Estimating Population Size, Density, and Occupancy of Lions (*panthera leo*), Leopards (*p. Pardus*), and Servals (*leptailurus serval*) Using Camera Traps in the Niokolo Koba National Park in Senegal, West Africa

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Abstract

Carnivore are undoubtedly among the most threatened of the mammal species in Africa because of the low density at which they occur and their large home range requirements that do not match with human propensity to develop and alter wildlife habitat. However, the degree of threat is unevenly distributed within the continent, with western and central African carnivores being the most threatened and the least studied. I estimated population size, density, and proportion of area occupied in relation to environmental factors of one medium-size (serval – *Leptailurus serval*) and two large carnivores (lion – *Panthera leo* and leopard – *P. pardus*) in the Niokolo Koba National Park, Senegal, West Africa, using remote camera surveys and both traditional (CR), spatially explicit capture-recapture (SECR) techniques for servals and leopards, and non-spatial (MR) and spatial mark resight (SMR) methods for lions. Lions selected optimal sites with both high tree density and prey activity; leopards occupied areas with high tree density but with less prey activity; and servals selected habitats with more dense canopy cover where leopards were absent. The presence of lions was favorable to serval presence, as we presume leopards avoid lions, although we did not have strong evidence to support it. Moreover, the half mean maximum distance moved (½ MMDM) method under CR methods appeared to overestimate leopard and serval density while full MMDM estimates were close to SECR methods density estimates. For lions, both ½ MMDM and full MMDM methods in MR framework overestimated density whereas the SMR method resulted in more reasonable estimates, especially in light of previous assessments of lion densities in West Africa.. These results are of high importance for conservation and management purposes of the imperiled Niokolo Koba carnivore community.

Dedications

Praise be to Allah, the merciful; peace and blessings upon his Prophet Muhammad.

I would like to dedicate this work to my wife Fama and kids Mahmoud and Amina, to my parents, and my brothers and sisters. It was very hard to be far from you all these years. I know it was hard for you too, particularly for my son and daughter who always asked me when I would be back. I love you so much!

Acknowledgements

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Chapter 1: Introduction, background, and status of carnivores and carnivore research, with particular focus on 3 target species, in the Niokolo Koba National Park, Senegal

Introduction

Africa harbors the largest variety of mammal species in the world possibly due to its large size and relative geological stability (Bothma and Walker 1999). In fact, the African continent comprises a large selection of biomes including rainforests, woodlands, deserts and savannahs that are suitable for a wide range of mammals (Bothma and Walker, 1999). However, the effects of habitat loss and fragmentation due to agricultural development and urbanization combined with direct hunting including poaching and retaliatory killing (Karanth et al. 2009; Barbault & Sastrapradja 1995) are drastically reducing mammal richness, thus restricting some species to very patchy habitats that cannot ensure their viability.

Large carnivore species are undoubtedly among the most threatened mammals in Africa because of their naturally low densities and their large home range requirements that conflict with human propensity to develop and alter wildlife habitat. However, the degree of threat is unevenly distributed within the continent. Southern and eastern African large carnivores are relatively well protected and conserved compared to western African carnivores. For instance, the lion (*Panthera leo*) is listed in the IUCN Red List as "regionally endangered" in West Africa while it is "vulnerable" overall (Bauer and Nowell, 2004; IUCN 2009).

Similarly, Ray et al. (2005) demonstrated that carnivore research displays a strong geographic bias, with most of the studies occurring in eastern and southern Africa. One of the main reasons lies in the fact that carnivore populations in western Africa occur at lower densities – 1 to 3 lions per 100 km^2 (Bauer and Van Der Merwe 2004; Riggio et al. 2013) compared to 2.6 and 8 lions per 100 km^2 in Eastern and Southern Africa respectively (Riggio et al. 2013). Fortunately, researchers have shown an increasing interest in West African large carnivores during the last two decades, with a strong focus on single species, principally the felids or wild cats.

Even with this new interest in West African species, carnivores of Niokolo Koba National Park (NKNP) in Senegal, one of the largest protected areas in West Africa, are poorly studied. The few existing studies focused mainly on lions even though several censuses of mammal species populations were conducted in the past. However, the methodologies used for these censuses were more adapted for mammalian herbivores than for carnivores. For instance, the last large-scale census conducted in May 2006 by the African Parks Foundation resulted in an alarmingly low number of mammal species. This lead to a large controversy about the methods used (terrestrial counts and aerial surveys using line transect methods) and specifically their inefficiency in estimating carnivore population sizes. Despite these protests, Niokolo Koba National Park was listed as a World Heritage site of UNESCO classified as "in Danger" one year later mostly because of these dramatically low species detection results.

To date, no other large-scale study had been conducted to address the weaknesses of previous studies despite the desire of the Senegalese Wildlife Department[1] to invest more effort in conserving the world heritage site. Managing such a huge park (9,130 km^2) requires better knowledge of population ecology of target species in order to implement effective conservation strategies designed to reverse the decline in mammal species richness Directly studying large carnivores is an efficient way to achieve that goal as most large carnivores function as both umbrella and keystone species, requiring large areas and having a crucial role in maintaining ecosystem structure, thus preventing shifts in habitat and species extinction via trophic cascades (Noss 1996; Terborgh et al. 1999, Terborgh et al. 2001). Therefore targeting carnivores for study can lead to more efficient and inclusive strategies that can aid in conserving a large number of other species within the park.

My proposed study planned to fill knowledge gaps regarding carnivore ecology by conducting surveys using methods more appropriate for carnivore species. Herein, I focused specifically on two large carnivores: lions (*Panthera leo*) and leopards (*Panthera pardus*), and one medium-size carnivore, the serval (*Leptailurus serval*). I used camera-trapping methodology known to be a suitable technique to estimate carnivore abundance and density through both traditional capture-recapture and spatially explicit capture recapture frameworks. I will also estimate occupancy of the three target species across the study area and use habitat and prey

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[1] Officially Direction des Parcs Nationaux du Sénégal (DPNS)

covariates to predict occupancy. In addition, the camera trapping methodology will yield substantial information on presence and habitat use for many smaller carnivores and herbivores simultaneously, providing an inventory of other species across the Niokolo Koba National Park.

This study has three objectives:

Objective 1: Estimate lion, leopard, and serval occupancy and their co-occurrence across the study site by examining site covariates such as micro-habitat features, prey trap success, and the presence of the other target species.

Objective 2: Estimate and compare the abundance and density of leopards and servals using camera-trap data using 4 capture-recapture estimation methods (2 non spatial and 2 spatial) in the Niokolo Koba National Park.

Objective 3: Estimate lion density using mark-resight models in a non-spatial and spatial framework in the Niokolo Koba National Park

Study site

The Niokolo Koba National Park (NKNP) was created in 1954 by the French colonial administration, and was enlarged four times by the Senegalese administration. The park is located in south-eastern Senegal, between 12°30' and 13°20' North and 18°30' and 13°42' West, in a well-watered region, unlike most parts of the country (Fig. 1.1). Its creation and successive extensions were radical and controversial as numerous villages were relocated and sometimes forcibly driven out by the Government, as a result of the expanding conservationist doctrine at that time (DPNS 2000).

The NKNP covers 9,130 km^2 and presents heterogeneous vegetation types, generated by complex soil and geologic formations that are distributed in three types of terrain: valleys, plateaus, and hills with the highest elevation at Mount Assirik – 311 meters (Fig. 1.2). The climate is of Sudanian type with a rainy season from June to October. The average annual rainfall ranges from 900 to 1,200 millimeters and the temperature from 25°C in December to 33°C in May (DPNS, 2000). The climate creates a transition vegetation type between Sudano-Guinean savanna and Guinean savanna. All the streams of the park belong to the catchment of

the Gambia River which crosses the park from southeast to northwest. The main tributaries are Niokolo Koba, Koulountou, and Nieriko. In addition to these streams, some permanent and temporary ponds and pools play an important role in water and fresh grass supply for the wildlife.

The canopy is mainly composed of deciduous species. Four types of savanna are clearly differentiated within the park (DPNS 2000), in addition to other types of vegetation cover as well as marshes. The main vegetation covers are:

- *Herbaceous* savannah: characterized by a continuous herbaceous strata dominated by *Andropogon gayanus*.

- *Shrub savannah:* located in the plateaus and hill slopes with a continuous herbaceous strata scattered with shrubs. The dominant plant family is Combretaceae.

- *Tree savannah:* also located in the plateaus and hill slopes with a tree cover of 5 to 25% (Adam, 1965) and a continuous closed herbaceous layer.

- *Wooded savannah:* located in the depressions between the hills and along the valleys and composed of trees and shrubs that cover 25 to 50% (Adam 1965). The trees can reach 7 to 12 meters. The herbaceous layer is dominated by the genera *Andropogon* and *Pennisetum*. It is the most common habitat that occupies 69% of the park (Sillero-Zubiri et al. 1997; Tappan 2012).

- *Open woodland:* located in floodplains of some rivers with soil coverage of 50 to 75%. This vegetation is characterized by a few dominant tree species that reach sometimes 15 meters with a prevalence of Sudanian species such as *Pterocarpus erinaceus*.

- *Gallery forest:* located in the wet valleys with good soil and hydrologic conditions representing 78% of the Senegalese forest gallery (DPNS 2000). Characterized by a great diversity of plant species with a prevalence of evergreen species, abundant lianas, tall trees, and dense vegetation. It generally occupies the entire valleys or the banks of the rivers.

- *Marshes:* characterized by annual and perennial grasses over 25 cm high and below 150 cm. The marshy meadow is usually located in the ponds and pools in the banks of the Gambia River and its tributaries. The prevalent aquatic species are sometimes different from one

pond to another because of the site conditions. Marshlands colonized by invasive species such as *Mitragyna stipulosa* and *Elaeis guineensis* are located at the source of some streams (DPNS 2000). Bamboo stands (*Oxytenanthera abyssinica*) are found in the valleys and along the hillsides, while palmaries (*Borassus aethiopium*) are located along the three main rivers.

Overall, 1,500 species of flowering plants are found in Niokolo Koba, representing 62% of the Senegalese flowering plant species in less than 5% of the country (Adam 1971; Schneider and Sambou 1982 cited by DPNS 2000).

The NKNP is an *in situ* repository of animal diversity due to the variety of its habitat types. According to the National Biodiversity Monograph (MEPN 1998), 80 mammal species, 330 bird species, 60 fish species and 36 reptile species are inventoried in the park. In addition, NKNP qualifies as the last refuge for large mammal species of the country such as the elephant (*Loxodonta africana*), the Derby eland (*Taurotragus derbianus derbianus*), and the chimpanzee (*Pan troglodytes*). The carnivore population of the park is also varied with 23 species – out of the 75 carnivore species in Africa – distributed within 6 families (Sillero-Zubiri et al. 1997). Some mammal species such as African wild dog (*Lycaon pictus*), Derby eland, chimpanzee, lion, leopard and caracal (*Caracal caracal*) occur in and around the park at their westernmost and northernmost distribution in Africa.

Because of its exceptional richness in animal diversity as well as in biotopes, Niokolo Koba was given double international recognition in 1981 as a Biosphere Reserve of UNESCO's Man and the Biosphere Program and as a World Heritage site under Criteria X. However, because of "*the degradation of the property and the imminent threats to its Outstanding Universal Value, in particular the critically low mammal populations, the ongoing management problems and the impacts of the proposed construction of a new dam on the Gambia river a few kilometres upstream of the park* (World Heritage Committee 2007)", the park was inscribed in the List of Word Heritage Sites in Danger in 2007. In fact, NKNP is threatened by increasing poaching and degradation of some habitats due to silting and colonization of some ponds by invasive species like *Mimosa pigra* and *Mitragyna inermis*. Other threats are caused by stray cattle and agriculture encroachment. However, the inscription of the park in the UNESCO list of

sites in Danger is mostly motivated by the results of the controversial African Park foundation inventory (Renauld et al. 2006) conducted in 2006

Target species

Lion: Panthera l. leo

The lion is the second largest felid in the world and one of the most charismatic wild animals. It once inhabited Europe, the Middle East, Asia, and Africa but was extirpated from Europe two millennia ago and from North Africa and the Middle East about 150 years ago (Nowell and Jackson 1996). Lions also were extirpated from Asia except in India where they exist in a small remnant population that is considered a distinct subspecies called *P. l. persica*, as opposed to *P. l. leo* known as the African lion (Nowell and Jackson 1996; IUCN 2013). In Sub-Saharan Africa, West, and Central Africa, lions are believed to have a different climatic history than eastern and southern African lions, which probably led to a genetic differentiation between the lion populations (Bertola et al. 2011). Bertola et al. (2011) argue that eastern and southern African lions show more genetic diversity than the West and Central Africa ones, which are more closely related to the Asian lion. This could also explain why West and Central African lions have a less developed mane than their eastern and southern cousins. Furthermore, Bertola et al. (2011) hypothesized that the lack of diversity in West and Central Africa lions is due to a shorter evolutionary history caused by extinction followed by recolonization from Indian refugia. These historical and genetic factors are probably the main causes for the uneven distribution of lions across Africa, with the largest populations occurring in eastern and southern Africa.

The lion is globally classified as 'Vulnerable' on the IUCN Red List but 'Endangered' in West Africa (IUCN 2013; Bauer and Van Der Merwe 2004). The latter classification is the consequence of two large-scale surveys of African lions conducted by Chardonnet (2002) and Bauer and Van Der Merwe (2004) which suggested that West African lion abundance ranged from 850 (Bauer and Van Der Merwe 2004) to 1,163 (Chardonnet 2002) individuals and accounted only for 2.95 to 3.7% of the total population size in Sub-Saharan Africa. Another more recent publication by Riggio et al. (2013) estimated West African lion abundance to be only 525 individuals. The main threats identified to lion populations are habitat loss, fragmentation, and depletion of the natural prey base – which results in human-lion conflicts – as

well as legal and illegal hunting (Nowell and Jackson 1996; Chardonnet 2002; Bauer and Van Der Merwe 2004; Sogbohoussou 2011; IUCN 2013). Ray et al. (2005) stated that lions lost 82.9% of their historical range across Africa. In West Africa, most lion populations are isolated and virtually occur only in protected areas (Bauer et al. 2001)

Lions prefer habitat consisting of open woodland and thick bush, and scrub and grass complexes where they can find sufficient cover for hunting and denning (Nowell and Jackson 1996). However, lions tolerate a wide range of habitats across Africa and are absent only from tropical rain forests and the interior of the Sahara desert (Nowell and Jackson 1996). The lion is the most social cat species, living in prides of related females remaining together with their cubs, while unrelated males form coalitions that compete for pride tenure. Average pride size is 4 to 6 lions (Nowell and Jackson 1996; IUCN 2013), however, pride sizes are lower in West Africa with an average of 2.6 (±1.7) in the Pendjari Biosphere Reserve in Benin (Sogbohoussou 2011). Sogbohoussou (2011) also investigated the lion's prey preference in the same study area and showed it consisted mainly of large ungulates such as buffalo (*Syncerus caffer*), kob (Kobus kob), hartebeest (*Alcelaphus busephalus*) and roan antelope (*Hippotragus equinus*).

Leopard: Panthera p. pardus

The leopard is the most widely distributed wild felid in the world (Nowell and Jackson 1996; Uphyrkina et al. 2001; IUCN 2013) and inhabits habitats ranging from desert to rain forest and from sea level to 5,700 m height on Mount Kilimanjaro (Nowell and Jackson 1996). Their coat color and pattern vary with habitat type (Nowell and Jackson 1996). Nine leopard subspecies are recognized worldwide from genetic analysis with the single subspecies *P. p. pardus* occurring in Africa (Uphyrkina et al. 2001; UICN 2013). In Sub-Saharan Africa, the leopard occupies all types of habitat but lost 36.6 % of its historical range and is now restricted to very patchy habitats even though they can persist in human-modified habitats in the absence of persecution (Ray et al. 2005). Leopard presence across such a range in geography is probably related to the leopard's solitary habits and its large range of prey varying in size from arthropods to adult male eland (Nowell and Jackson 1996) and consisting of 92 different species in Sub-Saharan Africa (Bailey 2005).

The leopard population size is smaller in West Africa than in any other Sub-Saharan region and leopards appear to be rarer than lions in the savannah regions (Nowell and Jackson 1996). However, the leopard is not classified as Endangered in West Africa as is the lion probably because of the absence of reliable estimates of abundance in the region and across Africa. The main threats to leopard persistence are human-related, with habitat conversion, trophy hunting – mainly in East Africa – skin and canine trade for traditional rituals in West and Central Africa. Despite the level of threats and their patchy distribution, the leopard population is considered stable across Africa and listed as "Near Threatened" under the IUCN Red List.

Serval: Leptailurus serval

The serval is a solitary cat found in Sub-Saharan Africa and Morocco (Nowell and Jackson 1996). Although widespread, they are mostly located along permanent water sources in long grass environments such as reed beds and other riparian vegetation types, but are absent in tropical rainforests and the Sahara deserts (Nowell and Jackson 1996; Ray et al. 2005; IUCN 2013). Servals are commonly recorded inside protected areas but their status outside is uncertain (IUCN 2013). They are highly tolerant of agricultural lands provided that water and cover are accessible (Ray et al. 2005). Their most common prey are rodents, birds, reptiles, and insects (Nowell and Jackson 1996; Sillero-Zubiri et al. 1997). According to Geertsema (1985), their lowest density in optimal habitat in Ngorongoro Crater was 42 individuals per 100 km^2. The same author estimated the home range size for male and female adult servals to be 11.6 and 9.5 km^2 respectively.

The major threats to serval persistence are wetland and riparian habitat losses – as they harbor high rodent densities – and degradation of grasslands (Nowell and Jackson 1996). Illegal pelt trade for traditional rites and medicine is also noted as a threat mainly in West African regions including Senegal (IUCN 2013). In addition, they are killed by indiscriminate predator control methods such as poisoning although their presence is thought to be beneficial to farmers as they control rodent populations and rarely prey upon livestock (Ray et al. 2005; ICUN 2013). Although unusual, large carnivores such African wild dog, spotted hyena (*Crocuta crocuta*), and

leopard also prey on servals (Ray et al. 2005). The serval is listed as "Least Concern" in the IUCN Red List (IUCN 2013).

Status of the target species in Senegal

The three carnivore species of main interest in this study have almost the same distributional range but with different levels of protection in the country. They all occur only in the southeast of Senegal which comprises the NKNP. Their range includes the Badiar National park in the northern part of the Guinea Republic and the western part of Mali. Based on available data from the 1980s, the Senegalese Government enacted the Game and Wildlife Protection Act[2] in 1986. Under that Act, the leopard is integrally protected (capture and hunting forbidden, except for scientific reasons) while the lion and serval are partially protected (can be captured or hunted under certain extreme conditions). For instance, shooting of lions is subject to a special authorization of the Senegalese President as the lion is the national emblem.

However, the Act formally forbids hunting in all six Senegalese national parks without any exception. Hunting is only authorized however, in special ranches that often surround national parks. Currently, this Act is heavily criticized by the Senegalese Wildlife Department because it is outdated and because the annual authorized takes – which are given by a different department – do not lie in scientific data according to the Department. Furthermore, there is no report of illegal carnivore hunting or persecution by humans due to the fact that most carnivores are restricted in protected areas and poaching usually targets ungulates.

Internationally, the lion is considered a "Vulnerable" species overall under the IUCN Red List and as "Endangered in West Africa", whereas the leopard is classified as "Near Threatened", and the serval as "Least Concern" (IUCN 2013).

Review of carnivore estimates in the NKNP

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[2] Officially Code de la Chasse et de la Protection de la Faune

The first mammal population census in Niokolo Koba was conducted in 1990. Prior to that, some rough estimates based on terrestrial and aerial observations, were made by Dupuy (1975), the first curator of the park, and his team from 1967 to 1975. Dupuy (1975) guess-estimated the population of lions at about one hundred individuals, and stated that leopards, caracals (*Caracal caracal*), and servals were numerous but difficult to estimate.

DPNS (1993) stated that, at the end of the 1980s and the beginning of the 1990s, the spotted hyena was common, and that caracals, servals, leopards, and African wild cats (*Felis silvestris*) were present. African wild dogs were estimated at 50 to 100 individuals and the population size of lions was between 100 and 200. However, this estimation, like the previous ones, did not rest on current scientific methodology and analysis.

In 1989, DPNS signed an agreement with the French Research Institute for Development (ORSTOM[3]) to perform periodic censuses of the Niokolo Koba's large and medium sized mammal populations. Therefore, two campaigns (1990-1993 and 1994-1998) were conducted (Galat et al 1992; Galat et al. 1996) and a compilation report comparing the results of these campaigns was produced in 1998. During the whole 9-year period, the line transect techniques were used and the count dates (14-16 of February) were the same. The counts were conducted by vehicles and on foot within the roads and trails of the park during daylight hours, from 7 to 11 am, and from 4 to 6:45 pm. The results were analyzed with the program DISTANCE (Laake et al. 1996). Even though the method was not appropriate for carnivore estimation in forested environments (carnivores are harder to detect because of their elusive and nocturnal behavior), the study estimated the lion population at 165 individuals, however with very large confidence intervals (62 – 441) (Galat et al., 1998). Leopard and serval population sizes were not estimated.

In 1997, in the time frame of the Project Grand Carnivores, a transboundary project between Niokolo Koba and the adjacent Badiar National Park in the Guinea Republic, other mammal population surveys were conducted by Sillero-Zubiri et al. (1997) specifically focusing on carnivore species. Line transects again were utilized and driven with a vehicle during daylight and night. In addition, audio broadcast stations with taped carnivore calls were set to attract some species like lions and hyenas. Overall, 21,668 km were surveyed in Niokolo Koba during 1,292

[3] Now IRD: Institute of Research for Development

hours including 1,419 km and 106 hours of night searches. Moreover, interviews were conducted with the park staff, visitors, and researchers to aid in collecting sightings of the target species. From that survey and based on previous estimates by Galat et al. (1998), they estimated population size and density for some carnivores for which they had encounters (Table 1.1).

In 2001, the French Global Environment Fund funded a census program of six month of surveys from January to June (5 days each month) consisting of 3 aerial and 2 terrestrial counts). Similar to the 1990-98 campaigns, this count program also used line transect techniques, which are usually more appropriate for detecting herbivore species. Consequently, the only carnivore species sighted during the whole six month period was a group of 9 African wild dogs.

The last large-scale census was conducted in 2006 by the African Parks Foundation whose aim was to be granted the management of the park in a public-private partnership. The objective of the count was to determine population sizes, densities, and spatial distributions of the mammal species by means of aerial and terrestrial counts. The terrestrial counts were used to confirm the aerial count result. Overall, 8,337 km were surveyed by plane, representing an area of 3,335 km^2, which is 40.3% of the area of the park. As for the terrestrial counts, 83 line transects were surveyed, representing 1,679 km. No carnivore species was seen during the aerial counts, while the terrestrial counts recorded 5 species (Table 1.2).

The African Parks Foundation report focused mainly on the aerial results. Population sizes and densities of carnivore species were not estimated for the terrestrial counts. Additionally, indices of abundance were presented without either calibration or further analysis.

The most recent census was conducted in March-April 2011 by Henschel et *al.* (2014) this time with a focus on carnivore species, specifically lions. They used line transects for track surveys combined with call stations. They estimated lion and leopard population size at 17 and 403 respectively, using the Funston et al. (2010) formula. Their derived densities were 0.2 and 4.4 individuals per 100 km^2 respectively (Table 1.3).

The large carnivore estimates described in the paragraph above share the same characteristics: estimation techniques not adapted for carnivores, short timeframes, indices of abundance not calibrated, and wide confidence intervals. In fact, most of these surveys were not intended to estimate carnivore populations, but rather all the mammal species instead. The two

studies that targeted carnivores (Sillero-Zubiri et al. 1997, Henschel et al. 2014) lacked precision, with large confidence intervals for both of them. This points to the need to use more appropriate techniques to estimate carnivore population densities within the Niokolo Koba National Park. Camera trapping and more recently, DNA sampling, methods are now considered more appropriate methods for surveying carnivores. These methods share the distinction of being noninvasive techniques, defined by Kelly et *al.* (2012) as "the gathering of data without capturing, handling, or otherwise physically restraining individual animals".

Camera-trapping techniques and CMR models

Camera trapping techniques employ remotely triggered cameras to document the presence of animals in a given area and, for uniquely marked animals, to estimate their densities and abundances using capture mark-recapture (CMR) models. In NKNP, leopards and servals have unique spot pattens and camera trapping can be used to estimate abundance and density. Camera trapping was first used by Karanth (1995) to estimate tiger (*Panthera tigris*) population size and density in Nagarahole National Park in India under capture – recapture modeling (Karanth 1995; Karanth and Nichols 1998). Since then, this noninvasive technique has been widely used by researchers to estimate density for individually recognizable animals (O'Connell et al., 2011) and its application has been broadened to determine survival, recruitment, habitat preference and to identify behavioral patterns (O' Connell et al., 2011). Camera trapping studies have significantly increased knowledge of ecology and demography for carnivore species, which are generally elusive and occur at low densities, making them very difficult to study. Similarly, camera models have evolved subsequently to meet the specific needs of researchers and are widely available at reasonable costs (Kelly et al. 2012).

However, camera trapping techniques have raised challenging issues for researchers to address in order to obtain unbiased estimates of the parameters of interest for target species (O'Brien 2011). For example, survey design for deployment of cameras in the field should attempt to be representative of the entire study area, as the purpose of the sampling is to draw inferences for a larger area. O'Brien (2011) pointed out however that representativeness is not easy to assess and often sampling areas are chosen because of their degree of accessibility.

Other issues include data treatment that relies heavily on capture-recapture analysis and model assumptions that require demographically and geographically closed populations. Geographic closure is a harder assumption to meet (Wilson and Anderson 1985) and makes it difficult to estimate the effective trapping area to which the sampling is applicable and further to estimate density. To address these two problems, the half mean maximum distance moved (½MMDM) by the target species suggested by Wilson and Anderson (1985) has been widely used. MMDM, as defined by Wilson and Anderson (1985), is "the average of the maximum distance between recaptures for animals caught at least twice". This metric is however more and more criticized because it tends to underestimate the radius of an average home range (Soisalo and Calvanti 2006; Dillon and Kelly 2008; Tobler and Powell 2013) and therefore overestimates densities. Instead, Soisalo and Calvanti (2006), Dillon and Kelly (2008) and Tobler and Powell (2013) recommended using the full MMDM as it potentially produces more accurate and precise estimates. They also noted the importance of knowing the home-range size of the target species in order to determine the appropriate camera spacing, buffer size, and total grid size.

