

**A camera trap assessment of factors influencing
leopard (*Panthera pardus*) habitat use in the
Nouabalé-Ndoki National Park, Republic of Congo**

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**Submitted in partial fulfilment of the requirements for the degree
of Masters of Science in Conservation Biology**

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TABLE OF CONTENTS

PLAGIARISM DECLARATION	5
ACKNOWLEDGEMENTS	6
ABSTRACT	7
1. INTRODUCTION	9
2.1. Study Area	14
Figure 1. Map of the Nouabalé-Ndoki National Park (NNNP) study area (dark green) showing the location of camera traps (dots within the two yellowish polygons) and the distribution of the different human settlement and crossroads surrounding the park, with Central African Republic Protected Area (CAR_PA), Djeke triangle (a 10,000-hectare forest block which lies about 5km outside of the Nouabalé-Ndoki National Park (NNNP) on the border of the. Central African Republic and Republic of Congo. It covers pristine unlogged rainforest set aside by a logging company following negotiations by the wildlife conservation society), the Congolaise Industriel de Bois roads (CIB roads), and limite UfaCIB indicates CIB logging concession boundaries. _	16
2.2. Human activities around the Nouabalé-Ndoki National Park	17
3. DATA ANALYSIS	20
3.1. Species richness	20
3.2. Relative Abundance (RA) of leopard prey species	20
3.3. Occupancy modelling of leopard habitat use	21
3.3.1. Predictor variables for use in the occupancy model	21
3.3.2. Occupancy modelling	21
4. RESULTS	24
4.1. Species richness	24
Table 1. List of mammal species camera trapped from 2009 to 2015 in the Nouabalé-Ndoki National Park, Republic of Congo with number of photographs in Northern cluster (No. photos.NC); number of photographs in Southern cluster (No. photos. SC); total number of photographs in Northern and Southern clusters (No. photos. NC & SC).	24
Figure 2. Species accumulation curves with 95% confidence intervals for the wildlife community detected by camera trapping within both northern (blue line) and southern (orange line) clusters in the Nouabalé-Ndoki National Park over the period of 2009-2015. Dashed lines signify the 95% confidence limits for each curve.	25
Table 2. A comparison of the observed animal species richness (Sobs), Abundance Coverage Estimator (ACE) and Incidence Coverage Estimator (ICE) across both northern and southern clusters within the Nouabalé-Ndoki National Park, based on camera trap data from 2009 to 2015	26
Table 3. EstimateS results of the number of species observed with confidence intervals within the northern cluster, Species estimate: S(est); Species estimate confidence interval Lower Bound: S(est) 95%CI Lower Bound; Species estimate confidence interval Upper Bound: S(est) 95%CI Upper Bound.	26

Table 4. Estimates of the number of species observed with confidence intervals within the southern cluster. Species estimate: S(est); Species estimate confidence interval Lower Bound: S(est) 95%CI Lower Bound; Species estimate confidence interval Upper Bound: S(est) 95%CI Upper Bound.	26
4.2. Relative abundance (RA) of leopard prey species	27
Figure 3. The mean relative abundance (RA) of select leopard prey species, based on camera trap data from 2009 to 2015 in the NNNP, within the Northern and Southern clusters.	28
4.3. Occupancy modelling of leopard habitat use	28
Table 5. Number of photographs and stations where leopards were captured in each cluster with trap effort and leopard independent captures over the whole period of study.	28
Table 6. Summary of model selection outputs using occupancy(ψ) covariates only while keeping detection (p) covariates constants, with Akaike's information criterion (AIC), delta AIC (Δ AIC), Akaike weight (AIC wgt), model likelihood, no. of parameters (k), 2log-likelihood (LL). Covariates include: blue duiker (M); red duiker (RD); red river hog (P); Nearest distance to villages (DV); Nearest distance secondary & crossroads (DC), Nearest distance to Park borders (PB), Distance to rivers (DR).	29
Table 7. Summary of model selection results indicating the effect of detection (p) covariates (while keeping ψ fixed) in determining probabilities of leopard detection and site use, with Akaike's information criterion (AIC), delta AIC (Δ AIC), Akaike weight (AIC wgt), model likelihood, no. of parameters (k), 2log-likelihood (LL). Covariates include: blue duiker (M); red duiker (RD); red river hog (P); Nearest distance to village(DV); Nearest distance secondary & crossroads (DC); seasons (S); NDVI(N); Effort(E); Clusters 1&2 (C), Nearest distance to Park borders (PB), Distance to rivers(DR).	31
4.4. Probability of occurrence and proportion of habitat use by leopards at camera trap stations and within each cluster	32
Figure 4: Site-specific output from seven years camera trapping showing spatial variation in leopard space use (based on the averaged model ($\sum w = 1$), with watercourses (blue line) occurring outside and inside the protected area surrounding therefore both northern and southern clusters, parks border (blue dots along the park peripheric).	32
Table 8. Proportion of leopard space use at camera trap stations and within both northern and southern cluster across the period of study, showing five level of space use, ranging from 0.15 to 95%.	33
6. CONCLUSION AND RECOMMENDATIONS	37
REFERENCES	39

PLAGIARISM DECLARATION

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ABSTRACT

Leopards (*Panthera pardus*) are faced with increasing levels of anthropogenic pressure resulting in population declines across much of their historical range. While there is relatively limited knowledge of leopards occurring in African rain forests, their abundance and distribution is assumed to be impacted by a combination of several anthropogenic factors, most notably loss of prey and habitat conversion. In this study I used a long-term camera trap array that forms part of the Tropical Ecology, Assessment and Monitoring (TEAM) project - Terrestrial Vertebrate (Camera Trapping) Monitoring Protocol, to estimate the species richness of mammals, the relative abundance of leopard prey species and leopard habitat use in the Nouabalé-Ndoki National Park (NNNP) in the Republic of Congo. I investigated the impact of different environmental and anthropogenic factors on leopard occurrence at two camera trap arrays (a northern and southern cluster) within the NNNP using occupancy modelling. While there were no significant differences in mammalian species richness between the two clusters there was a higher relative abundance of the preferred prey species of leopards in the northern cluster.

A total of 106 leopard photographic events were recorded across all camera traps and all survey years. The top occupancy model produced an average probability of site use (ψ) over all sites of 0.52 ± 0.14 (SE). The covariate specific β -coefficient estimate suggests that leopard occurrence and detectability were positively correlated with both the relative abundance of the blue duiker (*Philantomba monticola*) and the distance to the nearest river ($\beta = 0.062 \pm \text{SE } 0.053$ and $6.55 \pm \text{SE } 10.84$, respectively). Therefore there was no support for the prediction that the probability of leopard habitat use increases with a higher relative abundance of all potential prey species, nor was there support for the prediction that leopard

habitat use would be higher further away from human settlements ($\beta = 3.42 \pm \text{SE } 2.94$). Leopard habitat use was higher in the southern cluster which may be linked to the denser understory that would provide greater cover which is important for improved hunting success in leopards. Together, these results suggest that both the prey species and leopards appear to be thriving within the NNNP with limited evidence of anthropogenic impacts despite an increase in commercial logging and the itinerant bushmeat hunting in the peripheral area. It would be worth expanding the existing camera trap arrays to cover a greater spatial extent within NNNP and hence allow for a more detailed analysis of edge effects and to detect the potential impacts of anthropogenic activities which are predicted to increase in selected villages in the periphery of the park.

1. INTRODUCTION

The leopard (*Panthera pardus*) is the most widespread large felid, occurring across much of sub-Saharan Africa, and much of tropical and temperate Asia (Nowell & Jackson 1996; Sunquist, & Sunquist, 2017; Hunter et al., 2013).

Leopard habitat varies considerably and is associated with tropical forests, grassland plains, deserts, alpine areas (Jacobson *et al.*, 2016; Nowell & Jackson 1996), high mountains as well as the edge of urban areas (Wang *et al.*, 2009; Athreya *et al.*, 2016; Odden et al., 2014). As with other large carnivores, which are seen as keystone species of ecosystems (Gavashelishvili *et al.*, 2008), leopards are considered to play an important role in the functioning of ecosystems and have been shown to regulate prey populations in the African rain forest (Wilting et al., 2006 ; Silver et al., 2008 ; Wangchuk *et al.*, 2004).

Due to the important role leopards play in ecosystem functioning, they are used extensively as biodiversity indicators (Sergio et al. 2006). Leopards also contribute greatly to the ecotourism industry as visitors pay considerable sums of money to view and photograph these cryptic carnivores (Weaver, 2002). In addition, leopards play an undeniable cultural role in many African countries where their skins are used by certain tribes as traditional costume to worship divine entities in the coronation place (Adeola *et al.*, 1992).

