Assessing the conservation status of the bonobo (*Pan paniscus*): results from Salonga National Park (DRC), and suggestions for a range-wide approach towards a new action plan

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Photo: Barbara Fruth© LuiKotale Bonobo Project

To my father

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ABSTRACT

All great ape species and subspecies are currently classified as endangered or critically endangered in the IUCN Red List, with wild populations declining at unprecedented rates. Among them, the bonobo (*Pan paniscus*) is perhaps the least known. With only 30% of its geographical range having been surveyed, the data needed for assessing its status and trend were lacking until 2016, preventing an update of its conservation status.

Here, I investigated novel and traditional field methods for the assessment of bonobo populations, using data acquired in Salonga National Park (SNP), Democratic Republic of the Congo (DRC). First, I used 16,700 camera-trap videos to apply camera-trap distance sampling (CTDS), a recent method for estimating population density, to the bonobo and 13 other species. Second, I analysed 1,511 bonobo nests and 15 years of climatic data (2003–2018), to investigate factors involved in nest decay, evaluating the effects of inaccurate nest decay times on density estimates via traditional nest counts. Finally, I integrated datasets from 13 different surveys in SNP conducted over two time periods (2002-2008; 2012-2018) including detection/non-detection, count data and CTDS to estimate bonobo status and trend, using specifically calculated nest decay times.

I showed that CTDS was an excellent method providing wildlife density and abundance, particularly important for threatened species, and highlighted issues in the application to different species, with reactivity to the cameras being the main source of bias for the bonobo. I found that decreasing precipitation triggered longer decay times of bonobo nests in SNP, with the number of storms being the main factor driving nest decay although a behavioural adaptation with bonobos strengthening nest structure in response to harsh precipitation. In addition, I showed that failure to account for nest-specific biotic and abiotic conditions, would lead to bonobo estimates biased up to 60%. Finally, I showed that an integrated analysis helped mitigating biases peculiar to specific survey methods, revealing an important, stable bonobo population in SNP. Here, a pristine habitat and the presence of rangers exerted a positive effect on bonobo abundance, as did ancestral taboos.

The results of this thesis showed that new methodologies like CTDS, providing density estimates without the need of conversion factors, retain high potential for future population monitoring and conservation. Nevertheless, with necessary

precautions such as application of time specific decay rates, implementation of traditional methods still provides accurate assessment of status and trend. The methods and recommendations described here are meant to serve as basis for a range-wide assessment, informing the new bonobo conservation strategy due in 2022.

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DECLARATION

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

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LIST OF ABBREVIATIONS, TABLES AND FIGURES

List of abbreviations

A	Species specific Availability	**MIKE**	Monitoring the Illegal Killing of Elephants
ACa	Species-specific Availability following Cappelle et al. (2019)	**MNC**	Marked Nest Counts
AIR	Active Infrared Sensor	**MS**	Mark-reSight methods
ARo	Species-specific Availability following Rowcliffe et al. (2014)	**MYA**	Million Years Ago
BFT	Bonobo Feeding Trees	***N***	Abundance, i.e number of individuals
CR	Capture-Recapture models	**NA**	Not Available
CT(s)	Camera Trap(s)	**PAM**	Passive Acoustic Monitoring
CTDS	Camera Trap Distance Sampling	**PIR**	Passive Infrared Sensor
CI	Confidence Interval	**PP**	Ranger Patrol Post
CV	Coefficient of Variation	**PSIS**	Pareto Smoothed Importance Sampling
D	Density, i.e. individuals / km^2	**Recce**	Reconnaissance walks
DBH	Diameter at Breast Height	**REM**	Random Encounter model
DRC	Democratic Republic of the Congo	**REST**	Random Encounter and Staying model
DS	Distance Sampling	**ROR**	Relative Occurrence Rate
ELPD	Expected Log Predictive Density	**SCNC**	Standing Crop Nest Counts
GAM	Generalized Additive Model	**SDM(s)**	Species Distribution Model(s)
GIS	Geographic Information System	**SD**	Standard Deviation
GLM	Generalized Linear Model	**SE**	Standard Error
GPS	Geographic Positioning System	**SECR**	Spatially Explicit Capture Recapture models
iCAR	Intrinsic Auto-Regressive Component	**SNP**	Salonga National Park
ICCN	Institut Congolais pour la Conservation de la Nature	**STE**	Space to Event model
IPM(s)	Integrated Population Model(s)	**THV**	Terrestrial Herbaceous Vegetation
IS	Instantaneous Sampling	**TTE**	Time to Event model
IUCN	International Union for the Conservation of Nature	**uSECR**	Unmarked Spatially Explicit Capture Recapture model
LOOIC	Leave One Out Information Criterion	**WWF**	World Wide Fund
LTDS	Line Transect Distance Sampling	**ZSM**	Zoological Society Milwaukee

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CHAPTER 1

General introduction

1.1. Background

Since the industrial revolution, 200 years ago, the world human population has grown exponentially triggering a dramatic increase in the demand for natural resources such as food, energy, and space. Humans' pressure on the environment is now overwhelming natural processes, leading to environmental changes at multiple levels (Zalasiewicz et al., 2010). Never in the course of history, has a single species so profoundly influenced Earth's geology, atmosphere, and life forms (Crutzen, 2006; Steffen, Crutzen and McNeill, 2007).

One of the most pernicious effects of human activities on the planet is its impact on biodiversity, with species' extinction rates reported being 100 to 1000 times higher than the background rates estimated before the appearance of *Homo sapiens* on the planet (Ceballos et al., 2015). Although human activities also impact the biodiversity of vascular plants (Ellis, Antill and Kreft, 2012; Humphreys et al., 2019; López-Rojo et al., 2019), the animal kingdom is particularly affected: insects (Dunn, 2005; Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; van Klink et al., 2020); fish (Briggs, 2011; McCauley et al., 2015); amphibians (McCallum, 2007; Wake and Vredenburg, 2008); reptiles (Gibbons et al., 2000; Böhm et al., 2013); birds (Sanderson et al., 2006; Monroe et al., 2019) and both land and marine mammals (Ceballos and Ehrlich, 2002; Cardillo et al., 2005; Turvey et al., 2007; Ripple et al., 2015; Jaramillo-Legorreta et al., 2019), are threatened worldwide.

In addition, the geographical range of many species is also contracting as a result of human encroachment, and so are their population sizes i.e., their number in the wild (IUCN, 2020a). This is leading to an anthropogenic-induced global defaunation (Dirzo et al., 2014), with 30% of the living terrestrial vertebrate being in danger of extinction (IUCN, 2020a) and population sizes declining by 28% on average over the past 40 years (Dirzo et al., 2014). Large bodied species are reported being particularly affected, mainly as a result of 1) active selection by human hunters since the late Pleistocene (Sandom et al., 2014) to present days (Ripple et al., 2019), 2) slow reproduction rate and 3) big home range size (Cardillo et al., 2005; Karanth et al., 2010; Dirzo et al., 2014). Notorious examples are elephants (Blake et al., 2007; Maisels et al., 2013; Wittemyer et al., 2014), rhinoceros (Zafir et al., 2011; Brook et al., 2014) and big felids (Black et al., 2013; Henschel et al., 2014; Bauer et al., 2015; Brugière, Chardonnet and Scholte, 2015), but also marine mammals such as whales, dolphins and porpoises (Turvey et al., 2007; Pennisi, 2017; Jaramillo-Legorreta et al., 2019).

Similarly, also the great apes (Figure 5.1), belonging to our family, the *Hominidae,* are declining across their geographical range (Junker et al., 2012; Carvalho et al., 2021). Orangutans (*Pongo abelii* and *P. pygmaeus subspp.* and *P. tapanulii*), gorillas (*Gorilla gorilla subspp.* and *G. beringei subssp.*), bonobos (*Pan paniscus*) and chimpanzees *(P. troglodytes subspp.*) are large, slow reproducing species, inhabiting large home ranges in areas where human populations, and by that human activity are increasing steadily (Jāhāna, 2016). Several species and subspecies showed catastrophic population declines and local extinction, recent examples being the Sumatran (*P. abelii*) (Wich et al., 2016) and Bornean Orangutan (*P. pygmaeus*) (Santika et al., 2017), the Western chimpanzee (*P. t. verus*) (Kühl et al., 2017) and the Grauer's gorilla (*G. b. graueri*) (Plumptre et al., 2016). As a result, all 14 great ape species and subspecies are presently threatened and classified as Endangered or Critically Endangered in the Red List of Threatened Species issued by the International Union for the Conservation of Nature (IUCN, 2020a) (Table 1.1). The principal causes for this trend are strictly anthropogenic, with human borne infectious disease (Köndgen et al., 2008; Inogwabini and Leader-Williams, 2012; Dunay et al., 2018; Strindberg et al., 2018), habitat destruction (Junker et al., 2012; Wich et al., 2016; Voigt et al., 2018) and illegal hunting (Walsh et al., 2003; Hart et al., 2008; Kühl et al., 2009; N'goran et al., 2012; Strindberg et al., 2018) as major drivers. Importantly, a recent study on chimpanzees has demonstrated that not only does human activity negatively affects apes' population dynamics, but it also reduces their behavioural diversity. By that, part of the apes' behavioural and cultural repertoire is at risks to disappear, even before we could know its entire diversity (Kuehl et al., 2019).

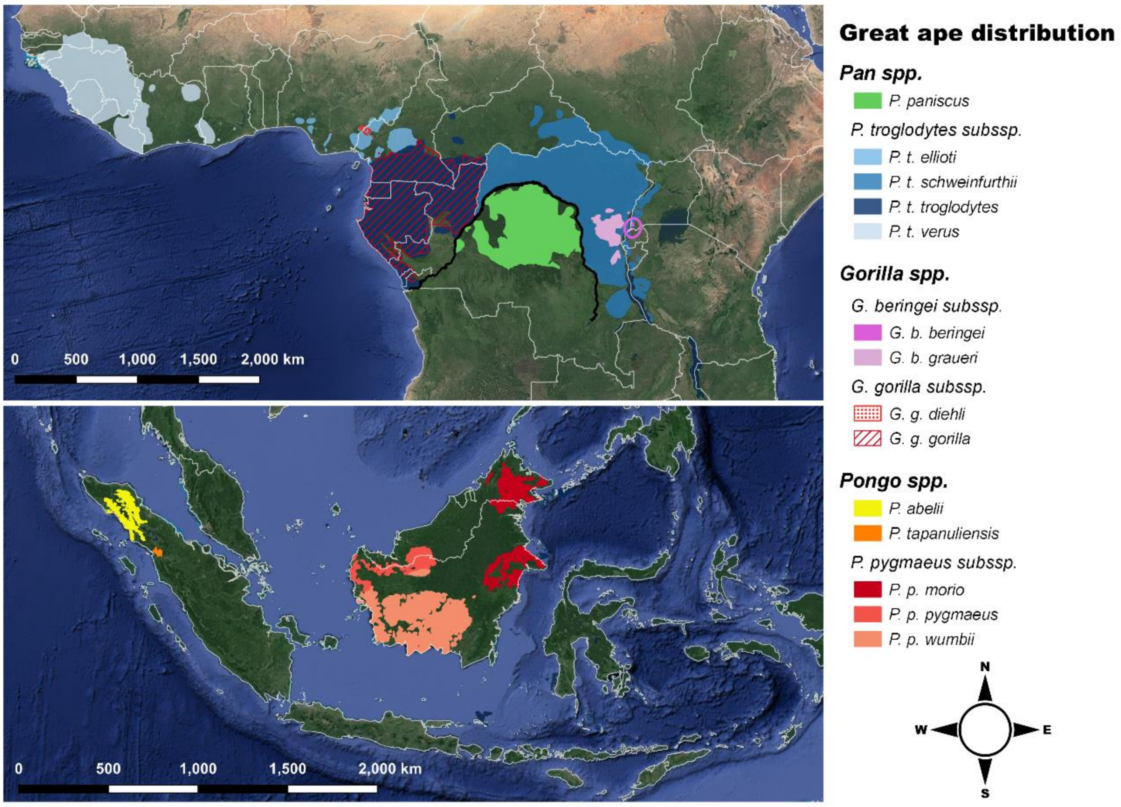
Given their current status, the remnants of great ape populations require immediate action and effective conservation strategies. Being flagship species, umbrella species and environmental indicator species, their conservation is of pivotal importance. In fact, by protecting great apes, also their habitat and the animal communities therein can be equally protected (Chapman et al., 2020). In addition, since the times of Charles Darwin (1809 - 1892) and Thomas H. Huxley (1825 - 1895), great apes, and particularly African apes, have been used as model species for the study of human evolutionary history (Darwin 1871; Huxley, 1863). In fact, the *Homo* lineage split from gorillas about 15.1 million years ago, and from the genus *Pan* (including chimpanzees and bonobo) as recently as 12.1 million years ago, according to the latest estimates (Moorjani et al., 2016), with chimpanzees and bonobos sharing 98% of their genome with us humans (Prüfer et al., 2012). Despite the close relatedness, with bonobo and chimpanzee having separated less than 1 million years ago (Won and Hey, 2005), these great apes show a remarkable diversity in their social structure and astonishing behavioural flexibility. By that, the study of living great apes allows us to glimpse into the origins of our species by evaluating great apes' plasticity in responding to environmental constraints with their subsequent evolutionary outcomes (Hockings et al., 2015). Therefore, not only would their disappearance be catastrophic from the point of view of their place in the planet's biodiversity, but also from an ethical and scientific perspective, depriving the world of our closest relatives and precluding our chances to understand the evolutionary history of our species (Wrangham, 1987; McGrew, 1992).

Table 1.1. Current conservation status of great apes' living species and sub-species. "Status": specific conservation status according to IUCN (2020): "EN" (Endangered); "CR" (Critically endangered).

Genus	Species	Subspecies	Common name	Status
Pan	*paniscus*		Bonobo	EN
	troglodytes	*verus*	Western chimpanzee	CR
		eliottii	Nigeria-Cameroon chimpanzee	EN
		troglodytes	Central chimpanzee	EN
		schweinfurthii	Eastern chimpanzee	EN
Gorilla	*gorilla*	*gorilla*	Western lowland gorilla	EN
		diehli	Cross River gorilla	CR
	beringei	*beringei*	Mountain gorilla	EN
		graueri	Eastern lowland gorilla	CR
Pongo	*abelii*		Sumatran orangutan	CR
	pygmaeus	*pygmaeus*	Northwest Bornean orangutan	CR
		morio	Northeast Bornean orangutan	CR
		wurmbii	Southwest Bornean orangutan	CR
	tapanuliensis		Tapanuli orangutan	CR

To protect great apes' remnant populations (Figure 1.1), we need to know their status in the wild, and particularly their 1) distribution across their geographical range, i.e. presence / absence; 2) relative abundance or density, i.e. number of individuals within a specified area at a given moment; 3) population trend, i.e. changes in population size across periods of time (Sutherland, 2006). These indicators are fundamental to the establishment of effective conservation strategies and action plans (IUCN, 2017). Importantly, they can be related to measures of habitat suitability and threats for the investigation of the factors driving ape density and distribution over the area of interest (Kühl et al., 2008). Consequently, the conservation of great apes requires carefully designed surveys, using appropriate field data collection techniques, as well as analytical methods providing accurate estimates of population status (Nichols and Williams, 2006).

Figure 1.1. Geographical distribution of great apes' living species and sub-species (IUCN, 2020a). African apes (top): bonobo, chimpanzee (*Pan spp.*) and gorilla (*Gorilla spp.*); Asian apes (bottom): orangutan (*Pongo spp.).*



1.2. Great apes survey methods

1.2.1. Detecting and counting great apes

Great apes inhabit the tropical rainforests of South-East Asia (orangutans) and sub-Saharan Africa (gorillas, chimpanzees and bonobos), where direct observation of unhabituated apes is hard due to poor visibility in thick vegetation (Kühl et al., 2008). They are hunted in most of their geographical range (Hart et al., 2008; Kühl et al., 2009; N'Goran et al., 2012) and tend to be elusive and wary of humans. For these reasons, great apes' monitoring using direct observations is restricted to known groups, habituated to human observers. As the process of habituation can take up to five years (Williamson and Feistner, 2003), direct monitoring is neither feasible nor cost effective over large landscapes. Therefore, until now great apes were monitored by using indirect signs of presence, counting apes' traces encountered in the environment rather than individual animals (Kühl et al., 2008). Great ape signs can be collected opportunistically, by recording any sign of ape presence encountered, or systematically, by walking 1) paths of least resistance through a survey area (Walsh and White, 1999), called "reconnaissance walks" or "recces"; 2) paths on predetermined lines systematically placed across the survey area (Buckland et al., 2001; 2015), called "line transects". In recces, the observer is allowed to deviate from his/her path, whereas no deviations are permitted on line transects, where the observer must strictly follow the predetermined line (Kühl et al., 2008).

In order to obtain reliable information on great ape distribution and density, carefully designed studies are key. According to the study objectives, surveys can be designed to maximize detections of a particular species, focusing on specific habitats or targeting locations such as trails and feeding sites to maximize the probability of encounters (Karanth and Nichols 1998, Head et al. 2013, Després-Einspenner et al. 2017). However, randomized designs are generally more appropriate (Buckland et al., 2001; Burton et al., 2015; MacKenzie et al., 2002, Rowcliffe et al. 2008). Systematic designs (with a random start-point), provide data representing the different habitats and features of the study area, ensuring accuracy in the resulting estimates of distribution and density (Buckland et al., 2001). These designs require an even coverage of the study area, as well as adequate randomization, replication (i.e. number of transects) and effort (i.e. length / duration of each sampling unit, according to the method used) are needed. This way, it is possible to mitigate biases arising from spatial variability in density / occurrence of indirect signs of great apes (Buckland et al., 2001; 2015; Burton et al., 2015; MacKenzie et al., 2003; 2015).

Great apes leave different signs of presence such as feeding remains and footprints. However, for monitoring purpose, researchers have mostly exploited great ape 1) excrements (i.e. dungs); 2) sleeping platforms, or “nests”; 3) vocalisations, or “calls” and 4) images, obtained remotely by devices permitting observations of individuals, i.e. camera-traps.

1) Great ape faeces are easily recognizable and trained field staff can accurately discriminate between the sympatric species gorilla and chimpanzee (Head et al., 2011). The use of dung for monitoring purpose is almost impossible for the arboreal orangutan, and studies are rare also for African apes (Takenoshita and Yamagiwa, 2008; Todd et al., 2008). However, dung surveys have gained momentum in recent years, as they were used in genetic studies (Arandjelovic et al., 2010; McCarthy et al., 2015; Brand et al., 2016). Here, faeces are collected *ad libitum* in the study area, maximizing sample size by targeting feeding and sleeping sites, or frequently used paths (Arandjelovic et al., 2011).

2) Every night weaned apes build structures called “sleeping platforms,” “beds” or “nests”. Although sometimes built on the ground (Tagg et al., 2013; Fruth, Tagg and Stewart, 2018), particularly in gorillas (Yamagiwa, 2001), nests are commonly constructed in trees, where small branches and twigs are bent and broken over a larger side branch, forming an oval, nest-like structure to sleep at night (Goodall, 1962), and sometimes during day (i.e. day nests) (Fruth and Hohmann, 1996). Great ape nests are constructed at predictable rates (of about 1 nest / day), last long in the forest, and are easily spotted by the human eye (Fruth and Hohmann, 1994). Because of these characteristics, nest counts have become the gold standard for monitoring great apes in the wild (Kühl et al., 2008).

3) Great apes exhibit a rich vocal repertoire (Boesch and Crockford, 2005; Clay, Archbold and Zuberbühler, 2015; Salmi, Hammerschmidt, and Doran-Sheehy, 2013; Spillmann et al., 2015). Of particular interest are loud calls, long distance vocalisations used to advertise fitness (Delgado, 2006), defending territorial boundaries (Wich and Nunn, 2002; Wrangham, Wilson and Hauser, 2007), coordinating group movements (Gruber and Zuberbühler, 2013) and signal the presence of food (Fedurek and Slocombe, 2013; Kalan and Boesch, 2015). Loud calls can be recorded by human observers while in the forest, or, more recently, by recording devices (Heinicke et al., 2015). First developed

in marine environments for detecting cetaceans (Zimmer, 2011), passive acoustic monitoring methods (PAMs) were recently adapted to terrestrial habitat and species (Blumstein et al., 2011), including great ape populations (Kalan et al., 2015; Spillmann et al., 2015; Kalan et al., 2016; Crunchant et al., 2020).

4) Great apes' images are typically obtained by using recording devices called camera-traps (CTs). Camera-trap studies have seen an exponential increase in the last decade (Burton et al., 2015), offering innovative approaches to monitor species in an economical and minimally invasive way (Rovero and Zimmermann, 2016). The passage of animals in the area in front of the camera activates infrared sensors designed to detect 1) movement (Active Infrared Sensor "AIR") or 2) differences in surface temperatures between the animal and the background (Passive Infrared Sensor "PIR"), with the latter being more common (Welbourne et al., 2016). By that, either still images or videos are obtained. CTs can be set at defined locations (such as feeding sites, or animal paths) to maximize the number of still images / videos obtained during a sampling session, or can be distributed systematically in the study area (e.g. according to an even grid generated from a random origin) to obtain standardized information, representative of the entire area of study (Rovero and Zimmermann, 2016).

1.2.2. Analytical methods

In order to analyse a species' status, we need to model its 1) distribution (location specific presence/absence data); 2) abundance (location specific count data), to estimate its density / abundance. Consequently, analytical methods specific to each data type were developed in the past (Kéry and Schaub, 2011)

1.2.2.1 Distribution

Species distribution models (SDMs) are used to predict a species' distribution across a landscape (Elith and Leathwick, 2009). They make use of presence / absence data, binary data useful to estimate a species' occurrence probability as function of environmental covariates. Consequently, any observation or indirect sign can be used to confirm a species' presence. However, although we can be certain a species is present if any sign of presence is found in the area, we can rarely be sure it is absent. In fact, even if a species is present in an area, we might miss it because of imperfect detection (MacKenzie et al., 2003; 2015). This is the most frequent scenario in wildlife surveys. In such cases, presence / absence data should more appropriately being referred to as detection / non-detection data (Kéry and Royle, 2015). Several methods were developed for the analysis of detection / non-detection data for estimating a species' distribution (reviewed in Guisan and Thuillers (2005) and Martinez-Minaya et al., (2018)). Below, I will describe three of the most common methods relevant to great apes.

A. Logistic regression

Detection / non-detection data can be modelled using logistic regression, a regression specific for the analysis of binary data, implemented using generalized linear (GLM) (McCullagh and Nelder, 1989) or generalized additive models (GAM) (Wood, 2017). Logistic regression can be used to estimate a species occurrence probability while investigating the influence of environmental and anthropogenic covariates (Elith and Leathwick, 2009). Although logistic regression models were used for assessing great ape distribution (Davies et al., 2019), they were unable to account for false absence (i.e. when a species is present but not detected) (Pearce and Boyce, 2006). As a result, some great ape researchers (Junker et al., 2012) combined logistic regression with methods requiring presence only data, such as maximum entropy models.

B. Maximum entropy models

Maximum entropy models (Phillips, Dudík and Schapire, 2004), became a popular framework for studies modelling a species distribution using presence-only data, particularly after the release of the open-source software Maxent (Phillips and Dudík, 2008). The Maxent approach models species distribution using a maximum entropy principle to determine the largest spread (i.e. maximum entropy) in a geographic dataset of species presence in relation to a set of background environmental variables (Elith et al., 2011). In practice, a survey grid is superimposed over the study area, where each cell (i.e. location) within the grid is assigned values of environmental factors potentially explaining the species distribution. Then, the software extracts a sample of background locations (where presence is unknown) and contrasts them against locations of known presence to estimate cell-specific relative occurrence rates (ROR). ROR values are a measure of a cell's suitability to the species of interest, but can be interpreted in different ways, including the species occurrence probability (Merow, Smith and Silander Jr, 2013). By that, it is possible to generate cells of pseudo-absence if ROR is estimated being e.g., lower than 0.5. Maximum entropy analyses were used in several studies modelling the distribution of gorillas (Kayijamahe, 2008; Van Gils and Kayijamahe, 2010; Etiendem et al., 2013; Thorne et al., 2013; Onojeghuo et al., 2015; Ginath Yuh et al., 2020; Kehou, Daïnou and Lagoute, 2021), chimpanzees (Torres et al., 2010; Junker et al., 2012; Fitzgerald et al., 2018; Ginath Yuh et al., 2020; Kehou, Daïnou and Lagoute, 2021), bonobos (Hickey et al., 2013) and orangutans (Rahman et al., 2019). The main advantages of this successful framework were the possibility to work with presence-only data and the suitability for investigating the factors explaining a species distribution (Elith and Leathwick, 2009). The main disadvantage, however, was their inability to explicitly account for imperfect detection (Guisan and Thuiller, 2005). This is exactly what the next family of models, so called occupancy models, are capable of.

C. Occupancy models

Occupancy models (MacKenzie et al., 2003; 2015), are hierarchical logistic regression models developed to address the issue of false absences in species distribution analysis involving detection / non-detection data (Kéry and Schaub, 2011). As suggested by Guisan and Thuiller (2005) the approaches described above had the main disadvantage of modelling a species apparent rather than the true distribution.

By jointly modelling a species' 1) occurrence probability and 2) detection probability, occupancy models simultaneously evaluate both the observational process generating the detection / non-detection data (including false absences) and the biological process, representing the true occupancy of the species of interest. However, they require replicated surveys (≥ 2) of the same locations and within a time of population closure, i.e. there is no birth /death or immigration / emigration, to correctly estimate a species detection probability. This can be achieved through 1) temporal replication, i.e. the same site is surveyed repeatedly at different times; 2) spatial replication, i.e. several sampling units (e.g. transects) are surveyed within the same site; 3) replication by independent observers, i.e. the same site is surveyed simultaneously by more than one observer.

In practice, an occupancy model is composed of two levels:

$$O_r \sim Bernoulli\,(\psi) \qquad \textit{Lev. 1}$$

$$o_{r,j}\,/\,O_r \sim Bernoulli\,(O_r\pi) \qquad \textit{Lev. 2}$$

Where O_r is the latent (i.e. true) occupancy at site *r* and ψ the occurrence probability*;* $o_{r,j}$ is the observed occupancy at site *r* for replicate *j* and π is the detection probability. Both ψ and π can be modelled as a function of covariates, equivalently to a logistic regression (Engler, Guisan and Rechsteiner, 2004). By that, a species' occurrence probability in cells that were found empty, is a function of the probability a cell was occupied (ψ) and the probability that the species was missed because of imperfect detection (1 - π). Occupancy models can be implemented with a frequentist, maximum likelihood approach (MacKenzie et al., 2003; 2015), in a Bayesian framework (Rue, Martino and Chopin, 2009) or with machine learning algorithms such as Random-Forest (Campos-Cerqueira and Aide, 2016)

Because replicated surveys could be highly costly in great ape habitats (Kühl et al., 2008), occupancy models were less successful than maximum entropy models (Plumptre et al., 2016; Santika et al., 2017; Szantoi et al., 2017; Plumptre et al., 2021). However, they recently found additional application in the analysis of acoustic detection / non-detection data (Kalan et al., 2015; Kalan et al., 2016; Crunchant et al., 2020).

1.2.2.2 Density and abundance

In community ecology, population size "N" (i.e. number of individuals per unit area) and density "D" (i.e. the rnumber of individuals per a defined area), are the most informative parameter, providing information for monitoring temporal trends in population status and comparing populations across sites (Nichols and Williams, 2006). As such, they are crucial information for effective wildlife conservation in general, and great apes in particular. The analytical methods used to estimate animal density and abundance require count data, which are typically collected following Distance Sampling (DS) protocols (Buckland et al., 2001; 2015) and analysed in the dedicated open-source software "Distance" (Thomas et al., 2010).

A. Line transect nest counts using distance sampling

Nests counts, rather than ape counts, were the gold standard for monitoring great ape density and abundance over the past 40 years (Kühl et al., 2008). Nests were most often counted along line transects (Figure 1.2) using DS (Buckland et al., 2001; 2015), either from the ground (Plumptre, 2000) or from the air, using helicopters (Ancrenaz et al., 2004) or drones (Wich et al., 2015; Bonnin et al., 2018). Line transect Distance Sampling (LTDS), account for the fact that objects i.e., animals or their indirect signs, are imperfectly observed in the field. In fact, the probability of detecting an object, decreases with its increasing distance from the observer (Buckland et al., 2001; 2015). Therefore, LTDS required counting great ape nests, but also measuring their distance from the transect (Buckland et al., 2012). DS then fits functions describing the decrease in detection probability with the increasing distance to the observer (Buckland et al., 2001; 2015). By that, estimates of the number of nests in the surveyed area can be obtained, even if some were missed (Buckland et al., 2012). However, density estimates of great ape nests can be considered reliable only if the following assumptions are fulfilled: 1) sampling units (e.g. line transects) are placed randomly with respect to the distribution of the nests; 2) nests located on the transect line are always detected; 3) observations of nests are independent events; 4) distances are measured accurately i.e. distance measurements are as close to the true distance as possible, and precisely, i.e. errors associated with distance measurement are as small as possible (Buckland et al., 2001; 2015). In addition, African great apes are social animals and nests are usually found in groups (Plumptre and Reynolds, 1997). To prevent violation of assumption (3), researchers used to measure distances to the nest group centre (rather than to the individual nests), including in the same group those nests estimated being constructed in the same night by their colour and degree of decomposition (Plumptre and Reynolds, 1997). In practice, individual nests were assigned to a particular “age class”, from fresh to very old (Tutin and Fernandez, 1984), and those assigned to the same class were considered a nest group. However, more recent works have clearly shown within group variation in the time needed for nests to decompose (Walsh and White, 2005). Therefore, it is now common practice to record distances to individual nests (Buckland et al., 2012). Violation of assumption (3) is not particularly problematic (Buckland et al., 2012), as point estimates of density are not affected. In contrast, the estimated variance can be affected by violation of (3), but estimators robust to violation are available (Fewster et al., 2009).

Conversion factors

If correctly applied nest count in combination with DS provide accurate and reliable estimates of great ape nest density (Kühl et al., 2008). However, for conservation and management purposes, ape density (rather than nests) is needed. Nest density must be converted into ape density using conversion factors, namely 1) proportion of nest builders in the population; 2) daily nest production rate; 3) nest decomposition time (in days).

1) *Proportion of nest builders in the population.* As only weaned apes build nests, the proportion of individuals constructing nests in the population of interest is a required parameter to estimate ape density using nest counts. However, this information is difficult to obtain unless specific observational studies of the community of interest are carried out. Such studies are rare, and so are the studies providing a value for this parameter, with reported values ranging between 0.7 and 0.9 (Kühl et al., 2008).

For these reasons, researchers avoided correcting estimated densities by the proportion of nest builders. Instead density is estimated for the number of weaned individuals, rather than all individuals in the population (Kühl et al., 2008).

2) *Daily nest production rate.* Great apes build a new nest every night, but the rate of construction has been found to be higher than 1 nest / day (Kühl et al., 2008). In fact, great apes build day-nests, which seldom differ in structure and appearance from those built at night, and might also reuse previously constructed nests (Fruth, Tagg and Stewart, 2018). Rates of construction are thus needed, correcting for biases arising for the construction of day nests and nest reuse. Ignoring day nests (i.e. apes constructing more than 1 nest/day) would result in underestimated densities. Not accounting for nest reuse (i.e. apes constructing less than 1 nest/day) would lead to overestimated densities (see Equations 1 and 2, below). However, here as well, rates are derived from observations of habituated apes, and very few nest production rate estimates are available in the literature, ranging between 1 and 1.9 nests / day (Kühl et al., 2008).

3) *Nest decomposition time.* The time needed for great ape nests to decompose and disappear from the environment is reported being highly variable across species, space, and time, with reported values ranging between a day and two years (Kühl et al., 2008; Mathewson et al., 2008; Mohneke and Fruth, 2008). Reliable estimates of density and abundance require survey-specific estimates of nest decomposition time (or nest decay). As nests built the same day and time by a group of apes show different decomposition times, nest specific factors are known to drive nest decay (Morgan et al., 2016; Walsh and White, 2005). Continuous monitoring of a large sample of nests representative for the period of survey returns the most reliable estimate by analysing nest survival (Mohneke and Fruth, 2008; Morgan et al., 2016; Lapuente et al., 2020). However, these studies are time consuming, and time-efficient methods such as Hidden Markov chain analysis (Mathewson et al., 2008) and logistic regression (Laing et al., 2003) have been developed and recommended (Kühl et al., 2008). Conversion factors are known to be highly variable and specific to each ape population, and values specific to the population of study are required to obtain accurate estimates (Kühl et al., 2008).

Types of nest counts

Standing Crop Nest Counts (SCNC) (Tutin and Fernandez, 1984) requires all three conversion factors described above. Transects are surveyed only once and field researcher must record all nest encountered regardless of their age. The estimated density of nests $\boldsymbol{\widehat{D}_{nests}}$ obtained by the application of DS, is then converted into ape density $\boldsymbol{\widehat{D}_{apes}}$ using the following formula:

$$\widehat{D}_{apes} = \frac{\widehat{D}_{nests}}{\hat{p} * \hat{r} * \hat{t}} \qquad \text{Equation 1}$$

where $\boldsymbol{\hat{p}}$ is the proportion of nest builders, $\boldsymbol{\hat{r}}$ is the nest construction rate and $\boldsymbol{\hat{t}}$ is the estimate nest decay time.

Marked Nest Counts (MNC) (Plumptre and Reynolds, 1996) does not require estimates of nest decomposition time. In a first passage, all nests encountered on a transect are marked. Then, in subsequent passages, only freshly built nests are counted. The intervals between passages must be short enough so that no new built nest could disappear before a new passage occur. Freshly built nest density $\boldsymbol{\widehat{D}_{fresh\,nests}}$ obtained by the application of DS, is then converted into ape density $\boldsymbol{\widehat{D}_{apes}}$ using the following formula:

$$\widehat{D}_{apes} = \frac{\widehat{D}_{fresh\,nests}}{\hat{p} * \hat{r} * \hat{c} * \hat{d}} \qquad \text{Equation 2}$$

where $\boldsymbol{\hat{p}}$ is the proportion of nest builders, $\boldsymbol{\hat{r}}$ is the nest construction rate, $\boldsymbol{\hat{c}}$ is the proportion of nests remaining until the next passage and $\boldsymbol{\hat{d}}$ is the inter-passage interval, in days.

Advantages and disadvantages

DS using nest counts is the most widely used method for monitoring great ape density and abundance. It has the remarkable advantages of requiring little field equipment, benefiting from a consolidated mathematical framework, open-source software and a vast community of users and developers, making the method easily accessible. However, the dependence on highly variable conversion factors scaling the number of estimated nests to the number of apes, is a major disadvantage. Estimating time and site-specific factors, is time consuming and many LTDS studies borrowed values published for different sites and/or time periods, potentially inducing bias in density estimates (Aebischer et al., 2017). In addition, great apes build nests in specific locations (Davies et al., 2019; Hernandez -Aguilar, 2009; Serckx et al., 2016). As such, nest counts might not provide information on ranging and foraging areas, and so fail to reflect the totality of great ape habitat requirements. Finally, in LTDS surveys, good random design with sufficient effort ensures representative sampling and therefore accuracy of nest density estimates. However, this significantly increases the labor needed with walking long distances in the remote areas typically inhabited by great apes (Kühl et al., 2008).

In Chapter 3, I describe the importance of obtaining accurate conversion factors, particularly nest decay time, to obtain unbiased estimates of great ape density and show biotic and abiotic factors affecting nest decomposition rate in natural conditions.

Figure 1.2. Field researchers walking a line transect in Salonga National Park, Democratic Republic of the Congo.

B. Camera-trap methods

To overcome the limitations of LTDS, great ape researchers have been looking for analytical methods providing estimates without the need for conversion factors. The technological advancements making genetic studies, acoustic devices, and camera-traps cheaper and more easily accessible, provided the basis for such developments. However, data from acoustic devices were mainly used for estimating great ape distribution (Kalan et al., 2015; Crunchant et al., 2020), despite methods for density estimation were recently proposed (Stevenson et al., 2021). Similarly, genetic studies still require laboratory analysis and equipment, inhibiting their wide application. Conversely, CTs (Figure 1.3) have become extremely successful tools for remotely monitoring wildlife in the past 20 years resulting in the development of different methods for the estimation of animal density (Rovero and Zimmermann, 2016). Some of these methods being also applicable to acoustic and genetic data. In the following paragraphs I will concentrate on methods developed for the analysis of CT images by reviewing the most common, with a particular focus on those used for great ape density estimation.

a. Capture-recapture methods

The first density estimators based on CT footage were designed for large, individually recognizable species, using a *capture-mark-recapture* (CR) framework (White, 1982; Karanth and Nichols, 1998). In CR, animals from a closed population had to be captured at least twice. In the first capture event, all captured animals were individually marked (or tagged), so that they could be recognized in subsequent capture events. Using the most basic model, capture probability must be constant, both between individual animals and capture events, and each individual in the population being sampled must have a non-zero probability of being detected. Enough time must occur between events so that captured animals can disperse in the study area, but not so much that the assumption of population closure is violated. For example, if the population in study shows seasonal migration, the study should be conducted before the migration occurs. Then, the method was based on the assumption that the proportion of marked individuals in the population is equal to the proportion of marked individuals in the recaptured population (White, 1982). Regardless, CR methods required individual recognition of the recorded animals, either via molecular methods, the classification of individual-specific calls (acoustic surveys) or by markings individually assigned to the animals, such as in felids being identified by their coat pattern (Jackson et al., 2006). The major disadvantage was that CR estimates were not connected to the spatial distribution of the population of study. With the effective surveyed area being difficult to estimate, CR methods estimated population size within an area of unknown size rather than density. In fact, if animals move in and out of the study area, abundance estimates would refer to a larger area than the one covered by the CT (Sollmann, Mohamed and Kelly, 2013).

To overcome the limitation of CR methods, *Spatially Explicit Capture Recapture* (SECR) methods were developed (Borchers and Efford, 2008). By determining the activity centers of individual animals and then estimating the number of activity centers in the study area, SECR provided both population density *D* and abundance *N* in a defined area. SECR incorporated information about the geographical distribution of traps in the study area and accounted for the fact that animals located closer to traps were more likely to be captured than those further away. By that, SECR methods modelled heterogeneity in detection probability and variable temporal sampling effort at different trap locations (Borchers and Efford, 2008; Efford, Borchers and Byrom, 2009; Borchers, 2012). Like CR methods, SERC required individuals in the population of study to be identifiable and that at least a proportion being detected more than once at different locations and that the probability of detection is > 0 for each individual in the population (Efford, Borchers and Byrom, 2009). SERC models were a promising advancement and proved efficient in many applied studies, including estimates of ape density, both by using CTs (Spehar et al., 2015; Després-Einspenner et al., 2017) (CTs-SECR), and genetic material obtained from faeces (genetic-SECR) (McCarthy et al., 2015). They also have potential for the analysis of acoustic data (Stevenson et al., 2021). However, by requiring individuals to be individually recognizable, the number of species that could be surveyed using CTs- and acoustic-SECR remains limited, whereas the applicability of genetic-SECR is limited by the costs of the laboratory analyses required.

Mark-resight models (Arnason, Schwarz and Gerrard, 1991), were similar to CR methods, but allowed for density estimates when only a subset of the animals was uniquely identifiable (Neal et al., 1993; Hein and Andelt, 1995; Rich et al., 2014). The sighting probability of the marked subset is assumed to be representative of the sighting probability of the entire population (Arnason, Schwarz and Gerrard, 1991). By that, spatially explicit mark-resight models were also developed, addressing the need to relate population estimates to an area of known size (Rich et al., 2014; Alonso et al., 2015). Although suitable for the analysis of CT images and genetic studies, MS models were never applied to great ape populations.

b. Unmarked methods

The need for the recognition of individuals was the main limitation of CR methods in CT studies. To overcome this issue, several methods have been developed in recent years, known as models estimating density of “unmarked” species (Gilbert et al., 2021).

The first method for estimating animal density from CT data in the absence of individual identification was the *random encounter model* (REM) (Rowcliffe et al., 2008). The REM adapted a mechanistic model of the collision rates between gas molecules (Hutchinson and Waser, 2007) to animal movements within their habitat. It required estimates of animal speed, average group size (only for species moving in groups) and of the CT detection area, to provide animal density using maximum likelihood methods (Rowcliffe et al., 2008). The main advantages of REM were 1) animals did not need to be individually identifiable, 2) estimates were referred to an area of known size (i.e. the CTs detection area), and 3) conversion factors were not required. Similar to DS methods, REM modelled estimated animal detectability as a function of the distances and angles at which animals were first detected (Rowcliffe et al., 2011). Consequently, assumptions of the REM were also similar to DS methods, with the population of study being closed, and observations being independent events. Animals were assumed to be detected with certainty within the CT detection zone and expected to move randomly in their space, according to the Hutchinson-Waser model. Consequently, animal should not react to the camera being attracted to it or avoiding it. Finally, CTs were to be deployed randomly within the study area (Rowcliffe et al., 2008). REM models have been applied to several species (Zero et al., 2013; Anile et al., 2014; Cusack et al., 2015; Caravaggi et al., 2016), but never to great apes. However, these studies highlighted the difficulties in correctly estimating animal speed and in fully satisfying certain assumptions (e.g. random animal movements and camera-placement). Therefore, despite continuous developments (Rowcliffe et al., 2011; Rowcliffe et al., 2013; Hofmeester, Rowcliffe and Jansen, 2017; Palencia et al., 2019), the broad applicability of REM is still being fully tested (Burton et al., 2015; Chauvenet et al., 2017; Gilbert et al., 2021).

A recent extension of REM models is the *Random Encounter and Staying Time model*, REST (Nakashima, Fukasawa and Samejima, 2017). Relying on the same assumptions and mathematical framework as REM, REST did not require estimates of animal speed, a significant improvement over classical REM (Gilbert et al., 2021). Instead, REST included the time animals spent in the CTs detection area, or staying time, which is easily extracted from CT footage (Nakashima, Fukasawa and Samejima, 2017). In a recent paper (Palencia et al., 2021) investigating red deer (*Cervus elaphus*), wild boar (*Sus scropha*) and red fox (*Vulpes vulpes*) populations, REST and REM were found to provide similar densities. Given its recent development, REST was never applied to great ape population.

Recently, the SECR methods described above for marked individuals, were extended to allow density estimates of unmarked populations. Using the same mathematical framework and assumptions of SECR, *unmarked-SECR* (uSECR) exploited the spatial correlation in counts at each location to estimate the number and location of individual activity centers (Chandler and Royle, 2013). However, this promising method required spatially intensive sampling effort, involving the deployment of many camera-traps and estimates were found to lack precision unless supplemented with ancillary data such as genetic sampling or telemetry (Evans and Rittenhouse, 2018; Linden, Sirén, and Pekins, 2018; Sollmann et al., 2014). At present, uSECR has not been applied to great apes.

More recently, Moeller et al., (2018) proposed three new methods for estimating density of unmarked animals from CT data.

1) The *Time To Event model* (TTE), as the REM, required estimates of animal movement rate and had similar assumptions. The TTE used detection rates within the camera's field of view, using the time until the first detection of an animal occurs (i.e., an event) within an arbitrarily defined sampling unit. It is mathematically similar to popular survival models, estimating the time needed until an animal's appearance (Efron, 1988). In the TTE, only the first detection of an animal within an arbitrarily defined sampling unit contributes information, and detection probability is assumed to be certain within the CTs' field of view (Moeller, Lukacs and Horne, 2018). These are among the main disadvantages of the method in its current formulation (Gilbert et al., 2021).

2) The *Space To Event model* (STE) did not use remotely triggered videos, but rather time-lapse images, taken at predefined moments and regardless of the presence of an animal (Gilbert et al., 2021). The STE then counts the animals captured at each

time-lapse photo within pre-defined sampling occasions (e.g. hourly periods). Although the STE relied on the same assumption of the TTE, perfect detection within the field of view was considered more likely with time-lapse photos (Gilbert et al., 2021). Animal density was estimated by calculating the sampled area multiplying the area covered by the camera field of view (up to the maximum distance at which the given species can be identified) by the number of time-lapses before an animal is first observed (Moeller, Lukacs and Horne, 2018).

3) Finally, the *Instantaneous Sampling* model (IS) is similar to the STE but uses counts of animals in view at each time-lapse photo, without considering sampling occasions (Moeller, Lukacs and Horne, 2018).

Moeller et al. (2018) tested these three methods mentioned above on an elk (*Cervus canadensis*) population showing that accuracy of the TTE model was sensitive to animal movement rates. They found the STE and IS methods to perform well, being unbiased when compared to aerial surveys of the area. However, at present this remains the only study applying these methods.

Recently, Howe et al. (2017) proposed to apply Distance Sampling theory to CTs data. *Camera trap distance sampling* (CTDS) extended point transect distance sampling by considering a CT as a human observer, whose field of view is restricted to the area covered by the CT. Animals captured by a CT are then associated to their distance from the CT using reference videos previously collected by field researchers (Howe et al., 2017). Distances are recorded at predefined moments called “snapshots” and detection probability is assumed to be certain at the camera, decreasing with distance to the camera (Howe et al., 2017). CTDS used a consolidated mathematical framework, open-source software and a large community of users and developers. These advantages resulted in several recent studies, validating the method and showing its applicability under different field conditions (Cappelle et al., 2019; Corlatti et al., 2020; Harris et al., 2020; Cappelle et al., 2021; Palencia et al., 2021; Amin et al., 2021). I describe CTDS in detail in Chapter 2.

Finally, Campos-Candela et al. (2018), and Luo et al. (2020), proposed density estimators for unmarked populations by using animal home-ranges and use of space in two simulation studies. These methods were never tested in the field, and the simulation study proposed in Campos-Candela et al. (2018), was criticized for being unable to properly account for realistic animal behaviour, in another study simulating its application to a moose (*Alces alces*) population (Abolaffio, Focardi and Santini, 2019). CT data could also be used in other popular frameworks such as the *N-Mixture model* (Royle, 2004), an approach evaluating both the observed and latent population by using replicated surveys at the same, independent locations. N-Mixture models require strict assumptions, including population closure, equal detection probability for all individuals and an animal being detected by a camera is not being detected in subsequent survey periods (Royle, Dawson and Bates, 2004). In addition, and similar to the CR models described above, they had the major disadvantage that the effective sampling area of cameras was unknown (Kéry and Royle, 2015), and that they are sensitive to assumption violations. As a result, it was suggested that N-Mixture models should be treated as indices of relative abundance, rather than estimators of animal density (Gilbert et al., 2021).

Photo: Jonas Abana Eriksson© PNS Survey®

Figure 1.3. Installing a camera-trap in the forest of Salonga National Park, Democratic Republic of the Congo.

1.2.2.3 Population trends

Another important information in great ape conservation is the status of a population across time, also called “trend” (Buckland, Goudie and Borchers, 2000). Here, field data from a minimum of two periods are required to model temporal changes with respect to density and abundance, assessing the impact of factors considered being important predictors of ape distribution (Strindberg et al., 2018). Defining if a population is stable, increasing or decreasing in the wild is crucial to the assessment of a species conservation status, for the definition of specific action plans and for the establishment of conservation strategies (IUCN, 2017). Recent studies investigating great ape population trends have shown catastrophic declines. This concerns the Western chimpanzee (Kühl et al., 2017), the Central chimpanzee and Western lowland gorilla (Strindberg et al., 2018), the Grauer's gorilla (Plumptre et al., 2016), and the Bornean (Santika et al., 2017; Voigt et al., 2018) and Sumatran orang-utan (Wich et al., 2016). These studies used nest count data and different analytical methods to compare past and present great ape abundance, including occupancy models (Plumptre et al., 2016), GLMs (Wich et al., 2016; Kühl et al., 2017; Voigt et al., 2018) and GAMs (Strindberg et al., 2018). However, Santika et al. (2017), made use of data coming from different sources, including traditional and aerial nest counts and presence data obtained from interviews, and integrated them in a single model jointly analysing orang-utan occurrence and abundance, an approach described below.