In Senegal, no work has been done so far in evaluating the home-range size of any carnivore nor in estimating their abundance using camera trap techniques. At the continental scale, especially in eastern and southern Africa, home range sizes have been estimated for all the target species of this study, and show that there is very large variation due to site specificity, species densities, sex, age, and type of vegetation (Ray et al., 2005).

Spatially Explicit Capture-Recapture (SECR) models

Newer analytical techniques have recently been developed, termed spatially explicit capture-recapture (SECR) models (Efford 2004; Borchers and Efford 2008; Royle and Young 2008; Royle et al. 2009), that do not suffer as much from the problems associated with camera spacing and extent or lack of information on home range size. Efford et al. (2004) was the first to formalize a method which directly estimates density without estimating effective trapping area. Their technique departs from the traditional approach and hypothesizes that animal range centers are distributed across the study area as a spatial point process with an unknown density (D), assuming that each animal possesses a home range centered at an unknown location, and that

each trap is set at a known location and can catch at most one animal, during a closed-population sampling session. Therefore, two unknown parameters that are a function of spatial area used to represent the capture process. The first parameter, g_0 is the probability of detection at a single detector placed in the center of the animal's home range, and the second parameter, σ, is the spatial scale over which capture probability declines. The parameters D, g_0, and σ and the trap locations define an individual-based model of the capture process. Ultimately, the three parameters can be estimated jointly by simulation and inverse prediction using conventional capture–recapture statistics as predictors (Borchers and Efford 2008). This technique was further improved by Borchers and Efford (2008) under maximum likelihood (ML) methods that are not only more flexible, but also allow AIC model selection and the inclusion of covariates. This maximum likelihood, spatially-explicit, capture-recapture framework can be implemented using software DENSITY (Efford et al. 2004).

In the same framework of estimating density without relying on trap specificity, Royle and Young (2008) developed a hierarchical spatial capture-recapture models and adopted a Bayesian analysis framework based on data augmentation and using Monte Carlo Markov Chain simulation. Their approach supposes two components: a biological process where each individual of a population has a center of activity around which its movements are randomly distributed (latent variables) according to some probability distribution function, and an observation model conditional to the latent variables (Royle and Gardner 2011). Their model was first implemented in WinBUGS, then in R package SCRbayes (Russell et al. 2012) in R (R Core Development Team 2009) and lately in R package SPACECAP (Gopalaswamy et al. 2012). Both spatially explicit model formulations estimate the density of home range centers and that is equivalent to the density of animals on the landscape.

In this analysis I use both traditional and spatially explicit capture-recapture models for marked species, the leopard and serval, providing a comparison of leopard results to each other and to previous leopard results from other studies that did not use carnivore specific methodology. I also provide the first density estimates for servals from any camera trap study.

Non-spatial and Spatial Mark-Resight Models

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Unlike traditional CMR and SECR models, mark-resight models are flexible enough to allow the use of both marked and unmarked individuals of a sample population to estimate population abundance, density and detection parameters (Royle et al. 2013). The fundamental assumption of mark-resight models is that the marked individuals are representative of the entire population in terms of sighting probabilities (McClintock 2011). This assumption implies that the number of marked individuals available for resighting needs to be known exactly, which was difficult to meet (McClintock et al. 2009). Fortunately, several mark-resight models that fit data with unknown number of marked individuals have been developed recently (McClintock et al. 2009, Royle et al. 2013). Non-spatial mark-resight models estimate abundance and must be divided by area surveyed to estimate density, thus, the same MMDM issues arise as described above for traditional capture-recapture models. In response, Sollmann et al. (2013) developed spatially explicit mark-resight (SMR) models using a Bayesian framework along similar lines as the SECR models developed by Royle and Gardner (2011). This technique has recently been applied to puma (*Puma concolor*) populations where a portion of the population is individually identifiable by scars, nicks, botflies, and tail kinks (Rich et al. 2014). A similar situation exists in NKNP, where lions are solid in color but numerous individuals are uniquely identifiable by scars, mane patterns, and nicks. Therefore, mark-resight models can be used.

In this study, I use mark-resight and spatial mark-resight models for the first time on lions to compare methods to each other, and to compare to past lion surveys that did not use carnivore specific methodology.

Occupancy estimation

Capture-recapture models require that individuals can be captured and marked or are reliably identified by natural marks. These requirements are not always met in nature because not all animals have individually distinct coat patterns or consist of partially marked populations and therefore, an alternative is to use an occupancy modeling approach. Occupancy is a state variable that can be defined as the probability that a patch or site is occupied by a species of interest (O'Connell and Bailey 2011). This maximum likelihood-based approach developed by MacKenzie et al. (2002) integrates two other concepts: presence-absence and detection-non-

detection. Presence-absence refers to whether or not the species is present in a given area and detection-non detection refers to the detectability (probability of detection) of the target species when it is present in that site. Presence-absence is advantageous to wildlife managers as it provides information about spatial distribution of species and habitat suitability (MacKenzie et al. 2005; O'Connell and Bailey 2011). Moreover, it can be used as a surrogate for population size or species abundance, by depicting changes in occupancy through time, especially at a large spatial scale for low-density, cryptic species (MacKenzie et al. 2003). Detection-non detection is also of a strong importance in occupancy modeling because not detecting an animal – which does not mean absence of the animal – could lead to a negatively biased estimation of the proportion of patches occupied, specifically when detection probability < 1.0 (MacKenzie, 2002).

Another advantage of using occupancy modeling is based on the fact that it is more flexible in the sense that it allows incorporation of both covariate information and missing observations (MacKenzie, 2002). In addition, the approach can be used simultaneously with closed -population, capture-recapture modeling, with further assumptions however. Occupancy and capture-recapture modeling are related by the fact that when sites are treated as the sampling units, the detection-non detection of each site becomes the equivalent of capture-recapture data in abundance estimation models (Vojka, 2005).

Occupancy modeling involves multiple surveys of species at the same targeted sites in order to collect detection-non detection information from that site, from which probability of detection is computed and hence, the proportion of occupied area estimated. This described model is the original occupancy approach (MacKenzie et al., 2002) and is also known as the "single-season" model, where multiple surveys are conducted during a single season. However, it should be noted that despite its wide use in wildlife dynamics, occupancy modeling shows limitations when detection probability is too low, especially lower than 0.3 (Vojka, 2005).

Pilot study

Before choosing the definite study area within the Niokolo Koba National Park, I conducted a pilot study from May 24th to July 7th 2012. The site was selected because it had the

highest frequency of carnivore sightings according to the park managers. We set up 25 camera trap stations that consisted mainly of film cameras. Twenty stations were placed on animal trails where we found carnivore tracks nearby and the other 5 were placed on human trails. Only the 5 stations on human trails yielded large to medium-size carnivore captures, confirming that carnivores often use clear trails and roads (Dillon and Kelly 2008; Soisalo and Calvanti 2006). This preliminary study also confirmed the feasibility of camera trapping in a wooded, savannah-dominated habitat.

This pioneer study is a keystone in carnivore conservation and management in Senegal in a context where the Niokolo Koba is listed as a World Heritage Site in Danger. Carnivore-focused studies can lead to more efficient and effective management actions that will benefit all other trophic level species due to the umbrella function of most of large carnivores. Additionally, this study will not only add knowledge about carnivore communities in West Africa, but it will also contribute to filling the huge knowledge gap in comparison to the southern and eastern African carnivores. Eventually, it aims to be a starting point in carnivore research in south-eastern Senegal by sparking interests of wildlife scientists and conservationists all around the world.

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Table 1.1: Guess-estimates of population size and density of 5 carnivore species in NKNP out of the 22 species encountered during the1997 survey

Carnivore species	Population size	Density (individuals/100 km^2)
Canis adustus	526 – 734	7
Panthera leo	50 – 150	0.5 – 1.5
Panthera pardus	100 - 300	1 - 3
Crocuta crocuta	200 - 500	2 - 5
Lycaon pictus	50 – 200	0.25 - 1

Reference: Sillero-Zubiri et al. 1997.

Table 1.2. Number of contacts (direct and indirect) and indices of abundance of 5 carnivore species from the terrestrial census during the 2006 large-scale survey

Species	Number of contacts		Index of abundance (Number of contacts/100 km)	
	Direct	Indirect	Direct	Indirect
Canis adustus	13	120	0.8	7.1
Panthera leo	1	5	0.1	0.3
Panthera pardus	2	19	0.1	1.1
Crocuta crocuta	-	43	-	2.6
Lycaon pictus	-	9	-	0.5

Reference: Renaud et al., 2006

Table 1.3. Indices of abundance, densities, and population sizes of the four largest carnivores of the Niokolo Koba during the 2011 survey. The estimates were generated from track counts using the Funston et al. (2010) formula.

Species	Index of abundance (tracks/100km)	Density (number of individuals/100km^2)	Population size
Panthera leo	1.0	0.2	16 (0-54)
Panthera pardus	14.29	4.4	403
Lycaon pictus	1.66	0.4	37
Crocuta crocuta	23.6	7.4	679

Reference: Ndao and Henschel, 2011; Henschel et al. 2014
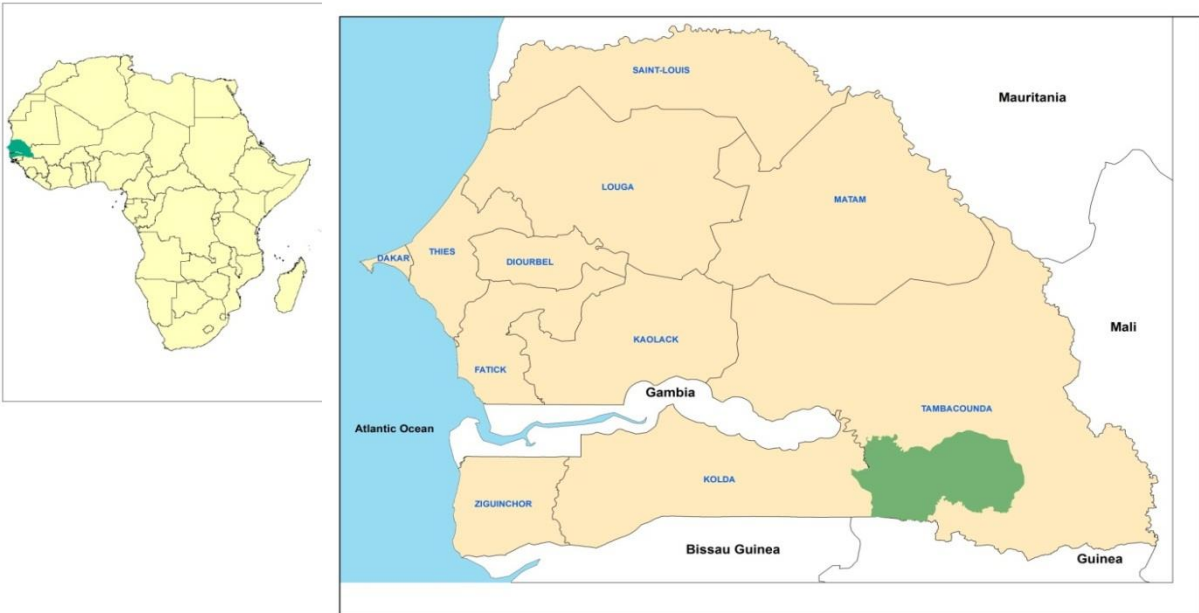
Figure 1.1. Location of Senegal in Africa (left corner) and the Niokolo Koba National Park (green) in South-East Senegal.
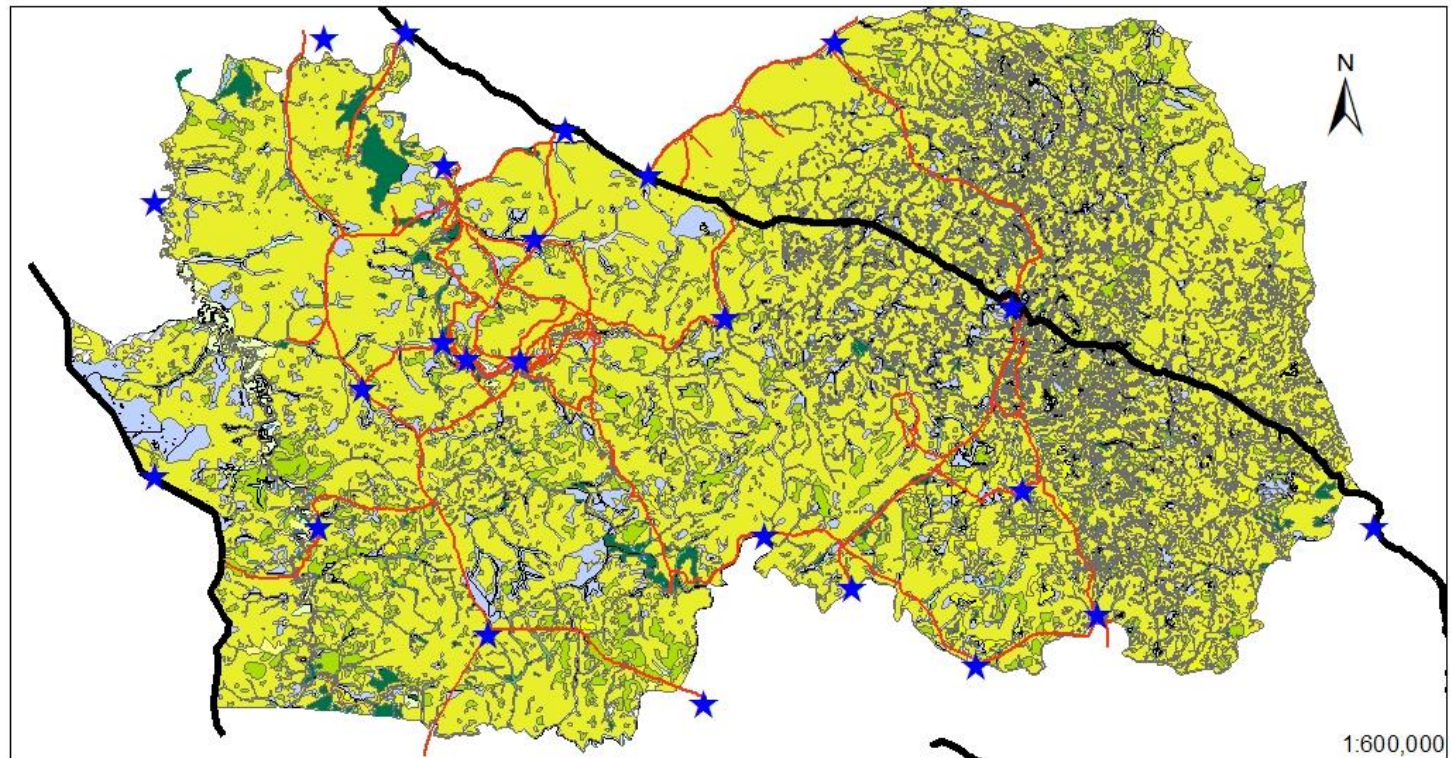
LEGEND

Habitat features

★ PostGuards	Shrub Savanna	Wooded Savanna	Open woodland in valleys
Highway	Herbaceous Savanna	Shrub\Tree Savanna on Bowe	Water bodies
Truck trails	Dense Forest	Open woodland	Wetland
	Gallery Forest	Riparian forest	

Figure 1.2. Niokolo Koba National Park habitat features and facilities. Land use/Land cover shapefiles from Tappan (2012).

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Chapter 2: Lion (*Panthera leo*), leopard (*P. pardus*) and serval (*Leptailurus serval*) occupancy across the Niokolo Koba National Park in Senegal

Abstract

Competition among carnivore species has been shown to be an important ecological factor that influences population distribution and habitat use. Lions, leopards, and servals are three felids species that often co-exist in African wild habitats. In the Niokolo Koba National Park (NKNP) in Senegal, the three felid species are known to be present, but very little is known about their ecology and behavior, as is the case for most carnivore communities in West Africa. We used an occupancy modeling framework implemented in program Presence to examine habitat use of lions, leopards, and servals in the NKNP from camera-trap data. Naïve occupancy estimates were 0.57 for leopards, 0.32 for lions, and 0.46 for servals. The single species occupancy modeling revealed that leopards had the highest occupancy ($\Psi = 0.78$; SE = 0.13) and occurred in dense areas but with low prey activity. Their probability of detection (p = 0.20; SE = 0.05) decreased with tree density. Lion probability of occupancy was 0.47 (SE = 0.12) and they occupied areas with high prey activity and high tree density. Unlike leopards, lion detectability increased with tree density (p = 0.29; SE = 0.09). Servals occupancy ($\Psi = 0.58$, SE = 0.13) and detection (p = 0.17, SE = 0.05) were both negatively influence by leopards activity as the only important predictor variable. Two species co-occurrence modeling confirmed the role of the three most important factors in the single species modeling (tree density, prey availability, and leopard trap success), but we only found evidence of co-occurrence between lions and servals. Lion presence increased serval occupancy and detection, possible because leopards avoided areas where lions were present. Although we did not find evidence of avoidance between lions and leopards and between leopards and servals, we believe that this is mainly due to lack of data (low number of sites and sampling without stratifying by habitat types) as many of the interaction models failed to converge. Our findings confirm a habitat selection strategy that consists of occupying dense areas likely to increase prey catching efficiency through ambushing. We also suggest leopard adaptability when constrained by competition. Interspecific interactions among carnivores are important to consider when designing a management plan targeting multiple threatened predators.

Introduction

Carnivore species are unquestionably among the most threatened species worldwide. The level of threat is mainly related to persecution by humans, habitat loss and fragmentation, as well as to some intrinsic factors such as large home range requirements, large body size, and naturally low population growth rates (Cardillo 2002, Purvis 2000). In addition, their position at the top of the food chain makes them vulnerable to ecosystem perturbations at any level (Mills 1991). However, humans are not the only threat to carnivore persistence. Competition among carnivore species has been shown to be an important ecological factor that influences populations of other carnivore species (Caro and Stoner 2003). Competition can take form of exploitative when species compete to directly access the same food resources, but can also be more radical when some species kill others species of the same guild to prevent them from accessing resources. As noted by Polis et al. (1989), intraguild predation is sometimes directed preferentially towards the closest potential competitors of the predator. Palomares and Caro (1999) also suggested that interspecific killing among mammalian carnivores accounts for up to 68% of known mortalities in some carnivore species. This results in specific behavior such as predator avoidance, which in turn causes spatial and temporal resource partitioning when species share a common range or distribution (Bischof et al. 2014). Furthermore, carnivores belonging to the same family generally exhibit similarities in their trophic attributes, and as a consequence, their niches often overlap more frequently than with other families (Donadio and Buskirk 2006), increasing the interference risk.

Lions, leopards, and servals, are three felids species that often co-exist in African wild habitats. As the apex carnivore, lions haven been shown to generally select the richest areas and thus are not restricted in their movements (Vanak et al. 2013). The leopard, which is the second largest and the closest competitor to lions, will avoid encountering them, even though they are ecologically separated by prey selection, with leopards displaying more diet flexibility (Nowell and Jackson 1996; Bothma and Walker 1999). Some instances of lions killing leopards and their cubs have been documented (Palomares and Caro 1999; Ray et al. 2005). The serval, which is much smaller than both leopards and lions, is believed to systematically avoid leopard presence as the leopard sometimes preys on it (Ray et al. 2005; Donadio and Buskirk 2006).

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In the Niokolo Koba National Park in Senegal, the three felid species are known to be present, but very little is known about their ecology and behavior, as is the case for most carnivore communities in West Africa. Ray et al. (2005) noted that there is a strong bias towards research activities in eastern and southern Africa compared to West Africa and therefore recommended initiating more research and conservation actions on carnivores in neglected areas such as southern Senegal.

Knowledge of how large and medium size carnivores spatially select and occupy their habitats is of a strong interest to conservationists for monitoring purposes, chiefly when the species of interest occur at very low densities, and therefore are hard to detect. In this context, occupancy, which may be defined as the proportion of patches/sites occupied by a species across the landscape (MacKenzie et al. 2002), can be a useful tool to assess the spatial distribution of a given species while accounting for probability of detecting the species if present. In addition, factors believed to influence species occurrence and spatial distribution can be incorporated as covariates in an occupancy modeling framework (MacKenzie et al. 2002), allowing prediction of probability of occurrence for other sites not surveyed (Sunarto et al. 2012).

We used occupancy modeling to examine the distribution patterns of lions, leopards, and servals in the Niokolo Koba National Park (NKNP) in Senegal from camera-trap data. However, since our sites (camera stations) are close together, this analysis is more equivalent to habitat use within an occupancy framework rather than true occupancy.

The goals of this study were (i) to investigate probability of occupancy of each of the three species of interest in relation to environmental and/or local habitat factors, and (ii) to explore species co-occurrence across the sampled area. We hypothesize that first, leopards would have the highest occupancy as they have the widest habitat range and would avoid lions, and second the main drivers of serval occupancy would be higher canopy and understory cover (they prefer riparian forest) and they would avoid leopards, as the competitor closer to their body size. We also hypothesize that lion and leopard occupancy would increase as prey availability increases. This study will contribute knowledge about how understudied carnivores of NKNP are distributed across, and select their habitats in, a wooded-savannah dominated environment. Determining and anticipating interspecific interactions is needed in order to more effectively conserve the diverse, yet threatened, felids in West Africa.

Material and methods

Study area

The study area is within a subzone situated in the core of the Niokolo Koba National Park with a dense network of trails. The park covers 9,130 km^2 and is located in the south-eastern Senegal (Fig. 2.1) in a well-watered region unlike most parts of the country. The climate is of Sudanian type with annual rainfall fluctuating between 900 and 1,200 millimeters from May to October. The vegetation is a transition between Guinean savannahs and Sudano-Guinean savannahs, creating a large array of habitat types, the dominant one being wooded savannah at 69% (Tappan 2012). The canopy is mainly composed of deciduous species distributed along valleys, plateaus and hills, with the highest elevation at Mount Assirik at 311 meters. All the streams of the park belong to the catchment of the Gambia River which crosses the park from southeast to northwest. The main tributaries are Niokolo Koba, Koulountou, and Nieriko. In addition to these streams, some permanent and temporary ponds and pools play an important role in water and fresh grass supply for wildlife. Because of its location in the extreme West of Africa and on the northern edge of the Sub-sahelian woodland belt, it harbors many mammal populations that are isolated and at the northern extreme of their distribution (Sillero-Zubiri et al. 1997a).

Field methods

The two study sites within the park were chosen because of the high probability for felid detection. Camera trapping sessions were conducted in Linguekountou area from February 04 to April 23, 2013, then in Niokolo area from April 30 to July 07 2013. Thirty camera stations were deployed on a dense network of human trails (Fig. 2.2) in each area and consisted of paired cameras mounted on trees 30 to 40 cm above the ground on opposing sides of established roads and trails. All stations were installed in 5 and 3 days in the first and second area respectively, and were checked every 13 to 15 days. Cameras were set to stamp date and time on the bottom of photographs to help construct capture histories at each site for each species. The average distance between two consecutive stations was 2.5 km and the minimum convex polygon surrounding camera stations was 285.4 km^2 in Linguekountou and 336.71 km in Niokolo (Fig. 2.1).

At each study site, we conducted microhabitat sampling at each camera trap location within a 100-meter radius buffer surrounding each camera station (following Davis et al. 2011). From each camera station location (center of the circle), we walked a 100-meter transect in 3 directions: 0, 120 and 240 degrees. Every 10m, for 100m, we stopped and use point intercept to determine if there is canopy cover or not and we described the canopy type on a 0 (no cover) to 10 (100% cover) scale. At the 50m and 100m points we used a 40m perpendicular transect to measure understory cover every 2 meters along the transect. We dropped a 2-m pole and used point intercept to describe whether vegetation hits the pole (1) or not (0) at $0 – 0.5$ m, $0.5 – 1$ m and $1. – 2$ m. We also conducted point-centered quarter at each station location (0m) and at 50, and 100 m points in each of the 3 transects. At each of the 7 points (centers), we measured tree height and tree diameter of the 4 nearest trees that fell into each quarter of the cardinal points. We also measured the distance between each center and the 4 nearest trees. This enabled us to estimate tree density, height, and basal area at each camera station.

Data analysis

We identified animals to species from camera trap photographs and calculated trap success for each species at each camera station (number of capture events of a given species per 100 trap-nights) following Dillon and Kelly (2007). A single capture event consisted of any distinctly different animal captured within a 30 minute time period regardless of the number of photographs. We considered each camera station as a site for occupancy modeling and for each of the three species of interest, we built capture histories for each site by collapsing the length of the camera trapping session into 8 encounter occasions (survey replications) of ~10 days each.

We used covariates from micro-habitat data, site trap successes of prey species, and macro-habitat features extracted from GIS to better understand species distribution patterns. At the micro-habitat level, we calculated for each site (camera station) the average canopy cover, the average understory cover at 3 levels ($0 – 0.5$ m, $0.5 – 1$ m and $1. – 2$ m), the average soil cover (3 categories: soil, rocky, and litter), the average tree basal area, the average tree height, and the mean tree density. From site trap successes, we created two categories of prey (large prey and medium and small prey combined) depending on their size. We defined prey as herbivorous

and omnivorous mammals than can potentially be preyed upon by lions, leopards, and servals. All preys smaller than bushbuck (45 kg) were considered as medium and small. These categories were based on lion (large prey) and leopard (medium prey) diet preference (Stuart and Stuart 2006; Nowell and Jackson 1996; Sogbohoussou 2011). Because we had only a few captures of small mammals such as rodents, which constitute the main diet of servals, we were not able to create a third category of very small mammals. We also used trap success of each of the three species of interest as covariates. These trap rates can be considered index of activity at each site rather than related to abundance. At the macro-habitat scale, we used ArcGIS (Version 10.1) to extract habitat information from a 2012 land cover map of the park. At each station, we created a 100 m and a 500-buffer to extract habitat features and calculate the percent cover for each habitat type. The habitat types are depicted in Figure 3.1.