Despite the value of leopards, they are at risk of extinction due to numerous threats arising from anthropogenic pressures (Schuette et al. 2013, Sharma et al. 2014). Habitat loss, prey depletion, conflict with humans, poaching for body parts, indiscriminate killing and increasing demand for their skins as cultural regalia are regarded as the major drivers of leopard range declines (Packer et al., 2011; Wolf & Ripple, 2016; Ray, Hunter & Zigouris, 2005; KANIARU 2013; Kissui, 2008; Myers, 1976; Breitenmoser et al., 2017; Odden et al., 2014; Athreya et al. 2011; Ray et al., 2005; Spalton et al., 2016; Breitenmoser et al., 2007;).

Due to the rapid population decrease, leopards are now classified as ‘Near Threatened’ by the IUCN Red List of Threatened Species (Stein *et al.* 2013). It therefore remains crucial to implement more comprehensive research efforts (Jacobson *et al.*, 2016), to assess the leopard’s conservation status across their distribution. Leopard management requires an understanding of habitat use patterns and the evaluation of anthropogenic factors that play a role in determining habitat use patterns (Farris *et al.*, 2015; Mackenzie, 2006).

Central Africa is a useful system for understanding patterns of habitat use and selection by leopards as it includes diverse biomes ranging from rainforests to savannas that sustain a wide range of mammal species including most of the large carnivores (Malhi *et al.*, 2013;).

Knowledge concerning the ecology of wildlife species, in particular the larger predators, is variable in West-Central Africa. While some species, such as lions (*Panthera leo*), have so far received scientific attention (Manthi *et al.*,2018;), less attention has been given to species such as leopards, or striped hyaenas (*Hyaena hyaena*) (Jacobson *et al.*,2016) . Most of these studies have focused on activity patterns, diet, behaviour, and home range use(Odden & Wegge, 2005; Achyut& Kreigenhofer, 2009; Bailey, 1993; Jackson, 1996) with more recent work exploring species habitat use(Simcharoen *et al.*,2008). However, Information concerning habitat utilization by leopards in Central Africa remains scarce (Ngoprasert *et al.*, 2007).

Within rainforests, habitat loss, poaching for body parts, bush-meat harvesting and direct persecution for livestock losses are all regarded as major contributors to current leopard range declines (Nowell *et al.*, 1996; Fahrig, 2003; Wolf & Ripple, 2016; Jacobson *et al.*, 2016; Jackson *et al.*, 2010; Lindsey *et al.*, 2013). These threats are more pronounced

outside protected areas because of hunting and poisoning, which are among the most important causes of death (Swanepoel et al.,2015).

Leopards and human hunters target species within the same size range, which has led to exploitative competition (Henschel et al., 2011) and a shift in leopard preference to smaller prey species. Prey depletion is considered to be one of the greatest threats to the persistence of leopards in rainforest areas (Datta ., 2008) and may explain their disappearance from parts of their former range (Rabinowitz et al.,1987). It is thus important to assess the leopard's status with regard to diverse current threats across its distribution if we are to slow the rate of their decline.

Due to the cryptic nature of leopards, low densities and their largely nocturnal or crepuscular activity patterns (Shehzad et al., 2012; Wang & Macdonald, 2009 ;Jenny & Zuberbühler, 2005)., it is difficult to obtain a robust population estimate using traditional large mammal monitoring methods (Obbard et al.,2010; Hunter and Barrett 20112012), including questionnaires and interviews with local people (Resnick,1999; Ramakrishnan et al., 1999; Athreya et al., 2016), track counts to assess relative abundance (Balme et al.,2009; Wilson& Delahay, 2001), and indirect evidence such as tree scratching and urine scraping(Ghoddousi et al.,2008; Ahlbom et al., 1986 ; Xu et al ,.2008) .

Camera traps have been identified as a reliable and efficient research tools to document rare, elusive animals such leopards (O'Connell et al., 2010). Nowadays, the potential of camera trapping for wildlife population assessment, including both relative and absolute density estimates, is obvious (Glen et al., 2013). Camera traps are non-invasive, minimise disturbance to wild animals and can be deployed without much effort while providing data of considerable conservation value (Schipper., 2007; Mackenzie and Royle 2005) . Camera traps have been used to estimate elusive terrestrial mammal presence and

abundance (Meek et al., 2012; Foster and Humphrey 1995), community structure and diversity and the density of individually recognisable species such as leopards (Ahumada et al., 2011; Otis et al., 1978; Silver et al., 2014). Camera traps have also been used to determine animal activity levels to construct energy budgets (Meek et al., 2012). In addition, and of importance to this study, camera trap data have been utilized to analyse species' habitat use and selection (Borchard et al., 2010; Harris *et al.*, 2010).

In the Republic of the Congo, relatively little is known about the population status or ecology of leopards. Results from a combination of track surveys and camera trapping in all suitable open habitat of Odzala-Kokoua National Park in northern Congo, revealed that the photographic capture rate for leopards was low, compared with camera-trap studies in rain-forest sites in Gabon (Henschel et al., 2014).. Leopards were only recorded at camera-trap stations in dense forest habitat. These observations suggested that leopards make little use of open savanna areas, potentially in response to competitive pressure from others dominant carnivores such as spotted hyenas (*Crocuta crocuta*) (Balme et al, 2007) or because for a stealth hunter access to dense cover is important for improved hunting success (Pitmann et al, 2013).

In this study, I analysed seven years of camera trap data on terrestrial vertebrates from the Tropical Ecology, Assessment and Monitoring (TEAM) project (<http://www.teamnetwork.org>) with the ultimate goal of understanding the predictors of leopard habitat use in the Nouabalé-Ndoki National Park in the Republic of Congo. TEAM is an international network that aims to understand both the underlying dynamics of biodiversity and the responses of biodiversity to major drivers of change (particularly changes in climate and land use or land cover). The TEAM terrestrial vertebrate monitoring protocol provides a standardized and efficient way to monitor the status of species and

communities of vertebrates using camera traps. I investigated the occupancy rates of leopards across two forest sites and examined the effect of landscape features and anthropogenic factors on leopard space use.

Specific objectives of the study were to: (i) determine distribution and estimate occupancy of leopards, (ii) evaluate landscape features and anthropogenic factors affecting habitat use over the whole period of study, (iii) explore and compare leopard habitat use across the two forest sites that differ in socio-economic pressures from the surrounding human communities. Finally, I explore whether selected environmental factors influenced leopard habitat utilization, specifically whether probability of occupancy of leopards varied based on site covariates. Leopard occupancy was predicted to be higher: 1) further away from roads and villages due to the high risk of anthropogenic pressure; 2) in areas where there are higher relative abundances of their preferred prey and 3) in habitat that affords them better cover to ambush prey species.

2. METHODS

2.1. Study Area

The Nouabalé-Ndoki TEAM site was established in 2009 in the Nouabalé-Ndoki National Park (NNNP), a 4,200 km² area of pristine, unlogged rainforest in the northern Republic of the Congo (2°28'N 16°27'E). Created in 1993 and extended in size in 2012, the NNNP is co-managed by the Ministry of Forest Economy and Sustainable Development and an international conservation group, the Wildlife Conservation Society (WCS) with a particular emphasis on local participation and co-management. Recently, a public-private partnership agreement between the two parties has been signed, giving the management of the Protected area to WCS (Ayar *et* Counsell., 2017). Additionally, a partnership between the Ministry, WCS, and the CIB (Congolaise Industriel de Bois) logging company dictates the management of several logging concessions surrounding NNNP wherein reduced-impact logging, law enforcement, and revenue sharing are practised.

The NNNP, together with the neighbouring Lobéké National Park (Cameroon) and Dzanga-Ndoki National Park (Central African Republic), forms the Sangha Tri-National (TNS), a world heritage site covering 7,542 km² of protected rainforest, which is surrounded by a 17,880 km² large buffer zone of mostly sustainably managed logging concessions. The continuous forest of the TNS is largely undisturbed and harbours viable populations of complete faunal and floral communities representing an important sanctuary for threatened biodiversity and a stronghold for threatened large mammals, such western lowland gorillas (*Gorilla gorilla gorilla*), forest elephants (*Loxodonta cyclotis*) and leopards. The TNS contains a diversity of habitats, including terra firma mixed species and monodominant *Gilbertiodendron* forest, swamp forest and a large diversity of natural forest clearings,

commonly known as ‘bais’, which are often associated with the Sangha hydrological system. (Dudley *et al.*, 2010).

