alpha 2_{w,s,j} + \gamma 1 \times \mathrm{V}_{w,j} + \cdots + \gamma n \times \mathrm{V}n_{w,j} + \mathrm{L}_{w,j} \tag{5}$$

were α2 is the intercept varying by sub-sector *s* and method *j*; γ1 to γ*n* are parameters specific to each variable V ($N = n$) included in the model (N max = 10: all variables), slopes for continuous variables, or factors for categorical variables; *L* represents the effort, i.e. transect length (nest counts) or camera-days (camera traps) for each transect *w*.

Within the same model and conditional on the transect having $d > 1$ (transects with $d = 0$ were modelled in Eq. 5), we then estimated μ, bonobo density on/for transect *w* for method *j* as

$$d_{w,j} \sim Gamma\left(\mu_{w,j} \times \theta_j, \theta_j,\right) \tag{6}$$

where $d_{w,j}$ is a matrix containing observed density (objects/km^2) estimated with Distance 7.3 (Thomas *et al.*, 2010) for transect *w* and method *j*; $\mu_{w,j}$ is the bonobo mean density for transect *w* and method *j;* and θ is the rate parameter for *j*. Consequently, the mean densities μ estimated above are only derived from those transects where a minimum of one nest was observed. As bonobo nest encounters mostly refer to group clusters (Serckx *et al.*, 2014), our estimates of bonobo mean density μ (Eq. 5) can be considered a proxy of bonobo party size. We modelled μ as a function of covariates as

$$\log\left(\mu_{w,j}\right) = \alpha 3_{w,s,j} + \delta 1 \times \mathrm{V}_{w,j} + \cdots + \delta n \times \mathrm{V}n_{w,j} \tag{7}$$

where α3 is the intercept varying by sub-sector *s* and method *j*; δ1 to δ*n* are parameters specific to each variable *V* ($N = n$) included in the model (N max = 10: all variables), slopes for continuous variables, or factors for categorical variables.

As field-derived variables were available for 11.7% of all considered transects, we used Bayesian imputation to estimate missing variable values. To do so, we assigned a distribution to the missing values as

$$Missing\_\mathrm{V}_v \sim Normal + (0, 1) \tag{8}$$

where *Missing_V* is a vector of length equal to the number of missing values for variable v. As all our variables had been standardised, we assigned a normal prior to the missing values: mean = 0 and SD = 1. For each field-derived variable, we obtained merged vectors of a length equivalent to the number of transects and composed of both observed and values estimated (i.e., imputed) within the same model. We developed the model in Stan (Carpenter *et al.*, 2017) and tested and fitted it using Rstan (Stan Development Team, 2020). We ran four chains of 5000 iterations each (warmup = 4000).

Distribution

We investigated the drivers of bonobo distribution by modeling bonobo occurrence probability $\psi_{i,t}$ as a function of covariates and thereby replacing Eq. 3, with the best model resulting from our selection procedure (see above). As no field-derived variable was available for recces, we included GIS-derived variables only which were available for both periods over the entire study area ($N = 5$: remotely derived variables only). We set weakly informative priors on the slopes and intercepts (Lemoine, 2019 — Appendix 3).

For drivers of bonobo density and distribution, we evaluated how (i.e., negatively or positively) the variables included in the models affected occurrence and density by computing the probability of direction *pd* (Makowski *et al.*, 2019) of the slope parameters in Eq. 3 and 7. This index represents the proportion of the posterior distribution having the same sign of the median, i.e., the probability that a parameter is positive or negative. As such, it varies between 0.5 and 1, and has been found to be highly correlated with the *p* value used in frequentist statistics (Makowski *et al.*, 2019). For example, assuming the median of a parameter x estimated to be negative, a *pd* of 0.55 indicates that 55% of the posterior is negative and 45% is positive, hence providing limited support for a negative effect of x on the response. Conversely, a *pd* of 0.99 would support a negative effect as only 1% of the posterior distribution would have positive sign. For simplicity, in this study we only consider a parameter to have a "significant" effect on the response when $pd \geq 0.99$ and considered any effect with $pd > 0.80$ in our discussion.

Ethical Statement

This study was purely observational, involving signs that are indicative of the presence of bonobos and remotely acquired bonobo images. The methods described above complied with the requirements and guidelines of the Congolese Wildlife Authority, adhered to the legal requirements of the host country, DRC, and followed ethical standards for camera trapping to protect the privacy of people inadvertently recorded during the survey (Sharma et al., 2020). The authors declare that they have no conflict of interest.

Data Availability The data and code used to generate the results of this study are available in GitHub (https://github.com/mattiabessone/Bonobo-Density-Distribution-SalongaNP-IJP-2024).

Results

Estimates of Bonobo Population Density and Distribution

Using period-specific nest decay time and the nest counts method including surveys in all sub-sectors, we estimated bonobo density in Salonga National Park and corridor during the period 2012–2018 to be 0.31 mature individuals/km^2 (percent coefficient of variation “CV” = 8.00%; range: 0.27–0.37; Table II), resulting in 12,119 weaned bonobos (CI = 8244–18,308). When we analysed specific surveys, we found the highest bonobo densities in the sectors Iyaelima, Lomela, and Etate/Watshikengo (Table II).

In 2012–2018, our occupancy model predicted a mean occurrence probability of 0.68 (SD = 0.47). As for the nest count model, Iyaelima, Lomela, and Etate/Watshikengo were among the sub-sectors where the estimated occurrence probability was highest (Fig. 2).

Table II Estimated bonobo density and abundance in Salonga National Park (SNP), Democratic Republic of the Congo, and its sub-sectors between 2012 and 2018 using different nest decay times. Density and abundance estimates (mean, range) from the analysis of standing crop nest counts

SNP sub-sector Area km^2	Density (weaned bonobos/km^2)		Abundance (number of weaned bonobos)	
	Fixed	Period-specific	Fixed	Period-specific
Etate ***708 km^2***	0.41 (0.22–0.75)	0.38 (0.21–0.69)	291 (158–533)	268 (146–491)
Iyaelima* ***7542 km^2***	0.36 (0.24–0.53)	0.33 (0.22–0.49)	2718 (1841–4012)	2503 (1695–3695)
Lokofa* ***2682 km^2***	0.14 (0.07–0.26)	0.13 (0.07–0.24)	366 (192–699)	337 (176–644)
Lomela ***4826 km^2***	0.46 (0.33–0.66)	0.43 (0.30–0.60)	2240 (1586–3164)	2075 (1461–2913)
Corridor ***8570 km^2***	0.23 (0.16–0.32)	0.21 (0.15–0.30)	1952 (1383–2756)	1798 (1273–2538)
Mondjoku ***4704 km^2***	0.27 (0.18–0.43)	0.25 (0.16–0.39)	1292 (829–2015)	1190 (763–1855)
Monkoto* ***2635 km^2***	0.17 (0.06–0.43)	0.15 (0.06–0.40)	435 (167–1134)	401 (154–1045)
South-West* ***4282 km^2***	0.18 (0.09–0.36)	0.16 (0.08–0.33)	756 (368–1552)	696 (339–1429)
Watshikengo ***5962 km^2***	0.52 (0.40–0.67)	0.48 (0.37–0.62)	3109 (2407–4016)	2863 (2217–3698)
Entire SNP ***41,911 km^2***	0.38 (0.31–0.43)	0.31 (0.27–0.37)	13,159 (8931–19,881)	12,119 (8224–18,308)

Nest decay times: Fixed (95.5 days) = calculated for the entire period of survey (2002–2018); *Period-specific* (103.7 days) = calculated for 2012–2018 only. * SNP, South block.

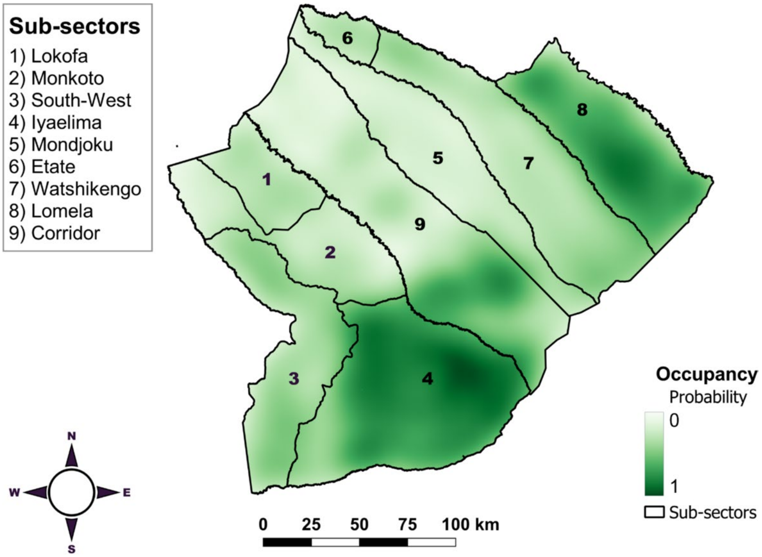

Fig. 2 Bonobo occurrence probability ψ predicted over Salonga National Park (sub-sectors 1–8), and corridor (sub-sector 9), Democratic Republic of Congo, between 2012 and 2018. A depiction of the uncertainty of the estimates is provided in Appendix 4.

