Population ecology, conservation status and genetics of the spotted hyena (*Crocuta crocuta*) in the Odzala-Kokoua National Park, Republic of Congo, including an assessment of the status of spotted hyenas in southeast Gabon

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1. Gutachter: Prof. Dr. Heribert Hofer

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In memory of Michael Bohm

CONTENT

Camera traps pictures of spotted hyenas and

other wildlife species from the Odzala-Kokoua National Park

The three following manuscripts are part of this dissertation:

1. BOHM, T., East, M.L. & Hofer, H. Camera-traps based assessment of the status of the endangered spotted hyena population in the Odzala-Kokoua National Park, Republic of Congo, with a new methodology to identify clan memberships in spotted hyena populations.

2. BOHM, T., Wachter, B., Bodendorfer, T., Henschel, P. & Hofer, H. Diet of spotted hyenas in the Odzala-Kokoua National Park, Republic of Congo.

3. BOHM, T. & Hofer, H. Population density and activity patterns of servals in the Odzala-Kokoua National Park, Republic of Congo.

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I had the unique opportunity to see the breathtaking beauty of the Odzala-Kokoua National Park and to walk thousands of kilometers through spotted hyenas' habitat. This gave me the chance to get first hand insights into the interesting life of spotted hyenas (and to experience a glimpse of the challenges they are facing in the wild - including fleeing from forest buffalo and elephant herds). I hope, future generations will still have the chance to see this beautiful animal in Odzala.

Chapter 1: General Introduction

1.1 Why study and conserve spotted hyenas?

With an estimated total population size of 27,000–47,000 animals, the spotted hyena (*Crocuta crocuta*) is the most abundant large carnivore in Africa (Hofer & Mills, 1998a). The species is widespread in Africa and is listed as *'Least Concern. Population Trend: Decreasing*' in the IUCN Red List of Threatened Species™ (Höner, Holekamp & Mills, 2008).

Its complex social behaviour has made the spotted hyena a model organism for researchers studying the evolution of sociality in mammals (Watts *et al.*, 2009). The species has a wide repertoire of vocalisations, making it an highly interesting research object for researchers studying the complexity of vocal communications in mammals (East & Hofer, 1991a, 1991b). Female spotted hyenas are highly masculinised with male-like genitals (Hamilton, Tilson & Frank, 1986). This 'abnormality' has caused scientists as well as philosophers much confusion over the centuries and no universally convincing explanation about the adaptive value of the females' masculinisation has been found until now (Watson, 1877; East, Hofer & Wickler, 1993; Glickman, 1995; Frank, 1997; Muller & Wrangham, 2002). In areas where the spotted hyena occurs, it is often the most abundant large carnivore species (Ogutu & Dublin, 1998; Höner *et al.*, 2005). Thus, it probably has a profound effect on the dynamics of their prey species (Kruuk, 1972), making it an interesting research object for studies on predator-prey relationships (Höner *et al.*, 2002). The spotted hyena has a wide habitat tolerance and, provided there is enough prey available and spotted hyenas are tolerated by local people, can cope well with human-driven habitat alterations and human-dominated landscapes (Hofer & Mills, 1998a; Abay *et al.*, 2010; Yirga *et al.*, 2013). In Ethiopia, spotted hyenas are regularly seen inside towns scavenging on and around garbage dumps (Yalden, Largen & Kock, 1980; Abay *et al.*, 2010; Girmay, Gadisa & Yirga, 2015). In Harar, Ethiopia, spotted hyenas are fed by hand by the 'hyena men' and have become an attraction for tourists (East & Hofer, 1998; Yalden *et al.*, 1980). Their adaptability to human-dominated landscapes might help to answer questions on how populations of large carnivores can deal with a growing human population in the future (Woodroffe, 2000; Linnell, Swenson & Andersen, 2001; Ripple *et al.*, 2014). Spotted hyenas have a strong immune system allowing them to withstand diseases that kill other animals (East *et al.*, 2001; Watts & Holekamp, 2009; Lembo *et al.*, 2011). To unravel the secrets of their innate immune response system fully will become one of the most interesting research topics in the future. The outcomes might help to better understand or even improve the immune response system in humans. Last but not least, spotted hyenas fulfil an important task in the ecosystem as their ability to eat bones and carcasses helps to 'clean' the environment (Sutcliffe, 1970). This ability is of great importance as it probably helps to prevent the spread of diseases in prey populations (Mills, 2005). Thinking one step further, this might also help to prevent transmissions of pathogen diseases towards humans.

Overall, the spotted hyena is certainly an animal worth to be studied and conserved. It helped to create jobs for researchers for decades. Several large long-term research projects on spotted hyenas exist, mainly in eastern Africa. Wild spotted hyenas were even transferred into research institutions outside Africa and studied under controlled conditions in enclosures like mice (Drea & Carter, 2009).

However, there is a big discrepancy between how spotted hyenas should be appreciated for their scientific and ecosystem value on the one hand and the actual appreciation they receive by Africans (as well as other people) and conservation stakeholders on the other hand. Spotted hyenas are not always seen as a 'target species for conservation' by conservation stakeholders, linked with a lack of interest in this species. Today, protected areas do not only serve as 'reservoirs' for animal populations but also as places which create revenues for governments, business companies and local people through tourism (Barnes, Schier & van Rooy, 1999; Wilkie & Carpenter, 1999a; Blom, 2000; Goodwin & Leader-Williams, 2000). Thus, conservation is often focused around so called 'sexy species', species which are the ones that mainly attract tourists and hence generate income (Ringer, 2002; Kerley, Geach & Vial, 2003; Okello, Manka & D'Amour, 2008). Spotted hyenas are not as majestic as lions (*Panthera leo*) nor are they as mystique as the secretive leopard (*Panthera pardus*), two species belonging to the 'Big Five', a collection of species promoted by the tourist industry as species that must be seen in Africa (Goodwin & Leader-Williams, 2000). Despite their enormous scientific and ecosystem value spotted hyenas have not yet fully received the appreciation they deserve and patiently wait in line, behind lions, leopards, elephants, buffaloes and rhinoceroses, to get noticed and appreciated in Africa.

The tolerance spotted hyenas actually receive by rural people in Africa is the other side of the coin. Rural populations in Africa often live in extreme poverty (Chen & Ravallion, 2007). In areas where prey is rare or where livestock has become easily available, spotted hyenas tend to prey on domestic animals and, thus, are mainly just seen as pest and threat to the economy (Patterson *et al.*, 2004; Kissui, 2008; Gusset *et al.*, 2009; Lindsey *et al.*, 2013). Moreover, spotted hyenas suffer from a bad reputation. Prejudices and myths about spotted hyenas have led to a biased view of spotted hyenas (Glickman, 1995). The majority of people still see spotted hyenas just as coward scavengers which steal prey from lions and other large carnivores (East & Hofer, 1998). While other large carnivores at least receive some 'protection' by being found as alluring because of their beauty and power (Macdonald, 2001), spotted hyenas do not have this bonus. Hundreds of years of false perception of spotted hyenas can not be reversed within shortest time but it is about time to change that and various reasons exist to do so: Spotted hyenas can be seen as indicators for the overall health status of a given protected area, as they, like other large carnivores, require large prey biomasses and large habitat areas (Caro & Durant, 1995). Thus, the natural occurrence of spotted hyenas in a protected area should be regarded as a reward for current and past protection activities. In contrast, due to the resilience of spotted hyenas a decline or even disappearance of a spotted hyena population in a protected area should be a warning sign for conservation stakeholders and tell them that there is something wrong (see Trinkel, 2009). Habitat might have become severely degraded, prey animals might have become rare or human disturbances might have become fatal for wildlife. Thus, to have an eye on spotted hyena populations helps conservation stakeholders to identify, and if possible, to reverse such trends. Moreover, outcomes from research on spotted hyenas will surely help us to understand and solve some of the current and future problems in biological sciences better. This will, in the long run, assist conservation stakeholders to preserve nature and environment in the future more effectively. Thus, spotted hyena conservation and research as well as wildlife tourism based of spotted hyenas should be promoted to a much greater extent.

1.2 Short introduction on the ecology and biology of spotted hyenas

Spotted hyenas are large carnivores with a dog-like appearance (Kingdon, 2004). Spotted hyenas are members of the family Hyaenidae and the only member of the genus *Crocuta* (Kingdon, 2004). Genetic analyses revealed that hyenas are closely related to a taxon consisting of mongooses and the Malagasy carnivore fossa (*Cryptoprocta ferox*) (Koepfli *et al.*, 2006).

Female spotted hyenas have developed male-like genitals with an elongated clitoris ('pseudopenis') resembling a male penis and a pseudoscrotum, created by fusion of the external labia, resembling male testes (Hamilton *et al.*, 1986; Frank, 1997). The pseudopenis is fully erectile and females give birth and mate through it (Frank, 1997). The adaptational value of this masculinization has been a question of debate for decades (Kruuk, 1972; East, Hofer & Wickler, 1993; Muller & Wrangham, 2002). Older hypotheses suggest that the pseudopenis evolved as an important element in the greeting ceremony (Kruuk, 1972) or that masculinization prevents unwanted copulations (East *et al.*, 1993). A newer hypothesis suggests that masculinization favours a sexual mimicry which functions as a defensive adaptation to infanticide (Muller & Wrangham, 2002).

Spotted hyenas live in social groups, so called ‘clans’ (Kruuk, 1972). Each clan consists of one to several matrilines of adult females and their offspring, as well as of one or several immigrant adult males (Frank, 1986a; Mills, 1990). Within a clan, linear dominance hierarchies among females and males are established (Frank, 1986a). However, within a clan all adult females and their cubs are dominant to all adult male immigrants (Drea & Frank, 2003). Females usually remain in their natal clan whereas males typically disperse from their natal clan at puberty and seek access to neighbouring clans (Frank, 1986b; Henschel & Skinner, 1991). Females which remain in their natal clan attain social ranks adjacent to those of their mothers (Smale, Frank & Holekamp, 1993; Jenks *et al.*, 1995; Engh *et al.*, 2000)

Females usually have a litter size of one or two, three cubs within a litter are rare (Mills, 1990; Cooper, 1993; Hofer & East, 2008). Females may give birth at the communal den or in a private birth den (Boydston, Kapheim & Holekamp, 2006). In the latter case, litter is then transferred to the communal den after several weeks (East, Hofer & Türk, 1989). The communal den is the clan's social activity centre. Dens are taken over from other species, mostly warthog, aardvark and bat-eared fox (Kruuk, 1972, Mills, 1990). Communal dens often have multiple entrances with entrances too narrow for adult hyenas or other large carnivores to enter (Kruuk, 1972; Mills, 1990). This network of small tunnels underground is of immense protective benefit for cubs as they allow them to quickly flee underground as soon as predators such as lions or leopards approach (East, Hofer & Turk, 1989). Besides their protective function communal dens serve important social functions as meeting place where adult clan members socially interact with each other as well as with cubs and where clan members form hunting and territory border patrol parties (Kruuk, 1972; Mills, 1990; White, 2007).

Spotted hyenas use a wide repertoire of senses, including vocalizations, odors and visual cues to recognize and communicate with each other individually (Gorman & Mills, 1984; Mills, 1990; East & Hofer, 1991a, 1991b). They are famous for their 'giggle' which sounds like a high-pitched human laughter (Mathevon *et al.*, 2010). A common call at nights in the African bush is the 'whoop' (East & Hofer, 1991a, 1991b). The 'whoop' is a long-distance vocalization emitted by hyenas to gather clan members together and to defend territory bounders, food resources, etc. (Mills, 1990). At communal dens, clan members whoop predominantly for self-advertisement (East & Hofer, 1991b).

Spotted hyenas generally exhibit a broad diet and tend to prey on the locally most abundant medium to large sized ungulate species, such as gazelles (*Gazella granti* and *G. thomsoni*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and buffalo (*Syncerus caffer*) in Eastern Africa (Holekamp *et al*. 1997; Höner *et al*. 2002) with preferences for juvenile individuals (Höner *et al*. 2002). In Southern Africa spotted hyenas mostly select gemsbok calves (*Oryx gazella*) (Mills, 1990), and in Western Africa buffalo is the most common prey species found in scats (Di Sivestre *et al.*, 2000). They are also known to exploit carrion as a food resource (Kruuk, 1972; Tilson, von Blottnitz & Henschel, 1980; Cooper, Holekamp & Smale, 1999; Höner *et al.*, 2002). In northern Ethiopia, spotted hyenas subsist entirely on domestic species (Abay *et al.*, 2010; Yirga & Bauer, 2010; Yirga *et al.*, 2013). But this preference is predominantly driven by the dramatic decline of natural prey species here (Abay *et al.*, 2010; Yirga *et al.*, 2013). Spotted hyenas are known as skilled hunters, killing a large percentage of their prey on their own (Cooper *et al.*, 1999; Höner *et al.*, 2002). A single spotted hyena can hunt down prey of the size of a wildebeest (Wasson, 1990), but often spotted hyenas hunt in groups to enhance hunting success and to prey down larger prey species, such as zebras (Mills, 1990; Holekamp *et al.*, 1997). Spotted hyenas can also adapt their hunting and scavenging behaviour to the co-occurrence of other large predators, in particular lions (Höner *et al.*, 2002). In areas where lion abundance is high and hence more prey can be acquired by kleptoparasitism or scavenging, spotted hyenas hunt less whereas in areas where lion abundance is low spotted hyenas hunt more (Cooper, 1991; Höner *et al.*, 2002). However, the opposite case holds true as well and lions often steal carcasses from spotted hyenas (Cooper *et al.*, 1999).

1.3 Notes on the status and distribution of spotted hyenas with special emphasis on Central Africa

Spotted hyenas inhabit continental Africa. In Africa, it is the most abundant hyena species and also has the greatest geographic distribution of all hyena species (Fig.1) (Hofer & Mils, 1998). The biggest spotted hyena populations exist in eastern Africa, particularly in the Serengeti ecosystem with a population number ranging from 7200 to 7700 animals (Hofer & Mills, 1998a). Large populations also exist in southern Africa, particularly in the Kruger National Park (1300–3900) (Mills, 1985). Other protected areas which support population sizes of several hundred animals are the Masai Mara Game Reserve, Kenya and the Selous Game Reserve, Tanzania (Hofer & Mills, 1998a). Notable populations with nationwide population sizes of more than 1000 animals exist in Botswana, Ethiopia, Namibia, Zambia and Zimbabwe (Hofer & Mills, 1998a). A continent-wide estimate puts the total world population of spotted hyenas at 27,000 to 47,000 animals (Mills & Hofer, 1998). Yet it is still the most abundant large carnivore in Africa and the species is listed as *Least concern* in the IUCN Red List of Threatened Species (Höner, Holekamp & Mills, 2008).

Their wide habitat tolerance and dietary flexibility appear to be the main reasons for their success (Hayward, 2006). In many African ecosystems the spotted hyena is the keystone predator (Trinkel, 2009). Spotted hyenas inhabit virtually all habitat types in sub-Saharan Africa; they can be found in savanna grasslands and desert zones (Fig. 1) (Tilson & Henschel, 1986; Mills, 1990) as well as in montane forests (Fig.1) (Sillero Zubiri & Gottelli, 1992). They are only absent from northern Africa and the extreme desert conditions north of the Sahel zone as well as from the dense rainforests in Central Africa (Fig. 1) (Hofer & Mills, 1998a).

Nevertheless, like other large carnivores, spotted hyenas suffer more and more from the demands of an increasing human population for land and natural resources. Human-caused mortality appears to be the primary source for mortality for hyenas today (Hofer, East & Campbell, 1993; Hofer & East, 1995). In the Serengeti about 8 % of the population's adult animals are killed each year as a result of snaring and poisoning by game-meat poachers (Hofer *et al.*, 1993). In areas where spotted hyenas are, rightly or mistakenly, regarded as threat to livestock, they are purposely killed by livestock owners (Gusset *et al.*, 2009; Pangle & Holekamp, 2010). In some areas, spotted hyenas are killed to make use of their body parts in traditional medicine or rituals (Hofer & Mills, 1998b). As a result, many spotted hyena populations are rapidly declining, even in protected areas, especially in eastern and western Africa (Hofer & Mills, 1998a). In addition, habitat fragmentation has led to the existence of highly isolated and often very small spotted hyena populations (Hofer & Mills, 1998a, b).

While spotted hyenas in eastern, western and southern Africa have been well studied, data on spotted hyenas in Central Africa is still deficient. A large part of Central Africa is covered by the tropical rainforests of the Congo Basin, extending from the Albertine Rift in the east to the Atlantic Ocean in the west (Fig. 1). Embedded in the Congo Basin lies the Batéké Plateaux area, which itself is part of the Western Congolian forest-savanna mosaic (Fig. 1 & 2) (Olson *et al.*, 2001). The Batéké Plateaux area is, with a size of roughly 200,000 km^2, a large forest-savanna mosaic, consisting of extensive areas of rolling grassy savannas, interspersed with gallery forests along watercourses. It covers almost $2/3^{rd}$ of the Republic of Congo (hereafter: Congo) and extends into Gabon to the west and Angola and Democratic Republic of Congo to the south respectively (Fig. 2). The actual plateaus are a series of six elevated areas which are primarily located in the Congo. In Gabon, the Batéké Plateaux area comprises the foothills of these Congolese plateaus. The plateaus are part of an ancient sand dune system called the Kalahari Sands and the dunes are believed to have been formed during the last glacial maximum 18,000–13,000 B.P. within a period of hyperarid conditions (Haddon, 2000; Heine, 1982).

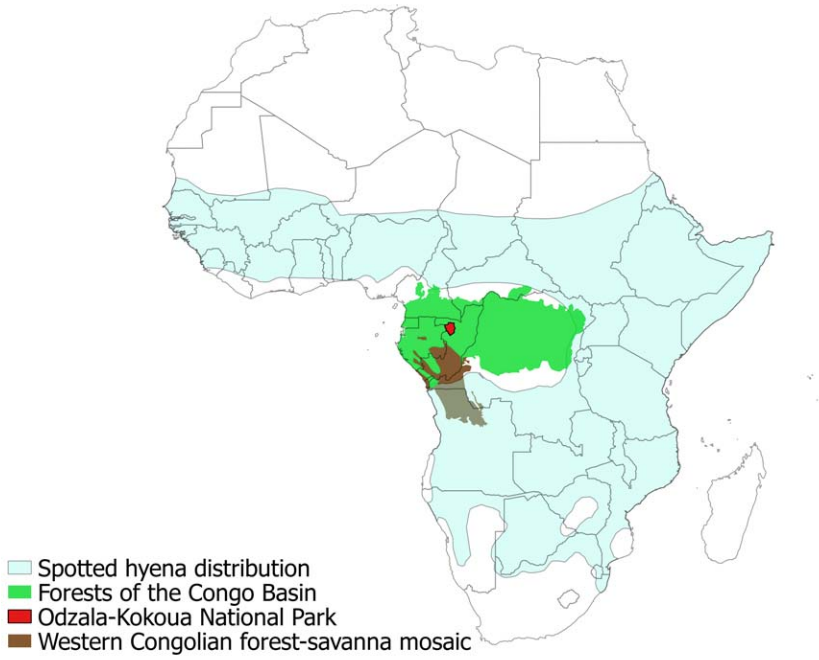

Figure 1. Map showing spotted hyena distribution in Africa according to IUCN and extent of the forests of the Congo Basin and the Western Congolian forest-savanna mosaic. Red area shows location of the Odzala-Kokoua National Park with current spotted hyena occurrence in Central Africa.

The savannas of the Batéké Plateaux were once a stronghold for spotted hyenas, lions and African wild dogs (*Lycaon pictus*) (Malbrant & Maclatchy, 1949). A dramatic decline occurred during the second half of the 20th century resulting in the complete extinction of lions and African wild dogs in the plateaus (Dowsett, 1995; Henschel, 2009). Simultaneously, the distribution range of spotted hyenas in the Batéké Plateaux has dramatically declined, resulting in only one remaining population inhabiting the Odzala-Kokoua National Park (OKNP) in the north of the Congo (Henschel, 2009) (Fig. 2). Within the last decades records of single individuals of this species were reported from several forest-savanna mosaics and forest sites in Congo, Gabon and Equatorial Guinea (Juste & Castroviejo, 1992; Hofer & Mills, 1998a; Henschel & Ray, 2003; Bout, Born & Spohr, 2010; Gessner, Buchwald & Wittemyer, 2013). However, none of these findings could prove that these spotted hyenas were remnants of distinct populations living in these areas (see also Chapter 8). Thus, it is more likely that these spotted hyenas represented unsuccessful dispersal events of spotted hyenas from the OKNP. The OKNP's spotted hyena population represents, in fact, the Batéké Plateaux' and, in addition, the Congo Basin's only spotted hyena population (Henschel, 2009). The spotted hyena population in the OKNP is more than 800 km separated from the nearest known spotted hyena populations in the Sahalian savannas in Cameroon and the Central African Republic by a wide band of contiguous rainforest (Fig. 1). This isolation makes the OKNP's population highly vulnerable to inbreeding depression and stochastic events, such as outbreaks of diseases. The OKNP's spotted hyena population is the subject of this dissertation. With my work I hope to make an important contribution to the preservation of the Congo Basin's last spotted hyena population.

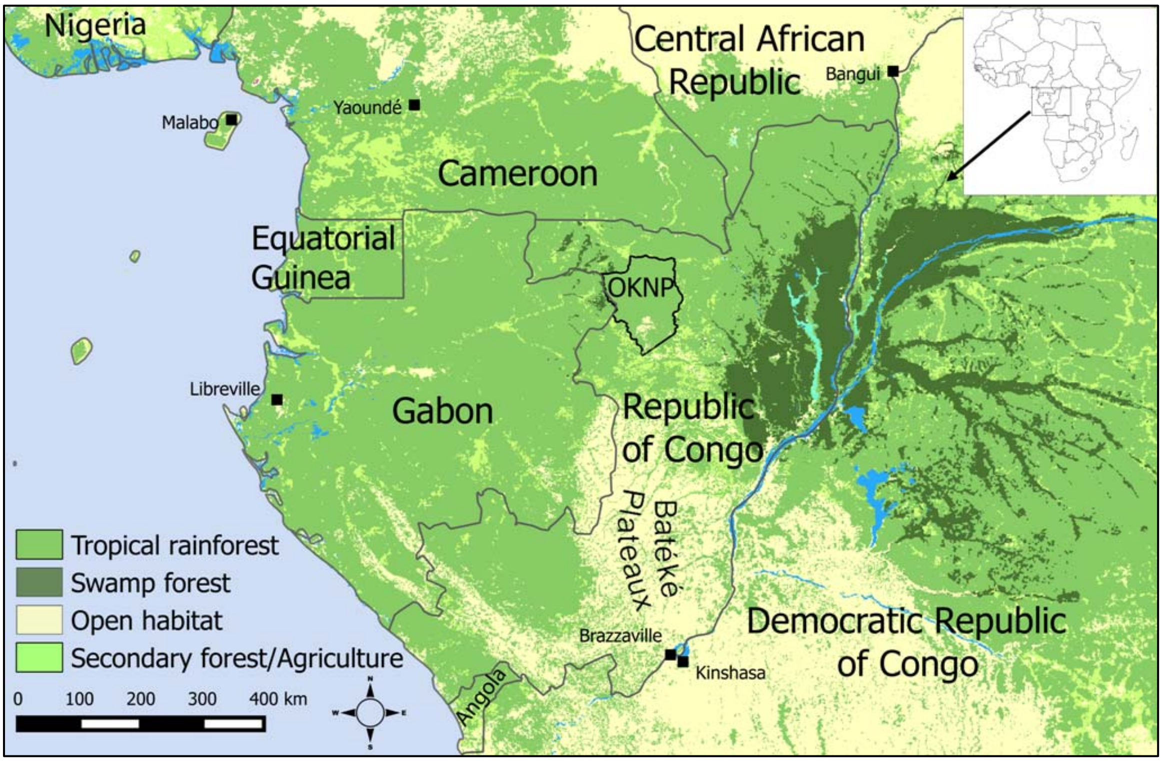

Figure 2. Map showing extent of the Batéké Plateaux and location of the Odzala-Kokoua National Park (OKNP).