The NNNP area of TNS is covered by a rich and diverse forest habitat, providing shelter and high quality food for its rich diversity of terrestrial and aquatic wildlife (Coppolillo *et al.*, 2004). The main forest types in the park are mixed *Sterculiaceae* – *Ulmaceae* semi-deciduous forest, divided into mixed humid forest on terra firma and liana or vine forest, with large patches of monodominant *Gilbertiodendron dewevrei* forest and swamp and flooded forests with a rich diversity of aquatic plants along most of the main rivers. The mixed humid forest on terra firma includes open and closed canopy, both with a high diversity of tree species. Closed canopy forest tends to have a distinct understorey and a high tree density and basal area. Open canopy forest has a low density of trees, and a dense cover of ground vegetation, usually terrestrial herbaceous vegetation, largely in the families’ Marantaceae and Zingiberaceae. Vine forest is relatively similar to the above types of forest but is characterized by dense understorey vegetation composed of lianas and terrestrial herbaceous vegetation and minimal canopy cover. Vine forest is usually close to rivers and sometimes has *Cleistanthus*, *Macaranga*, *Terminalia*, and *Pycnanthus* species. A gregarious *Caesalpinoid* legume, *Gilbertiodendron dewevrei* occurs as monodominant forest. This is a widespread vegetation type in the forest of the Congo Basin with a high tree density and basal area, very dense canopy and little understorey vegetation. This type of forest occurs both beside the watercourses of the area, and in large patches on the inter-fluvial plateaux of the park. The understorey is generally sparse, due to the dense canopy that admits little light. However, some areas have a dense *Haumania dankelmaniana* understorey, often with an abundance of *Palisota* spp. (Commelinaceae). Swamp forest is a mixed-species vegetation forest, usually in the floodplains of rivers, usually of low-canopy vegetation. The common species making up this vegetation type are *Alstonia congoensis*, *Guibourtia demeusei*,

Macaranga schweinfurthii, *Mitragyna (Hallea) ciliate*, *Nauclea pobeguineii* and *Symphonia globulifera*. The forest clearings comprise only a small percentage of the total surface area of the park and the neighbouring forests. They are, however, important for several species of large mammals of the region.

The Nouabalé-Ndoki National Park is home to important populations of forest elephants (*Loxondonta africana*), western lowland gorillas, chimpanzees (*Pan troglodytes*), bongo antelope (*Tragelaphus eurycerus*), and many other endangered large mammals.

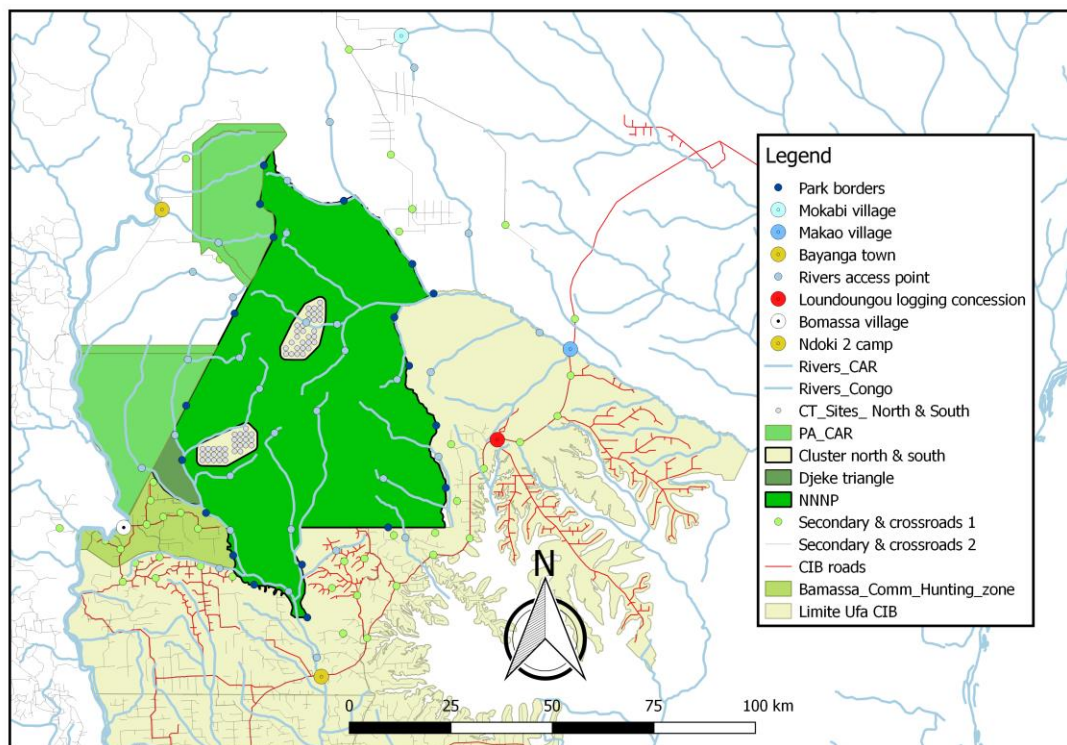


Figure 1. Map of the Nouabalé-Ndoki National Park (NNNP) study area (dark green) showing the location of camera traps (dots within the two yellowish polygons) and the distribution of the different human settlement and crossroads surrounding the park, with Central African Republic Protected Area (CAR_PA), Djéke triangle (a 10,000-hectare forest block which lies about 5km outside of the Nouabalé-Ndoki National Park (NNNP) on the border of the Central African Republic and Republic of Congo. It covers pristine unlogged rainforest set aside by a logging company following negotiations by the wildlife conservation society), the Congolaise Industriel de Bois roads (CIB roads), and limite UfaCIB indicates CIB logging concession boundaries.

2.2. Human activities around the Nouabalé-Ndoki National Park

The NNNP is surrounded by several human settlements occupied by residents of various ethnic groups and socio-economic background, including the Bambenjele and Bangombe Aka hunter-gatherers, and Bantu-speaking farmers, fishermen and immigrants working for the logging concession (Nsonsi *et al.*, 2017). There are six human settlements situated within 50km of NNNP and containing at least 100 inhabitants. Two of the villages, Bomassa and Makao, are both conservation focussed with Bomassa having been established as the NNNP headquarters in 1991. Wildlife populations around Bomassa are consequently relatively intact and poaching events are rare (Maisels *et al.* 2012). Makao is the second base of the NNNP but hosts fewer employment opportunities compared to Bomassa. Recent changes in livelihood activities have occurred since the establishment (5km from the village) of the Thanry-Congo logging camp in 2006, which has about 2,500 inhabitants (Nsonsi *et al.* 2017). Human presence and movement has increased between Makao and Thanry-Congo logging camps, where a large number of Aka people moved to the nearby logging town to provide help as hunters, collectors of non-timber forest products, or helpers on farms for new company employees (Riddell., 2013).. A bushmeat market was established with a related intensification of ivory poaching, leading to a significant reduction in the wildlife population near this village, including elephants (Poulsen *et al.* 2009). Kabo, in the south of the NNNP, is the third village and was originally a logging town which now focusses on agriculture with a conservation project to manage the buffer zone of NNNP. Ndoki 2, is logging concession camp situated in the southeast of the NNNP and it is having been managed by the Congolaise Industriel de Bois (CIB). Loundougou logging camp constructed in 2004 in the south-east of NNNP was established within pristine rain forest and soon attracted local hunters increasing rapidly in size in a few years to result in a local population of over 1000 people.

Unsustainable hunting practices near Loundoungou have resulted in a sharp fall in the number of ungulates in the vicinity of the logging concessions (Nsonsi et al., 2017). Mokabi village situated in the north of the NNNP, represents a real threat to the park, given the high level of pressure from legendary poacher coming from that locality, which constantly making the northern of the NNNP vulnerable. Furthermore, Bayanga, the town in which the Dzanga-Sangha National Park in the Centrafrican republic headquarters is based, has been taken into consideration in this study. Although situated in the Central African Republic, Bayanga town cannot be excluded from human settlement surrounding and negatively affecting the NNNP because of its proximity to that protected area and the high level of hunting in such locality. It is not uncommon to see in Bayanga, hunter, hold more than a hundred steel collars as well as some locally made guns (Mogba et al., 1998).