1.2.2.4 Integrating data from different sources

Until recently, studies evaluating a species' status exploited only part of the information available, using above mentioned occupancy models (MacKenzie et al., 2003; 2015) for the analysis of detection/non-detection data, Distance Sampling (DS) (Buckland et al., 2001; 2015), for the analysis of count data from standardized line and point transects and Capture-Recapture (CR) methods for investigating animal abundance while considering demographic parameters such as survival and recruitment (Lebreton et al., 1992). However, in recent years, there has been a growing interest in methods for the joint analysis of detection/non-detection, count, and demographic data. *Integrated Population Models* (IPMs) allow for the integration of count and capture-recapture data to investigate population dynamics, estimating parameters such as survival, recruitment, and fecundity. By integrating data from different sources (Plard et al., 2019), IPMs were found to improve the precision of the estimated parameters (Schaub and Abadi 2011) and were thus extended to more taxa. These included birds (Besbeas et al., 2002; Fay et al., 2019; Jansen et al., 2019; Margalida et al., 2020) and mammals such as tigers (*Panthera tigris*) (Dey et al., 2017), wolves (*Canis lupus*) (Horne et al., 2019), polar (*Ursus maritimus*) (Regehr et al., 2018) and black (*Ursus americanus*) (Sun, Fuller and Royle, 2019) bear; mule *(Odocoileus hemionus)* (Hatter, Dielman and Kuzyk, 2017) and Eld (*Panolia eldii*) (Bowler et al., 2019) deer. Importantly, the principles of data integration used in IPMs, were also extended to models permitting the joint analysis of detection/non-detection and count data, obtained with different methods. Data deriving from traditional ground surveys (Zipkin et al., 2017), camera-traps (Bowler et al., 2019), acoustic devices (Farr et al., 2021), interview surveys (Santika et al., 2017) and citizen science (Sun, Fuller and Royle, 2019), were all used to improve inference of population status and dynamics. In addition, these applications allowed investigating ecological drivers of specific distribution and abundance (Weegman et al., 2017), the assessment of impacts and threats (Dobbins et al., 2020), and the evaluation of conservation effectiveness (Saunders, Cuthbert and Zipkin, 2018). Great ape survey data are typically sparse, obtained from different sources which might entail different levels of standardization and accuracy (Moussy et al., 2021). Therefore, a framework such as described above, has a high potential for the study of ape populations in the wild. However, as mentioned above, only Santika et al. (2017) applied an integrated approach to the orangutan. In Chapter 5, I apply this method to the bonobo (*P. paniscus*) integrating detection/non-detection and count data obtained from reconnaissance walks, line transects and camera-trap surveys.

1.3. The bonobo

1.3.1. History

The great ape species subject of this thesis is perhaps the least known among the extant great ape species: the bonobo. First reason for our limited knowledge, is the bonobo's relatively recent discovery. Morphologically similar to the chimpanzee to the untrained eye, bonobos were mostly thought to be chimpanzees until the early 20th century, being recognized as a subspecies of the (then) western chimpanzee *Troglodytes niger* var. *marungensis* (Reichart, 1884). The *marungensis* populations were reported being distributed from the Marungu hills, on the shores of Lake Tanganyika, north-west of the Congo River, in what was the Congo Free State (1885 - 1908; Thompson, 2001). It was only in 1928 that the bonobo was first described as yet another chimpanzee subspecies, *Pan satyrus paniscus* (Schwarz, 1928), eventually becoming the species *Pan paniscus*, called Pygmy chimpanzee five years later (Coolidge Jr, 1933). The common name "Bonobo" was first used 21 years later by Tratz and Heck (1954), most likely a misinterpretation of the name "Bolobo", a town located in the ape's current geographical range (DeWaal and Lanting, 1998). Nevertheless, the name remained, and is now globally recognized. We also know that the individuals of the Marungu hills were chimpanzees, and that the two species, *Pan troglodytes* and *Pan paniscus*, separated between 0.83 and 0.86 MYA years ago (Won and Hey, 2005).

Bonobo and chimpanzee populations are geographically separated by the Congo River (Takemoto, Kawamoto and Furuichi, 2015), with the bonobo only being found on the river's left bank, north of the river Kasai (IUCN, 2020a). This area, 564,500 km^2 at the hearth of the Congo Basin, falls completely within the borders of the Democratic Republic of the Congo (DRC), making the bonobo endemic to the country (IUCN and ICCN, 2012). Largely covered by pristine lowland rainforest, accessibility to areas of bonobo presence have been limited by the lack of infrastructures and DRC's history of predatory colonialism until the country's independence (in 1960) and civil and political unrests, dictatorship, and war ever since. As a result, there are fewer bonobo field studies if compared to other African apes such as gorillas and chimpanzees. The first research in the wild dates to less than 50 years ago, with the pioneering work of Toshisada Nishida (Nishida 1972) and Arthur D. Horn (Horn, 1980) at lake Tumba, Alison and Noel Badrian (Badrian, 1977) at Lomako and Takayoshi Kano (Kano, 1980) at

Yalosidi. Since, other researchers have studied bonobos in the wild, expanding our knowledge of this unique species.

1.3.2. Ecology and behaviour

Like chimpanzees, bonobos live in fission-fusion societies of up to 80 individuals (Kingdon et al., 2013), inhabiting home ranges typically between 20 and 40 km^2 large (Hashimoto et al., 1998; Beaune et al., 2013), although reported ranging in areas as big as 80 km^2 (Terada et al., 2015). Social groups are characterised by male philopatry and female exogamy (Furuichi et al., 1998), with females typically emigrating from their natal groups as they approach sexual maturity and males remaining within their natal group (Kanō, 1992). However, whereas as in other male-philopatric species, in chimpanzees the strongest inter-individual affiliations are observed between males (Boesch, 1996), females are the most gregarious gender among bonobos, forming strong affiliations with other group members, despite being only distantly related to them (Kano, 1982; Hohmann et al., 1999; Furuichi, 2009). Male bonobos usually do not associate with one another (Parish, 1994; Hohmann et al., 1999), but rather form alliances with females, above all with their mother, with whom they build strong and lasting relationships (Hohmann and Fruth, 2003a). In contrast to chimpanzees, females have the higher status in bonobo communities (De Waal, 1995). In truth, the social system is rather egalitarian, with the female’s dominance status being enhanced by the strong alliances formed with other individuals within the community (Fruth and Hohmann, 2003). Bonobo communities are also reported to be more tolerant if compared to chimpanzee societies, with rarer episodes of aggressive behaviour (De Waal, 1995) (but see Fruth and Hohmann (2003)) and conflicts are settled within a rich frame of social behaviours, the most famous being the use of sexual interactions. Best example is the so called “genital rubbing”, a female-female interaction used as a way to reduce tensions and strengthen alliances between females in absence of genetic bonds (Parish, 1994; De Waal, 1995; Hohmann et al., 1999), a “social-grease” in the definition of Fruth and Hohmann (2006). Such a peculiar social structure has been mainly explained by the habitat inhabited by the bonobo. Although some populations are found in forest-savanna mosaic at the fringes of their geographical range (Serckx, 2014a), bonobos live in an equatorial region, dominated by evergreen lowland primary forests on *terra firma* as well as temporarily and permanently inundated soil (Fruth et al., 2016). These habitats are characterized by abundant food and limited seasonality, providing continuous and predictable food sources. Bonobos are frugivorous (Hohmann et al., 2012), with a diet mainly including fruit, leaves and herbs, but also honey, invertebrates (Badrian and Malenky, 1984; Bermejo, Illera and Pí, 1994; McGrew et al., 2007; Beaune et al., 2013), and meat from actively hunted vertebrates such as antelopes and monkeys (Hohmann & Fruth 1993, 2008; Surbeck and Hohmann, 2008). Such a stable and plentiful environment, and particularly the permanent presence of terrestrial herbaceous vegetation (Malenky and Wrangham, 1994), was proposed as the main driver releasing competition for food resources, hence allowing a more peaceful and tolerant society (White, 1998; Furuichi, 2009). As all other great ape species bonobos build individual nests, platforms in the trees obtained by intertwining branches, where they spend the night, safe from predators. Although infant apes also attempt to build nests, they never last. At night, they do not build own nests, sleeping jointly their mother (Fruth, Tagg and Stewart, 2018).

1.3.3. Conservation status

Similar to other great apes, the bonobo is threatened in the wild (Fruth et al., 2016). Already 40 years ago, the species was reported to be declining in DRC (Susman et al., 1981) because of its small geographical range, low densities, and patchy distribution (Fig 1.1). Today, we know that the threats to the bonobo include habitat destruction (Hickey et al., 2013), human transmitted diseases (Inogwabini and Leader-Williams, 2012) and poaching of adults for meat with surviving infants or immatures captured and sold as pets (Hart et al., 2008). In addition, DRC's political instability (Waller and White, 2016), annual population increases (Jāhāna, 2016), deforestation rate (Tyukavina et al., 2018) and the relaxation in recent generations, of the ancestral cultural taboos against bonobo's consumption (Thompson, Nestor and Kabanda, 2008), are also negatively affecting wild populations. The bonobo is currently classified as "Endangered" by the IUCN (Fruth et al., 2016). However, information of bonobo populations' status is lacking in 70% of its geographical range. In fact, most field studies carried out to date were concentrated in small areas, focussing on few bonobo groups (Furuichi et al., 1998; Eriksson, 1999; Dupain et al., 2000; Van Krunkelsven, Bila-Isia and Draulans, 2000; Hohmann and Fruth, 2003b; Reinartz et al., 2006; Inogwabini et al., 2008; Serckx, 2014b; Surbeck, Coxe and Lokasola, 2017). Given DRC's political and geographical setup, few attempted to cover larger areas (but see Kano (1984) and Grossmann et al., (2008)).

1.3.3.1 Bonobo survey methods: past-present-future

Like other great apes, until today bonobo abundance and distribution were assessed by using nest counts along line transects. The main objective of these surveys was to provide estimates of bonobo population density in specific sites, which was obtained via DS methods and analyses (Blake, 2005; Eriksson, 1999; Grossmann et al., 2008; Hart, 2009; Ikati et al., 2017; 2018; Maisels, 2015; Maisels, Nkumu and Bonyenge, 2010; Maisels et al., 2009; 2010; Omasombo, Bokelo and Dupain, 2005; Reinartz et al., 2006; 2008; Serckx, 2014; Van Krunkelsven, Inogwabini and Draulans, 2000; ZSM, 2017; 2018). Only one study focused on bonobo distribution across its entire range, using Maxent analyses to investigate the factors driving bonobo occurrence in DRC (Hickey et al., 2013).

Nest count surveys (using LTDS) were considered the method of choice for bonobo monitoring, a species rarely observed directly in the field. However, the application of LTDS was challenging in bonobo habitat, representing some of the remotest areas of the planet. Here, the lack of infrastructure prevented rapid deployment of survey teams, requiring days only to reach a survey starting point. In addition, LTDS required experienced researchers, who needed equipment and provisions that had to be back carried through the forest by teams of porters, a major task in the swamps and thickets typical of bonobo habitats. As such, bonobo LTDS surveys were highly costly in terms of field personnel and logistics.

The advent of novel survey methods using camera traps (described in Section 1.2) provided the possibility to survey bonobos with fewer workers, significantly reducing the costs associated with salaries and logistics (Cappelle et al., 2019). Here, spatially explicit capture-recapture methods (SECR) were applied to a known group of chimpanzees in Taï National Park, Cote d'Ivoire (Després-Einspenner et al., 2017), and could be applied to the bonobo. However, SECR requires the identification of individual apes, an issue significantly limiting its applicability for large-scale surveys. The recent development of machine learning algorithms allowing individual identification of animals in CT videos (Crunchant et al., 2017; Schofield et al., 2019), promises to extend the applicability of SECR to the bonobo in coming years. Similarly, novel unmarked CT methods (see section 1.2.2.2) retain high potential for future bonobo surveys. However, at present only one of these methods, i.e. CTDS, has been applied to a great ape, the chimpanzee (Cappelle et al., 2019). Although requiring fewer field personnel and time in the field (Cappelle et al., 2019), the time needed for processing and analysing the resulting images is a major disadvantage (Cappelle et al., 2019; Palencia et al., 2021). Here too, automatised methods are under development and could increase the applicability of CT methods in the future (Haucke et al.,2021; Norouzzadeh et al., 2021; Wei et al., 2020; Whytock et al., 2020). In Chapter 2, I show the applicability of CTDS, to the bonobo and another 13 sympatric species.

1.3.3.2 Salonga National Park

Salonga National Park (SNP), is situated in the centre of bonobo current range. With its 36,000 km^2, the size of Wales, it is the second largest forest protected area in the world and the largest in Africa. Established in 1970, SNP is divided in two blocks, north and south, separated by an inhabited corridor (9,000 km^2) where the majority of the population inhabiting the Park prior to its establishment were forcefully moved (Thompson, Nestor and Kabanda, 2008). However, 9 villages still exist within the park border (Figure 1.4).

Since 1970, SNP was managed by the national conservation authority the *Institut Congolais pour la Conservation de la Nature* “ICCN”, and since 2016, it is co-managed by the World Wide Fund for Nature “WWF”. Today, SNP consists of six sectors, administered by an ICCN head-quarter supervising several ranger patrol posts “PP”, responsible for the monitoring, control and law enforcement (Figure 1.4). In the late 1990s, following the outbreak of conflict, ICCN patrols were significantly reduced, and the park was left mostly unattended for almost a decade (Grossmann et al., 2008). Today, SNP conservation status has significantly improved, although it still raises serious concern mainly due to ongoing poaching, lack of surveillance and uncertainty of long-term funding (IUCN, 2020b).

From an elevation of 350 m increasing southwards to 500 m, SNP is comprised of more than 90% of pristine primary mixed rain forest, encompassing a low plateau covered by swamp forests, river terraces with an associated riverine forest and a high plateau with dry forest (Van Krunkelsven, Bila-Isia and Draulans, 2000). The remaining 10% are represented by savannahs, regenerating forest, cultivation, marshes, and water bodies. This large, pristine protected area harbors extraordinary biodiversity (Appendix 1), being recognized as one of the most important sites in the Congo basin for species such as the Congo peafowl (*Afropavo congensis*) and the forest elephant (*Loxodonta cyclotis*). At least eight monkey species are found in SNP: 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*). The ungulate community is also rich and includes forest buffalo (*Syncerus caffer*), sitatunga (*Tragelaphus spekii*) and the endangered bongo (*Tragelaphus eurycerus*). Top predators are represented by the leopard (*Panthera pardus*) and the African golden cat (*Caracal aurata*). The diversity of birds, reptiles, amphibians, fish and insects is unknown, but expected to be equally high and to include many species yet to be described (IUCN, 2020b). Most importantly for the purpose of this thesis, SNP is recognised as the stronghold of bonobos in the wild (Fruth et al., 2016).

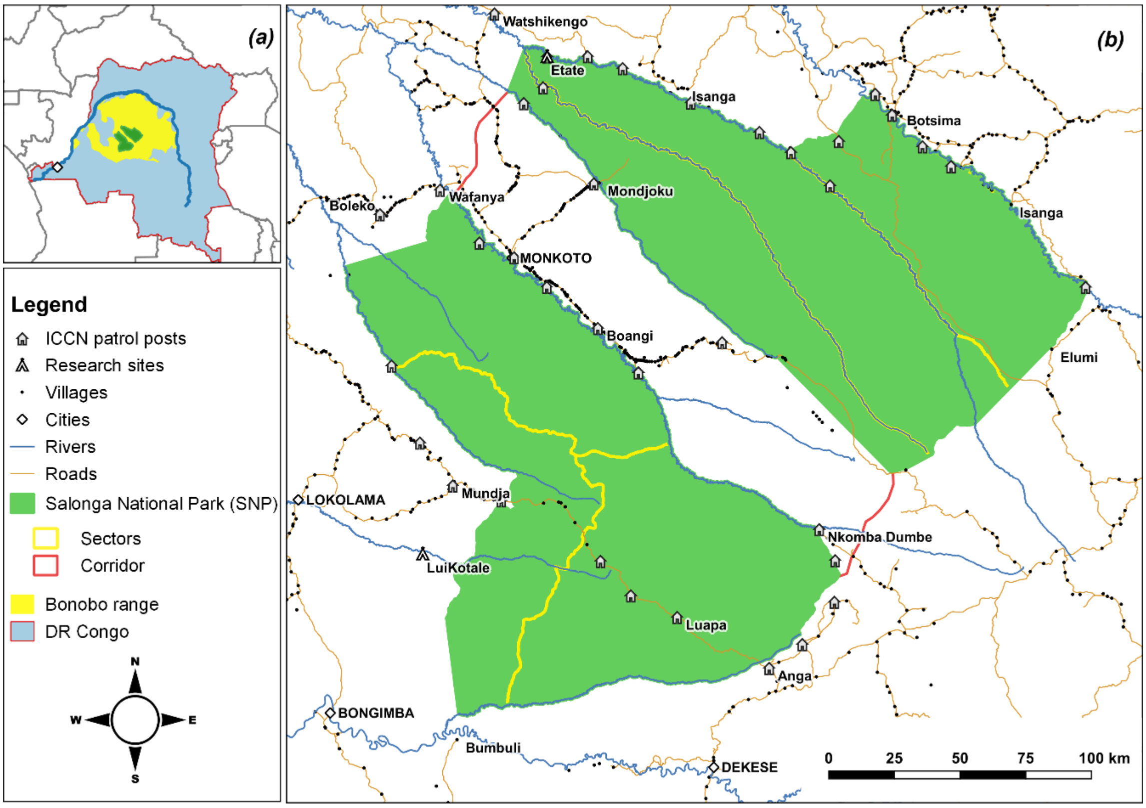


Figure 1.4. Location and main natural and administrative features of Salonga National Park (SNP).

Since its creation, very few ecological monitoring studies have been carried out in SNP. For the bonobo, the first preliminary survey was carried out by Kano (1992), who could not find confirmation of the ape's presence. Three years later, Kortland (1995) updated the distribution map proposed by Kano, including observations made in SNP whilst the first systematic surveys were conducted in small areas of the park by Van

Krunkelsven, Inogwabini and Draulans (2000) and Reinartz et al., (2006). Between 2003 and 2004, the programme MIKE, "Monitoring the Illegal Killing of Elephants", conducted a large survey of SNP also recording signs of bonobo presence, although its focus were elephant signs (Blake, 2005). The first intensive bonobo survey in SNP was finally carried out between 2006 and 2008, using a combination of recces and line transect distance sampling (Grossmann et al., 2008; Maisels, Nkumu and Bonyenge, 2010; Maisels et al., 2010). This survey also established the basis for long-term monitoring in an area close to the park head-quarter in Monkoto: Lokofa (Liengola et al., 2010). The early years 2000 saw the establishment of two research sites: Etate (Reinartz, 2003) in the block North, and LuiKotale (Hohmann and Fruth, 2003b) located in the buffer zone, close to the south-western fringe of the block South (Figure 1.4). The first conducted research on bonobo ecology and monitoring and stopped operating in SNP in 2019. The second is still operating and conducting research on the ecology and the social behaviour of three habituated bonobo groups. More recently, between 2012 and 2018, a large-scale inventory, including flagship species like the bonobo, was carried out by various organizations throughout the park and the corridor covering an area of almost 40,000 km^2 (IUCN, 2020b). I personally coordinated the collection of a major part of this dataset covering 17,127 km^2, from September 2016 to April 2018, in the block south of SNP, prior to commencing this PhD.

1.4. Preamble

The idea of this thesis sprouted in February 2018, in the village of Anga, Kasai, DRC, at the fringes of SNP, where I was coordinating the inventory of the block South of SNP. The inventory, led by my main supervisor, Prof. Barbara Fruth, was entering its final phases. At the time, several studies focusing on great apes other than the bonobo were investigating great ape status and trend, leading to updates of conservation status in the IUCN Red List of Endangered Species (Plumptre et al., 2016; Wich et al., 2016; Kühl et al., 2017; Santika et al., 2017). A similar assessment for the bonobo was impossible due to limited data (Fruth et al., 2016). Next to the traditional LTDS approach, we were pioneeringly applying CTDS, only recently described (Howe et al., 2017). Although we were not fully aware of the amount of data coming out of the project, the extent with over 400 LTs and over 700 CT locations, and data collected across 21 months was promising to fill an important gap. However, the person to analyse these valuable data was yet unknown.

An upcoming call for fully funded PhD scholarships at Liverpool John Moores University, where at the time Prof. Fruth was Reader in Primate Behaviour and Conservation, seemed the perfect opportunity to proceed with my academic career complementing my experience as field researcher. We proposed to use the new data collected in SNP to calibrate a model useful for the assessment of the range-wide bonobo population status and trend. Four months later, I wrapped up the project in SNP, and was on my way to Liverpool.

This dissertation is the result of two years of field work in SNP, and three years of desk work as a PGR student. It focuses on methodological aspects crucial to the assessment of bonobo populations, hence their conservation.

In Chapter 2 I use the CT data collected in the block South of SNP to apply CTDS to the bonobo and 13 other sympatric species. It involved months spent watching videos, processing more than 38,000 video clips. The results revealed the density of species underrepresented in the literature, including the first ever published for the Congo peafowl (*Afropavo congensis*), giant ground pangolin (*Smutsia gigantea*) and the cusimanses (*Crossarchus spp.*), an obscure genus of social mongooses. I describ issues and caveats in applicability, but also the high potential of this methodology for future bonobo population assessment.

Chapter 3 deals with problems arising when using inaccurate conversion factors in LTDS, focussing of nest decomposition time. The study was conceived in April 2020, during the first Covid lockdown. A few months earlier, with my supervisory team, I decided to analyse bonobo population status and trend in SNP using an integrated approach, exploiting all available sources of information and, most importantly, integrating traditional (LTDS) and novel methods (CTDS). This implied familiarization with Bayesian statistics, particularly with the coding language of Stan (Carpenter et al., 2017), an emerging, cutting-edge platform for Bayesian statistical modelling never used in great ape literature. The particularly complicated model I was aiming to develop could not be implemented using existing packages, implying I had to learn how to code it myself. As I was struggling to deliver a working model, we realized that to correctly scale nest density to bonobo density, we had to include *ad hoc* conversion factors, particularly nest decomposition time. To this aim, we decided to analyze a long-term database of 1,511 bonobo nest collected between 2002 and 2018 at the research site of LuiKotale, using a Bayesian approach in Stan. Working on a simpler survival model, I found that bonobo nest decay had lengthened by 17 days over the last 15 years as a result of declining rainfall in the Congo Basin, showing that failure to account for these changes would lead to largely overestimated population density. Importantly, I improved my coding skills and obtained a crucial parameter for my integrated model.

In Chapter 4 I estimate bonobo population status and trend in SNP over the past 10 years, by integrating the finding of previous chapters. Specifically, I used a unique dataset including detection/non-detection and count data from 13 surveys conducted between 2002 and 2018 by different organizations operating in SNP, including recces, line transects and CTDS, evaluated in Chapter 2. I included *ad hoc* period-specific nest decay times to convert nest abundance to bonobos (estimated in Chapter 3) and showed the influence of ecological and anthropogenic factors on the species presence and density. I found a stable bonobo population in SNP between two periods (2002-2008; 2012-2018) showing that the integration of different data sources can help to mitigate bias peculiar to specific survey methods. These results provided a rare positive story in great ape conservation by revealing the importance of pristine habitats, tolerance from local communities and law enforcement, strongly supporting the preservation of SNP. Most importantly, as the same approach could be used to estimates bonobo range-wide population status and trend, I set the basis for future studies and for the upcoming bonobo conservation action plan (IUCN and ICCN, 2012) due in 2022.

Finally, by summarizing the overarching results obtained in previous chapters, in Chapter 5 I highlight the implications for bonobo monitoring and conservation, providing suggestions for future applications and insights into ongoing research.

In the following pages, I will present each research chapter as a journal manuscript, either already published (Chapter 2 and 3) or currently in preparation (Chapter 4).

CHAPTER 2

Drawn out of the shadows: surveying secretive forest species with camera trap Distance Sampling

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This chapter was published in March 2020 and reformatted for consistency and LJMU-thesis requirements. All supplementary materials are included in the chapter or provided as an appendix.

2.1. Abstract

With animal species disappearing at unprecedented rates, we need an efficient monitoring method providing reliable estimates of population density and abundance, critical for the assessment of population status and trend.

We deployed 160 camera traps systematically over 743 locations covering 17,127 km^2 of evergreen lowland rainforest of Salonga National Park, block South, Democratic Republic of the Congo. We evaluated the applicability of camera trap distance sampling (CTDS) to species different in size and behaviour. To improve precision of estimates, we evaluated two methods estimating species' availability ("*A*") for detection by camera traps.

We recorded 16,700 video clips, revealing 43 different animal taxa. We estimated densities of 14 species differing in physical, behavioural and ecological traits, and extracted species-specific availability from available video footage using two methods 1) "*ACa*" (Cappelle et al., 2019) and 2) "*ARo*" (Rowcliffe et al., 2014). With sample sizes being large enough, we found minor differences between *ACa* and *ARo* in estimated densities. In contrast, low detectability and reactivity to the camera were main sources of bias. CTDS proved efficient for estimating density of homogenously rather than patchily distributed species.

Synthesis and applications. Our application of camera trap distance sampling (CTDS) to a diverse vertebrate community demonstrates the enormous potential of this methodology for surveys of terrestrial wildlife, allowing rapid assessments of species' status and trends that can translate into effective conservation strategies. By providing the first estimates of understudied species such as the Congo peafowl, the giant ground pangolin and the cusimanses, CTDS may be used as tool to revise these species' conservation status in the IUCN Red List of Threatened Species. Based on the constraints we encountered, we identify improvements to the current application, enhancing the general applicability of this method.

2.2. Introduction

The use of camera traps (CTs) to study wildlife has seen an exponential increase in the last decade (Burton et al., 2015), offering innovative approaches for obtaining species' distribution, density, abundance, behaviour and community structure in an economical and minimally invasive way (Rovero and Zimmermann, 2016). Animal density is an extremely informative parameter in community ecology, providing data for monitoring temporal trends in population status and comparing populations across sites (Nichols and Williams, 2006), crucial information for effective wildlife conservation.

The first density estimators based on camera trap footage were designed for large, individually recognizable species, using a *Capture-Recapture* (CR) framework (Karanth and Nichols, 1998). The method was applied to few mammals, mainly felids identified by their coat pattern (Karanth, 1995; Jackson et al., 2006). However, defining the effective surveyed area was problematic and CR methods estimated population size within an area of unknown size, rather than density (Sollmann, Mohamed and Kelly, 2013). *Mark-reSight* methods (MS) (Rich et al., 2014) and *Spatially Explicit Capture-Recapture* methods (SECR) (Efford, Borchers and Byrom, 2009) were a big improvement. By estimating the area effectively sampled, density estimates became statistically valid (Sollmann et al., 2014). However, requiring at least a proportion of individuals to be recognizable, they were not applicable to all species. Recently, the development of statistical estimators of animal density has overcome these limitations. SECR methods have been extended allowing density estimates of unmarked populations (Chandler and Royle, 2013). Here, sampling effort must be spatially intensive and estimates lack precision unless supplemented with auxiliary data such as genetic sampling or telemetry (Sollmann et al., 2014; Evans and Rittenhouse, 2018; Linden, Sirén and Pekins, 2018). *Random Encounter Models* (REMs) (Rowcliffe et al., 2008) were considered a promising development. REMs assumed a certain detection within an estimated area in front of the camera and, by using Hutchinson and Waser's gas model (2007) to describe animal movement, required estimates of average animal speed for estimating animal density. Animal speed however, is hard to estimate accurately , and REMs broad applicability is still being tested (Sollmann, Mohamed and Kelly, 2013; Chauvenet et al., 2017). To address these issues, recent studies have used a modified version of REMs. Nakashima, Fukasawa and Samejima (2017) replaced animal speed with the time detected animals remain in the camera field of view (obtained from recorded videos), whereas Campos-

Candela et al., (2017) in a simulation study and Moeller, Lukacs and Horne (2018) in a study on elks (*Cervus canadensis*), circumvented the need for animal average speed by collapsing sampling occasions into predetermined instantaneous moments where the surface covered by the camera field of view was known and 100% detectability assumed. Although these methods were a promising development for estimating density of unmarked species, they remain to be tested in various field situations and, as some (e.g. Nakashima, Fukasawa and Samejima (2017); Campos Candela et al., (2017)) are mathematically demanding, broad applicability without a user-friendly software seems unlikely.

Camera trap Distance Sampling (CTDS) (Howe et al., 2017) is another recently proposed method for density estimations of unmarked populations. It uses a Distance Sampling (DS) approach (Buckland et al., 2001; 2015), adjusting point transect distance sampling to the use of camera traps. Similarly to Moeller et al., (2018) and Campos-Candela et al., (2017), CTDS makes use of predetermined instantaneous snapshot moments, but assumes 100% detection at 0 m only, accounting for imperfect detection by modelling detectability as a function of distance. In addition, CTs only detect animals when available, a problem when studying arboreal or subterranean species. Therefore, CTDS requires estimates of species-specific availability "*A*", i.e. the proportion of time a species is available for detection. So far, two methods have been used for estimating "*A*": 1) "*ACa*" (Cappelle et al., 2019) refers to the time of activity "T_i" with T_i being defined as the number of 1 hour-intervals with at least one video. 2) "*ARo*" (Rowcliffe et al., 2014) estimates "*A*" by fitting a circular kernel distribution to times of independent detections, with the peak of activity defined by the maximum value of the kernel distribution. Importantly, in both methods "*A*" is extracted from the same videos used for estimating density. CTDS was applied to wild populations of Maxwell's duiker *Philantomba maxwellii* (Howe et al., 2017), and Western chimpanzees *Pan troglodytes verus* in Taï National Park, Côte d'Ivoire (Cappelle et al., 2019) returning unbiased estimates for the latter. In addition, by using a DS approach, CTDS takes advantage of a consolidated mathematical framework, open-source software and a vast community of users and developers, making the method easily accessible. Therefore, CTDS could be considered among the most promising methods to assess animal density, particularly suitable for habitats where species taking advantage of dense vegetation for their cryptic existence are rarely encountered.

Our planet's tropical rainforests, particularly the Amazonian and the Congo basins, provide these features. Disappearing with unprecedented speed, ecological information for the vast majority of terrestrial vertebrates is urgently required (IUCN, 2020a). Central Africa's Congo basin provides 1,620,000 km^2 of evergreen rainforests, with 1,000 bird and 400 mammal species currently known (Campbell, 2005). Its heart, the *Cuvette Centrale*, 800,000 km^2 in size situated south of the Congo River, Democratic Republic of the Congo (DRC), has the continent's largest protected area of pristine African lowland rainforest: Salonga National Park (SNP), an IUCN World Heritage Site. Here, we estimate vertebrate density by applying CTDS to the large and remote South block of Salonga National Park, assessing applicability of the methodology in relation to species-specific properties such as 1) size; 2) activity patterns; 3) sociality; 4) abundance; 5) distribution, and 6) reactivity to CTs. The latter referring to any responsive behaviour occurring because of the presence of an observer (i.e. the CTs) causing the animal to modify its travelling trajectory. This either by moving away from the camera (avoidance), by approaching it (attraction), or by stopping, standing in front of the camera.

2.3. Materials and methods

2.3.1. Study area

Salonga National Park (36,000 km^2), situated in the *Cuvette Centrale*, DRC (Figure 2.1a), consists of two blocks, North and South. We investigated block South (17,127 km^2), composed of 99% of primary lowland mixed forest, 1% of savannahs, regenerating forest, cultivation, marshes and water bodies (Bessone et al., 2019).

2.3.2. Data collection

Camera trap data were collected between September 2016 and May 2018 as part of a comprehensive biodiversity inventory (PNS-Survey©), conducted along 405 systematically placed sample units (i.e. line transects), generated from a random origin. The 1 km transects running east-west were evenly spaced by 6 km (Figure 2.1b). Two infrared camera traps (Bushnell Trophy CamTM, Model 119776), with angle of view θ = 45° and inter-trigger lag time = 1 s, were set up at 250 m and 750 m from the beginning of each transect (Figure 2.1c). To avoid disturbance caused by the passage of field teams, cameras were systematically positioned 50 m to the north or south of the transect line, oriented north between 70 and 90 cm above ground. Given the size of SNP and the limited number of devices (n = 160), the study area was divided into 37 sub-areas covering 380 km^2 on average (range = 72 – 1,188 km^2, SD = 274.8), each surveyed once. CTs were relocated to a new sub-area after a minimum of two weeks (average = 38.4 days, range 14 – 78, SD = 12.4). Of the 405 transects, 27 were not surveyed due to their proximity to major rivers, or armed poachers, resulting into 378 surveyed line transects (Figure 2.1B). Due to logistical constraints, one transect remained without, and four transects with only one CT each, resulting in 750 sampling locations. Time of installation, habitat type and GPS location were noted for each device. Cameras were active 24h/day and sensor sensitivity was set to “high”. For a discussion of potential limitations of our survey design, see Box 2.1.

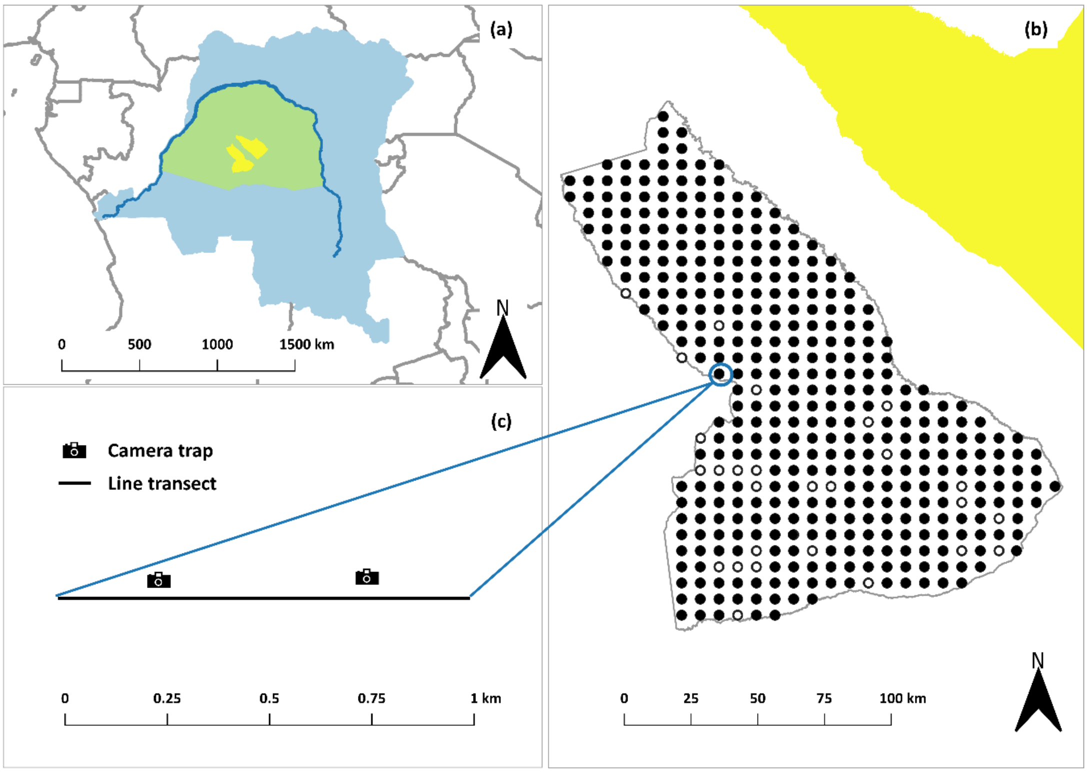


Figure 2.1. Location and Survey Design: *A)* Democratic Republic of the Congo (DRC; light blue) with Congo River (blue line), *Cuvette Centrale* (green) and Salonga National Park (SNP; yellow); *B)* SNP, block South with surveyed (black dots) and unsurveyed (white dots) line transects; *C)* Camera trap locations along line transect.

2.3.3. *Camera trap distance sampling*

2.3.3.1. Measurements

Following Howe et al., (2017) we measured distances between the CT's lens (i.e. 0m) and the midpoint of each detected animal (= radial distances) in each video at predetermined snapshot moments (= observations) by comparing animal locations to 1 m distance labels recorded during camera installation (from 1 to 12 m). Predetermined snapshot moments represent observations at specific times of day, starting with a snapshot at midnight 00h 00min 00sec with an interval between snapshots "*t*" set to 2 seconds, a value considered appropriate to obtain adequate sample sizes even for fast moving and rare species (Howe et al., 2017). Temporal effort is then determined by the value of *t* (the longer "*t*", the lower the effort - see Box 2.2).

We expected that species-specific features could potentially affect CTDS estimates. Therefore, for each observation we also recorded 1) individual maturity (immature / adult), 2) animal group size, and 3) reactive behaviours (see Box 2.3).

2.3.3.2. Species-specific availability

We corrected for species-specific availability "A" applying 1) "ACa" Cappelle et al., (2019); and 2) "ARo" Rowcliffe et al., (2014), calculating *ARo* by using the R package "activity" (R Core Team, 2019) (Figure 2.9). In order to ensure independence of observations of times of detection we used the number of capture events, defined as the first video recording the same individual / animal group, while subsequent videos of the same individual / group were discarded. A new event was recorded when a different individual / animal group entered the field of view.

2.3.3.3. Density estimation

Densities were estimated by applying the formula of Howe et al., (2017) (see Box 2.2 for further details). All operational days, excluding days of camera installation and retrieval, were considered when calculating survey effort. As reactivity to CTs is expected to induce bias (Buckland et al., 2001; 2015), we discarded all observations where animal behaviour indicated a reaction to CTs. Then, we left and / or right-truncated each dataset after visual inspection of the histogram of observed radial distances Fig 2.8. We fitted the detection functions to the remaining radial distances and calculated species-specific density in Distance 7.3 (Buckland et al., 2001; 2015), correcting for both *ACa* and *ARo,* and considered 6 CTDS models (half normal with 0 and 1 hermite polynomial adjustment terms; hazard rate with 0 and 1 cosine adjustments terms; uniform with 1 and 2 cosine adjustment terms). In CTDS violation of the assumption of independence of observations is expected. Violation does not affect point estimates of abundance (Buckland et al., 2001; 2015), but introduces "over-dispersion", which is partially addressed by defining predetermined instantaneous snapshot moments (Howe et al., 2017; Moeller et al., 2018). In addition, the assumption can be relaxed by estimating variances using a nonparametric bootstrap, resampling points with replacement (Buckland et al., 2001; 2015), and by using model selection methods adjusted for over-dispersed data. Accordingly, we estimated variance from 999 bootstrap resamples, with replacement across camera locations, and selected between competing models comparing QAIC scores, following a two-step method (Howe et al., 2019).

2.3.4. *Considered species*

Recorded species were considered suitable for density estimation if 1) the number of independent capture events was ≥ 20; 2) the number of recorded radial distances was ≥ 80 (Buckland et al., 2015). To test general applicability of the method, we selected species showing differences in size, activity, abundance and distribution patterns. Information on the following species-specific traits was acquired from published literature: 1) body mass, a proxy of body size (Smith et al., 2003); 2) activity pattern (diurnal, nocturnal or crepuscular); 3) sociality (gregarious or solitary); 4) expected abundance; 5) expected distribution (homogeneous or heterogeneous), (2-5: (Kingdon et al., 2013)); and 6) conservation status (IUCN, 2020a).

Box 2.1. Survey design limitations

The size of SNP block South prevented us from surveying the whole study area simultaneously, suggesting violation of the assumption of population closure. However, DS estimates are not severely affected by this violation (Buckland et al., 2001; 2015), and with our sampling locations covering an area of 36 km^2 each, area size is larger than home ranges published for 12 of the 14 species considered (Table 2.8). The remaining two were the elephant and the honey badger. Elephants can range over territories larger than 1000 km^2 (Blake et al., 2009). Thus, same individuals could have been detected in different sub-areas. However, elephants can be individually recognized by morphological characteristics (Goswami et al., 2012). When investigating our video footage, we did not detect double captures across sub-areas. Honey badgers were reported to have home ranges as large as 500 km^2 (Begg et al., 2005) in savannahs. Our average sub-area was 380 km^2 and rain-forest counterparts are likely to have smaller home-ranges (e.g. chimpanzee (Lindshield et al., 2017)), due to seasonality being less pronounced close to the equator. Therefore, double detections were unlikely as were dramatic fluctuations in population size over the 18 months of our study.

Box 2.2. *Estimating animal density with CTDS*

We estimated densities applying the following formula (Howe et al., 2017):

$$\widehat{D}= \frac{n_k}{\pi w^2 \, e_k \widehat{P}} * \frac{1}{A}$$

where n_k is the number of observations at camera *k*, *w* is the maximum distance between object and camera considered or truncation distance, $\widehat{P}$ is the estimated probability of detection of an animal at a snapshot moment and $e_k = \frac{\vartheta T_k}{2\pi t}$ is the sampling effort at camera location *k*. Here, T_k is the sampling effort at camera *k* in seconds, *t* is the time interval of predetermined snapshot moments (set to 2 s), θ is the horizontal angle of view of the camera in radians (i.e. 0.785), so $\frac{\theta}{2\pi}$ represents the proportion of a circle covered by the camera (i.e. 0.125).

Finally, *A* is the specific availability. This value is required for species that spend part of their active time e.g. feeding in trees or hidden in shelters, hence not being always equally available for detection.

A is defined by Cappelle et al., (2019) as:

$$ACa= \frac{n_T}{T_i * n_p}$$

where n_T is total number of videos of a species, T_i is the activity time represented as number of 1-hour intervals when the species was recorded, n_p is number of videos at peak time.

A is defined by Rowcliffe et al., (2014) as:

$$ARo = \frac{a(fx)}{2\pi \, fmax}$$

where *fx* is a circular probability density function fitted to a set of videos recorded at particular times of day (in radians), and *fmax* (= peak of activity) is the tangent to the maximum of *fx* in a 24-hour cycle (measured as radians from 0 (00:00:00h) to 2 π (23:59:59h). By assuming that in a 24-hour cycle, the entire population was continuously active at *fmax*, *ARo* is estimated as the ratio of the area under *fx* "*a(fx)"* and the area under *fmax* (Figure 2.2).

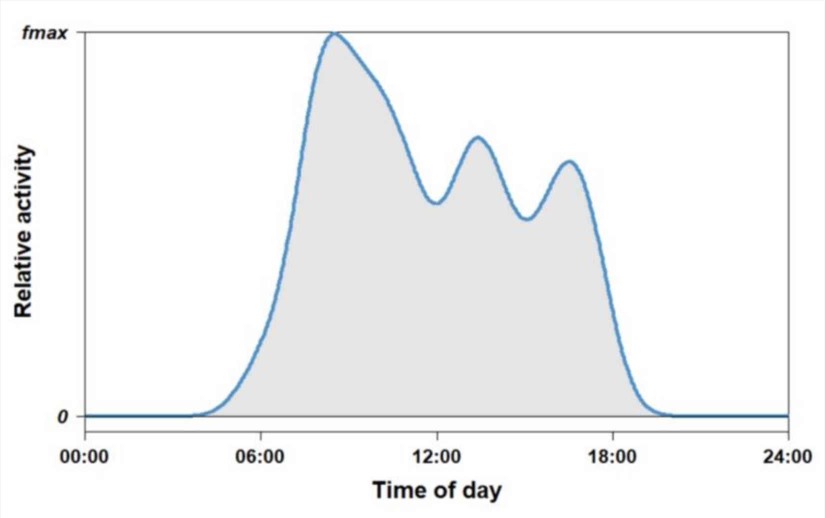
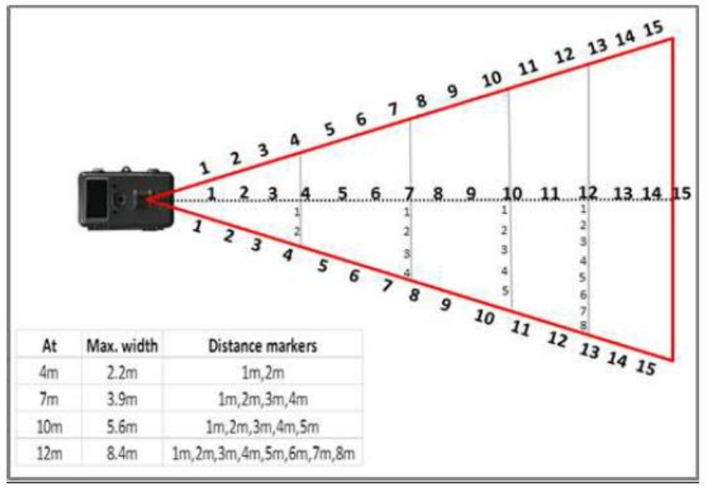


Figure 2.2. Species Specific Availability (*ARo)* exemplified for the Congo peafowl over a 24h-day following Rowcliffe et al., (2014). Availability is estimated as the ratio of the area under the blue line (*fx*) (shaded in grey), representing the relative species-specific activity extracted from video-clips, and the area within the rectangle (in white) defined by the maximum of the curve *(fmax)* equalling the peak of activity, and 0.

Box 2.3. *Measuring radial distances*

The application of CTDS requires the establishment of clearly visible distance categories. In practice, these were established using tape measures according to Figure 2.3, and by presenting numbered sheets for each metric interval in front of the active camera. Operators presenting the distance labels touched reference points (trees, branches, termite mounds, etc.) so that these specific areas could be easily identified during video-processing. These measurements were recorded on video-sequences (reference videos – Videos 1, 2, 3 and 4 in "Supporting Videos"), and used to measure the radial distance of the recorded animal to the camera at predetermined snapshot moments (cf. Video 5 in "Supporting videos"), by comparing animal locations to the 1 m distance labels (cf. "Supporting videos"). In Table 2.1, we provide an example of the data recorded at each snapshot moment (https://besjournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2F1365-2664.13602&file=jpe13602-sup-0013-VideoS1-S5.zip).

Figure 2.3. Measurements taken at indicated distance intervals from the camera-trap for reference videos (N'Goran et al., 2016).



At	Max. width	Distance markers
4m	2.2m	1m,2m
7m	3.9m	1m,2m,3m,4m
10m	5.6m	1m,2m,3m,4m,5m
12m	8.4m	1m,2m,3m,4m,5m,6m,7m,8m

Table 2.1. Radial distance and other relevant information recorded. Camera-trap: identifier of specific camera trap; Day: day of predetermined snapshot moment (year/month/day); Time: time of predetermined snapshot moment (hours: minutes: seconds); Individual: identifier for each individual within the field of view at Time of Day; Radial distance: Distance from Camera to individual at Time of Day; Age class: adult / immature for each individual at Time of Day; Reaction: Observation on reactivity to camera (yes = reacting ; no = non reacting)) of each individual at Time of Day.