Population Trend

Comparing bonobo density estimated with nest counts in 2002–2008 and 2012–2018 in sub-sectors surveyed twice ($N = 4$), we did not find statistically significant population trends (Fig. 3). Similarly, although our occupancy model predicted a 6% decrease in bonobo occurrence probability in the sub-sectors surveyed across periods ($N = 5$), we found no support for a negative trend ($pd = 0.66$).

Methods Comparison

Bonobo density and abundance did not vary significantly when using different decay times as part of the standing crop nest count method (Z test: z = 1.449, p = 0.075; Table II). Similarly, although our bonobo population trend analysis showed a negative trend both when using a fixed (11.39% decrease) and a period-specific decay time (27.33% decrease), neither of the comparisons were statistically significant (*Fixed*: z = 0.454, p = 0.330 | *Period-specific*: z = 1.160, p = 0.127; Fig. 3). When we compared estimated bonobo density based on nest counts data with estimates obtained using camera traps in Salonga South block, we found that camera trap estimates were higher (*Period-specific*: 0.21 | *Fixed*: 0.25 | *Camera traps:* 0.54; Fig. 4). However, due to the high coefficient of variation associated with the camera trap estimate mostly due to highly over-dispersed data (CV = 43.00%; Fig. 4), the difference was not significant (*Fixed* vs *Camera traps*: z = −1.278, p = 0.101 | *Period-specific vs Camera traps*: z = −1.460, p = 0.072).

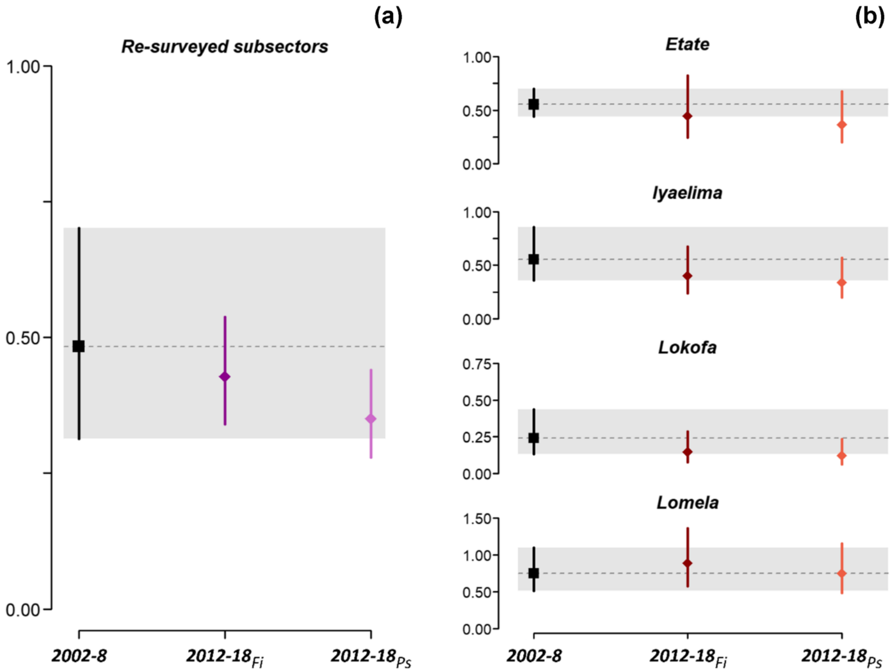

Fig. 3 Trend in bonobo density (individuals/km^2) in Salonga National Park, Democratic Republic of Congo, in the four sub-sectors surveyed in 2002–2008 and 2012–2018, estimated using standing crop nest counts with fixed (*Fi*) and period-specific (*Ps*) nest decay times. (**a**) Trend in all sub-sectors considered; (**b**) trend in specific sub-sectors. *Black squares* show reference estimates and *shaded grey area* shows 95% confidence interval for 2002–2008 (*2002–8*; reference estimate); *red diamonds* show estimates, and *vertical red lines* show 95% confidence intervals of estimates for 2012–2018 with fixed (*2012-18*$_{Fi}$ = 95.5 days; *dark red*) and period-specific (2012–18$_{Ps}$ = 103.7 days; *light red*) nest decay times.

Drivers of Bonobo Density and Distribution

In the model estimating bonobo mean density (μ), primate density and black mangabey density were highly collinear (Appendix 5). As black mangabey feeding habits overlap with those of the bonobo (Kingdon *et al.*, 2013), to investigate inter-specific competition we excluded primate density from all our tested models and included black mangabey density only (Table II).

Models describing the probability of finding bonobo signs on transects φ were not different from the null model (Appendix 6). Therefore, we discarded all proposed models and replaced Eq. 5 with an intercept-only regression, with intercept varying by method and sector (accounting for differences between institutions using different transect lengths and designs). Similarly, the simplest model with no varying slopes returned the best-fitting estimating mean density μ, and was selected for the analysis by replacing Eq. 7 (Appendix 6). When estimating bonobo occurrence probability ψ, we found no signs of collinearity. The model returning the best results

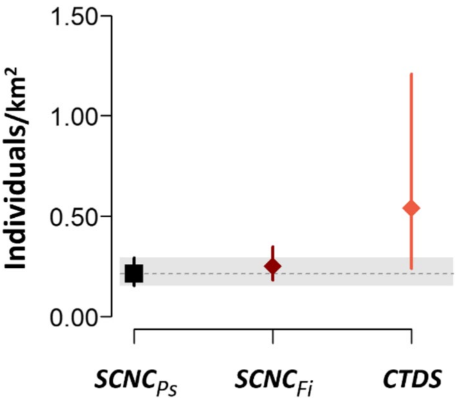

Fig. 4 Bonobo density compared by method: standing crop nest count (SCNC) versus camera trap distance sampling (CTDS) in 2012–2018 in Salonga National Park South block, Democratic Republic of the Congo. The *black square* shows the reference SCNC-estimate corrected by the period-specific (*Ps*) nest decay time (103.7 days), the *dark red diamond* shows the SCNC-estimate corrected by the fixed (*Fi*) nest decay time (95.5 days), the *light red diamond* shows the CTDS-estimate; *vertical lines* show 95% confidence intervals, the *shaded grey area* shows confidence interval of the reference estimate.

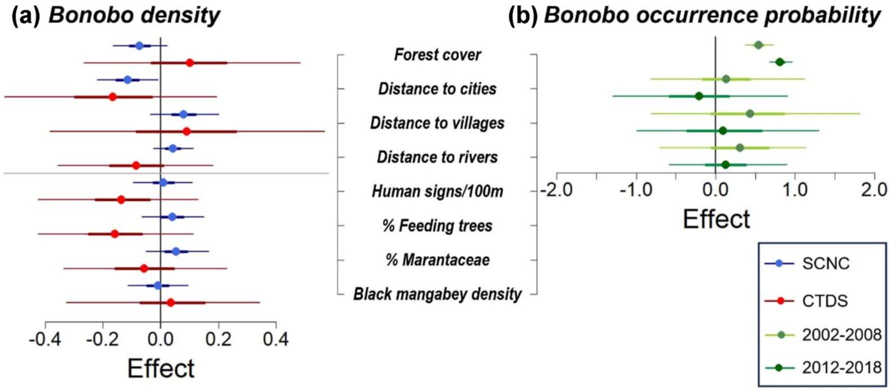

Fig. 5 Effect of drivers on (**a**) bonobo density μ and (**b**) bonobo occurrence probability ψ in in Salonga National Park, Democratic Republic of the Congo. (**a**) Effect on bonobo density (individuals/km^2) by method (standing crop nest counts: *SCNC, blue*; camera trap distance sampling: *CTDS, red*) in 2012–2018; (**b**) effect on bonobo occurrence by period (2002–2008: *light green*; 2012–2018: *dark green*). *Dots* represent the mean, *thick lines* the interquartile range, and *thin lines* the 95% confidence intervals. Explanatory variables 1–4 were included in both analyses (**a** and **b**); 5–8 in density analysis only (**a**).

included an intercept varying by sub-sector and slopes varying by sector and by proximity to a patrol post.

In contrast to our prediction, bonobo nest density (nest counts) was negatively affected ($pd = 0.93$) by the proportion of forest cover; in contrast, bonobo density (camera traps) was unaffected ($pd = 0.70$) (Fig. 5a). However, forest cover was a strong, significant, predictor of bonobo occurrence ψ (*pd* = 1.0) in both periods (Fig. 5b). Instead, bonobo nest density was weakly but positively affected by the proportion of *Marantaceae* understorey vegetation cover (*pd* = 0.83; Fig. 5a). Bonobo density from camera traps, however, was negatively affected by the encounter rate of human signs (*pd* = 0.83; Fig. 5a), whereas bonobo nest density was not (*pd* = 0.58; Fig. 5a). Conversely, we found no indication that the density of black mangabey affected either nest (nest counts) or bonobo (camera traps) density (*pd* = 0.56 and 0.60 respectively).