2.3. Data collection

The 'Reconyx- 'RM45 RAPIDFIRE' camera trap was used throughout the study. In total, 60 cameras were deployed for a minimum of 30 consecutive days each year on a fixed grid with 2km between each one in accordance with the TEAM Terrestrial Vertebrate Monitoring Protocol. Two sites within NNNP, designated 'northern cluster' and 'southern cluster', were used as they differ in vegetation structure and the degree to which they are subjected to anthropogenic pressures, including logging and human traffic. Surveillance sites were first mapped in QGIS version 2.14.0Essen, using various spatial layers to select suitable locations for the camera trap points. The anthropogenic, administrative, land use/cover, and natural characteristics of the sites were then determined. Spaced points or grid cells were generated over the core study area with the goal of subsampling using smaller camera trap arrays (Ahumada et al.,2011). The final two arrays of 30 points or grid cells each were selected to ensure that (1) they sampled a representative portion of the core study area; (2) they were accessible using the access points identified above; (3) they would be accessible

year-round; (4) they were not located along river banks or other edges; and (5), they were located in areas with existing trail systems to minimize disturbance and the need to cut new trails. Camera trap points were extracted from QGIS to produce a list of co-ordinates in decimal degrees using the WGS84 datum. However, the final position of the camera trap was subject to variation as placement was optimised to maximise the probability of capturing photographs of wild animals. Once the camera trap was affixed to a tree the field of view was roughly calculated using the 'Walk Test' mode in the camera trap to ensure optimal placement (height and orientation). Camera trap sites were cleared of anything that could inadvertently obstruct the beam and each camera trap was installed at heights of 30-50 centimetres off the ground. Camera traps were placed beside roads and well-used animal paths. Camera trapping was done in the dry season (months with less than 100 mm of rain (Silver *et al.*, 2004). Data collection varied with year according to the following schedule: 2009 ((December); 2010: (January, February, March, April, November and December); 2011 and 2012 (January, February, March and December); 2013, 2014 and 2015: (January, February, March, April and December); and in 2016 (January, February, March and April). No bait was used to attract animals to the points. At the end of the sampling period, all images were imported from the memory cards to the DeskTEAM program which is a dynamic software package developed by the TEAM network for processing camera trap and other types of data. All images were manually processed to identify animals present in each picture.

3. DATA ANALYSIS

3.1. *Species richness*

Species richness was measured separately for each site surveyed ('northern' and 'southern' cluster) using species accumulation curves (Colwell & Coddington, 1994; Gotelli & Colwell, 2001). Bird species were excluded from species counts, as camera traps are not generally regarded as a good tool for their detection (Brien & Kinnaird).

Accumulation curves were based on 100 randomized replicate runs and then 200 bootstraps using the EstimatesS software version 9.00 (Colwell, 2006). The combined total species richness was compared for both northern and southern clusters using the 95% confidence intervals of the species accumulation curves (Gotelli et al., 2011).

In order to estimate the number of rare species that had not been sampled inside each cluster, the mean incidence coverage estimator of species richness (ICE) was used in addition to the mean abundance coverage estimator of species richness (ACE) (Colwell et al., 2012). The ACE uses data that are relatively tied to 10 or fewer individuals in a sample. As for the associated incidence-based coverage (ICE) estimator, it is based on species found in 10 or less sampled units (Lee and Chao 1994, Chazdon et al., 1998, Magurran 2004).

3.2. *Relative Abundance (RA) of leopard prey species*

Relative abundance (RA) was exclusively calculated for prey species within the most preferred size category 10-40kg (Hayward et al.,2006). In total, six species were selected and considered as leopard preferred prey species. Four of them: peters' duiker (*Cephalophus callipygus*), yellow-backed duiker (*Cephalophus silvicultor*), bay duiker (*Cephalophus dorsalis*), and white-bellied duiker (*Cephalophus leucogaster*), were grouped into a single group named, "red duiker species". The two-remaining species, blue duiker (*Philantomba monticola*) and red river hog (*Potamochoerus porcus*) were independent during analysis.

Relative abundance of leopard prey species was calculated separately for each cluster. Each camera station was treated as a sampling unit, assuming that associated capture rates were independent. Prey species RA was calculated by dividing the number of independent captures at each camera trap station by the number of days the camera trap was active. An independent capture was defined as all photographs of a given species within an hour time period (Rovero et al., 2009).

3.3. Occupancy modelling of leopard habitat use

3.3.1. Predictor variables for use in the occupancy model

The following variables were used as predictors of habitat use: distance (km) to nearest village and secondary/crossroads (both as proxies for human presence), distance to the rivers, relative abundance of leopard preferred prey species, sampling effort (number of days each camera trap was active), cluster ('northern' or 'southern'), season (entire period in which data were collected), and the Normalized Difference Vegetation Indices (NDVI) downloaded from Google Earth Engine available at <https://earthengine.google.com/> (accessed October 2017). The distance of each camera trap to the nearest village and crossroads was calculated using the distance matrix tools from QGIS 2.14.0-Essen, a Geographic Information System software program (Boston,USA).

3.3.2. Occupancy modelling

A likelihood-based occupancy modelling approach (MacKenzie et al., 2002; MacKenzie & Royle, 2005) was used to estimate site occupancy (ψ), and detection probability (p) of leopards. Detection was defined as the capture of independent photographs of leopard taken within a fixed time period (1 hour) by a single camera trap. To increase the detection probability for each sampling period, multiple days were combined into a single survey occasion. Therefore, for each camera trap and for each month within every single

season survey, detections/non-detections was combined over a five-day period for each camera trap station, resulting in six sampling occasions. This sample interval provided the best balance between the number of sampling occasions and the probability of detection in any sampling occasion. Leopard detection histories were constructed for each camera trap site using a standard 'X-matrix format' (Otis *et al.*, 1978). Thus, for each site and each occasion, '1' indicated the detection (photograph) of a leopard, while '0' indicated non-detection during each five-day period. Following this, a two-step modelling process was performed, beginning with a model using occupancy (ψ) covariates only, to compare candidate occupancy models (MacKenzie 2006; Karanth *et al.* 2011) and to identify which model better explained heterogeneity in probability of space use. Models were ranked based on their Akaike Information Criterion (AIC), and were considered to be sufficiently supported when they had a $\Delta AIC < 2$ (Lukacs *et al.*, 2010). Models with $\Delta AIC > 6$ were removed from the analyses (Richards 2005), and all models considered had an AIC weight $> 95\%$. In the case of no single model possessing an AIC weight of over 0.95, a final candidate set of all models with $\Delta AIC < 5$, whose combined weights surpassed 0.95 (95% confidence set), was retained. Model averaging was performed on a set of models with a ΔAIC of up to five, which had a total Akaike weight of approximately 0.98. Following this, the best detection model from the first stage was used to run the candidate set of models to test the effects of detection (p) covariates (Royle & Nichols, 2003). Model fit was assessed by running bootstrap goodness-of fit tests ($n = 1000$ bootstrap samples), using the over dispersion parameter, \hat{c} , calculated in PRESENCE Version 12.7, (Symonds *et al.* 2011). Values of $\hat{c} > 1$ were taken to indicate more variation in the observed data than expected and that the associated AIC values should be adjusted in order to compare models (MacKenzie & Bailey, 2004). Values of $\hat{c} < 1$ were taken to indicate less variation than expected and that the data were not overdispersed, and thus appropriate for use (Burnham & Anderson, 2002). The

relative importance of each covariate was assessed using the sum of all AIC weights of models that included that covariate (Mackenzie & Royle 2005). The sign of the untransformed β -coefficients for each covariate represented the direction of influence of the covariate (i.e. positive or negative). Covariates were deemed to have a robust impact if the β -coefficient $\pm 1.96 \times \text{SE}$ did not include zero (MacKenzie 2006). Site-specific and overall estimates of habitat use were obtained by averaging values (with shrinkage) across models within the 95% confidence set, based on their relative weights (MacKenzie & Bailey 2004) and were used to generate a map of leopard occurrence in QGIS.

4. RESULTS

4.1. Species richness

Over seven sampling seasons at both clusters, a total of 14 995 camera trap-days yielding 423 938 images were accumulated. A total of 37 animal species were recorded, comprising 29 genera, 17 families, and seven orders (Table 1).

Table 1. List of mammal species camera trapped from 2009 to 2015 in the Nouabalé-Ndoki National Park, Republic of Congo with number of photographs in Northern cluster (No. photos.NC); number of photographs in Southern cluster (No. photos. SC); total number of photographs in Northern and Southern clusters (No. photos. NC & SC).