All covariate variables were standardized using the z-score scaling to have all values symmetrically distributed around zero (mean for each variable) for comparability before testing for normality in JMP (version 10.0.2, SAS Institute 2012), and only two covariates out of the 18 were normal. Then we performed a pairwise correlation test at $\alpha = 0.05$ to test for relationship between covariate variables (Table 2.1). When habitat variables were significantly correlated at the 0.6 level, we removed one of the two correlated variables from the dataset. We also removed all macro-habitat variables for three main reasons: first they were largely dominated by wooded savannah (75% for 100 m-buffer and 69% for 500 meter-buffer), second they were statistically significantly correlated to each other and to percent canopy cover from the micro-habitat sampling, and third when setting up camera stations, we did not stratify by vegetation type, therefore we did not have much variability in habitat type beyond wooded savannah. In this case, canopy cover from the microhabitat surveys may be the best surrogate for the macro-habitat variables. Because large and medium prey trap successes were highly positively correlated, we decided to combine them into one category called 'prey'. We also did the same for the 3 categories of understory cover for the same reason.

Habitat use was estimated using Program Presence (version 6.4, Hines, 2006) under single season-single species platform for each felid and single season-two species platform for species co-occurrence. We assumed that probabilities of occupancy and detectability are constant across all sites, an equivalent assumption to population closure in capture-recapture modeling.

Constant occupancy and detectability were probably met as we were studying long-lived species over a relatively short period (less than 3 months) within the same season. Since the species were identified from photographs and they were easily distinguishable, there was no misidentification.

The 8 most significant variables thought to predict species occupancy and detection were retained as covariates in the analyses. For each single species and each paired-species, we first set a priori candidate set of models to test our hypotheses (Table 2.2), then we developed different models using different combinations of the site covariates and tested for over-dispersion on the most parameterized model. Models were ranked based on Akaike Information Criterion for small sample size (AICc) model ranking (Burnham and Anderson 2002) and AIC weights. Models that did not converge were dropped from the analyses. We considered models competing if the ΔAICc was within 2.0 of the top model, and we model-averaged the parameter estimates from the competing models.

For species co-occurrence, we used the conditional two-species occupancy modeling or psi Ba parameterization – which allows the integration of covariates – developed by Richmond et al (2010). Under that parameterization, a species A is considered as dominant and a species B subordinate and occupancy and detection of the subordinate species is conditional on the presence or absence of the dominant species. In our case, the order of dominance would be lion, and in the absence of lion, leopard. Serval is always a subordinate species. We also assumed that occupancy probabilities were not independent because of interspecific competition, and therefore the dominant species would out-compete the subordinate one in habitat and food selection (Steen et al. 2014). The parameterization used the following parameters (from Richmond et al. 2010):

Ψ^A : probability of occupancy for species A

Ψ^{BA} : probability of occupancy for species B, given species A is present

Ψ^{Ba} : probability of occupancy for species B, given species A is absent

p^A : probability of detection for species A, given species B is absent

p^B : probability of detection for species B, given species A is absent

r^A : probability of detection for species A, given both species are present

r^{BA}: probability of detection for species B, given both species are present and species A is detected

r^{Ba}: probability of detection for species B, given both species are present and species A is not detected

To compare (i) occupancy and (ii) detection or co-detection of the subordinate species in presence/absence of the dominant species, we developed 4 baseline models (without covariates):

(1):　　Ψ^A (.), $\Psi^{BA} = \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} = r^{Ba}$ (.) – There is no interaction between the dominant and subordinate species for psi or p: (i) probability of occupancy of the subordinate species is the same either in presence (Ψ^{BA}) or absence (Ψ^{Ba}) of the dominant species, and (ii) probability of detection of the subordinate species is the same either in presence (r^{BA}) or absence (r^{Ba}) of the dominant species.

(2) Ψ^A (.), $\Psi^{BA} = \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} \neq r^{Ba}$ (.) – There is no interaction between the dominant and subordinate species for psi, but there is for p: (i) probability of occupancy of the subordinate species is the same either in presence (Ψ^{BA}) or absence (Ψ^{Ba}) of the dominant species, and (ii) probability of detection of the subordinate when the dominant species is present (r^{BA}) is different from the probability of detection of the subordinate when the dominant species is absent (r^{Ba})

(3):　　Ψ^A (.), $\Psi^{BA} \neq \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} = r^{Ba}$ (.) – There is interaction between the dominant and the subordinate species for psi, but not for p: (i) probability of occupancy of the subordinate species when the dominant is present (Ψ^{BA}) is different from the probability of occupancy of the subordinate when the dominant species is absent (Ψ^{Ba}); and (ii) probability of detection of the subordinate species is the same either in presence (r^{BA}) or absence (r^{Ba}) of the dominant species.

(4)　　Ψ^A (.), $\Psi^{BA} \neq \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} \neq r^{Ba}$ (.) – There is interaction between the dominant and the subordinate species for psi and for p: (i) probability of occupancy of the subordinate species when the dominant is present (Ψ^{BA}) is different from the probability of occupancy of the subordinate when the dominant species is absent (Ψ^{Ba}); and (ii) probability of

detection of the subordinate when the dominant species is present (r^{BA}) is different from the probability of detection of the subordinate when the dominant species is absent (r^{Ba})

For each of the baseline models, we developed various candidate set of models in which we allowed the parameters to vary depending on covariates. The covariates included were those from our *apriori* predictions in Table 3.2. Models were ranked based on AICc values and weighs. Models were considered as competing if ΔAICc was less than or equal to 2. In case of interactions, we calculated the species interaction factor (SIF) (Richmond et al. 2010) that we plotted against the most significant covariates. If the SIF > 1.0 the species are said to co-occur more often than by random chance, whereas if the SIF is < 1.0 they occur less often than chance. If the SIF = 1.0 or the confidence intervals overlap 1.0 the species are likely occurring independently.

Results

The duration of the camera trapping was 78 nights in Linguekountou where two cameras got stolen during the first 2 weeks of the study and therefore were discarded from the study. The effective sampling effort was 2014 trap-nights and 36 different species were "caught" in remote camera photographs. In Niokolo, the camera trapping session lasted 67 days with a sampling effort of 1707 trap-nights. Large prey (Fig. 2.3) had an average trap success of 2.27 and 1.54 captures per 100 trap-nights (TN) respectively in Linguekountou and Niokolo while medium and small preys (Fig. 2.4) had trap successes of 6.08 and 2.94. Leopards, lions, and servals had average trap successes of 1.9 (±0.59), 2.06 (±0.72), and 1.41 (±0.39) captures per 100 TN respectively in Linguekountou whereas in Niokolo, trap rates were much lower at 0.67 (±0.26), 0.30 (±0.18) and 0.42 (±0.19) captures per 100 TN (see appendix A.1 for details about trap success of each species caught at each site).

Leopards were caught 40 times at 16 sites, lions 43 times at 9 sites, and servals 29 times at 13 sites in Linguekountou, and 8 times at 8 sites, 3 times at 3 sites and 6 times at 6 sites respectively in Niokolo. Because of the low capture rates in Niokolo, we discarded this study site from the analysis due to large numbers of zeroes and hence little data to model. Therefore, all the following results were derived only from the Linguekountou site.

Naïve occupancy estimates were 0.57 for leopards, 0.32 for lions, and 0.46 for servals.

Single-species occupancy

Leopard occupancy was related to prey trap success and average tree density as both covariates are present in 4 out the 6 competing (within ΔAICc < 2) top-ranked models (Table 2.3) that accounted for 61% of model weight. Surprisingly, and opposite from our predictions, leopard occupancy was negatively associated with prey trap success (from top model: β = - 3.75; SE = 3.24) while tree density, as expected, was positively related: β = 2.15; SE = 1.84) (Fig. 2.5a; 2.5b). On the other hand, leopard detection decreased mainly with tree density (β = -0.75; SE = 0.26) (Fig. 2.5c). Parameter estimates were obtained from model averaging of the competing models. The mean probabilities of occupancy and detection for leopards were 0.78 (SE = 0.13) and 0.20 (SE = 0.049), respectively.

Our prediction was also observed for lions as the top-ranked models showed that occupancy was strongly positively related to prey trap success (β = 9.36; SE = 5.55) (Table 2.4; Fig. 2.6a). Like leopards, lion detection also increased with tree density (β = 2.13; SE = 0.58) (Fig. 2.6b) and slightly with prey trap success (β = 1.13; SE = 1.99). Lion mean probability of occupancy was 0.47 (SE = 0.12) and its average detection probability 0.29 (SE = 0.09).

For servals, the first three top-ranked models competed but each of them indicated that leopard trapping rate was negatively associated with serval occupancy as predicted (β = - 3.79; SE = 2.26) (Table 2.5; Fig. 2.7a). Detection also decreased with leopard trapping rate (Fig. 2.7b). The mean probabilities of occupancy and detection were 0.58 (SE = 0.13) and 0.17 (SE = 0.05), respectively. Percent overstory canopy cover did not play a role in serval occupancy as expected, certainly because of the placement of most of the camera stations on trails in wooded savannah habitat type and hence very little variability in this parameter.

When compared, leopards had the highest proportion of sites occupied (0.78) as predicted, followed by servals (0.58), then lions (0.47) (Fig. 2.8). Despite having the lowest occupancy rate, lions had the highest probability of detection (0.29) while servals had the lowest probability of detection (0.17).

Two-species occupancy

- *Lion vs. leopard*

All 3 top-ranked models (ΔAICc ≤ 2) and the next 3 others accounted for 64.01% of the AICc weight (Table 2.6) and were built from the baseline model (1) that assumed occupancy and detection of leopards were not influenced by the presence or absence of lions (no interaction). However, the best models confirmed that lion occupancy is strongly positively related to prey trap success (β = 4.85; SE = 2.64). The models also showed that leopard detection when lions were present (β = -1.20; SE = 0.31) or absent (β = -1.34; SE = 0.37) was negatively influenced by tree density, as in the single species models. We did not calculate a species interaction factor (SIF), because the top models all indicated no interaction (i.e. SIF = 1.0).

- *Lion vs. serval*

Similarly to lion vs. leopard, models based on the baseline model of no interactions (1) were top ranked (Table 2.7), although 10 models competed. In the top model, percent overstory canopy cover is surprisingly strongly negatively related to serval occupancy, but with high variability (β = -25.43; SE = 21.59) and no models that included understory cover were top models. Like in single species modeling, one of the competing models showed that serval detection is still, although more weakly influenced by leopard presence either in the presence or absence of lions (β = - 0.78; SE = 0.40). For lions, prey availability was still the main driver of its habitat selection (β = 4.91; SE = 2.79).

Among the competing models, one was derived from model baseline (2) that assumed equal serval occupancy but different detection in presence or absence of lion; and another from the baseline (3) model (interaction model) that supposed serval occupancy when lions are present is different from its occupancy when lions are absent, with overstory canopy emerging as the most important habitat factor with a negative relationship (β = -11.79; SE = 7.77). We also investigated the type of interaction between the two species by calculating the species interaction factor (SIF) which revealed, unexpectedly, that lions and serval co-occurred more frequently than expected by chance (mean SIF = 1.39) in areas with higher tree density favored by lion and denser canopy cover preferred by serval (Fig. 2.9 a and b).

- *Leopard vs. serval*

As in the two previous paired-species occupancy analyses, models based on the baseline model of no interactions (1) were top ranked (Table 2.8). This is completely different from our expectation of seeing model types (3) or (4) top-ranked, as we predicted that servals would avoid areas where leopards were present. However, there were 11 competing models and 3 were from the baseline model (2) which assumed different detection probabilities of serval in presence or absence of leopards. This in line with our previous finding that leopard trap success prevented serval detection, (in addition to occupancy). Moreover, leopard presence was still negatively related to prey availability (β = -3.57; SE = 2.49) while serval occupancy and detection were negatively influenced by tree density (β = -1.22; SE = 1.59). As with lions vs. leopards, we did not calculate SIF, because the top models all indicated no interaction (i.e. SIF = 1.0).

Discussion

Remote cameras has proven to be a very effective method to record presence/absence of target species (O'Connell et al. 2006; 2009). This study utilized remote cameras to estimate probabilities of occupancy and detection of two large and one medium carnivore. In our case, we are using occupancy over a relatively small scale (285.4 km^2) and hence our occupancy is equivalent to habitat use by the three carnivores within the site as also done in other studies (Sunarto et al. 2012). In addition, the assumption pertaining to species misidentification is less likely to be violated when using camera traps. However, the fact that camera trap protocol was primarily designed for large carnivore abundance and density estimation, may have resulted in low serval detection because of its smaller home range size.

The positive relationship between lion occupancy and both prey trap success and tree density is in accordance with most studies. Stephens and Krebs (1985) showed that carnivore habitat selection is mainly governed by prey availability and landscape attributes. This is also in line with the Hopcraft et al. (2005) findings, which suggested that lions specifically select habitats with dense vegetation, rather than areas where prey are most abundant, as prey in general, avoid dense areas where they may be easier to catch (Sinclair 1985). This strategy known as ambush-habitat hypothesis, as opposed to the prey-abundance hypothesis (Hopcraft

2005; Balme et al. 2007), proposed that it is more cost-effective for the predator to ambush since less time and energy is spent hunting. This strategy involves the selection of ambush sites of high prey vulnerability (Schmitz 2005) and may explain the strong positive relationship that we found in this study between lion probability of detection and tree density. On the other hand, areas with high tree density, may be more difficult to travel through and therefore, trails may play an important role in acting as good funnels for lion movement, increasing detectability in such areas. In this case, lions may be drawn to these areas initially due to high prey activity, and from a remote camera sampling standpoint, within these areas, as the habitat becomes more dense, they have increased detectability on established trails.

Unexpectedly, leopards occupied dense areas that were negatively related to prey activity, which is in contrast to the Balme et al. (2007) findings that suggested that leopards also used the same habitats and hunting strategy as lions. However, our surprising result may be explained by interspecific competition between lions and leopards, with lions selecting the optimal dense areas with high prey activity, forcing leopards to use more marginal habitat, as suggested by Vanak et al. (2013). Leopard occupancy increased with tree density yet declined with prey activity, thus, like lions, they also prefer dense areas, but within those dense areas they avoid places where lions are likely to occur (those areas with high prey activity). We also found a strong negative relationship between leopard probability of detection and tree density. Interestingly, the fact that that leopard detectability declined with tree density is the exact opposite from lions. Perhaps leopards are changing their behavior to become more cryptic in such areas – either to avoid lions or to hide better in order to hunt prey more successfully.

Our lack of an avoidance relationship in the 2-species models may be due to fact that both lions and leopards choose dense areas, but within those areas there were subtle differences and our samples sizes were too small, especially for the number of sites where lions were captured, to reveal these subtle differences. Nonetheless, this highlights the ability of leopards to adapt to local constraints (Nowell and Jackson 1996; Ray et al. 2005; Balme et al. 2007) such as competition with lions by switching to poorer quality areas (less prey activity) and/or becoming more cryptic in dense areas where lions might be present.

The serval, was not influenced by prey trap success nor by tree density. The serval is a small mammal specialist (Nowell and Jackson 1996) and more than 90% of the prey species

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captured by cameras in our study did not include these diet items. Additionally, the serval prefers habitats with permanent water sources and tall grass where it can find its prey (Ray et al. 2005). Therefore, the covariates used in our study were not likely the most appropriate for modeling serval occupancy and detection. Given the low probability of detection for servals, we presume that servals used trails to move between their preferred habitats, but tended to avoid areas where leopards were present, as leopards are known to kill servals (Ray et al. 2005; Donadio and Buskirk 2006). In fact the only important variable for serval occupancy was leopard trap success and this relationship was negative. Small sample sizes for servals may be one reason why the 2-species interaction models did not find an avoidance effect for servals and leopards despite leopard trap success negatively impacting serval occupancy in the single species model.

Interestingly, the two-species occupancy modeling revealed some support for co-occurrence between lions and servals, because the interaction model was a competing model and the SIF >1.0.. Lion presence appeared favorable for serval occupancy as serval probability of occupancy was greater when lions were present than absent. High co-occurrence was seen mainly in areas with higher canopy cover and tree density. Serval preference for areas with dense vegetation cover matched the habitats selected by lions in this study. It is possible that servals use areas where lions are present because leopards avoid lions, hence those areas provide refuge from leopards. A similar pattern was found among jaguars (*Panthera onca*), pumas, and ocelots (*Leopardus pardalis*) in Belize, where ocelots were more likely to occur when jaguars were present (Davis et al. 2011).

This pioneer study highlighted the distribution and habitat use patterns of three felids in the Niokolo Koba National Park. Our findings confirmed the lion habitat selection strategy that consists of occupying dense areas potentially to increase its efficiency in catching prey through ambushing. In addition, we suggest the leopard is adaptable, when constrained by competition and can exist in similar areas as lions, but more cryptically. The servals also exists in dense areas and appears benefit from the 'protection' of lions. Although, we did not find evidence of avoidance between leopard and lion and between leopard and serval from the two-species occupancy modeling, we believe that this is mainly due to lack of data (low number of sites and sampling without stratifying by habitat types), as many of the interaction models failed to converged in program PRESENCE.

We recommend that future development be oriented towards investigating a sample area representative of all Niokolo Koba habitat features. In addition, many more sites should be added in order to increase power to make better predictions about species distribution patterns in regards to habitat selection, as well as species behavior relative to interspecific competition. We also suggest expanding this approach over multiple seasons and conducting multi-season occupancy analyses. Park managers believe that large carnivores follow migration of prey animals within and outside the park, which could explain the rarity of carnivore sightings in our second study site during wet season. This could be verified by investigating carnivore occupancy using multi-seasons models. We still require crucial information assessing species distribution and habitat use on a bigger scale and we need to anticipate interspecific interactions, in order to implement sound predator management plans for the imperiled Niokolo Koba National Park.

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Table 2.1. Pairwise correlation test on the 18 candidate variables to be used as covariates in analyzing leopard, lion and serval occupancy across the Niokolo Koba National Park. Values in bold show high correlation (≥0.6).

Candidate Variables		Overstory	Understory cover			Ground cover			Dendrometry			Trap success					Percent wooded savannah	
		Canopy	0-0.5m	0.5-1m	1-2m	Soil	Litter	Rock	Tree density	Basal area	Tree height	Large preys	Medium preys	Leopard	Lion	Serval	Buffer 500m	Buffer 1 km
Overstory	Canopy	**1.00**																
Understory cover	0-0.5m	0.05	**1.00**															
	0.5-1m	-0.06	0.40	**1.00**														
	1-2m	0.06	0.11	**0.73**	**1.00**													
Ground cover	Soil	-0.22	0.31	-0.09	-0.35	**1.00**												
	Litter	0.16	-0.26	0.10	0.40	**-0.98**	**1.00**											
	Rock	-0.01	-0.14	-0.04	-0.24	0.08	-0.23	**1.00**										
Dendro-metry	Tree density	0.51	0.03	-0.19	-0.02	-0.24	0.25	-0.06	**1.00**									
	Basal area	0.29	-0.13	-0.04	0.08	-0.23	0.22	-0.06	0.17	**1.00**								
	Tree height	**0.65**	-0.01	0.10	0.19	-0.27	0.23	-0.15	0.45	0.67	**1.00**							
Trap success	Large preys	**-0.62**	0.11	0.03	0.03	0.44	-0.36	0.16	-0.25	-0.24	-0.52	**1.00**						
	Medium preys	-0.49	0.16	-0.17	-0.10	0.29	-0.22	0.21	-0.07	-0.10	-0.52	**0.81**	**1.00**					
	Leopard	0.08	0.16	0.07	-0.01	-0.12	0.08	0.21	0.19	-0.31	-0.01	-0.07	-0.02	**1.00**				
	Lion	0.28	0.44	0.25	0.07	0.03	0.00	-0.30	-0.05	0.02	0.29	-0.26	-0.21	0.15	**1.00**			
	Serval	-0.22	0.23	-0.10	0.08	-0.07	0.11	-0.04	0.06	-0.04	-0.13	0.12	0.31	0.11	-0.01	**1.00**		
Percent wooded savannah	Buffer 500m	**-0.72**	0.10	0.00	-0.33	0.36	-0.37	0.36	-0.53	-0.32	**-0.64**	0.55	0.42	0.04	-0.23	0.01	**1.00**	
	Buffer 1 km	**-0.62**	-0.16	-0.14	-0.44	0.29	-0.32	0.35	-0.55	-0.41	**-0.63**	0.43	0.26	0.06	-0.24	-0.10	**0.91**	**1.00**

Table 2.2. A priori hypotheses for lion, leopard, and serval single species and two-species analyses. (+) indicates hypothesized positive relationship, (−) indicates hypothesized negative relationship and (0) indicated no relationship.

Hypothesized variables	Occupancy			Detection		
	Leopard	Lion	Serval	Leopard	Lion	Serval
Overstory cover	+	-	+	+	+	+
Understory cover	+	+	+	+	+	+
Tree density	+	+	+	+	-	+
Prey availability	+	+	-	+	+	-
Lion trap success	-		-	-		-
Leopard trap success		0	-		0	-
Serval trap success	0	0		0	0	

Table 2.3. Results of the 'single species-single season' occupancy analysis for leopards. Models were developed using site covariates and ranked based on their AICc values. ΔAICc = AIC difference, K = number of parameters. Models in bold are competing (ΔAICc <2).

Models*	AICc	ΔAICc	Model weight	Model Likelihood	K
Ψ (Prey+Dens),p(Dens)	**159.47**	**0**	**0.1477**	**1**	**5**
Ψ (Prey),p(Dens)	**159.63**	**0.16**	**0.1364**	**0.9231**	**4**
Ψ (Prey+Dens),p(Dens+Lion)	**160.18**	**0.71**	**0.1036**	**0.7012**	**6**
Ψ (Dens),p(Dens)	**160.23**	**0.76**	**0.101**	**0.6839**	**4**
Ψ (p(Dens)	**161.21**	**1.74**	**0.0619**	**0.419**	**3**
Ψ (Prey+Dens),p(Dens+Preys)	**161.28**	**1.81**	**0.0598**	**0.4045**	**6**
Ψ (Lion),p(Dens)	161.77	2.3	0.0468	0.3166	4
Ψ (Lion),p(.)	161.9	2.43	0.0438	0.2967	3
Ψ (Lion+Dens),p(Dens)	162.04	2.57	0.0409	0.2767	5
Ψ (Prey),p(.)	162.2	2.73	0.0377	0.2554	3
1 group, Constant P	162.32	2.85	0.0355	0.2405	2
Ψ (Prey.),p(Cover)	163.25	3.78	0.0223	0.1511	4
Ψ (Prey),p(Lion)	163.5	4.03	0.0197	0.1333	4
Ψ (Prey),p(Prey)	163.51	4.04	0.0196	0.1327	4
Ψ (.),p(Cover)	163.66	4.19	0.0182	0.1231	3
Ψ (.),p(Lion)	163.66	4.19	0.0182	0.1231	3
Ψ (Lion+Dens),p(.)	163.85	4.38	0.0165	0.1119	4
Ψ (.),p(Prey)	164.04	4.57	0.015	0.1018	3
Ψ (.),p(.Und)	164.1	4.63	0.0146	0.0988	3
Ψ (.),p(Serval)	164.14	4.67	0.0143	0.0968	3
Ψ (Lion),p(Prey)	164.51	5.04	0.0119	0.0805	4
Ψ (Prey+Dens),p(Lion)	165.44	5.97	0.0075	0.0505	5
Ψ (Dens),p(Lion)	165.53	6.06	0.0071	0.0483	4

*Ψ = probability of occupancy; p = probability of detection; Preys = prey trap success; Dens = Tree density; Und = Understory cover; Cover = percent canopy cover; Serval = serval trap success; Leop = leopard trap success; Lion = lion trap success; 1 group, Constant p = null model (occupancy and detection constant across the study site); 1 group, Survey-specific P = probability of occupancy constant, probability of detection varies with visits; + = additive effects.

Table 2.4. Results of the single species-single season occupancy analysis for lions. Models were developed using site covariates and ranked based on their AICc values. ΔAICc = AIC difference, K = number of parameters. Models in bold are competing (ΔAICc <2)..

Models*	AICc	ΔAICc	Model weight	Model Likelihood	K
Ψ(Preys), p(Preys+Dens)	**109.95**	**0**	**0.7425**	**1**	**5**
Ψ (.), p(Preys+Dens)	113.44	3.49	0.1297	0.1746	4
Ψ (.), p(Preys+Density+Und)	114.74	4.79	0.0677	0.0912	5
Ψ (.), p(Dens)	116.83	6.88	0.0238	0.0321	3
Ψ (.), p(Preys+Cover)	118.28	8.33	0.0115	0.0155	4
Ψ (.), p(Dens+Und)	118.83	8.88	0.0088	0.0118	4
Ψ (Und.), p(.Preys+Und)	120.27	10.32	0.0043	0.0057	5
1 group, Survey-specific P	120.69	10.74	0.0035	0.0047	9
Ψ (.), p(Cover)	121.79	11.84	0.002	0.0027	3
Ψ (.), p(Preys)	122.22	12.27	0.0016	0.0022	3
Ψ (.), p(.Preys+Und)	123.33	13.38	0.0009	0.0012	4
Ψ (Preys), p(.Preys+Und)	123.36	13.41	0.0009	0.0012	5
Ψ (.), p(Serval)	124.54	14.59	0.0005	0.0007	3
1 group, Constant P	124.74	14.79	0.0005	0.0006	2
Ψ (Cover), p(.Preys+Und)	124.74	14.79	0.0005	0.0006	5
Ψ (Cover+Preys),p(.Preys+Und)	125.06	15.11	0.0004	0.0005	6
Ψ (Dens), p(.Preys+Und)	125.3	15.35	0.0003	0.0005	5
Ψ (.), p(Leop+Serval)	126.21	16.26	0.0002	0.0003	4
Ψ (.),p(BA)	126.34	16.39	0.0002	0.0003	3
Ψ (.),p(Leop)	126.47	16.52	0.0002	0.0003	3
Ψ (.),p(Und)	126.62	16.67	0.0002	0.0002	3

*Ψ = probability of occupancy; p = probability of detection ; Preys = prey trap success; Dens = Tree density; Und = Understory cover; Cover = percent canopy cover; Serval = serval trap success; Leop = leopard trap success; Lion = lion trap success; BA = mean tree basal area; 1 group, Constant p = null model (occupancy and detection constant across the study site); 1 group, Survey-specific P = probability of occupancy constant, probability of detection varies with visits; + = additive effects.

Table 2.5. Results of the 'single species-single season' occupancy analysis for servals. Models were developed using site covariates and ranked based on their AICc values. ΔAICc = AIC difference, K = number of parameters. Models in bold are competing (ΔAICc <2).