We found a trend toward higher nest-density when the distance to villages (*pd* = 0.91) and main rivers (*pd* = 0.89) increased (Fig. 5a). However, we found no similar trend in bonobo density from camera traps (*pd* = 0.64 and 0.73 respectively; Fig. 5a) nor bonobo occurrence probability (Fig. 5b) because sub-sectors responded differently (Appendix 3). We found geographical differences (varying by sub-sector) in the effect of proximity to cities on bonobo occurrence (Appendix 3), but bonobo nest density was generally higher closer to cities (*pd* = 0.98; Fig. 5a) and, although less markedly, so was bonobo density obtained from camera traps (*pd* = 0.80; Fig. 5a).

Finally, bonobo occurrence probability was positively influenced by the presence of a patrol post, a proxy of direct protection, in both periods (2002–2008: *pd* = 0.99, 2012–2018: pd = 1.00; Fig. 6a) and so was bonobo mean density (nest counts: *pd* = 0.93, camera traps: *pd* = 0.93; Appendix 3). The presence of a patrol post also influenced the effect of proximity to villages on bonobo occurrence probability (Fig. 6b and c). In the absence of a patrol post, sites further away from villages yielded higher occurrence probabilities, particularly in 2002–2008 (Fig. 6b and c). However, if a patrol post was present, the relationship was inverted in many cases showing higher occurrence probabilities closer to villages (Appendix 3). Interestingly, in 2012–2018, this trend was even more pronounced, particularly in Etate (Fig. 6b and c) where the positive effect of patrol post proximity increased over time (from *pd* = 0.80 to *pd* = 0.94). Exceptions were Iyaelima (*pd* = 0.93) and Mondjoku (*pd* = 0.83) during 2012–2018, as bonobo signs were found closer to villages in the absence of a patrol post (Appendix 3). In the corridor, where hunting is allowed, bonobo signs were consistently found more frequently farther away from villages (*pd* = 1.00; Fig. 6b and c).

Discussion

Based on our estimates, our study suggests that until 2018 a combination of highly suitable habitat, taboos in the local population, presence of law enforcement, and the size of the protected area contributed to maintaining a stable bonobo population in the protected Salonga National Park and its unprotected corridor. The area, equivalent in size to Rwanda and Burundi combined, remains a stronghold for wild bonobos. This finding is in line with assessments confirming improvements in the management and protection of this site (IUCN, 2020) as shown by the site's recent removal from the list of Endangered World Heritage Sites (UNESCO World Heritage Committee, 2021). The bonobo status in Salonga and the corridor contrast with most other great ape population trends that show dramatic declines

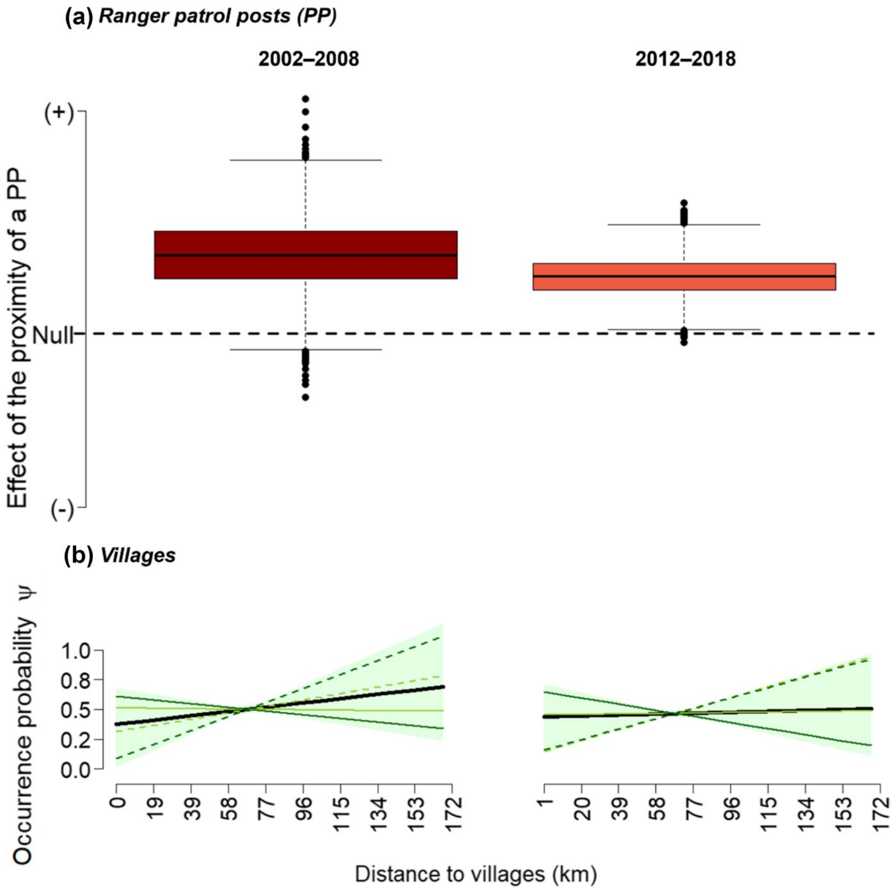

Fig. 6 Bonobo occurrence probability in Salonga National Park, Democratic Republic of the Congo, in relation to proximity to (**a**) ranger patrol posts (PP), and (**b**) villages in 2002–2008 and 2012–2018. (**a**) Effect of patrol post in proximity (15 km) between 2002–2008 (*dark red*) and 2012–2018 (*light red*). *Boxplots* show the second and third quartiles with *horizontal line* being the median; *whiskers* show the first and forth quartiles; *dots* represent outliers. *Dashed zero-line (Null)* represents no effect of proximity to patrol post on bonobo occurrence probability. (**b**) Effect of distance to villages (km) considering the presence (*dark green*) or absence (*light green*) of a patrol post (i.e., interaction between distance to village and proximity to a patrol post). *Dashed lines* show effects in the corridor; *solid lines* in Etate. *Black solid lines* show the main effect, *shaded areas* the 95% confidence interval.

in both protected and non-protected areas (Plumptre *et al.*, 2016; Kühl *et al.*, 2017; Santika *et al.*, 2017; Strindberg *et al.*, 2018). However, although not statistically significant, our results consistently suggest that the bonobo population of Salonga has experienced a decline from 2012 to 2018: a call for vigilance.

Using our results as a case study, we share caveats identified in conventional survey methodology. We provide practical recommendations for future monitoring programmes and insights into the analytical developments needed to improve future bonobo and, more generally, great ape population assessments.

Estimates of Bonobo Population Density and Distribution

By using nest counts and a period-specific nest decay time and accounting for corresponding climate conditions, we estimated the total number of bonobos in Salonga to range between 8,244 and 18,308 mature individuals (Table II). This estimate suggests that Salonga might hold as many bonobos as the minimum global population last estimated by the IUCN Red List assessment (Fruth *et al.*, 2016,) and confirms Salonga as the conservation stronghold of the species. However, our estimates must be considered with caution: the two conversion factors, nest production rate and decomposition time, needed in nest counts distance sampling analyses (used in this study) remain a source of concern when estimating great ape densities, as they affect the reliability of abundance estimates (Aebischer *et al.*, 2017). For example, if the real mean nest decay time was shorter than the applied value, which may be the case in areas located close to the Equator where higher precipitation may have accelerated nest decay time (Morgan *et al.*, 2016), nest counts could have underestimated bonobo density. Conversely, if nest construction rates in Salonga were higher than the value used in our analysis (1.37; Mohneke & Fruth, 2008), nest counts would have overestimated density. For example, the use of a construction rate of 1.92 estimated in Kokolopori (Wessling & Surbeck, 2023) would have returned 71% lower estimates.

Population Trend

When comparing bonobo population between periods (2002–2008 and 2012–2018), the trend indicated a decline, although it was not statistically significant. This result contrasts with the significant declines observed in other great ape populations (Plumptre *et al.*, 2016; Kühl *et al.*, 2017; Santika *et al.*, 2017; Strindberg *et al.*, 2018) and can be viewed as one of the rare positive stories in great ape conservation. Interestingly, however, the tendency for a decline was twice as high when using a period-specific nest decay time (Fig. 3). Given the evidence for climate change impacting nest decay time (Bessone *et al.*, 2021) and the fact that we were not able to account for potential variation in nest construction rates between periods or seasons (Wessling & Surbeck, 2023), interpretation of these results requires caution. Fluctuation in populations is a natural phenomenon due to stochastic effects in rates of birth and death and the occasional impact of severe environmental constraints or epidemic events. We recommend a regular monitoring scheme to continue assessing bonobo population trends across time and to corroborate the finding of this study (Kühl *et al.*, 2008).