No	Common name	Scientific name	No.photos.SC	No.photos.NC	No.photos.NC & SC
1	Aardvark	<i>Orycteropus afer</i>	192	221	413
2	African elephant	<i>Loxodonta africana</i>	29943	10643	40586
3	African brush-tailed porcupine	<i>Atherurus africanus</i>	508	724	1232
4	Agile mangabey	<i>Cercocebus agilis</i>	498	361	859
5	Water chevrotain	<i>Hyemoschus aquaticus</i>	24	712	736
6	African golden cat	<i>Caracal aurata</i>	327	583	910
7	African palm civet	<i>Nandinia binotata</i>	6	19	25
8	African buffalo	<i>Syncerus caffer</i>	22	223	245
9	Peters' duiker	<i>Cephalophus callipygus</i>	74708	41371	116079
10	Honey badger	<i>Mellivora capensis</i>	223	80	303
11	Moustac bleu	<i>Cercopithecus cephus</i>	592	246	838
12	African civet	<i>Civettictis civetta</i>	0	25	25
13	Bay duiker	<i>Cephalophus dorsalis</i>	16869	7593	24462
14	Giant rat	<i>Cricetomys emini</i>	296	416	712
15	Bongo	<i>Tragelaphus eurycerus</i>	12	5	17
16	Gambian rat	<i>Cricetomys gambianus</i>	249	594	843
17	Giant pangolin	<i>Smutsia gigantea</i>	57	174	231
18	Lowland gorilla	<i>Gorilla gorilla</i>	2274	3440	5714
19	Ribboned rope squirrel	<i>Funisciurus lemniscatus</i>	0	26	26
20	White-bellied duiker	<i>Cephalophus leucogaster</i>	865	93	958
21	Forest hog	<i>Hylochoerus meinertzhageni</i>	329	105	434
22	Blue duiker	<i>Philantomba monticola</i>	68523	66335	134858
23	Long-nosed mongoose	<i>Herpestes naso</i>	53	192	245
24	White-nosed guenon	<i>Cercopithecus nictitans</i>	83	3	86
25	Black-fronted duiker	<i>Cephalophus nigrifrons</i>	41	38	79
26	Black-footed mogoose	<i>Bdeogale nigripes</i>	543	343	886
27	Water mongoose	<i>Atilax paludinosus</i>	168	463	631
28	Leopard	<i>Panthera pardus</i>	1207	2649	3856
29	Red river hog	<i>Potamochoerus porcus</i>	15809	19658	35467
30	Fire-footed rope squirrel	<i>Funisciurus pyrropus</i>	3	16	19
31	Servaline genet	<i>Genetta servalina</i>	287	473	760
32	Yellow-backed duiker	<i>Cephalophus silvicultor</i>	13821	17823	31644
33	Sitatunga	<i>Tragelaphus speki</i>	12	55	67
34	African giant squirrel	<i>Protoxerus stangeri</i>	1573	1170	2743
35	Greater cane rat	<i>Thryonomys swinderianus</i>	0	12	12
36	African white-bellied pangolin	<i>Phataginus tricuspis</i>	30	39	69
37	Chimpanzee	<i>Pan troglodytes</i>	9996	6872	16868
		TOTAL	240143	183795	423938

Species accumulation curves for the whole study period indicated that more images were captured in the northern cluster (240 143 images) compared to the southern cluster (183 795) (Figure 2). However, the number of mammalian species photographs recorded in the southern cluster (37 species) was slightly higher than in the northern cluster (34 species) (Figure 2).

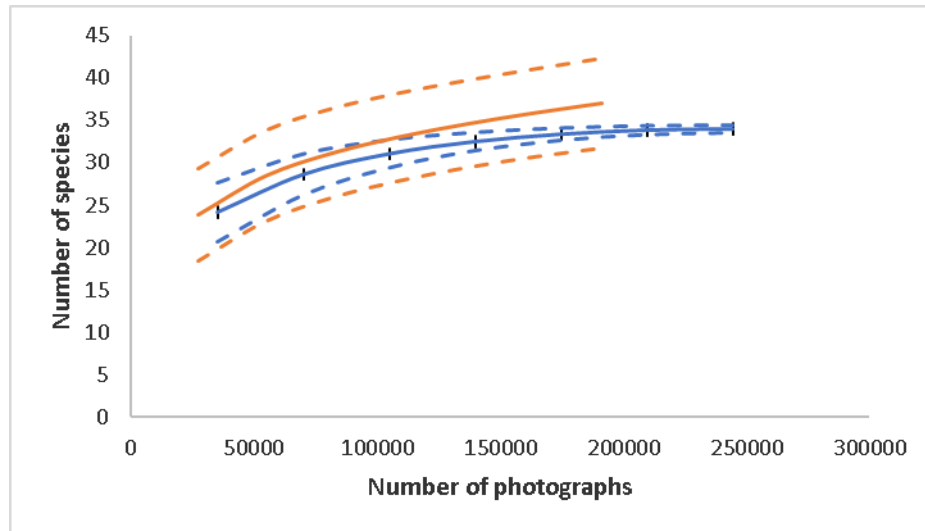


Figure 2. Species accumulation curves with 95% confidence intervals for the wildlife community detected by camera trapping within both northern (blue line) and southern (orange line) clusters in the Nouabalé-Ndoki National Park over the period of 2009-2015. Dashed lines signify the 95% confidence limits for each curve.

Three of the 37 species captured were only recorded in the southern cluster, namely, the ribboned rope squirrel (*Funisciurus lemniscatus*) (26 photographs); african palm civet (*Nandinia binotata*) (25 photographs) and the greater cane rat (*Thryonomys swinderianus*) (12 photographs). The remaining 34 species were found in both the northern and southern clusters. More than 100 photographs were recorded for 27 species, while seven species scored >20 and ≤ 100 images. Finally, three species scored ≤ 20 photographs, all of which were captured within the southern cluster. Finally, three species which had ≤ 20 photographs were all captured within the southern cluster.

Table 2. A comparison of the observed animal species richness (Sobs), Abundance Coverage Estimator (ACE) and Incidence Coverage Estimator (ICE) across both northern and southern clusters within the Nouabalé-Ndoki National Park, based on camera trap data from 2009 to 2015

Sites surveyed	Species richness estimators values across clusters	
	ACE Mean	ICE Mean
Northern cluster	34	34.36
Southern cluster	37	41.52

Although there was a slightly higher number of species recorded in the southern cluster, the large amount of overlap within the 95% confidence intervals of the observed species richness estimators within the both clusters, suggests that these differences were non-significant (Magurran, 2004) (Table 3, 4).

Table 3. EstimateS results of the number of species observed with confidence intervals within the northern cluster, Species estimate: S(est); Species estimate confidence interval Lower Bound: S(est) 95%CI Lower Bound; Species estimate confidence interval Upper Bound: S(est) 95%CI Upper Bound.

Seasons	Individuals (computed)	S(est)	S(est) 95%	
			CI Lower Bound	CI Upper Bound
2009	34890	24.1	20.6	27.7
2010	69780	28.6	26.2	31.1
2011	104670	31.1	29.4	32.7
2012	139561	32.5	31.4	33.6
2013	174451	33.4	32.6	34.1
2014	209341	33.9	33.3	34.4
2015	244231	34.0	33.5	34.5

Table 4. Estimates of the number of species observed with confidence intervals within the southern cluster. Species estimate: S(est); Species estimate confidence interval Lower Bound: S(est) 95%CI Lower Bound; Species estimate confidence interval Upper Bound: S(est) 95%CI Upper Bound.

Seasons	Individuals (computed)	S(est)	S(est) 95%	
			CI Lower Bound	CI Upper Bound
2009	27287	23.9	18.5	29.3
2010	54573	28.4	23.1	33.8
2011	81860	31.1	25.9	36.4
2012	109147	33.1	27.9	38.2
2013	136434	34.6	29.4	39.7
2014	163720	35.9	30.7	41.1
2015	191007	37.0	31.7	42.3

4.2. Relative abundance (RA) of leopard prey species

In total, 88 848 independent photographs of selected leopard prey species were obtained over the study period within both clusters. Pooling all sites, the most photographed prey species were: Blue duiker with 74785 photographs, followed by Peters' duiker with 9214 photographs, Yellow-backed duiker with 2163 photographs; Bay duiker with 2041 photographs, Red river hog with 525 photographs, and White-bellied duiker with 120 photographs. While all selected prey species were captured in all seasons, the White-bellied duiker was the only prey species recorded in only five of the seven years of the study period and was detected within each of the two clusters between 2011 and 2014. In 2015, White-bellied duikers were only photographed within the northern cluster. The remaining prey species were found in both clusters and detected in all years. Approximately 90.2% of all prey species photographs were taken in the northern cluster suggesting that leopard prey species are much more abundant within the northern cluster (Figure 3).