1.4 The Odzala-Kokoua National Park

The Odzala-Kokoua National Park (OKNP) has a size of approx. 13,600 km^2 (Fig. 3). The OKNP is the biggest national park in the Republic of Congo and is situated about 500 km^2 north of the capital Brazzaville (Fig. 2). Open-canopy Marantaceae-forest on *terra firma* with an almost impenetrable understorey dominated by the plants of the families Marantaceae and Zingiberaceae is the main habitat type in the park (Hecketsweiler, Doumenge, & Mokoko-Ikonga, 1991) (Fig. 4). Closed-canopy Marantacee-forest with a more open understorey can be found in the western section of the park (Fig. 4). Seasonal inundated forest (swamp forest) can be found along the two main rivers in the park, the Mambili and the Lékoli (Fig. 4). The rainforest in the park is part of the Northwestern Congolian Lowland Forest ecoregion (Olson *et al.*, 2001).

An open habitat consisting of a mosaic of savannas and gallery forests along rivers is situated in the south of the park (Fig. 4 & 5). This forest-savanna mosaic (hereafter FSM) is covering about 8 % of the park's entire surface and represents the northernmost extension of the Western Congolian FSM of the Batéké Plateaux. The savannas are dominated by Graminae (*Andropogon schirensis*) with scattered fire-resistant shrubs (Dowsett-Lemaire, 1996). The savannas are currently recolonized by the forest (e.g. *Lophira alata*, *Pentaclethra eetveldeana*, *Xylopia aethiopica*) (Dowsett-Lemaire, 1996). As a result, some parts of the savannas are covered by forest islands of up to 3 km^2 (Fig. 4, 5 & 6) or are characterized by high densities of shrubs and smaller trees (Fig. 7). Forest islands are important habitat types in the park, harbouring a rich diversity of bird species (Dowsett-Lemaire, 1995). Larger forest islands resemble open-canopy rainforest on *terra firma*, locally with an understorey of Marantacee, whereas smaller forest islands consist of an almost impenetrable understorey of lianes (Kouka, 2001).

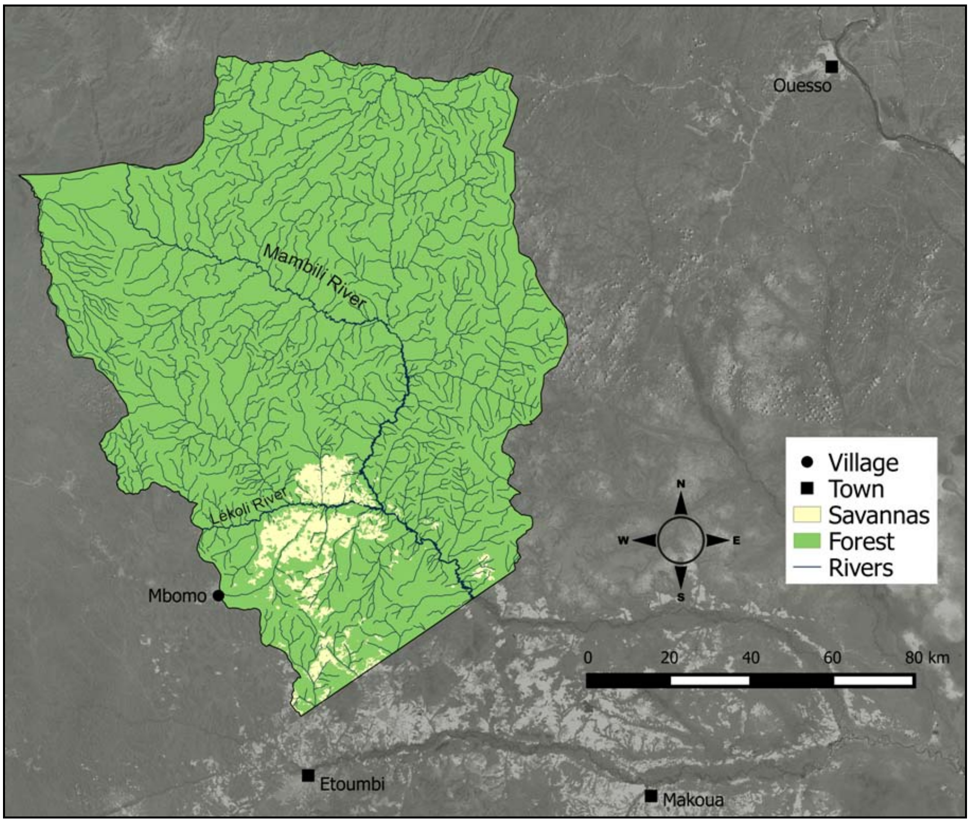

Figure 3. Satellite map showing the Odzala-Kokoua National Park.

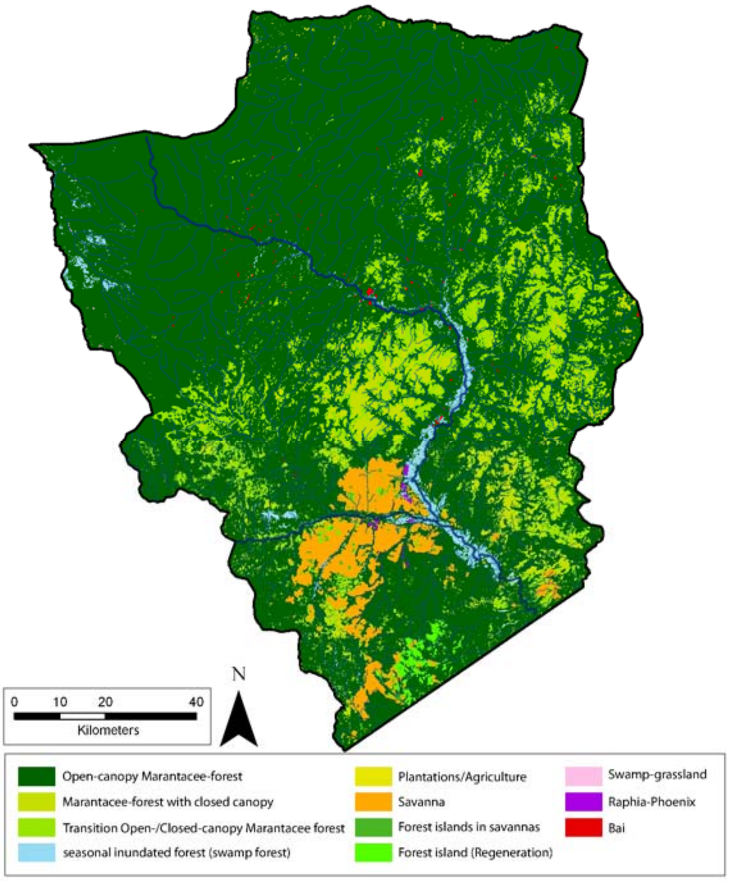

Figure 4. Map of the OKNP showing the different habitats in the park.

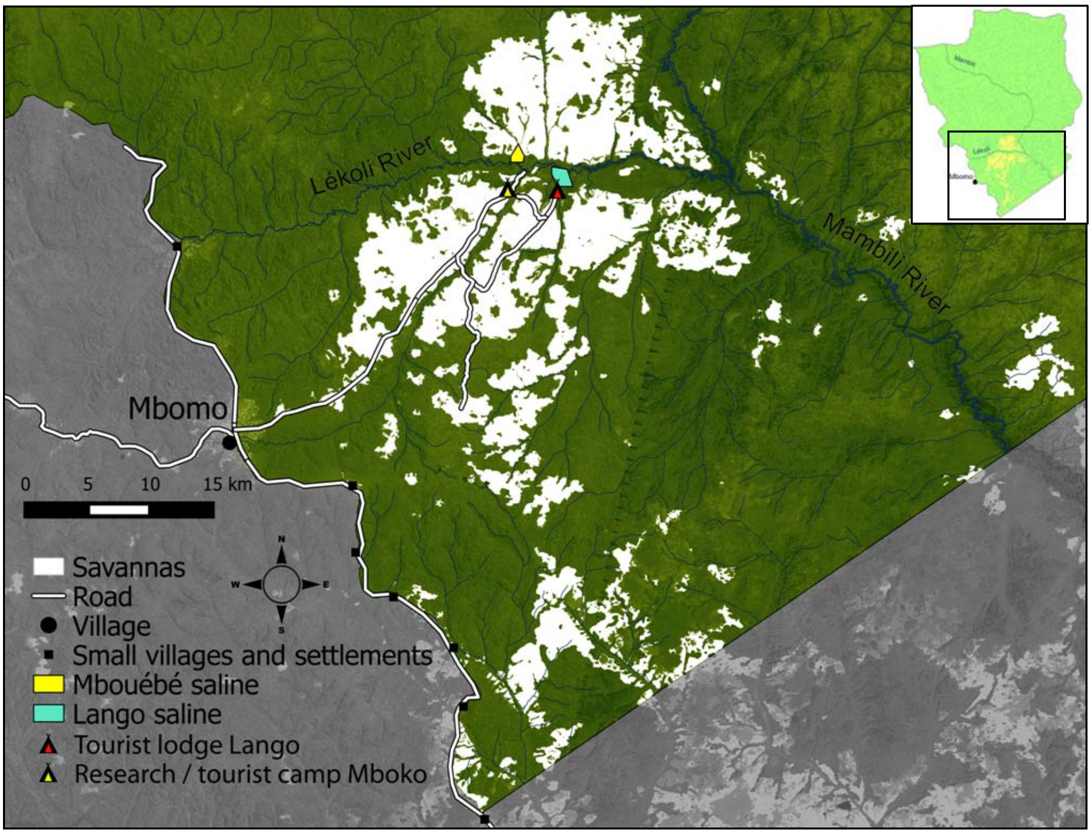

Figure 5. Map showing OKNP's forest-savanna mosaic and locations of salines, camps and villages.

Figure 6. Photo showing a forest island in the savannas of the OKNP. Photo: Torsten Bohm

Figure 7. Photo of the OKNP's forest-savanna mosaic. Photo: Torsten Bohm

Numerous forest clearings, so called *bais*, can be found in the forest bloc of the OKNP (Fig. 4). *Bais* are natural forest clearings which provide a year-round fresh vegetation and an important source for minerals for visiting mammals (Maisels, 1996). The largest known *bai* in the park is, with a size of approx. 0.18 km^2, 'Maya Nord' (Magliocca, Querouil & Gautier-Hion, 1999). *Bais* are regularly visited by larger forest mammal species, such as western lowland gorilla (*Gorilla gorilla gorilla*), forest elephant (*Loxodonta cyclotis*), sitatunga (*Tragelaphus spekeii*) and bongo (*Tragelaphus eurycerus*). Another type of clearings, *salines*, can be found along the Lékoli River (Fig. 5 & 8). *Salines* are large open clearings situated at the transition zone between savannas and forests (Maisels, 1996). They are situated next to the Lékoli River and extend into the forest with one or more tributaries of the Lékoli running through them. *Salines* have salt- and other mineral-rich soils and attract forest elephants as well as other mammals (Maisels, 1996). The *saline* Lango was the headquarters of an important local salt industry in the 19th century (Hecketsweiler *et al.*, 1991).

Figure 8. Forest buffaloes in the *saline* Lango. Photo: Torsten Bohm

The OKNP harbours a rich diversity of wildlife species and is one of the last strongholds for a variety of larger and smaller wildlife species in the Congo Basin (Maisels, 1996; Aveling & Froment, 2001). The OKNP hosts ten diurnal primate species which is the highest number in Central Africa and it probably also hosts the highest number of western lowland gorillas in Africa (Bermejo, 1999). However, gorilla population numbers have dramatically decreased by almost 50 % in the last two decades, which was mainly the result of severe Ebola outbreaks in the late 1990s and early 2000s (Walsh *et al.*, 2003; Bermejo *et al.*, 2006; Maisels *et al.*, 2013). The OKNP is a last stronghold for forest elephants in Central Africa. A census from 2012 showed that approx. 9600 forest elephants live in the park

(Maisels *et al.*, 2013). The population numbers in the park have been even increased since 2005 (7400 forest elephants) (Maisels *et al.*, 2013). However, this could be mainly the result of the poaching pressure outside the park resulting in an inward flow of forest elephants into the protected areas of the park. In addition, the OKNP is home of one of the biggest forest buffalo populations (*Syncerus caffer nanus*) in the Congo Basin (East, 1999; Aveling & Froment, 2001). The park harbours at least six different duiker species, e.g. yellow-backed duiker (*Cephalophus silvicultor*), as well as other large forest mammal species, such as bongo, sitatunga, giant forest hog (*Hylochoerus meinertzhageni*) and red river hog (*Potamochoerus porcus*).

The OKNP's FSM is home of the last population of spotted hyenas in the Congo Basin. Although spotted hyenas mainly occur in the park's FSM, they can also regularly be seen in the forest, *bais* and *salines* (Maisels, 1996; Bohm, 2008; pers. comment L. Lamprecht). The park's FSM is also a stronghold for a healthy population of servals (*Leptailurus serval*) (see chapter 4). Larger ungulate species such as bushbuck (*Tragelaphus sciptus*), forest buffalo and red river hog can also be regularly seen in the FSM (Maisels, 1996; Bohm, 2008). Forest buffaloes regularly aggregate in the savannas and groups containing 50–100 animals can often be seen in the FSM (Chamberlan, Maréchal & Maurois, 1998; Bohm, 2008). The park's FSM was once inhabited by the last population of lions in the Congo Basin but the last two lions were killed in the early 1990s (Dowsett, 1995).

The OKNP is surrounded by many small and large villages, with some of them directly situated at the park's border (Fig. 3 & 5). The largest village, with approx. 4000 inhabitants, is Mbomo (Fig. 3, 5 & 9). The town Etoumbi, located just 20 km south of the park, is with approx. 10,000–15,000 inhabitants the largest nearest town (Fig. 3). In the rural as well as in the town populations near the park there is a high demand for bushmeat (Hennessey & Rogers, 2008; Mbete *et al.*, 2010). Although villagers are allowed to hunt using legal forms of hunting, such as snaring with natural, local materials ('traditional hunting') or with licensed fire arms (http://faolex.fao.org) during hunting seasons in pre-defined regions, villagers do often not respect the laws and hunting for bushmeat is mostly carried out with illegal wire snares year round (Hennessey & Rogers, 2008; Mbete *et al.*, 2010). Hunting mostly occurs in the buffer zones and forest areas surrounding the park (Hennessey & Rogers, 2008; Mbete *et al.*, 2010). However, bushmeat hunting, as well as poaching for ivory, is still a big problem in the park itself and also affects areas in and around the savannas of the park (pers. comment L. Lamprecht; Vanwijnsberghe, 1996; Gami, 2000; Bohm, 2012; Maisels *et al.*, 2013). A large palm-oil plantation which is currently built at the south-western border of the park (pers. comment D. Zeller) will probably further fuel the bushmeat problem in this region.

The park is currently managed by African Parks, a NGO which has signed a 25-year mandate for the management of the OKNP with the Congolese government. African Parks successfully manages several parks in Africa and is currently implementing their unique approach, combining conservation practice with business expertise, in the OKNP. Priority is given to significantly decrease the amount of bushmeat and ivory poaching inside the park borders and, in the long term, to generate revenues from paying visitors of the park. An upmarket tourist lodge, situated at the saline Lango (Fig. 5), was opened in 2012 and a growing number of tourists is visiting the park since then.

Figure 9. Local market in Mbomo. Bushmeat is sold here on a daily basis. Photo: Torsten Bohm

1.5 Objectives of this study and structure of the dissertation

Knowledge of size and structure of a population can provide valuable information regarding its potential vulnerability for extinction. Populations in areas of 'less scientific attention' might differ in their genetic makeup and biology from populations that are well studied. Thus, implementation of effective conservation strategies can be hampered if basic information is not available or deficient. Furthermore, populations in different areas face different threats. In the Congo Basin, bushmeat is still the main source of protein for humans (Wilkie & Carpenter, 1999b; Fa, Currie & Meeuwig, 2003; Mbete *et al.*, 2011). In many areas bushmeat hunting is mostly carried out with wire snares (Noss, 1998; Fa & Yuste, 2001). This form of illegal hunting is undirected as it targets not only the desired food (Fa & Yuste, 2001; Becker *et al.*, 2013). Bushmeat hunting is often not sustainable and has already led to a decline in many local wildlife populations in the Congo Basin (Wilkie & Carpenter, 1999b; Fa & Brown, 2009). As large carnivores are on top of the food chain, they suffer indirectly from the depletion of potential prey base (Karanth & Stith, 1999; Henschel, 2009).

Furthermore, they are in direct competition for food with human hunters, as their diet, consisting mostly of small to large-sized ungulates (Hayward *et al.*, 2006), is also the preferred food of hunters (Fa & Yuste, 2001; Henschel *et al.*, 2011). Thus, to have accurate knowledge on the quantity of human-induced threats to large carnivore populations is of great importance for formulation and implementation of successful management strategies.

Wildlife researchers make us of various tools in order to collect data on wildlife populations. As wildlife researchers often have to deal with vulnerable or rare species, they have to choose tools which have little or in the best case no impact on the behaviour of the target species and the environment they inhabit (Long *et al.*, 2008). Several of such non-invasive tools which do not require direct handling of animals exist today. Camera traps have emerged as a key non-invasive tool in wildlife research over the last decades (Karanth & Nichols, 1998; O'Connell, Nichols & Karanth, 2011). They have proven to be effective in studying a variety of carnivores in remote areas (Trolle & Kéry, 2003; Silver *et al.*, 2004; Karanth *et al.*, 2006; Rayan & Mohamad, 2009). Data obtained from camera traps are usually used to estimate population sizes, but can also be used to give insights into habitat use, temporal activity patterns and population dynamics of the target species (Azlan & Sharma, 2006; Karanth *et al.*, 2006; Sarmento *et al.*, 2009; Borah *et al.*, 2013).

Analysis of fecal samples has been a powerful tool in large carnivore conservation practice for decades (Mills, 2005). Fecal (or scat) samples can be obtained relatively easy and provide valuable information on the occurrence, health status, diet and genetic make-up of wildlife populations (Sillero-Zubiri & Gottelli, 1992; Dalén, Götherström & Angerbjörn, 2004; Randall *et al.*, 2009; Spiering *et al.*, 2010; Caragiulo *et al.*, 2015; Olarte-Castillo *et al.*, 2015). Population genetics analysis based on scats has become one of the most powerful instruments for conservation (Waits, 2004; Hauffe & Sbordoni, 2009). Genetic monitoring of large carnivore populations has proven to be very effective at answering important management and ecological questions, especially in isolated areas or areas with small large carnivore populations (Gottelli *et al.*, 1994; Tallmon *et al.*, 2004; Liberg, 2005; Aspi *et al.*, 2008). Due to their extensive spatial requirements, large carnivores are principally threaten by habitat fragmentation, and genetic monitoring can help to understand the influences of habitat fragmentation on the survival chances of large carnivore populations.

Another tool which has found its way into large carnivore conservation practice is acoustic monitoring (Terry, Peake & McGregor, 2005). Many mammal species have a wide repertoire of vocalisations (Sousa-Lima, Paglia & Da Fonseca, 2002; Darden, Dabelsteen & Pedersen, 2003; Morisaka, Shinohara & Taki, 2005; Erb, Hodges & Hammerschmidt, 2013). Studies have shown that individual animals can be discriminated by features of their vocalisations (Tooze, Harrington & Fentress, 1990; Terry *et al.*, 2005; Pfefferle *et al.*, 2007; Salmi, Hammerschmidt & Doran-Sheehy, 2014). Moreover, information from vocal recordings can also provide information on the caller's age and stamina (Fischer *et al.*, 2002; Erb *et al.*, 2013). In addition, acoustic monitoring provides valuable service to conservation stakeholders as it also allows to record human disturbances and their impact on wildlife in conservation areas (Wrege *et al.*, 2010).

The main objective of this study was to collect data on the ecology and population status of spotted hyenas in the OKNP. Information from this allows an assessment of the species' conservation status and formulation of conservation strategies necessary to secure its survival in the OKNP. Furthermore, I estimated population density of the serval in the OKNP's FSM and analysed influence of spotted hyenas on the temporal and spatial behaviour of this species. In addition, I investigated composition and ecology of the mammal community in the OKNP's FSM. In particular, I investigated influence of human activity and habitat characteristics, such as forest cover, on distribution and behaviour of medium and large-sized mammals in the FSM. Finally, I investigated population status of spotted hyenas and other wildlife species in three Batéké Plateaux areas in southeast Gabon. Specifically, I wanted to answer the following questions:

a) How many spotted hyenas live in the OKNP?
b) Where do spotted hyenas live in the OKNP?
b) How is the population structured in terms of age classes and number of clans? What are the numbers of males and (reproductive) females in the population? Can camera traps be used to answer these questions?
c) Can camera traps be used to get information on demographic parameters of the OKNP's spotted hyena population?
d) Can acoustic analyses of spotted hyena vocalisations be used to determine number of individuals in a spotted hyena clan?
e) What are the characteristics of spotted hyena communal den sites in the OKNP and where are these located?
f) What is the diet of spotted hyenas in the OKNP? What information (temporal activity patterns, distribution, etc.) can be extracted from camera trapping data about spotted hyenas' main prey species in the OKNP?
g) Did the isolation of the OKNP's spotted hyena population already have a negative impact on the population's genetic make-up and how is the genetic diversity in the population in general?
h) What are the major threats to the OKNP's spotted hyena population? Is the population size sufficiently large to secure the long-term survival of the population?

i) How many servals live in the OKNP's FSM and how does the spotted hyena, the apex predator in the OKNP's FSM, influence temporal activity patterns and distribution of this medium-sized carnivore?
j) What mammal species inhabit the OKNP's FSM and surrounding areas? How do human activity and habitat characteristics influence their distribution and behaviour? What are the major threats to the FSM?
k) Do spotted hyenas inhabit Batéké Plateaux areas in southeast Gabon? Is there sufficiently protected habitat available and is prey base in these areas sufficient to support viable spotted hyena populations?

To answer these questions I used non-invasive tools such as camera-trapping, scat analysis and acoustic monitoring. Three chapters (2–4) present results of the study in the form of manuscripts.

Chapter 2

Here, I provide results on the population size and density of spotted hyenas in the OKNP. For analysis, data from camera trapping studies were used. With the help of camera traps pictures I was also able to identify sex, age and clan memberships of recorded individuals. The methods and analyses described in this manuscript provided a new methodological framework that can be used for studying compositions and distributions of clans in spotted hyena populations as well as of social units in populations of other social carnivores with the help of camera traps.

Chapter 3

This chapter focuses on the diet of spotted hyenas in the OKNP. Diet was analysed using scats and regurgitations samples. I also compared temporal activity patterns of spotted hyenas and their main prey species in the OKNP with the help of camera trapping data.

Chapter 4

This chapter provides data on size, density and structure of the serval population in the OKNP's FSM. For this, data from camera traps were used. For analysis of population size and density I used spatially-explicit capture recapture methods. In this chapter I also analysed and discussed the influence that spotted hyenas have on the distribution and temporal activity patterns of servals in the park's forest-savanna mosaic.

Chapter 5

This chapter is about denning behaviour of spotted hyenas in the OKNP and presents first results of acoustic monitoring. The aim of acoustic monitoring was to identify individual spotted hyenas from recorded vocalisations. For this, I placed an audio recorder at a spotted hyena communal den to record whooping bouts from spotted hyenas.