Camera-trap	Day	Time	Individual	Radial distance	Age class	Reaction
C1_T159	2017/05/23	9:46:26	1	4.5	Adult	no
C1_T159	2017/05/23	9:46:28	1	4.5	Adult	no
C1_T159	2017/05/23	9:46:30	1	4.5	Adult	no
C1_T159	2017/05/23	9:46:32	1	4.5	Adult	no
C1_T159	2017/05/23	9:46:34	1	4.5	Adult	no
C1_T159	2017/05/23	9:46:36	1	4.5	Adult	no
C1_T159	2017/05/23	9:46:36	2	2.5	Immature	no
C1_T159	2017/05/23	9:46:38	1	5.5	Adult	no
C1_T159	2017/05/23	9:46:38	2	2.5	Immature	no

2.4. Results

A total of 160 camera traps were fully functional and active at 743 locations. Total effort was 27,045 camera days, returning 16,734 videos showing animals belonging to 43 different taxa (Appendix 1). Average number of species per location was 4.7 (range 0 – 24, SD = 3.04). Of these 43 taxa, 29 provided adequate data for density estimation. Table 2.2 shows 14 out of these, selected due to their differences in biological (body mass), behavioural (activity pattern, sociality), ecological (abundance, distribution) and conservation (IUCN status) traits. Except for the endemic Congo peafowl, all chosen species were mammals. Table 2.3 shows

species-specific information obtained from Camera Traps (CTs), including activity times, availability according to Cappelle et al., (2019) and Rowcliffe et al., (2014) (examples provided in Figure 2.4), as well as truncation distance. Detectability positively correlated with body size, with small-sized species being undetected within the first 2 m from the camera (Figure 2.5).

Table 2.2 Species (Common name, *scientific name*) selected for method evaluation. Body mass (average in kg; (Smith *et al.*, 2003)); Activity pattern (*sD* = strictly diurnal; *sN* = strictly nocturnal; *mD* = mainly diurnal; *mN* = mainly nocturnal; *Cr* = crepuscular); Sociality (*G* = gregarious; *S* = solitary); Approximate expected abundance (*n* per km²) available from literature; Distribution available from literature; IUCN status (IUCN, 2020a). * *Genetta servalina* and *G. maculata*; ** *Crossarchus alexandri* and *C. ansorgei*. References: Kingdon et al., (2013)

ID	Species	Body mass (kg)	Activity pattern	Sociality	Approximate expected abundance [*n* / km²]	Distribution	IUCN status
1)	Congo peafowl[(a)] *Afropavo congensis*	1.4	*sD*	*G*	Unknown	Homogeneous	VU
2)	Forest elephant *Loxodonta cyclotis*	3940.0	*mD*	*G*	0.05	Heterogeneous	EN
3)	Bonobo *Pan paniscus*	34.0	*sD*	*G*	0.42	Homogeneous	EN
4)	Allen's swamp monkey *Allenopithecus nigroviridis*	4.7	*sD*	*G*	100	Heterogeneous	LC
5)	Honey badger *Mellivora capensis*	8.0	*mD*	*S*	0.03	Homogeneous	LC
6)	African golden cat	10.6	*mD*	*S*	0.04 – 0. 1[(b)]	Homogeneous	VU

	Caracal aurata						
7)	Genets *Genetta sp.*	2.0 – 1.9[*]	*sN*	*S*	0.8 – 4.5[*]	Homogeneous	LC
8)	Cusimanses *Crossarchus sp*	0.7 – 1.5[**]	*mD*	*G*	Unknown	Homogeneous	LC
9)	Aardvark *Orycteropus afer*	52.3	*sN*	*S*	1 – 2	Homogeneous	LC
10)	Giant ground pangolin *Smutsia gigantea*	33.0	*sN*	*S*	Unknown	Unknown	VU
11)	Sitatunga *Tragelaphus spekii*	78.0	*mD*	*S*	92 – 180	Heterogeneous	LC
12)	Water chevrotain *Hyemoschus aquaticus*	10.8	*sN*	*S*	1.5 – 5	Homogeneous	LC
13)	Brush-tailed porcupine *Atherurus africanus*	1.9	*sN*	*S*	2.4 – 13	Homogeneous	LC
14)	Four-toed sengi *Petrodromus tetradactylus*	0.2	*Cr*	*S*	210	Homogeneous	LC

a: McGowan, Kirwan and Sharpe (2019)

b: Bahaa-el-din et al., (2016)

Table 2.3 Species-specific information obtained from camera traps (CTs). Individual locations: Number of CT locations with detections > 0; Capture events: Number of video-clips; Total Radial distances: Total of measured radial distances; Radial distances “Immatures” (%): Number of radial distances of immature individuals (percentage of Total); Radial distances “Reactivity” (%): Number of radial distances of reactive individuals (percentage of Total); Activity time T_i [hr]: number of activity hours per 24h-day used when calculating specific availability after Cappelle et al., (2019); Availability *(ACa)*: specific availability calculated after Cappelle et al., (2019); Availability *(ARo)* (S.E.): specific availability (standard error) calculated over 24h after Rowcliffe et al., (2014); Truncation [m] left ; right: meter(s) of left and right-truncation of radial distances. * see Box 2.2.

ID	**Species**	**Individual locations**	**Capture events**	**Total Radial distances**	**Radial distances “Immatures” (%)**	**Radial distances “Reactivity” (%)**	**Activity time T_i [hr]***	**Availability (*ACa*)***	**Availability (*ARo*) (S.E.)***	**Truncation [m] left ; right**
1)	Congo peafowl	73	137	3,104	249 (8%)	240 (8%)	12	0.57	0.34 (0.04)	1 ; 8
2)	Forest elephant	14	20	840	68 (8%)	676 (80%)	24	0.15	0.34 (0.10)	0 ; 12
3)	Bonobo	66	100	5,604	1,376 (25%)	515 (11%)	14	0.45	0.34 (0.05)	0 ; 12
4)	Allen’s swamp monkey	12	49	1,067	81 (17%)	209 (19%)	12	0.31	0.39 (0.04)	3 ; 8
5)	Honey badger	18	21	217	None	48 (22%)	11	0.38	0.28 (0.07)	0 ; 7
6)	African golden cat	23	25	84	None	6 (7%)	13	0.34	0.45 (0.07)	0 ; 7
7)	Genets	63	95	431	None	None	11	0.61	0.43 (0.03)	2 ; 7
8)	Cusimanses	24	34	1,301	72 (5%)	None	13	0.44	0.44 (0.06)	2 ; 7
9)	Aardvark	46	54	354	None	25 (7%)	12	0.45	0.31 (0.04)	0 ; 6
10)	Giant ground pangolin	15	24	119	None	None	11	0.50	0.40 (0.07)	1 ; 8
11)	Sitatunga	10	23	417	101 (24%)	None	14	0.41	0.64 (0.11)	0 ; 7
12)	Water chevrotain	38	152	1,462	None	None	12	0.61	0.34 (0.03)	1 ; 6
13)	Brush-tailed porcupine	140	527	1,765	48 (3%)	None	12	0.62	0.34 (0.02)	2 ; 8
14)	Four-toed sengi	7	40	216	None	None	13	0.31	0.28 (0.05)	2 ; 5

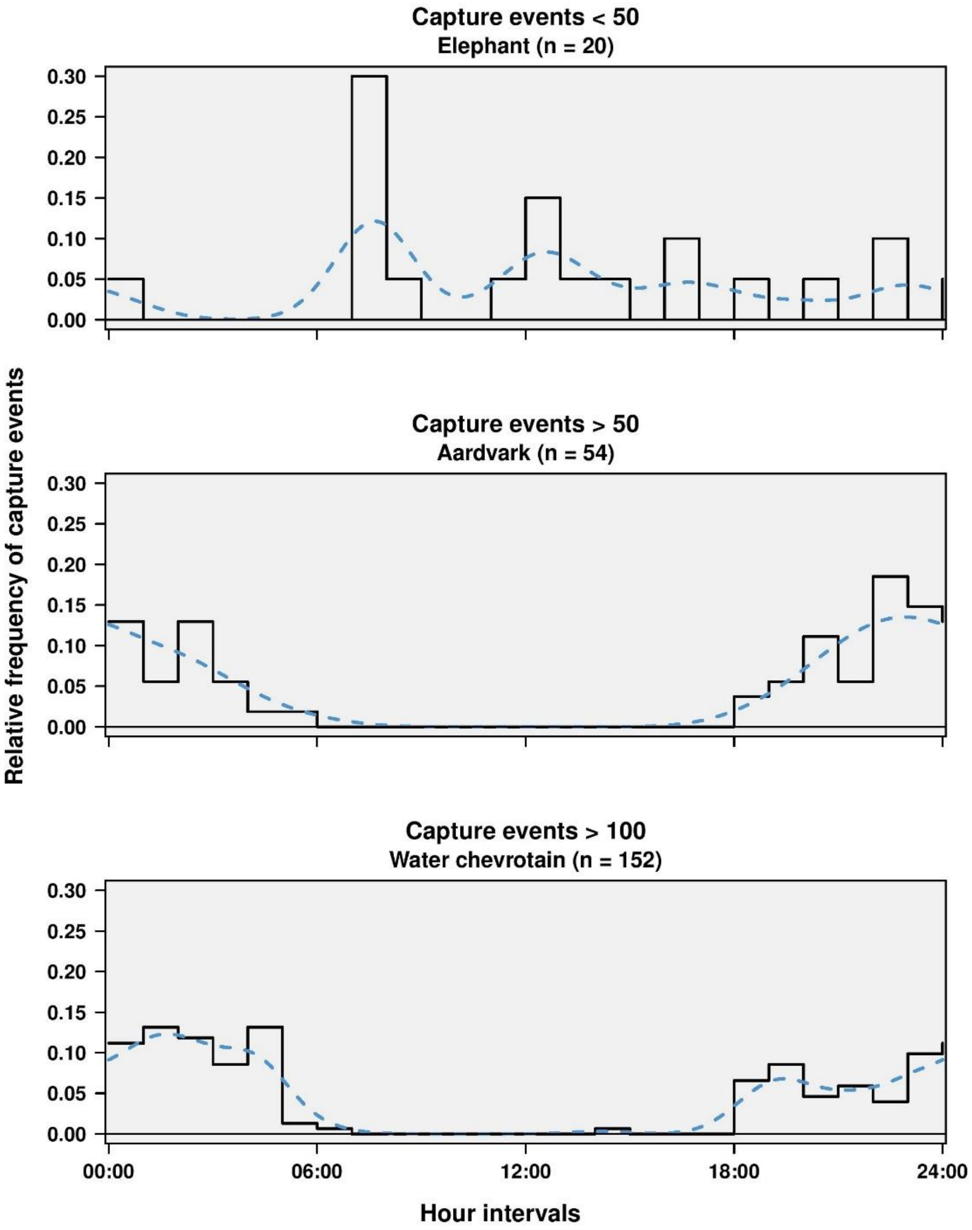


Figure 2.4. Camera trap-derived daily activity patterns for 1) Capture events < 50 (Elephant); 2) Capture events > 50 (Aardvark); 3) Capture events > 100 (Water chevrotain). Solid lines show availability (*ACa)* as relative frequency of capture events for each hour-interval according to Cappelle et al., (2019); Dashed blue lines show availability (*ARo)* as relative frequency of capture events fitted over 24 hours according to Rowcliffe et al. (2014).

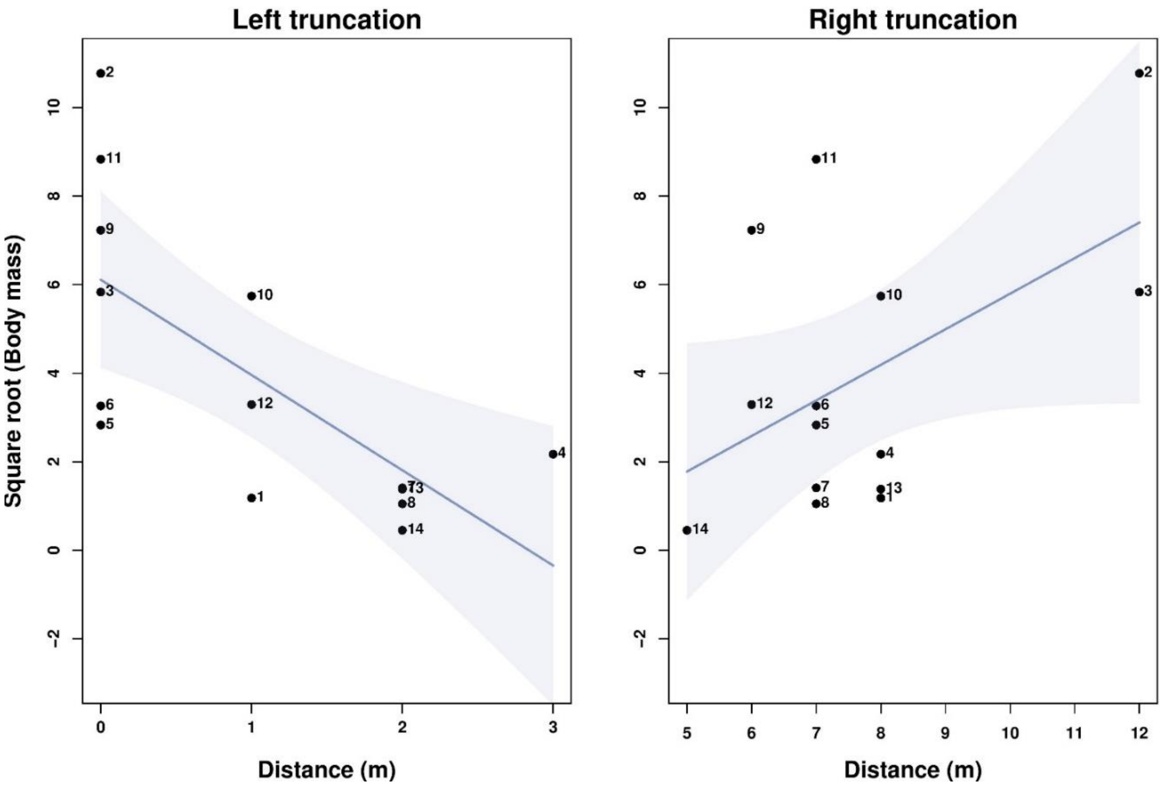


Figure 2.5. Species-specific truncation distances (m) for Left-truncation (left); and Right-truncation (right). Blue lines represent linear regression (left-truncation $R^2 = 0.48$, $p < 0.01$; right-truncation $R^2 = 0.19$, $p = 0.07$) with 95% confidence intervals (light blue areas). Black dot with number indicates species; numbers see "ID" in Table 1.

Of the 14 species, immature individuals were never detected in seven, made up less than 10% of observations in another four, and more than 10% in three species only (Table 2.3). Therefore, we decided to exclude observations of immature individuals, providing population estimates for adults only. Three different types of reaction to CTs (i.e. attraction, avoidance and olfactory) were recognised in seven species (Table 2.3); examples are provided in Figure 2.6.

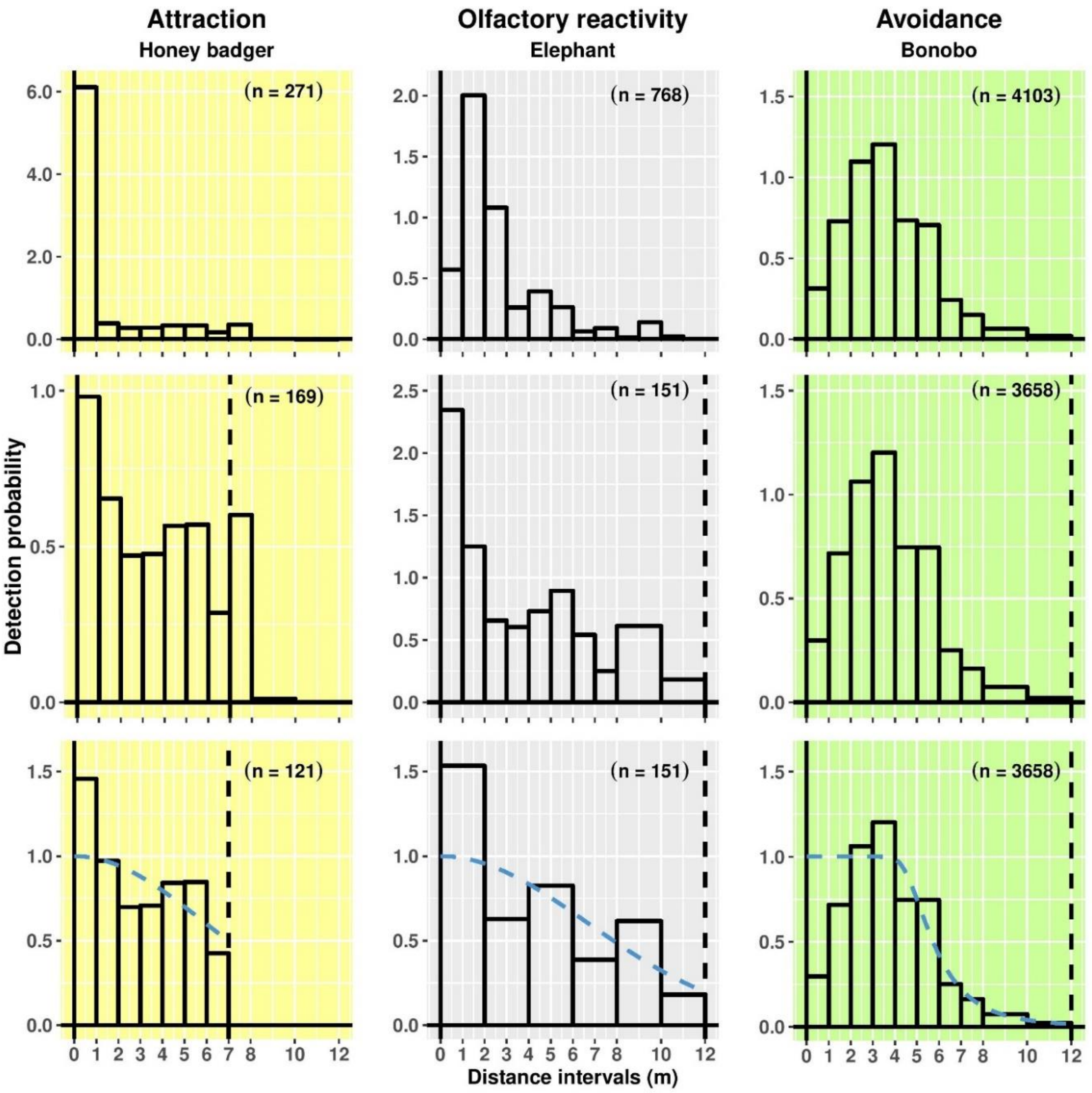


Figure 2.6. Reactivity to camera traps (CTs). Columns: Left (yellow): Attraction (honey badger); Middle (grey): Olfactory (elephant); Right (green): Avoidance (bonobo). Rows: Top: reactive observations included; Middle: reactive observation excluded; Bottom: final fitted model after right-truncation (honey badger); binning (elephant); as is (bonobo). Bars provide relative frequency of detections per distance interval prior to truncation (reactivity observations included); Dashed black lines show distances of truncation; Dashed blue lines detection probability as a function of distance (1.0 = 100%) after truncation (reactivity observations were discarded).

Table 2.4 shows density estimates for each species after bootstrapping, corrected for species-specific activity patterns, providing selected model and Coefficient of Variation.

Table 2.4 Species-specific density estimates. Selected model for density estimation showing a) key function (HN = Half normal; HR = Hazard rate; UNI = Uniform); b) series expansion (*co* = cosine; *hp* = hermite polynomial); c) adjustment terms; Radial distances (=observations): Number of measurements after truncation and discarding of immatures and reactive individuals ; Density (*ACa*) [ind/km^2] (95% Cis): Density of mature individuals per km² corrected for availability using *ACa* (Cappelle et al., 2019) with 95% confidence intervals (Cis); Density (*ARo*) [ind/km^2] (95% Cis): Density of mature individuals per km² corrected for availability using *ARo* (Rowcliffe et al., 2014) with 95% confidence intervals (Cis); CV: *ACa ; ARo*: Estimated coefficient of variation for 1) Density (*ACa*), 2) Density (*ARo*).

ID	**Species**	**Selected model a; b; c**	**Radial distances**	**Density (*ACa*) [*ind*/km^2] (95% Cis)**	**Density (*ARo*) [*ind*/km^2] (95% Cis)**	**CV: *ACa ; ARo***
1)	Congo peafowl	UNI ; *co* ; 1	2,383	**0.91** (0.66 – 1.27)	**0.76** (0.55 – 1.06)	0.17 ; 0.17
2)	Forest elephant	HN ; *hp* ; 0	151	**0.03** (0.01 – 0.07)	**0.02** (0.01 – 0.03)	0.44 ; 0.45
3)	Bonobo	HR ; *co* ; 0	3,658	**0.70** (0.32 – 1.53)	**0.54** (0.24 – 1.21)	0.41 ; 0.43
4)	Allen's swamp monkey	HN ; *hp* ; 0	691	**0.53** (0.24 – 1.14)	**0.20** (0.09 – 0.43)	0.41 ; 0.40
5)	Honey badger	HN ; *hp* ; 0	121	**0.05** (0.02 – 0.09)	**0.03** (0.01 – 0.06)	0.39 ; 0.41
6)	African golden cat	HN ; *hp* ; 0	78	**0.04** (0.02 – 0.07)	**0.02** (0.01 – 0.03)	0.36 ; 0.36
7)	Genets	HN ; *hp* ; 0	374	**0.27** (0.17 – 0.43)	**0.18** (0.11 – 0.28)	0.24 ; 0.23
8)	Cusimanses	HN ; *hp* ; 0	1,104	**1.16** (0.58 – 2.36)	**0.62** (0.31 – 1.26)	0.37 ; 0.37
9)	Aardvark	HN ; *hp* ; 0	255	**0.20** (0.10 – 0.34)	**0.15** (0.09 – 0.26)	0.27 ; 0.28
10)	Giant ground pangolin	HN ; *hp* ; 0	112	**0.05** (0.02 – 0.13)	**0.03** (0.01 – 0.08)	0.50 ; 0.54
11)	Sitatunga	HN ; *hp* ; 0	253	**0.12** (0.03 – 0.42)	**0.07** (0.02 – 0.25)	0.71 ; 0.74
12)	Water chevrotain	HN ; *hp* ; 0	1,250	**0.72** (0.38 – 1.35)	**0.68** (0.37 – 1.27)	0.33 ; 0.32
13)	Brush-tailed porcupine	HN ; *hp* ; 0	1,624	**0.71** (0.48 – 1.03)	**0.64** (0.44 – 0.96)	0.20 ; 0.20
14)	Four-toed sengi	HR ; *co* ; 0	191	**289.46** (2.67 – 31,294.00)	**181.09** (2.16 – 15,177.00)	17.20 ; 12.71

ACa corrected estimates consistently provided higher densities than *ARo*, with *ACa* and *ARo* corrected estimates being similar with at least 100 capture events (Table 2.3 and Figure 2.7). Estimates' precision significantly improved with a higher number of individual locations with at least one capture event (log-transformed – $R^2 = 0.63$; $p < 0.01$).

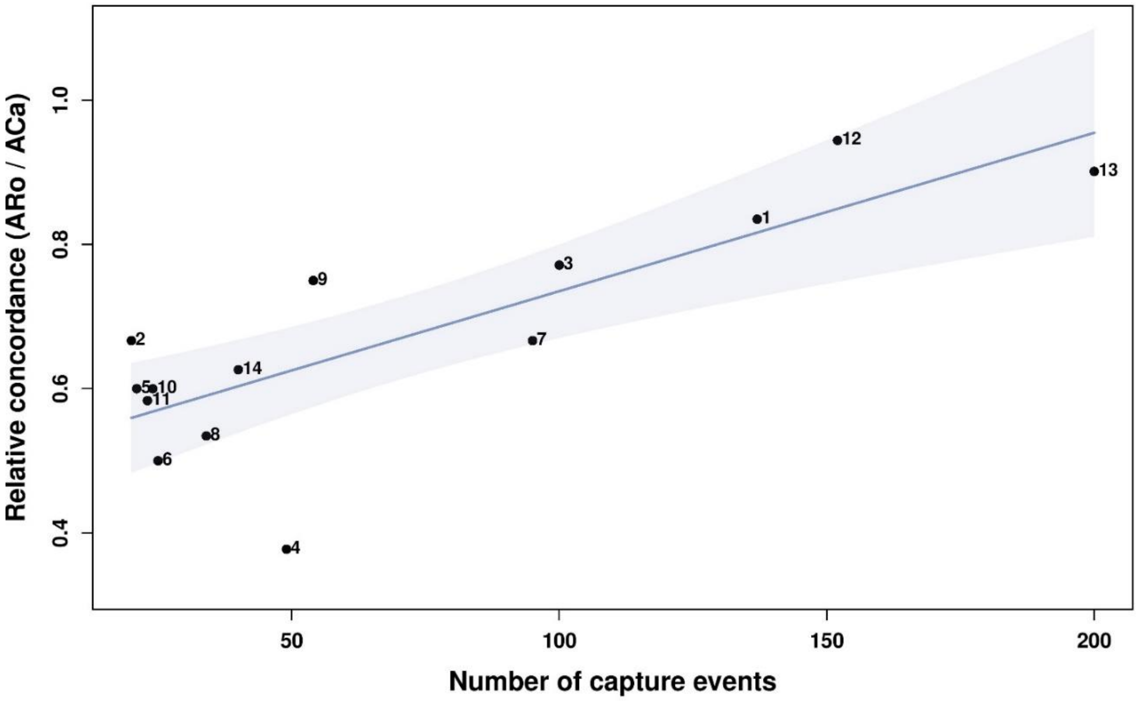


Figure 2.7. Relative species-specific concordance of density estimates corrected with *ARo* (Rowcliffe et al., 2014) and *ACa* (Cappelle et al., 2019) by number of capture events. Relative accordance (*ARo* / *ACa*): 1.0 = 100% accordance. Blue line represents linear regression ($R^2 = 0.62$, $p < 0.01$) with 95% confidence intervals (light blue area). Black dot with number indicates species; numbers see "ID" in Table 2.1.

A similar trend, with precision increasing with higher numbers of recorded radial distances or estimated densities, was not significant (see Figure 2.8). These results were confirmed by a multiple regression analysis, where precision was modelled as a function of the three aforementioned variables (see Table 2.5), suggesting precision was mainly driven by the number of individual locations and sample size.

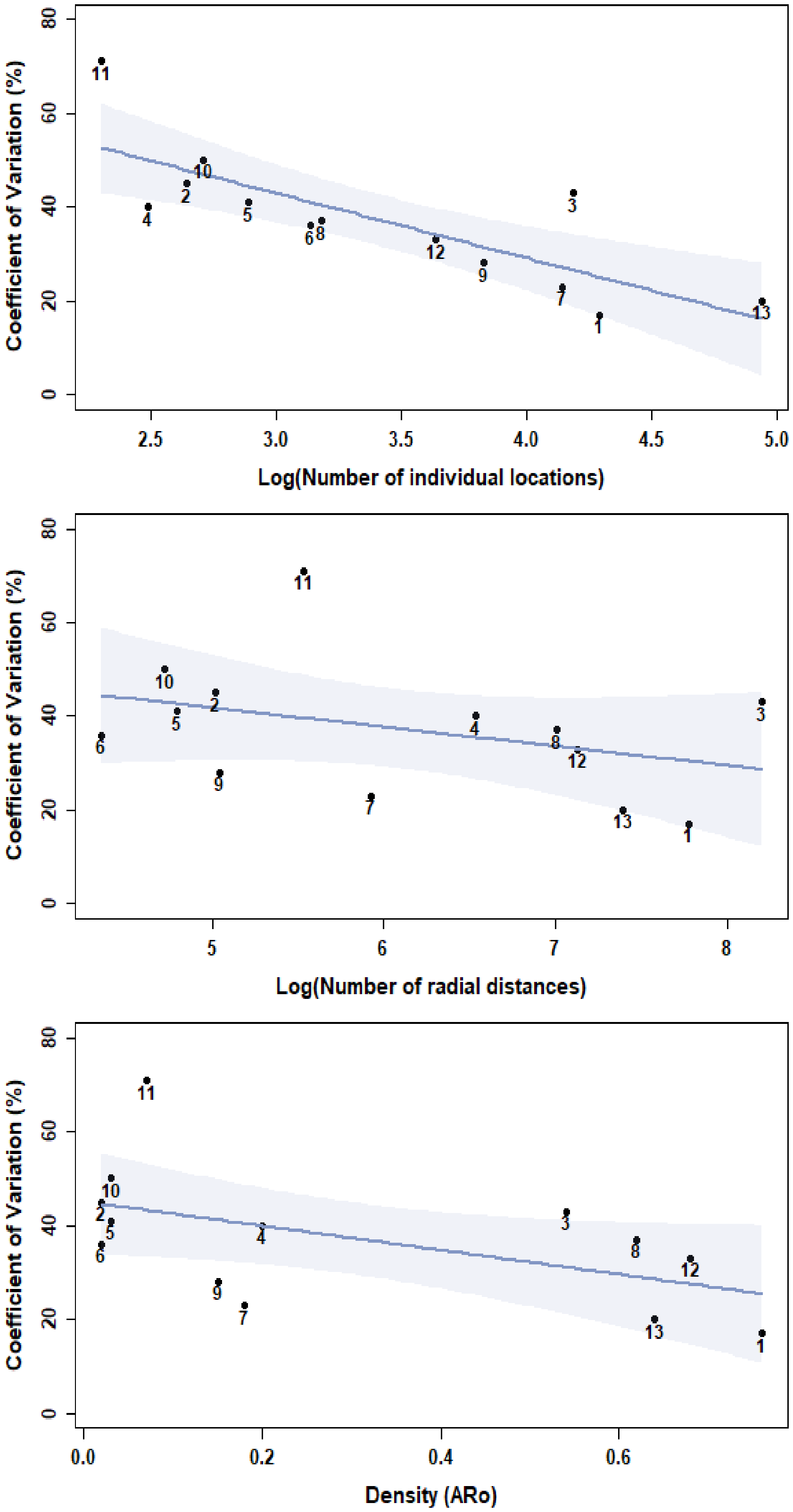


Figure 2.8 Relative species-specific precision (Coefficient of variation (%)) as a function of 1) log-transformed number of individual locations with at least one capture event (top – R^2 = 0.60; p < 0.01); 2) log-transformed number of radial distances used in the analysis (centre – R^2 = 0.14; *p* = 0.21); 3) density corrected for availability with *ARo* (Rowcliffe et al., 2014) (bottom – R^2 = 0.19; *p* = 0.08). After visual exploration of diagnostic plots for outlier and leverage, the Four-toed sengi data point (CV = 1271%) was excluded from analyses. Blue lines represent linear regression with 95% confidence intervals (light blue area). Black dot with number indicates species; numbers see “ID” in Table 1.

Table 2.5. Multiple linear regression ($R^2 = 0.71$; F = 5.16 (7,5); $p = 0.04$) predicting density estimate precision (i.e. coefficient of variation) as a function of seven explanatory variables (all log-transformed): 1) "Density (*ARo*)": density of mature individuals per km² corrected for availability using *ARo* (Rowcliffe et al., 2014); 2) "Locations": number of CT locations with detections > 0; 3) "Radial distances": total of measured radial distances used in the analysis; 4) "Density (*ARo*) **:** Locations": interaction of density (*ARo*) and number of individual locations; 5) "Density (*ARo*) : radial distances": interaction of density (*ARo*) and number of measured radial distances; 6) "Locations (n) : radial distances": interaction of number of individual locations and number of measured radial distances; 7) "Density (ARo) : Locations : Radial distances": interaction of density (*ARo*) and number individual locations and number of measured radial distances. *Estimated B*: estimated regression slopes*; S.E.*: standard error of estimated regression slopes B; *p value*: significance of explanatory variable (weakly significant values ($p < 0.1$) in bold). The Four-toed sengi (CV = 1,271%) was excluded from analyses after visual exploration of diagnostic plots for outlier and leverage (high leverage exerted). Such a large C.V was possibly mainly due to the small number of individual capture locations (n = 7, see Table 2.3), or to poor reliability of the detection function for this species, modelled using observations between 2 and 5 m only.

Explanatory variables	***Estimated B***	**S.E.**	**p value**
Intercept	957.82	399.41	**0.06**
1) Density (ARo)	47.29	110.48	0.69
2) Locations	-235.70	103.08	**0.07**
3) Radial distances	-118.83	54.39	**0.08**
4) Density (ARo) : Locations	-0.19	33.40	0.99
5) Density (ARo) : Radial distances	-4.17	17.91	0.82
6) Locations (n) : Radial distances	29.72	13.90	**0.08**
7) Density (ARo) : Locations : Radial distances	-3.35	5.50	0.57

2.5. Discussion

Our results are the first application of CTDS to a multi-species animal community and show the enormous potential of this method for biomonitoring. However, as in other CTs studies (Burton et al., 2015), biological, ecological and behavioural features affected specific detectability. In the following, we will discuss how six of these features could influence the applicability of CTDS: 1) body size/mass; 2) sociality; 3) activity pattern; 4) distribution; 5) abundance and 6) reactivity to the camera.

2.5.1 Body size / mass

Our results confirm previous studies (Tobler et al., 2008; Rowcliffe et al., 2011; Sollmann, Mohamed and Kelly, 2013), showing that body-size positively correlates with detectability (Table 2.3 and Figure 2.5). In such cases, we left-truncated our data when estimating density, a method known to effectively address low detectability at short distances (Buckland et al., 2001; 2015). However, left- truncation implies loss of data needed for achieving accurate estimates, especially for rare species. Therefore, we suggest that deploying cameras at a height of 50 cm above ground would increase detection rates of small-sized species. Although surprisingly found to be detected imperfectly within the first 2 m from the CT despite an average shoulder height of 95 cm (Figure 2.6), left-truncation was not applied to the bonobo, for reasons explained later ("2.5.6. Reactivity to camera"). As expected, elephants were detected at short distances. However, given their size both body length and width were considered when measuring radial distances, and fit was improved by binning data in 2 m intervals (Figure 2.6).

2.5.2. Sociality

When applying distance sampling to gregarious species, detection rates may be inflated, as detecting the first animal in a group increases the probability of detecting others (Treves et al., 2010). However, we found no clear evidence for overestimated density in gregarious species (Table 2.6) and obtained satisfactory coefficients of variation (< 25%) for both brush-tailed porcupine (solitary) and Congo peafowl (gregarious), with low precision equally affecting solitary and gregarious species when capture events were rare (Table 2.4).

Table 2.6. Density estimates as (in bold) for five gregarious species, using two different methodological approaches to CTDS. Density (*ARo*) [*ind*/km^2] (95% Cis; C.V.): species-specific density of mature individuals per km^2 corrected for availability using *ARo* (Rowcliffe et al., 2014) with 95% confidence intervals (CIs); Species (median group size; average group size; SD). Method 1: conventional CTDS; Method 2: *Group size covariate* (radial distances measured to the group centre and group size included as covariate (Plumptre and Cox, 2006)).

	Species				
	Congo peafowl (1 ; 1.73; 2.54)	*Forest elephant (1 ; 1.75; 0.94)*	*Bonobo (2 ; 2.74; 2.05)*	*Allen's swamp monkey (1 ; 1.90; 2.42)*	*Cusimanses (2 ; 2.24; 4.66)*
Method 1: conventional CTDS	**0.76** (0.55 - 1.06; 0.17)	**0.02** (0.01 - 0.03; 0.45)	**0.54** (0.24 - 1.21; 0.43)	**0.20** (0.09 - 0.43; 0.41)	**0.62** (0.31 - 1.26; 0.37)
Method 2: group size covariate	**0.67** (0.45 - 1.00; 0.21)	**0.02** (0.01 - 0.03; 0.37)	**0.52** (0.24 - 1.16; 0.42)	**0.21** (0.09 - 0.40; 0.41)	**0.50** (0.26 - 0.97; 0.34)

2.5.3. Activity patterns

Although differences in the specific availability calculated according to Cappelle et al., (2019), and Rowcliffe et al., (2014) were minor with large sample sizes, *ARo* presented major advantages: 1) calculations provided standard errors of estimated availabilities (that could be included in the estimation of total variance of density) and 2) values appeared to be less influenced by the peak of observation and stochasticity (Figure 2.4 and Table 2.3). Both methods rely on the assumption that at peak time, 100% of the population is available for detection (Rowcliffe et al., 2014), with asynchronous activity patterns of individuals within species leading to an overestimation of activity time, hence underestimated densities. Here, the visual analysis of the activity patterns obtained (Fig 2.9), seemed to suggest that the two carnivores (i.e. golden cat and honey badger) and the sitatunga might have shown asynchronous activity patterns in our study. *ARo* is consistently calculated over 24 hours, whereas *ACa* refers to the hour-intervals of observed activity, considering activity hours with one capture event only (Figure 2.4). In *ACa*, activity intervals may remain undetected due to low sample size, potentially causing underestimation of survey effort. For example, we observed elephants from 20 capture events only, revealing activity in 11 of 24 hour-intervals (Figure 2.4). Elephant activity however, is reported to occur throughout a 24h-day (Kely et al., 2019), suggesting we missed part of the species' activity time. While available knowledge could be used to interpret results according to species-specific ecology and behaviour, with *ARo* activity time fitted over 24 hours, additional sources of variation were avoided (Figure 2.4). In sum, sample sizes larger than 100 capture events allowed accurate and consistent estimates (Figure 2.7). Limited numbers of capture events however lead to underestimated *ACa*, inflating density values (Tables 2.3 and 2.4). Therefore, we recommend longer CT deployment, allowing a minimum of 100 capture events per species and the use *ARo* (Rowcliffe et al., 2014) for the calculation of specific availability. Unless supported by large enough sample sizes, comparing specific availability and density estimates across different studies is precarious and should be performed with care.

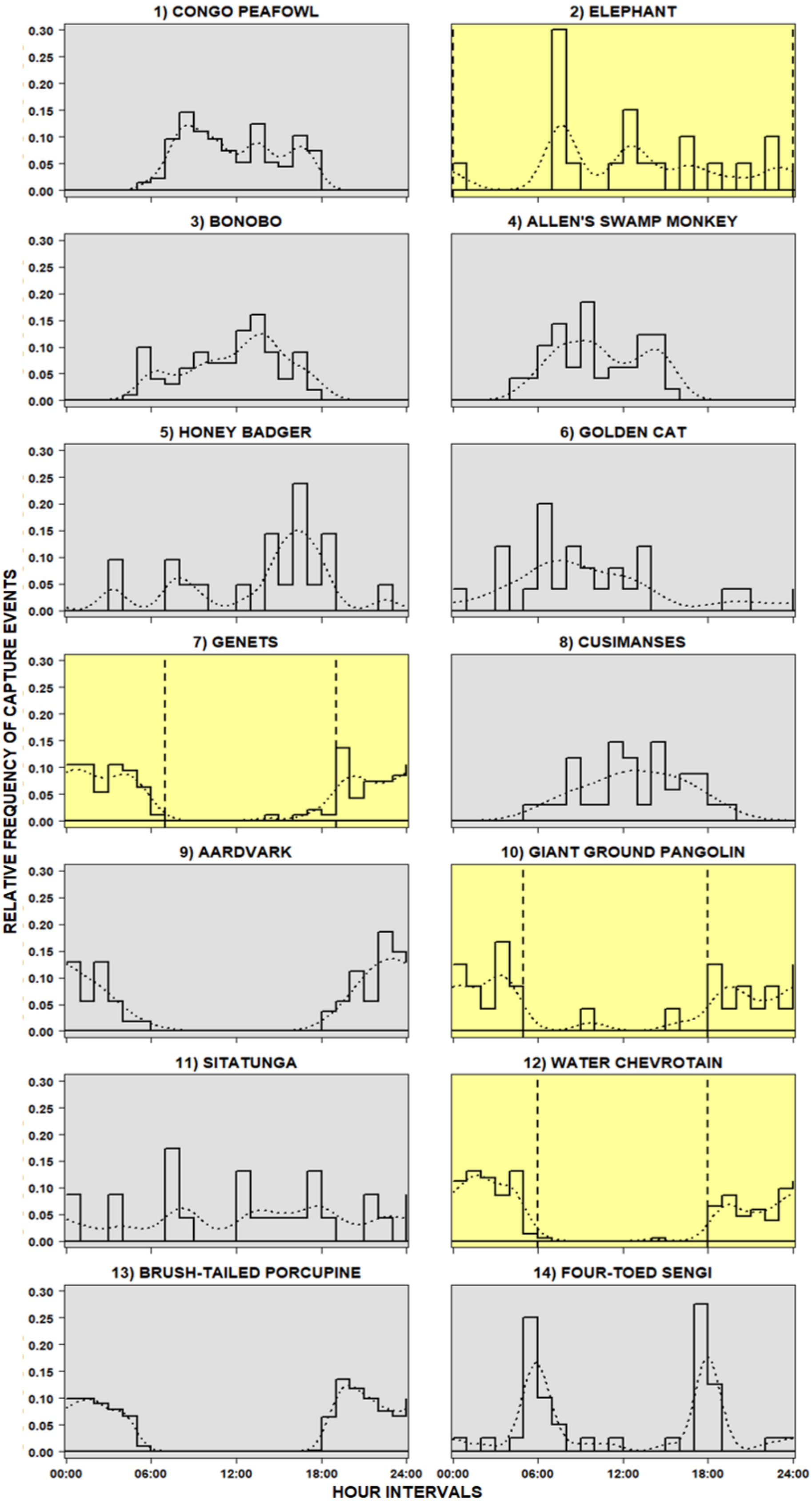


Figure 2.9. Species specific activity patterns PNS survey© 2016-2018. Bars show the relative frequency of capture events for each hour-interval; Vertical dashed lines show time-period considered (*ACa* analysis); Dotted line shows fitted availability function (*ARo* analysis). Plot colours: grey = all 1-hour intervals with capture events > 0 included in *ACa* calculation; yellow = some 1-hour intervals included or excluded in A*Ca* calculation.

2.5.4. Distribution

We expected high variability in encounter rates for heterogeneously distributed species, leading to imprecise density estimates due to spatial variation (Buckland et al., 2001; 2015). In fact, all the species we expected being heterogeneously distributed (Table 2.2), showed a coefficient of variation > 40%, due to low sample size and observations obtained from very few locations (Table 2.4 – but see also Figure 2.8). Future research should aim at increased spatial effort with synchronous camera deployment to reduce potential bias and strengthen precision (Buckland et al., 2015). When this is not possible, a stratified random design might increase estimate precision (Foster and Harmsen, 2012).

2.5.5. Abundance

Consequently, while precision was more satisfactory for abundant species, it was also good (CV below 35%) for rare, but widespread species such as the genets and the aardvark (Table 2.4 and Figure 2.8), with precision being mainly a function of sample size (i.e. number of radial distances) and heterogeneous distribution (i.e. number of individual locations with at least one capture event - Table 2.5). When estimating density of abundant species, a limiting factor was the time required for distance measurements from video-clips. To reduce time of analysis, 1) snapshot interval t could be increased, or 2) observations may be restricted to peak of activity only (Howe et al., 2017). For validation, we compared the full with the reduced methods for all species, and obtained consistent densities despite increased snapshot intervals and peak of activity observations only (Table 2.7). However, in the case of rarer species, the application of these methods would further reduce the number of exploitable radial distances, making safe estimates impossible.

Table 2.7. Species-specific density estimates (in bold) of mature individuals per km^2 corrected for availability using *ARo* (Rowcliffe et al., 2014) with 95% confidence intervals (in italics) (CI); Coefficient of variation (CV) using different analytical effort and number of radial distances used in each analysis (NA = analysis not performed due to low sample size (n < 60 radial distances)). Method: Full: full effort with distance measurement at each 2s snapshot moment; Reduced snapshot moments: decreased effort by increasing time between snapshot moments 1) t = 6s , 2) t = 30 s , 3) t = 60s; Reduced activity focus; decreased effort by focusing on peak of activity only; Parameters (Hours ; *t*): Hours = number of hourly intervals considered in the analysis , *t* = interval between snapshot moments; Estimates corrected for availability based on Rowcliffe et al., (2014); no correction for availability is performed when considering only the peak of activity (all animals are assumed to be active).

METHOD		**Full model**		**Reduced snapshot moments**						**Reduced activity focus**	
Parameters		**24 hours ; t = 2 s**		**24 hours ; t = 6 s**		**24 hours ; t = 30 s**		**24 hours ; t = 60 s**		**1 hour ; t = 2 s**	
ID	**Species**	*Radial distances*	*Density* *95% CI* *CV*	*Radial distances*	*Density* *95% CI* *CV*	*Radial distances*	*Density* *95% CI* *CV*	*Radial distances*	*Density* *95% CI* *CV*	*Radial distances*	*Density* *95% CI* *CV*
1)	Congo peafowl	2,383	**0.76** *0.55 - 1.06* 17%	787	**0.76** *0.54 - 1.07* 17%	147	**0.71** *0.50 - 1.00* 18%	79	**0.74** *0.50 - 1.08* 20%	319	**0.84** *0.46 - 1.52* 31%
2)	Forest elephant	151	**0.02** *0.01 - 0.03* 45%	52	NA	12	NA	6	NA	19	NA
3)	Bonobo	3,658	**0.54** *0.24 - 1.21* 43%	1,175	**0.53** *0.21 - 1.03* 42%	234	**0.52** *0.18 - 1.08* 45%	121	**0.56** *0.21 - 1.20* 43%	492	**0.45** *0.12 - 1.71* 77%
4)	Allen's swamp monkey	691	**0.20** *0.09 - 0.43* 40%	225	**0.21** *0.09 - 0.48* 44%	44	NA	15	NA	104	**0.11** *0.02 - 0.56* 99%
5)	Honey badger	121	0.03 *0.01 - 0.06* 41%	40	NA	7	NA	4	NA	45	NA
6)	African golden cat	78	**0.02** *0.01 - 0.03* 36%	24	NA	9	NA	5	NA	16	NA

7)	Genets	374	**0.18** *0.11 - 0.28* 23%	123	**0.20** *0.12 - 0.32* 25%	26	NA	10	NA	61	**0.27** *0.08 - 0.90* 67%
8)	Cusimanses	1,104	**0.62** *0.31 - 1.26* 37%	362	***0.63*** *0.31 - 1.29* 37%	69	**0.61** *0.29 - 1.28* 39%	33	NA	122	**1.57** *0.04 - 60.81* 505%
9)	Aardvark	255	**0.15** *0.09 - 0.26* 28%	87	**0.15** *0.09 - 0.23* 25%	22	NA	14	NA	67	**0.31** *0.12 - 0.84* 52%
10)	Giant ground pangolin	112	**0.03** *0.01 - 0.08* 54%	36	NA	10	NA	9	NA	35	NA
11)	Sitatunga	253	**0.07** *0.02 - 0.25* 71%	80	**0.05** *0.01 - 0.16* 70%	15	NA	7	NA	117	**0.35** *0.07 - 1.68* 93%
12)	Water chevrotain	1,250	**0.68** *0.37 - 1.27* 32%	427	**0.68** *0.36 - 1.30* 34%	98	**0.72** *0.35 - 1.47* 38%	47	NA	184	**0.72** *0.29 - 1.83* 50%
13)	Brush-tailed porcupine	1,624	**0.64** *0.44 - 0.96* 20%	527	**0.62** *0.45 - 0.99* 20%	97	**0.55** *0.31 - 0.95* 29%	52	NA	166	**0.66** *0.33 - 1.32* 37%
14)	Four-toed sengi	191	**181.09** *2.16 - 15,177* 1,271%	64	**266.49** *2.83 - 25,113* 1,450%	14	NA	5	NA	58	NA

2.5.6. Reactivity to the camera

Reactivity to the camera is known to bias density estimates, as it violates the assumptions of Distance Sampling (Buckland et al., 2001; 2015). Attraction to CTs, providing a high number of observations close to the camera has been previously addressed with left-truncation (Cappelle et al., 2019). However, to minimise induced bias we consistently excluded all snapshots showing evident reactivity to the camera from analysis, not only for species attracted to CTs, such as the honey badger (Figure 2.6), but also for the elephants, showing strong olfactory reactivity by insistently smelling the area in front of the camera (regardless of the distance interval). In elephants, when using all observations including the 80% showing reactivity, estimates were inflated up to two orders of magnitude (Figure 2.6). Avoidance is less frequent, but (Kalan et al., 2019) reported it for the bonobo. We confirm bonobos' avoidance of the camera, resulting in fewer observations within the first 2 meters (Figure 2.10). However, bonobos were not undetected, but rather observed further away, and left-truncation was not applicable. Lack of detection close to the camera can be levelled out by excess of detection further away (Buckland et al., 2015), but densities were inflated by 15% because bonobo neophobia seems to be coupled with curiosity from a secure distance. Therefore, we discarded all snapshots showing reactive behaviours. This study suggests reactivity to CTs being the most impacting form of bias in CTDS. Not accounting for reactivity could result in largely inflated density estimates, and future studies should carefully examine the videos to detect reactive behaviours. To reduce visual and olfactory reactivity, we recommend to either deploy CTs for at least one month prior to the survey, allowing animals to habituate to cameras; or record reference distance labels after the survey, reducing the time of CT set-up, and by that "contamination" with human odour. If neither is possible, methods not influenced by reactivity to CTs (e.g. SECR), is to be favoured over CTDS.