Models*	AICc	ΔAICc	Model weight	Model Likelihood	K
Ψ(Leop),p(.)	**138.5**	**0**	**0.3789**	**1**	**3**
Ψ (Leop),p(Dens)	**140.09**	**1.59**	**0.1711**	**0.4516**	**4**
Ψ (Leop),p(Leop.)	**140.31**	**1.81**	**0.1533**	**0.4045**	**4**
Ψ (Leop+Dens),p(Dens)	142.08	3.58	0.0633	0.167	5
Ψ (Leop),p(Lion+Leop.)	142.25	3.75	0.0581	0.1534	5
Ψ (Leop+Dens),p(Dens+Leop)	143.98	5.48	0.0245	0.0646	6
Ψ (.),p(.)	144.49	5.99	0.019	0.05	2
Ψ (Dens.),p(.)	144.6	6.1	0.0179	0.0474	3
Ψ (.),p(Leop)	145.04	6.54	0.0144	0.038	3
Ψ (Lion.),p(.)	145.79	7.29	0.0099	0.0261	3
Ψ (Und),p(.)	145.86	7.36	0.0096	0.0252	3
Ψ (Lion.),p(Lion.)	145.96	7.46	0.0091	0.024	4
Ψ (.),p(Cover.)	146.14	7.64	0.0083	0.0219	3
Ψ (.),p(Dens)	146.2	7.7	0.0081	0.0213	3
Ψ (.),p(Preys.)	146.31	7.81	0.0076	0.0201	3
Ψ (.),p(BA)	146.41	7.91	0.0073	0.0192	3
Ψ (.),p(Lions)	146.45	7.95	0.0071	0.0188	3
Ψ (.),p(Und.)	146.49	7.99	0.007	0.0184	3
Ψ (.),p(Dens+Leop.)	146.97	8.47	0.0055	0.0145	4
Ψ (.),p(Lion+Leop.)	147	8.5	0.0054	0.0143	4
Ψ (.),p(Dens+Prey)	147.01	8.51	0.0054	0.0142	4
Ψ (.),p(Cover+Dens)	147.86	9.36	0.0035	0.0093	4
Ψ (.),p(Cover+Und)	148.14	9.64	0.0031	0.0081	4
Ψ (.),p(Prey+Und)	148.2	9.7	0.003	0.0078	4

*Ψ = probability of occupancy; p = probability of detection ; Preys = prey trap success; Dens = Tree density; Und = Understory cover; Cover = percent canopy cover; Serval = serval trap success; Leop = leopard trap success; Lion = lion trap success; BA = mean tree basal area; 1 group, Constant p = null model (occupancy and detection constant across the study site); 1 group, Survey-specific P = probability of occupancy constant, probability of detection varies with visits; + = additive effects

Table 2.6. Results of the 'two-species-single season' occupancy analysis of lion (dominant species) vs. leopard (subordinate species) under PsiBa parameterization. Models were developed using baseline models (1), (2), (3) and (4) and site covariates. Models are ranked based on their AIC values. ΔAIC = AIC difference, K = number of parameters. Models in bold are competing (ΔAICc <2). **(1):** No interactions for psi or p - psiA (.), psiBA= psiBa (.), pA, pB ,rA, rBA= rBa (.); **(2):** No interactions for psi, interactions for p - psiA (.), psiBA = psiBa (.), pA,pB ,rA, rBA ≠ rBA; **(3)**: Interactions for psi, no interactions for p - psiA (.), psiBA ≠ psiBa (.), pA,pB ,rA, rBA^A= rBa (.); **(4):** Interactions for psi and p - psiA (.), psiBA ≠ psiBa (.), pA,pB ,rA, rBA ≠ rBa (.)

Model*	AIC	ΔAIC	AIC weight	Model Likelihood	K
psiA (Prey.) ,psiBA=psiBa (BA),pA,pB,rA,rBA=rBa (Dens) (1)	**287.72**	**0**	**0.232**	**1**	**9**
psiA (Prey.) ,psiBA=psiBa (BA),pA,pB,rA,rBA=rBa (.) (1)	**289.18**	**1.46**	**0.1118**	**0.4819**	**8**
psiA (Prey.) ,psiBA=psiBa (BA),pA,pB,rA,rBA=rBa (Dens+Und) (1)	**289.59**	**1.87**	**0.0911**	**0.3926**	**10**
psiA (Prey.) ,psiBA=psiBa (Prey.),pA,pB,rA,rBA=rBa (.) (1)	289.86	2.14	0.0796	0.343	8
psiA (Prey.) ,psiBA=psiBa (.),pA,pB,rA,rBA=rBa (.) (1)	289.99	2.27	0.0746	0.3214	7
psiA (Prey.) ,psiBA=psiBa (BA),pA,pB,rA,rBA=rBa (Preys) (1)	290.75	3.03	0.051	0.2198	9
psiA (Preys) ,psiBA=psiBa (BA),pA,pB,rA,rBA*rBa (.) (2)	290.85	3.13	0.0485	0.2091	9
psiA (Preys) ,psiBA*psiBa (BA),pA,pB,rA,rBA=rBa (.) (3)	291.14	3.42	0.042	0.1809	9
psiA (Preys) ,psiBA=psiBa (Preys),pA,pB,rA,rBA*rBa (.) (2)	291.55	3.83	0.0342	0.1473	9
psiA (Preys) ,psiBA=psiBa (.),pA,pB,rA,rBA*rBa (.) (2)	291.71	3.99	0.0316	0.136	8
psiA (Preys) ,psiBA*psiBa (.),pA,pB,rA,rBA=rBa (.) (3)	291.88	4.16	0.029	0.1249	8
psiA (Prey.) ,psiBA=psiBa (Dens.),pA,pB,rA,rBA=rBa (.) (1)	291.95	4.23	0.028	0.1206	8
psiA (Preys) ,psiBA=psiBa (Und),pA,pB,rA,rBA*rBa (.) (2)	292.16	4.44	0.0252	0.1086	9
psiA (Preys) ,psiBA*psiBa Und,pA,pB,rA,rBA=rBa (.) (3)	292.35	4.63	0.0229	0.0988	9
psiA (Preys) ,psiBA*psiBa (BA),pA,pB,rA,rBA*rBa (.) (4)	292.8	5.08	0.0183	0.0789	10
psiA (Preys) ,psiBA*psiBa (.),pA,pB,rA,rBA*rBa (.) (4)	293.61	5.89	0.0122	0.0526	9
psiA (Preys) ,psiBA=psiBa (Dens),pA,pB,rA,rBA*rBa (.) (2)	293.66	5.94	0.0119	0.0513	9

*psiA = probability of occupancy for species A; psiBA = probability of occupancy for species B, given species A is present; psiBa = probability of occupancy for species B, given species A is absent; pA = probability of detection for species A, given species B is absent; pB = probability of detection for species B, given species A is absent; r^A = probability of detection for species A, given both species are present; rBA= probability of detection for species B, given both species are present and species A is detected; rBA = probability of detection for species B, given both species are present and species A is not detected; Preys = prey trap success; Dens = Tree density; Und = Understory cover; Cover = percent canopy cover; Serval = serval trap success; Leop = leopard trap success; Lion = lion trap success; BA = mean tree basal area; 1 group, Constant p = null model (occupancy and detection constant across the study site); 1 group, Survey-specific P = probability of occupancy constant, probability of detection varies with visits. (1), (2), (3), (4) = baseline models from which models with covariates are developed (see methods)

Table 2.7. Results of the 'two-species-single season' occupancy analysis of lion (dominant species) vs. serval (subordinate species) under PsiBa parameterization. Models were developed using baseline models (1), (2), (3) and (4) and site covariates. Models are ranked based on their AIC values. ΔAIC = AIC difference, K = number of parameters. Models in bold are competing (ΔAICc <2). **(1):** No interactions for psi or p - Ψ^A (.), $\Psi^{BA} = \Psi^{Ba}$ (.), p^A, p^B ,r^A, $r^{BA} = r^{Ba}$ (.); **(2):** No interactions for psi, interactions for p - Ψ^A (.), $\Psi^{BA} = \Psi^{Ba}$ (.), p^A, p^B ,r^A, $r^{BA} \neq r^{Ba}$; **(3):** Interactions for psi, no interactions for p - Ψ^A (.), $\Psi^{BA} \neq \Psi^{Ba}$ (.), p^A, p^B ,r^A, $r^{BA} = r^{Ba}$ (.); **(4):** Interactions for psi and p - Ψ^A (.), $\Psi^{BA} \neq \Psi^{Ba}$ (.), p^A, p^B ,r^A, $r^{BA} \neq r^{Ba}$ (.)

Model*	AIC	ΔAIC	AIC wgt	Model Likelihood	K
psiA (Prey.) ,psiBA=psiBa (Cover),pA,pB,rA,rBA=rBa (.) (1)	**264.14**	**0**	**0.089**	**1**	**8**
psiA (.) ,psiBA=psiBa (Leop.),pA,pB,rA,rBA=rBa (.) (1)	**264.48**	**0.34**	**0.0751**	**0.8437**	**7**
psiA (Dens) ,psiBA=psiBa (Leop.),pA,pB,rA,rBA=rBa (Leop) (1)	**264.56**	**0.42**	**0.0722**	**0.8106**	**9**
psiA (.) ,psiBA=psiBa (Leop.),pA,pB,rA,rBA=rBa (Leopard) (1)	**264.69**	**0.55**	**0.0676**	**0.7596**	**8**
psiA (Preys) ,psiBA=psiBa (Cover),pA,pB,rA,rBA*rBa (.) (2)	**265.34**	**1.2**	**0.0489**	**0.5488**	**9**
psiA (Prey.) ,psiBA=psiBa (.),pA,pB,rA,rBA=rBa (.) (1)	**265.58**	**1.44**	**0.0433**	**0.4868**	**7**
psiA (Preys) ,psiBA*psiBa (Cover),pA,pB,rA,rBA = rBa (.) (3)	**265.81**	**1.67**	**0.0386**	**0.4339**	**9**
psiA (Prey.) ,psiBA=psiBa (Dens.),pA,pB,rA,rBA=rBa (.) (1)	**265.92**	**1.78**	**0.0366**	**0.4107**	**8**
psiA (Dens) ,psiBA=psiBa (Leop.),pA,pB,rA,rBA=rBa (.) (1)	**266.04**	**1.9**	**0.0344**	**0.3867**	**8**
psiA (.) ,psiBA=psiBa (Leop.),pA,pB,rA,rBA=rBa (Lion) (1)	**266.1**	**1.96**	**0.0334**	**0.3753**	**8**
psiA (Preys) ,psiBA*psiBa (Preys),pA,pB,rA,rBA*rBa (Cover) (4)	266.45	2.31	0.028	0.3151	11
psiA (.) ,psiBA=psiBa (Leop.),pA,pB,rA,rBA=rBa (Dens) (1)	266.47	2.33	0.0278	0.3119	8
psiA (Prey.) ,psiBA=psiBa (Und.),pA,pB,rA,rBA=rBa (.) (1)	266.6	2.46	0.026	0.2923	8
psiA (Preys) ,psiBA=psiBa (.),pA,pB,rA,rBA*rBa (.) (2)	266.67	2.53	0.0251	0.2822	8
psiA (Preys) ,psiBA*psiBa (.),pA,pB,rA,rBA=rBa (.) (3)	266.76	2.62	0.024	0.2698	8
psiA (Preys) ,psiBA*psiBa (Covers),pA,pB,rA,rBA*rBa (.) (4)	266.85	2.71	0.023	0.2579	10
psiA (Prey.) ,psiBA=psiBa (BA),pA,pB,rA,rBA=rBa (.) (1)	267.01	2.87	0.0212	0.2381	8
psiA (Preys) ,psiBA=psiBa (Dens),pA,pB,rA,rBA*rBa (.) (2)	267.06	2.92	0.0207	0.2322	9
psiA (Prey.) ,psiBA=psiBa (Prey.),pA,pB,rA,rBA=rBa (.) (1)	267.24	3.1	0.0189	0.2122	8
psiA (Preys) ,psiBA*psiBa (Preys),pA,pB,rA,rBA=rBa (Cover) (3)	267.34	3.2	0.018	0.2019	10
psiA (Preys) ,psiBA*psiBa (Dens),pA,pB,rA,rBA=rBa (.) (3)	267.6	3.46	0.0158	0.1773	9

*psiA = probability of occupancy for species A; psiBA = probability of occupancy for species B, given species A is present; psiBa = probability of occupancy for species B, given species A is absent; pA = probability of detection for species A, given species B is absent; pB = probability of detection for species B, given species A is absent; rA = probability of detection for species A, given both species are present; rBA= probability of detection for species B, given both species are present and species A is detected; rBA = probability of detection for species B, given both species are present and species A is not detected; Preys = prey trap success; Dens = Tree density; Und = Understory cover; Cover = percent canopy cover; Serval = serval trap success; Leop = leopard trap success; Lion = lion trap success; BA = mean tree basal area; 1 group, Constant p = null model (occupancy and detection constant across the study site); 1 group, Survey-specific P = probability of occupancy constant, probability of detection varies with visits. (1), (2), (3), (4) = baseline models from which models with covariates are developed (see methods)

Table 2.8. Results of the two-species-single season occupancy analysis of leopard (dominant species) vs. serval (subordinate species) under PsiBa parameterization. Models were developed using baseline models (1), (2), (3) and (4) and site covariates. Models are ranked based on their AIC values. ΔAIC = AIC difference, K = number of parameters. Models in bold are competing (ΔAICc <2). **(1):** No interactions for psi or p - Ψ^A (.), $\Psi^{BA} = \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} = r^{Ba}$ (.); **(2):** No interactions for psi, interactions for p - Ψ^A (.), $\Psi^{BA} = \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} \neq r^{Ba}$; **(3):** Interactions for psi, no interactions for p - Ψ^A (.), $\Psi^{BA} \neq \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} = r^{Ba}$ (.); **(4):** Interactions for psi and p - Ψ^A (.), $\Psi^{BA} \neq \Psi^{Ba}$ (.), $p^A, p^B, r^A, r^{BA} \neq r^{Ba}$ (.)

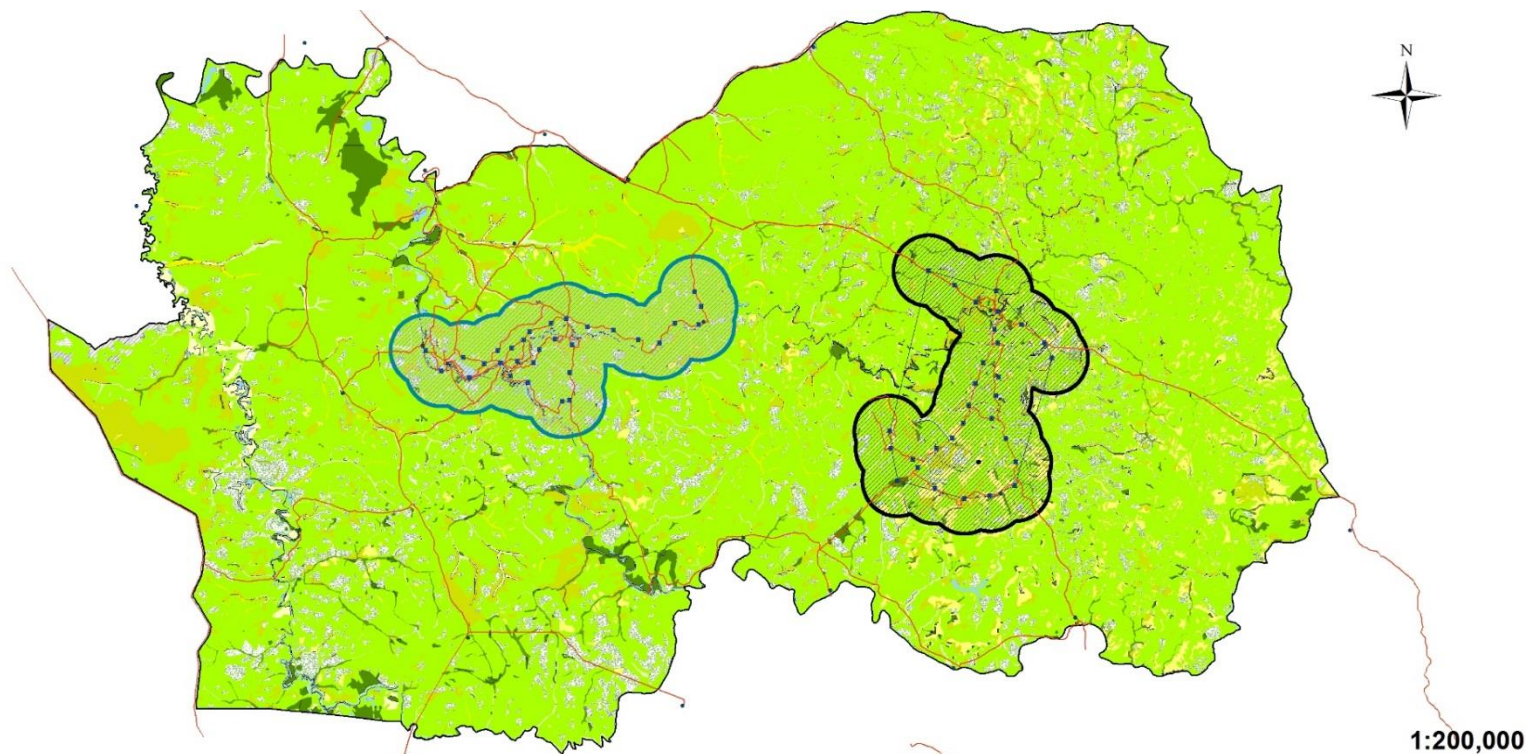| Model*	AIC	ΔAIC	AIC weight	Model Likelihood	K
psiA (Prey.) ,psiBA=psiBa (Dens.),pA,pB,rA,rBA=rBa (.) (1)	**310.35**	**0.00**	**0.07**	**1.00**	**8**
psiA (Prey.) ,psiBA=psiBa (.),pA,pB,rA,rBA=rBa (.) (1)	**310.36**	**0.01**	**0.07**	**1.00**	**7**
psiA (Prey.) ,psiBA=psiBa (Prey.),pA,pB,rA,rBA=rBa (.) (1)	**310.54**	**0.19**	**0.07**	**0.91**	**8**
psiA (Prey.) ,psiBA=psiBa (Dens.),pA(Dens),pB(Dens),rA,rBA=rBa (.) (1)	**310.83**	**0.48**	**0.06**	**0.79**	**10**
psiA (.) ,psiBA=psiBa (.),pA,pB,rA,rBA=rBa (.) (1)	**311.23**	**0.88**	**0.05**	**0.64**	**6**
psiA (Preys) ,psiBA=psiBa (.),pA,pB,rA,rBA*rBa (.) (2)	**311.45**	**1.10**	**0.04**	**0.58**	**8**
psiA (Preys) ,psiBA=psiBa (Preys),pA,pB,rA,rBA*rBa (.) (2)	**311.63**	**1.28**	**0.04**	**0.53**	**9**
psiA (Lion) ,psiBA=psiBa (.),pA,pB,rA,rBA=rBa (Dens) (1)	**311.77**	**1.42**	**0.04**	**0.49**	**8**
psiA (.) ,psiBA=psiBa (.),pA(.),pB(Preys),rA,rBA=rBa (.) (1)	**311.82**	**1.47**	**0.03**	**0.48**	**7**
psiA (Prey.) ,psiBA=psiBa (BA),pA,pB,rA,rBA=rBa (.) (1)	**312.11**	**1.76**	**0.03**	**0.41**	**8**
psiA (Preys) ,psiBA*psiBa (.),pA,pB,rA,rBA=rBa (.) (3)	**312.24**	**1.89**	**0.03**	**0.39**	**8**
psiA (Preys) ,psiBA*psiBa (.),pA,pB,rA,rBA = rBa (.) (3)	**312.24**	**1.89**	**0.03**	**0.39**	**8**
psiA (.) ,psiBA=psiBa (.),pA,pB,rA,rBA*rBa (.) (2)	**312.26**	**1.91**	**0.03**	**0.38**	**7**
psiA (.) ,psiBA=psiBa (.),pA,pB,rA,rBA*rBa (.) (2)	**312.26**	**1.91**	**0.03**	**0.38**	**7**
psiA (Prey.) ,psiBA=psiBa (Und.),pA,pB,rA,rBA=rBa (.) (1)	312.36	2.01	0.03	0.37	8
psiA (Preys) ,psiBA*psiBa (Preys),pA,pB,rA,rBA=rBa (.) (3)	312.52	2.17	0.02	0.34	9
psiA (.) ,psiBA*psiBa (.),pA,pB,rA,rBA=rBa (.) (3)	312.95	2.60	0.02	0.27	7
psiA (.) ,psiBA*psiBa (.),pA,pB,rA,rBA=rBa (.) (3)	312.95	2.60	0.02	0.27	7
psiA (Prey.) ,psiBA=psiBa (BA),pA,pB,rA,rBA=rBa (Dens) (1)	312.97	2.62	0.02	0.27	9
psiA (Preys) ,psiBA=psiBa (BA),pA,pB,rA,rBA*rBa (.) (2)	313.18	2.83	0.02	0.24	9
psiA (Lion) ,psiBA=psiBa (Lion.),pA,pB,rA,rBA=rBa (Dens) (1)	313.22	2.87	0.02	0.24	8
psiA (Dens.) ,psiBA=psiBa (.),pA,pB,rA,rBA=rBa (.) (1)	313.23	2.88	0.02	0.24	7

*psiA = probability of occupancy for species A; psiBA = probability of occupancy for species B, given species A is present; psiBa = probability of occupancy for species B, given species A is absent; pA = probability of detection for species A, given species B is absent; pB = probability of detection for species B, given species A is absent; r^A = probability of detection for species A, given both species are present; rBA= probability of detection for species B, given both species are present and species A is detected; rBA = probability of detection for species B, given both species are present and species A is not detected; Preys = prey trap success; Dens = Tree density; Und = Understory cover; Cover = percent canopy cover; Serval = serval trap success; Leop = leopard trap success; Lion = lion trap success; BA = mean tree basal area; 1 group, Constant p = null model (occupancy and detection constant across the study site); 1 group, Survey-specific P = probability of occupancy constant, probability of detection varies with visits. (1), (2), (3), (4) = baseline models from which models with covariates are developed (see methods)