Chapter 6

This chapter provides results of the genetic monitoring of the OKNP's spotted hyena population. Material for genetic analysis was obtained from fresh scat samples. Data was analysed with regard to genetic diversity, estimation of genetically effective population size and detection of recent bottleneck events.

Chapter 7

In this chapter I used camera trapping data to analyse distribution, occurrence and temporal activity patterns of wildlife species in the OKNP's FSM. Furthermore, I investigated influence of habitat characteristics and human activity on distribution and behaviour of the mammal community. The intention of this chapter is to provide baseline information which can help to support management of spotted hyenas and other wildlife species in the OKNP's FSM.

Chapter 8

This chapter gives information on three reconnaissance surveys and one camera trapping study which I did in southeast Gabon in 2011. The aim of these studies was to find out if viable spotted hyena populations are present in southeast Gabon. Apart from that, I collected data about current status of wildlife and levels of poaching in the surveyed areas.

Chapter 9

This chapter consists of a general discussion of the results of the dissertation. The discussion was focused on the methodologies I have used and their applicability in future studies on spotted hyenas. Furthermore, I shortly discuss implications of my findings for spotted hyena conservation in the OKNP and the need of follow-up studies.

A summary is given at the end, which shortly summarizes results and management implications from chapters 2–8.

Chapter 2: Camera-traps based assessment of the status of the endangered spotted hyena population in the Odzala-Kokoua National Park, Republic of Congo, with a new methodology to identify clan memberships in spotted hyena populations

2.1 Abstract

Despite being still the most abundant large carnivore in Africa, spotted hyena (*Crocuta crocuta*) populations are regionally declining. The Odzala-Kokoua National Park, situated in the northwest of the Republic of Congo, harbors the last population of spotted hyenas in the Central African Congo Basin. Accurate monitoring of this population is needed to preserve it for the future. We did three camera trapping studies to determine population size and trends in the population. In addition, we examined compositions of spotted hyena groups recorded by camera traps. Based on that, we were able to identify the members of the resident clans and the number of transients in the study areas from camera traps pictures. Including adults, older and younger cubs, the total population size in the park was estimated as 69 animals (6.42 individuals / 100 km^2) by the end of March 2014. We identified five clans, comprising 52 individuals, inhabiting the park's forest-savanna mosaic. Nine individuals were only recorded in forest clearings in the park's forest bloc and eight individuals were identified as transients in the park's forest-savanna mosaic. Urgent conservation actions are needed to preserve the last remaining spotted hyenas in the Congo Basin from extinction. Poaching with illegal wire snares is probably the main threat to the population. In our study we also investigated the peculiarities in spotted hyena societies and how these must be considered in analytical approaches, such as spatially-explicit capture-recapture methods, in the future.

2.2 Introduction

The spotted hyena (*Crocuta crocuta*) is a social large carnivore that lives in groups, so called clans (Kruuk, 1972). Each clan consists of one to several matrilines of adult females and their offspring, as well as of one or several immigrant adult males (Frank, 1986a; Mills, 1990). Females usually remain in their natal clan whereas males typically disperse from their natal clan at puberty and seek access to neighbouring clans (Frank, 1986a; Henschel & Skinner, 1987). Males which successfully joined another clan become immigrant males whereas males which cannot join a clan become nomads or transients (Mills, 1990; Smale, Nunes & Holekamp, 1997). Within a clan, linear dominance hierarchies among females and males are established (Frank, 1986b). However, within a clan all adult females and their cubs are dominant to all adult male immigrants (Drea & Frank, 2003). Clans inhabit territories with well-defined borders and clan members regularly patrol their territory (Mills, 1990; Henschel

& Skinner, 1991). The degree of territorial defence exhibited by clan members towards intruders as well as the degree of territorial activities in general seems to be related to competition over food. In areas where resident prey is abundant, such as the Ngorongoro Crater and Kruger National Park, spotted hyenas exhibit a highly territorial behaviour as revenues from prioritizing highly rewarding food sources overweight the costs for defence (Kruuk, 1972; Henschel & Skinner, 1991). In areas where territories are large due to widely dispersed prey (Namib, Kalahari) spotted hyenas show only enhanced territorial activities in the center as chances to detect intruders near the periphery are low (Tilson & Henschel, 1986; Mills, 1990). In the Serengeti, where prey is highly mobile and concentrated, single or groups of spotted hyenas commute over prolonged periods to areas with high prey concentrations (Hofer & East, 1993a, 1993b). As a results intrusion pressure is high and spotted hyenas adjust their territorial behaviour: commuters in 'transit' are ignored whereas commuters at kills are approached aggressively (Hofer & East, 1993b). Territorial as well as hunting activities is often carried out in groups (Holekamp *et al.*, 1997). Females play a major role in territorial activities and usually initiate and take the lead in clan wars and border patrols (Henschel & Skinner, 1991; Boydston, Morelli & Holekamp, 2001). Hunting in groups is carried out to hunt down larger prey and size of a hunting group strongly influences hunting success (Mills, 1990; Holekamp *et al.*, 1997; Trinkel, 2009).

The spotted hyena is widely distributed and still the most abundant large carnivore in sub-Saharan Africa (Hofer & Mills, 1998a). Healthy populations with nationwide population numbers of more than 1000 animals exist in eastern and southern Africa (Hofer & Mills, 1998b). However, in many regions population numbers are rapidly declining, even inside protected areas (Hofer & Mills, 1998a, b). Human-induced mortality appears to be the primary reason for the decline (Hofer, East & Campbell, 1993; Hofer & East, 1995). In Central Africa, spotted hyenas were once widely distributed in the open habitats of the Batéké Plateaux area (Malbrant & Maclatchy, 1949; Henschel, 2009), a large forest-savanna mosaic, covering almost two-thirds of the Republic of Congo and extending into neighbouring Gabon (Fig. 1). A dramatic decline occurred during the second half of the 20th century resulting in the nearby extinction of spotted hyenas in the Batéké Plateaux (Henschel, 2009). Today, spotted hyenas can only be found in the small forest-savanna mosaic of the Odzala-Kokoua National Park (OKNP) situated in the northwest of the Republic of Congo (Henschel, 2009). The OKNP'S spotted hyena population is separated from the nearest known spotted hyena populations in the Sahalian savannas in Cameroon and the Central African Republic by a wide band of contiguous rainforest (Hofer & Mills, 1998a). Hence, it remains the only spotted hyena population within the Batéké Plateaux and the Congo Basin.

The OKNP's spotted hyena population has been already the subject of a short-term camera trapping study (Henschel, Malanda & Hunter, 2014). For their analysis Henschel *et* *al.* (2014) used data from 24 trap stations which they placed in the park's forest-savanna mosaic aiming to find evidence for presence of lions (*Panthera leo*). Their trap stations were operational for 18–27 days (mean 17.67 trap days / trap station) from 21 July to 30 August 2007. They used one DeerCam 200 film-camera (Non Typical, Inc., Green Bay, Wisconsin) per trap station and their cameras produced 154 photos of spotted hyenas. For analysis they used a subset of 80 right-flank photographs and identified 46 different individuals. Population size and density was estimated as 88 ± 16.15 (CI 67–133) and 15.89 ± 3.92 individuals / 100km^2 respectively with 'conventional capture-recapture methods'. Camera traps are widely used for population size estimations of smaller and larger carnivores (e.g. Karanth & Nichols, 1998; Trolle & Kéry, 2005; Avgan *et al.*, 2014). Camera trapping studies are usually conducted within a closed capture-recapture framework (O'Connell, Nichols & Karanth, 2011). The mark-recapture models used for camera traps surveys are based upon closed populations that do not change by birth, death or migration over the course of the sampling period (Karanth, Nichols & Kumar, 2004). The sampling period is therefore restricted to a sufficiently short time frame whereas sampling periods of two to three months are usually used for long-lived animals with slow individual growth rates such as large carnivores (Silver *et al.*, 2004; Kalle *et al.*, 2011). Another assumption is that all individuals in the sampled area have "some" probability of encountering a camera trap, i.e. there is at least one camera trap within the range of an individual during duration of the sampling period (O'Connell *et al.*, 2011). An often used approach to satisfy this assumption is to adopt the smallest home range estimate for the target species as the minimum area in which there must be at least one camera trap site (Karanth *et al.*, 2004). Taking the biology of spotted hyenas into account, Henschel *et al.* (2014) have violated the above mentioned and other assumptions, which has likely resulted in highly inaccurate estimates of the population's size. First, spotted hyenas are territorial species which often do forays, which can last up to several weeks, outside their clan territories (Hofer & East, 1993b; Boydston *et al.*, 2005). Given the short duration of Henschel *et al.*'s (2014) study of about one month, with many camera traps sites that were operational considerably less than one month, it is likely that clan members which were foraging outside their territories were not detected. Henschel *et al.* (2014) placed 24 trap stations in an area of ca. 346 km^2 and aimed for approximately 5-km spacing between traps. However, as their Figure 1-B shows (Henschel *et al.*, 2014) camera trap placement was often locally clumped and large holes were left between trap stations. In some savannas of their study area camera traps were just placed at the savannas' edges resulting in holes of more than 32 km^2 (see Fig. 1-B in Henschel *et al.* (2014)), which is at least 3.5 times larger than the smallest reported home range of 9 km^2 for spotted hyenas (Höner *et al.*, 2005). Furthermore, spotted hyenas often travel and hunt in groups (Holekamp *et al.*, 1997). Thus, ideally, equipment should be used that enhances chances of photographing individuals following in close distance individuals which were photographed first. Henschel *et al.* (2014) used a film-camera with an interval of 60 s between trigger events (pers. comment P. Henschel). By using equipment that only allows to take consecutive pictures after a rather long interval, chances to miss individuals which often or exclusively travel in groups, such as females and younger individuals (Mills, 1990; Boydston, Morelli & Holekamp, 2001), are high.

Small and isolated populations are highly vulnerable to extinction. Enhanced levels of human poaching, lack of genetic diversity and stochastic events, such as outbreaks of diseases, are one of the key drivers which can bring small and isolated populations close to extinction (Kat *et al.*, 1995, 1996; Murray *et al.*, 1999). Small populations of large carnivores are especially threatened as their slow reproduction rate hampers them to bounce back after further retraction to population sizes sufficiently large to escape extinction (Burton *et al.*, 2011; Black *et al.*, 2013). The isolation of the OKNP's spotted hyena population makes it highly vulnerable to extinction and largely dependent from well-formulated management strategies. Lack of information or reliance on insufficient data can seriously hamper conservation strategies (Groom, Funston & Mandisodza, 2014). Thus, in order to support successful management strategies for the OKNP's spotted hyena population, detailed knowledge about their size, structure, dynamics and threats is needed.

Here we examine the situation of the spotted hyena population in the OKNP. We used data from three camera trapping studies to obtain direct estimates of size, structure and dynamics of the OKNP's spotted hyena population. In our camera trapping studies we considered the biology of spotted hyenas and adjusted trap design accordingly. We describe a new methodological framework based on camera traps that allows to identify clan memberships of individuals. This methodology can also be applied to determine compositions of social units in other social carnivore species. Discussion was focused around methodological considerations regarding optimal design of camera trapping studies on spotted hyenas and other social carnivores. We further discuss survival chances of the OKNP's spotted hyena population and recommend conservation actions. Finally, we discuss the value of Henschel *et al.*'s (2014) results and methods for the conservation of the OKNP's spotted hyena population in comparison with our results and methods.

2.3 Material and methods

Study area

The Odzala-Kokoua National Park is with approx. 13,600 km^2 the biggest national park in the Republic of Congo (Aveling & Froment, 2001). The main study site was situated in the southern area of the park which is characterised by a mosaic of savannas and gallery forests (Fig. 1). This mosaic makes up approximately 8% of the entire park surface and is completely surrounded by dense primary forest to the north, east and west respectively (Fig. 1). The savannas are dominated by Graminae (*Andropogon schirensis*) with scattered fire-resistant shrubs (*Hymenocardia acida* and *Annona senegalensis*) (Dowsett-Lemaire, 1996). The Lékoli River divides this forest-savanna mosaic (herafter FSM) into a southern and a northern savannas sector (Fig. 1). The savannas are currently being colonized by the forest (e.g. *Lophira alata*, *Pentaclethra eetveldeana*, *Xylopia aethiopica*) (Dowsett-Lemaire, 1996) and, as a result, some parts of the savannas were covered by forest islands of up to 3 km^2 or characterized by high densities of shrubs and smaller trees. Among the larger ungulates which can be found in the FSM are forest buffalo (*Syncerus caffer nanus*), bushbuck (*Tragelaphus scriptus*) and red river hog (*Potamochoerus porcus*). Spotted hyena and leopard (*Panthera pardus*) are the only remaining apex predators in the park (Maisels, 1996). Lions were extirpated by the mid-1990ies (Dowsett, 1995).

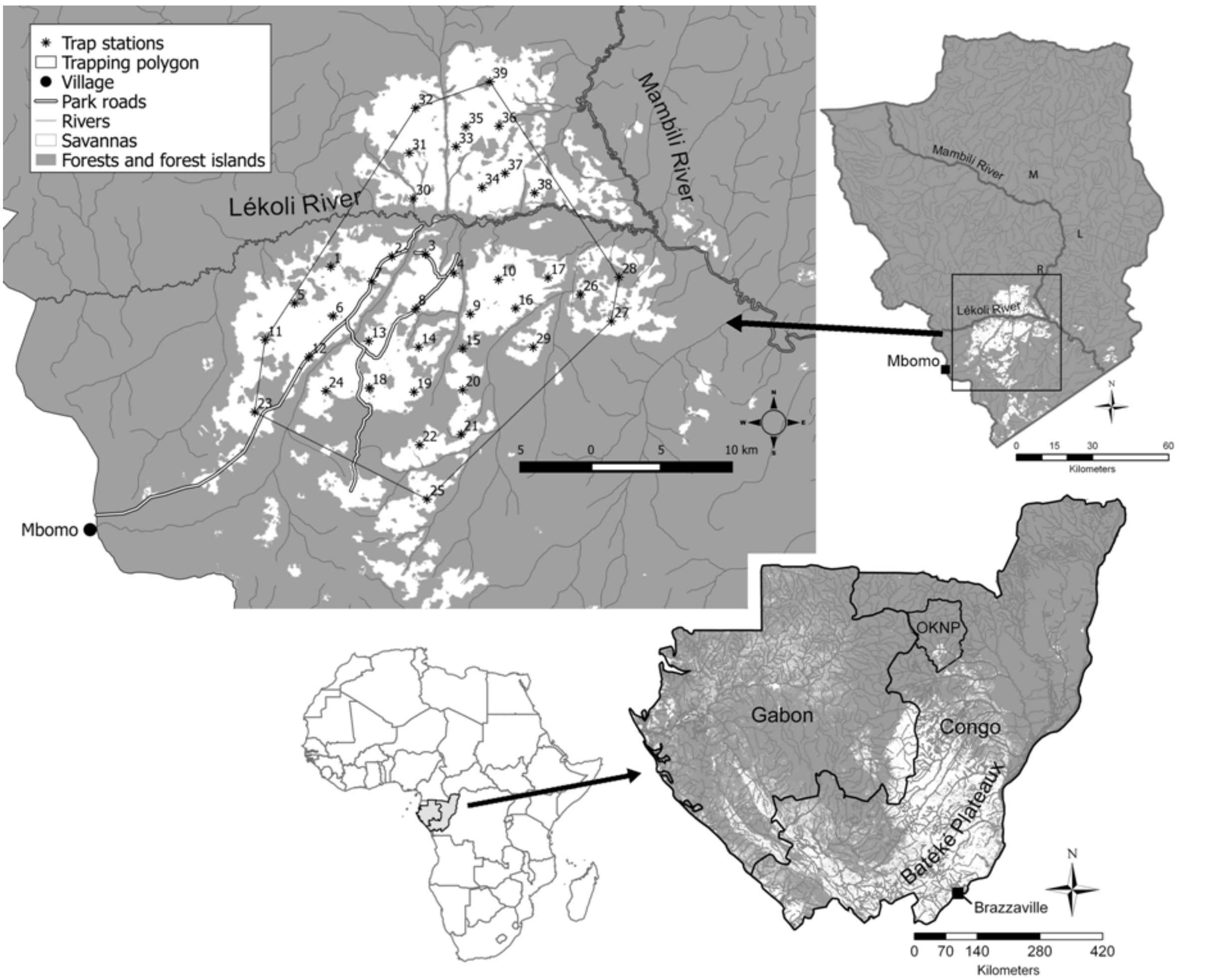

Figure 1. Maps showing locations of the Batéké Plateaux, Odzala-Kokoua National Park (OKNP), study area and trap stations in study area. L = *bai* Lokoué, R = *bai* Romani, M = *bai* Maya Nord.

Camera trapping

Trap stations were deployed in each cell of a 3.5 x 3.5 km grid. This spacing was chosen with respect to the known minimum home range sizes for spotted hyenas. The smallest reported home range for spotted hyenas is 9 km^2 (Höner *et al.*, 2005), which represents approximately the area of a circle that fully fills out the area within the grid cell. Trap stations were deployed at sites where capture probabilities for wildlife species were likely to be high, such as roads and wildlife trails.

We did camera trapping during two sampling periods: November 2011–January 2012 (hereafter CT study 1) and July 2013–March 2014 (hereafter CT study 2). During CT study 1 only the southern savannas sector was surveyed within two sampling blocks. Trapping block 1 (trap stations 1–11 in Fig. 1) was operational from mid-November for 32 days. Then trap stations were moved to trapping block 2 (trap stations 12–22 in Fig. 1) where they were operational for further 32 days. Each trap station was operated with one Reconyx HC500 and one Bushnell Trophy Cam camera trap. The mean inter-camera trap distance was 2.8 km and the total trapping area was 167 km^2. During CT study 2, 39 trap stations were installed in the southern and northern savannas sector. The same locations for trap stations 1–22 were used as in CT study 1. Installation of 38 trap stations began in mid-Jul and stations were active for eight months until end of March 2014. An additional trap station (no. 39 in Fig. 1) was installed in February 2014 and operational for one month. Mean inter-camera trap distance was 2.7 km and total trapping area was 456 km^2. At each trap station one Reconyx HC500 was installed. Fifteen additional cameras (Reconyx HC500 and Bushnell Trophy Cam) were temporally moved between trap stations so that some trap stations could be operated with two cameras at the same time during this study period. Twenty-nine stations were installed in savannas and ten stations were installed in forests and forest islands.

Reconyx were programmed to take pictures in RapidFire™ mode with 5 pictures per trigger event without interval between trigger events and pictures. Bushnell Trophy Cams were programmed to take 3 pictures per trigger event with the shortest available interval between trigger events (approx. 5–6 seconds).

In addition we used data from a camera trapping study conducted by the park management in the forest clearings Maya Nord, Lokoué and Romani in the forest bloc (Fig. 1) between December 2012 and May 2013. Smaller and larger forest clearing (*bais*) are numerous in the park and regularly visited by larger forest mammals, such as forest elephant (*Loxodonta cyclotis*) and western lowland gorilla (*Gorilla gorilla gorilla*). Spotted hyenas are also regularly seen in the *bais* (Maisels, 1996). Camera trapping study in the *bais* was conducted with Bushnell HD camera traps. Bushnell's were programmed to take 3 pictures per trigger event with an interval of 3 s between trigger events.

Data analysis

Individual identification and characteristics, clan memberships and sizes, population sizes and densities

Spotted hyenas were individually identified with the help of their unique spot patterns on both flanks. We defined each individually identified animal in a photo as independent capture event. Furthermore, consecutive photos of the same individual were considered as independent when there were taken at least one hour apart. Identified animals were further grouped into adults, subadults (older cubs) and cubs (very young cubs).

We often obtained dozens of pictures per trigger event and a large number of pictures showed close-ups with the animals' penis or clitoris (pseudopenis) and other sex characteristics, such as testicles, pseudoscrotum and swollen teats. Spotted hyena females are highly masculinised with genitals resembling male genitals (Hamilton, Tilson & Frank, 1986). A panel of experts was judging these pictures to determine sex of the photographed animals. In addition, we assessed the reproductive status of females. Reproductive females were grouped into the following categories: 1) lactating (swollen teats were visible), 2) in estrus (swollen clitoris was visible), 3) has given birth (disrupted clitoris was visible), 4) has had cubs (female was photographed suckling cubs in front of camera trap).

To determine clan membership we investigated grouping patterns from camera traps pictures. We considered animals photographed in the same photograph or following first photographed animal(s) within 10 minutes as animals belonging to the same group. For each combination of animals we recorded the number of times they were photographed in the same group. Clan memberships were visualized in a network diagram using software Gephi 0.8.2-beta (Bastian, Heyman & Jacomy, 2009). Each identified animal was considered as node in the network. The weight of the ties connecting the nodes was determined by the number of times animals were photographed together in the same group. We considered animals which were photographed in different territories and not in groups in the FSM as nomads/transients.

To determine trap effort needed to record all spotted hyenas in the study area we recorded the sampling occasion for each individual when it was first recorded. We then plotted the consecutive number of recorded individuals against the consecutive sum of trap nights of operational trap stations per sampling occasion. We defined a 24-hrs period between 6 am and 6 pm as one sampling occasion or as trap night for single trap stations respectively. Trap effort was determined independently for adult and subadult clan members as well as for transients and cubs. Determinations of trap effort could only be done with data from the FSM since park management could not provide relevant data from the *bais*.

We were further interested in location of the core area ('activity center') of each clan. The communal den is the social activity centre of a clan and the offspring of all clan members is raised at the communal den (Kruuk, 1972, Mills, 1990). Adult members regularly return to the communal den after foraging trips and border patrols (Mills, 1990; Boydston *et al.*, 2005). Very young clan members stay in the immediate vicinity of the communal den but start longer excursions as they grow older (Boydston *et al.*, 2005). Hence, it can be assumed that camera traps situated near a clan's communal den site record clan members, but especially young individuals, more often, whereas camera traps situated farther away from the communal den record clan members less often and, in general, rarely, if at all, very young individuals. We considered a communal den found in the study area as core area for the clan which was identified from camera traps occupying the area where the communal den was found. For clans for which no communal dens were found, we determined core areas from camera trapping data. For this, we investigated the mean hourly intervals between successive capture events for single members or groups of a particular clan at a trap station ('visit interval'). Then we looked if visit intervals between trap stations differed significantly for a clan using ANOVA and post-hoc Tukey's Honest Significant Difference Test and considered trap station(s) with the shortest visit intervals and differing significantly from visit intervals of other trap stations as trap station(s) near the clan's core area. If visit intervals between trap stations with the shortest intervals differed not significantly among each other we presented the core area as a polygon with the respective trap stations as vertices. In addition, we compared capture successes among age classes between trap stations near the core area and trap stations farther away using χ^2 - test.

For population density estimation we added the half mean maximum distance moved (½MMDM) of identified individuals which were photographed at more than one trap station as buffer around the trapping polygon to determine size of the sampling area. Population size was then divided by the size of the sampling area to obtain density. We used the total number of identified individuals as final number for the population size. The ½MMDM-approach is commonly used in capture-recapture studies (O'Connell *et al.*, 2011) and was also used by Henschel *et al.* (2014), making our estimates comparable to their estimates.

Changes in population and clan sizes

Duration of CT study 2 was long enough to determine loss of clan members within this period. For this, we investigated intervals between successive capture events for individuals. Spotted hyenas often do excursions outside their natal territories and stay outside their territories for several weeks (Hofer & East, 1993a; Boydston *et al.*, 2005). We used the number of sampling occasions from the animal which had the longest interval between successive capture events as threshold. Animals which were not photographed within this interval until the end of the study period were considered as animals which have died or left the study area.