Methods Comparison

Population density obtained from camera traps and nest counts differed remarkably in Salonga South block despite a slight overlap of confidence intervals [camera traps: 0.54 (range: 0.24–1.21; Bessone *et al.*, 2020); nest counts: 0.20 bonobo/km^2 (0.14–0.27; this study); Fig. 4]. In Taï National Park, Côte d'Ivoire, the application of camera trap distance sampling also provided higher chimpanzee density estimates than those obtained using nest counts (Boesch *et al.*, 2024). In addition to concerns with conversion factors, nest counts also underestimates ape density possibly because of difficulties in detecting nests in the canopy (Cappelle *et al.*, 2019; Boesch *et al.*, 2024). Conversely, although camera trap distance sampling was found to provide accurate estimates of chimpanzee density (Cappelle *et al.*, 2019), it may also overestimate bonobo mean density if the assumption that animals do not react to the observer (Buckland *et al.*, 2001; Buckland *et al.*, 2015; Cappelle *et al.*, 2021) is violated. Bonobos, however, are reported as being reactive to camera traps (Kalan *et al.*, 2019). There are several ways to discard snapshots to correct for such reactions, yet none seems to be fully satisfactory (Cappelle *et al.*, 2019; Palencia *et al.*, 2021; Houa *et al.*, 2022; Delisle *et al.*, 2023).

Our study shows that, due to diverse sources of bias, different methods can lead to contrasting results. However, we argue that, if sufficient funding is available, the simultaneous use of different survey methods remains the best approach, primarily because it allows us to question the results of the survey and provides the opportunity to better evaluate the status of the species of interest (Kühl *et al.*, 2020). However, if studies are financially constrained, we suggest that camera trap-based methods should be the option of choice. Without relying on conversion factors, they are comparable across sites and periods and require fewer operators and shorter field time (Cappelle *et al.*, 2019). We expect that the fast development of artificial intelligence algorithms automatising data-processing (Norouzzadeh *et al.*, 2021; Whytock *et al.*, 2021; Johanns *et al.*, 2022; Henrich *et al.*, 2024), together with a constant decrease in the price of devices (Piel *et al.*, 2022), would further expand the applicability of these methods in the future. Future studies aiming to use nest counts should invest in independent studies estimating nest construction rate and nest decay time during the period of study (Bessone *et al.*, 2021), and across different seasons (Wessling & Surbeck, 2023). Although these studies would involve high additional costs and, in the case of nest construction, require direct observation of habituated bonobos, they are crucial to ensure valid bonobo density estimates with nest counts.

Drivers of Bonobo Population Density and Distribution

An advantage of our approach is the separate evaluation of the drivers of both bonobo density and distribution. Bonobos form groups of variable size/composition that inhabit home-ranges of different size (Fruth & Hohmann, 2018). Given their fission–fusion social organisation, they range in subgroups of changing size and composition, called parties (Furuichi, 2009). Consequently, nest encounters refer most often to group clusters of varying size (Serckx *et al.*, 2014); this results in typically zero-inflated count data where most transects are devoid of nests while a few transects account for most nest observations. This process is largely a function of stochasticity, as shown by our model selection of φ, where models including covariates were not better than an intercept-only model (Appendix 6). By independently modelling the probability of observing objects on a transect φ, the mean densities μ estimated by our models can also be considered as proxy of bonobo party size (see Methods, Eqs. 4–6).

Our model results reveal that primary forest cover is the most important predictor of bonobo occurrence, confirming previous studies (Reinartz *et al.*, 2008). However, we did not observe the same pattern for nest density, a parameter that is mostly linked to ecological factors, such as food availability. Bonobos build both night- and day-nests in and around food resources. Both the proportion of *Marantaceae* vegetation and of feeding trees turned out to be among the most likely predictors of nest density, as in other studies (Reinartz *et al.*, 2008; Sercks *et al.*, 2016). In contrast, the proportion of forest cover seemed to negatively affect the number of nests observed on transects. Herbaceous vegetation and fruit availability can be higher in heterogeneous areas with lower forest cover, e.g., in patches including swamps (Mulavwa *et al.*, 2010), a pattern that can explain bonobo favouring areas of higher food availability as nesting sites. Alternatively, the result may be a sampling artifact: bonobo nests are harder to see in closed canopy and some may have been missed by observers. The observed discrepancy indicates that forest cover and understorey can vary independently of each other. Therefore, future surveys should consider both factors, including when modelling detection probability in occupancy models and detection function in distance sampling analyses.

Human presence (Reinartz *et al.*, 2008) and proximity to villages (Hickey *et al.*, 2013) have been reported as the most important drivers negatively affecting bonobo density and distribution. We observed an overall positive influence of distance to rivers on bonobo presence. As elsewhere in the Congo basin, large rivers are primary traffic routes into and within Salonga, with proximity to rivers coinciding with the likelihood to encounter humans. Alternatively, as shown in other areas (Terada *et al.*, 2015), this trend might show bonobo preference for nesting sites away from rivers and permanently inundated forest, where trees are usually further apart and possibly not well suited for nest construction. As in other areas (Kühl *et al.*, 2009), we also found that proximity to cities, hubs of the bushmeat trade, negatively affected bonobo occurrence in 2002–2018. However, in 2012–18, when all sub-sectors were included, we obtained more variable results and observed higher bonobo nest densities closer to large towns, possibly because of favourable bonobo habitats, with less inundated forest, being found rather towards the south of Salonga (Grossmann *et al.*, 2008), an area better connected to commercial cities outside the park. Alternatively, as we considered the estimated bonobo mean density as proxy of bonobo party size (see Methods, Eq. 4-6), this unexpected result could also indicate that in proximity to cities, bonobos aggregate in smaller but more cohesive communities, possibly because of higher human presence. For example, in chimpanzees, smaller community sizes are reported to result in higher cohesiveness and reduced fission–fusion dynamics (Lehmann and Boesch 2004), which may explain higher mean bonobo density closer to cities.

We observed an overall positive effect of distance to villages on both bonobo mean nest density (in 2012–2018 only) and occurrence probability. Similarly, bonobo mean density calculated from camera traps was (although weakly) negatively affected by the number of human signs, suggesting smaller party sizes with higher human presence. This positive relation between distance to villages and bonobo occurrence probability was also strong in the Corridor, where hunting of non-protected species is allowed (Fig. 6b and c). However, an exception was bonobo density close to the villages within the park's border, such as to those in the sub-sector Iyaelima (Grossmann *et al.*, 2008). In Iyaelima, eight villages have taboos against bonobo meat consumption (Thompson *et al.*, 2008) and exist next to suitable bonobo habitat. Cultural taboos are a positive driver of great ape abundance in central Africa (Strindberg *et al.*, 2018).

The presence of a patrol post had a positive effect (Fig. 6a) on bonobo occurrence probability; in most sub-sectors, bonobos were more likely to occur close to a village if a patrol post was found within 15 km. In areas such as Etate (Fig. 6a and b) where law enforcement patrols increased in recent years, the effect grew stronger over time. Interestingly, patrol posts did not have this effect when associated with Iyaelima villages (three cases). Thus, in Iyaelima, cultural taboos may protect bonobos regardless of rangers being present. To assess the overall importance of the presence of rangers in and around Salonga, it will be crucial to investigate its impact on species mostly targeted by the wild meat trade, such as ungulates (e.g., duikers) and arboreal primates, and to include patrol effort data in the analyses (Keane *et al.*, 2011).

Finally, the density of black mangabeys did not have an influence on bonobo density. This result occurred because we lacked proxies of drivers of inter-specific competition (such as availability of food targeted by both species); inter-specific competition may have levelled out by shared feeding areas; or mangabeys instead served as bonobo prey (Surbeck & Hohmann 2008). Alternatively, in contrast to our prediction, the absence of a significant effect might be explained by the minor inter-specific competition between the two species or by the food abundance of the forest in our study area that allowed large inter-specific overlap.

Implications and Relevance for Conservation

Based on our results and on the persisting concerns regarding its conservation status (IUCN, 2020), we advocate that Salonga National Park deserves the full attention of national and international conservation agencies. Although not significant, our comparative results point towards a decreasing bonobo population and demand further efforts to preserve Salonga's forests and the cultural heritage of the human population therein. Preservation efforts should include the buffer zone of Salonga, where bonobos may be eradicated more quickly should their habitat continue to be degraded at its current speed (Soliday *et al.*, 2023). This scenario is already a reality in the corridor of Salonga, where bonobos are absent in proximity to villages and where large areas of forest have been replaced by agricultural fields (Ikati *et al.*, 2018).

The factors enabling bonobo stability in Salonga do not exist in many other areas of the species' distribution range, where deforestation and hunting (Fruth *et al.*, 2016), as well as the lack or relaxation of traditional norms against killing of bonobos (Yokotsuka, 2023), pose threats to the viability of bonobo populations. Hence, conservation efforts through the bonobo's entire geographical range are imperative. Because of its limited geographical distribution, the bonobo remains vulnerable to deforestation, occurring at an annual rate of 1 million hectares in DRC (Tyukavina *et al.*, 2018), as well as other abrupt changes within its current range such as human population growth, urbanization, civil unrest, and war (Mitani *et al.*, 2024). In addition, climate change may also have dramatic co nsequences for bonobo survival by severely impacting forest productivity and composition (Bush *et al.*, 2020; Réjou-Méchain *et al.*, 2021). Consequently, preservation of sufficiently large suitable habitat remains the highest priority for the conservation of the bonobo.