Figure 2.1. Location of the two study areas in the Niokolo Koba National Park, Senegal. Camera-trapping was completed in Linguekountou from February to April 2013 and in Niokolo from April 30 to July 07 2013.Shapefiles from Tappan (2012).
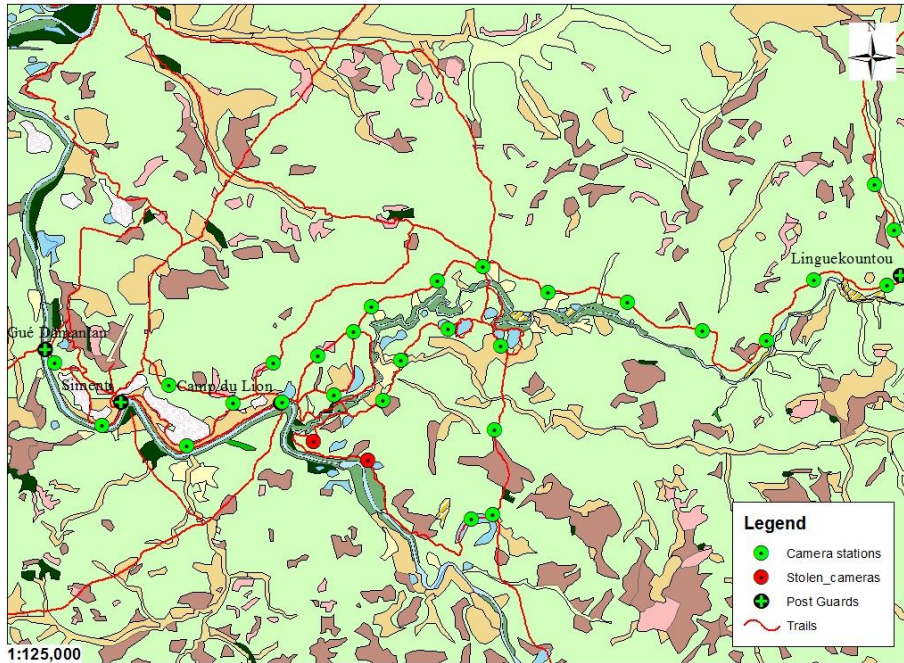
Figure 2.2a. Location of the 30 camera traps in Linguekountou, in the Niokolo Koba National Park, Senegal. Camera-trap was completed in the study area from February 4 to April 23 2013. Land use/Land cover shapelfiles from Tappan (2012).
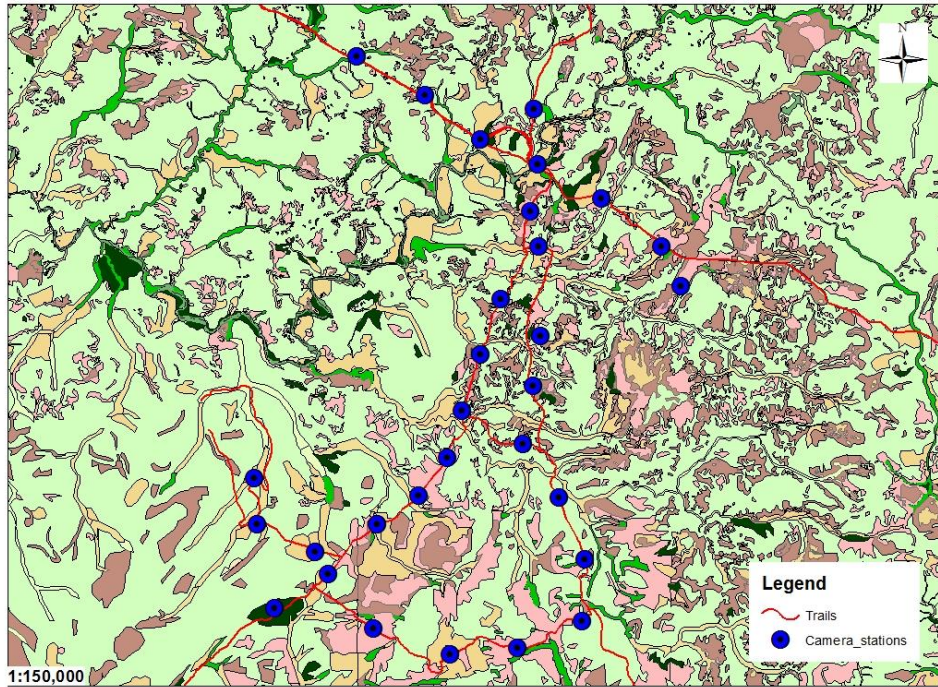
Figure 2.2b. Location of the 30 camera traps in Niokolo area, in the Niokolo Koba National Park, Senegal. Camera-trap was completed in the study area from April 30 to July 07 2013. Land use/Land cover shapelfiles from Tappan (2012).
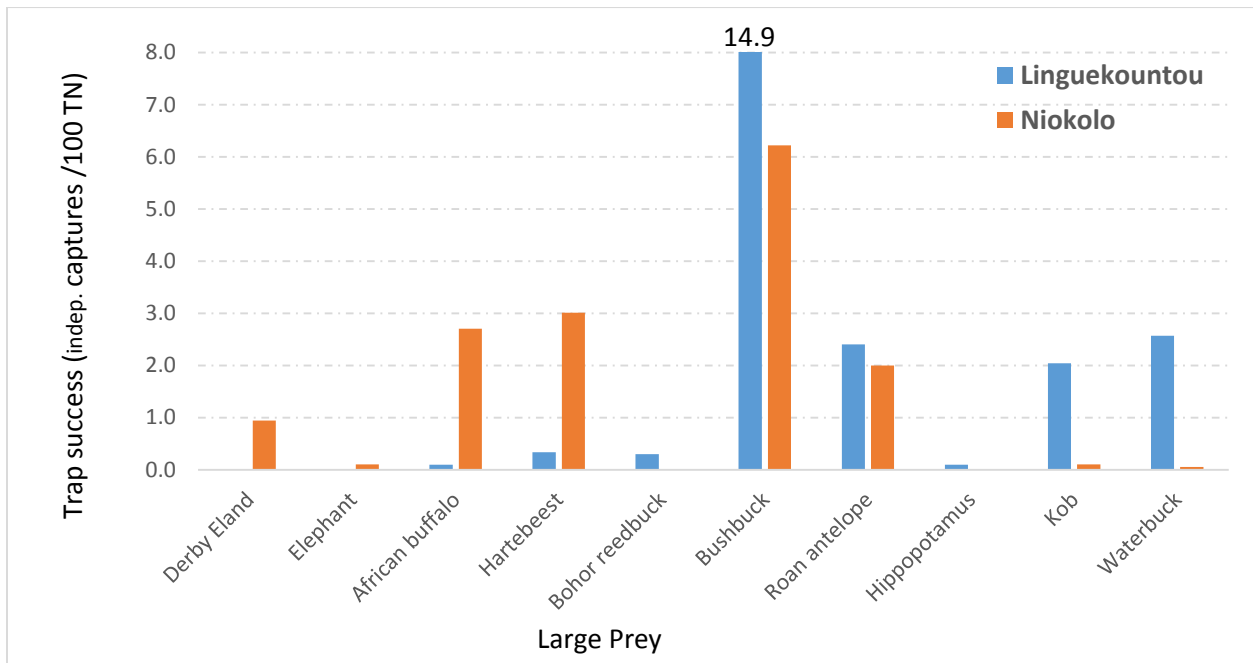
Figure 2.3. Large prey trap successes (number of independent captures per 100 trap-nights) during the camera trapping sessions in 2013 in Linguekountou and Niokolo in the Niokolo Koba National Park. Numbers above the bars indicate trap rates for species that go off the chart. Large prey is defined as all mammal herbivores and omnivores that weigh more than 45 kg and upon which lions and leopards potentially prey.
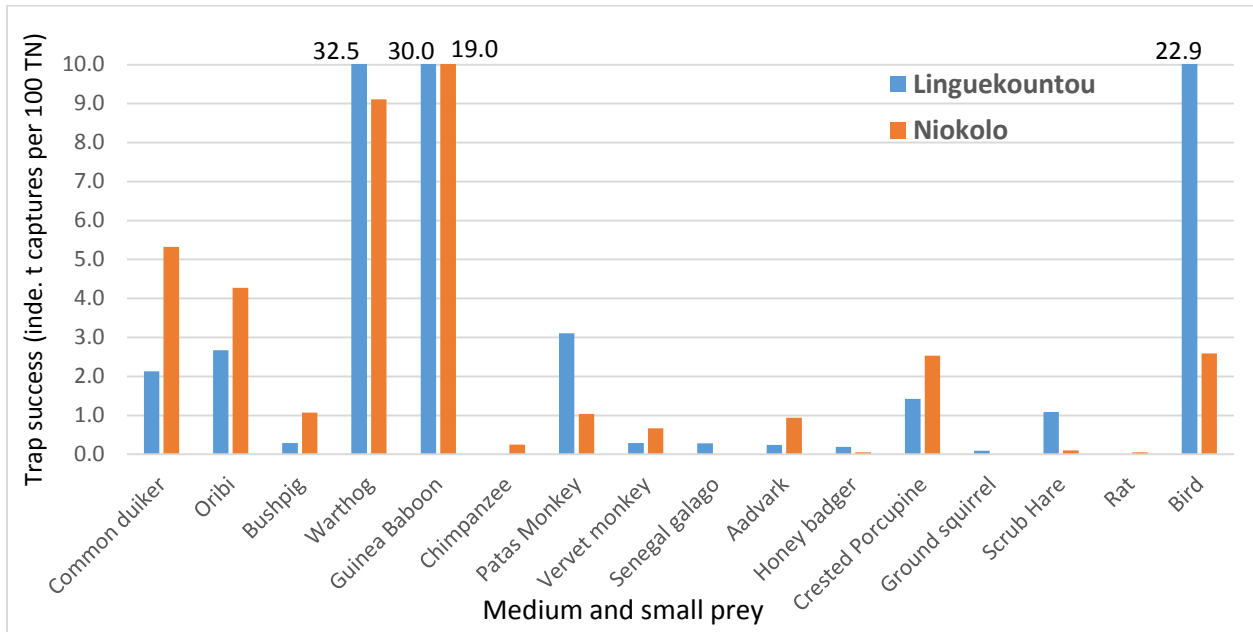
Figure 2.4. Medium and small prey trap successes (number of captures per 100 trap-nights) during the camera trapping sessions in 2013 in Linguekountou and Niokolo in the Niokolo Koba National Park. Numbers above the bars indicate trap rates for species that go off the chart. Medium and smalls preys are defined as all mammal herbivores and omnivores that weigh less than 45 kg and upon which lions and leopards potentially prey.
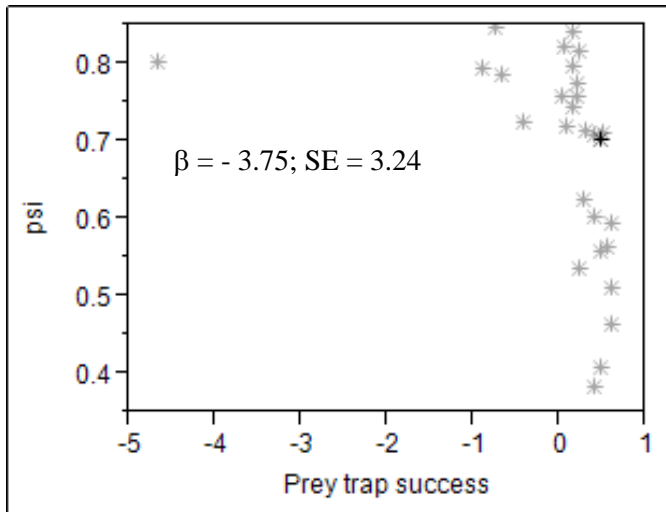
a
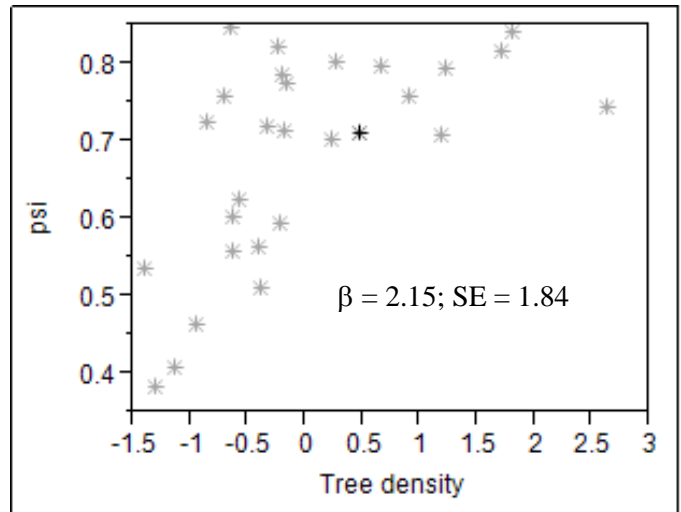
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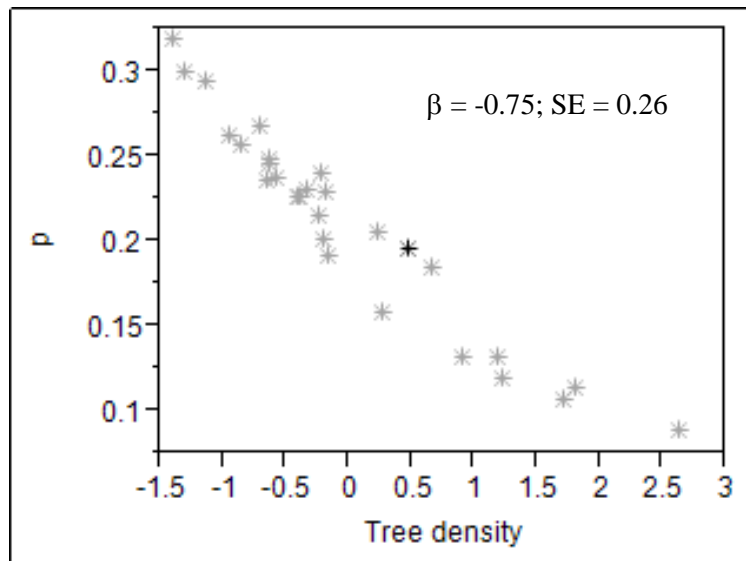
c

Figure 2.5. Based on logistic regression analysis in Program PRESENCE, the relationships between (a) leopard occupancy (psi) and prey trap success, (b) leopard occupancy and tree density (c) leopard probability of detection and tree density. Betas are from top-ranked model outputs in PRESENCE.
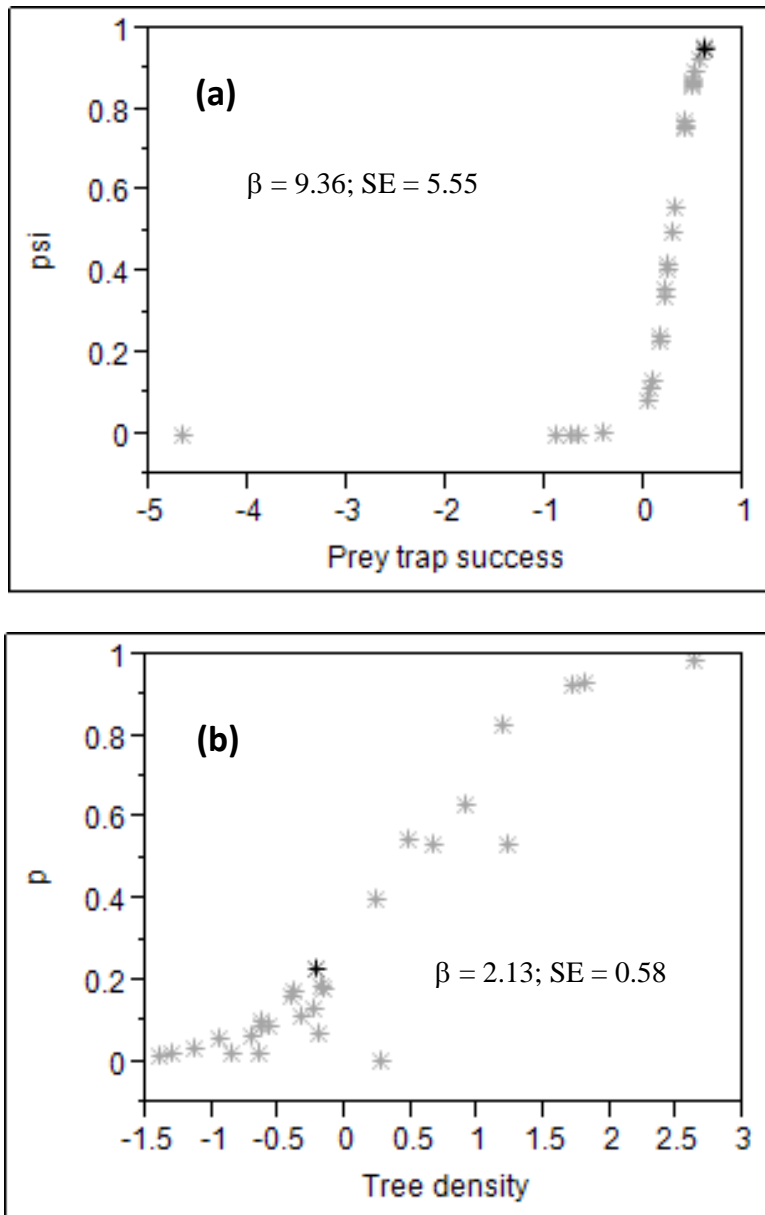
Figure 2.6. Based on logistic regression analysis in Program PRESENCE, the relationships between (a) lion occupancy (psi) and prey trap success, and (b) lion detection (p) and tree density. Betas are from top-ranked model outputs in PRESENCE.
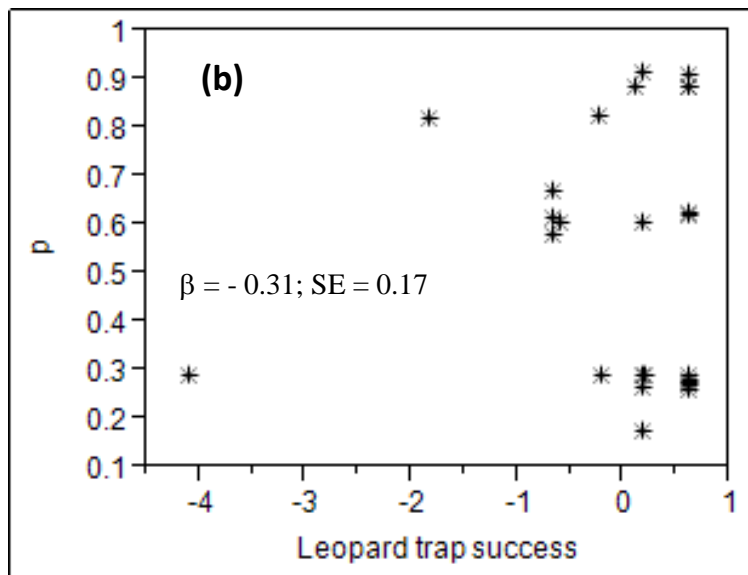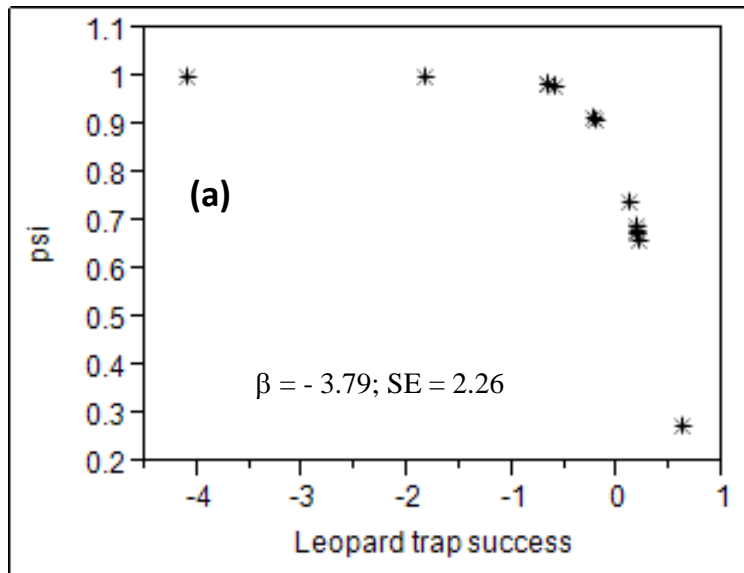
Figure 2.7. Based on logistic regression analysis in Program PRESENCE, the relationships between (a) serval occupancy (psi) and leopard trap success and (b) serval detection (p) and leopard trap success. Betas are from top-ranked model outputs in PRESENCE.
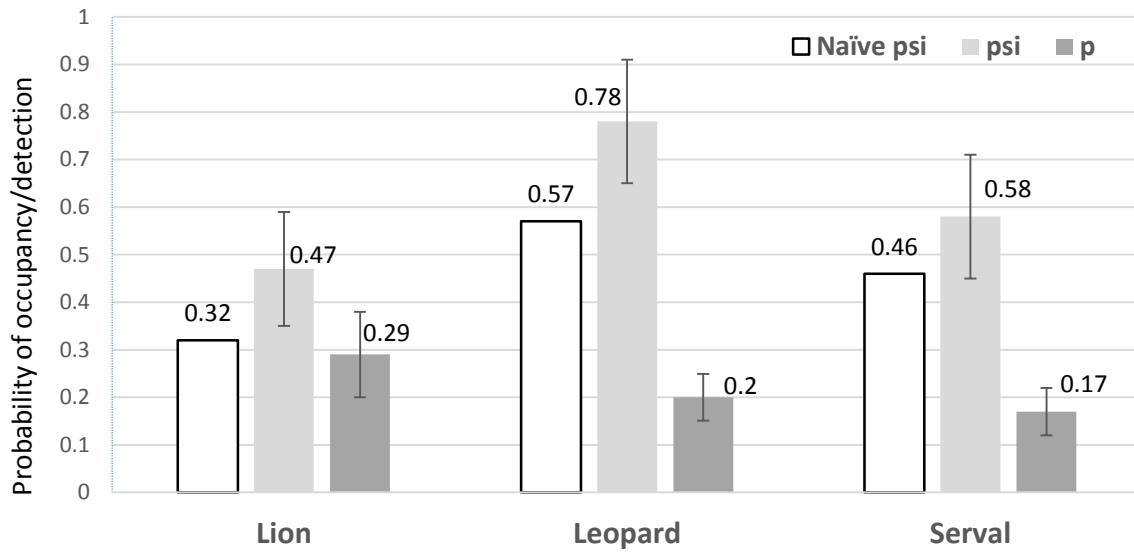
Figure 2.8. Comparison of lion, leopard, and serval naïve occupancies and probabilities of occupancy (psi) and detection (p) across the study site in the Niokolo Koba National Park.
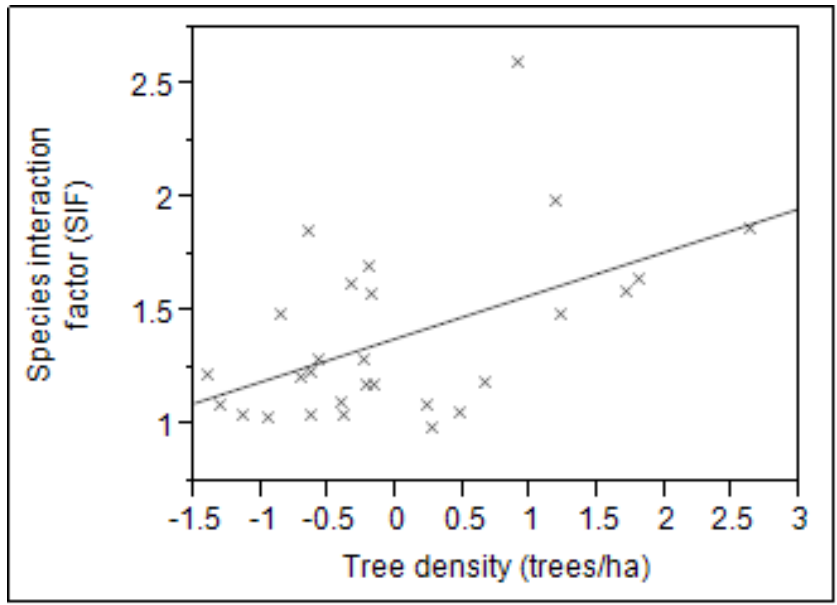
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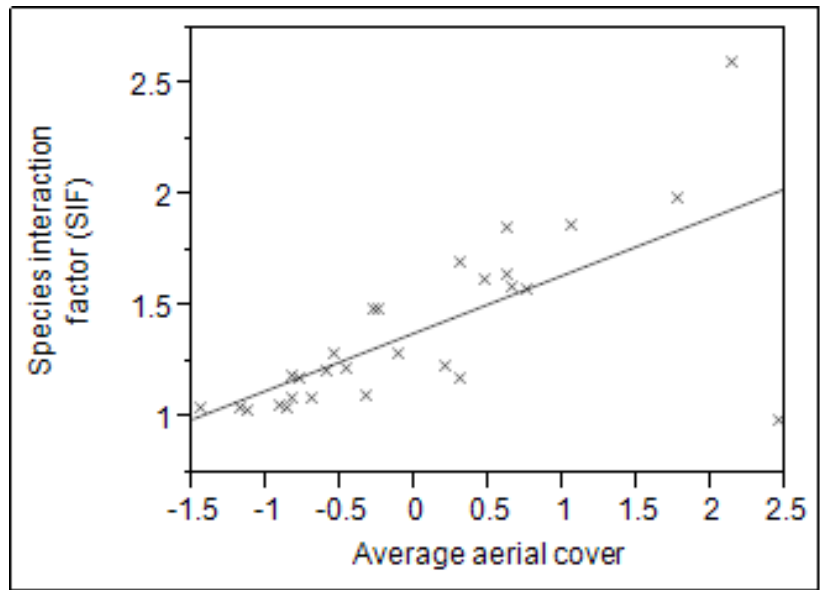
b

Fig. 2.9. Linear relationship between lions and servals species interaction factor (SIF) and (a) tree density; (b) aerial cover across the 28 camera station locations.

Appendix A.1: Trap successes (number of independent captures per 100 trap-nights) of all animals captured during the two camera trapping sessions in Linguekountou (February 4 to April 23 2013) and Niokolo (April 30 to July 07 2013) in the Niokolo Koba National Park, Senegal.

	Common names	Scientific names	Linguekountou	Niokolo
1	Aadvark	*Orycteropus afer*	0.24	0.94
2	African Buffalo	*Syncerus caffer*	0.10	2.71
3	African civet	*Civettictis civetta*	9.00	1.11
4	African wild cat	*Felis silvestris lybica*	0.54	0.00
5	African wild dog	*Lycaon pictus*	0.25	0.00
6	Banded mongoose	*Mungos mungo*	5.13	2.22
7	Birds		22.91	2.59
8	Bohor reedbuck	*Redunca redunca*	0.30	0.00
9	Bushbuck	*Tragelaphus scriptus*	14.93	6.22
10	Bushpig	*Potamochoerus larvatus*	0.29	1.07
11	Caracal	*Felis caracal*	0.00	0.42
12	Chimpanzee	*Pan troglodytes*	0.00	0.25
13	Common duiker	*Sylvicapra grimmia*	2.13	5.32
14	Common genet	*Genetta genetta*	3.26	1.45
15	Derby Eland	*Taurotragus derbianus*	0.00	0.94
16	Elephant	*Loxodonta africana*	0.00	0.10
17	Crested Porcupine	*Hystrix cristata*	1.43	0.00
18	Ground squirrel	*Xerus erythropus*	0.09	0.00
19	Gambian mongoose	*Mungos gambianus*	0.00	0.05
20	Guinea baboon	*Papio papio*	30.03	19.03
21	Hare	*Lepus saxatilis*	0.00	0.10
22	Hartebeest	*Alcelaphus buselaphus*	0.33	3.01
23	Hippopotamus	*Hippopotamus amphibius*	0.10	0.00
24	Honey badger	*Mellivora capensis*	0.19	0.05
25	Kob	*Kobus kob*	2.04	0.10
26	Large Grey Mongoose	*Herpestes ichneumon*	0.19	0.00
27	Leopard	*Panthera pardus*	1.91	0.67
28	Lion	*Panthera leo*	2.06	0.31
29	Oribi	*Ourebia ourebi*	2.67	4.27
30	Patas monkey	*Erythrocebus patas*	3.11	1.04
31	Crested porcupine	*Hystrix cristata*	1.43	2.53
32	Rat	*Rattus sp*	0.00	0.05
33	Roan antelope	*Hippotragus equinus*	2.40	2.00
34	Scrub Hare	*Lepus saxatilis*	1.08	0.00
35	Senegal galago	*Galago senegalensis*	0.28	0.00
36	Serval	*Leptailurus serval*	1.41	0.42
37	Side-striped Jackal	*Canis adustus*	2.61	1.12
38	Slender Mongoose	*Galerella sanguinea*	0.23	0.00

39	Spotted hyena	*Crocuta crocuta*	2.20	1.23
40	Vervet monkey	*Cercopithecus aethiops*	0.29	0.67
41	Warthog	*Phacochoerus africanus*	32.54	9.11
42	Waterbuck	*Kobus ellipsiprymnus defassa*	2.57	0.05
43	Water-marsh mongoose	*Atilax paludinosus*	3.42	1.45
44	White-tailed mongoose	*Ichneumia albicauda*	3.04	1.48

Chapter 3 – Estimating population size and density of the lion (*Panthera leo*), leopard (*P. pardus*) and serval (*Leptailurus serval*) using camera traps in the Niokolo Koba National Park in Senegal

Abstract

Effective management of threatened species requires precise estimates of abundance and density in addition to distribution. Camera-trapping techniques, combined with capture-recapture, have proven effective in estimating these parameters. We used camera-trapping techniques to assess population size and density simultaneously for 3 felid species: lions (*Panthera leo*), leopards (*Panthera pardus*), and servals (*Leptailurus serval*) in the imperiled Niokolo Koba National Park in Senegal. This is the first study estimating serval density, the first study in West Africa estimating leopard and lion densities from camera traps, and the first study to use mark-resight models for lion density estimation. We used 2 traditional capture-recapture (CR) and 2 spatially-explicit capture-recapture (SECR) methods for leopards and servals and we used non-spatial (MR) and spatial (SMR) mark resight models for lions. Leopard densities from the traditional CR using programs CAPTURE and MARK ranged from $1.88 - 2.23$ individuals per 100 km^2, while serval densities ranged from 2.44 to 4.73 individuals/100 km^2. The maximum likelihood SECR method, implemented in program DENSITY yielded leopard density estimates of 2.19 to 2.53 and serval density estimates of $3.49 - 4.08$ individuals per 100 km^2, while the Bayesian SECR executed with R package SPACECAP resulted in lower leopard densities between $1.78 - 1.82$ and lower serval densities ranging between 2.70 and 2.82. Unlike most studies that compared carnivore densities using the described techniques, our estimates from program DENSITY were similar or higher than those from traditional CR methods. SPACECAP yielded lower estimates, as expected. The MR model implemented in MARK estimated lion density at 2.56 (SE = 0.63) individuals per 100 km^2, while the SMR model resulted in an estimate of 1.74 (0.31). Our lion density is much higher than a previous estimate in NKNP that used line transect techniques (0.2 lions/100 km^2), which are known to be ineffective for large carnivores. This study proved that camera traps can be used in wooded savannah habitats to provide reliable estimates of carnivore density, providing much needed baseline information for

the park. We also confirmed that leopards and lions have lower densities in West Africa compared to southern and eastern Africa.