In addition, we compared results from the two camera trapping studies in the FSM to determine changes in population and clan sizes between these two periods. Spotted hyenas which were photographed during CT study 1 but not during CT study 2 were considered as animals which have died. We compared clan memberships based on network analysis from the two study periods to determine if animals have changed clans or become transients. Subadults and cubs from CT study 2 were considered as animals new to the population. Since more than 1½ years was between the two camera trapping studies we assumed that cubs and subadults identified in CT study 2 were born either after or during CT study 1. Thus, to consider these individuals as individuals new to the population is appropriate. We likely underestimated the number of new individuals as very young cubs that stayed at the communal den could not be recorded.

2.4 Results

Results from CT study 2 (July 2013 to March 2014) in the FSM and camera trapping study in the bais (December 2012 to May 2013)

During eight months of camera trapping in the FSM camera traps produced 2938 independent records of spotted hyenas. Total number of trap nights was 7081. Consequently trapping effort for spotted hyenas was 41.5 records / 100 trap nights. Spotted hyenas were recorded at all 39 trap stations. Of the 2938 records 2691 records were of sufficient quality allowing individual identification.

In total, we identified 72 individuals in the park's FSM (Table 1). Based on network analysis of grouping patterns we identified five different clans (hereafter clans 'Center', 'North', 'South', 'Southwest' and 'East') consisting of 45 adults, 10 subadults and 9 cubs (Table 1; Fig. 2). Mean number of animals per clan was 12.6 (range 6–25) (Table 1). Eight individuals were likely nomads/transients (Table 1). In total, we identified 15 males and 16 females, including eleven reproductive females (Table 1). Adult females were more frequently recorded than adult males (Males = 11, Females =16 (without transients); χ^2_{Yates} = 10.7, $P < 0.001$). Four clans were located in the southern savannas sector whereas one clan was located in the northern savannas sector (Fig. 3). With 1233 independent records, the clan Center had the highest number of records (Fig. 3). We only obtained 34 records from the clan East (Fig. 3). This was mainly due to prolonged periods of non-operational cameras here. Due to the low performance of these trap sites we could not obtain a complete network for this clan (Fig. 3). However, since these animals were exclusively and repeatedly photographed only in this area all animals photographed here were assigned to this clan.

Table 1. Overview on identified animals during CT study 2 (July 2013 to March 2014) in the FSM and camera trapping study in the *bais* (December 2012 to March 2013). In parentheses, changes at the end of March 2014. * Assuming that population size in *bais* has not changed

Age	# Animals	# Non-reproductive females	# reproductive females	# Males	# Unsexed
Clan Center					
Adult	15 (14)	2	4	4 (3)	5
Subadult	5 (3)	0	0	1	4 (2)
Cub	5 (4)	0	0	0	5 (4)
Total	25 (21)	2	4	5 (4)	14 (13)
Clan Southwest					
Adult	6 (5)	0	3	0	3 (2)
Subadult	3 (2)	0	0	0	3 (2)
Cub	2	0	0	1	1
Total	11 (9)	0	3	1	7 (5)
Clan North					
Adult	12 (11)	1	3	4 (3)	4
Subadult	1	0	0	1	0
Cub	2	0	0	0	2
Total	15 (14)	1	3	5 (4)	6
Clan South					
Adult	6 (3)	1 (0)	0	3 (2)	2 (1)
Total	6 (3)	1 (0)	0	3 (2)	2 (1)
Clan East					
Adult	6 (5)	1	1	0	4 (3)
Subadult	1 (0)	0	0	0	1 (0)
Total	7 (5)	1	1	0	5 (3)
All clans					
Adult	45 (38)	5 (4)	11	11 (8)	18 (15)
Subadult	10 (6)	0	0	2	8 (4)
Cub	9 (8)	0	0	1	8 (7)
Total	64 (52)	5 (4)	11	14 (11)	34 (27)
Mean clan size: 12.6 (10.4)					
Transients					
Adult	8	0	0	1	7
Total	8	0	0	1	7
Spotted hyenas in *bais*					
Adult	4	0	0	0	4
Subadult	5	0	0	0	5
Total	9	0	0	0	9
Total population size					
Adult	57 (50)	5 (4)	11	12 (9)	29 (26)
Subadult	15 (11)	0	0	2	13 (9)
Cub	9 (8)	0	0	1	8 (7)
Total	81 (69)*	5 (4)	11	15 (12)	50 (42)
Population density: 7.54 (6.42*) individuals / 100 km^2					

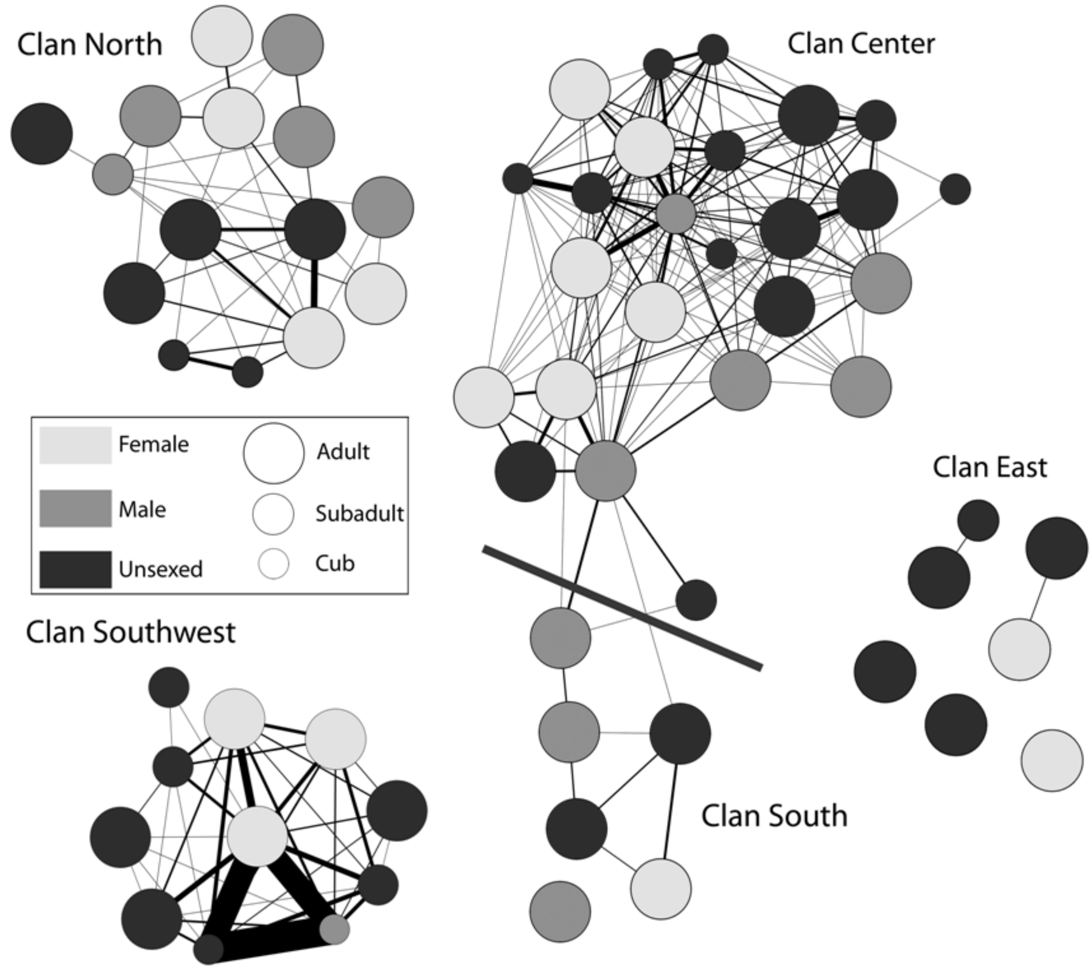

Figure 2. Results of network analysis based on grouping patterns obtained with data from CT study 2. Thickness of lines indicates how often animals were recorded in the same group (range 1–59). The animal which was not photographed in a group in the clan South was only photographed once at the beginning of the study period in the territory of clan South. Since it was regularly photographed with different clan members in this areas during CT study 1 it is assumed that this animal always belonged to this clan but has probably died or left the study area shortly after beginning of CT study 2.

Members of the clan Southwest were mainly photographed in the center and the south of the large savanna located in the southwest of the study area (Fig. 3). Trap station 12 had by far the most records for members of this clan and visit interval for this trap stations differed significantly from visit intervals of other trap stations (Tukey HSD; $P < 0.001$). In average, this trap station recorded every 29.4 (±SE 2.38) hours single members or groups of the clan Southwest. Cubs and subadults of this clan were significantly more photographed at this trap station than adults compared to all other trap stations where members of this clan were recorded ($\chi^2_{Yates} = 10.6$; $P < 0.05$). The two cubs of this clan were 75% of the times recorded at this trap station. They were exclusively recorded only here during beginning of the study and only one to two months later the first time at trap stations farther away. Members of the clan Center were mainly recorded in the northern part of the large savanna located in the center of the study area (Fig. 3). Trap stations 2, 3 and 8 had the shortest visit intervals and visit intervals differed significantly from visit intervals of other trap stations (Tukey HSD; $P < 0.01$) but not among each other (ANOVA: $F = 1.8$, $P = 0.17$). In addition, cubs from this clan where first photographed at these trap stations when they first showed up. In general, cubs and subadults of this clan were significantly more photographed at these three trap stations than adults compared to all other trap stations where members of this clan were recorded ($\chi^2_{Yates} = 7.6$; $P < 0.05$). Members of the clan North inhabit the savannas north of the Lékoli River (Fig. 3). For this clan, we could find its communal den site. Visit interval of trap station 34, which was with about 900 m nearest to the den site, was shortest and differed significantly from visit intervals of other trap stations (Tukey HSD, $P < 0.001$). In average, this trap station recorded every 13.3 (±SE 1.0) hours single members or groups of the clan North. In addition, the two cubs in this clan were only recorded at this trap station and at the second-nearest trap station 37. Sample size for cubs and subadults ($n = 3$) was too small for analysis of differences of records between ages and trap stations. Members of the clan South were mainly recorded in the small savannas located in the south of the study area (Fig. 3). Trap stations 19, 20, 21 and 25 had the shortest visit intervals and visit intervals differed significantly from visit intervals of other trap stations (Tukey HSD; $P < 0.001$) but not among each other (ANOVA: $F = 1.9$; $P = 0.13$). Members of the clan East were only recorded in the small savanna in the east of the study area. Due to the low trap success for members of this clan differences in visit intervals and trap success among age classes were not statistically tested.

In general, spotted hyenas were rarely recorded in territories other than their own, with the exception of members of the clans Center and South (Fig. 3). In particular, three members of the clan South were occasionally recorded deep inside the territory of clan Center. These three animals were former members of the Clan Center (see next section). Only two individuals living in the southern savannas sector and belonging to the clan Center were recorded seven times in the northern savannas sector (Fig. 3). Two members of the clan North were each recorded once in the southern savannas sector (Fig. 3). This suggests that spotted hyenas rarely cross the Lékoli River.

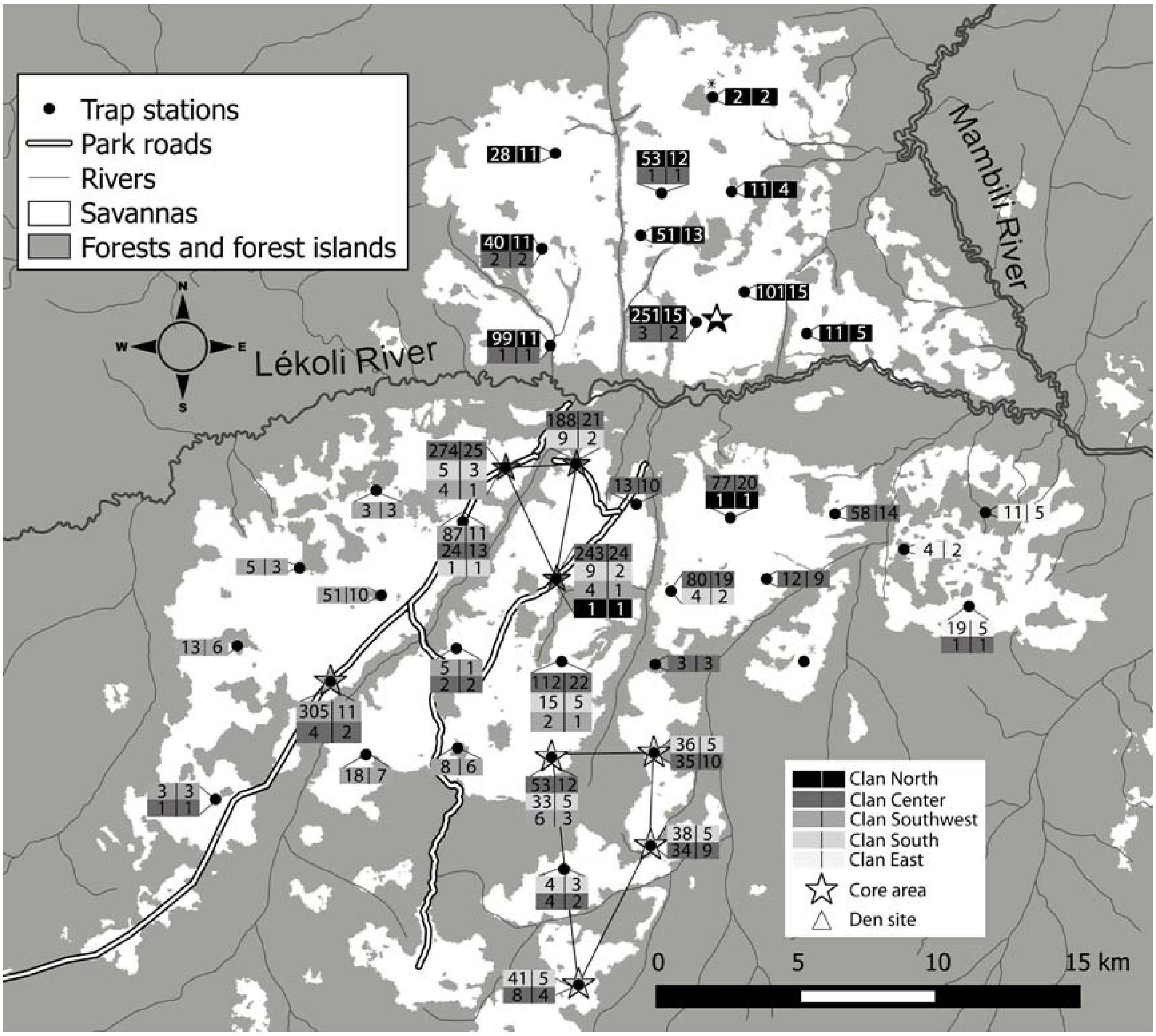

Figure 3. Map showing number of independent records (left number) and number of individuals (right number) recorded for different clans at trap stations in the FSM during CT study 2. Black asterisk indicated that this trap station was only operational for one month. Grey asterisk indicates that no known clan members were recorded at this trap station. For determination of core areas see text.

Spotted hyenas in the FSM were recorded 1944 times walking alone and 383 times walking in groups (Fig. 4). The largest group size was eight, with members of the clan Center (Fig. 4). In groups, spotted hyenas followed each other in the majority of the cases in very close distance. For example, groups with two animals were recorded 236 times. In 188 times (80.1%), the second animal was recorded within 60 seconds after the first animal. Cubs and subadults were significantly more photographed in groups than adults ($\chi^2_{Yates} = 344.0$, $P < 0.0001$; $\chi^2_{Yates} = 25.6$, $P < 0.0001$) (Fig. 5). For example, the two cubs of the clan Southwest were recorded 63 and 73 times respectively and 59 times they were walking in the same group (Fig. 2). Forty-eight times and 50 times respectively they were walking always with one particular female in the same group (Fig. 2) and 28 times they were photographed only with this female. This suggests that both cubs are probably littermates and that the female was likely their mother. Additionally, adult clan females were significantly more recorded in groups than adult clan males (Males = 11, Females = 16; $\chi^2_{Yates} = 66.4$, $P < 0.0001$).

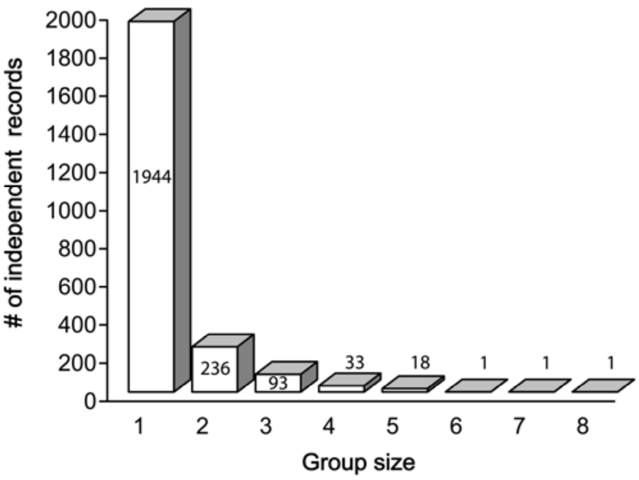

Figure 4. Number of times spotted hyenas were photographed in groups or solitary in the FSM during CT study 2.

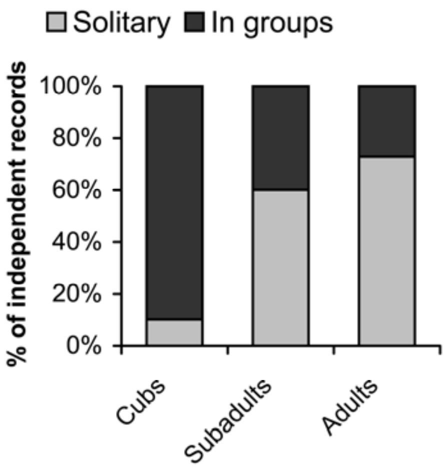

Figure 5. Percentage of records spotted hyenas of different ages were photographed in groups or solitary in the FSM during CT study 2.

Two members of the clan South were recorded in groups with members of the clan Center (Fig. 2). One of these animals was a former member of the clan Center (see next section). This suggests, that bonds from previous times still exist or that animals of either clans tried to establish bonds with members of the other clan in order to immigrate to the other clan.

All adult and subadult members of the five clans were recorded within a period of three months (Fig. 6). However, due to delayed installation of trap stations in the northern savannas section and the far eastern savannas there was some delay in the detection of animals in these areas. In total, it took one week to record all members of the clan North, four weeks to record all members of the clan Center, five weeks to record all members of the clan South and two months each to record all members of the clans Southwest and East. Cubs as well as transients showed up at the beginning, middle and end of the sampling period (Fig. 6).

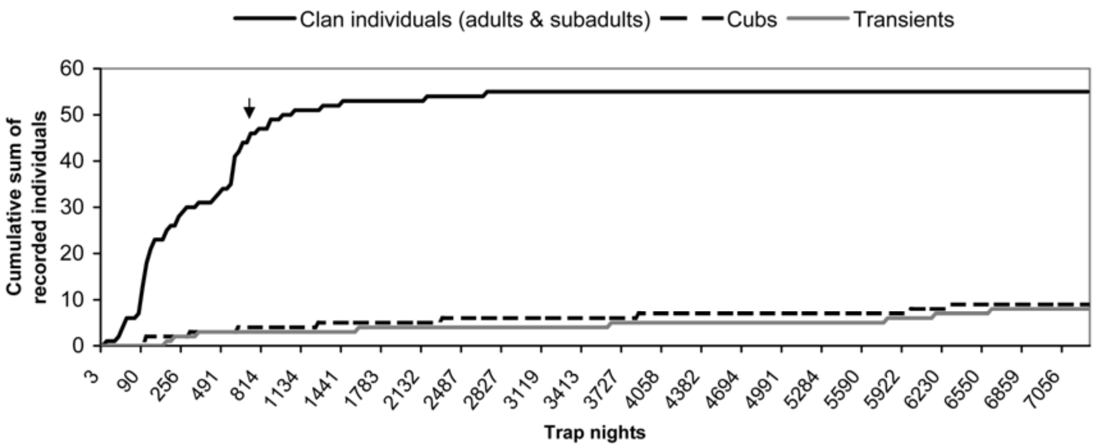

Figure 6. Graph showing a) trap effort needed to record all adult and subadult clan individuals in the FSM and b) sampling occasions when transients and cubs showed up during CT study 2. Arrow indicates sampling occasion when installation of all trap stations was completed. All adult and subadult clan individuals were photographed after 97 sampling occasions.

The maximum interval between two consecutive photographs for one clan member in the FSM was 81 sampling occasions. Twelve animals (seven adults, four subadults and one cub) were not photographed again within 81 sampling occasions before the end of the study period (Fig. 7), reducing the total number of clan members in the FSM at the end of this sampling period to 52 animals (Table 1).

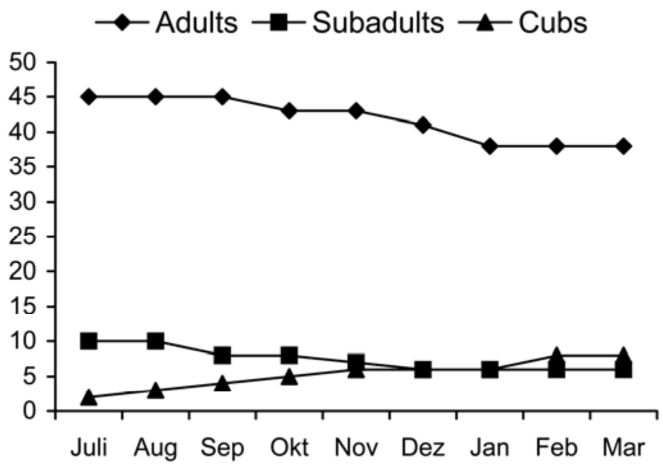

Figure 7. Graph showing loss of individuals in the FSM during course of CT study 2. All adult and subadults were presumed to be present in the study area already in July although they might have been photographed later. Graph for cubs shows when they were first recorded. In August, two new cubs showed up but another cub was not photographed since August. Animals which were not photographed again within 81 sampling occasions before the end of the study period were considered as lost.

We identified ten individuals at the *bais* Maya Nord and Romani (Table 1). With only 66 records, trap success in the *bais* was low. Spotted hyenas were photographed here 40 times walking alone, eleven times walking in pairs and once walking in a group consisting of four individuals. Animals photographed at the *bai* Maya Nord were not photographed at the *bai* Romani and vice versa. Hence, it can not be said if spotted hyenas from the *bais* belonged to one clan or to two clans. Thus, we grouped these animals into the group '*Bais*'. None of the hyenas recorded at *bais* were photographed in the FSM and vice versa with the exception of one individual which was first photographed in the *bais* and then several months later in the FSM. Since this individual was photographed in the FSM several months later we considered this individual as transient, which has probably no bonds with hyenas from the *bais* anymore.

Additionally, camera traps photographed two individuals from the clan North with cable snare wounds. In March 2014, T. Bohm photographed a spotted hyena with a cable snare wound on a park road.

Since no new individuals occurred after a period of approx. three months, with the exception of transits and cubs, we assumed that we recorded all resident spotted hyenas in the FSM. Trap design and equipment in the *bais* was different. But due to the long study duration of five months there, we assumed that nearly all *bai* spotted hyenas were recorded. 1/2MMDM for adult animals in the FSM was 6.15 (±SE 0.36) km. Consequently, size of the sampling area was 1074 km^2. This area comprises roughly the study area and surrounding areas shown in Fig. 1. The sampling area contained also forested areas. Spotted hyenas from the FSM were occasionally photographed in forests. Thus, they are likely to use these areas and to consider forested areas as part of the clans' territories is therefore appropriate. We included individuals from the *bais* in estimations of the total population size. It is unlikely that *bai* spotted hyenas have their core area in the *bais* but rather at the northernmost edge of the northern savannas from where they do forays to the *bais* from time to time. Using the total number of 81 identified spotted hyenas at the beginning of CT study 2, population density was calculated as 7.54 individuals / 100 km^2. Using the total number of 69 remaining spotted hyenas towards the end of CT study 2, population density has dropped to 6.42 individuals / 100 km^2.