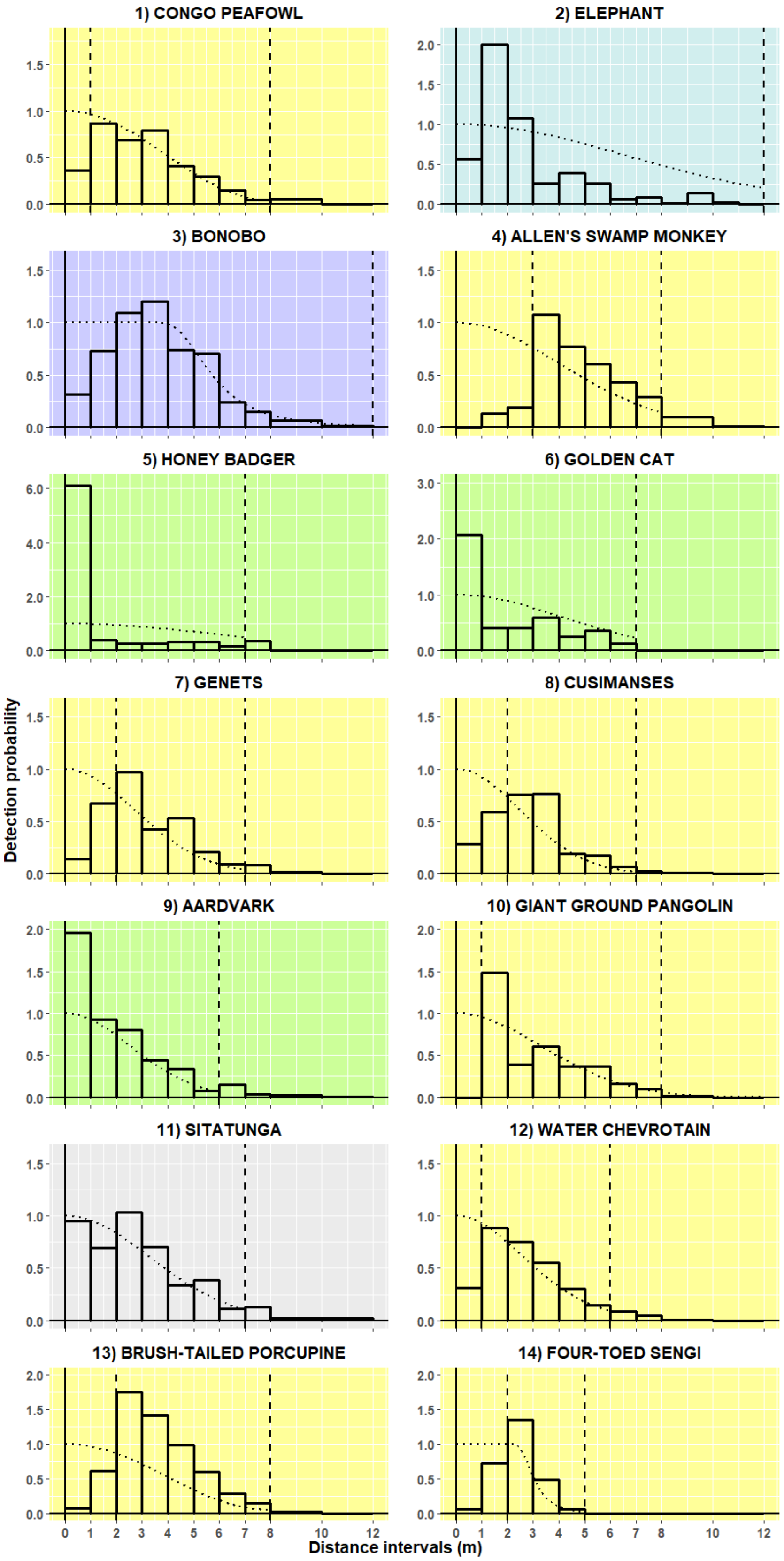


Figure 2.10. Species specific detection probability PNS survey © 2016 – 2018. Bars provide detection probability as function of distances prior to truncation (reactivity observations included); Dashed lines show distances of truncation; Dotted lines show probability density functions of detection probability as a function of distance after truncation (reactivity observations discarded). Plot colours: grey = no issues; yellow = low detection (body size); green = reactivity to camera (attraction); light blue = reactivity to camera (olfactory); purple = reactivity to camera (avoidance).

2.5.7. Conclusion

Camera trap distance sampling is an excellent survey method providing standardized and comparable information on wildlife density and abundance, particularly important for threatened species. Because of its highly diverse vertebrate community, SNP block South represents an excellent test-field, showing CTDS applicability to one of the remotest and least known rainforest areas of the globe. Density values for the Congo peafowl, the giant ground pangolin, and the cusimanses presented here, are the first ever obtained, and are of critical conservation importance providing the basis for IUCN Red Lists species assessments. Despite limitations in comparability due to methodological differences and a site-specific ecological set-up, eight out of 11 densities obtained fell within published ranges (Table 2.8). However, our estimates' accuracy remains to be confirmed: longitudinal assessments of density using standardised methods such as those detailed here will validate our results and shed light on the status of these cryptic species. Continuous monitoring and population trend evaluation are crucial information for wildlife conservation. Allowing simultaneous surveys of large portions of the terrestrial vertebrate community (Figure 2.11), rather than single species, the information CTDS can provide are of pivotal importance for the development of conservation plans of multi-species' communities. It may reveal the delicacy of location specific ecological equilibria, crucial for the conservation of the integrity of the few remnant intact habitats of our planet.

Table 2.8. Comparison of species-specific densities from CTDS (this study) to available literature. Species: common name of considered species or species group; CTDS density (this study; adults only): min-max: estimated density ranges from CTDS; Published density (immatures included): min-max: range from reference study (or point density when range unavailable); Survey method: used in the reference study; Reference: reference of cited study; Published home-range [km^2]: min – max: range from reference study (or point home-range when range unavailable); Reference: reference of cited study.* only nest-builders (infants excluded); ** adults only.

ID	**Species**	**CTDS density [ind/km^2] (this study)**	**Published density [ind / km^2]**			**Published home-range [km^2]**	
		(min - max)	*(min- max)*	*Survey method*	*Reference*	*(min- max)*	*Reference*
1)	Congo peafowl	0.55 - 1.06	Unknown	Not available	Not available	Unknown	Not available
2)	Forest elephant	0.01 - 0.07	0.03 - 0.06	Line transects Dung count	(Bessone et al., 2019)	25.90 - 2,226.30	(Blake et al., 2008)
3)	Bonobo	0.24 - 1.53	0.20 - 0.40*	Line transects Nest count	(Bessone et al., 2019)	12.30 - 31.50	(Hashimoto et al., 1998)
4)	Allen's swamp monkey	0.09 - 1.14	100.00	Deduced from size of 3 groups and their home ranges	(Kingdon *et al.*, 2013)	0.50 - 0.70	(Kingdon et al., 2013)
5)	Honey badger	0.01 - 0.09	0.03	Capture-recapture	(Begg, 2001)	126.00 - 544.00	(Begg et al., 2005)
6)	African golden cat	0.01 - 0.07	0.04 - 0.10	Camera-traps SECR	(Bahaa-el-din et al., 2016)	Unknown	Not available
7)	Genets	0.11 - 0.43	0.30 - 4.50	Spotlight Night counts	(Monadjem, 1998)	1.00 - 10.00	(Fuller, Biknevicius and Kat, 1990)
8)	Cusimanses	0.31 – 2.36	Unknown	Not available	Not available	Unknown	Not available
9)	Aardvark	0.09 – 0.34	0.70 - 0.80**	Telemetry	(Taylor and Skinner, 2003)	2.00 - 3.00	(Taylor and Skinner, 2003)
10)	Giant ground pangolin	0.01 - 0.13	Unknown	Not available	Not available	Unknown	Not available
11)	Sitatunga	0.02 - 0.42	150.00 - 180.00	Count in one forest clearing (gathering)	(Magliocca, Quérouil and Gautier-Hion, 2002)	0.09 - 12.00	(Kingdon et al., 2013)

12)	Water chevrotain	0.37 - 1.35	0.30 - 2.00	Drive counts with nets	(Hart, 2001)	0.22 - 0.30	(Kingdon et al., 2013)
13)	Brush-tailed porcupine	0.44 - 1.03	2.40 - 13.00	Drive counts with nets	(Noss, 1998)	0.11 - 0.22	(Kingdon et al., 2013)
14)	Four-toed sengi	2.16 - 31,294	210.00	Capture-recapture	(FitzGibbon, 1995)	0.01	(FitzGibbon, 1995)

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2.7. Data availability statement

Data available via the LJMU Data Repository: https://doi.org/10.24377/LJMU.d.00000052

Figure 2.11. Nine of 43 species captured by camera traps in Salonga National Park, DRC. Top: Congo peafowl, forest elephant, sitatunga; Middle: African golden cat, bonobo, giant ground pangolin; Bottom: yellow-backed duiker, aardvark, leopard.

CHAPTER 3

No time to rest: how the effects of climate change on nest decay threaten the conservation of apes in the wild

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3.1. Abstract

Since 1994, IUCN Red List assessments apply globally acknowledged standards to assess species distribution, abundance and trends. The extinction risk of a species has a major impact on conservation science and international funding mechanisms. Great ape species are listed as Endangered or Critically Endangered. Their populations are often assessed using their unique habit of constructing sleeping platforms, called nests. As nests rather than apes are counted, it is necessary to know the time it takes for nests to disappear to convert nest counts into ape numbers. However, nest decomposition is highly variable across sites and time and the factors involved are poorly understood.

Here, we used 1,511 bonobo (*Pan paniscus*) nests and 15 years of climatic data (2003–2018) from the research site LuiKotale, Democratic Republic of the Congo, to investigate the effects of climate change and behavioural factors on nest decay time, using a Bayesian gamma survival model. We also tested the logistic regression method, a recommended time-efficient option for estimating nest decay time.

Our climatic data showed a decreasing trend in precipitation across the 15 years of study. We found bonobo nests to have longer decay times in recent years. While the number of storms was the main factor driving nest decay time, nest construction type and tree species used were also important. We also found evidence for bonobo nesting behaviour being adapted to climatic conditions, namely strengthening the nest structure in response to unpredictable, harsh precipitation. By highlighting methodological caveats, we show that logistic regression is effective in estimating nest decay time under certain conditions.

Our study reveals the impact of climate change on nest decay time in a tropical remote area. Failure to account for these changes would invalidate biomonitoring estimates of global significance, and subsequently jeopardize the conservation of great apes in the wild.

3.2. Introduction

In the past 50 years, a marked increase in global mean temperature due to anthropogenic-induced climate change has affected tropical rainforests inhabited by the great apes, orangutans (*Pongo spp.)*, gorillas (*Gorilla spp.)*, chimpanzees (*Pan troglodytes subspp.)* and bonobos (*Pan paniscus*) (Malhi and Wright, 2004; Mba et al., 2018; Saeed et al., 2018). The rise in mean temperatures has induced a reduction in average precipitation in many areas of the tropics (Malhi and Wright, 2004; Maidment, Allan and Black, 2015; Tamoffo et al., 2019), increased the length of the dry season (Marengo et al., 2011; Asefi-Najafabady and Saatchi, 2013; Jiang et al., 2019) and disrupted the very functionality of rainforests worldwide (Walther et al., 2002; Bush et al., 2020). As such, climate change poses a threat to the conservation of great apes, animals that are highly endangered, with all species and subspecies currently classified as Endangered or Critically Endangered in the Red List of Threatened Species (IUCN, 2020a).

For effective monitoring and conservation of remaining populations, conservationists must have accurate knowledge of the size of these populations (Nichols and Williams, 2006). Great apes live at low densities and are difficult to observe directly in their habitat. However, they are unique among the non-human primates in that all weaned individuals, independent of sex and age (Fruth, 2016), build structures called "sleeping platforms," "beds" or "nests". The capability of building nests is learned rather than innate (Videan, 2006), with infants and occasionally juveniles sharing night nests with their mothers. Usually, the nest foundation is composed of a strong side branch, with smaller branches and twigs shaped over it, forming an oval, nest-like structure to accommodate a sleeping ape at night (Goodall, 1962), and sometimes for resting during the day (i.e. day nests) (Fruth, Tagg and Stewart, 2018). New nests are built every night; reuse of previously constructed nests occurs where construction material is limited (e.g. Hernandez-Aguilar (2009)) but is relatively rare (Fruth, Tagg and Stewart, 2018). Although sometimes built on the ground (Koops et al., 2007; Tagg et al., 2013), particularly in gorillas (Yamagiwa, 2001), nests are commonly constructed in trees. Several hypotheses for nest building in great apes have been proposed (Fruth, Tagg and Stewart, 2018), including increased comfort and sleep quality (Fruth and McGrew, 1998; Stewart, Pruetz and Hansell, 2007; van Casteren et al., 2012; Cheyne et al., 2013), enhanced thermoregulation (Samson, 2012; Stewart et al., 2018), reduced predation risk (Pruetz et al., 2008; Stewart and Pruetz, 2013) and insect avoidance (Largo, 2009; Samson, Muehlenbein and Hunt, 2013). Nest building in great apes is thought to have been a crucial component in hominid evolution (Fruth, Tagg and Stewart, 2018). Today, nest counts are used as proxies for assessing great ape population density and abundance in the wild, and thus are considered as an important conservation tool. As nests persist for long in the forest and are easily observed by the human eye (Fruth and Hohmann, 1994), nest counts, rather than ape counts, have become the gold standard for monitoring presence/absence, abundance and density of apes in the past 40 years (Tutin and Fernandez, 1984; Kühl et al., 2008; Stokes et al., 2010; Junker et al., 2012). Methods such as Standing Crop Nest Counts (SCNC) (Tutin and Fernandez, 1984), in combination with Distance Sampling (Buckland et al., 2001; 2015), have provided accurate density estimates requiring only a single visit to the field. However, there are some disadvantages. Nest production rate (Plumptre and Reynolds, 1997; Kühl et al., 2008; Kouakou, Boesch and Kühl, 2009) and nest decomposition or nest decay time (Walsh and White, 2005; Morgan et al., 2016)(i.e. conversion factors) are highly variable across species, space and time, but are required to scale down the number of counted nests to the number of apes (Kühl et al., 2008), in order to permit estimations of great apes (Buckland et al., 2012). Nest survey methods not requiring the use of conversion factors have been proposed (Plumptre and Reynolds, 1996), but they demand multiple visits to the survey site, which is often hard to implement. More recently, the advent of camera traps (Rovero and Zimmermann, 2016) has allowed an estimation of great ape abundance via the remote observation of individuals (Després-Einspenner et al., 2017; Cappelle et al., 2019). However, camera-trap methods have not yet been fully validated and they require more costly equipment than nest count methods. Thus, nest count surveys remain highly relevant, with SCNC being the most commonly used method for estimating ape density in the wild, both via traditional ground (Ndiaye et al., 2018; Akenji et al., 2019; Dias et al., 2019; Lapuente et al., 2020) or aerial (Wich et al., 2015; Simon, Davies and Ancrenaz, 2019) line transects. Finally, to investigate population trends, a crucial body of information in conservation science, it is necessary to compare estimates of ape population density obtained at different points in time (Kühl et al., 2017; Santika et al., 2017; Strindberg et al., 2018). It is generally recommended to apply site- and time-specific conversion factors to data generated from a particular survey (Kühl et al., 2008), ideally obtained by monitoring large samples of nests (representative of the survey period) until full decomposition (Kühl et al., 2008). However, as such studies could last several months, more time-efficient methods have been developed, such as the retrospective estimation of nest decay with a single revisit of a marked nest, using logistic regression (Laing et al., 2003), or hidden Markov chain (Mathewson et al., 2008) analysis. Nevertheless, with the exception of some authors who have modelled decomposition time across sites (Santika et al., 2017; Strindberg et al., 2018), published decay times have been applied to different sites (Walsh et al., 2003; Reinartz et al., 2008; Stokes et al., 2010; Haurez et al., 2014; Kühl et al., 2017) and/or time periods (Kamgang et al., 2018; Simon, Davies and Ancrenaz, 2019). This is problematic, as nest decomposition may differ with differing climate conditions, leading to inaccurate population density estimates (Morgan et al., 2006; Kühl et al., 2017). Nest-specific factors are known to drive nest decay; for example, nests built at the same time by members of the same group of apes exhibit different decomposition times (Morgan et al., 2016). However, rainfall is often reported as the most important variable affecting nest decomposition time, with lower rainfall resulting in longer decay times (Walsh and White, 2005; Kouakou, Boesch and Kühl, 2009; Morgan et al., 2016; Kamgang et al., 2020). Therefore, a drier climate would be expected to increase the time for which great ape nests would remain visible in the forest (Morgan et al., 2016). This knowledge has serious implications for great ape conservation. When using SCNC, applying an inappropriately short nest decay time would produce a falsely high population density result (Buckland et al., 2012). Therefore, if we do not use values obtained for the specific survey period and location in question, we cannot account for climate-related changes in mean decomposition time, thus hindering our ability to correctly estimate population trends.

Here, we used long-term data from the research site LuiKotale (Hohmann and Fruth, 2003b), Democratic Republic of the Congo (DRC), to investigate the impact of climatic conditions on nest decomposition. We investigated A) 15 years of daily rainfall and temperature data, and B) a total of 1,511 bonobo (*P. paniscus*) nests observed from construction to disappearance. As variables influencing nest decay time, we considered climate measured as 1) rainfall and 2) storms, as well as 3) habitat location (swamp versus dry forest), 4) construction type (height, position within tree, exposure), 5) construction behaviour, and 6) tree species.

1) **Rainfall:** as rain has been reported to be the most important factor affecting nest decay (Walsh and White, 2005; Kouakou, Boesch and Kühl, 2009; Morgan et al., 2016; Kamgang et al., 2020), we expected high levels of precipitation to accelerate decomposition.

2) **Storms:** some authors found no correlation between average rain and decay time (Mathewson et al., 2008). As rain can come in different forms (Liu, 2011), and thunderstorms with short and heavy rain may have a different influence on nest decay than continuous, lighter rain, we expected the number of storms, characterized by a high level of precipitation in a short time, to accelerate nest decay.

3) **Habitat location:** in contrast to heterogeneous primary forests on slopes and plateaus, those in riverine valleys and swamps are more protected from storms, due to their topographical position. Therefore, we expected nests built in heterogeneous dry forests to decompose faster than those built in swamps.

4) **Construction type:** if 1 or 2 were true, we would expect the effect to be more pronounced in nests built a) high rather than low in trees (Morgan et al., 2016), and b) on side branches rather than in the fork at the treetops. This is because the wind forces bend upper trunk parts more than lower ones, and distal positions more than central ones. We also expected nests to decay faster when c) open to the sky, as they would be more exposed to the elements than those protected by upper layers of foliage (Morgan et al., 2016); and when d) formed by the integration of material of several trees (Fruth and Hohmann, 1993), rather than of a single tree.

5) **Construction behaviour**: following recent findings (Stewart et al., 2018), we expected nests constructed for rainy or colder nights to persist longer, as more foliage is used for thermal insulation and solid branches in single trees are chosen over smaller branches integrated from several trees to withstand strong winds accompanying changes in weather.

6) **Tree species:** as tree species rather than nest characteristics have been reported to influence decomposition time (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004; Kouakou, Boesch and Kühl, 2009; Kamgang et al., 2020), we assessed differences between the most common trees used for nesting by the bonobos of LuiKotale.

We modelled the average time for a bonobo nest to fully decay in a Bayesian framework, using a gamma survival model describing the time between nest construction and full decomposition (Perry et al., 2019; Kelter, 2020). We then compared our results with those obtained using the recommended application of estimating nest decay with a single revisit of a marked nest, using logistic regression (Laing et al., 2003), a time-efficient and retrospective method.

3.3. Materials and methods

3.3.1. Study area

We collected data between 2003 and 2018 at the research site LuiKotale (2°45.610′ S, 20°22.723′ E), west of Salonga National Park (SNP), DRC, a World Heritage Site of Nature, and a stronghold for wild bonobos (Fruth et al., 2016) (Figure 3.1). The study site is situated in an area of lowland heterogeneous primary forest (Hohmann and Fruth, 2003b). Here, two bonobo communities were habituated to human observers by 2007 (Bompusa West; ca. 40km² home range) and 2015 (Bompusa East; ca. 30km² home range), respectively (Fruth and Hohmann, 2018). The climate at LuiKotale is equatorial, with abundant rainfall throughout the year, except for a short dry season in February and a longer dry season between May and August.

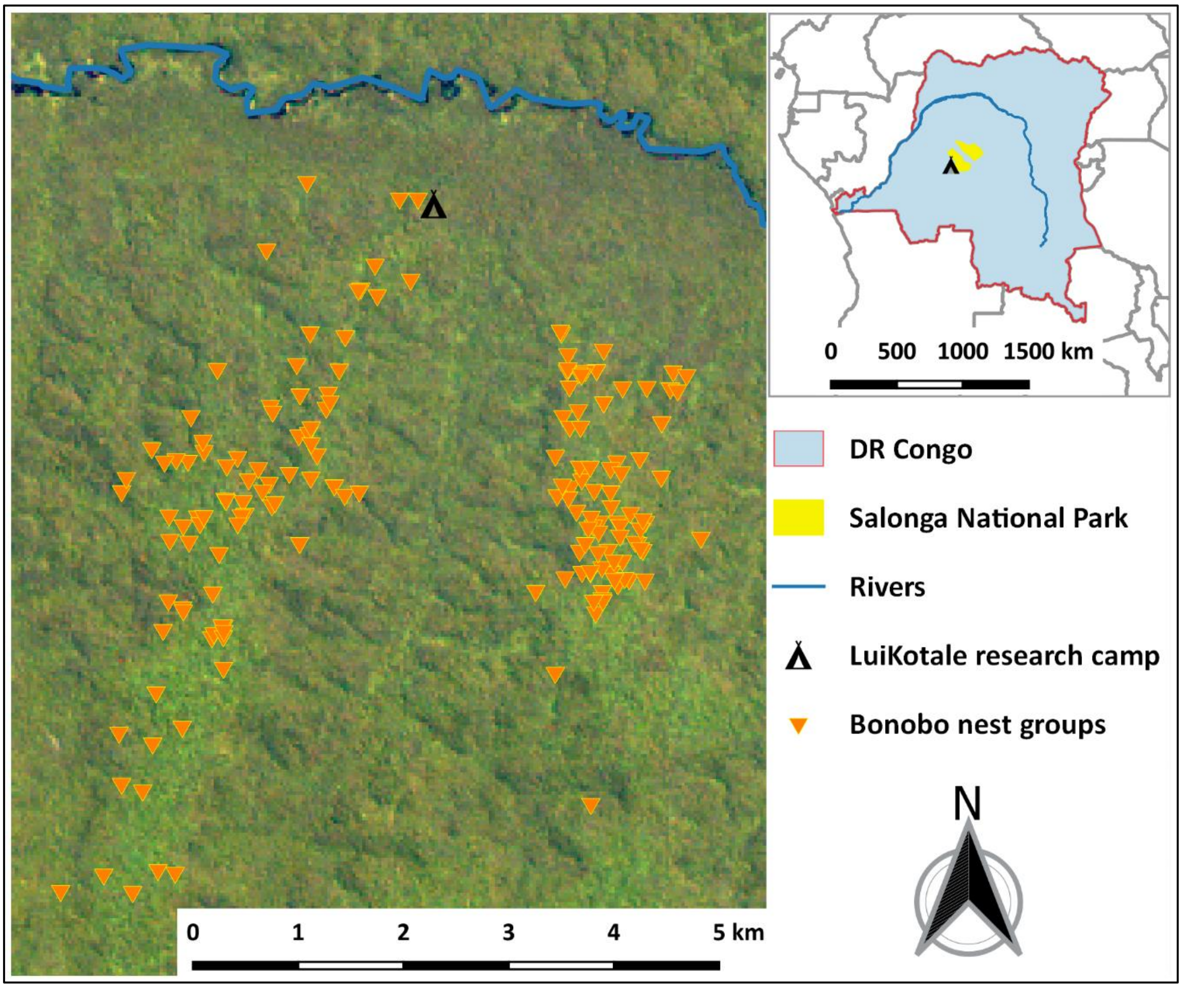

Figure 3.1. Nest groups (n = 182; orange triangles) monitored in the LuiKotale Study area (2003-2018) situated west of Salonga National Park (yellow) in the Democratic Republic of the Congo (light blue). Landsat-8 image courtesy of the U.S. Geological Survey.

3.3.2. Data collection

3.3.2.1. Climate data

We measured daily rainfall (mm/m^2) twice per day (at 6:00 and 18:00) using a rain gauge open to the sky. We measured minimum and maximum daily temperature (°C) using a thermometer in the forest. We recorded weather (i.e. rain, sun or clouds) in four time intervals: (a) 6:00–10:00; (b) 10:00–14:00; (c) 14:00–18:00; (d) 18:00–6:00 (i.e. night time); with interval (c) being the time during which bonobos built nests. This allowed us to extract the following variables: 1) daily rainfall throughout the lifetime of a nest; 2) daily number of storms throughout the lifetime of a nest, with storm being defined as a single interval of rain in an otherwise sunny day, with a minimum of 20 mm of rainfall within the time intervals mentioned above. The rain had to occur in the evening or night, as morning storms are extremely rare in the study area; 3) rain on construction date (i.e. if rain was recorded in interval (c), on the day of construction); 4) minimum temperature on construction date; and 5) differential temperature on construction date (max−min °C) to eliminate potential bias due to the use of different thermometers across time. We then compiled a full climatic database for the 15 years of study (2003–2018) to investigate 1) trends in climate conditions at LuiKotale and 2) differences between survey periods.

3.3.2.2 Nest decay data

We derived data on nests from direct follows of bonobos. Field staff marked the location of all nest sites included in this study in the evening, revisited them the morning after construction, and recorded GPS coordinates and habitat type. For each nest, we noted: 1) height (m); 2) exposure; 3) position in tree; and 4) construction type. For each nest tree, we recorded 5) height (m); 6) lowest branch (m); and 7) species (Table 3.1). We registered types of nest construction across two periods, nine years apart (Table 3.4). Period 1 (P1) included nests constructed across 35 months between August 2003 and July 2007. Period 2 (P2) included nests constructed across 24 months between July 2016 and June 2018. We further distinguished five surveys, lumping nests into ten to 13 consecutive months, reflecting a full year of data collection (Table 3.4): 1) August 2003–July 2004 (Survey 1, S1); 2) February 2005–December 2005 (Survey 2, S2); 3) July 2006–July 2007 (Survey 3, S3); 4) July 2016–June 2017 (Survey 4, S4); 5) July 2017–June 2018 (Survey 5, S5). S1 included the nests analysed by Mohneke and Fruth (2008), which included 24 fresh nest groups (n = 218 individual nests) between August 2003 and February 2004 and applied SCNC and marked nest count methods.

Although one person only (LB) estimated and followed the majority of nests, we divided nest height by tree height to use relative nest height accounting for possible differences in observer estimates. All relevant field research staff were trained in estimating nest and tree height using a clinometer. We visited nests on a weekly basis, recording age class, until complete decomposition. We defined five age classes (Tutin and Fernandez, 1984) distinguishing nests consisting of 1) fresh and green leaves; 2) green but dry leaves; 3) brown/black leaves; 4) no leaves but the structure of broken and bent branches still visible; and 5) nests recognizable only if the place of construction was known to the observer. We considered a nest fully decomposed when it entered class 5. We calculated nest "age" *post hoc* as the number of days between the day of construction and the day before it was found to be fully decomposed. If a nest was not fully decomposed at the end of the study, we included it as "censored" (Buckley and James, 1979). Consequently, in censored nests, the time to decay was smaller than the true but unknown time to decay.

This study was purely observational, involving nests left behind by bonobos. The methods described above complied with the requirements and guidelines of the ICCN and adhered to the legal requirements of the host country, DRC.

3.3.3. Statistical analysis

3.3.3.1. Defining factors

The following nest characteristics were binary: forest type (*F*), nest exposure (*E*), nest position (*P*), nest construction type (*C*) and rain at construction (*R*). As nests were constructed in 85 different tree species (*Sp*), we assigned a single category to the each of the most recurrent 10 tree species (1 to 10), and included all other species in a separate category (i.e. 11) (Table 3.1). Because the top 10 tree species varied between P1 and P2, we repeated this process for 1) all investigated nests; 2) nests constructed in P1; and 3) nests constructed in P2.

The following variables were continuous: nest height (*A*), relative nest height (*H*), average precipitation (*W*) and daily number of storms (*S*). We classified these into the following three categories based on their mean and standard deviation (SD): "Low" (mean – 1 SD), "High" (mean + 1 SD) and "Medium" (anything in between) (Table 3.1).

Some of the factors described in Table 1 measured the same phenomenon in different ways (i.e. absolute nest height / relative nest height; minimum temperature / differential temperature). To avoid problems of overfitting (McElreath, 2020), we fitted four different models including all possible combinations of these variables and selected the top ranked models by using Pareto-smoothed importance sampling (PSIS) (Vehtari, Gelman and Gabry, 2017). Average daily rainfall and average number of storms throughout the lifetime of a nest posed a similar issue, as we expected these two variables to be correlated (if there is a lot of rain, there are many storms). However, the phenomena they described were different and could both be important in driving nest decomposition. Therefore, we first fitted a model including both variables, and verified that the posterior distribution of the parameters was not correlated (i.e. no overfitting) following Vehtari et al., (2017). Then, we looked at the decrease in expected log predictive density (ELPD) given by removing one or the other covariate (Gabry et al., 2019). A big decrease would suggest that the removed covariate exerted a high contribution to the explanatory power of the model. A small decrease would suggest a low contribution. We applied the same process to all other variables, running different models and leaving one variable out at a time. By looking at the decrease in ELPD values given by removing a particular variable, we evaluated the importance of each factor in driving nest decomposition time. We performed model comparison and selection using the R package "loo" (Vehtari, Gelman and Gabry, 2017).

Table 3.1. Nest type categories definitions, and sample sizes used in this study.

Factor	**Description**	**Categories**		**Number of nests**
Forest type (*F*)	Primary heterogeneous inundated forest	Swamp		84
	Primary heterogeneous forest on *terra firma*	*Terra firma*		1,427
Nest exposure (*E*)	Nest closed to sky by above vegetation	Close		544
	Nest open to sky	Open		967
Nest position (*P*)	Side branch	Side branch		1,326
	Treetop	Top		185
Nest construction type (*C*)	Nest located in a single tree	Single tree		1,257
	Nest using branches of 2 or more adjacent trees	Integrated		254
Nest absolute height (*A*)	Nest height from the ground (m)	Low	=<13	326
		Medium	13–23	874
		High	>=23	311
Nest relative height (*H*)	Nest height from the ground (m) / Tree height (m)	Low	<0.8	234
		Medium	0.8–0.95	937
		High	>0.95	340
Average precipitation (*W*)	Average daily precipitation during a nest's lifetime (mm)	Low	<3	210
		Medium	3–9	1,056
		High	>9	245
Average storms (*S*)	Average daily number of storms during a nest's lifetime	Low	<0.02	196
		Medium	0.02–0.12	1,059
		High	>0.12	256
Minimum temperature (*T*)	Minimum temperature recorded on day of construction (°C)	Low	=<18	261
		Medium	18–22	1,084
		High	>=22	166
Differential temperature (*D*)	Difference between maximum and minimum temperature at day of construction (°C)	Low	=<4	302
		Medium	4–8	868
		High	>=8	341
Rain at construction (*R*)	No rain between 14:00 and 18:00 on day of construction	No		1,291
	Rain between 14:00 and 18:00 on day of construction	Yes		220
Tree species (*Sp*)	Tree species where nest was constructed. The 10 most recurrent species were assigned to a specific category. All other species were included in the eleventh category (including integrated nests).	1–11		See Table 3.8

3.3.3.2. Modelling nest survival

Nest survival analyses have been previously conducted using four main methods: Kaplan-Meier models (Mohneke and Fruth, 2008), survival analyses (Morgan et al., 2016) provided by the software MARK (White and Burnham, 1999), Hidden Markov chain analysis (Mathewson et al., 2008; Fleury-Brugiere and Brugiere, 2010) and logistic regressions (Laing et al., 2003; Kouakou, Boesch and Kühl, 2009). Here, we modelled the average time to full decay of a bonobo nest using a Bayesian gamma survival model describing the time between nest construction and full decomposition (Kelter, 2020). The gamma distribution properly describes the length of time between events and provides more flexibility than the typically used exponential distribution (Perry et al., 2019). In order to include censored nests (i.e. nests for which the exact time to full decay was not observed), we modelled fully decayed nests using a gamma cumulative probability distribution, which provided the probability that a nest has disappeared after a certain number of days. Conversely, we modelled censored nests by using the complementary cumulative probability distribution, which essentially returns the probability a nest has not disappeared after a certain number of days (Kelter, 2020).

In mathematical terms, for each fully decayed nest *i*, we modelled the days to full decay *Dd* as

$$Dd \sim gamma\ (k\ , \theta) \qquad \textit{Eq. 1}$$

And censored nests *Dc* as

$$Dc \sim 1 - gamma\ (k\ , \theta) \qquad \textit{Eq. 2}$$

where the shape parameter of the gamma distribution is *k*, defined as the mean decomposition time μ multiplied by the rate parameter θ

$$\mathrm{k} = \mu * \theta$$

The mean decomposition time μ for each nest *i* can be modelled depending on nest-specific factors, using a linear model with a log-link function, such as

$$\mu_i = \exp\,(\digamma_j[F_i] + \varepsilon_j[E_i] + \pi_j[P_i] + \gamma_j[C_i] + \alpha_j[A_i] + \eta_j[H_i] + \omega_j[W_i] \qquad \textit{Eq. 3}$$
$$+ \sigma_j[S_i] + \tau_j[T_i] + \delta_j[D_i] + \rho_j[R_i] + \psi_j[Sp_i])$$

where Greek letters represent specific parameters of variables estimated by the model for each category *j*, and capital letters represent variables (see Table 1). This allowed us to investigate differences in mean decomposition time for nests belonging to each category within our variables. We assigned a weakly informative prior to each parameter *y* in the linear model

$$y_n \sim normal\,(0\,,5) \qquad \textit{Eq. 4}$$

where *y* represents any of the parameters *n* in equation 3, and a positive weakly informative prior to the parameter θ in equations 1, 2 and 3

$$\theta \sim gamma\,(0.1\,,0.1) \qquad \textit{Eq. 5}$$

Finally, in order to validate our model, we used our gamma survival model to independently reanalyze a previously published dataset (Mohneke and Fruth, 2008). For that, we only included nests investigated in Mohneke and Fruth (2008), excluding all subsequent nests considered in this study.

Another method used in great ape conservation is logistic regression analysis (Laing et al., 2003). This method has the advantage of allowing average nest decay time to be estimated retrospectively, with only one revisit of marked nests. It has thus been recommended as the most cost-effective approach for obtaining site-specific nest decay time (Kühl et al., 2008; Stokes et al., 2010). Published studies using logistic regression analysis have focused on African great apes (Table 3.2), whilst orangutan researchers have mainly used the Hidden Markov Chain method (Mathewson et al., 2008) (but see Wich et al., (2016); Voigt et al., (2018)). Logistic regression studies differed considerably in terms of the number of nests included, survey length and the time between the day the nests were marked and the day they were revisited (Table 3.2).

However, nest decay is not constant across time (Walsh and White, 2005) and nests built at the same time could decay at different rates (Morgan et al., 2016). Therefore, if the sample of nests is of inadequate size, or not representative of the climatic variation across the period of study, average nest decay estimates can be biased (Laing et al., 2003). In order to assess the reliability of this method, we used logistic regression to estimate mean decomposition time of the same published dataset used to validate our model (Mohneke and Fruth, 2008), following the protocol described by Kouakou, Boesch and Kühl (2009). We investigated 1) different survey lengths: a) full length of study), and b) half-length of study; and 2) different intervals between nest marking and revisit: a) 2 weeks, b) 1 month, c) 3 months after the last nest group was marked, d) 3 months after each nest group was marked (Kamgang et al., 2020), and e) a random number of days (between 7 and 360) after the nest was marked (Serckx et al., 2014b). We then binary labelled the individual nests as

“Decayed” = 0, if the date of revisit occurred after the known date of decay, or “Alive” = 1, if the date of revisit occurred before the known date of decay. We compared the results to the known mean decay time (Mohneke and Fruth, 2008) and adopted the most reliable scenario to investigate the effect of sample size on the precision of the estimate. Here, we randomly selected a sample of nests comprising a) 75%, b) 50% and c) 25% of the nest groups included in the original dataset (10 random draws each) and compared the results with those obtained by 1) Mohneke and Fruth (2008) and 2) our gamma survival model. In addition, to further explore the effects of sample size on estimated decay time, we repeated the same analyses for a larger dataset: S4, presented in this study.

We developed our gamma survival model (Appendix 2) in ‘Stan’, a state-of-the-art platform for Bayesian statistical modelling (Carpenter et al., 2017), using the R interface RStan (Stan Development Team, 2020). We used R Version 4.0.2 (R Core Team, 2020) to run two chains for each survival model (4,000 iterations; 2,000 of warmup), to perform exploratory and logistic regression analyses and to create figures.

Table 3.2. Studies using a logistic regression for estimating the average decay time for great apes (Species) across different study areas. Sample (n): number of individual nests included in the study. Survey duration: the duration of the study in months. Revisit: time after which the nests were revisited.

References: [1] (Serckx et al., 2014b); [2] (Morgan et al., 2006); [3] (Kamgang et al., 2020); [4] (Kouakou, Boesch and Kühl, 2009); [5] (Murai et al., 2013); [6] (Tweh et al., 2015); [7] (Wich et al., 2016); [8] (Voigt et al., 2018)

Species	Study area	Sample (n)	Survey duration	Revisit
Pan paniscus	Lake Tumba; Democratic Republic of the Congo[1]	610	22 months	Weekly
Pan troglodytes troglodytes	Goualougo Triangle; Republic of Congo[2]	92	7 months	NA
Pan troglodytes troglodytes	Mbam Ndjerem National Park; Cameroon[3]	309	15 months	3 months after nest marking
Pan troglodytes verus	Tai National Park; Côte d'Ivoire[4]	141	6 months	Weekly, until 80% nests were decayed
Pan troglodytes verus	Rio Muni Landscape; Equatorial Guinea[5]	76	3 months	From 14 to 202 days after nest marking
Pan troglodytes verus	Several sites; Liberia[6]	165	5 months	From 6 to 310 days after nest marking
Pongo abelii	Several sites; Sumatra, Indonesia[7]	753	NA	NA
Pongo pygmaeus	Sabangau and Lesan; Borneo, Indonesia[8]	423 (Sabangau) 88 (Lesan)	118 months (Sabangau) 20 months (Lesan)	Weekly

3.4. Results

3.4.1. Climate

Between 2003 and 2018, the climate recorded in LuiKotale showed a significant trend of decreasing average rainfall (linear regression: $R^2 = 0.363$; $p = 0.013$) and differential temperature ($R^2 = 0.248$; $p = 0.049$), but revealed no difference in the number of storms per year (Figure 3.2). Consequently, in 2003−2007 (P1), average daily rainfall in the lifetime of a nest was higher than in 2016−2018 (P2) (Wilcoxon test: $W = 279021$, $p < 0.001$). P1 also showed larger temperature variation between day and night on construction date ($W = 257941$, $p < 0.001$). However, the daily number of storms in the lifetime of a nest was higher in 2016−2018 than in 2003−2007 ($W = 195465$, $p = 0.002$).

These results were also confirmed by the analysis of monthly climate data across our two study periods (Figure 3.3). When investigating average monthly rainfall and differential temperature, a marked decrease from P1 to P2 became evident; despite a tendency for more storms in P2, the number of storms per month was statistically similar across periods (Figure 3.4). Accordingly, 2003−2007 was a wetter period, with larger day/night temperature variation.

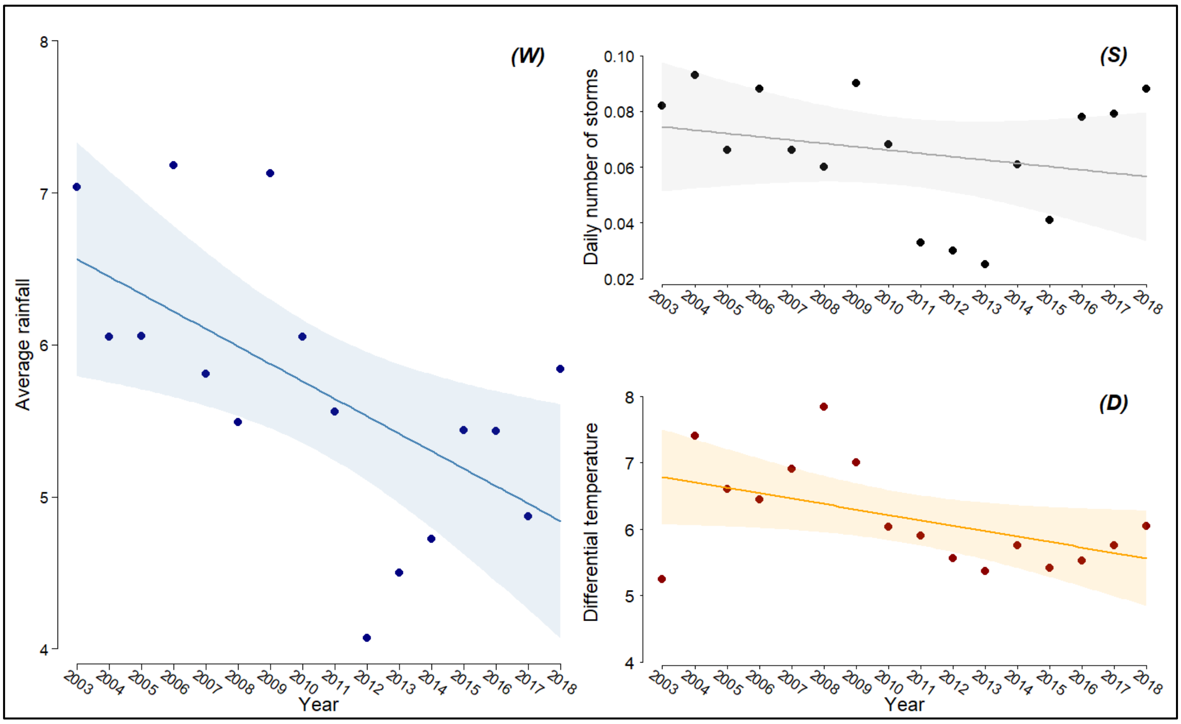

Figure 3.2. Climate in LuiKotale, Central Congo Basin, DRC (2003-2018). Left, “Average rainfall” (*W*): average rainfall per year (mm/m^2) shows a significant decreasing trend across the years (linear regression: $R^2 = 0.363$; $p = 0.013$); Top-right, “Daily number of storms” (*S*): average daily number of storms per year ($R^2 = 0.063$; $p = 0.348$; NS); Bottom-right, “Differential temperature” (*D*): average differential temperature (max-min °C) per year (C°) ($R^2 = 0.248$; $p = 0.049$).

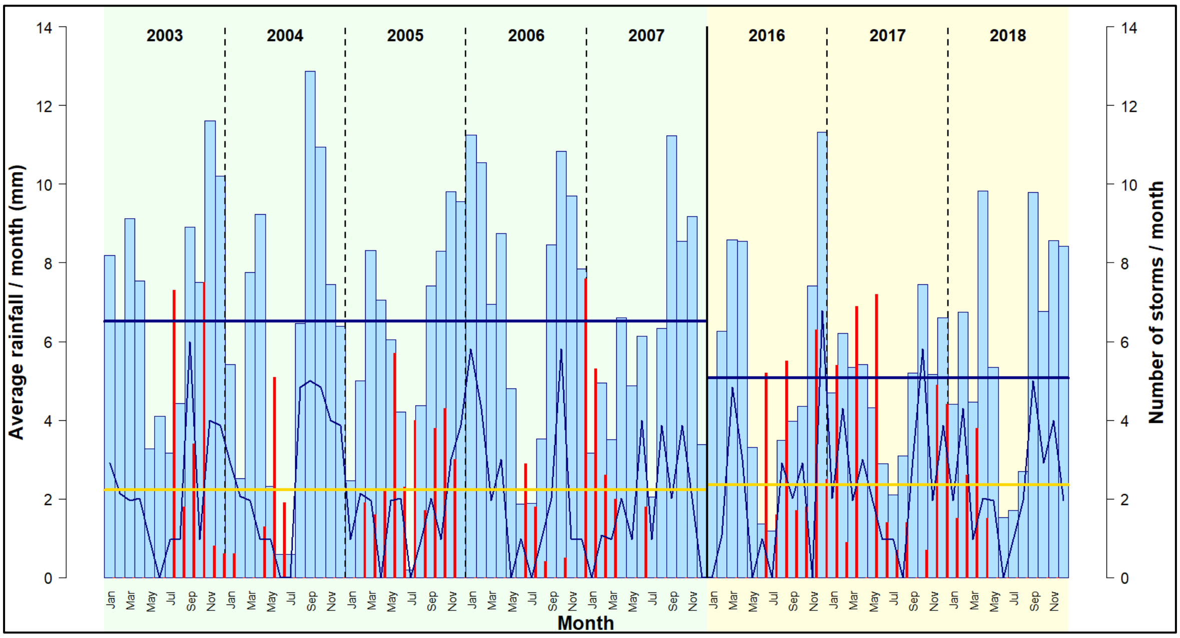

Fig 3.3. Monthly trend of average rain (light blue bars) and number of storms (dark blue line) across 1) periods (P1 = green background; P2 = yellow background), and 2) years (delimited by vertical lines). Horizontal solid lines represent 1) average monthly rainfall between periods (blue) and 2) average monthly number of storms between periods (yellow). Red vertical bars show the number of nests included in the study in each month (divided by 10, for graphical purposes).