Unfortunately, very few new sites have been surveyed since 2015, the latest survey to be included in the last IUCN assessment (Fruth *et al.*, 2016). Of the 156,211 km^2 considered to be suitable bonobo habitat within the bonobo's range (Hickey *et al.* 2013), only approximately 60% have been covered. Therefore, we reiterate calls from bonobo experts that stress the need to obtain data on bonobo occurrence and abundance in unsurveyed areas, those surveyed by scientists long ago, and particularly the non-protected areas (Fruth *et al.*, 2016). Our study adds ~5000 km^2 of bonobo habitat previously unsurveyed by scientists. However, our current data do not allow accurate assessment of a range-wide bonobo conservation status, currently listed as Endangered; the lack of more comprehensive information from areas across the range hinders future efforts aimed at preserving this species.

Our results show how the effects of ecological factors and anthropogenic threats in Salonga emerge depending on the scale and quantity of the investigation (Serckx *et al.*, 2016). To effectively inform conservation strategies aimed at mitigating specific threats, future studies should consider and evaluate the interaction between factors acting at different scales. In addition, our study also highlights the importance of integrating and evaluating different data sources and methodologies to improve population assessments based on heterogenous and often sparse information. Where financial and technical resources are available, the use of genetic sampling (Arandjelovic and Vigilant, 2018) or new methodologies allowing fast, large-scale multi-species investigations such as camera traps (Gilbert *et al.*, 2021) and passive acoustic monitoring devices (Ross *et al.*, 2023) may complement traditional applications, as they are not affected by conversion factors such as nest construction rate (Wessling & Surbeck, 2023) and decay time (Bessone *et al.*, 2021). The development of portable, cost-effective solutions for the analysis of genetic material (Jain *et al.*, 2016) and the progress of AI algorithms to help detect individual animal calls (Piel *et al.*, 2022) or images (Crunchant *et al.*, 2017) relating to individual apes are expected to boost the application of these technologies to great ape population assessments in the future.

However, particularly when resources are limited, integration of data already available is critically important. For example, rangers of the ICCN, the national conservation authority, regularly collect wildlife data during law-enforcement patrols, mainly in areas of different protection status within bonobo range. Joining forces with ICCN, sharing patrol data collected with the Spatial Monitoring and Reporting Tool (SMART), may expand the available information and contribute to long-term bonobo occurrence data across fully and partially protected areas in the country (Keane *et al.*, 2011). Additionally, to understand local ecological knowledge in non-protected areas (Charnley *et al.*, 2007), collaboration with local communities may help us to understand patterns of occurrence (Brittain *et al.*, 2022) and population trends (Kamgaing *et al.*, 2019).

Importantly, the analytical tools able to jointly analyse data deriving from sources as diverse as traditional ground surveys (Zipkin *et al.*, 2017), camera traps (Bowler *et al.*, 2019), acoustic devices (Doser *et al.*, 2020), citizen science (Sun *et al.*, 2019), and interview surveys (Santika *et al.*, 2017) are already available. In case of the bonobo, future modelling efforts should aim to fully accommodate the ecological and observational process generated by nest counts, camera traps, and recce data, extending previous studies (Bowler *et al.*, 2019; Farr *et al.*, 2021). This approach will provide a framework able to integrate all bonobo survey data available throughout the species' geographic range, improve the accuracy and precision of estimates (Schaub & Abadi 2011), and finally provide researchers with the tools needed for a range-wide update of bonobo conservation status (Fruth *et al.*, 2016). The same framework may be applied to other ape and primate species where tools for evidence-based quantitative assessment of species-specific conservation are lacking and hampering effective conservation efforts of primates worldwide (Junker *et al.*, 2020).

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Authors' Contributions M.Be., H.S.K. and B.F. conceived the study; M.Be., I.H., G.H., K.P.N., S.B., V.D., F.G., F.Mai., P.G., J.H., B.In., I.L., M.Mb., G.E.R., S.S., T.S., A.V., H.S.K., and B.F. organized data collection and contributed to data acquisition; P.A., M.Ba., P.B.D.C., M.E., F.G., E.D.B.F., B.B.I., M.D.I., O.I., M.A.K., F.Mal., M.M., S.M., M.Mb., D.B.M., M.N., P.N., P.M.N., J.K.W., and M.L.K.W. collected bonobo data; M.Bo., P.W.B., R.B., M.A.K., J.L.K.K, J.K.K., P.P.M, R.R., and S.M. collected vegetation data; I.B.I., P.K., G.H., J.A.D.M., and B.F. provided facilities and logistical support; M.Be. conducted the statistical analyses; M.Be. processed, analysed the data, and created the figures; M.Be. and B.F. wrote the manuscript with contributions from all co-authors.

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Declarations

Inclusion and Diversity Statement The author list includes contributors from the country (DRC) and location where the research was conducted, who participated in data collection and contributed to the interpretation of the findings.

References

Aebischer, T., Siguindo, G., Rochat, E., Arandjelovic, M., Heilman, A., Hickisch, R., Vigilant, L., Joost, S., & Wegmann, D. (2017). First quantitative survey delineates the distribution of chimpanzees in the Eastern Central African Republic. *Biological Conservation, 213*, 84–94.

Arandjelovic, M., & Vigilant, L. (2018). Non-invasive genetic censusing and monitoring of primate populations. *American Journal of Primatology, 80*(3), e22743.

Beaune, D., Bretagnolle, F., Bollache, L., Bourson, C., Hohmann, G., & Fruth, B. (2013). Ecological services performed by the bonobo (*Pan paniscus*): Seed dispersal effectiveness in tropical forest. *Journal of Tropical Ecology, 29*(5), 367–380.

Bessone, M., Bondjengo, N., Hausmann, A., Herbinger, I., Hohmann, G., Kuehl, H. S., Mbende, M., N'Goran, P. K., Soliday, V., & Fruth, B. (2019). *Inventaire de la biodiversité dans le bloc sud du parc national de la Salonga et développement d'une stratégie de suivi écologique pour améliorer la protection de la faune et de la flore menacées dans le parc. Final report.* ICCN - WWF - MPI - LMU, Berlin, Germany.

Bessone, M., Kuhl, H. S., Hohmann, G., Herbinger, I., N'Goran, K. P., Asanzi, P., Da Costa, P. B., Derozier, V., Fotsing, D. B. E., Ikembelo, B. B., Iyomi, D. M., Iyatshi, B. I., Kafando, P., Kambere, A. M., Moundzoho, B. D., Musubaho, L. K. & Fruth, B. (2023). Assessing the effects of survey-inherent disturbance on primate detectability: Recommendations for line transect distance sampling. *Primates*, *64*(1), 107-121.

Bessone, M., Kühl, H. S., Hohmann, G., Herbinger, I., N'Goran, K. P., Asanzi, P., Da Costa, P. B., Dérozier, V., Fotsing, E. D. B., Ikembelo Beka, B., Iyomi, M. D., Iyatshi, B. I., Musubaho, L. K. W., & Fruth, B. (2020). Drawn out of the shadows: Surveying secretive forest species with camera trap distance sampling. *Journal of Applied Ecology, 57*(5), 963–974.

Bessone, M., Booto, L., Santos, A. R., Kühl, H. S., & Fruth, B. (2021). No time to rest: How the effects of climate change on nest decay threaten the conservation of apes in the wild. *PLoS ONE, 16*(6), e0252527.

Boesch, C., Crunchant, A. S., Diarrasouba, A., Houa, A. N., & Normand, E. (2024). *Suivi des populations animales dans le Parc national de Taï, Côte d'Ivoire par caméra à déclenchement automatique – Phases 1 & 2*. Wild Chimpanzee Foundation.

Bonnin, N., Van Andel, A., Kerby, J., Piel, A., Pintea, L. & Wich, S. (2018). Assessment of chimpanzee nest detectability in drone-acquired images. *Drones*, *2*(2), 17–19.

Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics, I*(2), 377–385.

Bowler, D. E., Nilsen, E. B., Bischof, R., O'Hara, R. B., Yu, T. T., Oo, T., Aung, M., & Linnell, J. D. (2019). Integrating data from different survey types for population monitoring of an endangered species: The case of the Eld's deer. *Scientific Reports, 9*(1), 1–14.

Brittain, S., Rowcliffe, M. J., Kentatchime, F., Tudge, S. J., Kamogne-Tagne, C. T. & Milner-Gulland, E. (2022). Comparing interview methods with camera trap data to inform occupancy models of hunted mammals in forest habitats. *Conservation Science and Practice*, *4*(4), e12637.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling estimating abundance of biological populations*. Oxford University Press.

Buckland, S. T., Rexstad, E. A., Marques, T. A., & Oedekoven, C. S. (2015). *Distance sampling: Methods and applications*. Springer.