Comparison with results from CT study 1

In this study period, spotted hyenas were photographed 434 times. The total number of trap nights was 673 (64.59 records per 100 trap nights). We identified 51 individuals, among them were 38 adults, including nine females and eight males, 11 subadults and two cubs. Due to the smaller number of records, robust results on the reproductive status of females could not be obtained. However, at least one female was reproductive. This female was photographed suckling the two cubs in front of one camera. All spotted hyenas were recorded after 38 sampling occasions (402 trap nights). In total, it took 17 sampling occasions (170 trap nights) to record all spotted hyenas in trapping block 1 and 7 sampling occasions (69 trap nights) to record all spotted hyenas in trapping block 2. We did not estimate population density for this study period since not the entire FSM was surveyed.

As CT study 2 showed, no individuals of the clan East were photographed in areas other than the small savanna in the east (see Fig. 3) and members from the northern savannas sector visit the southern savannas sector rarely. Thus, we assumed that all individuals photographed in the study area belonged to the clans Center, South or Southwest. Based on network analysis of grouping patterns all animals could be assigned to either of these clans. Twenty-seven (53 %) of these animals were photographed again in the subsequent CT study 2 (Fig. 8). The biggest loss of individuals was determined for clan Center: 14 animals have died and five members immigrated into other clans (Fig. 8). The most striking loss occurred in the clan South: While still ten animals belonged to this clan in CT study 1, only six belonged to this clan at the beginning of CT study 2 and only three at the end of CT study 2 (Fig. 8).

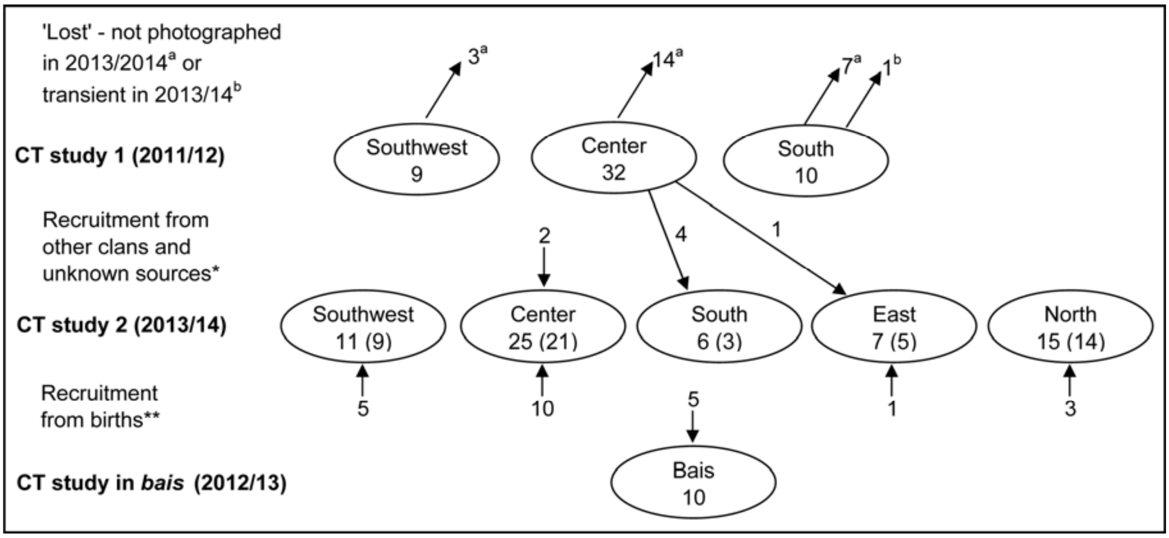

Figure 8. Changes in clan sizes between camera trapping studies in the FSM and towards end of CT study 2. In parentheses clan sizes for clans in the FSM at end of CT study 2. * Transients which have successfully joined this clan or undetected clan members from CT study 1. ** Recruitments include subadults and cubs since CT study 1.

2.5 Discussion

Methodological considerations

Camera traps have been extensively used to study solitary carnivores (e.g. Silver *et al.*, 2004; Kalle *et al.*, 2011). On the other hand, they have been used only very little in studies on social carnivores (e.g. Sequin *et al.*, 2003). As to our knowledge, we made the first attempt to study compositions of social units in a social large carnivore population with the help of camera traps. Based on analysis of grouping patterns we were able to identify clan memberships of recorded individuals. As our data showed, cubs, subadults and females often walk in groups, whereas especially cubs almost exclusively walk in groups and often with the same individuals. We used Reconyx camera traps which have a very fast trigger time of 0.2 s and record up to two pictures per second continuously. The short trigger time ensures that also fast-moving animals are photographed while continuous recording without intervals between successive pictures ensures that all animals of a group are recorded. Future camera trapping studies on spotted hyenas should therefore aim to use camera traps which have the same capabilities in recording groups otherwise a large proportion of information will get lost. Moreover, camera trapping studies on spotted hyenas should be sufficiently long. A too short study duration can result in non-detections of a) young individuals, which start to do longer excursions at a later point of time, and b) of animals which do forays outside their clan territories. We suggest a minimum duration of three months for camera trapping studies on spotted hyenas to ensure that at least all commuting adult individuals are recorded. Our study population consisted to 30 % of young individuals.

Camera trapping studies usually aim to determine only the number of adult individuals within a population (O'Connell *et al.*, 2011). But given the very low population size of the OKNP's spotted hyena population it was important to obtain accurate results on the entire number of animals in the population, including adults and immature individuals. However, this could only be achieved with a sufficiently long study. Furthermore, as young and older cubs do excursions mostly in the vicinity of the territory's center, big holes in the trapping grid should be avoided.

As our data showed, we have probably recorded all clan members during CT study 2 and camera trapping study in the *bais*. In addition, we documented the number of transients which occasionally showed up in the study areas. Thus, we refrained from doing population size and density estimates using capture-recapture methods as results from those would have probably not significantly improved estimates. Recently, so called spatially-explicit capture recapture (SECR) models have been evolved and improved population size and density estimates in capture-recapture studies (Royle *et al.*, 2014). SECR methods combine a state model (the distribution of activity centres of individuals) and an observation model (the spatial detection function) (Efford & Fewster, 2013; Royle *et al.*, 2014). The spatial aspect of SECR methods is of great use as it helps to understand individual heterogeneity in capture probabilities and movement patterns (Sollmann *et al.*, 2011). In SECR methods, spatial behaviour for different groups (e.g. males and females) can be explicitly modelled (Sollmann *et al.*, 2011). However, these models are still in its infancy and current models do not consider the special behaviour of social animals. As our study showed, for spotted hyenas, capture probability varies among sex and age classes and grouping behaviour has a significant influence on capture probability of individuals. Certain animals are recorded more or less often depending on how often they travel in groups, thus independency of records is not guaranteed. Furthermore, inadequate equipment (see above) can per se result in biased results of capture probabilities for certain animals. In addition, SECR models assume that activity centers for individuals are independent from each other (Royle *et al.*, 2014). However, group-living animals share the same activity center (core area), e.g. the communal den, and as our data showed, capture probability for members of the same clan decreases as distance from clans' core areas increases. To develop models that consider all these and other factors is a challenging task for a mathematically skilled researcher. With our approach we provided a methodology that helps to collect data on the above mentioned peculiarities in social carnivore populations and we gladly share our extensive data set with researchers who are interested to develop such models.

Reasons for decline and management implications

Our density estimate was less than half the density estimate of Henschel *et al.* (2014). However, Henschel *et al.*'s (2014) poor methods make their data and results difficult to interpret. Although it is important to have first results about an endangered population, it is questionable if data from quick and untargeted studies can lead to implementation of successful management strategies. Critically endangered small populations require the strongest possible science. With our study we provided updated and robust results on the current status of this unique spotted hyena population which are more useful for future management strategies.

The size of the OKNP's spotted hyena population is already very small and is further declining. Twenty-four of fifty-one animals which were photographed during CT study 1 have not been photographed during CT study 2 and have likely died. Population size in the FSM during CT study 2 has further declined although it can not be said if animals which were not photographed anymore towards the end of this study period have died or become nomads outside the study area. However, most losses occurred between December and January. This period marks a period during which villagers intensify hunting activities due to Christmas and New Year's Eve (pers. comment Leon Lamprecht). Hence, likelihood that these animals have become victims of poaching is high. Moreover, dispersing animals would usually try to join one of the neighbouring clans (Boydston *et al.*, 2005). Thus, it was surprising that animals which have disappeared were not photographed in neighbouring clans' territories shortly before their disappearance but rather disappeared from the FSM from one day to another, suggesting that these animals have also died from poaching.

Interestingly, on several occasions we recorded single spotted hyenas deep inside the territory of a clan of which they were once members of. In this case, they were probably using hunting grounds known from previous times. This behaviour, that single spotted hyenas occasionally hunt in territories of clans of which they were once members of, was also previously observed in the Serengeti (pers. comment East, M.L. & Hofer, H.).

Unfortunately, we were not able to survey the savannas which were situated south of the study area and near the park borders (see Fig. 1). As our data showed, spotted hyenas in the OKNP are highly territorial showing low intrusion pressure which is probably the result of the abundance of resident prey in their territories (Henschel & Skinner, 1991). During this study, larger and medium-sized ungulates were frequently recorded by camera traps in the clans' core areas, but, on the other hand, only rarely in the very south of the study area (T. Bohm, unpublished data). In general, wildlife abundance in the savannas near the park border is scarce (P. Henschel, unpublished data), suggesting that spotted hyenas' distribution is limited to the areas which were surveyed during our studies. However, to confirm the presence of other clans in the savannas near the park borders we propose a camera trapping study in these areas. Such a study should be conducted as early as possible to have still the opportunity to compare our data with newly obtained data.

Considering the current population size of 69 remaining animals, questions arise if the population can persist or if it is doomed to extinction. We recorded 11 reproductive females in the population. The number of breeding males and females per generation - genetically effective population size N_e - is the actual population size that allows populations to retain their evolutionary potential (Soulé, 1987). As a rule of thumb, the ratio of N_e to N (total population size) for wildlife populations is roughly 0.2–0.3 (Frankham, 1995; Kalinowski & Waples, 2002). Using this ratio, N_e for the OKNP population is 13.8–20.7 animals. As a guideline for conservation aspects, it should be avoided that N_e falls below 50 animals to avoid a possible increased risk of extinction because of genetic effects (Allendorf & Luikart, 2007). Considering this, the OKNP population has already reached a critical state. However, a genetic study is underway (T. Bohm, unpublished data) to get more robust results on N_e and to assess the population's genetic diversity in general. Due to the small population size and the high isolation, it is likely that deleterious genetic processes, such as inbreeding, have been already occurred. Disregarding the results of this genetic study, urgent actions are needed. Given the current trend, the population is likely losing individuals faster than it recruits. This can result in the extinction of this highly precious spotted hyena population within shortest time. Poaching is likely the main driver behind this trend. Camera traps photos as well as direct observations of spotted hyenas with cable snare wounds during CT study 2 were strong evidence for that. Smaller villages and settlements are situated at the eastern and southern borders of the park and the park's FSM is less than 20 km away from these. Bushmeat is still the main source of protein for the majority of the rural and town populations surrounding the park (Hennessey & Rogers, 2008; Mbete *et al.*, 2011). Smaller and medium-sized forest mammals are mainly hunted and hunting is mostly carried out with illegal wire snares in the forested buffer areas surrounding the OKNP (Hennessey & Rogers, 2008; Mbete *et al.*, 2011). However, during hunting excursions, hunters also penetrate deep into the park (Gami, 2000). Thus, we propose regular large-scaled de-snaring patrols in forests surrounding the FSM as these probably represent areas where spotted hyenas mainly do hunting excursions outside the FSM. Given the low population size, introduction of new individuals might be necessary. Apart from the positive effect that new individuals can have on the genetic diversity of small isolated populations (Vilà *et al.*, 2003), new individuals can also give the OKNP population a boost. In wildlife populations, behavioural mechanisms exist that prevent matings between close relatives (East *et al.*, 2003). In the long run, these mechanisms can lead to slow population growth in small and isolated populations since simply not enough unrelated mating partners are available (Vilà *et al.*, 2003). Thus, new individuals can significantly improve the potential for matings between unrelated individuals and, hence, boost population growth. Given the high isolation of the OKNP's spotted hyena population, animals from candidate populations can be found only very far away. Since data from the genetic study mentioned above will also be used for a continent-wide study on the genetic relatedness of spotted hyena populations, animals from candidate populations might be already available in the nearest future.

Until the early 1990ies, the OKNP was home to the last lion population in the Congo Basin (Henschel *et al.*, 2014). Henschel *et al.* (2014) discussed extensively the reasons why lions have disappeared from the OKNP and how large carnivore conservation can go terribly wrong. By that time, the OKNP was managed by the European Union-funded ECOFAC (Conservation and Rational Use of Forest Ecosystems in Central Africa) program. Despite large amounts of available funding, the opportunity was missed to assess the status of this last lion population in the Congo Basin and to implement conservation strategies necessary to save it from extinction (Henschel *et al.*, 2014). With our study, we provided urgently needed updated data on the status of the OKNP's spotted hyena population and we hope, the current park management uses these to improve the situation for spotted hyenas in the OKNP. This spotted hyena population has not only an enormous intrinsic value for being the only spotted hyena population in the Congo Basin but is also an indicator for the well-being of the ecosystem (Holekamp, 2010). Apparently, the spotted hyena population suffers, and with it, the whole forest-savanna ecosystem in the OKNP. Efforts should be made by the park management to find the main drivers for this and to reverse this trend. The OKNP harbors a unique wildlife, among them species, such as western lowland gorilla and forest elephant, which generate high revenues from tourism (Blom, 2000). However, spotted hyenas have always been an integral part of the FSM of the Batéké Plateaux (Malbrant & Maclatchy, 1949). Thus, the preservation of this precious and highly endangered spotted hyena population should be pursued as priority conservation goal by the park management.

2.6 Acknowledgments

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Chapter 3: Diet of spotted hyenas in the Odzala-Kokoua National Park, Republic of Congo

3.1 Abstract

Spotted hyenas (*Crocuta crocuta*) have received considerable attention in Eastern and Southern Africa, but little is known about their ecology and current status in Central Africa. The distribution range of spotted hyenas in the Republic of Congo has dramatically declined during the past decades, with only one remaining population inhabiting the Odzala-Kokoua National Park (OKNP) in the north of the country. An important aspect of conservation management is the knowledge of the diet of the concerned species. In this study, we investigated 402 scats and regurgitations of spotted hyenas from the forest-savanna mosaic in the OKNP to investigate their diet. In addition, we estimated the overlaps of temporal activity patterns between spotted hyenas and their main prey species through the coefficient Δ with data from eight months of camera trapping. Twenty-six different prey species were identified in the diet, with forest buffalo accounting for 25.2% of all prey items identified, followed by red river hog (17.5%) and bushbuck (16.4%). These species predominantly occur in the forest-savanna mosaic. Our data suggest that the long-term survival of spotted hyenas in the OKNP will likely depend on the abundance of these prey species. Despite its importance in the prey, there was little overlap between the highly nocturnal spotted hyena and their largest prey species, the cathemeral forest buffalo, suggesting that spotted hyenas invest high levels of energy searching for food. Natural repopulation of spotted hyenas from the OKNP into other protected forest-savanna mosaics in the Republic of Congo and neighbouring Gabon might be possible. For this, we suggest to establish protected wildlife corridors to connect the vast forest-savanna mosaic areas that run through both countries, and to maintain viable populations of the main prey species of spotted hyenas.

3.2 Introduction

Spotted hyenas (*Crocuta crocuta*) are widely distributed in sub-Saharan Africa, although many populations appear to be rapidly declining, particularly outside protected areas (Hofer & Mills, 1998a). The causes for population declines across the range of the species are either directly affecting spotted hyenas through illegal shooting, poisoning and accidental capture with wire snares set for game meat or indirectly through legal and illegal hunting of their prey populations (Hofer, East & Campbell, 1993; Hofer *et al.*, 1996; Hofer & Mills, 1998a; Henschel, 2009). In the Republic of Congo (hereafter: Congo), spotted hyenas historically occupied all suitable open habitat and were widespread in the late 1940ies (Malbrant & Maclatchy, 1949). The range loss that occurred during the following decades is assumed to be due to a continuous reduction in potential prey species of spotted hyenas in the savannas regions of the Congo (Henschel, 2009). By 1990, only two resident populations persisted in Congo; one in the Conkouati-Douli National Park on the coast in the southwest and one in the Odzala-Kokoua National Park (OKNP) in the north of the country (Hofer & Mills, 1998b). In recent years, however, no spotted hyena signs were recorded in the Conkouati-Douli National Park. Today, the OKNP's population is considered to be the only remaining spotted hyena population in the Congo (Henschel, 2009). The species is legally protected under Congolese law since 1983 (Hecketsweiler, 1990), but to date there have been no scientific studies or conservation actions focusing on spotted hyenas in this country (Henschel, 2009).

For the effective conservation of a species a sound knowledge of its behavioural ecology is required. Viable populations of large carnivores can only persist when food resources are sufficiently available and when their populations and those of their prey species are not challenged on the long-term. An important aspect of the behavioural ecology of a species is the composition of its diet. Spotted hyenas generally exhibit a broad diet and prey mainly on medium to large sized prey species. In Eastern Africa, they mainly prey on gazelles (*Gazella granti* and *G. thomsoni*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and buffalo (*Syncerus caffer*) (Holekamp *et al*., 1997; Höner *et al*., 2002) with preferences for juvenile individuals (Höner *et al*., 2002). In Southern Africa, spotted hyenas mainly prey on gemsbok (*Oryx gazella*) calves (Mills, 1990), and in Western Africa buffalo is the most common prey species found in scats (Di Silvestre, Novelli & Bogliani, 2000). While diet compositions are well documented in Eastern, Southern and Western Africa, such information is lacking from Central Africa.

Here we determine the diet of spotted hyenas in the OKNP in Congo using scats and regurgitations from the forest-savanna mosaic in the southern part of OKNP. In addition, we analysed activity patterns of spotted hyenas and their main prey species found in the diet using data collected during eight months of camera trapping. Our findings are discussed in respect to possible repopulations of spotted hyena in the Congo and neighbouring Congo Basin countries such as Gabon.

3.3 Material and methods

Study area

The OKNP is situated in the north of Congo, about 500 km north of the capital Brazzaville. The park covers an area of approximately 13,600 km^2 and is the largest national park of the Congo (Aveling & Froment, 2001). There are two rainy seasons and two dry seasons, and the mean annual rainfall in the park is always higher than 1500 mm (Maisels, 1996). Rainfall varies substantially within the park, with higher rainfall in the northern and lower rainfall in the southern area of the park (Maisels, 1996).

The main study site was situated in the southern area of the park (Fig. 1). It is characterised by a mosaic of savannas and gallery forests which makes up approximately 8% of the entire park surface (Fig. 1). The savannas are dominated by Graminae (*Andropogon schirensis*) with scattered fire-resistant shrubs (*Hymenocardia acida* and *Annona senegalensis*), and are currently being colonized by the forest (e.g. *Lophira alata*, *Pentaclethra eetveldeana*, *Xylopia aethiopica*) (Dowsett-Lemaire, 1996). As a result, some parts of the savannas were covered by forest islands of up to 3 km^2 or characterized by high densities of shrubs and smaller trees.

Apart from the spotted hyena the leopard (*Panthera pardus*) is the only other large predator in the OKNP. The distribution of the two predator species does not seem to overlap strongly. The spotted hyena is regularly observed in the open habitat in the southern area of the park and occasionally in the large forest clearings in the centre of the park, whereas leopard spoors are regularly seen in the entire forested area of the OKNP (Maisels, 1996), but only rarely in the open savannas (this study). In this study we therefore assumed that the prey remains found in spotted hyena scats and regurgitations originated from prey animals killed or scavenged by hyenas rather than kleptoparasitized from leopards.

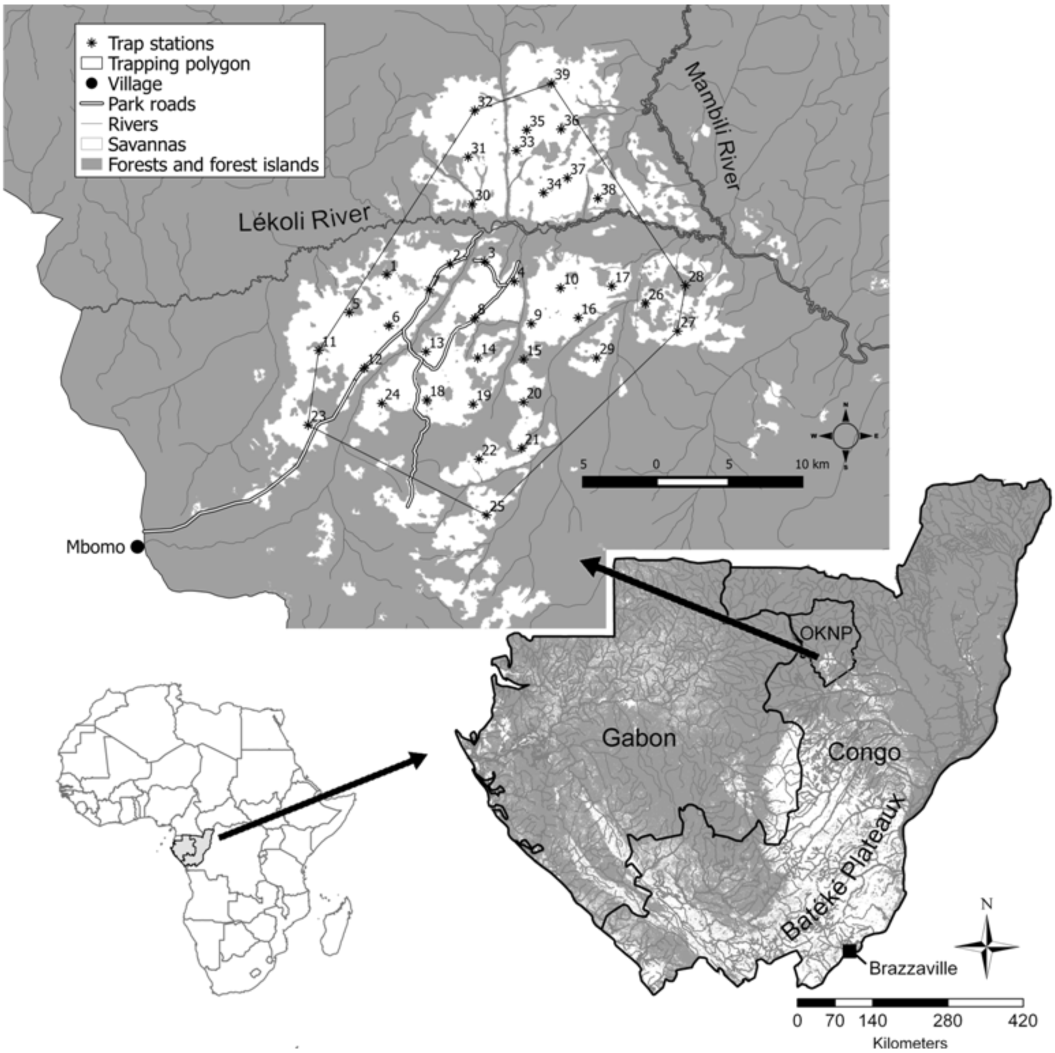

Figure 1. Map of Congo and Gabon indicating the savanna areas of the Batéké Plateaux and the Odzala-Kokoua National Park (OKNP) in Congo. The detailed map of the OKNP shows the study site and location of camera trap stations in the forest-savanna mosaic. Grey areas indicate rainforest, dark grey lines indicate rivers and white areas indicate savanna areas.