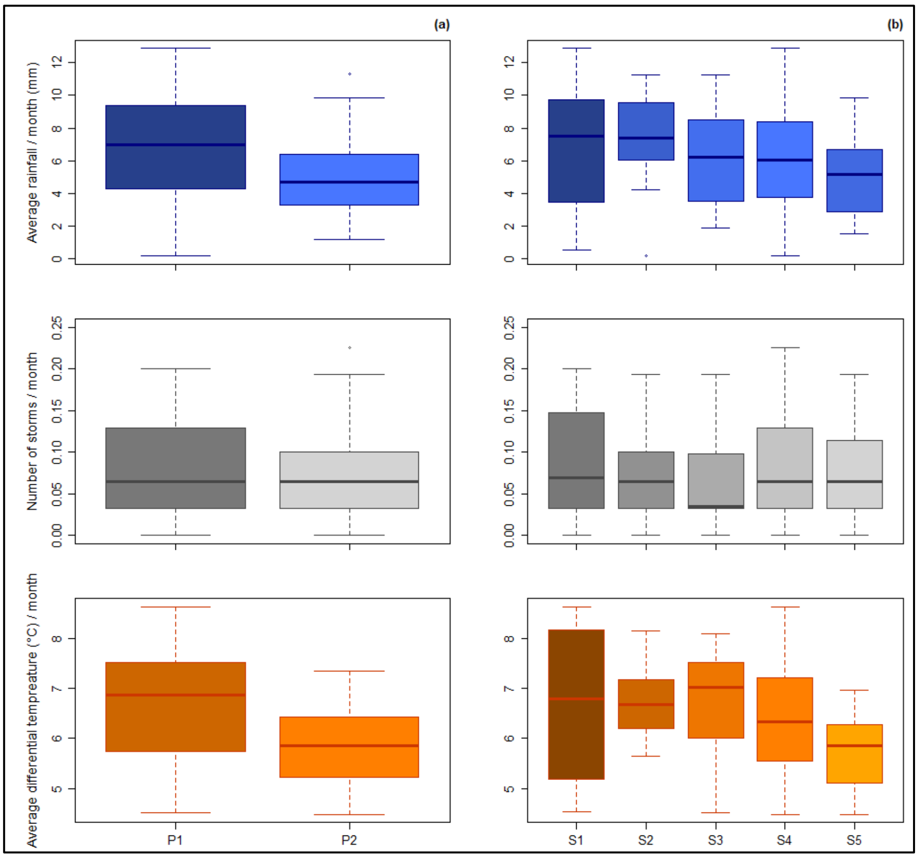

Figure 3.4. Monthly climate of a) Periods (2003-2007, P1, n = 44; 2016-2018, P2, n = 27), and b) Surveys (S1, n = 15; S2, n = 13; S3, n = 16; S4, n = 15; S5, n = 15). From top to bottom: 1) average monthly precipitation (mm); 2) Average monthly number of storms; 3) Average monthly differential temperature between night and day (C°).

3.4.2. Model diagnostic and validation

Following the results of the model selection procedure (Box 3.1), we included both average rainfall (*W*) and daily number of storms (*S*), defining the mean nest decomposition time μ for nest *i* by modifying Eq. 3 as follows,

$$\mu_i = \exp(\digamma_j[F_i] + \varepsilon_j[E_i] + \pi_j[P_i] + \gamma_j[C_i] + \eta_j[H_i] + \omega_j[W_i]\,\sigma_j[S_i] + \delta_j[D_i] + \rho_j[R_i] + \psi_j[Sp_i]) \qquad \textit{Eq. 6}$$

where Greek letters represent specific parameters of variables estimated by the model for each category *j*, and capital letters represent variables (see Table 3.1). All models converged well (Figure 3.5), with potential scale reduction factor, “Rhat” (Vehtari, Gelman and Gabry, 2017), being equal to 1 for all parameters. To assess the reliability of our estimates, we examined the Pareto *k* diagnostic (Vehtari, Gelman and Gabry, 2017), showing that our model was well specified (Table 3.3) and results were credible (Figure 3.6).

Finally, in order to validate the model accuracy, we reanalyzed the data from 2003−2004 published by Mohneke and Fruth (2008), for which average decomposition time was reported to be 75.5 days (n = 218 nests, 95 % confidence interval (95% CI) = 68.4−82.5). Our model returned an average decomposition time of 77.5 days (95 % CI = 71.3−84.2), fully within the confidence interval reported previously.

Fig 3.5. Trace-plots of the realized iterations (n=2000) for the main model (i.e. including all nests), for all factors listed in Table 1 (main text). The chains (n = 2) always indicate good mixing and

convergence. Similar results were obtained for all other models described in the study (i.e. by periods or by survey). Warmup iteration (n = 2000) are not shown.

Table 3.3. Model checking and diagnostic using Pareto smoothed importance-sampling (PSIS) leave-one-out cross-validation (Vehtari, Gelman and Gabry, 2017)**.** For each model we provide 1) Number of data-points: number of individual nests; 2) Number of parameters: number of parameters estimated by the model (* = tree species' parameters not included); 3) ELPD (SE): estimated log pointwise predictive density (ELPD) and relative standard error (SE), 4) p (SE): effective number of parameters (p) and relative standard error (SE); 5) looic: leave one out information criterion with relative standard error (SE); 5) Pareto *k* diagnostic values: reliability and approximate convergence of the PSIS-based estimates (values < 0.7 are considered acceptable (Vehtari, Gelman and Gabry, 2017)); 6) Monte Carlo SE of ELPD: pointwise values of the Monte Carlo standard error (SE) of ELPD. In S3, one data point was found having a Pareto *k* value > 0.7, indicating a highly influential data point, possibly biasing the estimated diagnostics. By re-running the model leaving out the influential data-point (Mohneke and Fruth, 2008), we obtained reliable estimates (model "S3 b").

Model	**Number of data points**	**Number of parameters**	**ELPD (SE)**	**p (SE)**	**looic (SE)**	**Pareto k diagnostic values**	**Monte Carlo SE of elpd**
MAIN	1,511	35	-7088.8 (67.9)	22.8 (1.0)	14177.7 (135.8)	1,511 < 0.5	0.1
P1	832	35	-3938.4 (47.0)	21.3 (1.1)	7876.8 (94.0)	832 < 0.5	0.1
P2	679	35	-3138.1 (49.7)	23.3 (1.6)	6276.0 (99.4)	679 < 0.5	0.1
S1*	278	23	-1167.1 (27.8)	13.3 (1.9)	2334.2 (55.5)	278 < 0.5	0.1
S2*	305	23	-1446.9 (26.3)	15.1 (1.6)	3113.9 (52.7)	305 < 0.5	0.1
S3*	249	23	-1155.3 (27.4)	12.6 (1.5)	2310.6 (54.8)	248 < 0.5 1 < 1.0§	NA
S3b*	248	23	-1149.0 (27.4)	11.5 (1.2)	2298.9 (54.7)	248 < 0.5	0.1
S4*	450	23	-2324.9 (27.0)	13.6 (1.2)	4649.8 (54.1)	450 < 0.5	0.1
S5*	229	23	-806.3 (35.9)	12.8 (1.8)	1612.7 (71.8)	226 < 0.5 3 < 0.7	0.1

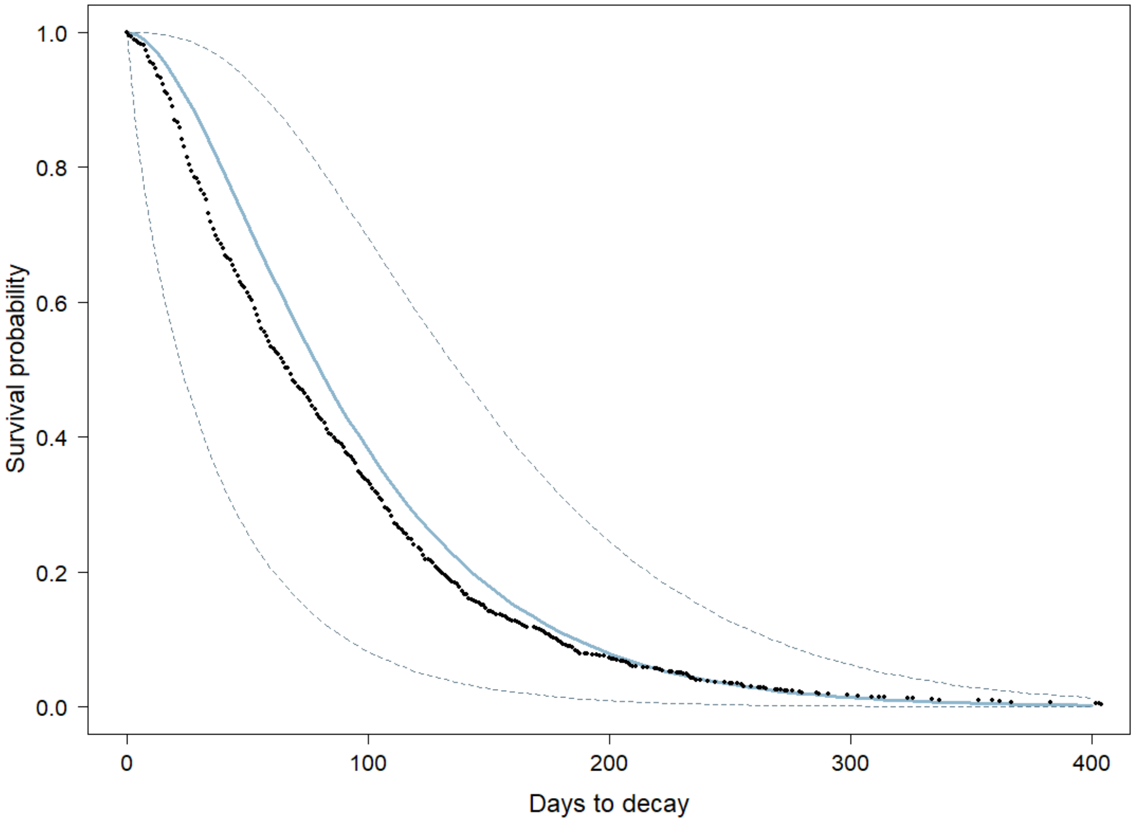

Figure 3.6. Nest survival curve. Survival curve including all nests (n = 1,511; blue solid line) with 95% confidence intervals (dashed blue lines). Black dots: proportion of nests still present after a certain number of days (censored nests (n = 203) included).

3.4.3. Nest decay time

We monitored 182 nest groups, totaling 1,511 nests across two periods (P1 and P2), 9 years apart. Monitored nests were constructed both in the dry (n = 643) and rainy season (n = 868), with all months being represented (average number of nests/month = 128; min = 50 (May), max = 180 (June)). Period- and survey-specific information are provided in Table 3.4.

The estimated average nest decomposition time for the full dataset was 95.5 days (SD = 1.93, see Figure 3.7a). When looking at differences between periods (i.e. 2003−2007 versus 2016−2018), we observed a significant increase, with an average nest decomposition time of 87.5 days (SD = 2.22) in P1 and 106.7 days (SD = 3.12) in P2 (Figure 3.7b). These results were only partially supported by the analysis of yearly nest decomposition cycles (i.e. specific surveys), with S1 and S3 in P1 showing average decomposition times consistently shorter than all other periods. Interestingly, S2, including 305 nests from February–December 2005, showed a mean decomposition time similar to those recorded in P2 (Figure 3.7c).

Table 3.4. Period- and survey-specific information.

Period	Survey	Study length (dates)	Number of nest groups	Number of individual nests	Number of censored individual nests (%)
P1	S1	12 months (08/2003–07/2004)	33	278	45 (16.2%)
	S2	10 months (02/2005–12/2005)	30	305	23 (7.5%)
	S3	13 months (07/2006–07/2007)	23	249	22 (8.8%)
Total (P1)		35 months (08/2003–07/2007)	86	832	90 (10.8%)
P2	S4	12 months (07/2016–06/2017)	57	450	26 (5.7%)
	S5	12 months (07/2017–06/2018)	39	229	87 (26.4%)
Total (P2)		24 months (07/2016–06/2018)	96	679	113 (16.6%)
Total (study)		59 months	182	1,511	203 (13.4%)

Using the dataset analyzed in Mohneke and Fruth (2008), we also conducted a logistic regression analysis. A randomly selected time to revisit (specific to each nest group) returned an average decomposition time of 78.2 days (95% CI = 77.3−80.6) (Table 3.5), which we used to analyze datasets with reduced sample size. A reduction to 75% of the original dataset had limited effect on the estimated decay time (Figure 3.8). In contrast, when reducing sample size to 25% of the original dataset, particularly for S4 of our study (Figure 3.8), results became variable. A similar trend was observed when analyzing the reduced dataset using our gamma survival model (Figure 3.9). However, here the estimated decay times were less variable than those obtained with a logistic regression analysis. Finally, the time interval between nest marking and revisit influenced the estimated decay time when analyzing the data from Mohneke and Fruth (2008) (n = 218), whereas results were more consistent for S4 (n = 450) (Table 3.5).

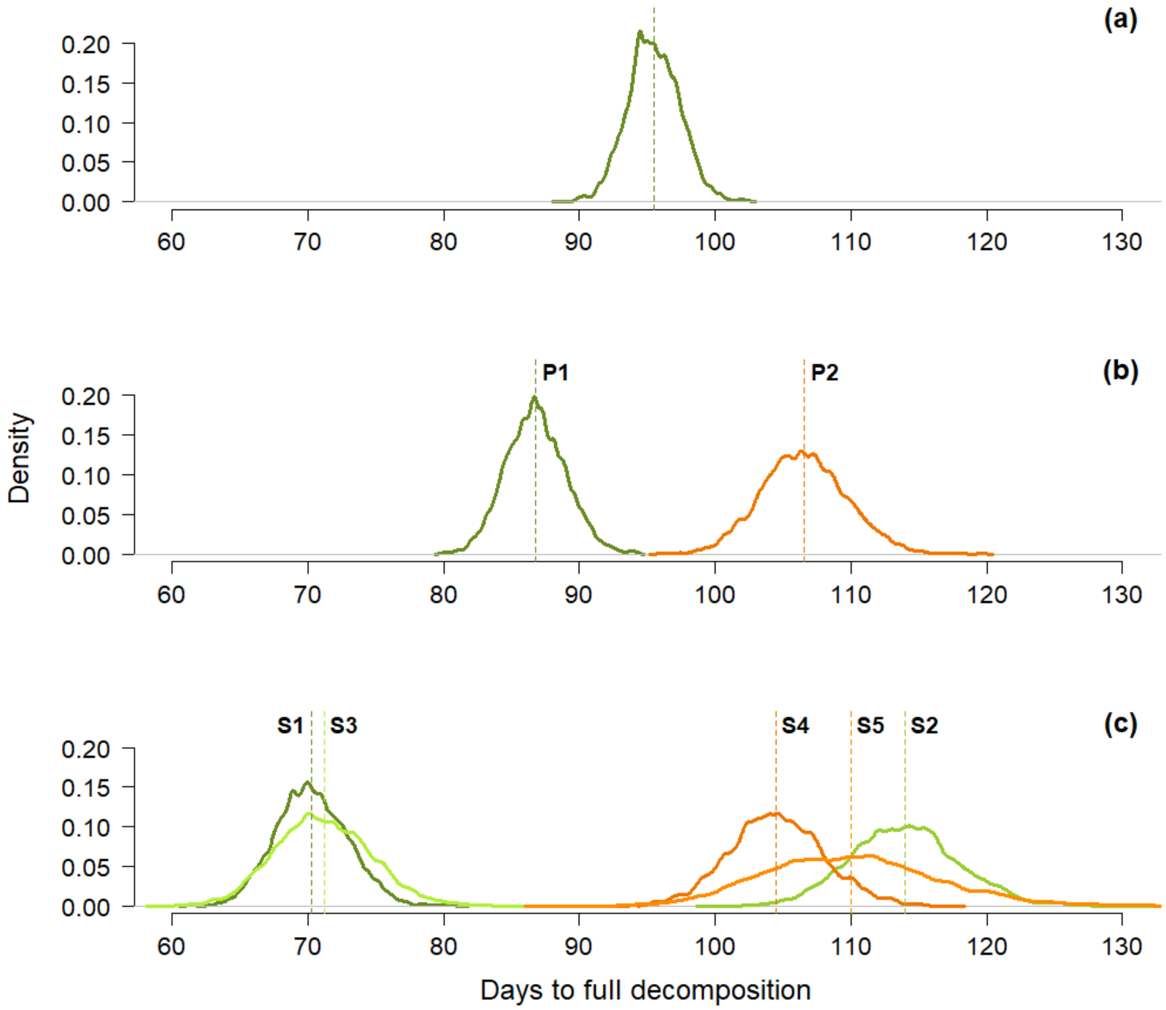

Figure 3.7. Posterior distribution of estimated mean decomposition time. a) All nests (n = 1,511); b) nests from the first (P1; n = 832; green) and second period (P2; n = 679; orange; c) nests from different surveys from P1 (S1 (n = 278); S2 (n = 305); S3 (n= 249); green curves) and P2 (S4 (n = 450); S5 (n = 229); orange curves). Coloured dashed lines show the mean values of the posterior distributions. Curves with larger breadth indicate higher uncertainty.

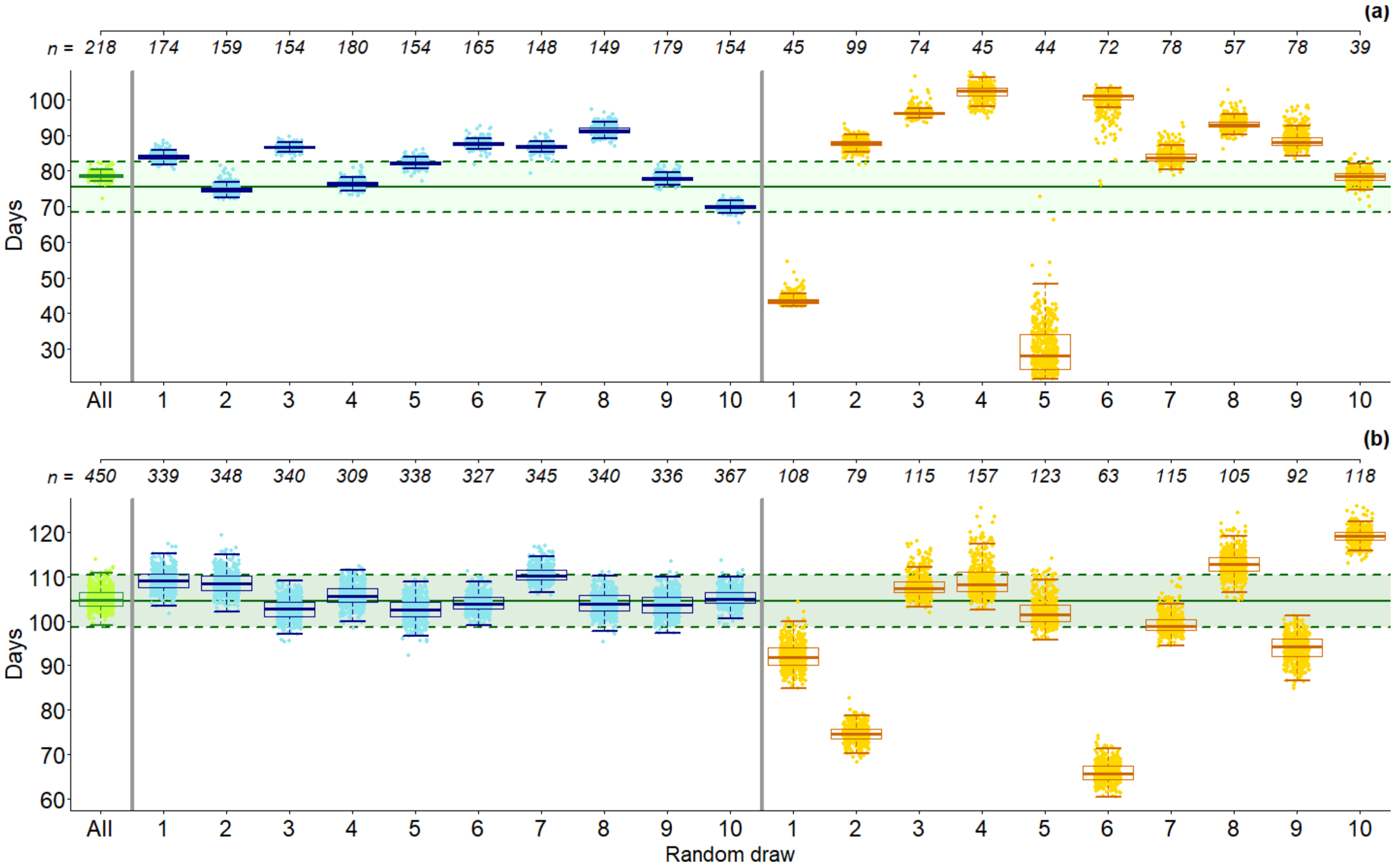

Fig 3.8. Estimated mean decay time of 10 datasets randomly selected from (a) Mohneke and Fruth (2008) and (b) S4 (this study), using logistic regression (Laing et al., 2003). Clouds of dots represent 500 mean decay times estimated via bootstrapping (Kouakou, Boesch and Kühl, 2009), with boxplots representing quartiles and variability of the bootstrap samples. From left to right: 1) full datasets (green) i.e. "All"; 10 random draws of 2) 75% of nest groups (blue); 3) 25% of nest groups (yellow). The upper x-axis shows the number of individual nests *n* in each draw. Green, horizontal lines show the reference decay value (mean, solid line) and 95% confidence intervals (dashed lines) for a) decay time for Mohneke and Fruth (2008); and b) S4 estimated via gamma survival model (this study).

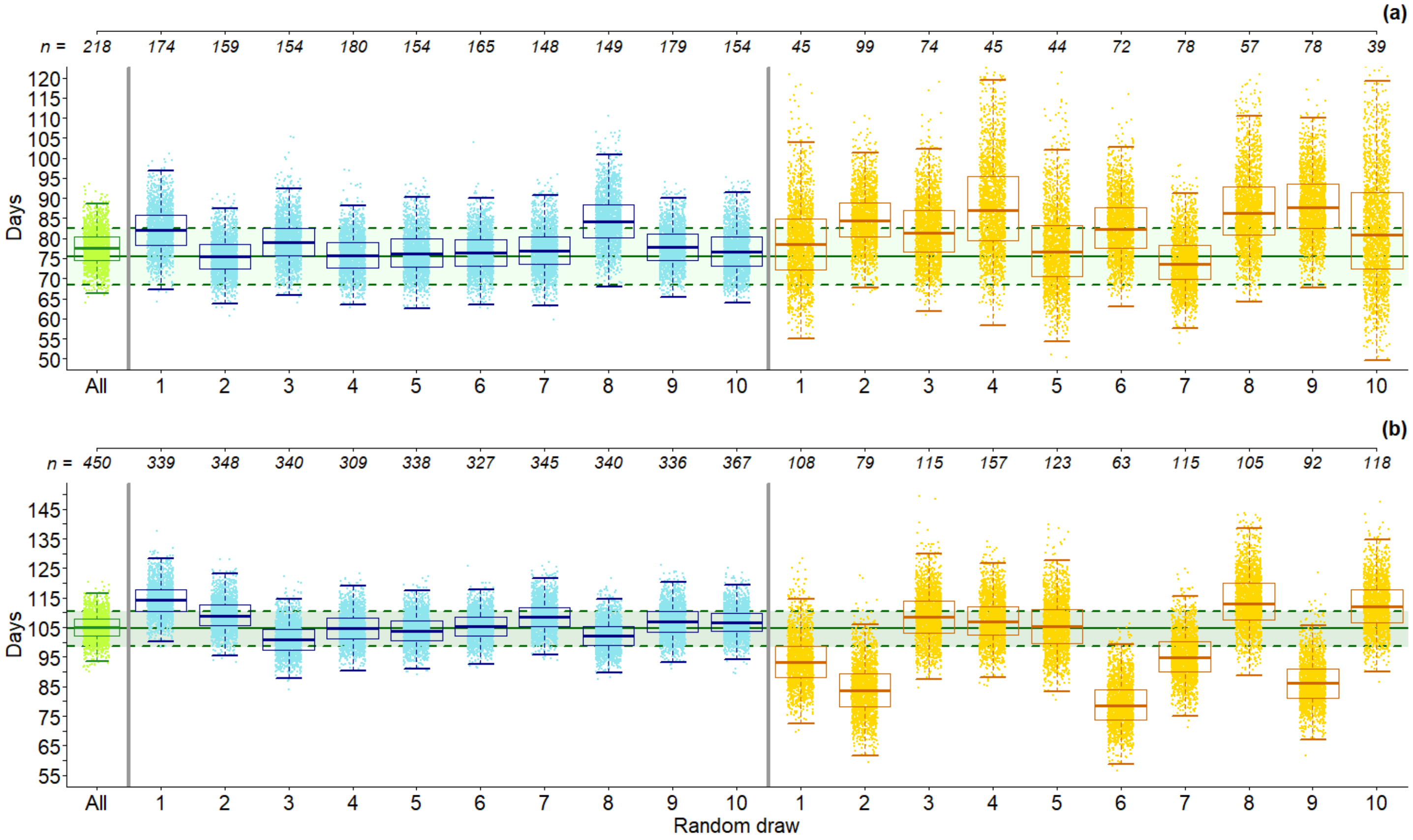

Figure 3.9. Estimated mean decay time of 10 datasets randomly selected from (a) Mohneke and Fruth (2008) and (b) Survey 4 "S4" (this study), using a gamma survival model. Clouds of dots represent 2,000 mean decay times extracted from the posterior distribution, with boxplots representing quartiles and variability of the samples. From left to right: 1) full datasets (green), i.e. "All"; 10 random draws of 2) 75% of nest groups (blue); 3) 25% of nest groups (yellow). The upper x axis shows the number of individual nests *n* in each draw. Green, horizontal lines show the reference decay value (mean, solid line) and 95% confidence intervals (dashed lines) for a) decay time for Mohneke and Fruth (2008); b) S4 estimated via gamma survival model (this study).

Table 3.5. Decay time (mean; (95% CI) of nests assessed for different survey times of 1) dataset published by Mohneke and Fruth (2008); 2) Survey 4 (this study), using a a) Logistic regression (Laing et al., 2003) investigating different times of revisit [Proportion of nests "Alive" at revisit]); b) Gamma survival model [this study]. 1) Different survey time (n = sample size): a) Full: complete dataset, b) Half 1: first half of the survey; c) Half 2: second half of the survey. 2) Different intervals between nest marking and revisit (for logistic regression only): a) 2 weeks = 2 weeks after the last nest group was marked; b) 1 month = 1 month after the last nest group was marked; c) 3 months = 3 months after the last nest group was marked; d) 3 months after marking = 3 months after each nest group was marked, e) Random = random number of days between 7 and 360 days after each nest group was marked. Observed mean decay time for the full dataset reported by Mohneke and Fruth (2008) was 75.5 days (95% confidence interval = 68.4 – 82.5).

		Logistic regression					**Gamma survival**
Dataset	**Survey time**	*2 weeks*	*1 month*	*3 months*	*3 months after marking*	*Random*	*NA*
Mohneke and Fruth [74]	*Full* *(n = 218)*	85.3 (84.0 - 89.8) [0.243]	78.2 (77.4 - 87.5) [0.170]	38.9 36.0 - 64.6 [0.004]	82.5 (79.7 - 84.2) [0.367]	78.2 (77.3 - 80.6) [0.238]	77.7 (71.0 - 84.9) [*NA*]
	Half 1 *(n = 125)*	66.4 (63.5 - 67.3) [0.536]	70.5 (68.2 - 71.9) [0.448]	86.1 (83.9 - 91.9) [0.192]	78.7 (78.1 - 83.2) [0.352]	68.1 (66.6 - 70.1) [0.248]	77.8 (69.9 - 86.6) [*NA*]
	Half 2 *(n = 93)*	90.9 (81.8 - 94.0) [0.419]	76.7 (74.3 - 82.4) [0.279]	*NA* *NA* [0.000]	84.7 (81.8 - 88.1) [0.387]	93.8 (92.9 - 97.6) [0.236]	78.5 (68.1 - 90.4) [*NA*]
S4 [this study]	*Full* *(n = 450)*	104.8 (103.6 - 107.5) [0.275]	105.4 (104.6 - 108.1) [0.238]	102.1 (100.6 - 112.5) [0.111]	96.9; (88.5 - 98.9) [0.464]	102.3; (100.6 - 109.1) [0.293]	104.6; (98.7 - 110.5) [*NA*]
	Half 1 *(n = 221)*	96.5 (92.5 - 98.4) [0.412]	91.42 (87.4 - 94.1) [0.326]	97.4 (94.7 - 100.6) [0.140]	84.4; (82.1 - 87.0) [0.389]	90.8; (87.9 - 95.5) [0.294]	87.2; (77.8 - 97.7) [*NA*]
	Half 2 *(n = 229)*	101.5 (100.2 - 103.1) [0.511]	102.4 (101.4 - 104.3) [0.441]	101.1 (100.3 - 109.9) [0.201]	103.7; (93.2 - 116.4) [0.537]	114.2; (111.6 - 126.4) [0.292]	109.1; (98.1 - 121.9) [*NA*]

3.4.4. Factors affecting decomposition time

Table 3.6 shows that bonobo nests tended to persist longer if constructed (*C*) with material from single rather than multiple trees (i.e. integrated) and, in contrast to our expectation, if exposed to the sky (*E*).

Bonobo nests also survived longer if built in the very top of a tree crown (*P*) (in contrast to side branches) and at lower heights (*HT*) (in contrast to nests built in upper parts of a tree). However, nests built on side branches in the apical section of a tree had a decomposition time 29 days shorter than those built in the fork at the top of the tree (i.e. top nests). As a result, nest height (*HT*) did not turn out to be a significant predictor of average nest decomposition time (Table 3.6; Figure 3.12 and Box 3.1). Forest type (*F*) had limited influence on nest decomposition time (Box 3.1). In contrast, our results suggest that tree species (*Sp*) was an important factor (Box 3.1), with nests constructed on species such as *Scorodophloeus zenkeri* showing a shorter decomposition time (average = 89.93; 95% CI = 74.16−107.55) than nests built on more solid species, such as *Anonidium mannii* (average = 109.82 ; 95% CI = 87.99−133.28). Table 3.8 shows the estimated nest decay time for the most recurrent tree species.

As expected, nests exposed to high levels of precipitation across their lifetime (*W*) showed the fastest decomposition (Figure 3.11). However, there were inconsistencies across periods regarding the conditions “intermediate” and “few” rains, with nests exposed to “few” lasting the longest in P1, and nests exposed to “intermediate” surviving the longest in P2 (Box 3.1). Conversely, the number of storms in the lifetime of a nest (*S*) was consistent across periods. In contrast with our prediction, nests exposed to fewer storms survived less than those exposed to numerous storms, with the longest decomposition time being exhibited by nests exposed to intermediate ones (Figure 3.11). Here, nest construction type differed significantly between the different categories. Among those exposed to a “Low” number of storms, the proportion of integrated nests was almost twice that observed for nests exposed to a “High” (Chi-squared test: X^2 = 5.2, p = 0.022) or “Medium” number of storms (X^2 = 15.2, $p < 0.001$). Conversely, the proportion of top nests was four times higher among the nests exposed to a “High” number of storms (X^2 = 17.3, $p < 0.001$). Finally, neither rainy condition (*R*) and/or differential temperature between day and night (*D*) at day of construction had a significant influence on nest decomposition time (Figure 3.12 and Box 3.1).

Table 3.6. Factors influencing nest decomposition time: results of the survival model. For each category (parameter) included in the model we show 1) Parameter mean: posterior mean with 95% confidence interval (95% CI) (log-scale); and 2) Average decomposition time: with 95% confidence interval (95% CI) (natural scale (Days)).

Factor	**Category**	**Parameter**	**Parameter mean (95% CI) Log-scale**	**Average decomposition time (95% CI) Natural scale (Days)**
Forest type (*F*)	Swamp	$\digamma_1$	0.52 (-6.13–7.48)	87.09 (75.00–100.01)
	Terra firma	$\digamma_2$	0.62 (-6.08–7.59)	95.96 (92.14–99.91)
Nest exposure (*E*)	Close	ε_1	0.42 (-6.13–6.94)	87.39 (82.20–92.61)
	Open	ε_2	0.56 (-6.01–7.06)	100.18 (95.52–104.99)
Nest position (*P*)	Side branch	π_1	0.52 (-6.16–7.02)	93.85 (89.95–97.84)
	Top	π_2	0.65 (-6.04–7.14)	107.11 (96.35–118.56)
Nest construction type (*C*)	Single tree	γ_1	0.67 (-5.53–6.89)	98.45 (94.41–102.62)
	Integrated	γ_2	0.50 (-5.69–6.74)	82.95 (75.61–90.60)
Nest relative height (*H*)	Low	η_1	0.43 (-5.02–5.79)	102.38 (93.05–112.04)
	Medium	η_2	0.37 (-5.05–5.74)	96.43 (91.98–100.97)
	High	η_3	0.29 (-5.13–5.61)	88.52 (81.31–96.06)
Average precipitation (*W*)	Low	ω_1	0.30 (-5.20–5.83)	92.41 (80.64–104.89)
	Medium	ω_2	0.35 (-5.17–5.88)	96.98 (92.81–101.21)
	High	ω_3	0.26 (-5.23–5.80)	89.08 (80.09–98.98)
Average storms (*S*)	Low	σ_1	-0.17 (-5.49–5.05)	46.05 (39.91–52.60)
	Medium	σ_2	0.70 (-4.64–5.88)	109.41 (104.56–114.37)
	High	σ_3	0.27 (-5.04–5.46)	71.82 (64.45–79.59)
Differential temperature (*D*)	Low	δ_1	0.32 (-5.18–5.87)	93.13 (85.82–100.55)
	Medium	δ_2	0.36 (-5.16–5.92)	96.70 (92.11–101.24)
	High	δ_3	0.33 (-5.17–5.88)	94.17 (87.40–101.51)
Rain at construction (*R*)	No	ρ_1	0.61 (-5.91–7.32)	95.23 (91.36–99.17)
	Yes	ρ_2	0.62 (-5.89–7.34)	96.86 (88.48–105.49)
Scale parameter		θ	0.02 (0.02–0.02)	*NA*

Box 3.1. *Results of model selection procedure.*

Models containing differential temperature (*D*) and relative nest height (*H*) returned a better fitting than those containing minimum temperature at construction (*T*) and absolute nest height (*A*) (Table 2 – Models 1 to 4). However, although the raw average daily amount of rainfall throughout a nest's life (*W*) and the raw average daily number of storms (*S*) were correlated (Spearman's correlation test: *rho* = 0.74, $p < 0.001$), we did not detect signs of correlation between *W* and *S* related parameters after reclassification (Figure 3.10).

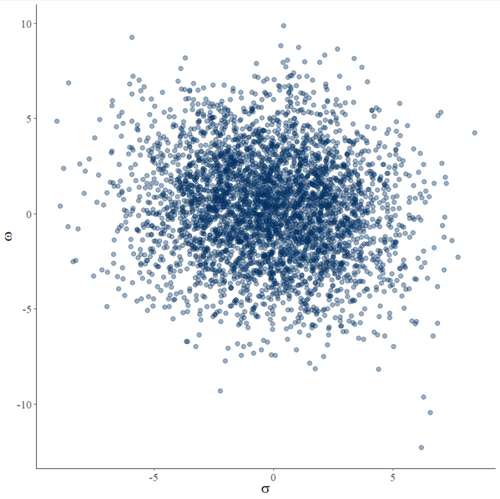

Figure 3.10. Scatter plots of the relationship between the posterior distributions of the parameters for 1) Average rain (ω) and 2) Average storms (σ).

(*S*) was the most important factor in our main model (including all nests, from both periods) (Table 3.7 – Models 5 to 15), with other important variables being nest exposure (*E*), nest construction type (*C*) and tree species (*SP*). All other factors added very little to the overall predictive power of the model.

Table 3.7. Differences in expected log predictive density (ELPD) between competing models and estimated standard errors of the differences. If the difference between models is higher than the standard error, models with higher ELPD are expected to have better predictive performance. Models 1 to 4 include all variables specified in Table 1, but with different combinations of those describing nest height (*A* vs. *H*) and temperature at construction (*T* vs. *D*), with model 4, including *H* and *D*, returning the best predictive performance (bold). ELPD differences of leaving out one variable at a time (4.a to 4.j) are then compared to the full model (Model 4). If an important variable is excluded, then the ELPD difference with the full model will be higher. The average number of storms in a nest's life is the most important factor describing nest decomposition time. Its exclusion returns the worst predictive performance, only better than the null model (5). * = variables significantly increasing the model's predictive performance.

Model	Model description	Difference in ELPD	Standard error
1	Differential temperature *D* & absolute height *A*	-11.8	5.7
2	Minimum temperature *T* & absolute height *A*	-9.4	5.7
3	Minimum temperature *T* & relative height H	-6.5	4.4
4	**Differential temperature *D* & relative height *H***	**0**	**0**
4.a	Model 4 – Differential temperature *D*	-0.2	1.7
4.b	Model 4 – Average rain *W*	-0.4	1.7
4.c	Model 4 – Forest type *F*	-1.1	1.7
4.d	Model 4 – Rain at construction *R*	-1.2	1.0
4.e	Model 4 – Relative height *H*	-1.9	2.6
4.f*	Model 4 – Nest position *P*	-2.8	2.5
4.g*	Model 4 – Construction type *C*	-7.2	3.4
4.h*	Model 4 – Species *SP*	-7.4	5.8
4.i*	Model 4 – Nest exposure *E*	-7.6	4.9
4.j*	Model 4 – Average storms *S*	-97.6	11.6
5	Null model	-181.0	17.9

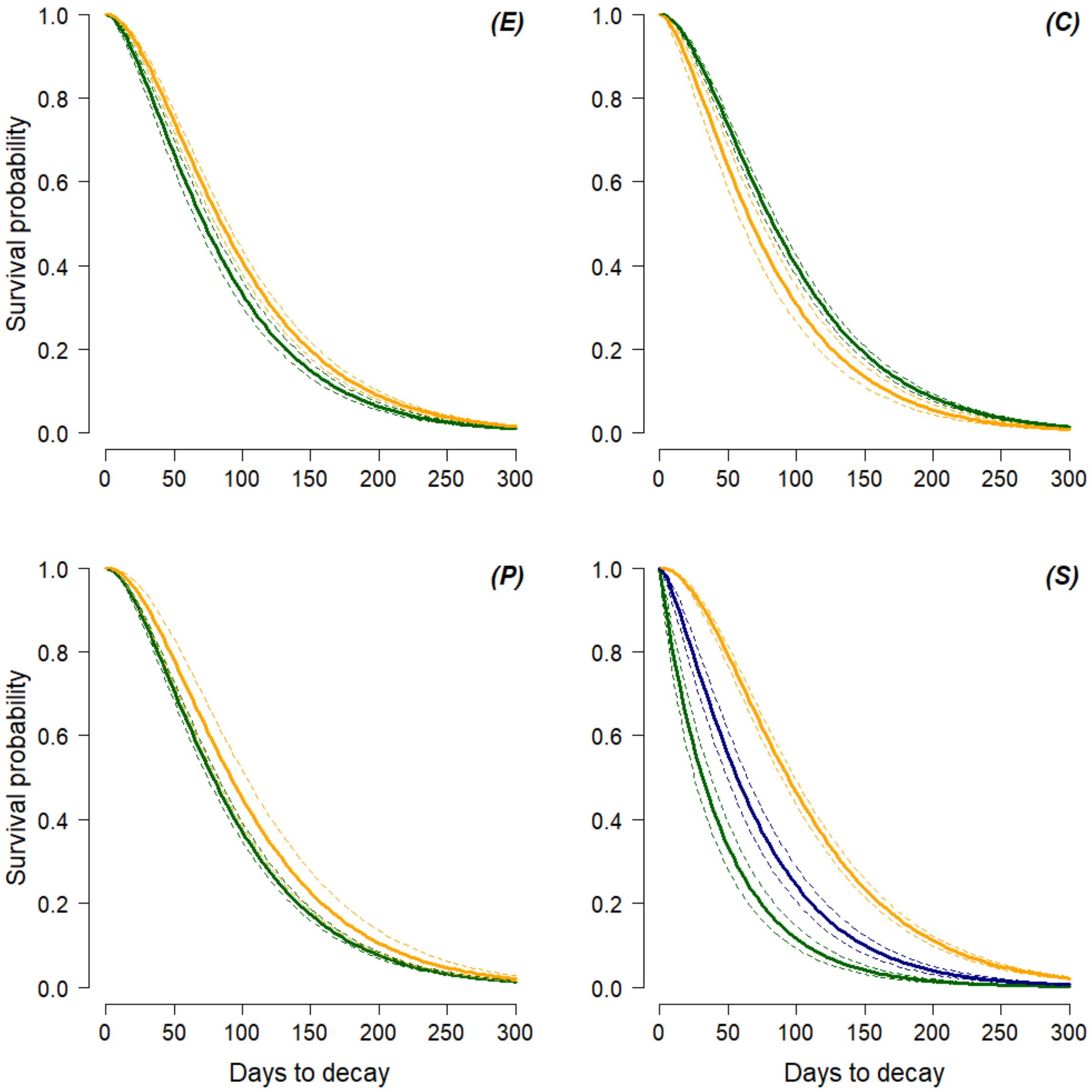

Fig 3.11. Factors influencing nest survival. Survival curves (bold, coloured lines) and 95% confidence intervals of the mean (dotted, coloured lines) for: (E) Exposure of nest: “Open” (orange) and “Closed” (green); (C) Construction type: “Integrated” (orange) and “Single tree” (green); (P) Position: “Side branch” (green) and ”Top” (orange); (S) Nest exposed to number of storms: “Low” (green),”Medium” (orange) and “High” (blue).

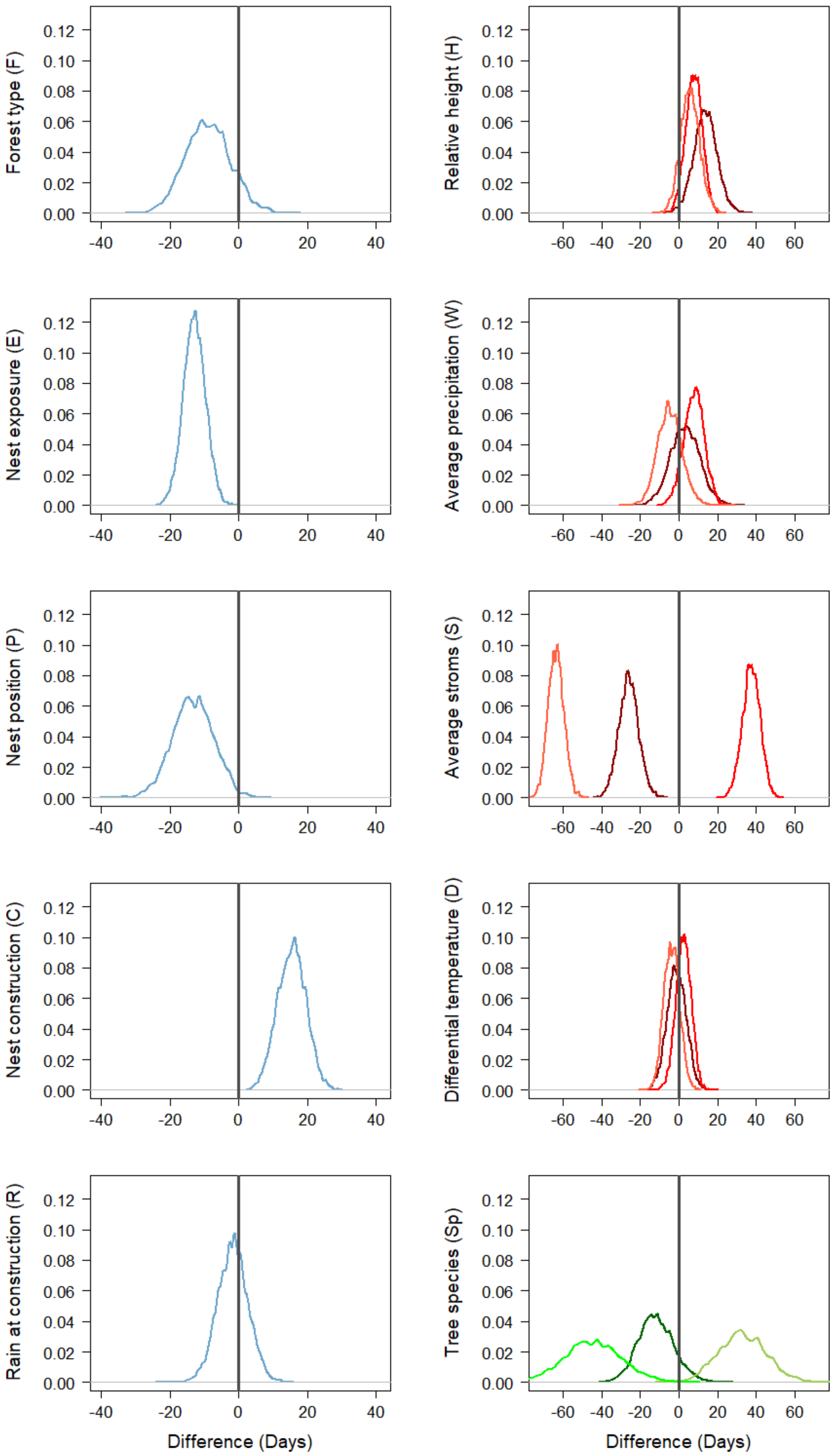

Figure 3.12. Posterior distribution of contrasts (differences in days) between categories within the factors listed in Table 1 (main text). If the mass of the contrasts (coloured lines) overlaps 0 (dashed grey line), then the difference between mean decay times for 2 categories is not significant. 1) Blue lines (left): contrasts of binary factors. 2) Red lines (right): contrasts of three level factors (Dark red = ”Low” - “High”; Red = “Medium” - “High”; Light red = “Low”- “Medium”). 3) Green lines (bottom-right): contrasts tree species (Dark green = *Scorodophloeus zenkeri* – “Other species”; Green = *Anonidium mannii* – “Other species”; Olive green = *Scorodophloeus zenkeri - Anonidium mannii).*

Table 3.8. Decay time for nest constructed in tree species (categories; parameters) in this study (All), and by survey period (P1, P2). Species: Genus and species name; Vernacular name: local (Lonkundu) name of tree species; Sample: number of individual trees for each category; Parameter mean (95% CI) log-scale: posterior mean with 95% confidence Interval of each parameter *j*; Average decomposition time (95% CI) natural scale (Days) with 95% confidence interval. Category 11 (i.e. "Other species"): all other tree species, including those of integrated nests.