Bush, E. R., Whytock, R. C., Bahaa-El-Din, L., Bourgeois, S., Bunnefeld, N., Cardoso, A. W., Dikangadissi, J. T., Dimbonda, P., Dimoto, E., Ndongo, J. E., Jeffrey, K. J., Lehmann, D., Mkaga, L., Momboua, B., Momont, L. W., Tutin, C. E. G., White, L. J. T., Whittaker, A., & Abernethy, K. (2020). Long-term collapse in fruit availability threatens Central African forest megafauna. *Science, 370*(6521), 1219–1222.

Cappelle, N., Després-Einspenner, M. L., Howe, E. J., Boesch, C., & Kühl, H. S. (2019). Validating camera trap distance sampling for chimpanzees. *American Journal of Primatology, 81*(3), e22962.

Cappelle, N., Howe, E. J., Boesch, C., & Kühl, H. S. (2021). Estimating animal abundance and effort–precision relationship with camera trap distance sampling. *Ecosphere, 12*(1), e03299.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software, 76*, 1.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances, 1*(5), e1400253.

Charnley, S., Fischer, A. P., & Jones, E. T. (2007). Integrating traditional and local ecological knowledge into forest biodiversity conservation in the Pacific Northwest. *Forest Ecology and Management, 246*, 14–28.

Crunchant, A.S. (2020). *Acoustically assessing apes: Chimpanzee conservation with passive acoustic monitoring*. PhD thesis, Liverpool John Moores University.

Crunchant, A. S., Egerer, M., Loos, A., Burghardt, T., Zuberbühler, K., Corogenes, K., Leinart, V., Kulik, L., & Kühl, H. S. (2017). Automated face detection for occurrence and occupancy estimation in chimpanzees. *American Journal of Primatology, 79*(3), e22627.

Delisle, Z. J., Henrich, M., Palencia, P., & Swihart, R. K. (2023). Reducing bias in density estimates for unmarked populations that exhibit reactive behaviour towards camera traps. *Methods in Ecology and Evolution, 14*, 3100–3111.

Després-Einspenner, M. L., Howe, E. J., Drapeau, P., & Kühl, H. S. (2017). An empirical evaluation of camera trapping and spatially explicit capture-recapture models for estimating chimpanzee density. *American Journal of Primatology, 79*(7), e22647.

Doser, J. W., Finley, A. O., Weed, A. S., & Zipkin, E. F. (2020). Integrating automated acoustic vocalization data and point count surveys for estimation of bird abundance. *Methods in Ecology and Evolution, 12*(6), 1040–1049.

Dupain, J., Van Krunkelsven, E., Van Elsacker, L., & Verheyen, R. (2000). Current status of the bonobo (Pan paniscus) in the proposed Lomako Reserve (Democratic Republic of Congo). *Biological Conservation, 94*(3), 265–272.

Eriksson, J. (1999). *A Survey of the Forest and a Census of the Bonobo (Pan paniscus) population between the Lomako and Yekokora Rivers in the Equateur Province, DRC*. Master thesis, Uppsala University.

ESRI. (2019). *ArcGIS Desktop*, v. 10.7. Environmental Systems Research Institute, Redlands, CA. https://desktop.arcgis.com/en/arcmap

Exelis Visual Information Solutions. (2020). *ENVI*, v. 5.5.3, Boulder, Colorado. https://www.nv5geospatialsoftware.com/Products/ENVI

Ezeh, A., Kissling, F., & Singer, P. (2020). Why sub-Saharan Africa might exceed its projected population size by 2100. *The Lancet, 396*(10258), 1131–1133.

Fa, J. E., Olivero, J., Farfán, M. Á., Márquez, A. L., Duarte, J., Nackoney, J., Hall, A., Dupain, J., Seymour, S., & Johnson, P. J. (2015). Correlates of bushmeat in markets and depletion of wildlife. *Conservation Biology, 29*(3), 805–815.

Farr, M. T., Green, D. S., Holekamp, K. E., & Zipkin, E. F. (2021). Integrating distance sampling and presence-only data to estimate species abundance. *Ecology, 102*(1), e03204.

Fruth, B., & Hohmann, G. (2018). Food sharing across borders. *Human Nature, 29*(2), 91–103.

Fruth, B., Hickey, J. R., André, C., Furuichi, T., Hart, J., Hart, T., Kuehl, H., Maisels, F., Nackoney, J., Reinartz, G., Sop, T., Thompson, J. & Williamson, E. A. 2016. Pan paniscus. *The IUCN Red List* *of Threatened Species*, e.T15932A102331567. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15932A17964305.en

Fruth, B., Hohmann, G. & McGrew, W.C. (1999). The Pan species. In: P. Dolhinow & A. Fuentes (Eds.). *The Non-Human Primates* (p. 64-72). Mayfield Publishing Company, Mountain View, CA.

Fruth, B., Tagg, N., & Stewart, F. (2018). Sleep and nesting behavior in primates: A review. *American Journal of Physical Anthropology, 166*(3), 499–509.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. *Primates, 50*, 197–209.

Furuichi, T., Idani, G. I., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C., & Kano, T. (1998). Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology, 19*(6), 1029–1043.

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M. & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, *182*(2), 389-402.

Gilbert, N. A., Clare, J. D., Stenglein, J. L., & Zuckerberg, B. (2021). Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology, 35*(1), 88–100.

Grossmann, F., Hart, J. A., Vosper, A., & Ilambu, O. (2008). Range occupation and population estimates of bonobos in the Salonga National Park: Application to large-scale surveys of bonobos in the Democratic Republic of Congo. In T. Furuichi & J. Thompson (Eds.), *The Bonobos: Behavior, Ecology and Conservation* (pp. 189–216). Springer.

Hart, T. (2009). *A new conservation landscape for bonobo: Discovery and conservation of the Tshuapa-Lomami-Lualaba landscape in the Democratic Republic of Congo*. Final Report. Lukuru Wildlife Research Foundation, Inc., U.S. Fish and Wildlife Service, Washington, DC, USA.

Hart, J. A., Grossmann, F., Vosper, A., & Ilanga, J. (2008). Human hunting and its impact on bonobos in the Salonga National Park, Democratic Republic of Congo. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology and conservation* (pp. 245–271). Springer.

Hashimoto, C., Tashiro, Y., Kimura, D., Enomoto, T., Ingmanson, E. J., Idani, G. I., & Furuichi, T. (1998). Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology, 19*(6), 1045–1060.

Heinicke, S., Mundry, R., Boesch, C., Amarasekaran, B., Barrie, A., Brncic, T., Brugière, D., Campbell, G., Carvalho, J., Danquah, E., Dowd, D., Eshuis, H., Fleury-Brugiere, M. C., Gamys, J., Ganas, J., Gatti, S., Ginn, L., Goedmakers, A., Granier, N., ..., & Kuehl, H. (2019). Advancing conservation planning for western chimpanzees using IUCN SSC APES—the case of a taxon-specific database. *Environmental Research Letters*, *14*(6), 064001.

Henrich, M., Burgueño, M., Hoyer, J., Haucke, T., Steinhage, V., Kühl, H. S., & Heurich, M. (2024). A semi-automated camera trap distance sampling approach for population density estimation. *Remote Sensing in Ecology and Conservation, 10*(2), 156–171.

Hickey, J. R., Nackoney, J., Nibbelink, N. P., Blake, S., Bonyenge, A., Coxe, S., Dupain, J., Emetshu, M., Furuichi, T., & Grossmann, F. (2013). Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. *Biodiversity and Conservation, 22*(13–14), 3085–3104.

Hohmann, G., & Fruth, B. (2003). Lui Kotal: A new site for field research on bonobos in the Salonga National Park. *Pan Africa News, 10*(2), 25–27.

Hohmann, G., Fowler, A., Sommer, V., & Ortmann, S. (2012). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: The influence of abundance and nutritional quality of fruit. *Feeding Ecology in Apes and Other Primates, 48*, 123.

Houa, N. A., Cappelle, N., Bitty, E. A., Normand, E., Kablan, Y. A., & Boesch, C. (2022). Animal reactivity to camera traps and its effects on abundance estimate using distance sampling in the Taï National Park, Côte d'Ivoire. *PeerJ, 10*, e13510.

Howe, E. J., Buckland, S. T., Després-Einspenner, M. L., & Kühl, H. S. (2017). Distance sampling with camera traps. *Methods in Ecology and Evolution, 8*(11), 1558–1565.

Ikati, B., Itamba, O., Wilondja, B., Iyondo, J. R., Naky, P., & Maisels, F. (2018). *Inventaire des grandes mammifères et impact humain réalisé dans le Corridor du Parc National de la Salonga*. Kinshasa Wildlife Conservation Society.

Ilambu, O. (2006). *Analyse spatiale de la distribution des Postes de Surveillance au Parc National de la Salonga*. Unpublished report.

Inogwabini, B.-I., Bewa, M., Longwango, M., Abokome, M., & Vuvu, M. (2008). The bonobos of the Lake Tumba-Lake Maindombe hinterland: Threats and opportunities for population conservation. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology and conservation* (pp. 273–290). Springer.

IUCN. (2020). *Salonga National Park - 2020 Conservation Outlook Assessment*. IUCN World Heritage Outlook. https://worldheritageoutlook.iucn.org.