Collection and analysis of scats and regurgitations

Scats and regurgitations from spotted hyenas were collected opportunistically at latrine sites, prey carcasses or along wildlife trails which were extensively used by spotted hyenas. Latrines are locations inside or at the borders of a territory of a spotted hyena clan, where clan members defecate on a regular basis (Kruuk, 1972). Only fresh scats with the typical shape, structure, colour and odour of hyena scats and older scats with the typical white colour (Kruuk, 1972) were considered to ensure that collected scats originated from spotted hyenas. During three study periods (January–June 2008, November 2011–February 2012 and July 2013–March 2014) latrines and trails in the study site in the forest-savanna mosaic were checked for scats approximately every fifth to seventh day, a time period likely to provide new samples originating from a feeding event independent from the previous one.

Regurgitations were mainly collected from trails and were identified as hyena regurgitations by the hyena hairs found in them and the fresh hyena spoors on the spot. Identified spotted hyena scats and regurgitations were sun dried and crushed. Hairs were washed in water and put for 24 h in 2 ml tubes filled with 96% ethanol to remove remaining dirt. Other remains such as nails, teeth, hooves and scales were separately used to determine prey species in samples.

Hyena scats and regurgitations of similar freshness collected on one day that contained prey hairs of only one species, were assumed to originate from one or more hyenas having eaten from one prey animal. In this case only one of the samples was considered for the analysis to prevent overrepresentation of this species in the results. However, if scats were clearly of different freshness, i.e. one scat was deposited several hours ago and had a strong odour and another scat was deposited a few days ago and had no odour, and contained prey hairs of only one species, the respective scats were treated as discrete samples and used for analysis.

Prey hairs were examined macroscopically by their shape, colour and structure, and microscopically by their scale pattern, medulla width and shape (Teerink, 1991). To examine the scale pattern and the medulla of a hair, two slide preparations were made. Scale patterns were visualized by producing imprints of the hairs. For this, fast-hardening glue was spread on a microscope slide with the round end of a spatula. A hair was placed on the glue for about five minutes. After the removal of the hair, the imprinted scale pattern on the glue was investigated under a microscope at 40x magnification. For the examination of the medulla temporary mounting oil was spread on a microscope slide, a hair embedded into the mounting oil and covered with a cover slip. The medulla in the hair became clearly visible under a microscope at 40x magnification.

For the identification of the prey animals a reference collection of prey hairs of species known to occur in OKNP was compiled prior to and during the studies. Hairs were taken from specimens stored at three museums in Germany (Senckenberg Museum Frankfurt, Landesmuseum Wiesbaden, Naturkundemuseum Mainz). Additionally, hairs from tame zoo animals (*Cephalophus silvicultor, Gorilla gorilla gorilla*) from the zoo in Wuppertal, Germany, were taken. In Congo, additional reference samples were collected from dead animals (*C. callipygus*, *C. dorsalis*, *Philantomba monticola, Potamochoerus porcus*, *S. c. nanus*) found in the field.

The percentage of a prey species i in the diet was calculated by using its occurrence n_i in the scats and the total number of scats N (= n_i/N*100) or the total number of prey items R in the scats (= n_i/R*100), respectively. The former is a measure of how often spotted hyenas feed on a particular prey item, whereas the latter is a measure of the relative importance of a particular prey item in the diet of spotted hyena. Since it was not possible to differentiate hairs from Peter's duikers and bay duikers, these species were grouped together.

Camera trapping and analysis of temporal activity patterns

Field data for spotted hyena and its presumed prey were collected in the study area with camera traps. Installation of 38 trap stations in the OKNP's forest-savanna mosaic started in July 2013 and camera traps were active for eight months until end of March 2014. An additional trap station (No. 39, Fig. 1) was installed in February 2014 and operational for one month. Trap stations were deployed in each cell of a 3.5 x 3.5 km grid, resulting in a mean inter-camera trap distance of 2.7 km. The total trapping area was 456 km^2. Trap stations were set along roads and wildlife trails, i.e. at sites where capture probabilities for wildlife species were likely to be high. At each trap station one Reconyx HC500 was installed and programmed to take 5 pictures per trigger event. Fifteen additional cameras from a product mixture of Reconyx HC500 and Bushnell Trophy Cam were temporally moved between trap stations so that some trap stations could be operated with two cameras at the same time during study period. Twenty-nine stations were installed in savannas and ten stations were installed in forests and forest islands. The camera trapping study covered the large rainy season (Sep–Nov) and small dry season (Dec–Feb) and partly the large dry season (Jul–Sep) and small rainy season (Mar–May) (Maisels, 1996).

Information on time recorded by camera traps on each photograph were used to investigate temporal activity patterns of spotted hyenas and their most important prey species. To quantify overlap between activity patterns of spotted hyenas and prey species we used a two-step approach developed by Rideout & Linkie (2009). For this, each activity pattern was first estimated separately with the help of kernel density estimates. In a second step, we calculated the coefficient of overlap Δ_4, recommended for large sample sizes, which varies from 0 (no overlap) to 1 (complete overlap) (Ridout & Linkie, 2009). Statistical analyses were implemented in the software R (R Core Team, 2015) using a script developed by Linkie and Ridout (2011). The 95 percent confidence intervals for Δ_4 were calculated as percentile intervals from 500 bootstrap samples.

3.4 Results

Diet composition of spotted hyenas in the forest-savanna mosaic

A total of 342 scats and 60 regurgitations from the study site in the forest-savanna mosaic were used for the analysis. The 402 samples contained 531 prey items from at least 26 different prey species (Table 1). Seventy-four scats and 22 regurgitations contained two prey items each, eight scats and four regurgitations contained three prey items each and two scats and one regurgitation contained four prey items each. Two regurgitations contained remains of human waste (rubber and paper), but these were not considered as prey items and excluded from the analysis.

In 33.3% of scats and regurgitations the remains of forest buffaloes were detected, which corresponds to 25.2% of prey items (Table 1). Red river hog and bushbuck (*Tragelaphus scriptus*) were identified in 17.5% and 16.4%, respectively, of prey items. Four duiker species were also identified regularly, but other large ungulates such as bongo (*Tragelaphus eurycerus*) and sitatunga (*Tragelaphus spekii*) were only occasionally eaten and accounted for 1.3% and 1.1%, respectively, of the prey items. The only primate species found in samples were the putty-nosed guenon (*Cercopithecus nictitans*) and grey-cheeked mangabey (*Lophocebus albigena*).

We did not record statistical differences in proportions for any of the prey species between the three study periods. There was a statistical difference between the proportions of remains of the white-bellied pangolin (*Manis tricuspis*) recorded in scat and regurgitation samples (χ^2-test, $\chi^2_{Yate's} = 20.8$, d.f. = 1, $P < 0.01$).

Two regurgitation and two scat samples contained only hairs from spotted hyenas and one of the two regurgitation samples also contained a spotted hyena claw. The size of the claw suggested that the hyena consumed was adult. Three regurgitations contained a completely preserved hoof from a forest buffalo calf and five other regurgitations contained completely preserved hooves from adult bushbucks. Additionally, three fresh carcasses of adult forest buffaloes (one female and two individuals of unknown sex) with hyenas feeding on them or with hyena signs around the carcasses were detected in 2008. In addition, in 2013 and 2014 tourists and park staff reported two incidents in which spotted hyenas successfully killed adult buffaloes after having chased them into mud wallows located next to park roads.

Table 1. Diet of the spotted hyena in the forest-savanna mosaic of the Odzala-Kokoua National Park based on the analysis of 342 scats and 60 regurgitations. The percentage of a prey species in the diet was calculated by using its occurrence n_i in the samples and the total number of samples N (= n_i/N*100) or the total number of prey items R in the samples (= n_i/R*100), respectively. Prey weights are from Stuart & Stuart (2007), except for Gambian sun squirrel, greater cane rat and grey-cheeked mangabey, which are from Kingdon (2004).

	Scats (N = 342, R = 438)			Regurgitations (N = 60, R = 93)			Scats + Regurgitations (N = 402, R = 531)			Prey weight (*kg*)		
Prey species	*n*	*n/N ×100*	*n/R *100*	*n*	*n/N ×100*	*n/R ×100*	*n*	*n/N ×100*	*n/R ×100*	♂	♀	*Ad.*
Forest buffalo *Syncerus caffer nanus*	114	33.3	26.0	20	33.3	21.5	134	33.3	25.2	320	260	-
Red river hog *Potamocheorus porcus*	78	22.8	17.8	15	25.0	16.1	93	23.1	17.5	-	-	46–82
Bushbuck *Tragelaphus scriptus*	76	22.2	17.4	11	18.3	11.8	87	21.6	16.4	45	30	
Yellow-backed duiker *Cephalophus silvicultor*	37	10.8	8.4	5	8.3	5.4	42	10.4	7.9	-	-	45–80
Peter's duiker / Bay duiker *Cephalophus callipygus / Cephalophus dorsalis*	34	9.9	7.8	6	10.0	6.5	40	10.0	7.5	-	-	15–24/ 19–25
White-bellied pangolin *Phataginus tricuspis*	11	3.2	2.5	13	21.7	14.0	24	6.0	4.5	-	-	2–3
Greater cane rat *Thryonomys swinderianus*	16	4.7	3.7	3	5.0	3.2	19	4.7	3.6	-	-	2.6–7.5
Blue duiker *Philantomba monticola*	12	3.5	2.7	1	1.7	1.1	13	3.2	2.4	-	-	3–6
Manidae undetermined	7	2.0	1.6	3	5.0	3.2	10	2.5	1.9	-	-	-
Sciuridae undetermined	6	1.8	1.4	2	3.3	2.2	8	2.0	1.5	-	-	-
Bongo *Tragelaphus eurycerus*	4	1.2	0.9	3	5.0	3.2	7	1.7	1.3	300	240	-
Sitatunga *Tragelaphus spekii*	5	1.5	1.1	1	1.7	1.1	6	1.5	1.1	115	55	-
Large grey mongoose *Herpestes ichneumon*	6	1.8	1.4	-	-	-	6	1.5	1.1	-	-	2.5–4
African brush-tailed porcupine *Atherurus africanus*	3	0.9	0.7	2	3.3	2.2	5	1.2	0.9	-	-	2–4
Reptile undetermined	4	1.2	0.9	1	1.7	1.1	5	1.2	0.9	-	-	-
Spotted hyena *Crocuta crocuta*	2	0.6	0.5	2	3.3	2.2	4	1.0	0.8	-	-	60–80
African civet *Civettictis civetta*	4	1.2	0.9	-	-	-	4	1.0	0.8	-	-	9–15
Duiker undetermined	3	0.9	0.7	-	-	-	3	0.7	0.6	-	-	-
Putty-nosed guenon *Cercopithecus nictitans*	3	0.9	0.7	-	-	-	3	0.7	0.6	-	-	8–10
Giant ground pangolin *Smutsia gigantea*	1	0.3	0.2	2	3.3	2.2	3	0.7	0.6	-	-	30–35
Muridae undetermined	2	0.6	0.5	-	-	-	2	0.5	0.4	-	-	-
Water chevrotain *Hyemoschus aquaticus*	2	0.6	0.5	-	-	-	2	0.5	0.4	-	-	8–13
Marsh mongoose *Atilax paludinosus*	2	0.6	0.5	-	-	-	2	0.5	0.4	-	-	2.5–5.5
Grey-cheeked mangabey *Lophocebus albigena*	2	0.6	0.5	-	-	-	2	0.5	0.4	6–11	4–7	-
Mammal undetermined	2	0.6	0.5	-	-	-	2	0.5	0.4	-	-	-
Turtle	-	-	-	1	1.7	1.1	1	0.2	0.2	-	-	-
Bird undetermined	1	0.3	0.2	-	-	-	1	0.2	0.2	-	-	-
Eggshells	1	0.3	0.2	-	-	-	1	0.2	0.2	-	-	-
Gambian sun squirrel *Heliosciurus gambianus*	-	-	-	1	1.7	1.1	1	0.2	0.2	-	-	0.25–0.35
Giant forest hog *Hylochoerus meinertzhageni*	-	-	-	1	1.7	1.1	1	0.2	0.2	-	-	130–235
Total	438	128.1	100.0	93	155.0	100.0	531	132.1	100.0	-	-	-

Temporal activity patterns of spotted hyena and its four most important prey species

We obtained a total of 6310 independent records of spotted hyenas and their four main prey species (Table 2). Spotted hyenas, yellow-backed duikers and red river hogs showed intensive nocturnal activity (91%, 82% and 72% respectively of records between 06:00 and 18:00). Bushbucks were predominantly diurnal (70% of records between 06:00 and 18:00) whereas forest buffaloes appeared to be cathemeral (52% of records between 06:00 and 18:00). The average Δ_4 across spotted hyenas' prey species was 0.65 (±SE 0.10). The highest overlap with 0.87 was recorded for the yellow-backed duiker and the lowest with 0.40 for the bushbuck (Fig. 2).

Table 2. Number of records and capture rate (per 100 trap nights[a]) for spotted hyena and its four most important prey species in the forest-savanna mosaic of the OKNP. Column number four indicates the number of trap stations[b] at which these species were recorded.

Species	Records	Capture rate	# Trap stations
Forest buffalo	1161	16.4	39
Red river hog	904	12.8	33
Bushbuck	1226	17.3	34
Yellow-backed duiker	81	1.1	22
Spotted hyena	2938	41.5	39

[a] Trap nights = 7081 , [b] Total number of trap stations = 39

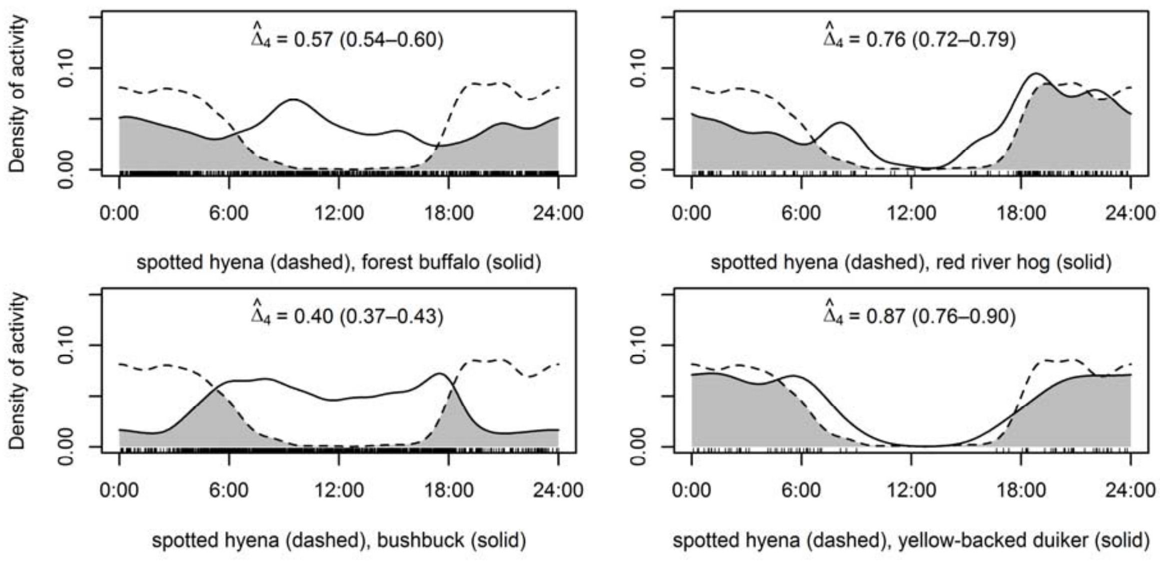

Figure 2. Coefficient of overlapping Δ_4 between the spotted hyena and its four main prey species in the forest-savanna mosaic of the OKNP. Sample sizes: spotted hyena (N = 2938), forest buffalo (N = 1161), red river hog (N = 904), bushbuck (N = 1226), yellow-backed duiker (N = 81).

3.5 Discussion

Diet

Spotted hyenas in the OKNP fed on a wide range of prey species. A minimum of 26 different prey species were identified in the diet, including mammals, reptiles and birds. Ungulates constituted the majority of the diet of spotted hyenas. Members of all ungulate genera, except the rare and elusive hippopotamus (*Hippopotamus amphibius*) (Maisels, 1996; this study), were detected in the samples. Ungulate species that predominantly occur in the forest-savanna mosaic such as bushbuck, buffalo, red river hog and yellow-backed duiker (Maisels, 1996; this study) dominated the spotted hyena diet in this area. Ungulate species that occur predominantly in the forest such as Peter's duiker / Bay duiker (Maisels, 1996; this study) contributed also substantially to the diet in the forest-savanna mosaic, whereas the swamp-dwelling water chevrotain (*Hyemoschus aquaticus*) and sitatunga were identified only rarely in hyena scats and regurgitations in the mosaic. Forest buffalo was the most frequent prey of the hyenas in the forest-savanna mosaic and hyenas fed on adult individuals as well as calves. The predominance of forest buffalo in the hyena diet might be due the high occurrence of buffaloes in the savannas (Chamberlan, Maréchal & Maurois, 1998; Brouet, 2002; this study). Forest buffaloes also have approximately the same size as wildebeests in East Africa (Kingdon, 2004), which are the preferred prey species of spotted hyenas (Höner *et al.*, 2002). The little overlap in the activity patterns between spotted hyenas and forest buffaloes might indicate that spotted hyenas invest high levels of energy searching for this highly rewarding prey species. Accordingly, spotted hyenas in the park do not adjust their activity to reduce foraging energy expenditure, as stated by the opportunistic hunting theory (Sunquist & Sunquist, 1989). Thus, their highly nocturnal activity might be more related to the increasing human activities by tourists and park staff in the park rather than to the activity patterns of their principal prey species.

The only detected remains of primate species were from putty-nosed guenons and grey-cheeked mangabeys in five scats. Previous studies also reported that hyenas sometimes prey on primate species (Breuer, 2005; Sillero-Zubiri & Gottelli, 1992). The OKNP hosts ten diurnal primate species which is the highest number in Central Africa and it probably also hosts the highest number of western lowland gorillas in Africa (Bermejo, 1999). Despite being the key predator in the park, spotted hyenas are unlikely to be a main factor of mortality for great apes in the OKNP.

The semi-arboreal white-bellied pangolin (Kingdon, 2004) was also regularly reported in the diet. The importance of white-bellied pangolin in the diet might have been underrepresented if we would have collected only scat samples. Thus, showing the importance of including spotted hyena regurgitations in the analysis as it allowed a more comprehensive picture of the spotted hyena diet in the OKNP.

No hairs from domestic animals were detected in the samples. Domestic animals present in the villages were domestic dogs and cats, poultry, goats and sheep (Vanwijnsberghe, 1996; pers. observation T. Bohm). Poultry, goats and sheep live and forage in close proximity to their owners' houses (Vanwijnsberghe, 1996; pers. observation T. Bohm), thus spotted hyenas have to enter a village to prey on them. Attacks from spotted hyenas on goats and sheep were reported by villagers of the nearby village Mbomo (Fig. 1) in 2010 and 2011 (L. Lamprecht, pers. comm.). Shortly after these incidents the park management built night enclosures for sheep and goats in Mbomo. No attacks on livestock by spotted hyenas were reported ever since. Overall, attacks on livestock by spotted hyenas were just temporally restricted events and did not occur regularly over a prolonged period (L. Lamprecht, pers. comm.). However, during discussions with villagers T. Bohm noted general negative attitudes by villagers towards spotted hyenas and villagers were concerned having spotted hyenas in their nearest surroundings as spotted hyenas are principally regarded as a threat to humans' and livestock's well-being. But a probably sufficient prey biomass in the park might explain why attacks on livestock by spotted hyenas were just rare incidents so far. However, in the long run, conservation actions such as described above and others have to be implemented by the park management to raise acceptance and awareness in the villagers towards spotted hyenas.

Management implications

A viable spotted hyena population in the OKNP will depend on the availability of their main prey species in the long-term (*Höner et al.*, 2002). Outside the OKNP, prey species of spotted hyenas are allowed to be hunted in defined areas and during specific seasons. Hunting is restricted to certain forms of hunting, such as snaring with natural, local materials ('traditional hunting') or with licensed fire arms (http://faolex.fao.org). However, hunting is carried out almost entirely with illegal metallic snares (wire snares) and in general with little respect to law restrictions (Vanwijnsberghe, 1996; Hennessey & Rogers, 2008). Hofer *et al.* (1996) showed that hunters from communities adjacent to the Serengeti National Park, Tanzania travel far distances away from their home villages to hunt for game within the park. The mean distance at which poachers were arrested away from their home village was 30.2 ± 1.0 km (Hofer *et al.*, 1996). In northern Congo, bushmeat hunting heavily affects areas adjacent to villages, towns and logging camps and is increasing and facilitated by an expanding network of logging roads (Wilkie *et al.*, 2000; Laporte *et al.*, 2007; Hennessey & Rogers, 2008). Villagers at the eastern border of the OKNP travelled distances up to 15 km and 24 km, respectively, to their hunting areas (Gami, 2000). Within the OKNP, despite increasing law enforcement actions by the park management, the rewards to hunt are high. Thus, hunters from the villages located at the borders of the OKNP, such as Mbomo (Fig. 1), extend their hunting areas deep into the park, including areas of the forest-savanna mosaic of the park (Vanwijnsberghe, 1996; Maisels, 1996). Bushmeat hunting in the park can therefore become a serious direct or indirect threat for spotted hyenas, either through accidental captures in snares, which is the most important mortality factor for adult spotted hyenas in the Serengeti (Hofer *et al.*, 1996), or depletion of their prey base. Moreover, we have evidence that spotted hyenas are directly affected by poaching as pictures from our camera traps showed two hyenas with wire snare wounds; another hyena with a wire snare wound was seen on a park road by T. Bohm in March 2014. For an effective protection of spotted hyenas in the park, future management efforts should therefore primarily focus on the effective reduction of poaching in the park and especially in the forest-savanna mosaic.

The protection of this last spotted hyena population in Congo is also important for ecotourism, an increasing industry in Congo (RAPAC, 2008), because it offers income opportunities to local communities adjacent to the park. Most tourists visit OKNP to see the gorillas, chimpanzees and forest elephants, but also the key predator of the park, the spotted hyena. Other National Parks in Congo and also in neighbouring countries, particularly Gabon which borders to the OKNP (Fig. 1), could profit from a healthy viable hyena population through ecotourism. Establishment of other spotted hyena populations in suitable open habitats in Central Africa is therefore proposed, whereas the OKNP population could help to repopulate these areas. Because human-managed translocations are subject to high financial and logistic investments, and often do not consider the social and ecological needs of the carnivore species, such translocations might not be successful (Mills, 1991; Mills, 1998). Therefore, we recommend "natural" translocations through the provision and protection of wildlife corridors.

Additional savanna areas that are suitable as prime habitats for spotted hyenas extend from the south of the OKNP into unprotected area (Fig. 1). These savanna areas are linked with the vast forest-savanna mosaics of the Batéké Plateaux further south covering almost two third of Congo and extending into Gabon (Fig. 1). Until the middle of the 20th century these habitats were inhabited by spotted hyenas (Malbrant & Maclatchy, 1949), including the recently established Batéké Plateaux National Park in south-eastern Gabon. For decades, no evidence of spotted hyenas was reported from Gabon. Only in 2008, spoors from four spotted hyenas were discovered in a forest-savanna mosaic approximately 30 km north-west of the Batéké Plateaux National Park (Bout, Born & Spohr, 2010). A subsequent study showed that these hyenas were not remnants of a distinct population in Gabon in this area (Bohm, 2012). Whether these hyenas originated from the OKNP is not known, but by protecting wildlife corridors within the huge area of forest-savanna mosaics inhabited by low density of humans (CIESIN & CIAT, 2005), long distance movements and exchange of spotted hyenas could be supported.