Introduction

Effective management of protected areas requires accurate and precise estimates of abundance and density as well as distribution of wildlife population (Sheng et al. 2010). Various animal census methods can be employed but only some are appropriate for estimating the abundance of elusive, cryptic, and rare wildlife species such as carnivores. Recently developed camera-trapping techniques using a capture-recapture framework (Karanth 1995) have proven effective in estimating population size and density of such species, which formerly were only estimated using ineffective techniques. Silveira et al. (2003) compared camera trapping with line transect and track surveys and found that camera trapping was "most appropriate for mammal inventory in all environmental conditions, allowing a rapid assessment of wildlife conservation status". Camera trapping for carnivores, especially felids, is now widely used for abundance and density estimation, which greatly improves our knowledge of, and effectiveness in, wildlife population ecology and management.

In Africa, camera trapping has been used in several studies targeting elusive species such as carnivores (Kauffman et al. 2007, Marnewick et al. 2008, Balme et al. 2010, Henschel et al. 2010, Pettorelli et al. 2010) but most of these studies occurred in southern and eastern Africa, following the same trend as the strong bias in carnivore research in Africa (Ray et al. 2005, Henschel et al. 2014). This is likely due to the fact that carnivores are thought to occur in lower densities in western and central Africa compared to eastern and southern Africa. For instance, the lion is classified as "Regionally Endangered" by the IUCN Red List in West Africa while it remains only "Vulnerable" overall (Bauer and Nowell 2004, IUCN 2013). To date, no study using camera trapping to estimate carnivore abundance and/or density has been conducted in West Africa, despite the growing interest in these carnivore populations during the last two decades.

As in other parts of West Africa, very few estimates of carnivore population size have been conducted in Senegal. The most important carnivore community in Senegal is thought to occur in the Niokolo Koba National Park (NKNP). The only study that specifically targeted all

carnivores in that park was conducted by Sillero-Zubiri et al. (1997a) who used line transects and calling stations to investigate distribution and encounter rates of the NKNP carnivores. Henschel et al. (2014) focused solely on the lion population, which they estimated at 16 individuals with low precision (0-54 individuals) using track surveys and calling stations. Our goal in this study is to use carnivore specific techniques (i.e. camera trapping) to estimate abundance and density of three felid species simultaneously and thus add more reliable information about carnivore status in the Niokolo Koba National Park. This study estimates population size and density of one medium-size (serval) and two large (lion and leopard) carnivores using both a traditional capture –recapture (CR) framework and a spatially explicit capture-recapture (SECR) framework. For servals and leopards, I compared density estimates from 2 CR methods and 2 SECR methods, whereas for lions I used both non-spatial (MR), and spatial, mark-resight (SMR) models to calculate density.

I hypothesized that, lion and leopard abundance and density will be lower than serval abundance because of their biological traits (larger home range requirements, larger body size, and slower life history) as theorized by Purvis et al. (2000). Of the larger two species, lions should have lower density than leopards for similar reasons and because of the lion's preference for larger-bodied prey (Stuart and Stuart 2006), populations that are being drastically depleting according to Renaud et al. (2006). Additionally, because of the multiple threats that the park is facing (poaching, habitat loss and fragmentation), densities will be low for all three species in comparison to southern and eastern Africa following the general trend in West African protected areas. I also hypothesize that capture probabilities of the 3 species will be heterogeneous because each individual is expected to have a different trapping response, as found in most camera-trap carnivore studies (Foster et al. 2012; Tobler and Powell 2013). Behavioral response may also be found for all three species because of night camera flash that might frightened them (Wegge et al. 2004). Finally, I predict that density estimates for lions and leopards from this study will be more precise than those from Ndao and Henschel (2011, unpublished data) and Henschel et al. (2014) who used track counts and calling stations. We believe that their methods overestimated leopard density and underestimated lion density. This study is the first to use camera trapping to estimate population size and density of carnivore species in Senegal and possibly in West Africa as a whole.

Knowledge of carnivore ecology is crucial in managing protected areas as most of them are indicators of ecosystem health because of their trophic position, which makes them vulnerable to ecosystem perturbations at any level (Mills 1991). In addition, most carnivores, especially large ones, likely play the role of umbrella and keystone species as they have large area requirements and play a crucial role in maintaining ecosystem structure, thus preventing shifts in habitat and species extinction via trophic cascades (Noss et al. 1996, Terborgh et al. 2001, Gittleman et al. 2001). Because of their threatened status and conflicts with humans, conserving these species has become a global challenge, despite the fact that wild carnivores are also viewed as charismatic, flagship species that attract human attention for many reasons (Karanth and Chellam 2009). In the specific context of the Niokolo Koba, this study will not only confirm the feasibility of camera trapping in wooded savannahs, but it will also shed light on carnivore status, specifically for the lion, since the most recent estimate done without carnivore specific methods (Henschel et al. 2014) indicates that the lion is on the verge of extinction in the park. Therefore, my study will be able to confirm, refute, or at the very least, refine, this assertion with more carnivore specific methodology and analyses.

Material and methods

Study site

The Niokolo Koba National Park was created in 1954 and is located in south-eastern Senegal, between 12°30' and 13°20' North and 18°30' and 13°42' West, in a well-watered region, unlike most parts of the country (Fig. 3.1). It covers 9,130 km^2 and contains heterogeneous vegetation types, generated by complex soil and geologic formations that are distributed in three types of terrain: valleys, plateaus, and hills with the highest elevation at Mount Assirik – 311 meters. The climate is of Sudanian type with a rainy season from May to October. Average annual rainfall ranges from 900 to 1,200 millimeters and temperature ranges from 25°C in December to 33°C in May (DPNS, 2000). The climate creates a transitional vegetation between Sudano-Guinean savanna and Guinean savanna, with wooded savannah composing nearly 69% of the habitat types (Tappan 2012). All the streams of the park belong to the catchment of the Gambia River, which crosses the park from southeast to northwest. The

main tributaries are Niokolo Koba, Koulountou, and Nieriko. In addition to these streams, some permanent and temporary ponds and pools play an important role in water and fresh grass supply for wildlife. Because of its location in the extreme west of Africa and on the northern edge of the sub-sahelian woodland belt, it harbors many mammal populations that are at the northern extreme of their distribution (Sillero-Zubiri et al. 1997a).

Field methods

We decided on camera trap locations within NKNP after consultation with the park managers and a pilot study in 2012. For the pilot study, we systematically placed each camera station within a 3 X 3 km grid cell spread across the landscape, deploying 5 camera stations along human trails and the remaining 20 on wildlife game trails. Although we did not photograph any of the target species, most of the other carnivore captures occurred on human trails, consistent with other carnivore-oriented studies (Foster and Harmsen 2012; Tobler and Powell 2013). Subsequently, we decided to place all cameras used for this study on human trails (surveillance and touristic trails) and roads. However, before setting up a station, we first searched for carnivore signs such as tracks and scats to target those areas in order to potentially increase capture rates.

Camera trapping was conducted at two study sites: Linguekountou between February 4th and April 23rd 2013 and Niokolo between April 30th and July 07th. Due to very low capture rates at Niokolo we could not use the data for capture-recapture analyses. Therefore the following information in this chapter is all from our first study site, Linguekountou. We deployed 30 stations in 5 days across the dense network of human trails and roads from 5 km north of the old guard post of Linguekountou to the guard post of Gué Damantan (Fig 3.2), resulting in a minimum convex polygon surrounding cameras of 285.4 km^2. The less frequently used trails and roads were sometimes bushy and were cleared out before setting up a station. Two camera stations were stolen during the first two weeks without replacement. The average distance between two consecutive cameras was 2.5 km (SD = 0.68; min = 0.82; max = 3.2 km). Cameras were mounted on trees at 30 to 40 cm above the ground, and consisted of two cameras at each station placed on the opposing side of a trail or road (mean road/trail width = 3 m), with a slight

offset to avoid mutual flash interference. Each station comprised at least one digital and one film camera to capture both flanks of passing animals and to ensure that stations will still be functional even if analog cameras – which are more prone to failure – run out of film or batteries. Seven stations consisted of two digital cameras. We used 37 digital cameras comprised of 31 Moultrie L50 and 06 Moultrie D55 cameras and 23 DeerCam 300 and 200. Digital cameras were set to take two consecutive pictures for each trigger event with a delay of one minute while the film cameras were adjusted to take one picture per capture event, with a delay of 30 seconds between pictures. Both types of cameras were also set to stamp date and time on the bottom of the photographs, even though most of the film cameras failed to do so. Cameras were checked every 13 to 15 days to replace batteries, film, memory cards or malfunctioning cameras.

Data analysis

Individual identification and capture histories

Photographs of distinct individual animals taken within a 30 minute-time interval were only recorded once (i.e. as a single capture event), regardless of the number of photographs in calculating trap success. Trap success was calculated for all mammal species (including humans) caught at each station as the number of capture events of a given species per 100 trap-nights, following Dillon and Kelly (2007). A trap-night is defined as a 24-hour period where the station is fully active (at least one of the 2 cameras is functional).

Individual leopards and servals were identified by their distinct natural markings by two independent investigators who, in our case, always agreed on serval identifications. Blurry photographs and unidentifiable individuals were discarded from analysis. However, because most of the film cameras malfunctioned or took blurry photographs, often only a photograph of one side of the animal was available for identification. We therefore built two capture histories for each left and right side for each individual and analyzed them separately. We collapsed daily encounter occasions into 8-day blocks due to large numbers of zeroes on a daily basis, which can cause computational problems. For lions, most of trap events occurred at stations that had two digital cameras and most times we had both sides of the same individual. While lions do not have clear natural markings, 3 investigators worked separately and compared results based on subtle

marks such as scars, missing tail tips, mane size and shape, and markings on the interior side of hind legs, following Kelly et al. (2008).

Servals and leopards abundance estimation

Abundance of servals and leopards was calculated for each flank separately using traditional, non-spatial, capture-recapture models (CR) under program CAPTURE (White et al. 1978, Rexstad and Burnham 1981) and program MARK (version 6.2, White and Burnham 1999). We statistically tested the population closure assumption for each species under program CAPTURE before estimating abundance and compared models using the program's discriminant function analysis selection procedure. As for MARK, we explored different candidate sets of models under Huggins Full Heterogeneity Closed Capture framework, using heterogeneity, time, behavior, and mixed combinations, and selected the top-ranked model based on Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson 2002) and Akaike weights. We considered models competing if the delta-AICc was within 2.0 of the top model.

Serval and leopard density estimation using CR models

Densities were derived from population size estimates after computing the effective sample areas (ESA) from ArcGIS. ESA for each of the three species was obtained by applying to the camera stations a buffer radius equal to ½ the Mean Maximum Distance Moved (MMDM) (Karanth and Nichols 1998; Nichols and Karanth 2002) by a feline caught at least twice at two different stations. We also used the full MMDM, following Soisalo and Cavalcanti (2006), Dillon and Kelly (2008), and Tobler and Powell (2013), since authors suggested that in the absence of home range size estimates from radio-telemetry data, the ½ MMDM may be too small and hence overestimates density. Due to very low samples sizes for a single flank, MMDMs for leopards and servals were calculated by combining both left and right flank capture histories to increase precision. Densities and their standard errors were estimated following the delta method (Nichols and Karanth 2002).

Serval and leopard density estimation using SECR models

Maximum likelihood SECR

We also used a spatially explicit capture-recapture framework to directly estimate leopard and serval densities through maximum likelihood (SECR-ML, Efford 2004; Borchers and Efford 2008) using program DENSITY (version 5.0; Efford 2012). Under full likelihood and homogeneous Poisson distribution in DENSITY (Efford 2014), we selected the jackknife heterogeneity model estimator M(h) since this model was nearly always selected as the best model in CAPTURE. To determine how large our state space surrounding cameras should be, we varied the buffer size from 3 to 4 times the Root Polled Squared Variance (RPSV), which is a measure of the scale determined by inter-trap movements, pooled across individuals (Efford et al. 2004; Wilson et al. 2007), until the models converged to a relatively stable results using a final buffer size of 14,000 m. Then we explored all three available detection functions (half normal, negative exponential, and hazard rate) and ran a set of combined models with parameters g_0 (capture probability at home range center) and sigma (spatial scale over which detection declines) varying with time, behavior, and individual heterogeneity as a 2 class-mixture model. The models were ranked based on their AICc values and weights, and density estimates were taken from the top model for each data set (left and right sides) separately.

Bayesian SECR

We also used a spatially explicit Bayesian (SECR-B, Royle et al. 2013) capture-recapture approach implemented in the R package SPACECAP v.1.0.6 (Singh et al. 2010, Gopalaswamy et al. 2010). In SPACECAP, we used the default values of the model definition (trap response absent (i.e. no behavior effect), half normal detection function, and capture encounters following a Bernoulli distribution) and additionally, we ran a model where trap response is present. For leopards, we created a file of hypothetical potential home range centers spread across the state space at 1 km intervals whereas for servals, we used a modified script in SPACECAP (provided by Gopalaswamy) adapted for animals with smaller home ranges and created a mesh of a potential home range centers at 0.5 km intervals. We gradually increased the number of Markov Chain Monte Carlo (MCMC) iterations (min = 150,000) and burn-in period (min = 50,000) and

set the data augmentation value 5 to 8 times the expected population size in the larger state-space (Gopalaswami et al. 2012) until model convergence was reached, as indicated by the Geweke diagnostic (Gopalaswami et al. 2012).

Lion density estimation using non-spatial mark-resight model

Because not all lions were individually identified, meaning that only a portion of the population was individually identifiable, we estimated population density using both non-spatial mark-resight (MR) and spatial mark-resight models (SMR) following Rich et al. (2014). Under the MR framework, we built encounter histories that included 3 components: the number of times each individually marked lion was caught, the total number of unmarked animal events, and the total count of marked individuals that were not identifiable (e.g. due to ambiguity caused by partial photos or bad angles), and implemented models in program MARK (McClintock and White 2010). Since we sampled from a naturally unmarked population, we set the number of marked lions as unknown. We assumed that the lion population was geographically and demographically closed and used the zero-truncated, Poisson log-normal estimator (McClintock et al. 2009; McClintock and White 2010; McClintock 2012) as we sampled with replacement. Following Rich et al. (2014), we implemented two different MR models in program MARK as we had only one sampling session and used no covariates. In the first model, all 3 parameters – intercept for mean resighting rate (α), individual heterogeneity (σ), and number of unmarked individuals in the population (U) – were kept constant (heterogeneity model), whereas for the second model, σ was fixed to 0 (null model). Models were ranked based on their AICc values and the estimates of abundance and overall mean resighting rate (λ) were derived from the top ranked model. To estimate density, we used both ½ MMDM and full MMDM from which we calculated ESA as described above.

Lion density estimation using spatial mark-resight model

We also used a spatial mark-resight model (SMR) to directly estimate lion density implemented within a Bayesian framework (Sollmann et al. 2013; Rich et al. 2014). We fit the

model in JAGS (Plummer 2009) using the rjags package (Plummer 2014) for the software R 3.0.2 (R Core Team 2013). We imposed a state-space of 10,431.25 km^2 representing a buffer around the trap coordinates approximately three times what we thought was a reasonably large estimate for lion movement (14 km, derived from Sogbohoussou 2011 from telemetry data). We created capture histories for each marked individual, and an accumulated count of unmarked individuals, including the coordinates of the camera trap locations (J) for each detection and non-detection. We also accounted for days each camera trap was in operation (K) over the total days of the survey (K_{max}). We estimated density of marked individuals and unmarked individuals using a joint parameter for lambda, or the detection rate of individuals if the detector was placed at the animal's home range center (s_i), and sigma, the distance over which detection declines from the individual's activity centers. Mark-resight models assume detection is constant across marked and unmarked individuals. We used a data augmentation value of 150 to represent potential capture histories of individuals that were marked but never detected (m_{max}), and a data augmentation value of 100 to represent potential capture histories of unmarked individuals that were never detected (M). The parameters ψ and ψ_m estimate the probability that an augmented activity center represents an actual unmarked or marked (respectively) individual in the state-space. Density was estimated directly by dividing the total sum of activity centers for marked and unmarked individuals, and the sum of augmented activity centers for marked and unmarked augmented activity centers, by the total state-space area. Following Rich et al (2014) we ran the model for 200,000 iterations following a 100,000 burn in period, and assessed chain convergence using Gelman-Rubin's R-hat statistic (Gelman et al. 2004) in the R package coda (Plummer et al. 2009), with convergence indicated if R-hat ≤ 1.1.

Results

Trap success

The 78 days of camera-trapping with 28 stations resulted in a sampling effort of 2014 effective trap-nights. The total number of capture events was 5,121 and consisted of 3,432 photos of mammals (Table 3.1). Thirty five mammal species were photographed including 14 carnivore species among which 4 were large carnivores (lion, spotted hyena, leopard, and

African wild dog). Spotted hyenas (*Crocuta crocuta*) were the most photographed large carnivore with an average trap success of 2.20 (±0.86) captures per 100 trap-nights (TN), while the common genet (*Genetta genetta*) had the highest average trap rate among all carnivores at 9.00 (±2.39) captures/100 TN (Table 2.1). As for all mammal species, warthogs (*Phacophoerus africanus*), Guinea baboons (*Papio papio*) and bushbucks (*Tragelaphus scriptus*) had the highest trap success rates at 32.54 (±11.73), 30.03 (±13.15) and 14.93 (±5.13) capture events per 100 TN respectively. Trap success for humans was 36.16 (±4.90) although all captures consisted of authorized people (rangers, tourists, researchers, and other workers) in the park, showing how intensely trails are used by humans.

We obtained 40 independent captures of leopards, 43 of lions, and 29 of servals during the length of the study, resulting in a mean trap success per 100 TN of 1.9 (±0.59), 2.06 (±0.72), and 1.41 (±0.39) respectively (Table 3.1). Leopards were captured at 15 different camera stations, lions at 9 stations, and servals at 14 stations. We identified 11 different leopard individuals from the left side-view and 12 from right side-view, whereas for servals, we identified 9 and 10 individuals from the right and left side-views, respectively. Leopards had the same number of recaptures for both sides while for servals, there were more recaptures from the right side than the left.

As for lions, most of the captures occurred at 6 of the 9 stations where both digital cameras were present making it easier to identify individual lions from both sides. We individually identified 9 different lions in 32 photographs from subtle marks, while only 7 other photographs total were considered unmarked or marked but unknown. The remaining 4 photographs were discarded due to poor quality.

Abundance and density estimates of leopards from CR methods

The closure test in program CAPTURE indicated that closure was met for both leopard capture histories (Table 3.2). The heterogeneity model (Mh) – which indicates that each individual has a unique probability of capture – was ranked as the top model for both capture histories (Table 3.2; Appendix B.1). Similarly, the top-ranked model in Program MARK revealed that behavior and heterogeneity in combination with time (additive and interactive

effects) affected both captures and recaptures in both capture histories (Table 3.2; Appendix B.3). Average capture probabilities from the top-ranked model (Mh) in program CAPTURE were 0.12 and 0.11 respectively for leopard left and right capture histories and from MARK they ranged from 0.13 to 0.38.

Leopard population size was estimated at 16 (SE = 4.2) and 19 (SE = 4.98) respectively for left and for right capture histories under Program CAPTURE and similarly for Program MARK, abundance for the respective capture histories was estimated at 16.41 (SE = 4.41) and 17.52 (SE = 4.47) (Table 3.3).

The ½ MMDM for leopards was 3.82 km resulting in an ESA of 417.23 km^2 and derived density estimates from program CAPTURE of 3.83 (SE = 1.71) and 4.55 (SE = 2.02) individuals per 100 km^2 for leopard left and right flank capture histories, respectively. Density estimates from program MARK were very similar to program CAPTURE and ranged from 3.93 (SE = 1.42) to 4.20 (SE = 1.85) respectively for left and right flanks (Table 3.3).

Using the full MMDM, ESA was 851.05 km^2 and resulted in density estimates from program CAPTURE of 1.88 (SE = 0.68) and 2.23 (SE = 0.81) individuals per 100 km^2 for left and right leopard capture histories, respectively. For Program MARK, the estimates were, again, very similar at 1.93 (SE = 0.58) and 2.06 (SE = 0.74) for lefts and rights, respectively (Table 3.3).

Abundance and density estimates of servals from CR methods

Similar to leopards, the closure test for servals was also met for both capture histories and the heterogeneity model (Mh) in CAPTURE was ranked as the top model (Table 3.4; Appendix B.2). AICc tables from program MARK indicated that behavior and heterogeneity and time (additive and interactive effects) affected capture probability (Table 3.2; Appendix B.4). Average capture probabilities from CAPTURE were estimated at 0.04 and 0.05 respectively for serval left and right flanks while from MARK both estimates were 0.26. Program CAPTURE estimated serval population size at 31 (SE = 9.37) for left capture histories and 23 (SE = 8.09) for the right ones, while in MARK abundance was 24.76 (SE = 14.23) and 15.99 (SE = 6.64) respectively (Table 3.4).

The ½ MMDM was 2.99 km for servals resulting in an effective sampled area of 331.43 km^2, with corresponding left and right flank density estimates of 9.35 (SE = 4.61) and 6.94 (SE = 3.64) individuals per 100 km^2 from program CAPTURE. Estimates from program MARK were lower, but with overlapping confidence intervals, at 7.47 (SE = 5.19) and 4.82 (SE = 2.75) for the respective flanks (Table 3.4).

When using the full MMDM method, ESA was estimated at 655.4 km^2 for servals. Serval left and right flank density estimates from CAPTURE were 4.73 (SE = 1.94) and 3.51 (SE = 1.57) individuals per 100 km^2 respectively, while from MARK they were also lower, but again with overlapping confidence intervals, at 3.78 (SE = 2.41) and 2.44 (SE = 1.22) (Table 3.4).

Density estimates of leopards and servals using SECR methods

The SECR-ML framework implemented in program DENSITY indicated the null model with the negative exponential detection function as the top-ranked for both leopard capture histories (Table 3.2; Appendix B.5). Leopard density estimates were 2.19 (SE = 0.99) for left side capture histories and 2.53 (SE = 1.81) for the right flank (Table 3.5). For the Bayesian, SECR-B implemented with SPACECAP, only the models with trap response present (behavior model) in SPACECAP converged for both flanks (i.e. the Geweke diagnostic was <1.6) and resulted in lower density estimates of 1.82 (SE = 1.50) and 1.78 (SE = 1.24) for left and right flank respectively (Table 3.5). Confidence intervals were large for these estimates.

For servals, the top model using the SECR-ML approach for both sides was the null model (Table 3.2; Appendix B.6) with negative exponential detection function, similar to leopards, and densities were estimated at 4.08 (SE = 2.94) and 3.49 (SE = 2.47) servals/100 km^2 respectively for left and right flanks (Table 3.6).

Finally, for Bayesian SECR-B, again only the models with trap response present (behavior model) in SPACECAP converged for both flanks (Geweke diagnostic < 1.6) and again resulted in lower density estimates than other methods for servals at 2.82 (0.53) and 2.51 (SE = 0.56), but this time with much better precision (Table 3.6).

Abundance and density estimates of lions

The non-spatial mark resight estimator revealed the heterogeneity model (where $\sigma \neq 0$ and constant) was the top ranked model over the null (Table 3.6). The derived estimate of lion abundance from the top-ranked model was 12.44 (SE = 2.52). The ½ MMDM was 2.23 km and resulted in an effective sampled area of 251.82 km^2 and, for the full MMDM an ESA of 486.03 km^2, with respective density estimates of 4.94 (SE = 1.39) and 2.56 (SE = 0.63) lions per 100 km^2 (Fig. 3.4).

The spatial mark-resight models resulted in a lower density estimate of 1.74[4] (SE = 0.31) lions per 100 km^2.

Discussion

This study is a pioneer in investigating leopard, lion, and serval abundances and densities from camera-trap data using both traditional capture-recapture and spatially explicit capture-recapture frameworks in West Africa, and probably the first in Africa. It confirmed that the Niokolo Koba National Park still has a diverse carnivore community, although some species seem to occur at very low densities. It also confirms the feasibility of camera-trapping in a landscape dominated by wooded savannah at 69%. In addition, camera-trapping is more suitable for carnivores than the line transects formerly conducted in the park and is less demanding in human investment. Camera trapping also provides proof of persistence of some species such as elephants, African wild dogs, and caracals that have not been photographed in the park for a decade.

Placement of cameras on human trails and roads was advantageous as almost all captures of large and medium-sized carnivores occurred on heavily used trails, as confirmed by the high human trap rate (36.16 per 100 TN). This is in contrast with our pilot study when 80% of the cameras were placed on small animal trails and we had no captures of large and medium sized carnivores. In addition, we obtained fewer large and medium size carnivores on abandoned or slightly used trails than on regularly maintained ones. The Moultrie L50 cameras were more

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[4] Preliminary results

reliable and performed better as none of them ran out of batteries or malfunctioned during the entire camera-trap session. Their performance was mitigated however, by the fact that sometimes they failed to trigger, or triggered too slowly, when animals passed by. In contrast the Moultrie D55 cameras ran out of batteries twice during the course of the study and triggered randomly every 1 to 5 minutes, making it difficult to process the numerous photos. Finally, the DeerCam 200 and 300 film cameras were the less reliable and they ran out of film and batteries very quickly and most of them malfunctioned by the end of the study.

This study has provided the first abundance and density estimates for servals from camera-trap studies anywhere, and the first for lions and leopards via camera trapping from West Africa, and the first for lions using non-spatial and spatial mark-resight models. Servals were easier to individually recognize from their black spots and bars than leopards (personal experience). In fact, the two investigators that identified individual servals were in 100% agreement. For leopards, there was approximately 80% convergence in individual identification between the two investigators, with the remaining disagreement due to poor quality photographs that eventually were discarded. Surprisingly, most lion individuals were relatively easy to distinguish from each other by the presence of subtle scars, spots and dark coloration on their hind legs, mane development and shape, and missing tail tips. The three investigators who examined lion photographs agreed on 7 of the 9 individual lions then worked together to identify the remainder or to classify them as unmarked, or marked but unable to identify.