IUCN (2024). *The IUCN Red List of Threatened Species*. Version 2020-1. https://www.iucnredlist.org.

Jain, M., Olsen, H. E., Paten, B., & Akeson, M. (2016). The Oxford Nanopore MinION : Delivery of nanopore sequencing to the genomics community. *Genome Biology, 17*, 239.

Johanns, P., Haucke, T., & Steinhage, V. (2022). Automated distance estimation for wildlife camera trapping. *Ecological Informatics, 70*, 101734.

Junker, J., Petrovan, S.O., Arroyo-RodrÍguez, V., Boonratana, R., Byler, D., Chapman, C.A., Chetry, D., Cheyne, S.M., Cornejo, F.M., Cortés-Ortiz, L., Cowlishaw, G., Christie, A.P., Crockford, C., Torre, Stella De L., De Melo, F.R., Fan, P., Grueter, C.C., Guzman-Caro, D.C., Heymann, E.W., …, & Kühl, H.S. (2020). A severe lack of evidence limits effective conservation of the world's primates. *Bioscience*, *70* (9), 794–803.

Kalan, A.K., Hohmann, G., Arandjelovic, M., Boesch, C., McCarthy, M.S., Agbor, A., Angedakin, S., Bailey, E., Balongelwa, C.W., Bessone, M., Bocksberger, G., Coxe, S., Deschner, T., Déspres-Einspenner, M.L., Dieguez, P., Fruth, B., Herbinger, I., Granjon, A.C., Head, J., …, & Kühl, H.S. (2019). Novelty response of wild African apes to camera traps. *Current Biology*, *29*(7), 1211–1217.

Kamgaing, T. O. W., Dzefack, Z. s. C. B. & Yasuoka, H. (2019). Declining ungulate populations in an African rainforest: Evidence from local knowledge, ecological surveys, and bushmeat records. *Frontiers in Ecology and Evolution*, *7*, 249.

Kano, T. (1984). Distribution of pygmy chimpanzees (*Pan paniscus*) in the central Zaire basin. *Folia Primatologica, 43*(1), 36–52.

Karanth, K. U., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology, 79*(8), 2852–2862.

Keane, A., Jones, J. P., & Milner-Gulland, E. (2011). Encounter data in resource management and ecology: Pitfalls and possibilities. *Journal of Applied Ecology, 48*(5), 1164–1173.

Kidney, D., Rawson, B. M., Borchers, D. L., Stevenson, B. C., Marques, T. A., & Thomas, L. (2016). An efficient acoustic density estimation method with human detectors applied to gibbons in Cambodia. *PLoS ONE, 11*(5), 1–16.

Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. (2013). *Mammals of Africa*. A&C Black.

Kühl, H. S., Maisels, F., Ancrenaz, M., & Williamson, E. A. (2008). *Best practice guidelines for the surveys and monitoring of great ape populations* (p. 32). IUCN SSC Primate Specialist Group (PSG).

Kühl, H. S., Nzeingui, C., Yeno, S. L. D., Huijbregts, B., Boesch, C., & Walsh, P. D. (2009). Discriminating between village and commercial hunting of apes. *Biological Conservation, 142*(7), 1500–1506.

Kühl, H. S., Sop, T., Williamson, E. A., Mundry, R., Brugière, D., Campbell, G., Cohen, H., Danquah, E., Ginn, L., Herbinger, I., Jones, S., Junker, J., Kormos, R., Kouakou, C. Y., N'Goran, P. K., Normand, Emma, Shutt-Phillips, K., Tickle, A., Vendras, E., … Boesch, C. (2017). The Critically Endangered western chimpanzee declines by 80%. *American Journal of Primatology, 79*(9), e22681.

Kühl, H. S., Bowler, D. E., Bösch, L., Bruelheide, H., Dauber, J., Eichenberg, D., Eisenhauer, N., Fernández, N., Guerra, C. A., & Henle, K. (2020). Effective biodiversity monitoring needs a culture of integration. *One Earth, 3*(4), 462–474.

Lehmann, J., & Boesch, C. (2004). To fission or to fusion: Effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology, 56*, 207–216.

Lemoine, N. P. (2019). Moving beyond noninformative priors: Why and how to choose weakly informative priors in Bayesian analyses. *Oikos, 128*(7), 912–928.

Maisels, F., Nkumu, P., & Bonyenge, A. (2009). *Salonga National Park, DRC, Terrestrial wildlife and human impact monitoring programme. Survey report - Salonga Corridor*. Kinshasa Wildlife Conservation Society.

Maisels, F., Nkumu, P., & Bonyenge, A. (2010). *Salonga National Park, DRC, Terrestrial wildlife and human impact monitoring programme. Survey report — Eastern sector of Park*. Kinshasa Wildlife Conservation Society.

Makowski, D., Ben-Shachar, M. S., Chen, S. A., & Lüdecke, D. (2019). Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology, 10*, 2767.

Malenky, R. K., Kuroda, S., & Ono, E. (1996). The significance of terrestrial herbaceous foods for bonobos. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee Cultures* (pp. 59–76). Harvard University Press.

McElreath, R. (2021). *Statistical rethinking: A Bayesian course with examples in R and Stan*. CRC Press.

McLester, E. (2022). Golden-bellied mangabeys (*Cercocebus chrysogaster*) consume and share mammalian prey at LuiKotale, Democratic Republic of the Congo. *Journal of Tropical Ecology, 38*, 254–258.

Mitani, J. C., Abwe, E., Campbell, G., Giles-Vernick, T., Goldberg, T., McLennan, M. R., Preuschoft, S., Supriatna, J., & Marshall, A. J. (2024). Future coexistence with great apes will require major changes to policy and practice. *Nature Human Behaviour, 8*(4), 632–643. https://doi.org/10.1038/s41562-024-01830-x

Mohneke, M., & Fruth, B. (2008). Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, Democratic Republic of Congo: Common methodology revisited. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology and conservation* (pp. 151–166). Springer.

Morgan, D., Sanz, C., Ononónga, J. R., & Strindberg, S. (2016). Factors influencing the survival of sympatric gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes troglodytes*) nests. *International Journal of Primatology, 37*(6), 718–737.

Moussy, C., Burfield, I. J., Stephenson, P., Newton, A. F., Butchart, S. H., Sutherland, W. J., Gregory, R. D., McRae, L., Bubb, P., & Roesler, I. (2021). A quantitative global review of species population monitoring. *Conservation Biology, 36*(1), e13721.

Mulavwa, M., Furuichi, T., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G. I., Ihobe, H., Hashimoto, C., Tashiro, Y., & Mwanza, N. (2008). Seasonal changes in fruit production and party size of bonobos at Wamba. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology and conservation* (pp. 121–134). Springer.

Mulavwa, M. N., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Mwanza, N. N., & Furuichi, T. (2010). Nest groups of wild bonobos at Wamba: Selection of vegetation and tree species and relationships between nest group size and party size. *American Journal of Primatology, 72*(7), 575–586.

N'Goran, P. K., Kuehl, H., Hohmann, G., Fruth, B., Herbinger, I. & Mbende, M. (2016). *Biomonitoring dans le Bloc Sud du Parc national de la Salonga, RDC. Protocole general de collecte de donnees sur les mammiferes*. ICCN - WWF - MPI - LMU, Berlin, Germany

Nakashima, Y., Fukasawa, K., & Samejima, H. (2018). Estimating animal density without individual recognition using information derivable exclusively from camera traps. *Journal of Applied Ecology, 55*(2), 735–744.

Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. *Trends in Ecology & Evolution, 21*(12), 668–673.

Norouzzadeh, M. S., Morris, D., Beery, S., Joshi, N., Jojic, N., & Clune, J. (2021). A deep active learning system for species identification and counting in camera trap images. *Methods in Ecology and Evolution, 12*(1), 150–161.

Oberauer, K. (2022). The importance of random slopes in mixed models for Bayesian hypothesis testing. *Psychological Science, 33*(4), 648–665.

Palencia, P., Rowcliffe, M. J., Vicente, J., & Acevedo, P. (2021). Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology, 58*(8), 1583–1592.

Piel, A. K., Crunchant, A., Knot, I. E., Chalmers, C., Fergus, P., Mulero-Pázmány, M., & Wich, S. A. (2022). Noninvasive technologies for primate conservation in the 21st century. *International Journal of Primatology, 43*(1), 133–167.

Pennec, F., Gérard, C., Meterreau, L., Monghiemo, C., Ngawolo, J. C. B., Laurent, R., & Narat, V. (2020). Spatiotemporal variation in bonobo (*Pan paniscus*) habitat use in a forest–savanna mosaic. *International Journal of Primatology, 41*(4), 1–25.

Plumptre, A. J., & Cox, D. (2006). Counting primates for conservation: Primate surveys in Uganda. *Primates, 47*(1), 65–73.

Plumptre, A. J., Nixon, S., Kujirakwinja, D. K., Vieilledent, G., Critchlow, R., Williamson, E. A., Kirkby, A. E., & Hall, J. S. (2016). Catastrophic decline of world's largest primate: 80% loss of Grauer's Gorilla (*Gorilla beringei graueri*) population justifies critically endangered status. *PLoS ONE, 11*(10), e0162697.