Besides the habitat requirements, a sufficient availability of potential prey species of spotted hyenas will also be an important prerequisite if other areas in Central Africa are to provide suitable habitats for spotted hyenas. Forest buffalo was the most important prey species of spotted hyena in the forest-savanna mosaic in the OKNP. The continuous disappearance of forest buffaloes from open habitats in Congo during the last decades (East, 1999) might be a reason for the simultaneous disappearance of spotted hyenas in these areas. Thus, it is advisable that conservation and park managers of Central African areas with confirmed or suspected occurrences of spotted hyenas or who wish spotted hyenas to repopulate their forest-savanna mosaic consider also a forest buffalo management. In addition to this, other possible factors that might have led to the extinction of spotted hyenas in their former Central African distribution range should be identified and considered for spotted hyena repopulation plans.

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Chapter 4: Population density and activity patterns of servals in the Odzala-Kokoua National Park, Republic of Congo

4.1 Abstract

Despite its wide distribution in continental Africa, the serval has received only little scientific attention so far. We did camera trapping in the forest-savanna mosaic of the Odzala-Kokoua National Park, located in the northwest of the Republic of Congo. The park's savannas represent the northernmost extension of the savannas of the Batéké Plateaux, a large ecoregion of open habitat in Central Africa. During eight months of camera trapping we recorded 51 individuals, among them were four kittens, four subadults and 43 adults. Almost two-thirds of the individuals recorded belonged to the servaline morph, which has a pattern mutation of small 'freckled' spots. Using spatially explicit capture-recapture methods the serval density in the park's forest-savanna mosaic was estimated as 11.20–11.71 individuals per 100 km². Data from camera trapping showed that male servals were largely nocturnal whereas female servals were mainly diurnal with a peak in the morning hours. Differences in capture rates and activity patterns between male and female servals were likely related to the occurrence of spotted hyenas, the dominant predator in the park. Spotted hyenas were highly nocturnal and, consequently, had a higher overlap in activity patterns with male servals. Our study provided the first robust density estimates for a medium-sized carnivore in Central Africa. We recommend further studies on this species whereas co-occurrences of larger predators should be considered in study planning.

4.2 Introduction

Most of Central Africa is covered by the tropical rainforests of the Congo Basin. For decades, wildlife in Central Africa has suffered from illegal wildlife trade, habitat degradation and an unsustainable off-take for bushmeat (Nasi, Taber & van Vliet, 2011; Abernethy *et al.*, 2013). Many populations of Central Africa's iconic large forest mammal species, such as gorilla (*Gorilla spec.*) and forest elephant (*Loxodonta cyclotis*), are therefore rapidly declining (IUCN, 2014; Wittemyer *et al.*, 2014). Past research efforts and conservation actions in Central Africa have mainly focused on forest areas and, in general, more on the iconic large forest mammals (Magliocca, Querouil & Gautier-Hion, 1999; Stokes *et al.*, 2010). Only little data are available on the bulk of the other species inhabiting Central Africa (e.g. Ray, 1997; Ray & Sunquist, 2001; Henschel *et al.*, 2011) and, in general, open habitats, such as savannas and forest-savanna mosaics (hereafter FSM), have been only poorly-studied in Central Africa so far.

With a size of roughly 200,000 km^2, the Batéké Plateaux area is a large FSM in Central Africa (Olson *et al.*, 2001) (Fig. 1). It covers almost $2/3^{rd}$ of the Republic of Congo (hereafter Congo) and extends into Gabon to the west and Angola and Democratic Republic of Congo to the south. It consists of extensive areas of rolling grassy savannas, interspersed with gallery forests along watercourses. The Batéké Plateaux is unique insofar as it harbours a diversity of species distinctive from the surrounding forests of the Congo Basin (Bout, 2006). But, as other regions in Central Africa, also faces threats like poaching and habitat alterations, which has already led to a dramatic decline in population numbers of a wide range of mammal species (Henschel, 2009). The Batéké Plateaux once harboured healthy populations of large savanna carnivore species, such as lion (*Panthera leo*), African wild dog (*Lycaon pictus*) and spotted hyena (*Crocuta crocuta*) (Malbrant & Maclatchy, 1949). While lions and African wild dogs have been gone extinct in the Batéké Plateaux by now, spotted hyenas still persist in the FSM of the Odzala-Kokoua National Park, north-western Congo (Henschel, 2009) (Fig. 1). Reduction of prey base and increased levels of persecution are believed to have been the main reasons for their decline / extinction (Henschel, 2009). Whereas the distribution of large carnivores and the reasons for their decline in the Batéké Plateaux have been well-documented (Henschel, 2009), virtually nothing is known on the distribution and population status of smaller savanna carnivores. Just until recently, servals (*Leptailurus serval*) were thought to be extinct in Gabonese ecosystems (Bout, 2010). Bout (2010) reported, for the first time for over more than five decades, observations of servals in Gabon. Also just recently, camera traps produced three photos of servals inside the FSM of the Odzala-Kokoua National Park (Henschel *et al.*, 2014). But due to their poor data, Henschel *et al.* (2014) could not provide density estimates. Their records included only servals of the so called *servaline* morph, which have a pattern mutation of small 'freckled' spots (Kingdon, 2004). In previous times, *servaline* servals were recorded at various locations in central, east and west Africa (Pocock, 1907; Allen, 1924), although it is commonly believed that this pattern mutation most frequently occurs in west Africa (Nowell & Jackson, 1996).

In general, despite its wide distribution all over continental Africa (Breitenmoser, Henschel & Sogbohossou, 2008) surprisingly little data on the ecology and status of the serval are available. In fact, Ramesh & Downs (2013) recently published study on population densities of servals on farmlands in South Africa was the first attempt to determine serval population densities making use of camera trapping, a tool which has emerged as a key non-invasive tool in wildlife research over the last decades (Karanth & Nichols, 1998; O'Connell, Nichols & Karanth, 2011). Apart from this, servals are often reported as 'bycatch' in camera trapping studies (Pettorelli *et al.*, 2010; Treves *et al.*, 2010; Henschel *et al.*, 2014) while in the best case data on habitat use for this species are reported (Pettorelli *et al.*, 2010).

Results from recent studies suggest that the serval can survive in degraded open habitats in Central Africa (Bout, 2010). However, our knowledge on population status and ecology of this species in its Central African range is yet too poor to draw final conclusions on its well-being in this part of Africa. Central Africa faces a future in which more and more land will be converted into human-dominated landscapes (Justice *et al.*, 2001) and in which protected areas will remain the only refuges for wild animal populations (Struhsaker, Struhsaker & Siex, 2005). To understand how also so far poorly-studied wildlife species can cope with these challenges in the future, more data on ecology and status of these are needed. Given the uniqueness of the Batéké Plateaux as being the only large savanna ecosystem in Central Africa, it is important to also include this region in research efforts.

The aim of this article is to provide population size and density estimates for servals in its Central African range. We carried out camera trapping in the FSM of the Odzala-Kokoua National Park, Congo and analysed results with conventional and spatially explicit capture-recapture methods. Using information from camera trapping, we also compared temporal activity patterns of servals and spotted hyenas, the dominant large predator in the park, to give cues on how co-existing large predators might influence serval capture success in camera trapping studies. We focused our discussion around methodological considerations regarding design and analysis of camera trapping studies on servals as well as on implications for the conservation of this species in Central Africa.

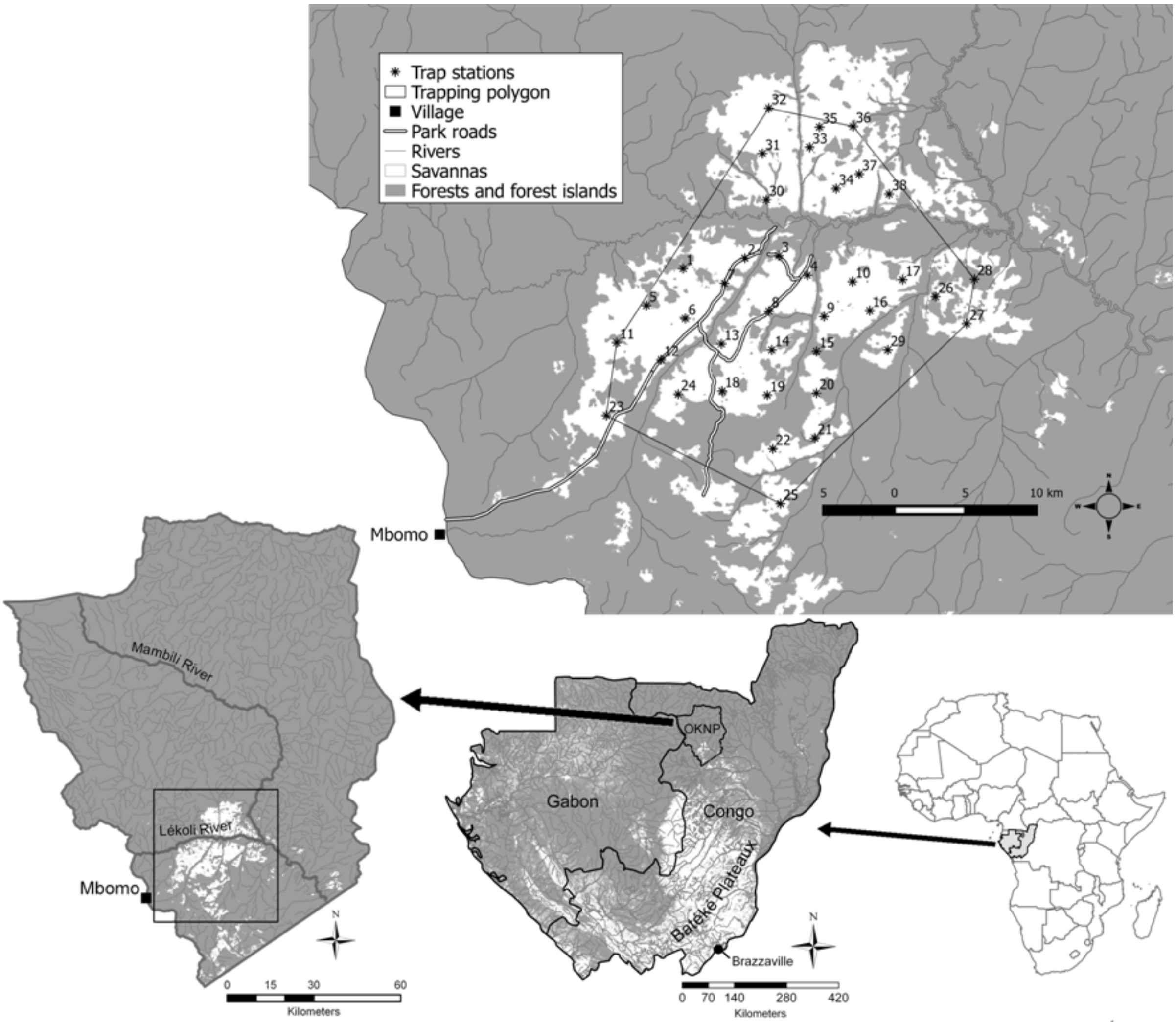

Figure 1. Maps showing extent of the Batéké Plateaux in Congo and Gabon, locations of OKNP, study area and camera tap stations inside study area. White areas = savannas, light grey = forests, dark grey = rivers.

4.3 Material and methods

Study area

The Odzala-Kokoua National Park (hereafter OKNP) has a size of approx. 13,600 km^2 and is the largest national park of the Congo (Aveling & Froment, 2001). Open-canopy Marantaceae-forest on *terra firma* with an almost impenetrable understorey dominated by the plants of the families Marantaceae and Zingiberaceae is the main habitat type in the park (Hecketsweiler, Doumenge, & Mokoko-Ikonga, 1991). A FSM of the size of ca. 800 km^2 is found at the very south of the park (Fig. 1). The savanna vegetation is dominated by Graminae (*Andropogon schirensis*) with scattered fire-resistant shrubs (*Hymenocardia acida* and *Annona senegalensis*) (Dowsett-Lemaire, 1996). The Lékoli River divides the park's savannas into a northern and a southern savannas block (Fig. 1). Larger and smaller forest islands, so called b*osquets*, are numerous in the savannas of the OKNP and the result of the continuous recolonization of savannas by the forest (Dowsett-Lemaire, 1996) (Fig. 1). Besides servals and spotted hyenas the OKNP harbours various other carnivore species, such as leopard (*Panthera pardus*) and African civet (*Civettictis civetta*) (Maisels, 1996).

Camera trapping

The study site was located within the park's FSM (Fig. 1). We divided the part into 38 3.5 x 3.5 km grid cells and deployed a camera-trap station in each cell, resulting in a mean inter-camera trap distance of 2.7 km. The field study was part of a spotted hyena population survey and trap stations were spaced according to the known minimum home range sizes for this species. The smallest reported home ranges for servals of 9.5 km^2 (Geertsema, 1985) are similar to those reported for spotted hyenas (9 km^2) (Höner *et al.*, 2005), which represents approximately the area of a circle that fully fills out the area within the grid cell. Trap stations were deployed at sites where capture probabilities for wildlife species were likely to be high, such as roads and wildlife trails. Installation of trap stations started in mid-July 2013 and was completed after five weeks. In total, trap stations were active for eight months until end of March 2014. The total trapping area was 431 km^2. At each trap station one Reconyx HC500 was installed and programmed to take five pictures per trigger event without intervals between trigger events. Fifteen additional cameras (Reconyx HC500 and Bushnell Trophy Cam) were used as second cameras for trap stations and switched between trap stations during the study period. Twenty-nine stations were installed in savannas and nine stations were installed in forests and forest islands. The study covered the large rainy season (Sep–Nov) and small dry season (Dec–Feb) and partly the large dry season (Jul–Sep) and small rainy season (Mar–May) (Hecketsweiler *et al.*, 1991).

Data analysis

Camera traps pictures of servals were transferred into a picture database and servals were individually identified with the help of their unique spot patterns on both flanks. If possible, individuals were sexed and grouped into adults, subadults and kittens. For population size and density estimates we used conventional capture-recapture (hereafter CCR) as well as maximum likelihood based spatially explicit capture-recapture (hereafter: SECR) and Bayesian based SECR models. The software MARK (White, 2008) was used for analyses with CCR methods. MARK allows analysis of capture-recapture data with a set of pre-defined capture-recapture models, allowing capture probabilities ($\hat{p}$) to vary among individuals, time and with trap response behaviour (White, 2008). SECR models have an advantage as they, unlike CCR methods, estimate density taking into account the spatial relationships between animals and trap locations (Efford & Fewster, 2013). SECR methods combine a state model (the distribution of activity centres of individuals) and an observation model (the spatial detection function) (Efford & Fewster, 2013; Royle *et al.*, 2014). The spatial aspect of SECR methods is of great use as it helps to understand individual heterogeneity in capture probabilities and movement patterns (Sollmann *et al.*, 2011). Most species of cats show sexual variation in ranging behaviour and activity (Simcharoen *et al.*, 2008; Sollmann *et al.*, 2011) which, as a result, affect capture probability as males patrol larger home ranges and, thus, are more likely to be photographed by camera traps (Sollmann *et al.*, 2011; Gray & Prum, 2012). In MARK the Mh-model deals with this problem of heterogeneous capture probability (White, 2008). In SECR methods, spatial behaviour for different groups (e.g. males and females) can be explicitly modelled (Sollmann *et al.*, 2011). Furthermore, SECR methods provide with 'sigma' (σ) an additional spatial scale parameters, which is related to the home range radius (Royle *et al.*, 2014) and, hence, can give deeper insights into the distinct spatial behaviour of the groups in question.

For SECR analyses we used the R packages secr 2.9.3 (maximum likelihood based SECR) (Efford, 2015) and SPACECAP 1.1.0 (Bayesian based SECR) (Gopalaswamy *et al.*, 2012). In secr we compared models in which detection probability (g_0) and sigma were either constant or varying with sex. SPACECAP does not support analyses with covariates. Due to heterogeneity of the habitat we built a habitat mask containing points of suitable and unsuitable habitat which was used for computations in secr and SPACECAP. We defined savannas, including forest islands, as suitable habitat. Dense forests surrounding savannas are likely non-suitable serval habitats (Kingdon, 2004) and, thus, were defined as non-habitat. We chose a distance of 500 m between points, resulting in a resolution of 0.25 km^2. The habitat mask contained the trapping polygon and a 11 km buffer around the trapping polygon to ensure that all individual home ranges within reach of cameras were included (Efford, 2015). Model-selection in secr was based on Akaike’s information criterion (AIC) (Efford, 2015). We determined the final density estimate as weighted average of density estimates from competing models whose Δ is in a range of 2-7 (Burnham & Anderson, 2002; Burnham, Anderson & Huyvaert, 2011). In SPACECAP we ran 60,000 iterations, of which the initial 7,000 were discarded as the burn-in period. We used a thinning rate of four and specified an augmentation value of 350 individuals, which was assumed to be well above the expected number of individuals . We created a density map with estimated serval densities per pixel of size 0.25 km^2 from SPACECAP output file using ArcGIS 9.3.

Density estimates with CCR methods were made using full (FMMDM) and half (1/2MMDM) mean maximum distance moved of individuals captured more than once. FMMDM and 1/2MMDM were added as a boundary strip to the trapping polygon to calculate sizes of Effective Trapping Areas (ETA) (Karanth & Nichols, 1998). In our case, an exceptionally large size of non-suitable habitat would be included in the resulting ETAs. Thus, we only used the size of suitable habitat inside the ETAs for densities calculations (Sollman *et al.*, 2011). We used FMMDM and 1/2MMDM of males obtained over the whole period of eight months for calculations of ETAs.

The used capture-recapture methods assume that the analysed population is geographically and temporally closed (White *et al.*, 1982). Due to the long study period we used a secondary study period for analyses, short enough to adequately approximate closure assumptions. Installation of all 38 trap stations was completed after 33 days. We allowed the population to 'adapt' to stations for further 53 days and chose a secondary period of 75 sampling occasions (trap nights) between the 10/10/2013 and 23/12/2013. For SECR and CCR analyses each of the 75 sampling occasions was included in the calculation. To check population closure during sampling period we used the software CloseTest (Stanley & Richards, 2005).

Activity patterns

To analyse differences in activity patterns between servals and spotted hyenas we assigned independent capture events for spotted hyenas as well as for male and female servals to the categories morning (05:30–11:00), afternoon (11:01–17:30), dusk (17:31–18:30) and night (18:31–05:29) and tested differences in activity periods using χ^2-tests. To quantify overlap between activity patterns of serval males or females and spotted hyenas we used the approach developed by Rideout & Linkie (2009). For this, each activity pattern was first estimated separately using kernel density estimates. In a second step, we calculated the coefficient of overlap Δ_4, recommended for large sample sizes, which varies from 0 (no overlap) to 1 (complete overlap) (Rideout & Linkie, 2009). Analyses were done using an adaptation of the R (R Core Team, 2015) code made available by Linkie & Rideout (2011). We calculated the 95 percent confidence intervals for Δ_4 as percentile intervals from 500 bootstrap samples.

4.4 Results

Trapping effort over the course of the entire study was 7048 trap nights. Servals were photographed 285 times at 29 trap stations, resulting in a capture rate of 4.04 photos/100 trap nights. Cameras produced more pictures of servals of the servaline morph, among them were two individuals with a sandy-coloured pelt with almost no spots on the flanks (Fig. 2). Two hundred and sixty photos were of sufficient quality for individual identification. Of 28 individuals pictures of their left and right flank respectively were available. In addition, for servaline morphs as well as for big-spotted morphs more individuals showing photos of the left flank were available and, thus, we included only these individuals in further analyses, summing up the total number of identified individuals to 51, of which, to conclude, 35 (69 %) were of the servaline morph whereas 16 (31 %) were of the big-spotted morph (Table 1).

Of these 51 individuals, 43 were adults, four were subadults and four were kittens (Table 1). We identified 25 females (incl. one subadult) and 17 males (Table 1). Only two individuals were, in total, seven times (2.5%) photographed in forests or forest islands, suggesting that forested areas are predominantly avoided. The MMDM pooled over all adult individuals was 4,261.06 (±SE 512.46) m (n = 18). For adult males MDMM was 4,765.25 (±SE 711.52) m (n = 12) and for adult females MDMM was 3,252.67 (±SE 382.19) m (n = 6) respectively.

Figure 2. Morphs of servals photographed in the OKNP. Left picture: big-spotted morph (female), middle picture = servaline morph (male), right picture = servaline morph with a sandy-coloured pelt and almost no spots on the flanks (male).

Table 1. Total number of servals *Leptailurus serval* and number of individuals based on sex, location and morph recorded during eight months of camera trapping in the OKNP's FSM.

Age	Total # individuals	Savannas blocks		Morph		Sex		
		Northern	Southern	Big-spotted	Servaline	Females	Males	Unknown
Kitten	4	4	0	0	4	0	0	4
Subadult	4	2	2	2	2	1	0	3
Adult	43	14	29	14	29	24	17	2
Total	51	20	31	16	35	25	17	9

The analysed secondary period contained 78 photos of 31 animals (18 adult females & 13 adult males). Nine females and five males respectively were photographed only once whereas nine females and eight males were recaptured up to seven times each. One male was photographed at three stations, four at two stations, and eight at one station. Seventeen females were photographed at one station and only one female was photographed at two stations. Statistical test for population closure supported the closure assumption (Table 2). In MARK the highest-ranking model was the heterogeneity model Mh. Capture probabilities among the heterogeneous groups were 0.06 and 0.02 respectively and population size based on this model was 42.79 (±SE 8.17). Using FMMDM and 1/2MMDM of males densities were estimated as 10.37 (±SE 4.88) and 11.81 (±SE 4.45) individuals/100 km^2 respectively (Table 2).

Table 2. Population size and density estimates for servals in the OKNP based on CCR methods. ETA = Effective trapping area (suitable habitat) based on MMDM and 1/2MMDM of male servals, $\hat{p}$ = Capture probability, $\hat{N}$ = Population size, D = Serval density (individuals/100km^2), SE = Standard error, CV (coefficient of variation) = SE[$\hat{N}$] / $\hat{N}$ × 100.

Closure test		Highest-ranking model	ETA (km^2)	$\hat{p}$	$\hat{N}$ (±SE)	D (±SE)	CV (%)
χ^2	P						
58.66	0.19	M(h)	412.50 ± 177.46	0.06 & 0.02	42.79(±8.17)	10.37(±4.88)	19.09
-	-	-	362.25 ± 117.59	-	-	11.81(±4.45)	-

Using maximum likelihood SECR, the highest ranking model was a model in which sigma varied with sex (Table 3). The detection probability for this model was 0.05. The averaged population size over all competing models was 50.83 (±SE 9.72). The size of suitable habitat within the area containing the trapping polygon and 11 km buffer was 434 km^2 and consequently averaged density was 11.71 (±SE 2.24) individuals/100 km^2. Results from Bayesian SECR are given in Table 3 and Figure 3.

Table 3. Population size and density estimates for servals based on maximum likelihood (ML) and Bayesian SECR methods. ω = Weight of support for each model, g_0 = Detection probability, λ_0 = expected encounter frequency at trap location considered as home range centre, σ (sigma) = spatial scale parameter, Psi = Data augmentation parameter, $\hat{N}$ = Population size, D = Serval density (individuals/100km^2), CV (coefficient of variation) = SE[$\hat{N}$] / $\hat{N}$ × 100, [•] = Parameter constant. Averaged population size and density estimates are given in bold.