All top-ranked models from all methods for estimating serval, leopard, and lion population sizes included heterogeneity, which is in line with most camera-traps studies reviewed by Foster et al. (2012). Heterogeneity is expected because individual activity and ranging behavior vary with biological traits such as sex, age, and territoriality (Harmsen et al. 2010; Foster et al. 2012). Top-ranked models in MARK also included behavior, heterogeneity, and time effects for leopards and servals. Time was not expected to affect capture probabilities since the study area is thought to hold a consistent population of large and medium carnivores from December (when trails are cleared and water abundant) to May (before the beginning of the rainy season), the period that coincided with our field study. We did not see any pattern such as increasing or decreasing capture probability through time, but rather different time periods had different capture probabilities. As expected, behavioral or trap-shy response possibly due to

animals fearing the white flash of the cameras, affected capture probabilities but was only revealed sometimes in MARK and the SECR-B approach using SPACECAP. We presume that the other approaches failed to detect it because of low sample size of number of captures and recaptures or because it is a relatively weak effect. Only one other study has found a behavioral effect (trap shyness) for tigers in Nepal (Wegge et al. 2004). In all cases, we are cautious about the best descriptive models from the different estimators due to low sample sizes and associated low capture probabilities for both leopards and servals. As for lions, we only investigated the heterogeneity model because it is the only one available in the mark-resight platform in program MARK and we had a larger sample size (when marked and unmarked are pooled) and more recaptures.

Comparison of density estimation methods

When comparing densities from left and right capture histories, we found that for leopards, right flank point estimates were almost always slightly higher (range from 1.78 to 4.55) compared to the left flanks (range 1.82 to 3.83) across the 5 methodologies, but in general they were very similar with overlapping confidence intervals. Conversely, serval left capture histories estimates were always higher than right with more separation for traditional ½ MMDM methods, although the large confidence intervals still overlapped. This may be explained by the fact that we had more right flank captures than left flanks for leopards and the inverse for servals. In addition, confidence intervals for both species and for both flanks were always large for traditional ½ MMDM methods and some runs of Program DENSITY for both species, and for SPACEAP for leopards. Confidence intervals were always larger for serval left flanks than for the right ones, but were similar for both leopard flanks.

When density estimates were compared across methods (Figures. 3.3; 3.4), we found that CAPTURE and MARK estimates using ½ MMDM were always higher for both leopard and servals. Leopard density estimates from DENSITY were higher than the full MMDM method from both CAPTURE and MARK, but they were very close for servals. Density estimation for traditional capture-recapture methods depend on ad hoc approach to estimating the effective trapping area, using either half or full MMDM as a proxy of the home range size. In both case,

the buffer width depends on camera station spacing and animal recaptures at multiple stations (Tobler and Powell 2013). Therefore, using ½ MMDM often results in a small ESA, which in turn tends to overestimate density by a factor of 3 to 5 times the density SECR methods (Tobler and Powell 2013). On the other hand, the use of full MMDM will decrease the positive bias and increase precision as it is thought to be a better proxy for home range radius than ½ MMDM (Parmenter et al. 2003; Soisalo and Calvanti 2006; Dillon and Kelly 2008), even though there is no theoretical basis for using it.

Density estimates from program DENSITY (SECR-ML) for servals were similar to those from full MMDM for CAPTURE and MARK but were higher for leopards. This is in contrast with most studies that compared CR to SECR estimates and found that SECR-based estimates were always smaller than CR-based ones (Obbard et al. 2010; Gerber et al. 2011; Noss 2012). Nevertheless, this result can be tempered by the fact that top-ranked mixture models (heterogeneity, behavior 2-class mixture and their combination) failed to produce real estimates of density likely because of low numbers of recaptures – and thus were discarded. On the other hand, density estimates from SPACECAP (SECR-B) were the lowest of all methods for servals consistent with findings by the same authors, but were nearly the same as the full MMDM methods for leopards. Because we have no explanations to why the ad hoc full MMDM methods resulted in apparently good estimates of density, we advocate for the use of SECR methods, which have a stronger theoretical basis, do not depend as heavily on trap layout, and can handle data from somewhat linear-shaped trap layouts like in our study (Obbard et al. 2010; Tobler and Powell 2014).

Lion MMDM was lower (4.46 km) than expected given their large size and in comparison to leopards (7.64 km) and servals (5.99 km), because most of our lion recaptures occurred at the same station. This MMDM was also about half of lion home range radius of 9.03 km derived from the average home range size of 256 km^2 from radio-telemetry data in Benin (Sogbohoussou 2011). Therefore, we believe that both ½ MMDM and full MMDM resulted in inflated lion density estimates due to small ESA, and we consider the spatially explicit MR model as more appropriate for density estimation in this case.

Interestingly, lion density estimates from mark-resight models (Fig. 3.5) showed more precision than for leopards and servals using both CR and SECR methods. This is consistent with

the findings of Rich et al. (2014) who used the same models for estimating densities of partially marked puma populations. This is likely explained by the use of both marked and unmarked individuals in the datasets, which increased the baseline sample size.

In comparing the densities of the 3 felids to each other, serval density was highest as expected based on its smaller body size followed by leopards. Unexpectedly lion densities were surprisingly similar to leopards. Previous censuses (Sillero-Zubiri 1997; Ndao and Henschel 2011; Henschel et al. 2014) found higher leopard densities and lions. For servals, this study is the first to estimate their density in the park, regardless of the method. Because their diet is composed mainly of rodents, we believe that their population should be stable as long as the riparian vegetation of the park is preserved. These results are also in line with most extinction risk studies (Purvis et al. 2000; Cardillo 2002, Cardillo et al. 2005) that suggest that species with large body size and at higher trophic level in the food chain occur at lower densities and are more likely to go extinct. Unfortunately, large prey are thought to be depleted due to poaching in NKNP (Renaud et al. 2006) and prey depletion is thought to be the main driver of lion decrease (World Heritage Committee 2007).

Comparison of density estimates with previous studies in the park

Since the early nineties, several estimates of carnivore population sizes have been conducted in the Niokolo Koba, with various methods ranging from day light and nighttime distance sampling, to calling stations and track counts. However, the first actual carnivore-focused census occurred in 1997 by Sillero-Zubiri et al. who estimated leopard density at 1 to 3, and lion density at 0.5 to 1.5 individuals per km^2. The second and last estimation was conducted in 2011 by Ndao and Henschel (see Henschel et al. 2014 for lion, unpublished data for leopards) who extrapolated density estimates from track counts using the Funston et al. (2010) formula. They estimated leopard and lion densities at 4.4 and 0.2 individuals per 100 km^2 respectively. Our study's estimates of leopard density were much lower than Ndao and Henschel from the full MMDM and SECR methods ranging from 1.78 to 2.53 individuals per 100 km^2 and were remarkably similar to the range of 1 to 3 individuals per 100 km^2 approximated by Sillero-Zubiri (1997b). On the other hand, our estimates of lion density from full MMDM and SECR methods

ranged from 1.71 to 2.56 and are higher than both of the two previous estimates. Henschel et al. (2014) estimated 16 lions in NKNP based on his density estimates, but our extrapolated density estimates, to the entire park, results in 106 lions, if we consider that 2/3 of the park habitats are suitable for lions (we excluded areas with human disturbance and high elevations). Because camera trapping techniques are known as more robust, less biased, and more appropriate for cryptic terrestrial carnivores, especially felids, than estimates based on indices or line transect distance estimation, we believe that the 2011 census overestimated leopard density and both other studies underestimated lion density.

Assessment of population sizes and densities of wildlife populations, specifically for large carnivores, is crucial in a management perspective. Knowledge of carnivore population trends can help implement broader impact conservation management actions that will benefit other species, as most large carnivores are umbrella species. Because of the position of the Niokolo Koba National Park as the most northern limit of distribution of lions and leopards, loosing these charismatic species would be detrimental to biodiversity and global conservation efforts, especially as West African lions are believed to be genetically different from southern and eastern African lions. We find that lion densities, while still low, are much higher than previous recorded and perhaps the situation, while still urgent, is not as dire a previous thought.

We provide the first reliable and precise estimates of carnivore density for 3 species simultaneously through a combination of camera trapping and capture-recapture modeling. This study represents a way forward in population monitoring for West Africa, which has seen very little use of remote cameras for wildlife surveys. Future research can expand this technique to other carnivore species and should focus on continuation of such surveys in order to determine trends in abundance through time. This information in essential for effective conservation of our dwindling, threatened and endangered top predators in Senegal.

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Table 3.1. Number of photographs, photo events, and trap success (number of photos per 100 nights) of mammal species caught at Linguekountou during the camera trapping session from February to April 2013, in Niokolo Koba National Park, Senegal.

	Common names	Scientific names	Number of photos	Number of photo events	Trap success
CARNIVORES					
1	African civet	*Civettictis civetta*	260	190	9.43
2	African wild cat	*Felis silvestris lybica*	20	11	0.55
3	African wild dog	*Lycaon pictus*	9	5	0.25
4	Banded mongoose	*Mungos mungo*	25	106	5.26
5	Common genet	*Genetta genetta*	98	67	3.33
6	Large Grey Mongoose	*Herpestes ichneumon*	6	4	0.20
7	Leopard	*Panthera p. pardus*	53	40	1.99
8	Lion	*Panthera l. leo*	82	43	2.14
9	Serval	*Leptailurus serval*	45	29	1.44
10	Side-striped Jackal	*Canis adusdus*	90	55	2.73
11	Slender Mongoose	*Galerella sanguina*	4	4	0.20
12	Spotted Hyena	*Crocuta crocuta*	59	45	2.23
13	Water-marsh mongoose	*Atilax paludinosus*	41	27	1.34
14	White-tailed Mongoose	*Ichneumia albicauda*	88	63	3.13
HERBIVORES					
15	Aadvark	*Orycteropus afer*	7	5	0.25
16	African buffalo	*Syncerus caffer*	4	2	0.10
17	Bohor reedbuck	*Redunca redunca*	7	6	0.30
18	Bushbuck	*Tragelaphus scriptus*	596	310	15.39
19	Bushpig	*Potamochoerus larvatus*	6	6	0.30
20	Common duiker	*Sylvicapra grimmia*	71	44	2.18
21	Crested Porcupine	*Hystrix cristata*	50	29	1.44
22	Ground squirrel	*Xerus erythropus*	3	2	0.10
23	Guinea Baboon	*Papio papio*	769	621	30.83
24	Hartebeest	*Alcelaphus buselaphusus*	19	7	0.35
25	Hippopotamus	*Hippopotamus amphibus*	4	2	0.10
26	Honey badger	*Melivora capensis*	9	4	0.20
27	Kob	*Kobus kob*	73	39	1.94
28	Oribi	*Ourebia ourebi*	92	55	2.73
29	Patas Monkey	*Erythrocebus patas*	93	64	3.18
30	Roan antelope	*Hippotragus equinus*	65	49	2.43
31	Scrub Hare	*Lepus saxatilis*	30	22	1.09
32	Senegal galago	*Galago senegalensis*	8	6	0.30
33	Vervet monkey	*Cercopithecus aethios*	9	6	0.30
34	Warthog	*Phacochoerus africanus*	936	663	32.92
35	Waterbuck	*Kobus ellipsiprymnus*	108	54	2.68
Humans		*Homo s. sapiens*	1282	747	37.09

99

Table 3.2. Top-ranked models for abundance and density estimation by software program for servals and leopards in Niokolo Koba National Park, Senegal. See appendices for model rankings for each program.

Species	Capture histories	Top-ranked model by Program			
		CAPTURE	MARK	DENSITY	SPACECAP
Serval	Left	Mh	{p(het*t) c(het+t)}	g0[b]s[.]	Trap response present
	Right	Mh	{p(het*t) c(het+t)}	g0[.]s[.]	Trap response present
Leopard	Left	Mh	{p(het*t) c(het*t)}	g0[b]s[.]	Trap response present
	Right	Mh	{p(het*t) c(het*t)}	g0[.]s[.]	Trap response present

Mh: Heterogeneity model; *p(het*t) c(het+t)*: Heterogeneous and time specific (interactive effects) capture probabilities and heterogeneous and time specific (additive effect only) recapture probabilities. *p(het*t) c(het*t)*: Heterogeneous and time specific (interactive effects) capture and recapture probabilities; *g0[b]s[.]:* behavioral effect in capture probabilities and constant spatial scaler ; *g0[.]s[.]:* Null model (constant capture probability and spatial scaler).

Table 3.3. Leopard individuals captured in remote camera traps from Niokolo Koba National Park, Senegal, and population size and density estimates from **Traditional Capture-Recapture** methods. Estimates were derived from top-ranked model in Programs CAPTURE and MARK and were computed for left and right side capture histories separately. Effective sampled area was calculated in ArcGIS 10.1 by applying a buffer size equal to half the mean maximum distance moved (½MMDM) and to full MMDM to the camera station locations.

Program	Capture histories	Number of individuals captured	Population size		Effective sampled area (km^2)		Density (leopards/100 km^2)			
							½ MMDM		Full MMDM	
			N-hat	SE	½ MMDM	Full MMDM	D-hat	SE	D-hat	SE
CAPTURE	Left	11	16	4.2	417.29	851.05	3.83	1.71	1.88	0.68
	Right	12	19	4.98			4.55	2.02	2.23	0.81
MARK	Left	11	16.41	4.41	417.29	851.05	3.93	1.42	1.93	0.58
	Right	12	17.52	4.47			4.2	1.85	2.06	0.74

Table 3.4. Serval individuals captured in remote camera traps from Niokolo Koba National Park, Senegal, and population size and density estimates from **Traditional Capture-Recapture** methods. Estimates were derived from top-ranked model in Programs CAPTURE and MARK and were computed for left and right side capture histories separately. Effective sampled area was calculated in ArcGIS 10.1 by applying a buffer size equal to half the mean maximum distance moved (½MMDM) and to full MMDM to the camera station locations.

Program	Capture histories	Number of individuals captured	Population size		Effective sampled area (km^2)		Density (servals/100 km^2)			
							½ MMDM		Full MMDM	
			N-hat	SE	½ MMDM	Full MMDM	D-hat	SE	D-hat	SE
CAPTURE	Left	10	31	9.37	331.43	655.41	9.35	4.61	4.73	1.94
	Right	09	23	8.09			6.94	3.64	3.51	1.57
MARK	Left	10	24.76	14.23	331.43	655.41	7.47	5.19	3.78	2.41
	Right	09	15.99	6.64			4.82	2.75	2.44	1.22

Table 3.5. Leopard and serval density estimates from **Spatially Explicit Capture-Recapture** methods. Estimates were directly obtained from maximum likelihood (SECR-ML) methods in program DENSITY and from Bayesian (SECR-B) methods in SPACECAP.

Program	Capture histories	Density (leopards/100km^2)	SE (leopards)	Density (servals/100km^2)	SE (servals)
DENSITY	Left	2.19	0.99	4.08	2.94
	Right	2.53	1.81	3.49	2.47
SPACECAP	Left	1.82	1.50	2.82	0.53
	Right	1.78	1.24	2.51	0.56

Table 3.6. Candidate models to estimate population size (N) and mean resighting rate (λ) of lions using **non-spatial Mark-Resight** analysis in program MARK. AIC_c = Akaike's information criterion with small sample size; ΔAIC_c = differences in AIC_c; Deviance = maximized log-likelihood; K = number of estimable parameters.

Model[1]	AIC_c	ΔAIC_c	AIC_c Weights	Model Likelihood	K	Deviance	N (SE)	λ (SE)
$\alpha(.)\,\sigma(.)\,U(.)$	47.47	0	0.83	1	3	37.47	12.43 (2.51)	2.28 (0.85)
$\alpha(.)\,\sigma(0)\,U(.)$	50.67	3.19	0.17	0.20	2	44.95	12.06 (1.31)	2.69 (0.59)

[1]α = mean resighting rate; σ = individual heterogeneity level; U = number of unmarked
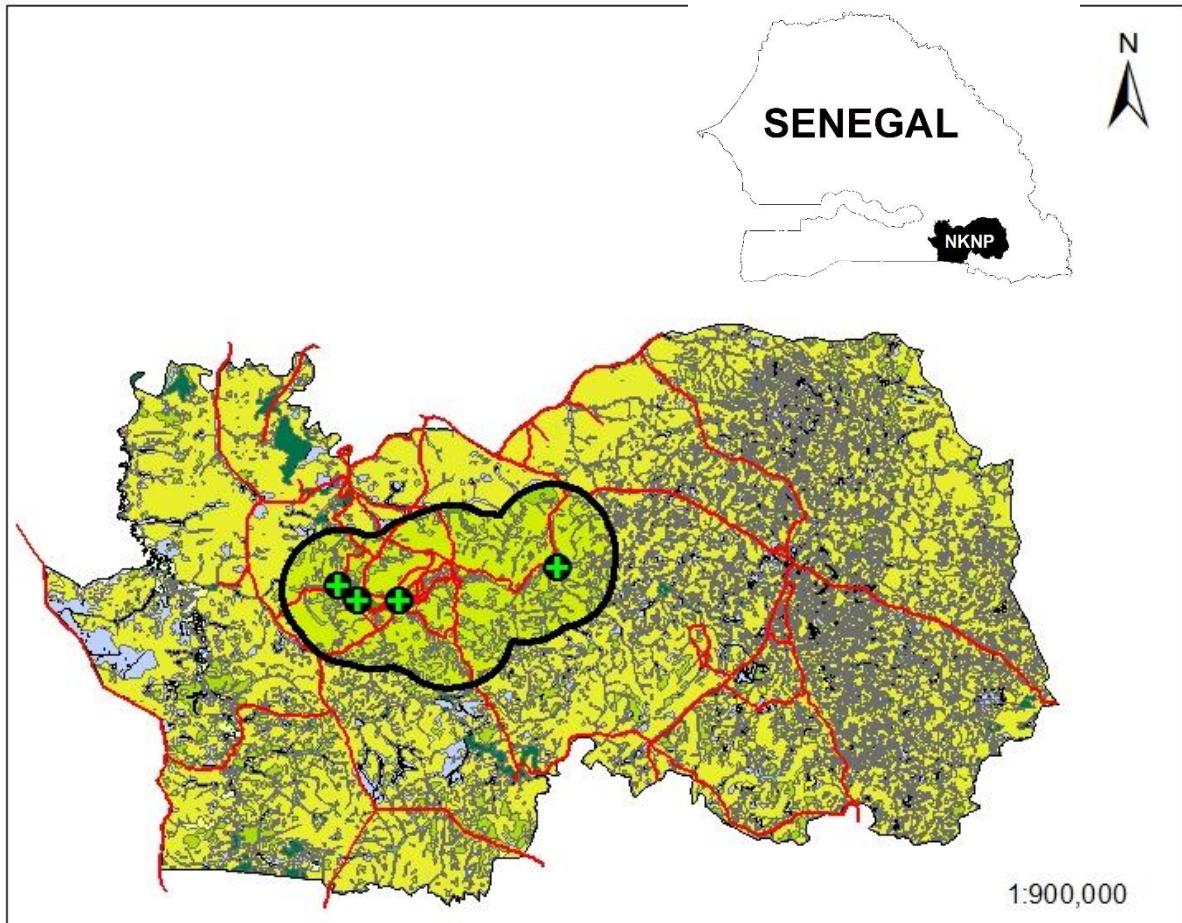
Figure 3.1. Location of the study area in the Niokolo Koba National Park (NKNP), Senegal. The camera-trap survey area is outlined in black, and was conducted from February to April 2013. Land use/Land cover shapefiles from Tappan (2012).
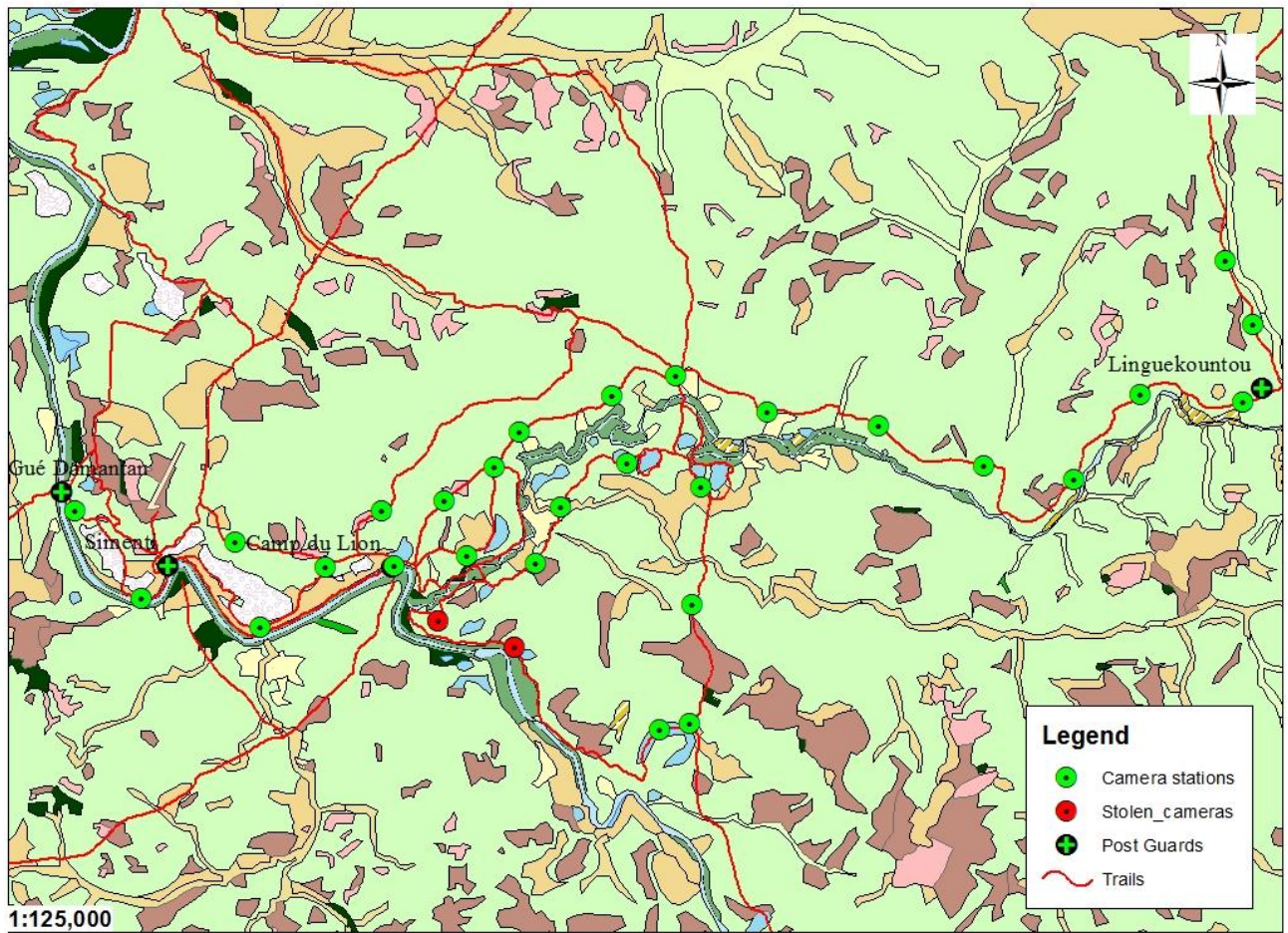
Figure 3.2: Locations of the 30 camera stations placed along trails between Linguékountou and Gué Damantan post guards in the Niokolo Koba National Park in Senegal. Land use/Land cover shapefiles from Tappan (2012).
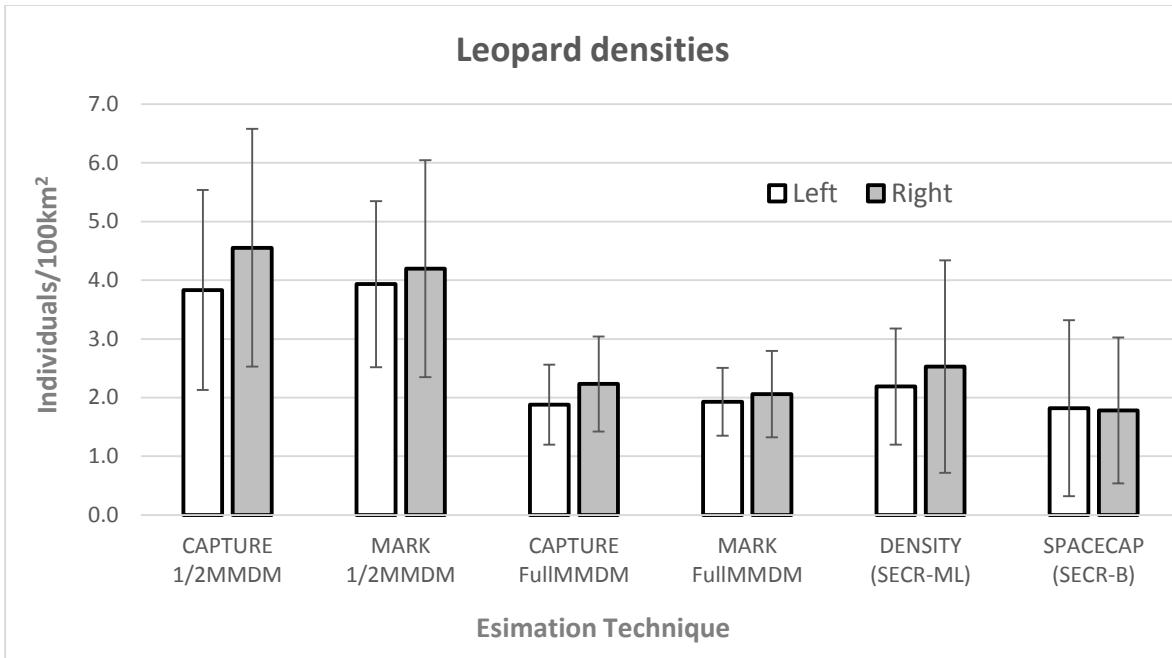
Figure 3.3: Comparison of leopard density estimates from left and right side capture histories calculated from ½ MMDM and full MMDM buffer sizes (derived from programs CAPTURE and MARK abundance estimates), DENSITY, and R package SPACECAP.
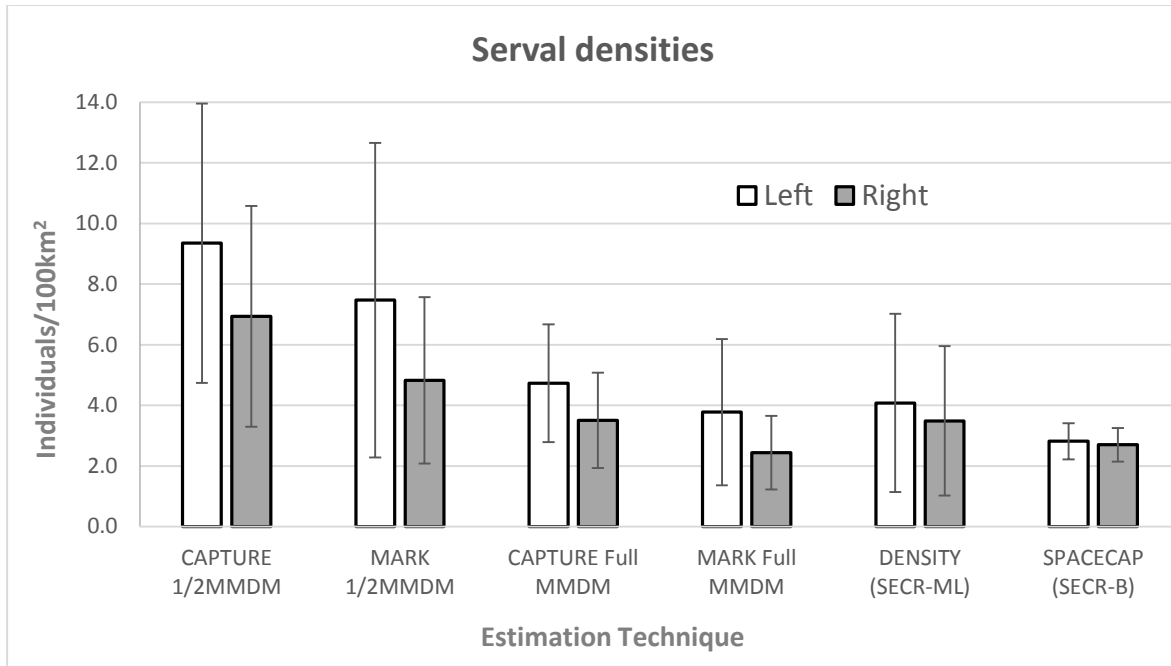
Figure 3.4: Comparison of density estimate from serval left and right capture histories calculated from ½ MMDM and full MMDM buffer sizes (derived from programs CAPTURE and MARK abundance estimates), DENSITY, and R package SPACECAP.
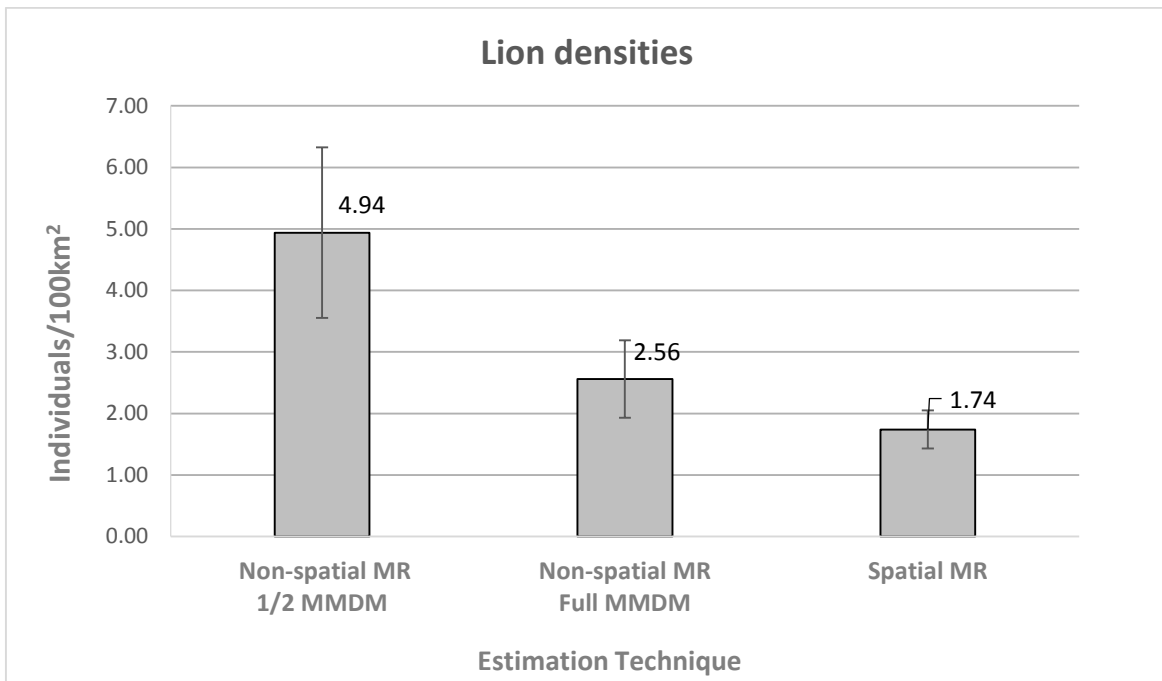
Lion densities