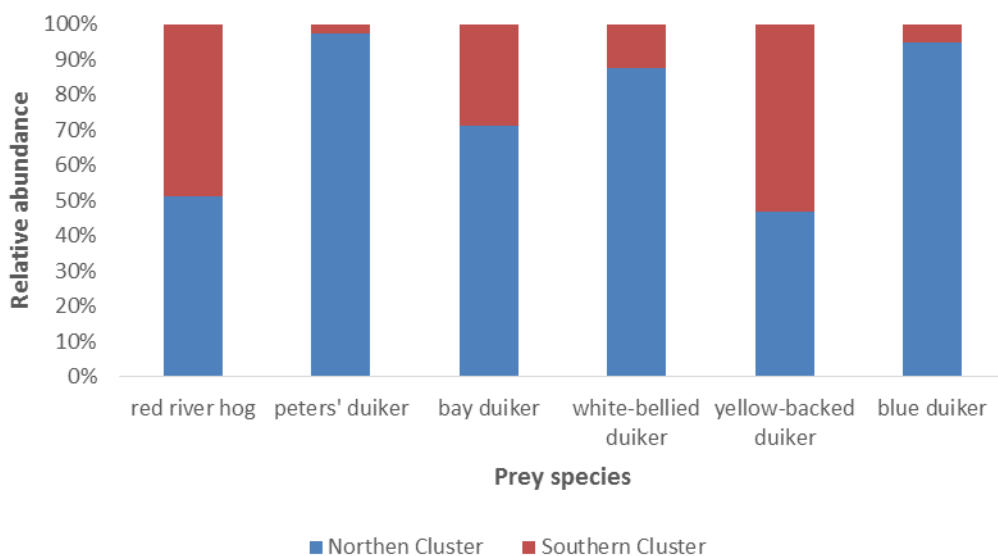


Figure 3. The mean relative abundance (RA) of select leopard prey species, based on camera trap data from 2009 to 2015 in the NNNP, within the Northern and Southern clusters.

4.3. Occupancy modelling of leopard habitat use

The effective sampling effort of 14995 camera trap days resulted in 106 leopards detections at 44 locations over 7431 and 7564 days within the northern and southern clusters, respectively in the NNNP (Table 5).

Table 5. Number of photographs and stations where leopards were captured in each cluster with trap effort and leopard independent captures over the whole period of study.

Cluster	Total number of locations	Number of locations where leopard photographed	Trap effort over seven years	Number of independent photographs
North	30	24	7431	65
South	30	20	7564	41
Total	60	44	14995	106

In the first stage of modelling, various combinations of occupancy (ψ) covariates were tested while keeping detection (p) constant. Ranking the models according to AIC score, resulted in ten candidates models which had a Δ AIC of less than two, with “ ψ (.), p (.)”, (the null model assuming that occupancy and detection constant across the study site), ranking highest (AIC weight =0.0967) (Table 6). The combined AIC weight set of the ten top-ranked models was 0.57, suggesting a 57% chance that one of these ten models contained the best-performing model (Symonds & Moussali 2011). However, the low AIC weights of these models suggest that none of these were very well-supported. Although significant, the occupancy covariates β -coefficient estimated that no environmental covariates significantly affected the probability of leopard use (β = -0.298573 \pm SE 0.316504).

Table 6. Summary of model selection outputs using occupancy(ψ) covariates only while keeping detection (p) covariates constants, with Akaike's information criterion (AIC), delta AIC (Δ AIC), Akaike weight (AIC wgt), model likelihood, no. of parameters (k), 2log-likelihood (LL). Covariates include: blue duiker (M); red duiker (RD); red river hog (P); Nearest distance to villages (DV); Nearest distance secondary & crossroads (DC), Nearest distance to Park borders (PB), Distance to rivers (DR).

Model	AIC	Δ AIC	AIC wgt	Model Likelihood	K	LL
$\psi(\cdot),p(\cdot)$	814.95	0	0.097	1.000	2	810.95
$\psi(\text{RD}+\text{M}),p(\cdot)$	815.1	0.15	0.090	0.928	4	807.1
$\psi(\text{M}+\text{P}),p(\cdot)$	816.19	1.24	0.052	0.538	4	808.19
$\psi(\text{M}+\text{DV}),p(\cdot)$	816.21	1.26	0.052	0.533	4	808.21
$\psi(\text{M}+\text{Dist_DC}),p(\cdot)$	816.21	1.26	0.052	0.533	4	808.21
$\psi(\text{M}+\text{Dist_PB}),p(\cdot)$	816.21	1.26	0.052	0.533	4	808.21
$\psi(\text{M}+\text{DR}),p(\cdot)$	816.21	1.26	0.052	0.533	4	808.21
$\psi(\text{P}+\text{Dv}),p(\cdot)$	816.21	1.26	0.052	0.533	4	808.21
$\psi(\text{DV_PV}),p(\cdot)$	816.86	1.91	0.037	0.385	4	808.86
$\psi(\text{DC}),p(\cdot)$	816.91	1.96	0.036	0.375	3	810.91
$\psi(\text{DR}+\text{M}+\text{RD}),p(\cdot)$	816.95	2	0.036	0.368	5	806.95
$\psi(\text{PB_}+\text{M}+\text{RD}),p(\cdot)$	816.96	2.01	0.035	0.366	5	806.96
$\psi(\text{RD}+\text{M}+\text{P}),p(\cdot)$	817.07	2.12	0.034	0.347	5	807.07
$\psi(\text{P}+\text{DC}),p(\cdot)$	817.45	2.5	0.028	0.287	4	809.45
$\psi(\text{P}+\text{PB}),p(\cdot)$	817.55	2.6	0.026	0.273	4	809.55
$\psi(\text{P}+\text{DR}),p(\cdot)$	817.57	2.62	0.026	0.270	4	809.57
$\psi(\text{DC}+\text{DV}),p(\cdot)$	817.8	2.85	0.023	0.241	4	809.8
$\psi(\text{DR}+\text{M}+\text{P}+\text{RD}),p(\cdot)$	817.95	3	0.022	0.223	6	805.95
$\psi(\text{RD}+\text{P}),p(\cdot)$	818.12	3.17	0.020	0.205	4	810.12
$\psi(\text{DV}+\text{DR}),p(\cdot)$	818.14	3.19	0.020	0.203	4	810.14
$\psi(\text{RD}+\text{PB}),p(\cdot)$	818.3	3.35	0.018	0.187	4	810.3
$\psi(\text{RD}+\text{DR}),p(\cdot)$	818.3	3.35	0.018	0.187	4	810.3
$\psi(\text{RD}+\text{DC}),p(\cdot)$	818.31	3.36	0.018	0.186	4	810.31
$\psi(\text{RD}+\text{DV}),p(\cdot)$	818.31	3.36	0.018	0.186	4	810.31
$\psi(\text{DC}+\text{DR}),p(\cdot)$	818.53	3.58	0.016	0.167	4	810.53
$\psi(\text{DR}+\text{P}+\text{RD}),p(\cdot)$	818.67	3.72	0.015	0.156	5	808.67
$\psi(\text{PB}+\text{P}+\text{RD}),p(\cdot)$	818.68	3.73	0.015	0.155	5	808.68
$\psi(\text{PB}+\text{DV}+\text{RD}),p(\cdot)$	818.76	3.81	0.014	0.149	5	808.76
$\psi(\text{DR}+\text{DV}+\text{RD}),p(\cdot)$	819.83	4.88	0.008	0.087	5	809.83
$\psi(\text{DR}+\text{PB}+\text{RD}),p(\cdot)$	820.3	5.35	0.007	0.069	5	810.3
$\psi(\text{PB}+\text{RD}),p(\cdot)$	820.3	5.35	0.007	0.069	5	810.3
$\psi(\text{PB}+\text{DR}+\text{RD}),p(\cdot)$	820.89	5.94	0.005	0.051	5	810.89
$\psi(\text{M}+\text{S}),p(\cdot)$	825.78	10.83	0.000	0.004	10	805.78
$\psi(\text{S}+\text{RD}+\text{M}),p(\cdot)$	825.85	10.9	0.000	0.004	11	803.85
$\psi(\text{S}),p(\cdot)$	826.75	11.8	0.000	0.003	9	808.75
$\psi(\text{P}+\text{S}),p(\cdot)$	827.21	12.26	0.000	0.002	10	807.21
$\psi(\text{DV}+\text{S}),p(\cdot)$	827.67	12.72	0.000	0.002	10	807.67
$\psi(\text{DC}+\text{S}),p(\cdot)$	827.96	13.01	0.000	0.002	10	807.96
$\psi(\text{RD}+\text{S}),p(\cdot)$	828.28	13.33	0.000	0.001	10	808.28
$\psi(\text{DR}+\text{S}+\text{RD}),p(\cdot)$	830.16	15.21	0.000	0.001	11	808.16
$\psi(\text{PB}+\text{S}+\text{RD}),p(\cdot)$	830.26	15.31	0.000	0.001	11	808.26