Survey	Category	Species	Vernacular name	Sample	Parameter	Parameter mean (95% CI) Log-scale	Average decomposition time (95% CI) Natural scale (Days)
ALL	1[a]	*Dialium spp.*	Maku pembe	383	ψ_1	-0.04 (-2.87 - 2.79)	87.39 (81.31 - 93.52)
	2[b]	*Dialium spp.*	Maku rouge	139	ψ_2	-0.03 (-2.86 - 2.80)	88.65 (79.25 - 99.07)
	3	*Greenwayodendron suaveolens*	Bodzinda	99	ψ_3	0.2 (-2.65 - 3.06)	111.47 (98.43 - 125.50)
	4	*Plagiostyles africana*	Bondenge	48	ψ_4	0.21 (-2.62 - 3.07)	113.1 (94.71 - 132.26)
	5	*Monopetalanthus microphyllus*	Bokese	40	ψ_5	-0.05 (-2.89 - 2.79)	86.91 (68.98 - 105.51)
	6	*Scorodophloeus zenkeri*	Bopidji	42	ψ_6	-0.08 (-2.89 - 2.73)	84.31 (67.60 - 102.17)
	7	*Santiria trimera*	Botalala	40	ψ_7	0.12 (-2.74 - 2.96)	103.37 (84.55 - 124.06)
	8	*Anonidium mannii*	Bodzingo	34	ψ_8	0.34 (-2.51 - 3.17)	128.93 (105.77 - 153.04)
	9	*Cynometra sessiliflora*	Eaka	27	ψ_9	0.23 (-2.57 - 3.04)	114.9 (87.89 - 145.59)
	10	*Gilbertiodendron dewevrei*	Bolapa	25	ψ_{10}	-0.02 (-2.89 - 2.78)	89.57 (66.22 - 113.90)
	11	*Other species*		634	ψ_{11}	0.05 (-2.80 - 2.89)	96.05 (90.74 - 101.64)
P1	1[a]	*Dialium spp.*	Maku pembe	203	ψ_1	-0.08 (-2.77 - 2.84)	79.11 (72.49 - 86.54)
	2[b]	*Dialium spp.*	Maku rouge	74	ψ_2	-0.08 (-2.76 - 2.85)	79.30 (67.61 - 91.56)
	3	*Greenwayodendron suaveolens*	Bodzinda	59	ψ_3	0.19 (-2.42 - 3.16)	104.47 (89.03 - 120.45)
	4	*Monopetalanthus microphyllus*	Bokese	27	ψ_4	-0.18 (-2.86 - 2.71)	72.64 (55.44 - 92.45)
	5	*Cynometra sessiliflora*	Eaka	24	ψ_5	0.15 (-2.52 - 3.10)	100.77 (77.67 - 128.09)
	6	*Gilbertiodendron dewevrei*	Bolapa	21	ψ_6	-0.05 (-2.67 - 2.93)	82.80 (59.71 - 105.65)
	7	*Scorodophloeus zenkeri*	Bopidji	18	ψ_7	-0.14 (-2.80 - 2.76)	75.70 (54.57 - 100.22)
	8	*Santiria trimera*	Botalala	16	ψ_8	0.19 (-2.48 - 3.16)	104.97 (79.65 - 133.60)
	9	*Maesobotrya bertramiana*	Kalanga	16	ψ_9	-0.09 (-2.86 - 2.85)	79.78 (57.20 - 105.06)
	10[c]	*Diospyros spp.*	Mandza	14	ψ_{10}	-0.12 (-2.78 - 2.75)	77.18 (51.44 - 105.91)
	11	*Other species*		359	ψ_{11}	0.07 (-2.63 - 3.01)	92.18 (85.59 - 98.69)
P2	1[a]	*Dialium spp.*	Maku Pembe	180	ψ_1	-0.17 (-2.69 - 2.63)	96.27 (87.13 - 106.41)

2[b]	*Dialium spp.*	Maku Rouge	65	ψ_2	-0.13 (-2.61 - 2.64)	99.94 (84.29 - 117.23)
3	*Greenwayodendron suaveolens*	Bodzinda	40	ψ_3	0.07 (-2.44 - 2.83)	121.86 (99.85 - 144.63)
4	*Plagiostyles africana*	Bondenge	36	ψ_4	0.08 (-2.44 - 2.91)	123.83 (100.54 - 150.77)
5	*Scorodophloeus zenkeri*	Bopidji	24	ψ_5	-0.18 (-2.62 - 2.72)	95.50 (72.08 - 121.39)
6	*Anonidium mannii*	Bodzingo	24	ψ_6	0.10 (-2.40 - 2.91)	126.65 (97.49 - 158.92)
7	*Santiria trimera*	Botalala	24	ψ_7	-0.03 (-2.52 - 2.82)	111.60 (84.60 - 143.76)
8[d]	*Grewia spp.*	Bopfumo	10	ψ_8	-0.32 (-2.85 - 2.65)	84.21 (52.61 - 119.40)
9	*Trichoscypha arborescens*	Bohungwu	12	ψ_9	-0.41 (-2.89 - 2.42)	76.94 (50.99 - 107.96)
10	*Monopetalanthus microphyllus*	Bokese	13	ψ_{10}	0.00 (-2.53 - 2.85)	115.08 (78.27 - 158.39)
11	*Other species*		252	ψ_{11}	-0.01 (-2.48 - 2.81)	112.39 (101.93 - 123.22)

[a] Includes five *Dialium* species identical by vernacular name: *D. angolense; D. gossweileri; D. kasaiense; D.pachyphyllum; D. tessmannii*

[b] Includes two *Dialium* species identical by vernacular name: *D. corbisieri; D. zenkeri*

[c] Includes five *Diospyros* species identical by vernacular name: *D. bipendensis; D. gilletii; D. iturensis; D. melocarpa; D. zenkeri*

[d] Includes three *Grewia* species identical by vernacular name: *G. coriacea; G. oligoneura; G. pinnatifida*

3.5. Discussion

Long-term studies have revealed the dramatic impact of climate change on Central African rainforests. Only recently, an analysis of phenological data covering a 32-year period raised severe concerns of the impact of climate change on Central African forests (Bush et al., 2020). Our study, although only covering 15 years of climate data, reaffirms that climate change is impacting upon the very heart of the second largest forest area on our planet, the Congo Basin. Here, we showed the steady decline of rainfall across years, and the impact of this on bonobo nest decay times. This connection is relevant to all great ape density estimations using distance sampling, and is therefore of major importance to the interpretation of all biomonitoring estimates, past, present and future, inferring global significance in the conservation efforts of great apes in the wild.

Many studies have reported an effect of climate on great ape nest decomposition time, with drier conditions resulting in longer decay times (Kouakou, Boesch and Kühl, 2009; Stewart, Piel and McGrew, 2011; Morgan et al., 2016; Kamgang et al., 2020). Our study links the decomposition of 1,511 bonobo nests to climatic data spanning a 15-year period, and supports this claim. In LuiKotale, bonobo nests constructed in 2016–2018 showed a mean decay time 19 days longer than nests constructed in 2003–2007, when average monthly rainfall was higher (Figure 3.7). We also found that average nest decay time varied significantly from one year to another in the same period, with nests in S2 exhibiting a decomposition time one month longer than those constructed in the previous (S1) and subsequent (S3) years. The year 2005 (S2) was characterized by a very short dry season, with a single month (July) of extremely limited precipitation. In addition, most rain and storms in that year were concentrated at the end of the survey (between November and December 2005) (Fig 3.7). Therefore, a long dry climate at the beginning of the survey (February–August) may have triggered a longer decay time for most nests. Indeed, nests constructed between February and August 2005 showed an average decay time 20 days longer than those constructed after the end of the dry seasons, highlighting the atypical conditions of that year. This clearly demonstrates how using a decay time estimated in a different period, or in a different survey (e.g. S2), could result in a severe bias in bonobo density estimates.

3.5.1 Factors affecting decomposition time

Several studies have reported the amount of rain occurring in the lifetime of a nest as the most important factor affecting nest decomposition time (Kouakou, Boesch and Kühl, 2009; Morgan et al., 2016; Kamgang et al., 2020). However, others did not find a clear pattern in support of this claim (Mathewson et al., 2008). Here, we assumed events of extreme precipitation (i.e. storms) to affect nest decomposition time more than continuous rains. By investigating both factors, we found that the occurrence of storms, rather than rainfall, was the most important parameter explaining differences in nest decay time (Table 3.6, Figure 3.10 and Box 3.1). As expected, high values of rain were related to faster decomposition time (Table 3.6). However, the correlation was not significant (Figure 3.12), and the observed pattern varied between periods, with P1 showing no differences between rain categories, and P2 showing nests experiencing a "Medium" amount of rain lasting longer than nests experiencing both "Low" and "High" amounts of rain (Table 3.6 and Appendix 3). In contrast, the number of storms showed a consistent, yet unexpected pattern. In line with our expectations, "High" numbers of storms triggered a decomposition time 24 days faster than the mean value of 95 days. However, "Low" numbers of storms were associated with a decomposition 49 days faster (Table 3.6). With 88% of nests experiencing "Low" numbers of storms being constructed in the dry season, either in February, or between May and August, our results suggest a shorter decay time for nests constructed in the dry season, at odds with the expectation of a longer decay time. We suspect that the reasons for such a pattern are behavioural. It has been recently suggested that chimpanzees adjust nest construction type in response to the weather (Stewart et al., 2018). Chimpanzees built thicker, more insulated nests in colder conditions, increasing the number of broken branches and choosing larger support branches, in moister and windier weather (Stewart et al., 2018). Here, we found no influence on decay time of rain and temperature at the time of nest construction, the proxies we chose to investigate a behavioural influence on nest decomposition time (Tables 3.6 and Figure 3.12). In addition, we did not record nest construction measures, such as those described in (Samson and Hunt, 2014; Morgan et al., 2016; Stewart et al., 2018). However, we found nests experiencing a "Low" number of storms to be less frequently constructed in the treetop, and more frequently comprising materials from more than one tree (i.e. integrated nests). Indeed, our results showed that integrated nests lasted 15.5 days fewer than those constructed using material from a single tree, whilst a nest in the treetop exhibited a longer decomposition time than one built on side branches (Table 3). These results suggest that bonobos in LuiKotale exhibit flexible nest building behaviour, constructing less durable (e.g. located on side branches) but more comfortable (e.g. integrated) nests during the dry season when strong nest support is not required because of a predictable absence of storms. Although involving significantly fewer rains, we observed a similar number of storms per month in 2016–2018 (P2) as in P1 (2003–2007) and a less obvious dry season (Figure 3.3 and Figure 3.4). This suggests that, in P2, rain was less predictable and was more likely to appear during a storm. Bonobos might have adapted to such a climate by strengthening nest structure to cope with unpredictable and intense precipitation, thus enabling longer decay time.

Other studies found nests exposed to the open sky to decay faster than those protected by upper foliage (Morgan et al., 2016). However, we found an opposite trend, with “Open” nests surviving longer than “Closed” nests (Table 3.3 and Figure 3.11). The reason for this may also be behavioural. Building a nest open to the sky allows an ape to dry quicker, avoiding exposure to persistent dripping water from above foliage after rain (Baldwin et al., 1981). Such open nests may require stronger support and a thicker structure to resist wind (Stewart et al., 2018), potentially resulting in open nests lasting longer than those shielded by vegetation but not built as strong. In addition, and in contrast to our expectations, the difference between the height of the nest and its survival was not statistically significant, further supporting the importance of bonobo nest-building behaviour on decay time.

In order to better understand the adaptability of great ape nesting behaviour to climatic conditions, future studies should record nest structure in greater detail. In particular, such detail includes measures of nest thickness and strength (Samson, 2012; Samson and Hunt, 2014; Stewart et al., 2018), material used (Fruth and Hohmann, 1994; Morgan et al., 2016) and nest position on the branches (i.e. distance from the trunk).

Here, we defined a storm in a rather crude way, looking at single, abundant bursts of rain (minimum of 20 mm/m^2), following bright sunshine in the afternoon or clear sky at night. However, a more sophisticated classification would incorporate wind speed (Stewart et al., 2018). Indeed, it is likely that strong winds, in combination with heavy rain, are very effective in dismantling great ape nests, particularly those constructed further away from the tree trunk or with flimsier supports.

Habitat (i.e. forest type) did not significantly affect decomposition time in LuiKotale (Figure 3.11), probably because of the limited number of nests in our study constructed in swamp forest (5%). However, in accordance with other studies (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004; Kouakou, Boesch and Kühl, 2009; Kamgang et al., 2020), we found that the tree species had an important influence on nest decomposition time (Box 3.1). Here, we observed a large variation between and within species (Table 3.8). *Dialium* species were the most frequently used, with "Maku pembe" (comprising 5 species) being used in 25% of nests (Table 3.8). However, *Dialium* is the most frequently occurring genus in LuiKotale (Beaune et al., 2013). We also found that nests constructed in species such as *Anonidium mannii* (129 days) or *Plagiostyles africana* (113 days) lasted considerably longer than those constructed in trees such as *Scorodophloeus zenkeri* (84 days) or *Trichosypha arborescens* (77 days; only used in P2) (Table 3.8). To further investigate this phenomenon, future studies should include information on the phenotypes and biomechanical properties of the nesting tree species (Samson, 2012; Samson and Hunt, 2014).

3.5.2. Nest decay and great ape conservation

Nest decay values are widely used in the monitoring of great ape populations to convert nest density into ape density (Kühl et al., 2008) and are therefore of great importance when assessing IUCN extinction risk categories. In recent years, new protected areas have been created following nest count studies and great ape conservation strategies, such as Moyen-Bafing National Park, Guinea (Boesch et al., 2020). Management plans and conservation strategies continue to be based on nest count surveys, as are studies assessing the effectiveness of conservation interventions (Stokes et al., 2010; Kablan et al., 2019).

Many studies have shown that the average nest decomposition time is extremely variable (Plumptre and Reynolds, 1997; Mathewson et al., 2008), thus recommending the use of values reflecting time- and site-specific nest decomposition (Laing et al., 2003; Kühl et al., 2008). However, until 2008, the few published decay times were commonly applied to all great ape surveys (Morgan et al., 2016); subsequently, best practice guidelines for great ape monitoring were published, discouraging such decisions (Kühl et al., 2008). In recent years, some studies have included survey-specific decay time by either observation (Fleury-Brugiere and Brugiere, 2010; Serckx et al., 2014b; Voigt et al., 2018; Lapuente et al., 2020) or modelling (Spehar et al., 2010; Murai et al., 2013; Tweh et al., 2015; Santika et al., 2017; Strindberg et al., 2018; Heinicke et al., 2019a). Others have incorporated values obtained in the same area from an earlier survey (Gregory et al., 2012; Carvalho, Marques and Vicente, 2013; Piel et al., 2015; Plumptre et al., 2016; Simon, Davies and Ancrenaz, 2019), from a site close to the surveyed area (Mathewson et al., 2008; Stokes et al., 2010; Danquah et al., 2012; Haurez et al., 2014; Spehar et al., 2015; Dias et al., 2019), or from averaged published values (Aebischer et al., 2017). Our findings highlight the problematic nature of this approach. Even within a short period of 3 years (P1 in this study), decay time showed a between-years fluctuation of as many as 44 days (Figure 3.7). As an example, if a bonobo SCNC survey was performed at LuiKotale in 2005, in which a constant nest production rate (= 1.37 nest/individual (Kühl et al., 2008)) and decay time calculated from the year before (i.e. S1) were applied, a real bonobo population of 30 individuals would be overestimated by 60%, to 48 individuals. In addition, our results suggest that it is problematic to model nest decay using tree species only (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004), or abiotic factors such as rainfall and habitat type (Santika et al., 2017). Both abiotic and biotic factors must be included in order to obtain reliable estimates, reflecting the high variability observed in our study.

The most reliable estimates of nest decomposition time are obtained via continuous monitoring of a sample of nests large enough to be representative of the period of survey (Kühl et al., 2008). However, such a protocol is infeasible in most cases, where financial and time resources are limited. Therefore, more time-efficient methods, such as the retrospective estimation of nest decay with a single revisit of a marked nest (Laing et al., 2003), are recommended (Stokes et al., 2010). Using a logistic regression on subsets of our long-term data, we obtained consistent estimates in many cases (Figure 3.8 and Table 3.5). However, we also found a considerable amount of variation, mainly due to 1) unrepresentative sample size and 2) inappropriate interval between nest marking and revisit.

When we mimicked a smaller sample size by randomly reducing our full dataset to 75 and 25 % to investigate decay representativity, biased decay time estimates became more apparent the smaller the sample (Figure 3.8 and Figure 3.9). This effect was more pronounced for the 1-year (S4; July 2016–June 2017), than for the 6-month survey (Mohneke and Fruth, 2008). In field conditions, this happens when nest groups included in the decay study do not represent the possible factors affecting decay (Walsh and White, 2005). According to our results, the time between nest marking and revisit also affected the precision of decay time estimates. Here, inconsistent estimates became apparent when reanalyzing the survey by Mohneke and Fruth (2008), while the analysis of S4 returned consistent estimates, possibly because of the larger sample size. This was more pronounced when evaluating different times of revisit for half the survey time (i.e. 3 months in (Mohneke and Fruth, 2008); 6 months in S4) (Table 3.5). Great ape nests do not decay steadily (Walsh and White, 2005), but short periods of heavy rains, for example, can accelerate decomposition of many nests at a time. Therefore, including or excluding such periods can affect the precision of the estimates, regardless of the method used for analysis and particularly when sample sizes are small. This was unlikely to be an issue in our study due to the sampling of 1,511 nests. However, with lower sample sizes, the inclusion of a random effect for nest group might allow controlling for the issue, both in logistic regressions and survival analyses. In addition, when we set the revisit time at 3 months after the last nest group was marked, in the analysis of the dataset from Mohneke and Fruth (2008), all nests (except one) were already decayed at revisit, rendering the method invalid. It is thus important to select a revisit time that corresponds to the known or expected decay time for the area of study. While too few days can exclude or include periods of fast nest decay, excessively long times can result in no nests being “alive” at revisit, thus making analysis impossible altogether.

In sum, logistic regression provides an excellent method for effectively estimating survey-specific nest decay time with only two visits. However, it remains imperative to use a sample size that is representative of the whole nest population, and an appropriate time between visits. To best reflect the conditions to which nests are exposed, nest decay studies must start before the survey and continue throughout, with revisits taking place during or immediately after the survey (Laing et al., 2003).

Concerning sample size, Buckland et al., (2001) recommended a minimum of 50 individual samples to allow reliable modelling of dung decay time using logistic regression. However, as bonobo nest decay time is not only affected by ecological parameters such as habitat, rainfall or number of storms, but also by behavioural factors such as construction type and choice of tree species, the decay time of bonobo nests shows a larger variation than that of dung. Therefore, we found that for bonobo nests, a minimum of 250 nests are needed for reliable estimates (Figure 3.8).

3.5.3. Conclusions

The Congo region plays a key role in assessing global warming conditions. Due to the lack of real data from this region, models that prospect the impact of climate change into the future are so far contradictory (Haensler, Saeed and Jacob, 2013; Hua et al., 2019). Here, 15 years of data collection revealed a marked decrease in yearly rainfall and differential temperature between 2003 and 2018, but a constant number of storms. As a result, most of the rain in recent years at LuiKotale has come in the form of storms. Drier conditions have resulted in longer nest decay times, suggested to be further prolonged by the building of stronger nests necessitated by rarer, but harsher and more unpredictable, precipitation. Climate change is a reality in the middle of the Congo Basin, and this trend is likely to extend across the range of great ape distribution. As climate change continues to affect both the process of nest decomposition and ape nest construction behaviour (Figure 3.13), great ape nest decomposition times are likely to increase further in future years. This will create an opportunity for the erroneous conclusion of increasing ape numbers even when populations are stable or decreasing. In conclusion, we stress the absolute necessity to obtain and apply accurate, survey-specific nest decay estimates. Failure to account for the variation of decay time both between and within sites will lead to unreliable population estimates, having serious implications for our understanding of the dynamics of great ape populations and jeopardizing the very foundations of the conservation of great apes.

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3.7. Data availability statement

Data available via the EDMOND repository: https://dx.doi.org/10.17617/3.6e.

Photo: Bernard Ikembelo© PNS Survey®

Figure 3.13. Bonobo nests observed in Salonga National Park, Democratic Republic of the Congo.

CHAPTER 4

Integrated analysis of present and past abundance and distribution reveals a stable bonobo population in a natural world heritage site

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4.1. Abstract

The iconic great apes, a group of high conservation value, have declined dramatically over the past decades. Among them, the bonobo (*Pan paniscus*), is considered endangered in the IUCN Red List. However, with only 30% of its geographical range having been surveyed, detailed information is missing.

Here, we used a unique dataset comprising detection/non-detection and count data from 13 surveys conducted between 2002 and 2018, including 8,310 km of reconnaissance walks and line transects and 27,045 camera trap-days in Salonga National Park (SNP) and buffer zone, an area of 45,000 km^2 in total. We obtained data on bonobo presence and density in order to compare 2 time periods (2002-2008; 2012-2018), provide a population trend and investigate the influence of ecological and anthropogenic factors on the species. To do so, we jointly modelled bonobo occurrence and density data in a purposely developed Bayesian model, explicitly accounting for method specific detection probability and spatial autocorrelation.

We found that SNP is a bonobo stronghold with a population ranging from 13,288 and 20,208 mature individuals. Forest cover and herbaceous understorey were good predictors of bonobo abundance, while proximity to villages and the number of human signs negatively affected its numbers. Notably, we detected a positive effect of the presence of rangers on bonobo occurrence, as well as higher bonobo densities in areas where the local communities showed ancestral taboos against the killing of these great apes.

Our results also suggest that the integration of different data sources can help mitigate biases linked to specific methods providing an approach useful for the assessment of species lacking detailed survey data. Confirming a stable bonobo population, we provide an encouraging story in great ape conservation and advocate continued preservation of the integrity of SNP and its biological and cultural heritage in order to sustain this stronghold for wild bonobo.

4.2. 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), with 30% of the living terrestrial vertebrates being endangered by extinction (IUCN 2020a).

Knowing a species' geographical distribution, population size (i.e., number of individuals), density (i.e., number of individuals per specified area), population trend, (i.e., changes in abundance across time) and the main threats to the species are pivotal for its viability assessment, informing both international and national conservation authorities of specific conservation strategies. As a consequence, wildlife conservation efforts require appropriate field data and analytical methods providing accurate estimates of population status (Nichols & Williams 2006). Field data may include direct observation of animals or animal signs (Plumptre 2000), acoustic records (Blumstein et al., 2011) and camera-trap observations (Rovero & Zimmermann 2016) that provide information on presence (i.e., detection/non-detection), count (i.e., number of observed objects in the surveyed area) or demographic data (e.g., survival and recruitment rates). Frequently, field data for a particular species are spatially and temporally limited. They are typically sparse, are obtained from different sources, and entail different levels of standardization and accuracy (Moussy et al., 2021). For example, count data collected for monitoring purposes retain more information (Nichols & Williams 2006) but are usually spread over smaller areas than presence data gathered by citizen scientists (Altwegg & Nichols 2019) or law-enforcement patrols (Keane et al., 2011).

Until recently, studies evaluating a species' status used only part of the available information. The gold standard in ecological modelling were a) Occupancy models (MacKenzie et al., 2003; 2015) for the analysis of detection/non-detection data and b) Distance Sampling (DS) (Buckland et al., 2001; 2015), for the analysis of count data from systematic line and point transects. In addition, DS data were exploited in spatial modelling using generalized linear (GLM) and generalized additive models (GAM) (Miller et al., 2013), and incorporated in hierarchical models for the analyses of population status and trends (Bowler et al., 2019; Farr et al., 2021; Santika et al., 2017; Sollmann et al., 2015), including state-space models (Clark & Bjørnstad 2004) and dynamic N-mixture models (Royle 2004). The latter required multiple visits of a site conducted over a minimum of two periods, in order to evaluate changes in population abundance across periods by modelling site-specific survival and recruitment (Chandler & Clark 2014).

These successful frameworks provided the basis for the development of models jointly analyzing detection/non-detection, count, and demographic data. Developed first in fishery studies (Maunder & Punt 2013), Integrated Population Models (IPMs) improved previous methods by increasing the precision of the estimated parameters (Schaub & Abadi 2011). From fisheries, IPMs were extended to a large number of species (Besbeas et al., 2002; Dey et al., 2017; Hatter et al., 2017; Bowler et al., 2019; Horne et al., 2019; Jansen et al., 2019) and more recently used for the joint analysis of detection/non-detection and count data deriving from traditional ground surveys (Zipkin et al., 2017), camera-traps (Bowler et al., 2019), acoustic devices (Doser et al., 2020), aerial and interview surveys (Santika et al., 2017) and citizen science (Sun et al., 2019). These applications enabled the investigation of ecological drivers of specific distribution and abundance (Jansen et al., 2019), the assessment of impacts and threats (Dobbins et al., 2020), and the evaluation of conservation effectiveness (Saunders et al., 2018), showing the high potential of data integration for wildlife conservation (Kühl et al., 2020).

With all 14 species and subspecies classified as endangered or critically endangered in the Red List of Threatened Species issued by the International Union for the Conservation of Nature (IUCN 2020a), great apes (orangutans*: Pongo spp.*; gorillas: *Gorilla spp.*; bonobos: *Pan paniscus*; and chimpanzees: *P. troglodytes*) are of the highest conservation importance. Inhabiting thick tropical forests, they are rarely observed directly and are thus commonly monitored by taking advantage of their unique habit of sleeping in purposely built structures called “nests” (Fruth et al., 2018). Ape nests last long and are easily counted by field researchers, typically by applying Standing Crop Nest Counts (SCNC) (Tutin & Fernandez 1984), a method requiring a single visit and analyses in a DS framework (Buckland et al., 2001). However, SCNC requires conversion factors scaling the number of counted nests to the number of apes. Nest production rate, the average daily number of nests built by an ape, and nest decay time, the average number of days a nest would take to disappear from the forest (Buckland et al., 2001), are key. With both values being known to be highly variable across space and time, it was recommended to use purposely estimated, survey-specific conversion factors to obtain unbiased estimates (Kühl et al., 2008). While SCNC has been found to bias the true population size due to inaccurate conversion factors in some cases (Aebischer et al., 2017), estimating ad hoc values is time- and resource-demanding and not always performed (Kühl et al., 2008). Recently, camera-traps (CTs) allowed primatologists to move away from classical nest counts (Spehar et al., 2015; Després-Einspenner et al., 2017; Cappelle et al., 2019;). However, CT-based methods still present caveats, requiring full validation (Spehar et al., 2015). Consequently, the integration of nest counts with other sources of information is expected to provide more precise estimates of great ape abundance and population trend, particularly when analyzing sparse data collected with different methods (Horne et al., 2019). Recent studies of great ape population trends, have modelled nest count data only, using occupancy models (Plumptre et al., 2016), GLM (Wich et al., 2016; Kühl et al., 2017; Voigt et al., 2018) or GAM (Strindberg et al., 2018). An analysis integrating traditional SCNC, aerial nest counts and presence data from interviews (Santika et al., 2017) has only been applied to the Bornean orangutan (*P. pygmaeus*).

Here, our objective was twofold. First, we wanted to demonstrate how data integration could improve the effective assessment of species status. And second, we aimed to show how such integrated approach can inform conservation management, providing pivotal information with regards to the socio-ecological setting favoring species persistence.

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). With its density and distribution unknown in 70% of its geographic range, and the remaining 30% being surveyed sparsely (Fruth et al., 2016), this ape is an ideal candidate on which to develop a trend analysis that integrates diverse and limited available information. At the heart of the species' distribution range, lies Salonga National Park (SNP), a World Heritage Site considered a bonobo stronghold (Fruth et al., 2016). Remarkably, SNP 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 (Table 4.1). First, between 2002 and 2008 with a combination of reconnaissance walks "recces", and SCNC. Then, between 2012 and 2018, using a combination of recces, SCNC, and Camera-Trap Distance Sampling "CTDS" (Howe et al., 2017), a recent method estimating animal density by extending point transect DS to the use of CTs.

Here, we exploit this unique database integrating bonobo detection and density data over 2 periods, applying 3 different methods. We developed a single Bayesian model to estimate bonobo abundance and distribution. By that, we assess past and present bonobo population status in SNP and provide a population trend over the past 10 years. By integrating CTs and traditional nest count data, we show how bonobo presence and abundance is affected by ecological predictors, anthropogenic threats, and proxies of protection considering area-specific socio-cultural factors.

4.3. Materials and methods

4.3.1. Study area

Salonga National Park (36,000 km^2), DRC, is divided in 2 blocks, north and south, separated by an inhabited corridor (9,000 km^2). From an elevation of 350 m increasing southwards to 500 m, SNP is composed of more than 90% primary mixed lowland rain forest, the remaining 10% represented by savannahs, regenerating forest, cultivation, marshes, and water bodies. SNP consists of six sectors, administered by a head-quarter of the national conservation authority 'Institut Congolais pour la Conservation de la Nature' (ICCN) supervising several ranger patrol posts "PP" (Figure 4.1).

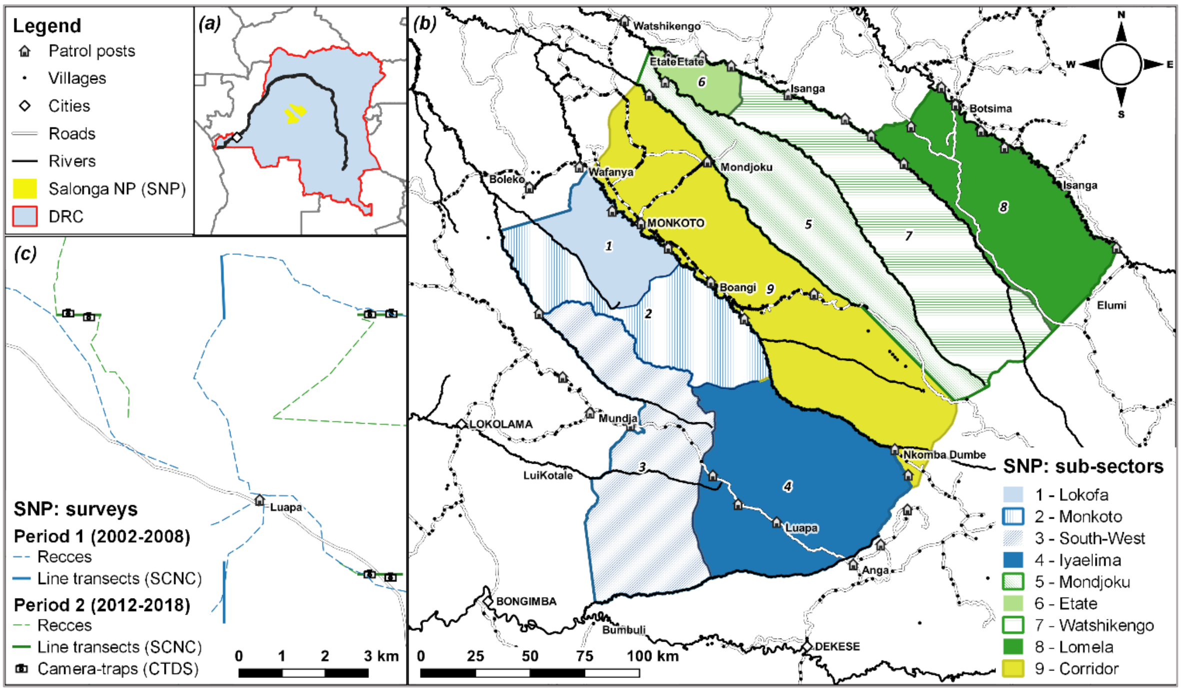

Figure 4.1. Location of Salonga National Park (SNP) in DRC (a); sub-sectors surveyed (b); and details of survey methods (c). Sub-sectors (solid colours; 1, 4, 6 and 8) surveyed in both periods of study (P1 [2002-2008] and P2 [2012-2018]); sub-sectors (patterns; 2, 3, 5, 7) surveyed in P2 only. The corridor (9) was surveyed with recces in P1 and with standing crop nest counts (SCNC) in P2.

4.3.2. Bonobo data

We included data on bonobo presence and abundance from 13 different surveys (Table 4.1), 10 of which were obtained from the IUCN SSC A.P.E.S. database (Heinicke et al., 2019b) conducted between 2002 and 2018 over 9 sub-sectors (Figure 4.1b) and within 2, 7-year periods: 2002 - 2008 (P1), and 2012 – 2018 (P2). In P1, we included detection / non-detection data from recces and SCNC obtained in 5 sub-sectors, using count data from 4 sub-sectors only. In P2, we included detection / non-detection data from recces, SCNC and CTDS (IUCN, 2020b), obtaining count data from SCNC for all 9 sub-sectors (Figure 4.1b). CTDS was only applied in 4 sub-sectors (Figure 4.1b). Overall, our analyses included 4,352 km of recces, 3,958 km of line transects (SCNC), and footage from 27,045 days of camera trap footage (CTDS) (Table 4.1). In P1, we surveyed 2,617 km of recces and 362 km of line transects in 5 sub-sectors, revealing density for 4 sub-sectors. In P2, we surveyed all 9 sub-sectors, including 1,735 km of recces, 3,596 km of line transects and 27,045 CTDS-days, allowing a comparative approach for 4 sub-sectors. In all surveys (except one), sample units were evenly spaced and deployed systematically from a random origin (Fig 4.2). We georeferenced the location of bonobo signs including direct observations, nests, dung, and other indirect signs, using tracklogs of the paths walked and waypoints recorded by the survey teams.

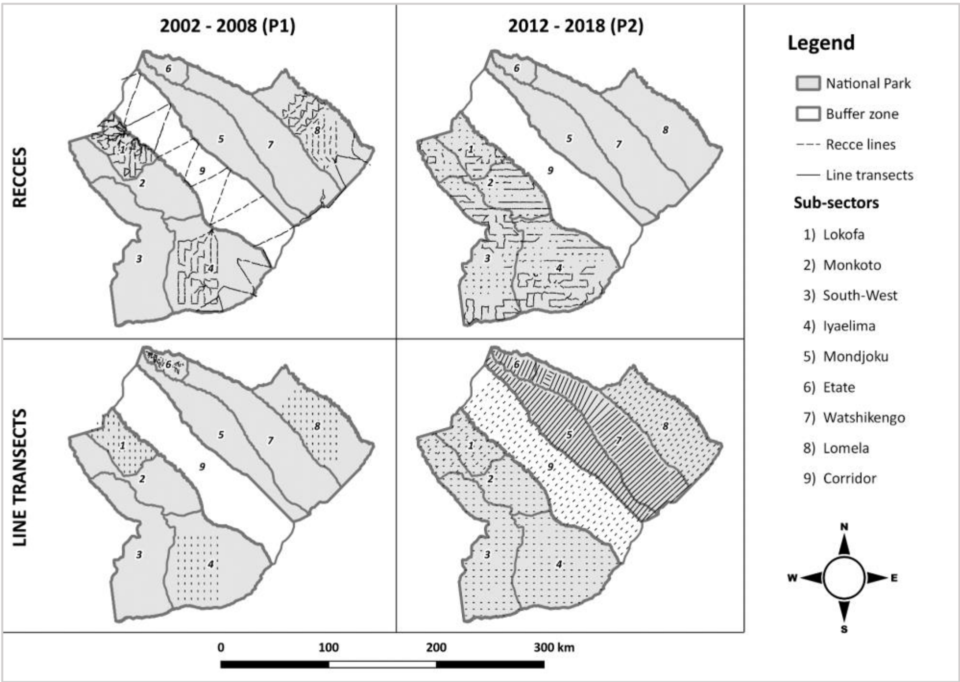

Figure 4.2. Maps of the study area and bonobo surveys in period 1 "P1" (2002 – 2008) and period 2 "P2" (2012 – 2018). Top row: reconnaissance walks "Recces"; right). Bottom row: line transects. Camera-traps were located along line transects in sub-sector 1 to 4 (P2 only).

Table 4.1. Surveys included for period 1 (P1: 2002 - 2008) and period 2 (P2: 2012-2018). Bonobo density (n/km^2) is scaled using a fixed nest construction rate (=1.37) and the period-specific nest decay applied in this study (P1 = 90.5; P2 = 103.7 days). Original studies used a nest decay time of 78 days (Mohneke and Fruth, 2008). Recces” = reconnaissance walks; “SCNC” = Standing Crop Nest Counts; “CTDS” = Camera Trap Distance Sampling.

Period	Dates	Sub-sectors	Method	Effort (km)	Bonobo density (n/km^2)	Reference	Comment
P1	Jul 2003 May 2004	All	Recces	123	/	(Blake, 2005)	1 km transect lines. Focus on elephant. Included for detection / non-detection only.
	Apr 2006 Jun 2006	Iyaelima	Recces	511	/	(Grossmann et al., 2008)	1.4 km transect lines. In Lokofa, perpendicular distances taken to the mid-point of nest group and analysis performed accordingly (Buckland et al., 2001). Iyaelima and Lomela not entirely surveyed.
			SCNC	88	0.43		
	Mar 2005 May 2005	Lokofa	Recces	583	/		
			SCNC	77	0.23		
	Oct 2006 Nov 2006	Lomela	Recces	515	/		
			SCNC	95	0.72		
	Oct 2007 Dec 2007	Corridor	Recces	476	/	(Maisels et al., 2009)	/
	Nov 2008 Dec 2008	Corridor	Recces	409	/	(Maisels et al., 2010)	/
	Nov 2004 Apr 2008	Etate*	SCNC	102	0.58	(Reinartz et al., 2008; Reinartz et al., 2006)	Transects lines of different length (range = 236 – 8,111 m). Repeated passages in Etate core-area (only first passage used); single passage in remaining area, including random and targeted transects. Not entirely surveyed.
P2	Jan 2014 May 2017	Mondjoku	SCNC	1,085	0.27	(ZSM, 2017; 2018)	Long transect lines (range = 1,042 – 47,160 m), segmented in 1 km lines for analyses.
	Feb 2012 Mar 2016	Etate, Watshikengo	SCNC	1,370	0.47		
	Apr 2015 May 2015	Lokofa	SCNC	66	0.18	(Maisels, 2015)	2 km transect lines
	Nov 2015 May 2016	Lomela	SCNC	300	0.50	(Ikati et al., 2017)	
	Sep 2017 Jun 2018	Corridor	SCNC	402	0.20	(Ikati et al., 2018)	
	Sep 2016 Apr 2018	Iyaelima, Lokofa, Monkoto, South-West	Recces	1,735	/	(Chapter 2, this thesis)	1 km transect lines
			SCNC	373	0.27		
			CTDS	27,045 CT-days	0.54		

Bonobo nesting sites are known to be linked to fine-scale local conditions (Serckx et al., 2016). Therefore, for the analysis of detection/non-detection data, we superimposed a fine scale grid (cell size = 1 km^2; number of cells = 44,898) on SNP and corridor (Figure 4.3). We coded each cell with either "1" (bonobo detected), "0" (not detected), or a missing code (not surveyed). We calculated method-specific survey effort as the length of the paths (transect or recce) in each cell (or number of camera days) and extracted 5 GIS-derived covariates: forest cover, a proxy of environmental suitability, distance to the closest city, village, river, all proxies of anthropogenic threats, and whether a cell was within 15 km from a PP, accounting for direct protection from rangers.

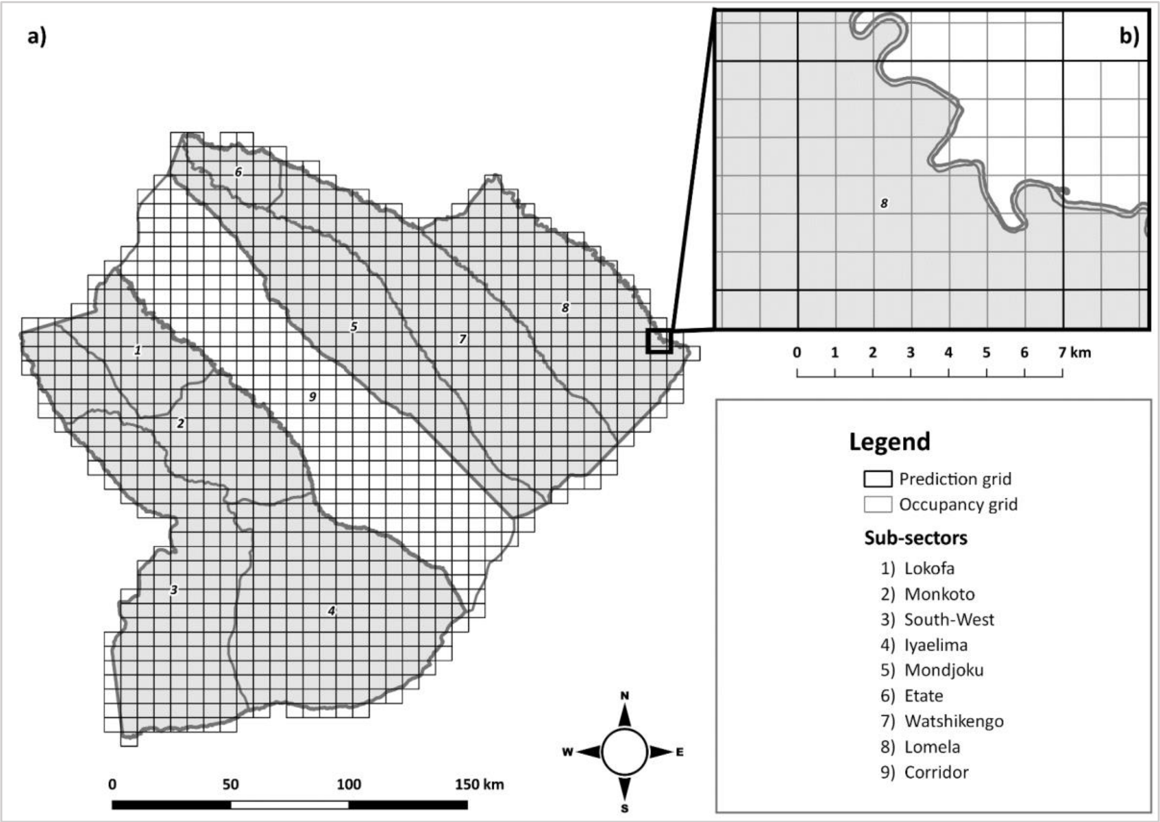

Figure 4.3. Grids used for data analysis and prediction, superimposed over the study area. a) Prediction grid (cell size = 42 km^2); b) detail of occupancy grid used for the analysis of detection / non-detection data (cell size = 1 km^2).

4.3.3. Ecological and anthropogenic variables

GIS-derived variables were extracted from the analysis of spatial data and Landsat-8 satellite imagery (courtesy of the U.S. Geological Survey) in different Geographic Information System (GIS) software, particularly QGis 3.2.0 (QGis Development Team 2020), ArcMap 10.7 (ESRI 2019) and ENVI 5.5.3 (Exelis Visual Information Solutions 2020).

1) 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). In addition, they are also known to use secondary and seasonally inundated forest (Hashimoto et al., 1998) at times of high fruit availability (Mulavwa et al., 2008; Serckx et al., 2014b) and were seen in forest-savannah mosaic habitats (Pennec et al., 2020; Serckx, 2014b).

Hypothesis: The proportion of forest coverage F is positively correlated to both bonobo occurrence probability and bonobo mean density.

To test our hypothesis, we first extracted habitat types in SNP and corridor from Landsat 8 satellite imagery in ENVI 5.5.3 (Exelis Visual Information Solutions, 2020), creating a raster (grain size = 1 ha) distinguishing 5 habitat types: 1) forest (including seasonally inundated lowland and secondary forest); 2) swamps and permanently inundated forest along main rivers; 3) savannahs; 4) human settlements (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 (2-5). Finally, we assigned values of *F*, by calculating the proportion of forest within each 1 km^2 cell (occupancy model), and each transect-buffer, with width equalling twice the specific truncation distance used in the DS analysis (count models).

2) Distance to cities *C*. Here, we defined Cities (C) as urban areas of more than 5,000 people. In Central Africa, cities are known to be hubs of the commercial bushmeat trade, affecting great ape abundance even more than local hunting (Kühl et al., 2009). SNP has a long history of intensive poaching, mainly driven by the high demand of cities such as Kinshasa, Mbandaka, and Ilebo (Hart et al., 2008), with commercial poaching reported to be ongoing (IUCN 2020b).

Hypothesis: Distance to cities C positively correlates to bonobo abundance and distribution.

To test the influence of *C*, we first created a cost distance raster to the most important cities around SNP (grain size = 1 ha) in ArcMap 10.7 (ESRI 2019), using the “Cost distance” algorithm provided in the “Spatial analyst” license. Then, we accounted for differences in travelling speed according to habitat type, weighing according to field observations (MB, *pers. obs.*) with the least costly obtaining the value 1, and the costliest 10. Values were allocated as follows: 1) forest (5); 2) swamps and permanently inundated forest (10); 3) savannahs (2); 4) human settlements (2); and 5) roads and rivers (1). Finally, we averaged the obtained cost distance raster values within each 1 km^2 cell (occupancy model), each transect-buffer (count models) and within each 42 km^2 cell (predictions) to obtain site-specific cost distance to cities *C*.

3) Distance to villages *V*. Here, we defined villages (V) as human settlements ranging between 50 and 5,000 people. The proximity to human settlements is reported to be among the most negative drivers of bonobo abundance and distribution in DRC (Hickey et al., 2013). However, SNP is peculiar in having villages within its border, where some authors found high bonobo densities (Grossmann et al., 2008; Thompson et al., 2008).

Hypothesis: Distance to villages positively affects bonobo abundance and distribution.

We expected the effect to vary with area of SNP. To test the influence of *V*, we followed the above procedure (see "Distance to cities *C*").

4) Distance to rivers *R*. Access to areas of great ape distribution in Central Africa, such as distance to roads, have been shown to negatively affect ape abundance (Strindberg et al., 2018). Within DRC, particularly around SNP, rivers replace roads, connecting SNP to both cities and villages.

Hypothesis: Distance to rivers (R) positively affects bonobo abundance and distribution.

To test the influence of *R*, we followed the above procedure (see "Distance to cities C").

5) Proximity to ranger patrol post *K*. The conservation status of SNP is still of serious concern due to ongoing poaching (IUCN 2020b). For its protection, currently 31 ranger patrol posts (PPs) with usually less than 10 rangers each, are permanently based near or within a village. From PPs, rangers operate anti-poaching patrols and monitor the bushmeat trade (Ilambu 2006).

Hypothesis: Proximity of a PP (K) positively affects bonobo abundance and distribution.

To test the influence of *K*, we used distance to PP as a proxy. First, we designated a buffer of 15 km radius around each PP in QGIS. This radius has been reported being the furthest distance invested for subsistence hunting in other sites in sub-Saharan Africa (Fa et al., 2015). Second, we dummy coded each 1 km^2 cell (occupancy model), each transect-buffer (count models) and each 42 km2 cell (prediction) as "1" when intersecting the 15 km buffer, and "0" if not. By that we obtained the binary, factorial variable *K*.

For the analysis of count data, we fitted method- and survey-specific detection functions in Distance 7.3 (Thomas et al., 2010), obtaining density estimates of bonobos (CTDS) and bonobo nests (SCNC). Around line-transects, we extracted the same GIS-derived covariates listed above within a buffer of width equal to the specific truncation distance used in the DS analysis on each side of the transect (width = truncation distance x 2). Here, we focused on strips around the transects to account for fine-scale environmental features important for bonobo nesting sites (Serckx et al., 2016). In SNP Block South, we also recorded the number of human signs/100 m, a proxy of human presence and hunting intensity, the proportion of bonobo feeding trees and the proportion of *Marantaceae* coverage (i.e., a family of herbaceous plants consumed by bonobos (Reinartz et al., 2008)), accounting for food availability, and the density of black mangabeys (*Cercocebus aterrimus*) and other primates, proxies of inter-specific competition.

6) Human encounter rate *H*. Human activities such as hunting and logging have been reported as the most important drivers of great ape decrease worldwide (Kühl et al., 2017; Plumptre et al., 2016; Walsh et al., 2003; Wich et al., 2016). In SNP, higher encounter rates of human signs were negatively correlated with bonobo density (Maisels et al., 2009, 2010; Reinartz et al., 2006).

Hypothesis: Human encounter rate negatively affects bonobo abundance and distribution. For this, we first recorded the number of human signs (direct observations of humans, hunting and fishing camps, snares, gun shells, paths, machete cuts, and felled trees (N'Goran et al., 2016)) along line transects in the field. By that, we obtained transect specific values of human signs per 100 m of transect *H*. Finally, for prediction from M1 (Block South only, in P2), we assigned the value of *H* recorded in the field to the specific 42km^2 cell containing the transect and estimated the value of *H* in unsurveyed 42 km^2 cells (n = 27) by mean of a GAM using the mgcv package in R 4.0.4 (R Core Team, 2020). We specified a Tweedie distribution, log link and an iterative search to estimate the power parameter. The model included 4 GIS extracted explanatory variables: i) forest cover *F* (normalized), ii) distance to villages *V* (normalized), iii) distance to rivers *R* (normalized), iv) longitude and latitude of the cell centroid. The latter was transformed to km north and east of the centre of the survey region, making the covariate isotropic (Miller et al., 2014). Here, we fitted the model using thin plate regression splines for *F*, *V* and R, and a two-dimensional smooth function for longitude/latitude, accounting for spatial correlations associated with location (Miller et al., 2014).