QGis Development Team. (2020). *QGIS geographic information system —Open source geospatial foundation project*. http://qgis.osgeo.org

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Version 4.0.5, http://www.r-project.org/

Réjou-Méchain, M., Mortier, F., Bastin, J.-F., Cornu, G., Barbier, N., Bayol, N., Bénédet, F., Bry, X., Dauby, G., Debaluwe, V., Doucet, J. L., Doumenge, C., Fayolle, A., Garcia, C., Kibmbe Lubamba, J. P., Loumeto, J. J., Ngomanda, A., Ploton, P., Sonkeé, B., … Gourlet-Fleury, S. (2021). Unveiling African rainforest composition and vulnerability to global change. *Nature, 593*(7857), 90–94.

Reinartz, G. E., Isia, I. B., Ngamankosi, M., & Wema, L. W. (2006). Effects of forest type and human presence on bonobo (*Pan paniscus*) density in the Salonga National Park. *International Journal of Primatology, 27*(2), 603–634.

Reinartz, G. E., Guislain, P., Bolinga, T. M., Isomana, E., Inogwabini, B. I., Bokomo, N., Ngamankosi, M., & Wema, L. W. (2008). Ecological factors influencing bonobo density and distribution in the Salonga National Park: Applications for population assessment. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology and conservation* (pp. 167–188). Springer.

Ross, S. R. J., O'Connell, D. P., Deichmann, J. L., Desjonquères, C., Gasc, A., Phillips, J. N., Sethi, S. S., Wood, C. M., & Burivalova, Z. (2023). Passive acoustic monitoring provides a fresh perspective on fundamental ecological questions. *Functional Ecology, 37*(4), 959–975.

Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology, 45*, 1228–1236.

Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics, 60*(1), 108–115.

Santika, T., Ancrenaz, M., Wilson, K. A., Spehar, S., Abram, N., Banes, G. L., Campbell-Smith, G., Curran, L., d'Arcy, L., & Delgado, R. A., Erman, A., Goossens, B., Hertanto, H., Houghton, M., Husson, S. J., Kuehl, H., Lackman, I., Leiman, A., Llano Sanchez, K., …, & Meijaard, E. (2017). First integrative trend analysis for a great ape species in Borneo. *Scientific Reports*, *7*(1), 4839.

Schaub, M., & Abadi, F. (2011). Integrated population models: A novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology, 152*(1), 227–237.

Serckx, A. (2014). *Eco-ethology of a population of bonobos (Pan paniscus) living in the western forest–savannah mosaics of the Democratic Republic of Congo*. Université de Liège.

Serckx, A., Huynen, M. C., Beudels-Jamar, R. C., Vimond, M., & Kühl, H. S. (2016). Bonobo nest site selection and the importance of predictor scales in primate ecology. *American Journal of Primatology, 78*(12), 1326–1343.

Sharma, K., Fiechter, M., George, T., Young, J., Alexander, J. S., Bijoor, A., Suryawanshi, K., & Mishra, C. (2020). Conservation and people: Towards an ethical code of conduct for the use of camera traps in wildlife research. *Ecological Solutions and Evidence, 1*(2), e12033.

Soliday, V., Louat, A., Miezi, E., & Fruth, B. (2023). Investigating the impact of a long-term research and conservation project on the expansion of land use and land cover in a remote area of central DRC. *Trees, Forests and People, 11*, 100368.

Sollmann, R., Gardner, B., Chandler, R. B., Royle, J. A., & Sillett, T. S. (2015). An open-population hierarchical distance sampling model. *Ecology, 96*(2), 325–331.

Spehar, S. N., Loken, B., Rayadin, Y., & Royle, J. A. (2015). Comparing spatial capture–recapture modeling and nest count methods to estimate orangutan densities in the Wehea Forest, East Kalimantan, Indonesia. *Biological Conservation, 191*, 185–193.

Stan Development Team. (2020). *RStan: The R interface to Stan*. R package version 2.21.2. https://mc-stan.org/

Strindberg, S., Maisels, F., Williamson, E. A., Blake, S., Stokes, E. J., Aba'a, R., Abitsi, G., Agbor, A., Ambahe, R. D., Bakabana, P. C., Bechem, M., Berlemont, A., Bokoko de Semboli, B., Boundja, P. R., Bout, N., Breuer, T., Campbell, G., De Wachter, P., Akou, M. E., ..., & Wilkie, D. (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Science Advances*, *4*(4), eaar2964.

Sun, C. C., Fuller, A. K., & Royle, J. A. (2019). Incorporating citizen science data in spatially explicit integrated population models. *Ecology, 100*(9), e02777.

Surbeck, M., & Hohmann, G. (2008). Primate hunting by bonobos at LuiKotale, Salonga National Park. *Current Biology, 18*(19), R906–R907.

Surbeck, M., Coxe, S., & Lokasola, A. L. (2017). Lonoa: The establishment of a permanent field site for behavioural research on bonobos in the Kokolopori Bonobo Reserve. *Pan Africa News, 24*(2), 13–15.

Terada, S., Nackoney, J., Sakamaki, T., Mulavwa, M. N., Yumoto, T., & Furuichi, T. (2015). Habitat use of bonobos (*Pan paniscus*) at Wamba: Selection of vegetation types for ranging, feeding, and night-sleeping. *American Journal of Primatology, 77*(6), 701–713.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R., Marques, T. A., & Burnham, K. P. (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology, 47*(1), 5–14.

Thompson, J. M., Nestor, L. M., & Kabanda, R. B. (2008). Traditional land-use practices for bonobo conservation. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology and conservation* (pp. 227–244). Springer.

Tutin, C. E., & Fernandez, M. (1984). Nationwide census of gorilla (Gorilla g. gorilla) and chimpanzee (Pan t. troglodytes) populations in Gabon. *American Journal of Primatology, 6*(4), 313–336.

Tyukavina, A., Hansen, M. C., Potapov, P., Parker, D., Okpa, C., Stehman, S. V., Kommareddy, I. & Turubanova, S. (2018). Congo Basin forest loss dominated by increasing smallholder clearing. *Science Advances*, 4(11), eaat2993.

UNESCO World Heritage Committee. (2021). *Decisions adopted during the extended 44th session of the World Heritage Committee (WHC/21/44.COM/18).* Fuzhou (China)/Online meeting, 16–31 July 2021. https://unesdoc.unesco.org/ark:/48223/pf0000379267

Van Krunkelsven, E. (2001). Density estimation of bonobos (*Pan paniscus*) in Salonga National Park, Congo. *Biological Conservation*, *99*(3), 387-391.

Vehtari, A., Gelman, A. & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*(5), 1413-1432.

Walsh, P. D., Abernethy, K. A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M. E., Huijbregts, B., Mambounga, D. I., Toham, A. K., & Kilbourn, A. M. (2003). Catastrophic ape decline in western equatorial Africa. *Nature, 422*(6932), 611.

Wessling, E. G., & Surbeck, M. (2023). Failure to account for behavioral variability significantly compromises accuracy in indirect population monitoring. *Animal Conservation, 26*(4), 558–572.

White, F. J. (1998). Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *International Journal of Primatology*, *19*(6), 1013-1027.

Whytock, R. C., Świeżewski, J., Zwerts, J. A., Bara-Słupski, T., Pambo, A. F. K., Rogala, M., Bahaa-eldin, L., Boekee, K., Brittain, S., Cardoso, A. W., Henschel, P., Lehmann, D., Momboua, B., Opepa, C. K., Orbell, C., Pitman, R. T., Robinson, H. S., & Abernethy, K. A. (2021). Robust ecological analysis of camera trap data labelled by a machine learning model. *Methods in Ecology and Evolution, 12*(6), 1080–1092.

Wich, S., Dellatore, D., Houghton, M., Ardi, R. & Koh, L. P. (2015). A preliminary assessment of using conservation drones for Sumatran orang-utan (*Pongo abelii*) distribution and density. *Journal of Unmanned Vehicle Systems*, *4*(1), 45-52.

Wich, S. A., Singleton, I., Nowak, M. G., Atmoko, S. S. U., Nisam, G., Arif, S. M., Putra, R. H., Ardi, R., Fredriksson, G., & Usher, G. (2016). Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Science Advances, 2*(3), e1500789.

WorldPop. (2024). *Africa continental population datasets (2000–2020) version 2.0*. https://hub.worldpop.org/geodata/summary?id=139

Yokotsuka, A. (2023). Taboo against eating bonobos and its degradation. In T. Furuichi, G. Idani, D. Kimura, H. Ihobe, & C. Hashimoto (Eds.), *Bonobos and people at Wamba: 50 years of research* (pp. 419–442). Springer.

Zipkin, E. F., Rossman, S., Yackulic, C. B., Wiens, J. D., Thorson, J. T., Davis, R. J., & Grant, E. H. C. (2017). Integrating count and detection–nondetection data to model population dynamics. *Ecology, 98*(6), 1640–1650.

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