Fig. 3.5. Lion density estimates from two non-spatial mark-resight methods (using ½ MMDM and full MMDM buffer sizes) implemented in program MARK and 1 spatial-mark resight model implemented in R.

Appendix B.1. Program CAPTURE closure test, model selection, abundance estimates, standard errors, probability of capture and recapture, and confidence intervals for leopard left and right capture histories from camera trapping survey in Niokolo Koba National Park, Senegal.

Leopard capture history	Closure test	Model*	Model selection	Number captured	Abundance estimates	Standard error	Prob of capture p-hat	Prob of recapture c-hat	95% confidence interval	
									Lower	Upper
Left side photo-capture	z-value = 1.878 p < 0.97	M(o)	0.95	11	17	4.92	0.12	-	13	35
		M(h)	0.94	11	16	4.20	0.12	-	13	31
		M(tbh)	0.94	11	-	-	-	-		
		M(b)	0.61	11	11	0.90	0.33	0.11	11	11
		M(bh)	0.89	11	11	0.90			11	11
Right side photo-captures	z-value = 0.38 p < 0.65	M(h)	0.98	12	19	4.98	0.11	-	14	36
		M(o)	0.88	12	19	5.86	0.11	-	14	41
		M(bh)	0.87	12	12	1.16	-	-	12	19
		M(b)	0.66	12	12	1.16	0.31	0.10	12	19
		M(tbh)	0.86	12	19	6.19	-	-	14	43

* M(o) = Null model; M(h) = heterogeneity in capture probabilities model; M(b) = behavior model; M(bh) = heterogeneity and behavior model; M(tbh) = time, behavior and heterogeneity model

Appendix B.2. Program CAPTURE closure test, model selection, abundance estimates, standard errors, probability of capture and recapture, and confidence intervals for serval left and right capture histories from camera trapping survey in Niokolo Koba National Park, Senegal.

Serval capture history	Closure test	Model*	Model selection	Number captured	Abundance estimates	Standard error	Prob of capture p-hat	Prob of recapture c-hat	95% confidence interval	
									Lower	Upper
Left side photo capture	z-value = -1.155 p < 0.1241	M(h)	1.00	11	31	9.37	0.04		19	58
		M(o)	0.95	11	45	39.75			17	212
		M(tbh)	0.88	11						
		M(bh)	0.72	11	10	0.94			10	10
		M(b)	0.60	11	10	0.94	0.32	0.02	10	10
Right side photo capture	z-value = -0.395 p < 0.3465	M(tb)	1.00	12	9	0.82			9	9
		M(h)	0.99	12	23	8.09	0.05		15	49
		M(b)	0.99	12	9	0.32	0.37	0.04	9	9
		M(o)	0.97	12	16	6.85			11	43
		M(bh)	0.97	12	9	0.32			9	9

* M(o) = Null model; M(h) = heterogeneity in capture probabilities model; M(b) = behavior model; M(tbh) = time, behavior and heterogeneity model; M(h) = heterogeneity in capture probabilities model; M(b) = behavior model; M(bh) = heterogeneity and behavior model; M(tb) = time and behavior model

Appendix B.3. Program MARK model selection and abundance estimates and standard error for leopard left and right capture histories from camera trapping study in Niokolo Koba National Park, Senegal. Models were ranked based on Akaike Information Criterion adjusted for small sample sizes (AICc) and AICc weights. K = number of parameters; Deviance = -2 log(likelihood)

Leopard capture history	Models*	AICc	Delta AICc	AICc Weights	Model Likelihood	K	Deviance	Estimates		95% Confidence interval	
								N-hat	SE	Lower	Upper
Left side photo captures	{p(.) c(.)}	82.44	0.00	0.49	1.00	1	68.19	16.41	4.41	12.34	32.94
	{p(b) c(b)}	82.85	0.41	0.39	0.81	2	66.51	11.96	1.63	11.10	20.44
	{p(h) c(h)}	85.68	3.25	0.10	0.20	3	67.20	21.73	11.20	13.00	68.73
	{p(t) c(t)}	88.45	6.01	0.02	0.05	8	58.42	15.73	4.00	12.12	30.97
Right side photo captures	{p(het*t) c(het*t)}	87.99	0.00	0.87	1.00	7	58.88	17.52	4.47	13.37	34.23
	{p(b) c(b)}	93.75	5.76	0.05	0.06	2	75.53	12.45	0.91	12.04	17.48
	{p(t) c(t)}	95.01	7.02	0.03	0.03	10	58.88	17.52	4.47	13.37	34.23
	{p(bh) c(bh)}	95.85	7.86	0.02	0.02	3	75.53	13.08	0.00	13.08	13.08
	{p(.) c(.)}	96.10	8.11	0.02	0.02	1	79.95	19.09	5.41	13.88	38.77
	{p(het+t) c(het+t)}	97.44	9.44	0.01	0.01	11	58.88	17.52	4.51	13.36	34.43

*p(b) c(b): behavior effect in both capture and recapture probabilities; p(.) c(.); null model; p(t) c(t); time effect both capture and recapture probabilities; p(h) c(h): heterogeneity in both capture and recapture probabilities; p(het*t) c(het+t) : heterogeneous and time specific (additive and interactive effect) capture probabilities and heterogeneous and time specific (additive effect only) recapture probabilities; p(b) c(b): behavior effect in both capture and recapture probabilities; p(het*t) c(het*t) : heterogeneous and time specific (additive and interactive effect) capture and recapture probabilities; p(bh) c(bh); behavior and heterogeneity effects in both capture and recapture probabilities

Appendix B.4. Program MARK model selection and abundance estimates and standard error for serval left and right capture histories from camera trapping study in Niokolo Koba National Park, Senegal. Models were ranked based on Akaike Information Criterion adjusted for small sample sizes (AICc) and AICc weights. K = number of parameters; Deviance = -2 log(likelihood)

Serval capture history	Models*	AICc	Delta AICc	AICc Weights	Model Likelihood	K	Deviance	Estimates		95% Confidence interval	
								N-hat	SE	Lower	Upper
Left side photo captures	{p(het*t) c(het+t)}	56.81	0.00	0.89	1.00	6	36.38	24.76	14.23	13.01	82.29
	{p(b) c(b)}	63.38	6.58	0.03	0.04	2	51.73	10.85	1.52	10.08	18.92
	{p(bt*t) c(bt*t)}	63.43	6.62	0.03	0.04	7	40.68	20.03	10.28	11.90	62.80
	{p(.) c(.)}	64.61	7.81	0.02	0.02	1	55.05	29.08	17.62	14.09	98.91
	{p(bh) c(bh)}	65.51	8.70	0.01	0.01	3	51.73	10.85	1.52	10.08	18.92
	{p(t) c(t)}	66.38	9.57	0.01	0.01	10	36.38	24.76	14.14	13.03	81.79
	{p(het) c(het)}	66.70	9.89	0.01	0.01	2	55.05	29.08	17.62	14.09	98.91
	{p(het*t) c(het+t)}	53.82	0.00	0.94	1.00	5	38.52	15.99	6.64	10.45	42.68
Right side photo captures	{p(b) c(b)}	60.12	6.30	0.04	0.04	2	51.40	9.11	0.37	9.00	11.52
	{p(bh) c(bh)}	62.26	8.44	0.01	0.01	3	51.40	9.11	0.37	9.00	11.52
	{p(.) c(.)}	65.27	11.45	0.00	0.00	1	58.64	18.21	8.18	11.06	50.09
	{p(t) c(t)}	65.89	12.07	0.00	0.00	10	38.52	15.99	6.57	10.47	42.25
	{p(het) c(het)}	67.36	13.54	0.00	0.00	2	58.64	18.21	8.18	11.06	50.09
	{p(het) c(het+t)}	68.49	14.67	0.00	0.00	11	38.52	15.99	6.57	10.47	42.25
	{p(bt) c(bt)}	70.52	16.71	0.00	0.00	11	40.55	12.89	4.21	9.69	30.89

*p(het*t) c(het+t) : heterogeneous and time specific (additive and interactive effect) capture probabilities and heterogeneous and time specific (additive effect only) recapture probabilities; p(b) c(b): behavior effect in both capture and recapture probabilities; p(.) c(.); null model; p(t) c(t); time effect both capture and recapture probabilities; p(het) c(het): heterogeneity in both capture and recapture probabilities; p(bh) c(bh); behavior and heterogeneity effects in both capture and recapture probabilities; p(bt*t) c(bt*t): additive and interactive behavior and time effects in both capture and recapture probabilities; p(het*t) c(het+t*t) : heterogeneous and time specific (additive and interactive effect) capture and recapture probabilities; p(bt) c(bt); behavior and time effects in both capture and recapture probabilities

Appendix B.5. Program DENSITY Model selection and estimates (using Mh Jackknife estimator) for leopard left and right capture histories for camera trap study in Niokolo Koba National Park, Senegal. Models were ranked based on Akaike Information Criterion adjusted for small sample sizes (AICc) and AICc weights. K = number of parameters; g0 = capture probability at home range center; sigma = spatial scale over which detection declines.

Leopard capture history	Detection function*	Models**	K	AICc	Delta AICc	Model weight	Density (leopards per 100km^2)	SE Density	g0	SE g0	Sigma (m)	SE Sigma
Left side photo-captures	Negexp	g0[.]s[.]	3	169.21	0.00	0.64	2.19	0.99	0.10	0.06	1744.07	644.17
	Negexp	g0[.]s[b]	4	172.46	3.25	0.13	2.09	1.47	0.19	0.13	2254.94	963.58
	Negexp	g0[b]s[.]	4	172.65	3.44	0.12	1.38	1.38	0.33	0.29	1749.29	608.10
	Hazard	g0[.]s[.]	4	172.76	3.55	0.11	2.75	2.21	0.11	0.14	1523.86	1612.57
	Negexp	g0[b]s[b]	5	178.74	9.53	0.01	2.10	1.47	0.21	0.31	2184.89	1455.69
Right side photo captures	Negexp	g0[.]s[.]	3	175.87	0.00	0.47	2.53	1.81	0.06	0.04	3065.42	1522.56
	Halfnorm	g0[.]s[.]	3	176.23	0.36	0.39	2.66	1.53	0.02	0.01	4643.15	1598.35
	Hazard	g0[.]s[.]	4	179.58	3.71	0.07	3.02	1.23	0.01	0.01	7961.79	280.99
	Negexp	g0[.]s[b]	4	180.55	4.68	0.05	1.75	6.28	0.07	0.08	3659.19	8890.82
	Negexp	g0[b]s[b]	5	182.25	6.38	0.02	11.68	13.06	1.00	NA	388.57	220.71

*Negexp = negative exponential; Hazard = hazard rate; Halfnorm = Half normal

** *g0[b]s[.]:* behavioral effect in capture probabilities and sigma ; *g0[.]s[.]:* Null model; *g0[.]s[b]:*constant capture probability and sigma varies with behavior; *g0[b]s[b]:* behavioral effects in g0 and sigma

Appendix B.6. Program DENSITY Model selection and estimates (using Mh Jackknife estimator) for serval left and right capture histories for camera trap study in Niokolo Koba National Park, Senegal. Models were ranked based on Akaike Information Criterion adjusted for small sample sizes (AICc) and AICc weights. K = number of parameters; g0 = capture probability at home range center; sigma = spatial scale over which detection declines

Serval capture history	Detection function*	Models**	K	AICc	Delta AICc	Model weight	Density (servals per 100km^2)	SE Density	g0	SE g0	Sigma (m)	SE Sigma
Left side photo captures	Halfnorm	g0[.]s[.]	3	116.40	0.00	0.48	4.08	2.94	0.04	0.03	1429.49	649.55
	Negexp	g0[.]s[.]	3	116.75	0.35	0.41	9.98	9.30	0.09	0.08	961.15	544.58
	Halfnorm	g0[b]s[.]	4	121.20	4.80	0.04	4.50	2.99	0.15	0.16	1396.18	610.66
	Halfnorm	g0[.]s[b]	4	121.63	5.23	0.04	4.26	3.71	0.09	0.08	1781.83	860.34
	Hazard	g0[.]s[.]	4	122.06	5.66	0.03	11.5	8.66	0.02	0.01	2763.77	80.48
Right side photo captures	Negexp	g0[.]s[.]	3	125.09	0.00	0.53	3.49	2.47	0.14	0.10	1550.67	697.60
	Halfnorm	g0[.]s[.]	3	127.01	1.92	0.20	2.91	1.96	0.04	0.03	3112.74	1196.32
	Hazard	g0[.]s[.]	4	127.70	2.61	0.14	4.85	5.6	0.39	0.31	451.51	389.14
	Negexp	g0[.]s[b]	4	129.41	4.32	0.06	1.67	1.11	0.35	0.27	1883.84	832.45
	Negexp	g0[b]s[.]	4	129.59	4.50	0.06	0.02	1.95	1.18	0.60	1410.51	606.10

*Negexp = negative exponential; Hazard = hazard rate; Halfnorm = half normal;

**_g0[.]s[.]:_ Null model; _g0[.]s[b]:_ constant capture probability and sigma varies with behavior.

Addendum

An additional objective for this study was to estimate carnivore abundance and density from genetics using both traditional capture-recapture and spatially explicit capture-recapture models. Unfortunately, due to low number of scat samples collected, we were not able to do so and therefore we will just present the field and lab methods and the results of the genetics analysis from the cat samples.

Methods

Field methods

We systematically and opportunistically collected cat samples within the preset camera trapping grids in Linguekountou and Niokolo during the length of the camera trapping sessions. At each camera station, we walked on the trail at distance of 200 m before and 200 m after the location of the station at each visit (6 for the Linguekountou and 5 for Niokolo, during the camera checkups and micro-habitat sampling). We also searched opportunistically when walking micro-habitat transects. Scat samples were stored in 2.0 ml storage vials filled with 1.5 ml of DET buffer and the sample occupying the remaining 0.25 ml. DET buffer has been shown to have a better amplification rate among other buffers (Wultsch et al. In Review) and is more appropriate for warm, tropical climates. To avoid contamination, samples were handled with gloves, a mask, and wooden sticks. For each sample, we recorded parameters such as time of collection, GPS coordinates, conditions of the scat (moisture, presence of mold, etc.) and degree of certainty relatively to its depositor. The samples were stored at room temperature in paper bags to avoid any contamination.

Lab methods

Fecal DNA extraction and species identification

The QIAamp DNA Stool Mini Kit protocol (Qiagen, Inc., Valencia, CA, USA) was used to extract DNA from all fecal samples. An extraction negative was added to each extraction run to control for

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contamination. To identify species, four mitochondrial gene regions were amplified including cytochrome *b* (H15149, Kocher et al. 1989; Farrell-R, Farrell et al. 2000)*, 12S* (L1085, H1259, Kitano et al. 2007), *16S* (L2513, H2714, Kitano et al. 2007), *16Scp* (16Scp-F, 16Scp-F, Kitano et al. 2007), and adenosine triphosphate-6 (ATP6-DF3, ATP6-DR2, Chaves et al. 2012). DNA sequences were edited and matched with reference samples from the Global Felid Genetics Program at the American Museum of Natural History (New York, NY) using Geneious, v. 6.1.5. (Biomatters Ltd., Aukland, New Zealand).

- *Microsatellite amplification and genotyping*

We used 12 polymorphic microsatellite loci (Menotti-Raymond & O'Brien 1995; Menotti-Raymond et al. 1999) arranged in five PCR multiplex reactions (multiplex 1 – FCA032, FCA100, FCA124; multiplex 2 – FCA126, FCA212, FCA229; multiplex 3 – FCA096, FCA132, FCA275; multiplex 4 – FCA075, FCA208; multiplex 5 – FCA225). Multiplex 1 consisted of 10 μL 1 x concentrated Qiagen Master Mix (Qiagen, Inc., Valenica, CA, USA), 4.4 μL of primers (0.4μM for FCA032, 0.6μM for FCA100, 0.1μM for FCA124), 2.0 μL of 0.5 x concentrated Qiagen Q solution (Qiagen, Inc., Valencia, CA, USA), 0.6 μL H_2O, and 3.0 μL DNA extract. Multiplex 2 consisted of 10 μL 1 x concentrated Qiagen Master Mix (Qiagen, Inc.), 2.4 μL of primers (0.2μM for FCA126, 0.2μM for FCA212, 0.2μM for FCA229), 2.0 μL of 0.5 x concentrated Qiagen Q solution (Qiagen, Inc.), 0.6 μL H_2O, and 5.0 μL DNA extract. Multiplex 3 consisted of 10 μL 1 x concentrated Qiagen Master Mix (Qiagen, Inc.), 2.4 μL of primers (0.2μM for FCA096, 0.2μM for FCA132, 0.2μM for FCA275), 2.0 μL of 0.5 x concentrated Qiagen Q solution (Qiagen, Inc.), 0.6 μL H_2O, and 4.0 μL DNA extract. Multiplex 4 consisted of 10 μL 1 x concentrated Qiagen Master Mix (Qiagen, Inc.), 4.0 μL of primers (0.2μM for FCA075, 0.8μM for FCA208), 2.0 μL of 0.5 x concentrated Qiagen Q solution (Qiagen, Inc.), and 3.0 μL DNA extract. Multiplex 5 consisted of 10 μL 1 x concentrated Qiagen Master Mix (Qiagen, Inc.), 3.0 μL of primers (0.8μM for FCA225), 2.0 μL of 0.5 x concentrated Qiagen Q solution (Qiagen, Inc.), 1.8 μL H_2O, and 3.0 μL DNA extract. Microsatellite PCR amplifications were conducted starting with an initial denaturation step of 15 min at 95 °C; followed by 13 cycles of 30 s at 94

°C for denaturation, 1.5 min at 60.4 °C for multiplex 1, 62.4 °C for multiplex 2, 59.4 °C for multiplex 3 and 4, 57.4 °C for multiplex 5 with a decrease in annealing temperature of 0.3 °C in each cycle, and 1 min elongation at 72 °C; followed by 32 cycles of 30 s at 94 °C for denaturation, 1.5 min at 58 °C for multiplex 1, 60 °C for multiplex 2, 57 °C for multiplex 3 and 4, 55 °C for multiplex 5 for annealing, and 1 min elongation at 72 °C; and 30 min at 58 °C for multiplex 1, 60 °C for multiplex 2, 57 °C for multiplex 3 and 4, 55 °C for multiplex 5 for final elongation. A PCR negative was included in each group of PCR reactions to control for contamination.

Primers were fluorescently labeled and we visualized PCR products using an ABI 3730xl DNA analyzer (Applied Biosystems™, Carlsbad, CA, USA). Genotypes were identified using the software GENEMAPPER, version 5.0 (Applied Biosystems™, Carlsbad, CA, USA). To finalize the consensus genotypes and to minimize genotyping error, a multi-tube approach (Taberlet et al. 1996) was used with a minimum of 4 repetitions for each microsatellite multiplex and lion or leopard sample. To confirm the individual identification and assess the resolving power of the 12 microsatellite loci, we used GIMLET, version 1.3.3. (Valiere 2002) to calculate the probabilities of identity, $P_{(ID)}$, the probability of identity and $P_{(ID)sibs}$, the probability of identity between siblings.

Results

We collected a total of 43 scat samples from our survey efforts in both study areas. Of those samples that did amplify, 12 were confirmed as leopards and comprised 9 different individuals and 7 were confirmed as lions and comprised 3 different individuals (Table 4.1; 4.2)

We hope that this can provide a baseline of information for a future study with expanded scat sampling and genetic analyses to address not only questions of carnivore abundance and density, but also questions surrounding genetic health such as genetic diversity, population structure, and genetic connectivity across the landscape. This would add much needed information regarding the imperiled carnivores of Niokolo Koba National Park.

Table 4.1. Leopard identification summary

IND ID	ANMH ID	Original ID	Probabilities of Identity	
			P(ID)	P(ID)sibs
SENLEP01			0.0000	0.0008
	SEN052	L27		
SENLEP02			0.0000	0.0077
	SEN054	L31		
	SEN069	L59		
SENLEP03			0.0000	0.0079
	SEN055	L32		
SENLEP04			0.0000	0.0135
	SEN056	L34		
SENLEP05			0.0000	0.0014
	SEN059	L39		
SENLEP06			0.0000	0.0028
	SEN063	L49		
SENLEP07			0.0000	0.0026
	SEN075	L69		
SENLEP08			0.0000	0.0130
	SEN084	N06		
SENLEP09*			0.0003	0.0417
	SEN064	L50		

* P(ID)sibs < 0.05; remaining samples have P(ID)sibs < 0.01

Leopard samples (species ID confirmed, individual ID unconfirmed)			
	SEN079	N01	UNID
	SEN086	N08	UNID

Results	
No. of leopard samples (species ID confirmed):	12
No. of leopard samples (individual ID confirmed):	10
No. of individual leopards:	9
No. of indiviuals recaptured:	1

Table 4.2 Lion identification summary

IND ID	ANMH ID	Original ID	Probabilities of Identity		
				P(ID)	P(ID)sibs
SENLE001					
	SEN047	L03			
SENLE002					
	SEN048	L04			
	SEN061	L47			
SENLE003					
	SEN058	L36			

* P(ID) values could not be calculated due to low sample size

Leopard samples (species ID confirmed, individual ID unconfirmed)			
SEN067	L57	UNID	
SEN068	L58	UNID	
SEN083	N05	UNID	

Results	
No. of lion samples (species ID confirmed):	7
No. of lion samples (individual ID confirmed*):	4
No. of individual lions:	3
No. of individuals recaptured:	1

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