7) Proportion of bonobo feeding trees *T*. Food availability is a critical factor driving spatial distribution and abundance of bonobos (Hohmann et al., 2012; Mulavwa et al., 2008; Serckx et al., 2014b; White 1998).

Hypothesis: Density of bonobo feeding trees (T) positively affects bonobo abundance and distribution.

For this, we first identified all tree species with a diameter at breast height (DBH) >= 20 cm along 500m of each transect within 1,5m to 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, providing the transect specific proportion of bonobo feeding trees *T*. For prediction, we assigned the value of *T* recorded in the field to the specific 42 km^2 cell containing the transect and estimated *T* in unsurveyed cells by means of a GAM model using a Binomial distribution, logit link and an iterative search to estimate the value of *theta* parameter. The model included 2 GIS extracted explanatory variables i) forest cover *F* (normalized), ii) longitude and latitude of the cell centroid (transformed, see above).

8) Proportion of *Marantaceae M*. Terrestrial herbaceous vegetation (THV), particularly species of the family *Marantaceae (M)* (Malenky et al., 1996; Serckx et al., 2016; Terada et al., 2015), were found to be a good predictor of bonobo nest density in SNP in a previous study (Reinartz et al., 2008).

Hypothesis: Density of Marantaceae (M) positively affects bonobo abundance and distribution.

For this, we first recorded the understorey beneath each tree recorded in the 500x3m-strip described above, discriminating between 4 understorey types: 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* (3), and “0” in all other cases (1-2, 4). By that, we calculated the transect specific proportion of *Marantaceae M*. For prediction, we assigned the value of *M* recorded in the field to the specific 42 km^2 cell containing the transect and estimated *M* in unsurveyed cells by means of a GAM model using a Binomial distribution, logit link and an iterative search to estimate the value of *theta* parameter. The model included 2 GIS extracted explanatory variables i) forest cover *F* (normalized), ii) longitude and latitude of the cell centroid (transformed, see above).

9) Other primates' density *P.* Hunting of diurnal primates by bonobos was observed at Lilungu (Sabater Pi et al., 1993) and LuiKotale (Surbeck and Hohmann 2008), the study site closest to SNP.

Hypothesis: Density of primates (P) positively affects bonobo abundance and distribution. However, field observations from LuiKotale (Fruth pers. comm.) suggest high primate densities impacting bonobos due to inter-specific competition over food. At least 8 monkey species are present in SNP (Appendix 1): 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*). For this, we first recorded perpendicular distance to the centre of each monkey group observed along the line transects used for bonobo nest counts. From these data, we calculated transect specific primate density *P* in Distance 7.3 (Thomas et al., 2010), taking into account group size (Plumptre and Cox 2006). As above, for prediction we assigned the value of *P* recorded in the field to the specific 42 km^2 cell containing the transect and estimated *P* in unsurveyed cells by means of a GAM model using a Tweedie distribution, log link and an iterative search to estimate the power parameter. The model only included a two-dimensional smooth function for longitude/latitude, accounting for spatial correlations (transformed, see above).

10) Black mangabey density *B.* Of all primate species mentioned above, black mangabeys were the most likely food competitors of bonobos given their overlapping repertoire (Kingdon et al., 2013), and their abundance in SNP (Bessone et al., 2019).

Hypothesis: Density of black mangabey (B) negatively affects bonobo abundance and distribution.

For this, we calculated transect-specific black mangabey density *B* in Distance and extracted the values of *B* needed for prediction as described above.

4.3.4. Statistical analysis

4.3.4.1 Model definition

We integrated heterogeneously collected data across different areas and time periods. As CT data were only available for the South Block in P2, we first developed "M1", a single-period model integrating detection/non-detection and count data from recces, SCNC and CTDS, where additional ecological variables allowed a more detailed analysis of the factors important to bonobos (Box 4.1). Our model estimated bonobo occupancy *O* by explicitly accounting for method specific detection probability π. Estimating π requires multiple visits to the same site, but we surveyed only 507 cells (1.3%) with all methods simultaneously, imputing values for unsurveyed cells (McElreath 2020). Therefore, we estimated bonobo detection probability π and occurrence probability ψ from cells where we applied all methods. We modelled ψ as a function of covariates, and π by accounting for method-specific survey effort only. Here, although some environmental features might have influenced π, we did not include other covariates as the variable we expected to be important, i.e. the proportion of *Marantaceae M*, a proxy for understorey thickness, was not available for the recces. We also expected forest type to influence π in recces, with lower probability of detection in swampy areas, where attention was possibly lower due to the difficulties in 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, i.e. forest cover *F*, also included savannahs and open areas, where detection probability was expected to be high due to good visibility. Therefore, we decided to model π as a function of survey effort only. To account for spatial autocorrelation, we included an intrinsic Conditional Auto-Regressive component (iCAR), taking advantage of a specifically developed prior (Morris et al., 2019) computing the pairwise difference of neighbouring elements (i.e., cells) of a random spatial variable λ. By encoding the neighbour relations between cells in 2 vectors, this approach is more efficient than specifying a full adjacency matrix and required less memory and computational power (Morris et al., 2019).

We modelled count data *N* using a zero inflated model. Here, we assumed our density data to be representative of bonobo abundance in the study area, which is true when, like in this study, the distribution of sampling effort is random throughout the study area (Miller et al., 2013). Specifically, we first estimated ϕ, the probability of observing nests on a line transect using a logistic regression model. Then, we used a gamma regression to model method specific μ, representing the number of nests (SCNC) or bonobos (CTDS) on each transect. In a second model “M2" (Box 4.2), we extended M1 by including bonobo presence and abundance data collected in P1, in the North Block and corridor. By that, we estimated the updated park-wide bonobo abundance for P2 and bonobo population trend between periods. We excluded the observations obtained by CTs and estimated method specific detection probability π from cells surveyed (n = 805) with recces and SCNC simultaneously (P1: n = 266; P2: n = 539), accounting for survey effort (i.e. line length). By that, we aimed to control for differences in survey protocols and design, specific to each organisation (Table 4.1). Then, we estimated ψ as a function of GIS-derived covariates in an occupancy model, imputing values for cells not surveyed and accounting for spatial autocorrelation. Bonobos live in communities of several individuals and have large home ranges (Fruth and Hohmann, 2018). Therefore, to provide biologically meaningful predictions of bonobo occurrence, we first predicted occupancy probability ψ in 1 km^2 cells, and then averaged the values obtained over 42 km^2 cells (Figure 4.3), approximatively matching bonobo home-range sizes in the area (Fruth and Hohmann 2018). In both models, we predicted bonobo occurrence and abundance in each 42 km^2 cell of the superimposed grid (Figure 4.3), considering a cell to be occupied if 1) we recorded at least one bonobo sign (i.e. occurrence probability was assumed to be equal to 1); 2) the predicted occurrence probability was > 0.5. Similarly, we modelled count data separately for each period using the zero inflated regression described above, although here we modelled survey-specific probabilities of observing nests on a line transect ϕ, controlling for differences in survey protocols and design, specific to each organisation (Table 4.1). Finally, we predicted bonobo density μ conditional on ϕ, in all 42 km^2 cells predicted to be occupied. We deliberately avoided extrapolating bonobo abundance to areas not surveyed during P1 and estimated population trend only in sub-sectors surveyed twice.

To provide some limited information on the estimated parameters without affecting the posterior distribution, we set weakly informative priors (Lemoine, 2019). In logistic regressions, we used *Normal* (0,1.4) for the intercepts (Northrup and Gerber 2018) and *Normal* (0,0.5) for the slopes (McElreath 2020), assigning a specifically developed prior for the iCAR component λ and a standard normal prior for its standard deviation σ, *Normal* (0,1) (Morris et al., 2019). In gamma regressions, we used *Normal* (0,5) for the intercepts and *Normal* (0,0.5) for the slopes, constraining the rate parameter θ to being positive. θ was set wider in M1 (Box 4.1), *Gamma* (0.3,0.3) where μ was estimated for two methods returning largely different density estimates (nests vs bonobos); and narrower in M2 (Box 4.2), where we estimated nest density only, *Gamma* (0.1,0.1). For the estimation of nest decay time η, we set a weakly informative prior *Gamma* (10,0.1) and a positive informative prior on ε, *Gamma* (0.1,0.1).

We investigated the influence of different nest decomposition time, scaling estimated nest abundance to bonobo abundance by using 3 approaches. First, a period-specific nest decay time, using nests constructed from 3 months before the beginning of each of the two periods until their end. Second, a fixed, purposely calculated nest decay time. For these approaches, we estimated nest decomposition times from 1,511 bonobo nests followed from construction to decomposition between 2004 and 2018 at LuiKotale research site (Hohmann and Fruth, 2003b), located in Salonga National Park (SNP) buffer zone (02° 45.610' - 20° 22.723') (see Chapter 3). Finally, a literature nest decay time for all periods and surveys, used in previous surveys in SNP (Mohneke and Fruth 2008).

Box 4.1 *Model 1 – M1*

M1 integrated detection non-detection data from reconnaissance walks (recces), standing crop nest count (SCNC) and camera trap distance sampling (CTDS) and density data from SCNC and CTDS in SNP block south, between 2016 and 2018. It included 1) a single season occupancy model estimating the latent bonobo occupancy accounting for method-specific detection probability; 2) a gamma regression, modelling density data conditional on bonobo occupying a site. We modelled the latent bonobo occupancy O for all sites (n = 17,010) in 4 sub-sectors as

$$O_i \sim Bernoulli\,(\psi_i)$$
$$o_{i,j} \,|\, O_i \sim Bernoulli(O_i \text{ x } \pi_{i,j})$$

Eq. 1

where O_i is the latent occupancy and ψ_i the occurrence probability at site *i; $o_{i,j}$* is the observed occupancy for site *r* and method *j* and π_j is the average detection probability for method *j* estimated above.

We estimated detection probability π using only the observations obtained from sites *i* (n = 507) surveyed with *J* methods (n = 3) and modelled as a function of survey effort $L_{i,j}$, with logit-link

$$\text{logit}(\pi_{i,j}) = \alpha_j + L_{i,j}$$

Eq. 2

where α is the intercept for method *j.*

We modelled ψ_r as a function of covariates, with logit-link (Appendix S6)

$$\text{logit}(\psi_i) = \alpha 1_s + \beta 1 F_i + \beta_{s,k} C_i + \beta 3_{s,k} V_i + \beta 4_{s,k} R_i + \beta 5_k + \lambda_i \sigma$$

Eq. 3

where α1 and β5 are the intercepts and β (1 to 4) are covariate-specific slopes, varying by sub-sector *s* (n = 4) and by *k* (n = 2) i.e., being within 15 km from a patrol post or not *K* (except for β1, fixed). *λ* is the spatial autocorrelation component for site *i*, with *σ* being its standard deviation. Here we exploited Bayesian imputation (McElreath 2020) to include sites we did not visit and retained no detection data.

Finally, we predicted bonobo occupancy in SNP block south, *OSNPs* by averaging the predicted ψ in each 1 km^2 cell, over 42 km^2 cells (n = 405), approximatively the size of a bonobo home range (Fruth & Hohmann, 2018). Here, each 42 km^2 cell was assumed being certainly occupied (ψ = 1) if we recorded any sign of bonobo presence.

We modelled bonobo density *D* conditional on 1) the site being occupied 2) the transects having bonobo signs. Both SCNC and CTDS transects are typically zero-inflated, with transects bearing no bonobo signs for two main reasons. First, if there were no bonobos in the area, we conditioned *D* on occupancy *O* (i.e., if a site is predicted to be empty, then density on the transect would be 0, see Eq. 7). Second, if bonobos were present in the area, but the transect bore no signs of their presence, we estimated ϕ, the probability of finding bonobo signs on transect *w* for method *j*. We modelled ϕ for each method *j*, conditional on bonobos having been detected with any method either on the transect, or within a 42 km^2 area around the transect (i.e., the transect was within the home range of a bonobo community) as

$$z_{w,j} \sim Bernoulli\,(\phi_j)$$

Eq. 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 then estimated μ*,* bonobo density at transect *w* for method *j* as

$$d_{w,j} \sim Gamma\,(\mu_{w,j}\theta_j, \theta_j)$$

Eq. 5

where $d_{r,j}$ is a matrix containing observed density (objects/km2) estimated with Distance 7.3 (Thomas et al., 2010), for transect *r* and method *j*, $\mu_{w,j}$ is the mean bonobo density for transect *w* and method *j* and θ is the rate parameter for *j*.

Box 4.1 *Model 1 – M1*

We modelled μ as a function of covariates (with log-link), conditional on the transect having *d* > 1 (transects with *d* = 0, where modelled above), as

$$\log(\mu_{w,j}) = \alpha3_{s,j} + \delta1_{j}F_{w} + \delta2_{j}C_{w} + \delta3_{j}V_{w} + \delta4R_{w} + \delta5H_{w} + \delta6_{j}T_{w} + \delta7_{j}M_{w} + \delta8_{j}B_{w} + \delta9_{j,k} \qquad Eq.\ 6$$

where α3 is the intercept varying by sub-sector *s* and method *j;* δ (1 to 8) are covariate-specific slopes varying by method *j*, and δ9 is an additional intercept varying by method *j* and by *k* i.e., being within 15 km from a patrol post or not.

Finally, we predicted bonobo density in SNP block south D_{SNPs} for method *j* in 42 km^2 cell *q* (n = 405) the size of a bonobo home range, conditional on the cell bearing bonobo signs and on the cell being occupied (as predicted by the occupancy model) as

$$D_{SNPs_{q,j}} = D_{q,j} \text{ x } Z_{q,j} \text{ x } O_{SNPs_{q}} \qquad Eq.\ 7$$

Here, $D_{SNPs_{q,1}}$ estimated with SCNC, returned bonobo nest density, whilst $D_{SNPs_{q,2}}$ estimated with CTDS, returned bonobo density. Therefore, we first scaled bonobo nest density to bonobo density using the following formula (Tutin and Fernandez 1984)

$$scaled\ D_{SNPs_{q,1}} = \frac{D_{SNPs_{q,1}}}{1.37 \text{ x } \eta} \qquad Eq.\ 8$$

where 1.37 is the fixed nest production rate (Mohneke and Fruth 2008) and η is the average nest decomposition specifically calculated between 2016 and 2018 from 679 bonobo nests *n* followed from construction to full decomposition, and modelled as

$$y_{n} \sim Gamma\ (\eta\varepsilon, \varepsilon) \qquad Eq.\ 9$$

where ε is the rate parameter of the gamma distribution.

By that, we obtained bonobo abundance in SNP block south N_{SNPs} by averaging bonobo density obtained from SCNC and from CTDS in cell *q* and multiplying by 42 (km^2), the grain size of our prediction grid

$$N_{SNPs_{q}} = \frac{42\ x\ (scaled\ D_{SNPs_{q,1}} + D_{SNPs_{q,2}})}{2} \qquad Eq.\ 10$$

Box 4.2 *Model 2 – M2*

M2 integrates detection non-detection data from recces and SCNC and density data from SCNC in SNP and its corridor in two periods, P1 (2002 - 2008) and P2 (2012 and 2018). It includes 1) two single season occupancy models estimating period-specific latent bonobo occupancy; 2) two period-specific gamma regressions, modelling bonobo nest density data conditional on bonobo occupying a site.

We modelled the latent bonobo occupancy *O* in SNP and corridor for site *i* (n = 44,898) in period *t* as

$$\begin{aligned} O_{i,t} &\sim Bernoulli\ (\psi_{i,t}) \\ o_{i,j,t} \,/\, O_{i,t} &\sim Bernoulli\ (O_{i,t}\ \pi_{j}) \end{aligned} \qquad \textit{Eq. 11}$$

where $O_{i,t}$ is the latent occupancy and $\psi_{i,t}$ the occurrence probability at site *i* in period *t;* $o_{i,j,t}$ is the observed occupancy array for site *i*, method *j* and period *t*; π_j is the average detection probability for method *j* estimated above. We estimated the detection probability π*,* using only observations obtained from sites (n = 805) surveyed with both methods*,* modelled as a function of survey effort $L_{i,j}$ and as

$$\mathrm{logit}(\pi_{i,j}) = \alpha_j + L_{i,j} \qquad \textit{Eq. 12}$$

where α is the intercept for method *j*.

We modelled $\psi_{i,t}$ as a function of covariates

$$\mathrm{logit}(\psi_{r,t}) = \alpha 1_{s,t} + \beta 1_t F_i + \beta 2_{s,t} C_i + \beta 3_{s,t} V_i + \beta 4_{s,t} R_i + \beta 5_{s,k,t} + \lambda_{i,t}\sigma \qquad \textit{Eq. 13}$$

where α1 is the intercept and β (1 to 4) are covariate-specific slopes, varying by sub-sector *s* and period *t*, β5 is an additional intercept varying by *s*, *t* and *k* i.e., being within 15 km from a patrol post or not, and λ is the spatial autocorrelation component, with σ being its standard deviation. Here too, unsurveyed cells were included using data imputation.

Finally, we predicted bonobo occupancy in SNP and corridor, *OSNP* by aggregating ψ in 42 km^2 cells (n = 1,069), assuming a cell being certainly occupied (ψ = 1) if any sign of bonobo presence was recorded. As in M1, we modelled bonobo density *D* conditional on the site being occupied and the transects having bonobo signs. We estimated ϕ*,* the probability of finding bonobo signs on transect *w* for method *j* in period *t* conditional on bonobos having been detected with either method on the transect, or within a 42 km^2 area around the transect as

$$z_{w,j,t,} \sim Bernoulli\ (\phi_{u,t}) \qquad \textit{Eq. 14}$$

Where $z_{w,j,t}$ is an array where transects were dummy coded as 0 if no bonobo signs were found (*d* = 0) and 1 if bonobo signs were recorded (*d* > 0). We modelled ϕ fixed for each period *t*, accounting for differences in survey designs from different organizations *u* (Table 4.1).

We then estimated *D,* bonobo density at transect *r* in period *t* as

$$d_{r,t} \sim Gamma\ (\mu_{r,t}\theta_t, \theta_t) \qquad \textit{Eq. 15}$$

where $d_{r,t}$ is a matrix containing observed nest density (nests/km^2) estimated with Distance 7.3 (Thomas et al., 2010), in the area surveyed by transect *w* in period *t*, $\mu_{r,t}$ is the mean nest density in the area surveyed by transect *w* in period *t* and θ is the rate parameter for period *t.* We modelled μ as a function of covariates (with log-link), conditional on the transect having estimated nets density > 0 (transects with *d* = 0, where modelled above), as

$$\log(\mu_{w,j}) = \alpha 3_{s,t} + \delta 1_t F_w + \delta 2_t C_w + \delta 3_t V_w + \delta 4_t R_w + \delta 5_{k,t} \qquad \textit{Eq. 16}$$

where α3 is the intercept varying by sub-sector *s* and period *t;* δ (1 to 4) are covariate-specific slopes varying by period *t*, and δ5 is an additional intercept varying by period *t* and by *k*, i.e. being within 15 km from a patrol post or not. We imputed μ for transects that bore no bonobo signs.

Box 4.2 *Model 2 – M2*

Finally, we predicted bonobo nest density in SNP and corridor D_{SNP} in 42km^2 cell q (n = 1,069) the size of a bonobo home range conditional on the cell bearing bonobo signs on transects Z and on the cell being occupied (as predicted by the occupancy model) as

$$D_{SNP\,q,t} = D_{q,t} \text{ x } Z_{q,t} \text{ x } O_{SNP\,q,t} \qquad Eq.\ 17$$

D_{SNP} needed scaling to bonobo density using Eq. 8. However, here we were also interested in looking at the effect of different decomposition time on our estimates. Therefore, we modelled nest decomposition as

$$y_n \sim Gamma(\eta_g \varepsilon, \varepsilon) \qquad Eq.\ 18$$

where y is a vector (n = 1,511) of nest decomposition times n, η is the average decomposition time for study g (n = 5) and ε is the rate parameter of the gamma distribution.

Then, we first obtained bonobo density in SNP and corridor *DSNP* under three scenarios: 1) single η (i.e. η = mean(η1:5); 2) period-specific η (i.e. η1 = mean (η1:3); η2 = mean(η4:5); 3) survey-specific η (i.e. $\eta 1_g$). We then obtained bonobo abundance in SNP and corridor *NSNP* by multiplying $DSNP_q$ by 42 (km^2), the grain size of our prediction grid under the three different scenarios.

4.3.4.2 Simulation study

Before running our models, we investigated their accuracy and precision in a simulation study where we varied 1) the percentage of surveyed cells and 2) the number of transects. For the purpose, we used a simplified version of the model described above, including two covariates only and fixed nest decomposition time.

First, we simulated the true occupancy (*O_real*) by generating a vector of occurrence probability ψ, mimicking 17,000 survey cells as a function of two continuous variables (F1 and H1) in three sub-sectors I with specific intercepts α1 and slopes β1 and β2. By that, we obtained sector-specific mean occurrence probability ψ_i. Then, we simulated the observed occupancy (*O*), for three different methods *j* with specific, fixed detection probability πj. We investigated 4 survey coverages: 5%, 10%, 15% and 20%, simulating coverages similar to our surveys (M1: P2 = 13%; M2: P1 = 7%, P2 = 16%). In each scenario, we selected only cells surveyed with all methods to estimate π as a function of survey effort *L* in a reduced occupancy model. Finally, we estimated the remaining parameters in the main occupancy model, with method-specific fixed π_j.

Second, we simulated a varying number of survey units *R* (i.e. transects) independent of the cells generated above. We investigated 200, 600, 1200 and 3600 transects to assess the effect of sample size on the model accuracy, mimicking the number of transects in our surveys (M1: P2, n = 377; M2: P1, n = 272; P2, n = 3200). We set a fixed method-specific probability of observing bonobo signs on transect ϕ_j, and simulated μ_r, the mean density for each transect (conditional on ϕ being positive) for two methods (i.e., SCNC and CTDS) from a gamma distribution as a function of covariates *F2* and *H2* (obtained from the same distribution used for *F1* and *H1*), with method specific rates θ_j, obtaining a matrix of observed bonobo nest (SCNC) and bonobo (CTDS) density d. When simulating μ, we set sector-specific intercepts for each method, $\alpha2_i$ and $\alpha3_i$, and method-specific slopes, $\gamma1_j$ and $\gamma2_j$ for each variable. Finally, we defined fixed conversion factors (nest decomposition time = 95 days; nest construction rate = 1.37) to scale the simulated nest density obtained with method 1, to bonobo density (simulated in method 2). We then assumed the true density D, to be the average estimated by the two methods. By that, we obtained average density $\mu_{i,j}$, in each sector and for each method. For each scenario, we generated 10 databases and run 1 chain of 2,000 iterations (warmup = 1,000) repeatedly (n = 10) in R 4.0.4 (R Core Team 2020) using Rstan 2.21.2 (Stan Development Team 2020). Finally, we verified the accuracy of our model by comparing the posterior distribution of the estimated parameters (from the 10 samples aggregated) with the true values.

4.3.4.3 Model selection

As our study estimated bonobo density and distribution over a large area, we expected geographical differences in the effects of our explanatory variables in the park. Similarly, nest counts provided data on bonobo nesting sites only whilst CTs provided information on the full range of bonobo spatial use, including travelling, foraging, and nesting. Therefore, we were interested in estimating sub-sector- and method-specific parameters (see Eq. 2, 4, 6, 8 - Box 4.1; Eq. 14, 16, 18, 20 - Box 4.2).

To do so, we first wrote a set of candidate linear models addressing our research questions by including different combination of varying intercept and slopes for our three main parameters: 1) occurrence probability (ψ); 2) probability of a transect having bonobo signs (ϕ); 3) bonobo mean density (μ). Then, we evaluated potential collinearity between variables, by examining pairs plots of the posterior distribution (Gabry et al., 2019) and re-ran the models by excluding one variable from each collinear pair based on our research questions. We used data from the block South of SNP in P2, where a larger number of covariates were available and 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 run 1 chain of 2,000 iterations (warmup =1000) for all candidate model using RStan (Stan Development Team 2020), comparing their predictive power by evaluating the expected log predictive density (ELPD) using the R package "loo" (Vehtari, Gelman and Gabry, 2017). Here, the model with the lowest ELPD provided the best fit to the data and was set as the reference for comparing other models by calculating the difference in ELPD (Δ-Elpd) from the best fitting model. If a model fitted best one method (e.g. CTDS) but poorly another (e.g. SCNC), 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.

We developed our models in Stan (Carpenter et al., 2017), using RStan (Stan Development Team, 2020) in R 4.0.4 (R Core Team, 2020) and fit the final models by running 2 chains of 10,000 iterations each (warmup = 9,000).

This study was purely observational, involving signs left behind by bonobos and remotely acquired images. The methods described above complied with the requirements and guidelines of the ICCN and adhered to the legal requirements of the host country, DRC.

4.4. Results

4.4.1. *Preliminary analyses*

4.4.1.1 Simulation study

In our simulation study, the true value of the parameters was consistently included within the 95% confidence interval of the posterior distribution estimated in our model (Table 4.2 and 4.3). Consequently, our model satisfactorily estimated sector specific ψ, method-specific ϕ, and sector- and method specific μ, the main quantities of interest (Figure 4.4 and 4.5).

Table 4.2. Mean value and 95% CI of parameters modelling detection probability ψ for 4 different scenarios: 5%; 10%; 15% and 20% coverage of the area of study, compared with the real value used to generate the data.

Model	**Parameter**	**Real value**	**Estimated mean value for varying coverage (95% CI)**			
			5%	**10%**	**15%**	**20%**
ψ	$\alpha1_1$	2.00	1.54 (0.68 – 2.84)	1.59 (0.82 – 2.61)	1.62 (0.88 – 2.64)	1.60 (0.28 – 2.57)
	$\alpha1_2$	1.00	0.67 (0.18 – 1.34)	0.71 (0.27 – 1.24)	0.73 (0.31 – 1.21)	0.68 (0.28 – 1.22)
	$\alpha1_3$	-1.00	-1.09 (-1.44 – -0.77)	-1.17 (-1.45 – -0.91)	-1.10 (-1.36 – -0.85)	-1.13 (-1.38 – -0.89)
	$\beta1_1$	0.60	0.44 (0.05 – 0.92)	0.51 (0.16 – 0.94)	0.46 (0.21 – 0.81)	0.50 (0.25 – 0.92)
	$\beta1_2$	0.40	0.33 (0.13 – 0.58)	0.33 (0.13 – 0.56)	0.33 (0.16 – 0.51)	0.36 (0.24 – 0.51)
	$\beta1_3$	0.00	0.04 (-0.27 – 0.51)	0.07 (-0.18 – 0.30)	0.07 (-0.08 – 0.23)	0.05 (-0.09 -0.21)
	$\beta2_1$	-0.20	-0.13 (-0.62 – 0.47)	-0.21 (-0.58 – 0.10)	-0.19 (-0.52 – 0.10)	-0.17 (-0.45 – 0.08)
	$\beta2_2$	-0.50	-0.42 (-0.86 – -0.15)	-0.43 (-0.67 – -0.22)	-0.45 (-0.67 – -0.28)	-0.43 (-0.63 – -0.28)
	$\beta2_3$	0.00	0.09 (-0.18 – 0.36)	-0.05 (-0.31 – 0.19)	-0.04 (-0.22 – 0.14)	-0.04 (-0.20 – 0.13)

Table 4.3. Mean value and 95% CI of parameters modelling the probability of detecting bonobo sings on a transect ϕ and mean density μ for 4 different scenarios: 200; 600; 1200 and 3600 transects, compared with the real value used to generate the data.

Model	**Parameter**	**Real value**	**Estimated mean value for varying number of transects (95% CI)**			
			200	**600**	**1200**	**3600**
ϕ	ϕ_1	**0.60**	0.61 (0.51 – 0.70)	0.61 (0.56 – 0.65)	0.60 (0.56 – 0.64)	0.60 (0.57 – 0.63)
	ϕ_2	**0.30**	0.31 (0.23 – 0.40)	0.30 (0.26 – 0.35)	0.30 (0.26 – 0.34)	0.30 (0.28 – 0.32)
μ	$\alpha2_1$	**5.00**	4.98 (4.89 – 5.08)	5.01 (4.95 – 5.06)	5.00 (4.95 – 5.05)	5.00 (4.97 – 5.02)
	$\alpha2_2$	**4.00**	3.99 (3.85 – 4.11)	3.99 (3.92 – 4.05)	4.01 (3.93 – 4.07)	4.00 (3.97 – 4.03)
	$\alpha2_3$	**2.00**	1.94 (1.57 – 2.29)	1.96 (1.73 – 2.17)	2.02 (1.86 – 2.16)	2.00 (1.91 – 2.10)
	$\alpha3_1$	**0.20**	0.05 (-0.78 – 0.74)	0.17 (-0.19 – 0.51)	0.22 (-0.20 – 0.27)	0.22 (0.07 – 0.38)
	$\alpha3_2$	**0.00**	-0.13 (-0.67 – 0.40)	-0.02 (-0.35 – 0.30)	0.03 (-0.20 – 0.27)	-0.03 (-0.18 – 0.12)
	$\alpha3_3$	**-0.50**	-0.60 (-1.70 – 0.36)	-0.57 (-1.00 – -0.09)	-0.49 (-0.79 – -0.18)	-0.53 (-0.74 – -0.34)
	$\gamma1_F$	**0.50**	0.51 (0.42 – 0.59)	0.50 (0.45 – 0.55)	0.50 (0.46 – 0.54)	0.50 (0.48 – 0.52)
	$\gamma1_H$	**-0.30**	-0.31 (-0.39 – -0.22)	-0.31 (-0.35 – -0.27)	-0.30 (-0.33 – -0.27)	-0.30 (-0.32 – - 0.28)
	$\gamma2_F$	**0.20**	0.17 (-0.23 – 0.53)	0.18 (0.01 – 0.34)	0.18 (0.04 – 0.32)	0.20 (0.14 – 0.27)
	$\gamma2_H$	**-0.05**	0.02 (-0.27 – 0.33)	-0.05 (-0.21 – 0.11)	-0.04 (-0.17 – 0.10)	-0.05 (-0.11 – 0.03)
	θ_1	**0.10**	0.11 (0.07 – 0.15)	0.10 (0.08 – 0.12)	0.10 (0.08 – 0.11)	0.10 (0.09 – 0.11)
	θ_2	**0.50**	0.60 (0.31 – 1.16)	0.52 (0.38 – 0.71)	0.50 (0.38 – 0.63)	0.51 (0.44 – 0.59)

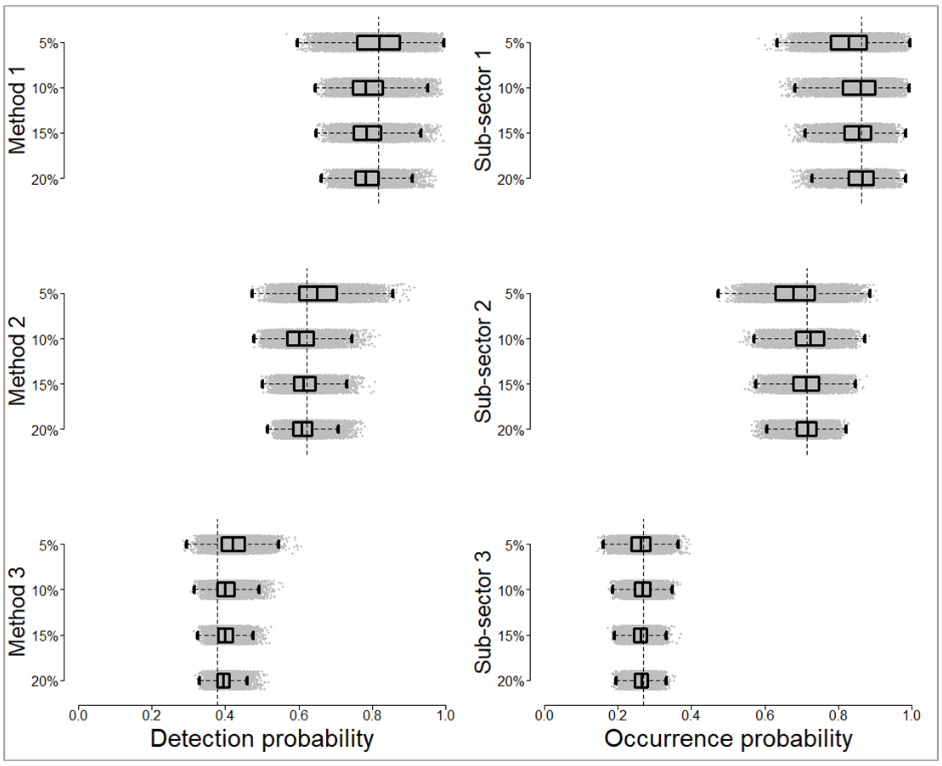

Figure 4.4. Estimated detection probability π (by method, 1 = SCNC, 2 = Recces, 3 = CTDS) and occurrence probability ψ (by sub-sector, n =3) for 4 survey coverages (5%, 10%; 15%; 20%). Grey dots represent 10,000 draws from the posterior distribution, with boxplots representing quartiles and variability of the samples.

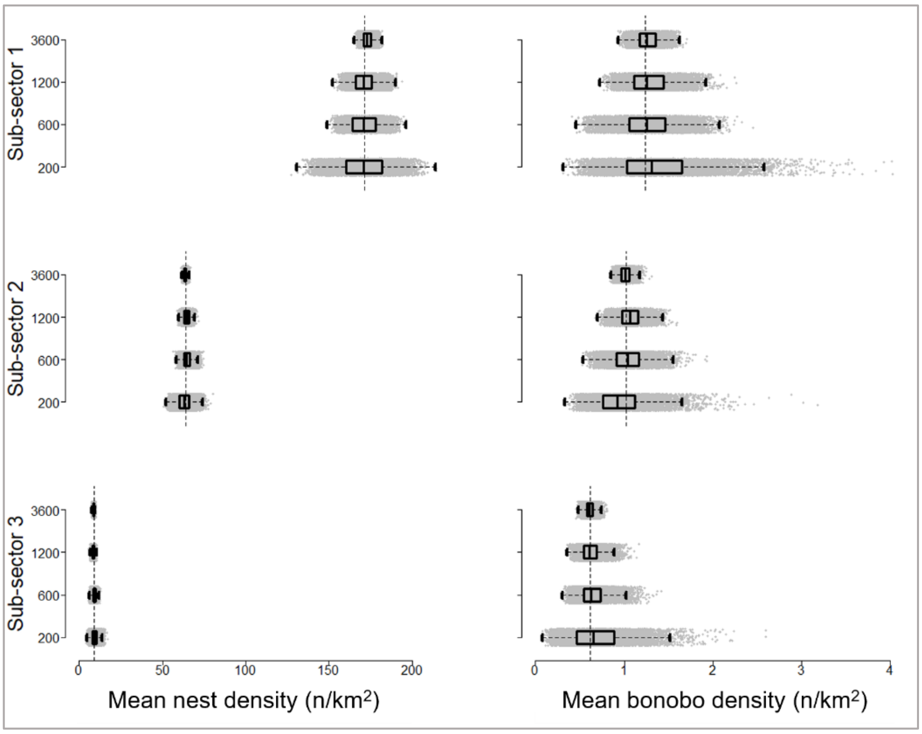

Fig. 4.5. Estimated mean nest and bonobo density (by sub-sector, n =3), simulating standing crop nest counts (SCNC - left) and camera trap distance sampling (CTDS - right) estimated densities μ, for 4 survey efforts (200; 600, 1,200; 3,600 transects). Grey dots represent 10,000 draws from the posterior distribution, with boxplots representing quartiles and variability of the samples. Vertical dashed lines show the true value of simulated parameters.

4.4.1.2 Model selection

We selected explanatory variables and random effects following our model selection procedure. Here, we found no signs of collinearity in models estimating ψ. The model returning the best results included an intercept varying by sub-sector and slopes varying by sector and by proximity to a patrol post "PP" (Table 4.4). However, in models estimating ϕ and μ we found monkey density (*P*) and black mangabey density (*B*) (Figure 4.6) to be highly collinear. As black mangabeys were the most common species in SNP block south, the two variables were providing the same information. Therefore, we decided to exclude *P*, including only *B* in our models. Black mangabey feeding habits overlap with the bonobo's (Kingdon et al. 2013). Therefore, *B* was more interesting as it provided the chance to investigate inter-specific competition.

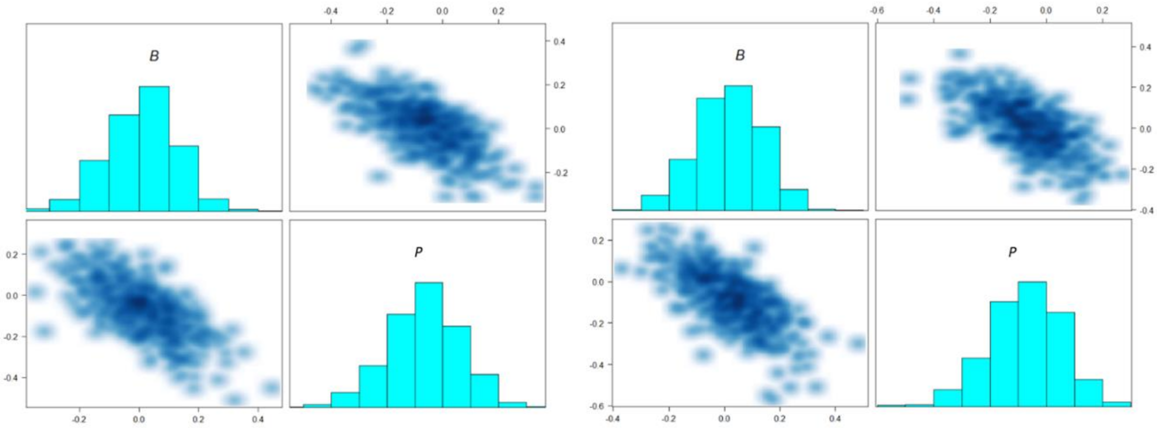

Figure 4.6. Pair plots of the posterior distribution of parameters describing the effect of black mangabey density *B* against primate density *P* on mean density μ from (left) SCNC, and (right) CTDS. Both plots show a strong correlation and indicates issues of collinearity.

Models describing the probability of founding bonobo signs on transects ϕ, were not different from the null model (Table 4.5), suggesting the process was mostly driven by chance. Therefore, we discarded all proposed models and selected an intercept-only regression, with intercept varying by method in M1, and by period (accounting for differences between surveys using different transect lengths and designs) in M2.

Similarly, the simplest model, which assumed homogeneity of slopes, returned the best fit when estimating mean density μ and was selected for the analysis (Table 4.5).

Table 4.4. Comparison of models estimating occurrence probability ψ. Greek letters represent parameters estimated by the model, italics capital letters represent variables and italics subscripted letters represents indexed varying intercepts and slopes. Here, *i* indicates the parameter varying by sub-sector *I,* and *k* indicates parameters varying by proximity to a patrol post *K*. The models in bold fitted the data best and were include in the final models.

Model	ID	Model	***Δ*-Elpd (SE)**			**Sum *Δ*-Elpd**
			Recces[a]	SCNC[b]	CTDS[c]	
ψ	1	$\alpha1_i + \beta1F + \beta2C + \beta3V + \beta4R + \beta5_k$	-528.4 (10.8)	-81.7 (5.5)	-100.4 (7.2)	-710.5
	2	$\alpha1_i + \beta1F + \beta2_iC + \beta3_iV + \beta4_iR + \beta5_k$	-398.8 (11.0)	-123.9 (6.2)	-160.1 (7.0)	-682.8
	3	$\boldsymbol{\alpha1_i + \beta1F + \beta2_{i,k}C + \beta3_{i,k}V + \beta4_{i,k}R + \beta5_k}$	**0.0 (0.0)**	**0.0 (0.0)**	**0.0 (0.0)**	**0.0**
	4	$\alpha1_{i,k} + \beta1F + \beta2_iC + \beta3_iV + \beta4_iR + \beta5_k$	-336.6 (8.5)	-160.3 (7.6)	-260.1 (8.7)	-757.0
	5	$\alpha1_{i,k} + \beta1F + \beta2_{i,k}C + \beta3_{i,k}V + \beta4_{i,k}R + \beta5_k$	-16.1 (1.8)	-19.3 (1.5)	-18.1 (6.9)	-53.5
	6	$\alpha1_i$	-2077.9 (24.2)	-495.4 (15.5)	-1896.4 (31.3)	-4469.7

Table 4.5. Comparison of models estimating the probability of finding bonobo sings on a transect ϕ and mean bonobo density μ. Greek letters represent parameters estimated by the model, italics capital letters represent variables and italics subscripted letters represents indexed varying intercepts and slopes. Here, *i* indicates the parameter varying by sub-sector *I,* and *k* indicates parameters varying by proximity to a patrol post *K*. The models in bold fitted the data best and were include in the final models.

Model	**ID**	**Model**	**Δ Elpd (se)**		**Sum**
			SCNC[a]	CTDS[b]	**Δ Elpd**
ϕ	1	$\alpha3_{i,j} + \delta1_jF + \delta2_jC + \delta3_jV + \delta4_jR + \delta5_jH + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k} + Ld_j$	0.0 (0.0)	-2.3 (3.2)*	0
	2	$\alpha3_{i,j} + \delta1_jF + \delta2_{i,j}C + \delta3_{i,j}V + \delta4_{i,j}R + \delta5_{i,j}H + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k} + Ld_j$	-1.0 (2.2)*	-1.1 (1.8)*	0
	3	$\alpha3_{i,j} + \delta1_jF + \delta2_{i,j,k}C + \delta3_{i,j,k}V + \delta4_{i,j,k}R + \delta5_{i,j,k}H + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k} + Ld_j$	-3.6 (6.2)*	0.0 (0.0)	0
	4	$\alpha3_{i,j,} + \delta1_jF + \delta2_{i,j}C + \delta3_{i,j}V + \delta4_{i,j}R + \delta5_{i,j,k}H + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k} + Ld_j$	-1.6 (2.6)*	-2.0 (1.7)	-2.0
	5	$\alpha3_{i,j} + \delta1_jF + \delta2_{i,j}C + \delta3_{i,j}V + \delta4_jR + \delta5_jH + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k} + Ld_j$	-0.7 (1.5)*	-3.4 (3.0)*	-3.4
	6	**$\alpha3_j$**	**-3.8 (11.0)***	**-2.6 (8.5)***	**0**
μ	**1**	**$\alpha3_{i,j} + \delta1_jF + \delta2_jC + \delta3_jV + \delta4_jR + \delta5_jH + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k}$**	**0.0 (0.0)**	**0.0 (0.0)**	**0**
	2	$\alpha3_{i,j} + \delta1_jF + \delta2_{i,j}C + \delta3_{i,j}V + \delta4_{i,j}R + \delta5_{i,j}H + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k}$	-3.6 (1.8)	-3.5 (1.3)	-7.1
	3	$\alpha3_{i,j} + \delta1_jF + \delta2_{i,j,k}C + \delta3_{i,j,k}V + \delta4_{i,j,k}R + \delta5_{i,j,k}H + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k}$	-0.8 (3.3)*	-5.3 (1.7)	-5.3
	4	$\alpha3_{i,j,} + \delta1_jF + \delta2_{i,j}C + \delta3_{i,j}V + \delta4_{i,j}R + \delta5_{i,j,k}H + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k}$	-6.0 (1.7)	-4.1 (3.1)	-10.1
	5	$\alpha3_{i,j} + \delta1_jF + \delta2_{i,j}C + \delta3_{i,j}V + \delta4_jR + \delta5_jH + \delta6_jT + \delta7_jM + \delta8_jB + \delta9_{j,k}$	-3.1 (0.9)	-2.3 (0.5)	-5.4
	6	$\alpha3_j$	-13.7 (6.7)	-41.9 (6.4)	-55.1

* Model score considered equal to the one returning the lower ELPD; [a] Standing crop nest counts; [b] Camera trap distance sampling.

4.4.2. Main results

4.4.2.1 Bonobo status and trend in SNP

Using purposely obtained nest decay times (P1 = 87.5 (SD = 2.22) days; P2 = 106.7 (SD = 3.12) days), we estimated the present bonobo density in SNP to be 0.37 individuals/km^2 (SD = 0.04; range = 0.29 – 0.45), resulting in 16,468 weaned bonobos (SD = 1,766; CI = 13,289 – 20,208). For P2, our models predicted that bonobos occupied 66% of the park and corridor, with bonobo abundance in SNP and corridor varying considerably when using different decay times (Table 4.6 and 4.7). We found the highest bonobo densities in SNP in the southern portion of the sub-sectors, namely in Iyaelima, Lomela and Watshikengo (Table 4.6 and Figure 4.7). Comparing P1 and P2, bonobo population trend was positive (increasing) when using a fixed decay time, and stable when using a period-specific decay time (Table 4.7 and Figure 4.8).

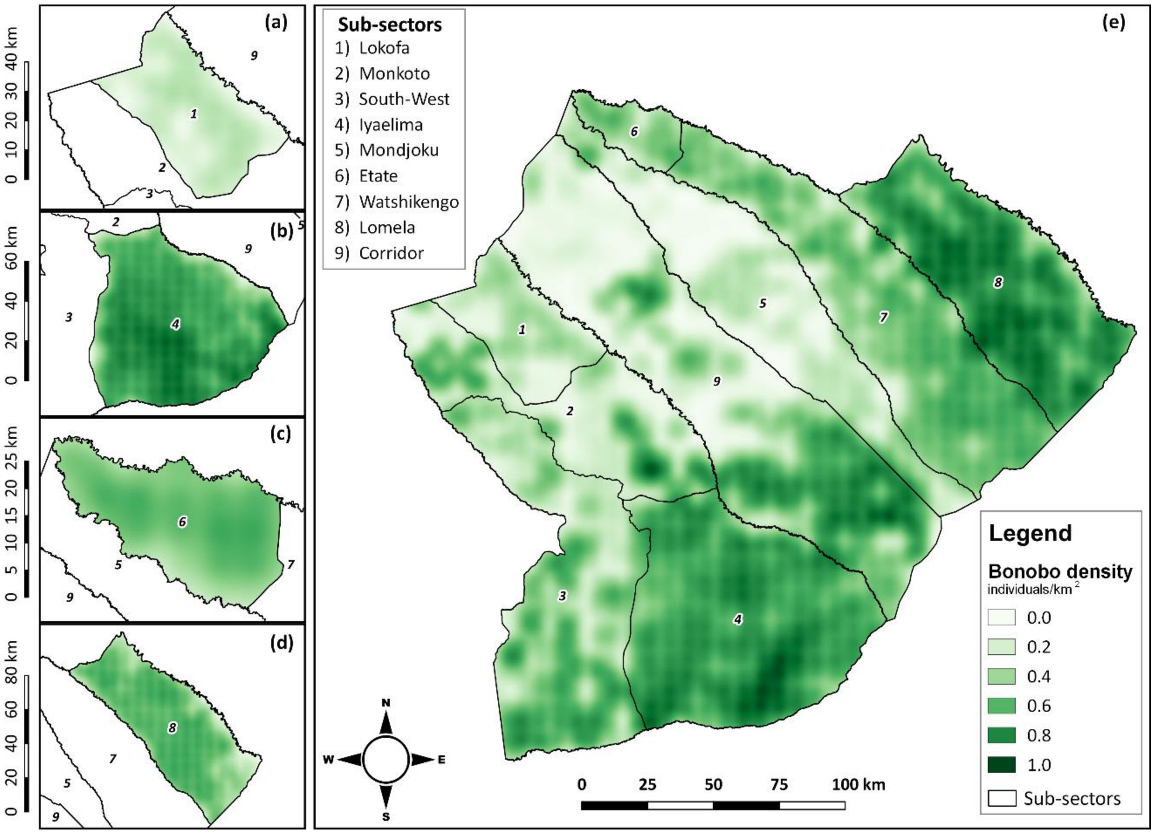

Figure 4.7. Predicted bonobo density in Salonga National Park (SNP). Squares from (a) to (d) show densities predicted for the 4 sub-sectors surveyed in period 1 (P1: 2002-2008); square (e) shows predictions for SNP and corridor in period 2 (P2: 2012-2018).