Effort, NDVI, and both northern and southern clusters were included as relevant detection variables through different combinations with the candidate set of models previously selected in the first stage of modelling. The results suggested that “ ψ (Monticola+Dist_rivers), p (NDVI)”, (hereafter “ ψ (M+DR), p (N)”), best explained heterogeneity in detection probability (AIC weight =0.804) (Table 7). No model was well-supported, and consequently a set of models with a Δ AIC of less than six was included in model averaging (Table 7). The covariate specific β -coefficient estimate suggests that leopard use and detectability correlate positively with both increasing relative abundance of Blue duiker and increasing distance to rivers (β =0.062 \pm SE 0.053 and 6.55 \pm SE 10.84, respectively). This means that as the abundance of Blue duiker increases, the probability of space use by leopard increases. Similarly, as the distance to the river increases, there is an increased chance of detecting leopards (Table 7). In contrast, NDVI did not have any discernible effect on leopard habitat use (β =-0.366163 \pm SE 0.086733). The model averaged ($\sum w > 95\%$) probability of site use (ψ) over all sites was 0.52 \pm SE 0.14, indicating that leopards utilized 52% of the surveyed area. This estimate reveals that the naïve estimates for the site use (0.19), represents a 33% underestimation of the actual proportion of the leopard habitat use. There was no evidence of a lack of fit ($P=0.47$) or over dispersion ($\hat{c}=0.65$), as indicated by the goodness of fit test for the global standard occupancy model. There was therefore no evidence of support for the prediction that the probability of leopard habitat use increases in the habitat with higher capture rate of potential prey (duikers and red river hog) as well as the prediction that leopard habitat uses decreases with proximity to human settlements (β =3.42 \pm SE 2.94).

Table7. Summary of model selection results indicating the effect of detection (p) covariates (while keeping ψ fixed) in determining probabilities of leopard detection and site use, with Akaike's information criterion (AIC), delta AIC (Δ AIC), Akaike weight (AIC wgt), model likelihood, no. of parameters (k), 2log-likelihood (LL). Covariates include: blue duiker (M); red duiker (RD); red river hog (P); Nearest distance to village(DV); Nearest distance secondary & crossroads (DC); seasons (S); NDVI(N); Effort(E); Clusters 1&2 (C), Nearest distance to Park borders (PB), Distance to rivers(DR).

Model	AIC	Δ AIC	AIC wgt	Model Likelihood	K	LL
ψ (M+DR),p(N)	812.26	0	0.085	1.000	5	802.26
ψ (M+DC),p(N)	812.61	0.35	0.071	0.840	5	802.61
ψ (M+DV),p(N.)	812.61	0.35	0.071	0.840	5	802.61
ψ (M+DB),p(N)	812.78	0.52	0.065	0.771	5	802.78
ψ (DV+DB),p(N)	813.24	0.98	0.052	0.613	5	803.24
ψ (DV+DR),p(N)	813.6	1.34	0.043	0.512	5	803.6
ψ (RD+DV),p(N)	813.65	1.39	0.042	0.499	5	803.65
ψ (P+DV),p(N)	813.87	1.61	0.038	0.447	5	803.87
ψ (DC+DV),p(N)	813.96	1.7	0.036	0.427	5	803.96
ψ (DC+DR),p(N)	814.08	1.82	0.034	0.403	5	804.08
ψ (P+DC),p(N)	814.15	1.89	0.033	0.389	5	804.15
ψ (RD+DR),p(N)	814.17	1.91	0.033	0.385	5	804.17
ψ (RD+PB),p(N)	814.27	2.01	0.031	0.366	5	804.27
ψ (P+M+RD),p(N)	814.38	2.12	0.029	0.347	6	802.38
ψ (M+P),p(N)	814.58	2.32	0.027	0.314	5	804.58
ψ (P+PB),p(N)	814.86	2.6	0.023	0.273	5	804.86
ψ (P+DR),p(N)	814.88	2.62	0.023	0.270	5	804.88
ψ (P+DC),p(E)	814.95	2.69	0.022	0.261	2	810.95
ψ (.),p(CN+CS)	815.19	2.93	0.020	0.231	4	807.19
ψ (M+DV),p(E)	815.72	3.46	0.015	0.177	5	805.72
ψ (RD+M+P),p(N)	815.72	3.46	0.015	0.177	6	803.72
ψ (M+DR),p(E)	815.75	3.49	0.015	0.175	5	805.75
ψ (M+DC),p(E)	815.75	3.49	0.015	0.175	5	805.75
ψ (M+DC),p(E)	815.77	3.51	0.015	0.173	5	805.77
ψ (DR+P+RD),p(N)	816.12	3.86	0.012	0.145	6	804.12
ψ (PB+P+RD),p(N)	816.21	3.95	0.012	0.139	6	804.21
ψ (RD+P),p(N)	816.26	4	0.012	0.135	5	806.26
ψ (DV+PB),p(E)	816.35	4.09	0.011	0.129	5	806.35
ψ (M+P),p(E)	816.51	4.25	0.010	0.119	5	806.51
ψ (RD+M),p(N)	816.52	4.26	0.010	0.119	5	806.52
ψ (RD+M),p(E)	816.58	4.32	0.010	0.115	5	806.58
ψ (PB+M+RD),p(E)	816.84	4.58	0.009	0.101	6	804.84
ψ (P+DV),p(E)	817.45	5.19	0.006	0.075	5	807.45
ψ (RD+M+P),p(E)	817.53	5.27	0.006	0.072	6	805.53
ψ (RD+DV),p(E)	817.62	5.36	0.006	0.069	5	807.62

4.4. Probability of occurrence and proportion of habitat use by leopards at camera trap stations and within each cluster

Leopard habitat utilization was unequally distributed across the two clusters in NNNP with leopard space use slightly in the southern than northern cluster (Figure 4).

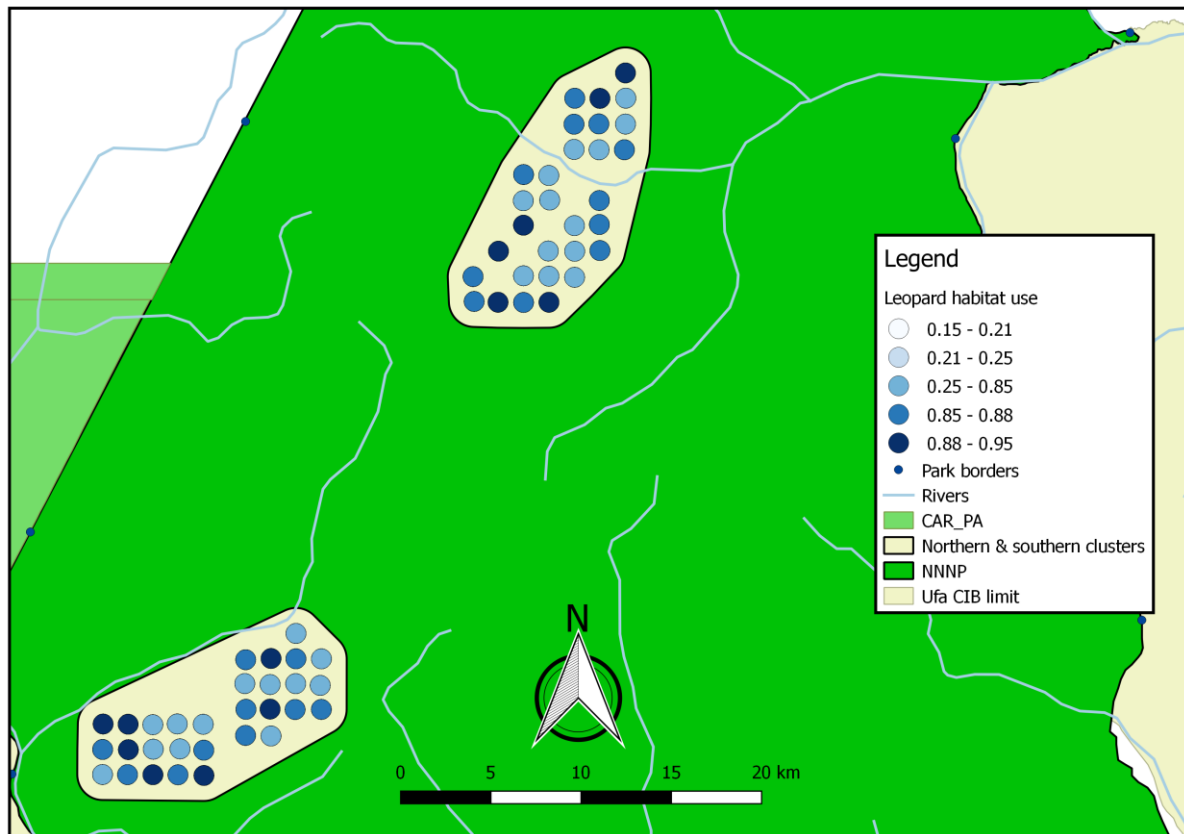


Figure 4: Site-specific output from seven years camera trapping showing spatial variation in leopard space use (based on the averaged model ($\sum w = 1$)), with watercourses (blue line) occurring outside and inside the protected area surrounding therefore both northern and southern clusters, parks border (blue dots along the park peripheric).