Table 4.6. Posterior distribution of bonobo density (*D*), abundance (*N*) and population trend in Salonga National Park (SNP) and its sub-sectors, estimated by our models by applying a period-specific nest decay time. Total abundance estimates and population trend (sub-sectors surveyed twice, n = 4), were obtained from the analysis of standing crop nest counts (SCNC) only. In SNP block South (4 sub-sectors*), estimated abundances are compared with those obtained by integrating density data obtained from camera-trap distance sampling (CTDS).

		SNP (SCNC)				SNP Block South (SCNC and CTDS)
Sub-sector		Period 1 (2002 - 2008)	Period 2 (2012 - 2018)			Period 2 (2012 - 2018)
Etate	*D* =	0.43 (0.16 – 0.78)	0.34 (0.03 – 0.80)			
	N =	431 (166 - 785)	346 (27 – 810)			
Iyaelima*	*D* =	0.56 (0.35 – 0.81)	0.56 (0.32 – 0.83)			0.51 (0.05 – 0.86)
	N =	3,758 (2,341 – 5,456)	3,738 (2,172 – 5,610)			3,251 (315 – 5,418)
Lokofa*	*D* =	0.18 (0.04 – 0.41)	0.22 (0.05 – 0.48)			0.33 (0.03 – 0.93)
	N =	391 (77 – 894)	470 (118 – 1,042)			662 (59 – 1,836)
Lomela	*D* =	0.40 (0.23 – 0.63)	0.55 (0.35 – 0.79)			
	N =	2,281 (1,299 – 3,564)	3,128 (1,999 – 4,494)			
				Trend		
	Total N	6,861 (4,904 – 9,297)	7,682 (5,647 – 10,139)	1.15 (0.73 – 1.71)		
Corridor	*D* =		0.29 (0.18 – 0.43)			
	N =		2,685 (1,622 – 3,971)			
Mondjoku	*D* =		0.15 (0.05 – 029)			
	N =		678(235 – 1,324)			
Monkoto*	*D* =		0.28 (0.11 – 0.52)			0.28 (0.02– 0.82)
	N =		981 (378 – 1,799)			922 (65 – 2,686)
South-West*	*D* =		0.35 (0.17 – 0.59)			0.37 (0.03 – 0.74)
	N =		2,072 (1,010 – 3,524)			2,023(164 – 4,040)
Watshikengo	*D* =		0.39 (0.23 – 0.60)			
	N =		2,388 (1,374 – 3,630)			
	Total N		16,486 (13,289 – 20,208)		*Total N*	6,858 (4,200 – 10,629)

Table 4.7. Posterior distribution of estimated bonobo abundance (*N*) and population trend in Salonga National Park (SNP), calculated applying different nest decay times. We obtained total abundance estimates and population trend in sub-sectors surveyed twice (n = 4) in both periods (Period 1 and Period 2) from the analysis of standing crop nest counts (SCNC) only. Total abundance for the entire SNP was obtained in P2 only from SCNC data and included all sub-sectors (n = 9). Provided abundances refer to weaned bonobo only.

	Sub-sectors surveyed twice			**Entire SNP**
Applied nest decay time	**Bonobo abundance *N***		**Population trend**	**Bonobo abundance *N***
	Period 1 (2002 - 2008)	**Period 2 (2012 - 2018)**		**Period 2 (2012 - 2018)**
Period-specific nest decay time (this study)	6,861 (4,904 – 9,297)	7,682 (5,647 – 10,139)	1.15 (0.74 – 1.71)	16,486 (13,289 – 20,208)
Fixed nest decay time (Bessone et al., 2021)	6,391 (4,604 – 8,606)	8,203 (6,043 – 10,855)	1.31 (0.85 – 1.91)	17,604 (14,214 – 21,545)
Literature nest decay time (Mohneke & Fruth, 2008)	7,640 (5,433 – 10,413)	9,805 (7,136 – 12,903)	1.31 (0.85 – 1.91)	21,046 (16,724 – 25,789)

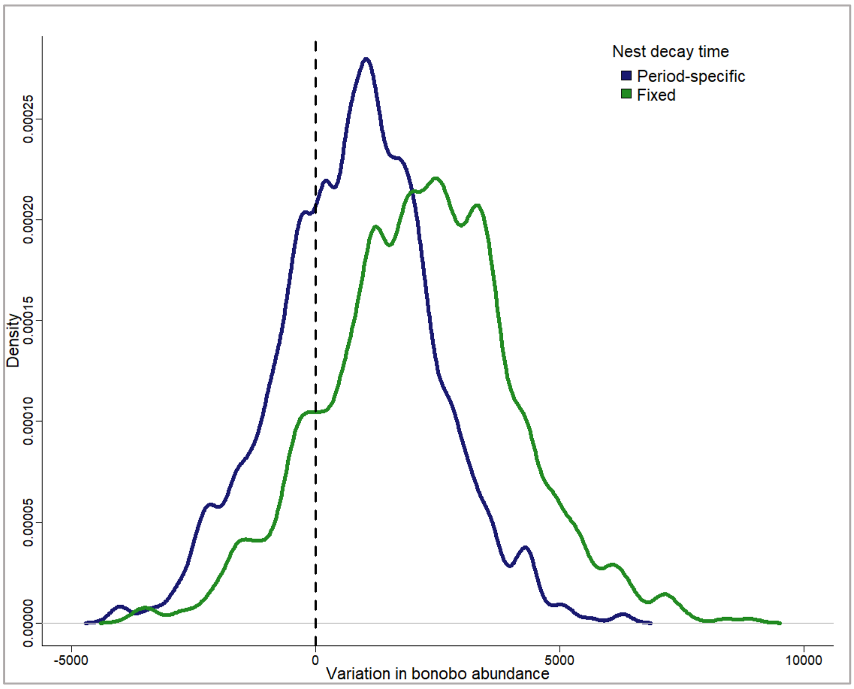

Figure 4.8. Posterior distribution of bonobo population trend in Salonga National Park (SNP), calculated using a 1) period-specific (blue) and 2) fixed (green) nest decay time. No changes in bonobo abundance between periods would result in a variation = 0, indicated by the dashed vertical line.

4.4.2.2 Integrating camera trap and nest count data

When integrating CTDS data, we estimated higher densities in the South Block than when using SCNC data alone (0.41 vs 0.35 bonobo/km^2). However, with CTDS estimates (percent coefficient of variation "CV" = 43%) being highly variable, our model's precision (CV = 21%) (Table 4.6) remained similar to the one obtained by SCNC analysis using the Distance software (CV = 17%) (see Chapter 2).

4.4.2.3 Drivers of bonobo abundance and distribution

Forest cover was a positive predictor of bonobo occurrence in both models and periods (Figure 4.9a and Appendix 6), although neither bonobo-nest- (SCNC), nor bonobo-density (CTDS) were affected (Appendix 7 and 9). Instead, bonobo nest density was positively correlated to the proportion of *Marantaceae* (Figure 4.9), but not to the proportion of feeding trees (Appendix S6). In addition, black mangabey density was not an important predictor of either nest (SCNC) or bonobo (CTDS) density (Appendix 7). Bonobo occurrence was positively influenced by the presence of a PP, a proxy of direct protection, in both models and periods (Figure 4.10c), but not bonobo mean density (Appendix 7 and 9). Bonobo density from CTDS however, was negatively affected by the encounter rates of human signs (Figure 4.9e). The presence of a PP also influenced the effects of proximity to villages. In general, sites further away from villages yielded higher occurrence probabilities (Figure 4.10a and b). However, if a PP was present, the relation was inverted in many cases, with higher occurrence probabilities closer to villages (Appendix 6 and 8).

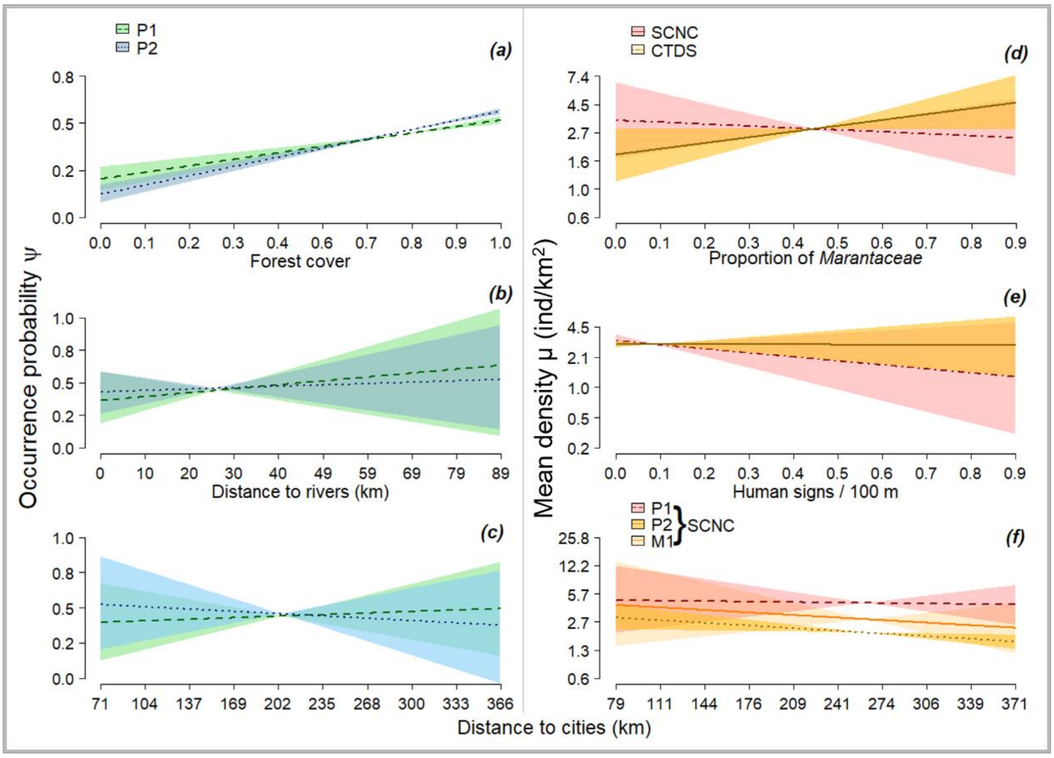

Figure 4.9. Importance of explanatory variables (mean [lines] and 95% CI [shaded areas]) on bonobo occurrence, by period (P1: 2002-2008; P2: 2012-2018), and abundance, by method (SCNC; CTDS). Occurrence probability ψ (left): forest cover (a), distance to rivers (b), distance to cities (c). Mean density μ (n/km^2) (right): proportion of *Marantaceae* (d), human signs per 100 m (e); distance to

cities (f). In (f), we only show the effects on nest density from SCNC by period (P1 and P2), and as estimated in P2 when integrating more variables (M1).

Interestingly, we observed the same trend more markedly in P2, particularly in Etate, where the positive effect increased over time (Figure 4.10a and b). Exceptions were Iyaelima and Mondjoku in P2, where bonobo signs were found closer to the villages in the absence of a PP (Appendix 9). In the corridor, where hunting is allowed, bonobo signs were consistently found further away from villages (Figure 4.10a and b). Bonobo signs were found more frequently further away from main rivers with some exceptions (Figure 4.9b, Appendix 6 and 8), although we found no similar trends with regards to nest density (Appendix 7 and 9). Finally, we found contrasting effects of proximity to cities on bonobo occurrence, with bonobo signs occurring more frequently further away from cities in P1 and closer to cities in P2 (Figure 4.9c). Conversely, bonobo nest density was higher closer to cities in P2, whilst we observed no significant effects in P1, nor when analysing the South Block alone (Figure 4.9f).

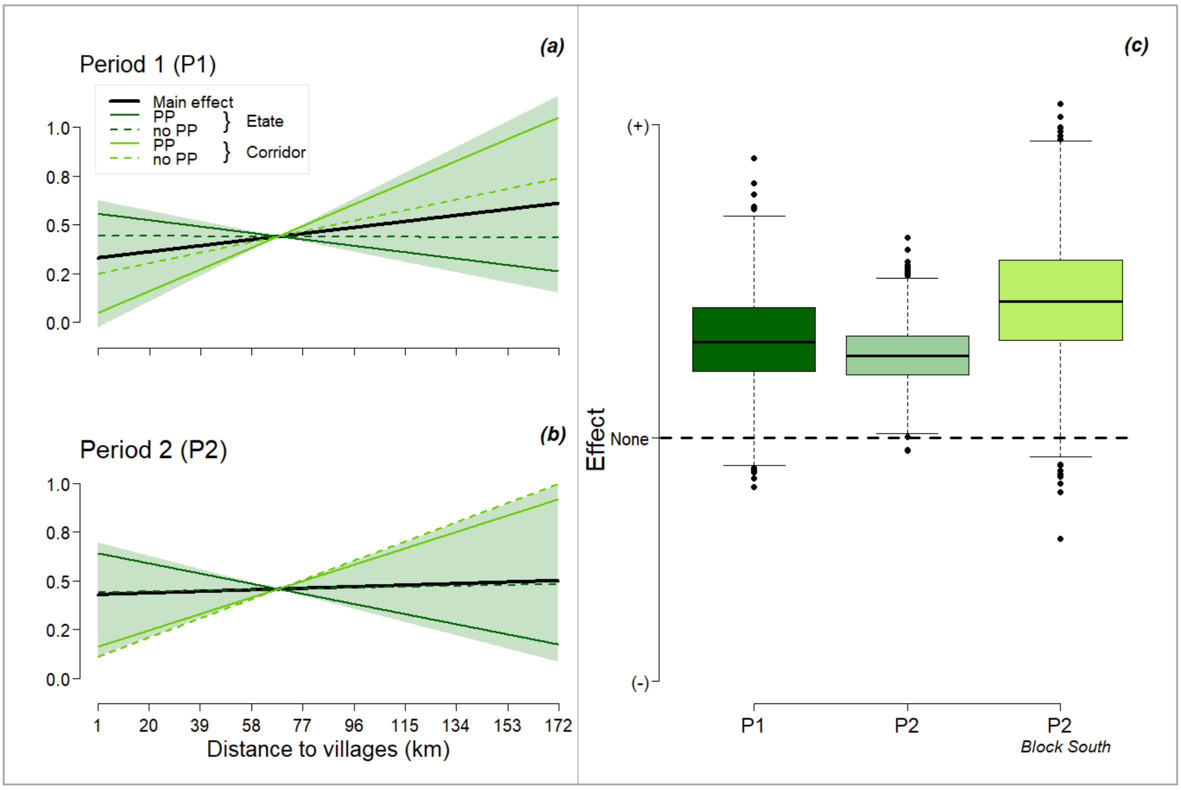

Figure 4.10. Effects of distance to villages, presence of ranger patrol posts (PP) and their interaction on bonobo occurrence probability. Left: main effect (black solid lines) and 95% CI (shaded areas) of distance to villages between (a) period 1 (P1: 2002-2008) and (b) period 2 (P2: 2012-2018), showing a consistent positive effect in the corridor (light green) regardless of the presence of a PP (solid lines) and a reversed trend in Etate (dark green) in P2 if a PP was present, significantly improving from P1, when the presence of a PP made no difference. Right: the main effect of proximity to a PP was positive in both periods (P1: dark green box; P2: green box), even when including camera-trap data in the Block South (P2: light green box).

4.5. Discussion

We estimated that the bonobo population in SNP, an area equivalent in size to Rwanda and Burundi combined, including protected (80%) and non-protected (20%) areas, remained stable over the past 10 years, confirming recent improvements in the management and protection of this World Heritage Site of Nature (IUCN 2020b; UNESCO World Heritage Committee, 2021). As such, we also confirmed SNP as a stronghold for the species. By using a period specific nest decay time, accounting for corresponding climate conditions, our model estimated the number of bonobos to range between 13,289 and 20,208 (Table 4.6), with a mean population density of 0.37 individuals/km^2. This finding contrasts to other great ape studies that have shown dramatic declines in protected and non-protected areas (Plumptre et al., 2016; Wich et al., 2016; Kühl et al., 2017; Santika et al., 2017; Strindberg et al., 2018; Voigt et al., 2018). We also demonstrated that the application of a fixed nest decay rate from the literature (Mohneke & Fruth 2008) would have increased the estimated bonobo population by 22% and suggested an increasing population trend over the past decade (Table 4.7).

4.5.1. *Integrating camera trap and nest count data*

The conversion factors needed in SCNC remains a source of concern in estimating individual animal densities, as they potentially affect the reliability of estimates (Aebischer et al., 2017). For example, in SNP South Block, the application of conventional CTDS and SCNC yielded a population density of 0.54 (range = 0.24 – 1.21) and 0.27 bonobo/km^2 (0.20 – 0.40) respectively (see Chapter 2). Although confidence intervals overlapped, the discrepancy could be due to SCNC underestimating bonobo density if the real mean nest decay was lower than the applied value, which seemed to be the case in Lokofa, the only sub-sector where the integration of camera-trap data yielded higher densities in our model (Table 4.6). Lokofa is an area of seasonally and permanently inundated rainforest located close to the Equator, where higher precipitation may have accelerated nest decay time (Morgan et al., 2016). Alternatively, CTDS could have overestimated bonobo mean density. Although CTDS was found to provide accurate estimates of chimpanzee density (Cappelle et al., 2019), the assumption of animals not reacting to the observer (Buckland et al., 2001; 2015) might be violated by bonobos, reported being particularly reactive to CTs (Kalan et al., 2019). There are several ways to correct for such reactions, yet none seems to be fully satisfactory (Cappelle et al., 2019; Palencia et al., 2021). By allowing the joint analysis of data from different sources, our modelling approach mitigated these effects. One final advantage of our modelling approach is the possibility to evaluate drivers of bonobo presence and density separately. In addition, 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. In fact, bonobo usually nest and travel in groups (also called parties), resulting in higher densities on areas where large bonobo (or nest) groups were observed.

In this study, we did not apply a dynamic N-mixture model (Santika et al., 2017) for 3 main reasons. First, we did not survey the same locations in P1 and P2 (average distance = 1,985 m, range = 43 - 7,621 m). As bonobo nesting sites are known to be linked to fine-scale local conditions (Serckx et al., 2016), we were unable to evaluate site-specific changes in bonobo nest density. Second, whilst orangutans are solitary, bonobos live in fission-fusion communities and have larger home-ranges (Fruth & Hohmann 2018). Consequently, bonobo nests are mostly found in groups (Serckx et al., 2014) and count data are typically zero-inflated, with most transects being found with no nests and a few with very high nest densities. 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 (Table 4.6). This result also supports the validity of the systematic surveys included in our study (Table 4.1), designed to provide an even coverage of the study area, representative of the different habitat features important to the bonobo. Third, GLM were reported being indistinguishible from N-Mixture models for sparse data such as those of this study (Barker et al., 2018). As we were not considering demographic parameters we decided to use the simplest approach.

Our model represent a simple solution for the integration of occurrence and count data, where the uncertainty associated with each stage of modelling (occupancy, density and decay time) propagates into the final estimates. By first modelling bonobo latent occupancy, and then estimating abundance in occupied sites only using a traditional regression analysis, our approach modelled occupancy and abundance independently. In doing so, we assumed our observed densities to be representative of the average bonobo density in the study area (Buckland et al., 2015). However, occupancy and abundance are dependent measures and future developments should aim to fully accommodate the ecological and observational process generating SCNC, CTDS and recce data, extending previous studies (Bowler et al., 2019; Farr et al., 2021).

4.5.2. Drivers of bonobo abundance and distribution

Our model indicated that forest cover was an important predictor of bonobo occurrence, confirming previous studies (Reinartz et al., 2008). However, we did not observe the same pattern for bonobo mean nest density, which is possibly mostly linked to ecological factors, such as food availability. Indeed, the proportion of *Marantaceae* was a good predictor of nest density in our model, supporting previous findings (Reinartz et al., 2008). However, bonobo density from CTDS was not affected, presumably because thick herbaceous understorey could have masked some individuals in CT videos. Conversely, we found no effect of the proportion of feeding trees on bonobo density, likely because our data did not include phenological observations. Similarly, the density of black mangabeys did not have an influence on bonobo density, either because we were lacking proxies of drivers of inter-specific competition (such as food availability), or inter-specific competition may have been levelled out by shared feeding areas, or because mangabeys serve as bonobo prey (Surbeck & Hohmann 2008).

Human presence (Reinartz et al., 2008) and proximity (Hickey et al., 2013) have been reported as the most important drivers of bonobo populations, negatively affecting density and distribution. Here, we observed an overall positive influence of distance to rivers, which are primary traffic routes in SNP, on bonobo presence, with occurrence probability being higher where human presence is scarce. Similar to other areas (Kühl et al., 2009), we found that proximity to cities, hubs of the bushmeat trade, affected bonobo occurrence in P1. However, in P2, when all sub-sectors were included, we obtained more variable results and observed higher bonobo nest densities closer to cities. This could be due to larger bonobo party sizes as a response to human presence, or to favorable bonobo habitats being found towards the south of SNP (Grossmann et al., 2008), an area better connected to commercial cities around the park. Indeed, the effect of proximity to cities on nest density was not detected when more ecological data were included in M1. Finally, we observed an overall positive effect of distance to villages on bonobo occurrence probability in both periods. Importantly, the presence of a PP had a positive effect (Figure 4.10), with bonobos being more likely to occur close to a village if a PP was found within 15 km in most sub-sectors, improving with time in areas such Etate (Figure 4.10a and b) where law enforcement patrols increased in recent years (ZSM, 2018). Nonetheless, we observed an opposite trend in Mondjoku and Iyaelima, with bonobos being more likely to occur further away from a village if a PP was present. During the second Congo war (1998 – 2003), the

Mondjoku sub-sector had high poaching levels even in proximity of the ICCN head-quarter (GR, *personal observation*), located close to villages (Figure 4.1), which could explain bonobo absence in areas where PP are present (Figure 4.7). The Iyaelima sub-sector is peculiar in having villages within the park borders. Here, rangers based in a PP often bonded with villagers, depending on their food, and were thus unlikely to enforce anti-poaching measures around their "home-village". Remarkably, in the Corridor, where hunting of non-protected species is allowed, the positive correlation between distance to villages and bonobo occurrence probability was consistently strong (Figure 4.10a and b). In addition, our model estimated bonobo mean nest density to be positively correlated to distance from villages (in P2 only), and bonobo mean density from CTDS, to be negatively affected by the number of human signs, suggesting smaller party sizes with higher human presence. However, an exception is that bonobos are more abundant in sub-sectors such as Iyaelima, where villages exist within the park's border (Grossmann et al., 2008). Here, excellent bonobo habitats are available, but also taboos against bonobo meat consumption (Thompson et al., 2008), an important driver of great ape abundance in central Africa (Strindberg et al., 2018). Consequently, in Iyaelima cultural taboos might protect bonobos regardless of rangers being present in the area. Therefore, although our results suggest that the presence of rangers help improve bonobo conservation, to assess the overall importance of the presence of rangers in SNP, it will be crucial to investigate its impact on species mostly targeted by the bushmeat trade, such as ungulates (e.g. duikers) and arboreal primates, including patrol effort data (Kablan et al., 2019). In addition, future field studies should aim to survey the same areas repeatedly, enabling the application of dynamic models (Santika et al., 2017) that evaluate population dynamics and conservation effectiveness.

4.5.3. Conservation relevance and perspectives

Although being a pivotal parameter to evaluate a species conservation status, the population trend of 42% of the mammal species assessed in the IUCN Red List is currently unknown (IUCN, 2020a). Using the bonobo as an example, our study suggest that an integrated approach could be crucial for future assessments of these species. Specifically, the method described here could be used for the range-wide assessment of population status and trend advocated by bonobo experts (Fruth et al., 2016). As bonobo survey data are sparse and localized in few areas (Fruth et al., 2016), our approach would allow integration of all data collected thus far across the species' geographical range, explicitly accounting for method-specific detection probability. This way, law enforcement (Keane, Jones and Milner-Gulland, 2011) and interview data (Santika et al., 2017) could also be included, expanding the range of exploitable data.

In addition, with increasing evidence showing the reliability of CTDS (Amin et al., 2021; Cappelle et al., 2019; Corlatti et al., 2020; Harris et al., 2020; Palencia et al., 2021) for multi-species investigation of cryptic and understudied species of high conservation value such as the Giant ground pangolin (*Smutsia gigantea*) and the Congo peafowl (*Afropavo congensis*) (see Chapter 2), our study provide a simple method for the integration of novel and traditional methods mitigating specific limitatons.

We suggest, that for these and other species, an integrated analysis could improve current assessments based on few studies providing sparse information. The approach used here can be adapted to a wide range of species, inhabiting diverse areas of the world, and tailored to accommodate different sources of information. In that way, it could become an essential tool to assess the population status and trend of species, like the bonobo, lacking large-scale survey information or long-term monitoring data, evaluating the effectiveness of conservation strategies.

Specifically, our study suggests that a combination of highly suitable habitat, taboos in the local population and presence of law enforcement, contributed to maintaining a stable bonobo population in SNP (Figure 4.11), which remains the species' strongholds in DRC. Although recently removed from the List of World Heritage Sites in Danger (UNESCO World Heritage Committee, 2021), the conservation status of SNP is still of considered of concern (IUCN 2020b). Our results provide a rare positive story in great ape conservation and strongly support further efforts to preserve the SNP's pristine forests and the cultural heritage of the human populations therein.

4.6. Acknowledgments

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4.7. Data availability statement

Data will be available via the EDMOND repository

Photo: Mattia Bessone© PNS Survey®

Figure 4.11. Salonga National Park viewed from the village of Anga, Kasai, Democratic Republic of the Congo.

CHAPTER 5

General conclusions

The main objective of this thesis was to improve previous methods used for estimating the status of bonobos in the wild.

Great ape nests have been studied since the late 19th century (reviewed in Fruth and Hohmann (1996)) and they have been used to assess density and abundance for more than 30 years, with standing crop nest counts (SCNC) (Tutin and Fernandez, 1984), being the method of choice. However, more recently, the limitations of traditional nest counts for estimating great ape density became apparent, due to the difficulties in correctly estimating conversion factors needed to translate nest to ape density (Kühl et al., 2008).

Several studies have estimated survey specific nest decomposition time by either observation of the full decomposition (Fleury-Brugiere and Brugiere, 2010; Serckx et al., 2014b; Lapuente et al., 2020) or modelling decomposition based on partial observation (Kouakou, Boesch and Kühl, 2009; Morgan et al., 2016; Spehar et al., 2010; Murai et al., 2013; Tweh et al., 2015; Wich et al., 2016; Santika et al., 2017; Strindberg et al., 2018; Voigt et al., 2018; Heinicke et al., 2019a). However, due to difficulties in carrying out such studies when time and resources are limited, others have used values obtained from the same area in previous years (Danquah et al., 2012; Gregory et al., 2012; Carvalho, Marques and Vicente, 2013; Piel et al., 2015; Plumptre et al., 2015; Simon, Davies and Ancrenaz, 2019), or even from other areas (Mathewson et al., 2008; Stokes et al., 2010; Haurez et al., 2014; Spehar et al., 2015; Dias et al., 2019). The same applies to the other conversion factor needed for estimating density via SCNC, the production rate of nests. Here, as long-term observational studies of habituated great ape communities are required, available values are much rarer (Kühl et al., 2008), with the only value available for the bonobo, being obtained in Lomako, DRC, back in 1995 (Mohneke and Fruth, 2008). Although the bias induced by an inaccurate nest production rate, expecting between-population differences in the order of decimals, is likely to be smaller than the bias induced by inaccurate nest decay times causing differences of several days, it remains a source of serious concern as recently demonstrated (Wessling and Surbeck, 2022).

For these reasons, recent years have seen the development of monitoring methods exploiting different sources of information, like genetic material, acoustic recordings, and camera-trap images (presented in Chapter 1). Any of these sources, including nests, can inform with regards to species distribution, allowing the application of the SDMs described in Chapter 1. However, for the estimation of species density, CT-methods have been particularly successful (Burton et al., 2015), allowing estimation of density of both unmarked and marked animals.

5.1. Main findings

In my thesis, I analysed a dataset including 5,213 bonobo nests observed on 3,596 km of line transects and 38,000 video clips collected at 743 different locations in Salonga National Park (SNP), bonobo's stronghold in Democratic Republic of the Congo (DRC). I also investigated the decomposition time of 1,511 bonobo nests, collected at the research site of LuiKotale, located in SNP's buffer zone. By that, I tested the applicability of a novel CT method (Chapter 2) and investigated the reliability of traditional survey methods (Chapter 3). Finally, I used state-of-the-art analytical methods integrating data collected using both of the former methods (Chapter 4). In Chapter 2, I applied camera trap distance sampling (CTDS) (Howe et al., 2017), a novel camera-trap based field method, to estimate bonobo density (and for another 13 species), in the largest forested protected area of the African continent, Salonga National Park (SNP). I identified issues in the applicability, and tested methods improving the estimation of required parameters, such as specific availability (Rowcliffe et al., 2014). I showed that CTDS provided higher density estimates than traditional SCNC, with CTDS returning a population density of 0.54 bonobo/km^2 against 0.27 bonobo/km^2 estimated by SCNC. However, confidence intervals overlapped (CTDS = 0.24 – 1.21; SCNC = 0.20 – 0.40), showing that CTDS can be successfully used to estimate bonobo density. Indeed, CTDS was found to return accurate density in all studies following the publication of my findings (Corlatti et al., 2020; Harris et al., 2020; Cappelle et al., 2021; Palencia et al., 2021).

Nevertheless, the accuracy of bonobo estimates presented in Chapter 2 could have been hindered by the species reactivity to CTs (Kalan et al., 2019). Although I excluded all snapshots where I found bonobos to be reacting to the CTs, I was unable to know whether or not a bonobo reacted to the camera before entering the field of view. This is a common issue in CTDS (Cappelle et al., 2021). To date, there is not a consensus on the best approach for dealing with reactive behaviours (Palencia et al., 2021), although the recent development of methods using species-specific ethograms to objectively identify reactive behaviours in CT videos (N. Cappelle, *personal communication*), promise to reduce reactivity-induced bias in future studies. In addition, bonobo CTDS estimates showed large coefficient of variation (43%), similar to an antecedent small-scale study on chimpanzees (Cappelle et al., 2019). The reason for large confidence intervals can be explained by bonobos showing a large variance of encounter rate, which is reported being associated with low estimate precision (Cappelle et al., 2021), possibly due to a few large bonobo groups, using the area in front of CTs for long timespans. Here, precision could be improved by increasing spatial and / or temporal effort (Cappelle et al., 2021). However, future studies should also consider discarding snapshots of animals lingering in front of the CTs, regardless of reactive behaviours.

Despite these limitations, when bonobo reactivity is minimized, for example by deploying CTs a few weeks before beginning the study, giving bonobos the time to acclimatize to their presence, CTDS remain a promising method for the estimation of bonobo density in the wild, with the additional advantage of allowing for simultaneous multi-species assessment of other sympatric species, including rare species (Palencia et al., 2021). Here, a minimum of 80 radial distances is recommended for reliable density estimates from point transects DS (Buckland et al., 2015), a threshold that might require intensive survey effort. However, the use of Multi Covariate DS (MCDS - Buckland et al., 2015), including species as a factor, would allow the combination of observations from several species sharing similar size and behaviour (i.e. similar detection probability). This way, density estimates can also be obtained for species returning few observations. Even more important for bonobos and other great apes, CTDS and other unmarked CT-based methods have the advantage of not requiring estimates of factors needed to convert nest to bonobo density.

In fact, in Chapter 3 I confirmed that estimates of bonobo density using traditional SCNC are highly dependent on one factor converting nest to bonobo density, namely nest decomposition time (Kühl et al., 2008). I showed that bonobo nest decay time in LuiKotale, located at the south-west fringe of SNP, has lengthened by 17 days over the last 15 years as a result of declining rainfall. I also found that whilst rainfall decreased, the number of storms did not decrease accordingly, suggesting that in recent years, precipitation was harsher and less predictable. As a result, bonobos changed their nesting behaviour, building stronger nests to endure the new conditions. These findings strongly suggest that density estimates using SCNC would be biased unless, biotic, abiotic, and behavioural factors specific to the population of study are considered. In Chapter 3, I showed that when applying nest decay time from only a year earlier, estimates were biased by as much as 60%; whilst in Chapter 4, I found that using a nest decay from previously published nest decay time from the same site of LuiKotale (Mohneke and Fruth, 2008), would have inflated density estimates up to 25%. However, as studies involving continuous monitoring of nest degradation are long and costly, I also provided recommendations for the application of time and cost-effective, single revisit methods, such as the logistic regression (Laing et al., 2003), recommending a minimum of 150 individual nests and carefully selected time to revisit, for accurate assessments of bonobo nest decay in future studies.

Chapter 4 brought these findings together to develop a model able to integrate survey data obtained at different times and with different methods. This allowed to include SCNC and CTDS estimates, as well as ad hoc nest decays. By that, I presented a modelling approach able to exploit multiple sources of information, mitigating method-specific biases and providing accurate assessments of bonobo status and trend. The method shown in Chapter 4 can be applied to other species, but it is particularly suitable to the bonobo, a species lacking information for more than 70% of its current range (Fruth et al., 2016), in which data, if available, were collected sparsely, entailing different levels of standardization and accuracy. The model allowed the separate evaluation of the drivers of bonobo occurrence and density, showing the importance of intact suitable habitat, tolerance from the local population and law enforcement, to maintain stable bonobo populations. This study, representing one of the rare positive stories in great ape conservation, fits perfectly ongoing research trends demanding the integration of different data sources towards more effective biodiversity monitoring (Kühl et al., 2020), and strongly supports further efforts for the preservation of SNP's pristine forests and of the cultural heritage of the human populations inhabiting it.

Together, these results have important implications for bonobo conservation. First, I showed the applicability of CT-methods able to complement data derived from traditional nest surveys. Second, I provided methodological recommendations to avoid biasing future estimates due to inaccurate nets decay values using traditional SCNC. Nest count, however, are still highly relevant because investigating population trends requires estimates of ape population density obtained at different points in time, ideally but not necessarily with the same methodology (Nichols and Williams, 2006). As previous surveys were collected using traditional methods such as SCNC, and CT-based survey methods such as CTDS are still under development (Gilbert et al., 2021), the latter are unlikely to fully replace traditional nest counts. In addition, as shown in Chapter 4, data from different sources can be integrated to provide more accurate estimates accounting for method-specific bias. With methods exploiting new sources of information being developed, tested, and validated, analytical methods like the one presented in Chapter 4 will provide the basis for simultaneously exploiting both traditional and new data. Here, I confirmed the findings of earlier studies (Arnold et al., 2018; Saunders, Cuthbert and Zipkin, 2018; Horne et al., 2019; Jansen et al., 2019; Plard et al., 2019; Dobbins et al., 2020) and showed how an integrated approach allowed a better understanding of the processes driving bonobo population dynamics and allowed mitigating method-specific limitations. Similarly, I showed that data integration can improve our capability in evaluating the efficacy of conservation strategies in SNP, specifically the positive effect of the presence of rangers on bonobo distribution.

5.2. Costs of line transects and camera trap methods

From a scientific point of view CTs studies allow the detection and investigation of a higher number of species than line transect surveys. In SNP block South, CTs recorded 43 species against only 25 recorded along line transects. In addition, the number of species providing a suitable sample size for investigation using CTDS (n = 31, see Appendix 1) was 4 times higher than using LTDS, which provided density estimates for 5 arboreal primates, the elephant and the bonobo only. As shown in Chapter 3, LTDS using indirect signs, like nests, is complicated by the need for correction factors such as nest decay time. In addition, LTDS nest counts provide information on nesting sites only, that are usually restricted to the heterogenous primary forests of the *terra firma*. In contrast, CT studies reflect the totality of great ape habitat use, including ranging and foraging areas such as temporarily and permanently inundated forests. Finally, CTs studies also provide additional insights into the natural history, ecology and behaviour of the species of interest (Alempijevic et al., 2021), including information on daily activity patterns (Palencia et al. 2019), demographic composition (McCarthy et al., 2018) and breeding behaviour (Maputla et al., 2020).

The two methods also differ in the associated monetary and practical costs. Cappelle et al. (2019) showed that line transects sampling is a cheap but time-consuming method, when compared to CT methods. The latter required less field time and staff but were more expensive in terms of equipment and time needed for video processing and analysis. Although detailing the multiple costs associated with each method was beyond the scope of this thesis, my work supports these findings. The monetary cost of CT devices alone (not including batteries and data storage devices, i.e. SD cards) totalled roughly £ 32,000 (£ 200 for each of the 160 units used in Chapter 2) and was 3 times higher than fully equipping 5 monitoring teams for line transect surveys with: 5 GPS devices (1 per team), 5 binoculars, 5 compasses, 5 smartphones for data collection, 5 satellite phones, 5 Topofil® for marking the transect line, measuring tapes, machetes, and secateurs (about £ 10,000 in total). However, data collection required longer time in LTDS, with an average of 4.5 hours needed to survey 1 km of transects. In comparison, the installation of 1 camera trap, including recording of reference videos (see Chapter 2) required about 30 minutes time. Although monitoring teams were composed by 4 people only, in LTDS longer time in the field translated into a larger number of porters needed to transport food (i.e., 10 to 15 porters per team). In contrast, CTs would require teams of about 6 people only (i.e., 1 trained researcher, 1 assistant and 4 porters), making the method cheaper in terms of salaries, food provisions and transport. However, the employment of many people represented an additional value of LTDS. By involving local communities in conservation activities, LTDS monitoring provided more work opportunities and salaries, which can be beneficial for the successful implementation of conservation measures in the long term.

With regards to the training needed for field applications, the methods were similar. However, incorrect installation of the CTs would result in loss of data, as some devices would need to be discarded from the analyses. For example, installing the CT in front of vegetation that repeatedly triggers the device drains batteries within 1 or 2 days, greatly reducing data acquisition. In contrast, when line transect data are not properly collected, e.g. survey teams violating the assumption of 100% detection probability on the transect line (see Chapter 1, section 1.2.2), the resulting data might be unusable altogether, hindering the reliability of an entire survey. In contrast, CTDS required longer time for data analysis, mainly because the method was new at the time of this thesis (Chapter 2). However, the main limiting factor of CTDS was the time required for processing the videos, identifying the species (i.e. roughly 500 videos / day), and estimating the radial distances needed for density estimates (i.e. between 30 and 50 videos / day, depending on the species in study). Both of these aspects have been the subject of studies and developments since the publication of Chapter 2, in March 2020. I discuss recent advancements in the next section.

5.3. Ongoing research and future perspectives

The results of my thesis show how novel methods and an integrated approach are critical tools for the assessment of bonobo conservation status. However, some issues still hinder the large-scale application of CT survey methods such as CTDS.

One of the major limiting factors of CT-studies, was the time needed to watch and code each video (Glover-Kapfer, Soto-Navarro and Wearn, 2019), a task made more laborious by false triggers i.e., videos retaining no animals. Chapter 2 of this thesis is the result of months spent watching CT videos (n = 38,344), singling out those with the species of interest, and compiling the data in an Excel sheet. To speed-up the labeling process, some studies have used citizen science to label large datasets of CT videos (McCarthy et al., 2021), whilst others have integrated citizen science and machine learning algorithms (Green et al., 2020).

The latter have been particularly successful. To date, Machine learning models provide different levels of degree of automation: 1) labelling of detections / non detections; 2) coding of CT videos, including recognition of species therein; 3) individual recognition of animals in the videos, for certain species; 4) estimation of radial distances in CTDS.

1) The simplest models allowed to discriminate between false-triggers and videos with animals (Wei et al., 2020). By identifying false triggers, the algorithm, contemporary to the publication of Chapter 2 of this thesis, would have halved the time needed to code my database (43% false triggers).

2) More sophisticated models were recently designed to identify the species in the footage (Whytock et al., 2020; Norouzzadeh et al., 2021), making use of training videos to calibrate the algorithm. Although showing high performance (Tabak et al., 2019), these algorithms were reported being poor in generalizing to other surveys (Schneider et al., 2020), and having difficulties in identifying rare species, given the limited number of training videos available for validation (Whytock et al., 2020). Nevertheless, the advantages of such models available at the beginning of my thesis would have been enormous.

3) Even more sophisticated models attempted to individually identify animals in CT videos. Thus far, these studies have been restricted to great apes, using individual facial features (Crunchant et al., 2017; Schofield et al., 2019). Although suffering from the same problems of (2), these models allow larger applicability of the marked-SECR methods described in Chapter 1.

4) Finally, given the growing application of CTDS studies (Howe et al., 2017; Cappelle et al., 2019; Corlatti et al., 2020; Harris et al., 2020; Cappelle et al., 2021; Palencia et al.,

2021, Amin et al., 2021), researchers are developing methods addressing two of the main limiting factors of the method, a) the time needed to estimate radial distances of animals to the CT (discussed in Chapter 2); b) the radial-distances themselves, with estimates using reference videos (Howe et al., 2017) being prone to some level of observer's subjectivity. Recently, Zuleger, Holland and Kühl (2021) proposed a photogrammetry approach to automatically derive radial distances observation distance from reference videos. Similarly, Haucke et al., (2021), described a method allowing estimation of radial distances in a fully automatized way from reference images, using image processing and pattern recognition. Estimated distances were reported as being extremely accurate, achieving a mean distance error of 0.14 m, and reducing the time for estimation with reference videos by a factor 18. Lastly, Johanns, Haucke and Steinhage (2022), proposed a fully automatic approach to estimate radial distances without the need of reference image, using monocular depth estimation (MDE). They found a distance estimation error of only 0.986 m.

One final source of concerns in CTDS, was the reactivity of animals to the CTs, which I identified as the main source of bias (Chapter 2). Here, objective methods assessing reactive behaviours using species-specific ethograms are under development and promise to reduce reactivity-induced bias in future studies (N. Cappelle, *personal communication*).

By that, technological and methodological advancements are expected to further expand the use of CT-based methods in coming years. In addition, acoustic surveys are also being quickly developed. Initial applications to great apes were limited to the assessment of distribution (Heinicke et al., 2015; Kalan et al., 2015; Spillmann et al., 2015; Campos-Cerqueira and Aide, 2016; Crunchant et al., 2020) but methods able to estimate species' density using acoustic recordings are becoming increasingly available (Stevenson et al., 2015; Stevenson et al., 2021). Although only applied to one frog species (*Arthroleptella lightfooti*), the latter retains high potential for being extended to other vocal species, including great apes.

As novel methods provide additional data useful to the assessment of a species status, the use of IPMs is also expected to further increase in coming years. As reviewed in Chapter 1, advancement in computing power and in the efficiency of statistical algorithms (Carpenter er al., 2017), are making the application of IPMs available to a larger number of users and practitioners, including ecologists and conservationists (Arnold et al., 2018; Saunders, Cuthbert and Zipkin, 2018; Horne et al., 2019; Jansen et al., 2019; Plard et al., 2019; Dobbins et al., 2020; Farr et al., 2021).

5.4. Conservation relevance

The results of this thesis are of the highest conservation importance for the bonobo, at different levels.

1) In Salonga National Park, this dissertation will serve as a basis for future monitoring of the bonobo population. Continuous surveys, repeated at regular intervals (e.g., five years), will provide the data needed for assessing population trend and, by that, for evaluating the efficacy of conservation strategies. Ideally, future surveys should be conducted in the same areas or, even better, on the very same transects surveyed between 2012 and 2018. By surveying the same areas, such a design will account for the fact that bonobo habitat use is driven by small-scale habitat features, particularly when it comes to choosing nest locations (Serckx et al., 2016). In addition, it will allow the application of methods analysing parameters of population dynamics, such as Dynamic N-Mixture models (Chandler and Clark, 2014; Santika et al., 2017), which will shed light on the factors involved in bonobo survival and patterns of dispersal. Along the same lines, the use of CTs seems highly advisable. CTs complement nest data by providing information on bonobo ranging and foraging areas. For example, bonobos are known to forage in inundated forest and swamps, but they rarely nest there (Fruth, 1995; Mulavwa et al., 2010). An integrated approach combining the two methods, would reflect the totality of bonobo habitat use and allow a thorough investigation of the drivers affecting the viability of bonobo population in SNP. Here, long term monitoring using CTs at fixed locations, would allow the bonobo to acclimatize to their presence, mitigating the bias induced by reactive behaviour. Although, the camera height used in this study (70 - 90 cm) was adequate to detect bonobos at close distances, it was too high for smaller species, which were frequently missed within the first 2 m from the camera lens. In order to fully exploit the potential of CTDS for multispecies monitoring, future studies should consider reducing CT height to 50 cm. In addition, technological advancements in CT-studies described above, will make data-processing faster and easier, whilst software allowing recognition of individual apes will provide the information needed for integrating demographic data, improving the estimates' precision (Schaub and Abadi, 2011; Regehr et al., 2018; Margalida et al., 2020).

If nest counts are to be used in future monitoring programs, the estimation of bonobo nest decay in different areas of SNP is highly advisable. Here, logistic regression methods (see Chapter 3) could be applied to minimize the time and costs needed for nest monitoring. The inclusion of patrol data with information on hunting pressure will provide an understanding of the efficacy of the park's protection, while acoustic devices recording gun shots may provide additional information on hunting pressure in the future (Dobbins et al., 2020). Finally, bonobo conservation and monitoring should consider including local communities in monitoring activities (Plumptre et al., 2021). In SNP, 9 villages are still present within the park borders, precisely in the areas where high bonobo densities are found (i.e. Iyaelima and Lomela). These communities have ancestral taboos against the killing of bonobos (Thompson 2008), but the unlawful hunting of other species in SNP is their only source of protein intake and income. Integrating these villages in future bonobo monitoring programs, might provide an alternative source of income in return for valuable information on bonobo presence, ongoing commercial hunting and poaching of endangered species. In addition, these communities still hunt with traditional methods such as bow and arrow. These methods have been considered sustainable in other areas of the Congo basin (Fa et al., 2020). Sustainable hunting programs of non-protected species, restricted to traditional hunting methods within a buffer area around the villages, seem like a workable solution to preserve the forest from large scale slash and burn practices, by at the same time sustaining the very people that had allowed bonobos to thrive in SNP for centuries.

2) At the national level, the methods and recommendations discussed in this thesis will provide the opportunity to assess the range-wide bonobo status and trend, integrating all available data collected thus far in DRC. An Integrated population models can be extended by including additional data, such as acoustic records (Doser et al., 2021), interviews (Santika et al., 2017) and ranger patrol data (Keane, Jones and Milner-Gulland, 2011; Kablan et al., 2019), allowing a better understanding of the drivers of bonobo occurrence and abundance in the wild (Arnold et al., 2018; Saunders, Cuthbert and Zipkin, 2018; Horne et al., 2019; Dobbins et al., 2020). With the new bonobo global conservation strategy due in 2022, this study is of highest importance (IUCN and ICCN, 2012), and will serve as basis for preserving the remnant wild population of this extraordinary ape.

Whilst the bonobo was the focus in this dissertation, its results are not restricted to this species. If Chapter 3, investigating bonobo nest decomposition, provided recommendations applicable to other great apes, the results of Chapter 2 and 4 can be extended to a large number of species, with the overarching findings of this dissertation being of highest interest for a broad audience of researchers, wildlife managers and conservationists. Chapter 2 has already had a considerable impact in the scientific community. Having received 19 citations since its publication in March 2020, it contributed to the development of CTDS. It also raised interest in the larger public. Having been featured (among others) by The Conversation and The Independent, it showcased some of the species inhabiting the Congolese rainforest, and the importance of preserving them and their habitat.

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