In Table 8, higher leopard space use (88-95%) was recorded at seven camera stations within the southern cluster, whereas six camera stations captured the same proportions (88-95%) of leopard site utilization in the northern cluster. Eighty percent of the camera stations in the northern cluster had between 85 and 88% use by leopards compared to approximately 77% in the southern cluster.

Table 8. Proportion of leopard space use at camera trap stations and within both northern and southern cluster across the period of study, showing five level of space use, ranging from 0.15 to 95%.

Leopard habitat use	Number of camera trap station	
	Nothern cluster	Southern cluster
0.15-0.21	0	0
0.21-0.25	0	0
0.25-0.85	0	0
0.85-0.88	24	23
0.88-0.95	6	7
Total	30	30

5. Discussion

Species richness

A total of 37 mammal species, including leopards, were detected at the 44 camera trap locations across the seven-year study period in the Nouabalé-Ndoki National Park. These estimates are high and similar to other studies that have estimated species richness of mammals in tropical forests with for example 32 species being recorded in the Udzungwa Mountains of south-central Tanzania (Rovero *et al.*, 2014). There was no significant difference in the species richness of mammals between the north and south clusters while the relative abundance of wildlife was substantially higher in the north cluster. This result was unexpected given that the northern section of NNNP is widely regarded as being more impacted by human activities (Boukoulou *et al.*, 2010) ;. Increased logging activities and access roads along the northern boundary have been linked to an increase in illegal bushmeat hunting and a significant decline in the neighbouring wildlife population (Riddell, 2013) .

By contrast wildlife in the south section of the park is less impacted by poaching (Maisels *et al.*, 2012) as human settlements are far and the nearest village Bomassa is benefiting more from conservation and people show better attitudes to wildlife conservation (Nsonsi *et al.* 2016).

Ruiz *et al.* (2005) revealed that species richness estimates were affected by vegetation type in the areas surveyed. However, it is possible but unlikely that these trends reflect differences in the detectability of wildlife species in the two clusters. The vegetation within the northern cluster is characterized by the mixed open understorey forest, which does not restrict animal movement as much as the mixed closed understorey forest typical of the southern section. A closed understorey is more likely to force animals onto paths and roads when they are travelling. Biases in detection because of camera placement relative to habitat

type and presence of paths/roads have been recorded in other studies including the importance of effort, spacing and trap placement (Mohamed *et al.*, 2013). However, given camera traps were preferentially placed on paths or roads it follows that detection rates should have been higher for this reason in the southern section. Importantly the camera traps were successful in detecting a number of species that are poorly detected using more traditional survey methods such as line transects (Rovero *et al.*, 2014). For example, *Cercocebus agilis* (is an IUCN- least Concern monkey with a wide distribution range. Generally, arboreal, the species spends between 15 and 20% of its total on the ground (Shah, 2003). Despite this, the species was recorded in 859 independent photographs. Among other commonly detected species, the relatively high ranking of *Cercopithecus cephus* (838 pictures) is also surprising given this is known as an arboreal dweller. The pool of the least - detected species contains a diverse suite of common (e.g. *Tragelaphus spekii*, *Tragelaphus eurycerus*, *Civettictis civetta*), animals found in the NNNP.

Relative abundance of leopards prey species

The relative abundance of preferred leopard prey species was higher in the northern cluster of the park with 90.2% of all prey species being detected here. Peters' duiker (*Cephalophus callipygus*) and blue duiker (*Philantomba monticola*) were the most commonly detected prey among all species. In fact, Peters's duiker was 88% more likely to be detected in the northern cluster than in the south. On the other hand, the blue duiker was the most abundant species, with 3.68% of these detected in the south, while the relative abundance of other prey was less than 1%. These results suggest that ungulates avoided areas of increased net productivity that are highly utilized by leopards (southern cluster), instead favouring habitat types with less vegetation cover (northern cluster). A similar pattern was previously reported by Creel *et al.*, (2014) who found that ungulate distributions are primarily determined by the risk of predation from a single dominant predator in a given area.

Avoidance of the southern cluster by ungulates could therefore be primarily driven by the high risk of being stalked and caught by leopard due to the high vegetation density. The northern cluster by contrast is more sparsely vegetated and hence provides less cover for leopards. Avoidance of high predation risk areas is a common strategy of many prey species (Thomson *et al.*, 2006) and is a well-established antipredator strategy in forest habitat (Maria *et al.*, 2011).

Habitat use

I found that habitat use by leopards in the NNNP was strongly influenced by a combination of ecological and anthropogenic factors with top-ranked models suggesting that no individual covariate has a strong significant impact on leopard habitat use (see Table 6, 7). Stephens and Krebs (1985) argued that, the selection of habitat by carnivores is driven mainly by the availability of prey in conjunction with landscape attributes. This is in line with the findings of this study with leopard habitat use positively correlated with the abundance of the blue duikers specifically (*Philantomba monticola*), as well as the proximity to rivers. This study confirms the importance of water availability in terms of habitat suitability for leopards (Mosheh *et al.*, 2009). Water can be seen as a passive trap for prey, strongly influencing leopard habitat use. The river system within the southern cluster is an important water supply for wildlife, attracting leopard prey species. A similar pattern was observed in Tanzania's Ruaha Landscape, with leopard favouring habitats close to watercourses (Abade *et al.*, 2014). Furthermore, Aritra *et al.*, (2017) who studied leopard habitat requirements in Golestan National Park reported that leopard distribution was positively linked to both prey density and proximity to watercourses. Although the occurrence of prey species was higher in the north than the south cluster, this was not linked to an increase in the leopard's use of the northern cluster. Balme *et al.*, (2007) reported that leopard habitat preference is strongly influenced by their relative ability to catch prey rather than the absolute abundance of prey

with leopards tending to avoid less densely vegetated areas as this decreases their hunting success (Hayward *et al.*, 2006).

There was no support for the prediction that leopard habitat use would be higher further from human settlements. Although not present in the best model, “distance to the village” was included in the highest-ranked models according to AIC, with a small but positive effect on leopard habitat use. This suggests that in NNNP leopards occupancy is not affected by human activity. Similar findings have been found for leopard in Indonesia (Gunawan *et al.*, 2017) and many other parts of Africa (Pitman, 2012) where leopard frequently prey on domestic livestock.

6. CONCLUSION AND RECOMMENDATIONS

Estimates of the status of wild animal species are critical for guiding conservation decisions and assessing the success of conservation initiatives (Gray & Prum 2012). This study provides estimates of species richness, relative abundance estimates and the predictors of leopard habitat use within the Nouabalé-Ndoki National Park. Species richness estimates for the park based on this survey are healthy and there is little evidence that anthropogenic activity on the park edges particularly in the North are having an impact on the mammalian fauna. This demonstrates that law enforcement activities have been very effective within the NNNP borders during the study period. Thus, NNNP remains an important refuge for wildlife and can act as a source for the periphery in the future.

Leopards were recorded in both the northern and southern camera trap clusters of the park across all years and at most camera stations. Probability of use was higher in the Southern cluster where the abundance of prey species was lower. This unexpected result suggests that factors other than abundance are important for influencing leopard presence in

NNNP. I propose that higher use of the southern cluster by leopards reflects the greater ground cover that provides them with cover when stalking prey.

A limitation of the current study is the restricted spatial extent of the camera trap arrays. With camera traps clustered in two small regions of the entire park it is difficult to determine the effects of distance to the park edge, villages or important landscape features on leopard use. Camera traps should ideally have been placed more evenly across the Ndoki landscape of the NNNP with analyses conducted at the level of individual camera traps rather than entire clusters to provide a resolution more applicable to managing threats to wildlife in the park and its periphery. In addition, a better spatial and temporal spread of camera traps would allow for higher recaptures of individual leopards and with that the opportunity to use the more informative, from a management perspective, density estimates that are derived from spatially explicitly capture- recapture modelling approaches.

This study represents an important attempt to assess the species richness of wildlife in the Nouabalé-Ndoki National Park and leopard use in particular using an occupancy framework. Managers of the NNNP will be heartened by the finding that mammalian species richness is high and proximity to known areas of bushmeat harvesting are not impacting on either diversity or abundance estimates. Long-term monitoring of these clusters in addition to extending the area under surveillance would be valuable contributions to assessing anthropogenic changes to the park and the surrounding areas. It is hoped that the data presented here will provide a valuable baseline from which future comparisons can be drawn and hence interventions put in place should declines in species richness or leopard use be apparent in future.

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