Method	Model	AIC	dAIC	ω	g_0 (±SE)	σ (±SE) m	$\hat{N}$ (±SE)	D (±SE)	CV (%)
ML SECR	g_0[•] σ[Sex]	865.68	0	0.60	0.05 (±0.01)	♂: 2,140.47 (±366.36) ♀: 1,370.24 (±112.07)	50.72 (±9.68)	11.69 (±2.23)	19.09
	g_0[Sex] σ[Sex]	866.50	0.83	0.40	♂: 0.03 (±0.02) ♀: 0.04 (±0.01)	♂: 2,520.86 (±594.23) ♀: 1,444.35 (±144.47)	51.00 (±9.77)	11.75 (±2.25)	19.16
	-	-	-		-	**Averaged results**	**50.83 (±9.72)**	**11.71 (±2.24)**	**19.11**

	Psi (±SE)	λ_0 (±SE)	σ (±SE)	$\hat{N}$ (±SE)	D (±SE)	CV (%)
Bayes. SECR	0.13 (±0.02)	0.04 (±0.01)	1,261.82 (±94.88) m	48.59 (±5.85)	11.20 (±1.35)	12.04

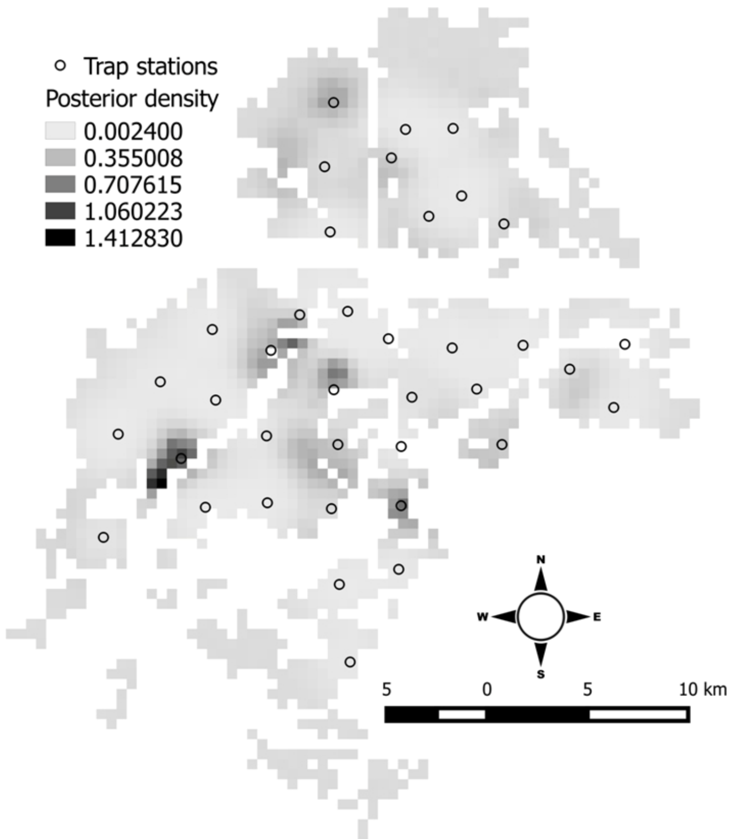

Figure 3. Density of servals per pixel of size 0.25 km² in the FSM of the OKNP based on density estimates by program SPACECAP.

Activity patterns

Male servals were mainly active during the night (59 %) whereas females were mainly active during daylight hours (78 %) with a peak in the morning hours (Fig. 4). The difference between males and females in the activity periods was significant (χ^2-test, $\chi^2 = 31.46$, d.f. = 1, $P < 0.01$), suggesting that both sexes have different activity periods. Spotted hyena was photographed ten times more frequently than servals (n = 2938). Spotted hyenas were highly nocturnal (Fig. 4) and coefficient of overlap with serval males was 0.72 (CI = 0.64–0.78) whereas with females overlap was 0.38 (CI = 0.31–0.45).

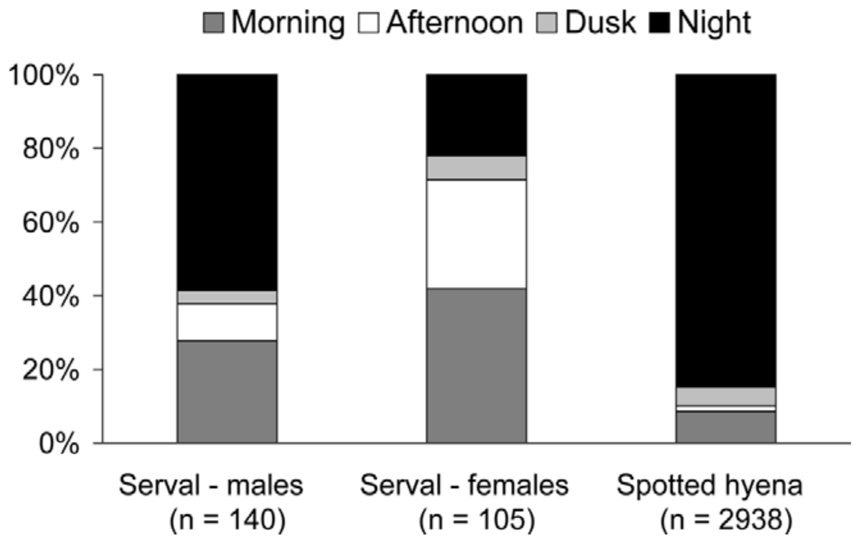

Figure 4. Activity patterns of servals and spotted hyenas. Morning: 0530-1100, Afternoon: 1101-1730, Dusk: 1731-1830, Night: 1831-0529.

4.5 Discussion

During eight months of camera trapping we photographed 43 adult individuals in a trapping polygon of 431 km^2. A consequence of this long sampling period was probably that highly mobile animals may have temporarily moved on and off of the study area. Most of the animals were photographed several times over several months, whereas others were only photographed twice or even once. The latter could have in fact represented highly mobile individuals moving on and off the study area. This scenario can decrease precision in density estimates with CCR methods, since these, unlike SECR methods, are prone to violations of the geographic closure assumptions (Kendall, 1999). Thus, we used a subset of data for analyses to approximate temporal (and for CCR methods also geographical) closure assumptions. We achieved sufficient precision in density estimates in several ways: Firstly, our CVs were in all analyses less than 20 %. CVs of less than 20 % are considered as 'fair' and suitable for management implications (Linkie *et al.*, 2008; Foster & Harmsen, 2012). Secondly, our study area was quite large and as a result we recorded a great number of individuals. Greater numbers of individuals lead, in general, to more precise results of density estimates (Linkie *et al.*, 2008; Foster & Harmsen, 2012). Thirdly, estimates for sigma showed that serval movement was at least (ML SECR) or almost (Bayesian SECR) half the distance between traps. Under these circumstances SECR models perform well, even if most of the animals are captured only once (Sollmann, Gardner & Belant, 2012). Additionally, this showed that our chosen grid cell size was appropriate. However, overall capture rate over the entire study was low for some individuals. In general, the serval is a hard-to-detect-species (Thiel, 2011). In our case, the occurrence of a co-predator, the spotted hyena, must be considered. Camera traps produced thousands of pictures of spotted hyenas and ungulate species but, in comparison, much smaller numbers of pictures of other carnivore species, including servals (see results; T. Bohm, unpublished data). The savanna areas in the park are completely surrounded by dense forests to the east, north and west, reducing the size of available habitat for savanna-dwelling species. Spotted hyenas are highly mobile animals (Mills, 1990) and other carnivores are part of their diet (di Silvestre, Novelli & Bogliani, 2000). Hence, they likely force servals, and other carnivores in the park's FSM to live a more secretive life and to actively avoid areas, such as trails or roads, which hyenas often use. We mainly placed camera traps in the savannas on larger trails, so called elephant boulevards, which connect distant forest areas. Traps placed here produced very high capture rates for larger ungulates and spotted hyenas. In fact, future studies on servals aiming to examine differences in capture probabilities on different trail types in areas in which servals co-exist with larger predators would be of great use and might help to improve detectability and, hence, density estimates for this species.

In addition, differences in capture rates and activity patterns between males and females might reflect sex-specific adaptations to the presence of spotted hyenas. As females solely take responsibility for offspring (Nowell & Jackson, 1996), they have to be more vigilant to avoid predation of their offspring by larger carnivores. Hence, serval females in the study area were mainly diurnal with little overlap in activity patterns with spotted hyenas, which were highly nocturnal. On the other hand, serval males were less vigilant, photographed more often and mainly nocturnal.

Our study provided first robust density estimates for the serval in Central Africa. The serval density in the OKNP of 10.37–11.81 ind./100 km² is higher than the density recorded on farmlands in South Africa (6.5–7.6 ind./100 km²) (Ramesh & Downs, 2013), but much lower than the density of 42 ind./100 km² recorded in the Ngorongoro Crater (Geertsema, 1985), although the latter estimate could be the result of a methodological artefact. Apart from these, no other density estimates are available. Ramesh & Downs (2013) based their analyses on CCR, Bayes- and ML-SECR methods but did not include sexes in their models. As our data showed, subtle differences in behaviour and movement pattern between males and females can cause differences in detectability. Thus, future studies on servals should also aim to determine sex of recorded individuals and make use of the capability of SECR methods that account for sex-specific differences in detection and movement.

Our estimates from CCR, Bayes- and ML-SECR methods differed not significantly from each other. However, the ad hoc approach used in CCR methods to determine size of the sampling area has certain drawbacks, mainly because it does not include the spatial relationships between animals and trap locations like SECR methods (Noss *et al.*, 2012). But, since CCR methods are still widely used we also provided the results from those here.

Almost two-thirds of the individuals recorded in our study population were of the servaline morph. Apparently, the servaline morph is the dominant genetic morph in the park and genetic studies on servals in the OKNP are recommended. Apart from that, further studies on servals in the savannas of the Batéké Plateaux are recommended. With the Léfini Faunal Reserve in southeast Congo, the Batéké Plateaux National Park (BPNP) in southeast Gabon and the 800 km^2 of open habitat in the OKNP, less than 5 % of the savannas of the Batéké Plateaux is actually under formal protection. Whereas the presence of this species in the Léfini Faunal Reserve has not yet been confirmed (Mathot, Ikoli & Missilou, 2006), recent findings suggest that servals are present in the BPNP (N. Bout, PPG, pers. comment). Large savanna carnivores are absent from the BPNP (Henschel, 2009) and a field study in the park is strongly recommended. Besides that, studies in unprotected FSMs where servals were recently recorded (Bout, 2010) are also recommended. Unless such studies can prove the existence of viable serval populations, the OKNP's serval populations remains the only known population in the Batéké Plateaux so far, and, is hence, crucial for the persistence of this medium-sized carnivore in Central Africa.

4.6 Acknowledgements

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Chapter 5: Characteristics of spotted hyena den sites in the Odzala-Kokoua National Park and acoustic monitoring

5.1 Introduction

Within a spotted hyena clan, the communal den is the centre of social activity and is regularly visited by all clan members (Mills, 1990). In a clan's territory there is always only one communal den, in rare cases a clan can have two communal dens (pers. comment M. East). A communal den is usually occupied for several months or even years (Boydston *et al.*, 2006). How long a clan occupies a communal den depends on several factors. Infestation by ectoparasites appears to be the main reason why spotted hyenas abandon a den site (Boydston *et al.*, 2006). Human activities can also persuade spotted hyenas to leave their den site (Mills, 1990). Likewise, environmental factors, such as flooding of den sites, can force spotted hyenas to leave their den site (Hofer & East, 1993). Besides rearing and protection of cubs, the communal den serves the establishment and maintenance of social bonds (Mills, 1990; Boydston *et al.*, 2006). Adult clan members meet at the communal den to interact with each other and with cubs and to form hunting and territory border patrol groups (Mills, 1990). Clan members also regularly whoop at the communal den, predominantly for self-advertisement (East & Hofer, 1991b). Whoops are emitted as a series of calls ('whooping bout') (East & Hofer, 1991a). Whooping bouts usually start with a short initial whoop followed by a series of symmetrical or asymmetrical whoops in the mid sequence and end with one or more terminal whoops (East & Hofer, 1991a) (Fig. 1). Asymmetrical whoops begin at a low frequency and end abruptly with an increase in pitch (Fig. 1). Symmetrical whoops begin at a low frequency, rise and fall in the middle and terminate with a low frequency section at the end (Fig. 1). Terminal whoops usually last longer than the previous whoops and show no rise in frequency (Fig. 1). Whoops of adult can be heard as far as 5km (East & Hofer, 1991a).

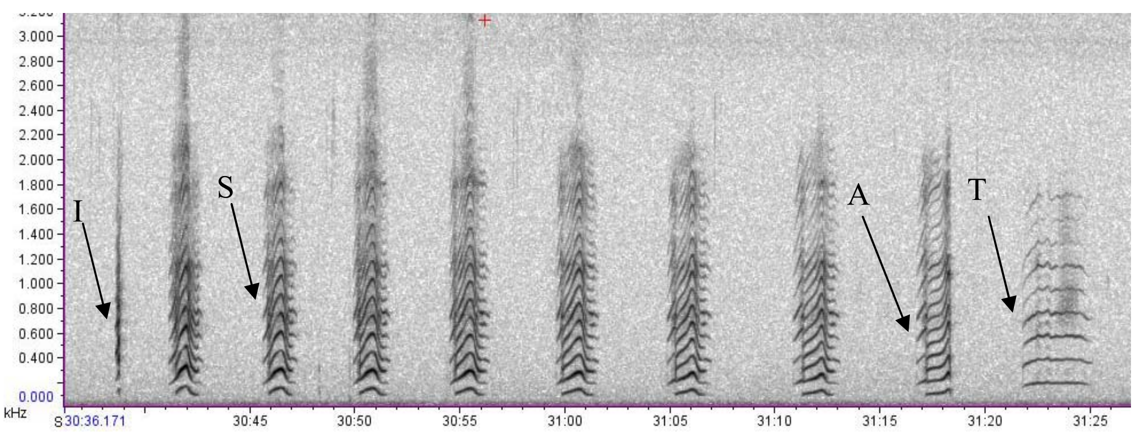


Figure 1. Sound spectrogram of a whooping bout from an adult animal recorded at a den site in the OKNP. I = initial whoop, S = symmetrical whoop, A = asymmetrical whoop, T = terminal whoop.

Cubs start to produce whoops in their first month of life (East & Hofer, 1991a). Whoops from cubs substantially differ from whoops from adults as they usually consist only of a few harmonics and have a higher fundamental frequency (Fig. 2).

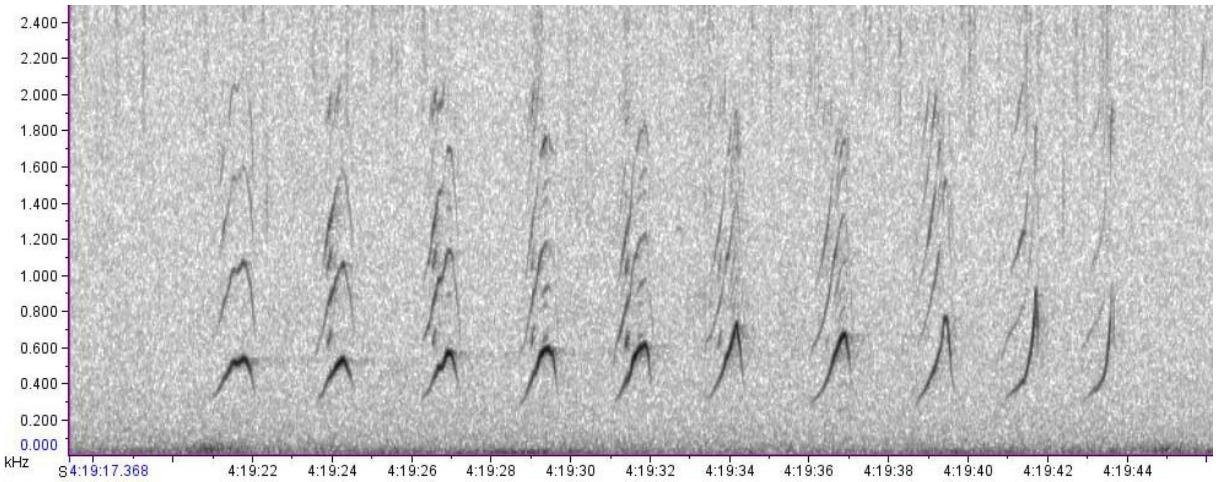


Figure 2. Sound spectrogram of a whooping bout from spotted hyena cub recorded at a den site in the OKNP.

East & Hofer (1991a) found that the structure of calls from individuals remain relatively stable over several years and that there is considerable variation in the structure of whoops between individuals, suggesting that animals can be individually identified with the help of their whoops. In addition, due to the difference in the structure of whoops between adults and cubs it can be assumed that acoustic monitoring can be used not only to identify the number of adult animals but also the number of cubs in a clan. To answer the question if the number of adult animals and cubs in a clan can be determined with the help of recordings of vocalisations I conducted acoustic monitoring in the park. For this, I installed an acoustic recorder at a communal den over a period of several months.

5.2 Methods and results

During the study periods Nov 2011 to Feb 2012 and Jul 2013 to March 2014 I regularly walked the study area accompanied by field assistants. During the first study period a total of 818 km was walked (Fig. 3). During the second study period a total of 2000 km was walked (Fig. 4). In 2013, a motorbike, kindly provided by the park management, was used to reach farther distances on the park's road network over a period of 3 months. To cross the Lékoli River a small canoe was used during the second study period. To reach areas which were not accessible by motorbike or during a one-day field trip, longer field trips lasting several days were done. During longer field trips, nights were spent in field camps which were built up near water courses.

Den site selection and characteristics

During field trips in the forest-savanna mosaic of the OKNP I found several den sites (Fig. 5). Spotted hyena den sites in the OKNP could be identified as distinct groups of termite mounds standing closely together, where clear signs of current or past extensive use by spotted hyenas, e.g. spotted hyena tracks, especially from hyena cubs, or circular areas of bare soil around termite mounds, could be observed (Fig. 6–9). A characteristic large termite mound with a varying number of large entrances served as main den. Several smaller dens could be found in the nearest surroundings of this main den. These smaller dens were smaller termite mounds with only one entrance and footprints of cubs seen at the entrance suggest that cubs occasionally make use of these smaller dens, probably as short-term shelter. Burrows in these termite mounds were likely excavated by aardvarks and giant pangolins, although the latter probably play just a minor role. Aardvarks were recorded several times with camera traps (see chapter 7) unlike giant pangolins which were not photographed. However, giant pangolin was recorded in scats samples (see chapter 3) but it can not be said if it was preyed in the savanna or the forest.

In 2011 and 2012 I found two abandoned den sites. One of the den sites was just 10 m away from the recently built road (den site 2 in Fig. 5). This den site showed signs of recent use, suggesting that hyenas have left the den site during or shortly before construction phase of the road. In 2013, I found an occupied den site (den site no.1 in Fig. 5). This den site was the communal den of the clan 'North' (see chapter 2). This communal den was situated in the large western savanna in the savannas sector north of the Lékoli River just 100 m away from a large lake ('Mare') (Fig. 5). In addition, during my study in the OKNP in 2008 (Bohm, 2008) I found one occupied den site and one abandoned den site (den sites 4 & 5 in Fig. 5). During one visit of the occupied den site I observed a cub with an adult hyena.

Acoustic monitoring

On the 19th October 2013 an acoustic recorder was deployed next to the den site 1 (Fig. 10). For recordings of spotted hyena vocalisation a Song Meter^{TM} SM2 (Wildlife Acoustics, Inc; Concord, Massachusetts) acoustic recorder was used. The acoustic recorder was housed in a waterproof case and attached to tree branch at a height of about 4 m (Fig. 10). This tree was the only larger tree in the nearest surroundings of the den site and situated about 20–25 m away from the 'main den'. The recorder was operated by 4 internal Mono D batteries or one external lantern battery. Lantern batteries which were connected with a cable to the recorder and stored in the case together with the recorder normally have a capacity sufficient for 2–3 weeks of autonomous recordings. Unfortunately, all of the lantern batteries, except 2, which I have bought in 2011 and stored in Mbomo after my departure from Odzala in 2012, were empty for unknown reasons even though the ones which were used in 2012 worked properly and those which were not used were sealed in a box showing no signs of use. Thus, later, a set of 4 rechargeable Mono D Nimh batteries was used. Capacities of these batteries were only sufficient to keep the recorder running for 7–8 days. Thus, frequent visits of the recorder were necessary to replace the batteries. Later, a second recorder was put in the case and programmed to start recording after 7 days, e.g. after the first recorder stopped recording. Recorders were programmed to take recordings in mono from 5 pm to 7 am (14 hours), at a sample rate of 16000 Hz. Recorders were operational until 26t^{h} February 2014.

In total, the recorder recorded 62 complete 14-hours periods and five incomplete 14-hours periods, summing up to a total of 907 hours of recordings. Sound files were visually examined for whooping bouts with the help of the software Audacity. Whooping bouts were further separated into whooping bouts from adults and whooping bouts from cubs. In total, 411 whooping bouts were recorded. Of these, 223 were of sufficient quality fur further analysis. One-hundred-and-forty-one whooping bouts were identified as whooping bouts from adults, whereas 92 whooping bouts were identified as whooping bouts from cubs. Sound files of whooping bouts were analysed in the programs Avisoft and Raven Pro. The following general parameters were measured:

- number of whoops in a bout
- composition of the bout (number of I, A, S & T whoops)
- occurrence of additional elements, such as subharmonics and sidebands in the bout
- length of the whole bout

In addition, the following parameters where measured from the first whoop, if whooping bouts contained no initial whoops or from the first whoop after the initial whoop:

- total duration of whoop
- number of subharmonics below 2000 Hz
- if first whoop was a S-whoop: begin and end of the 'mountain' in a S-whoop, length of the sequence before the 'mountain' in a S-whoop, length of the sequence after the 'mountain' in a S-whoop
- if first whoop was a A-whoop: duration and position of the 'mountain' in an A-whoop

Due to difficulties during analyses, results on the above mentioned parameters are not available yet.

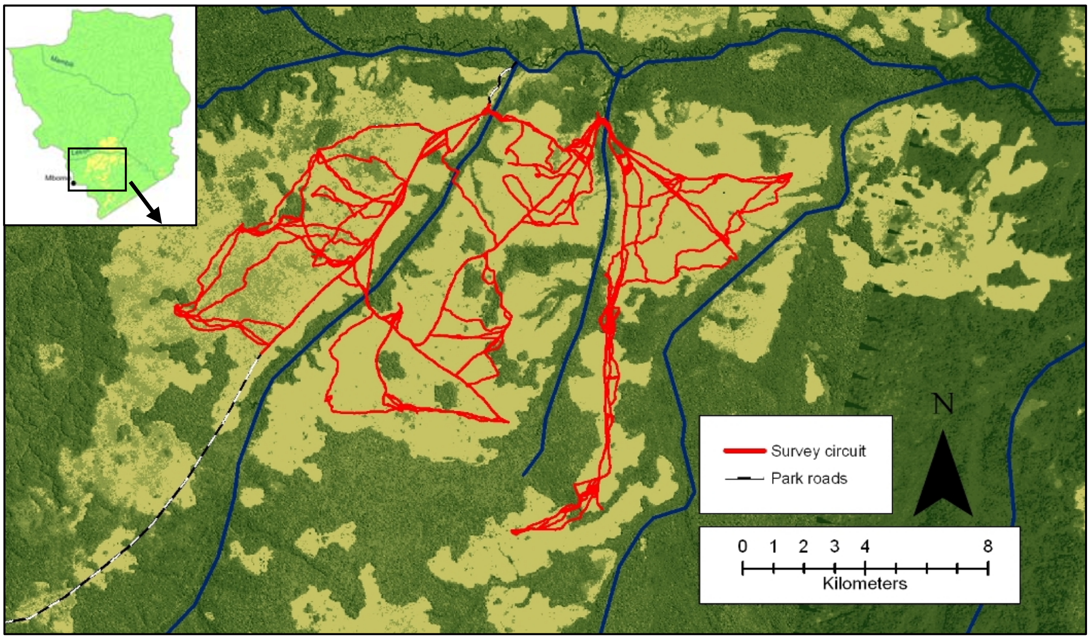


Figure 3. Map of the study area showing the survey circuit during study period Nov 2011–Feb 2012.

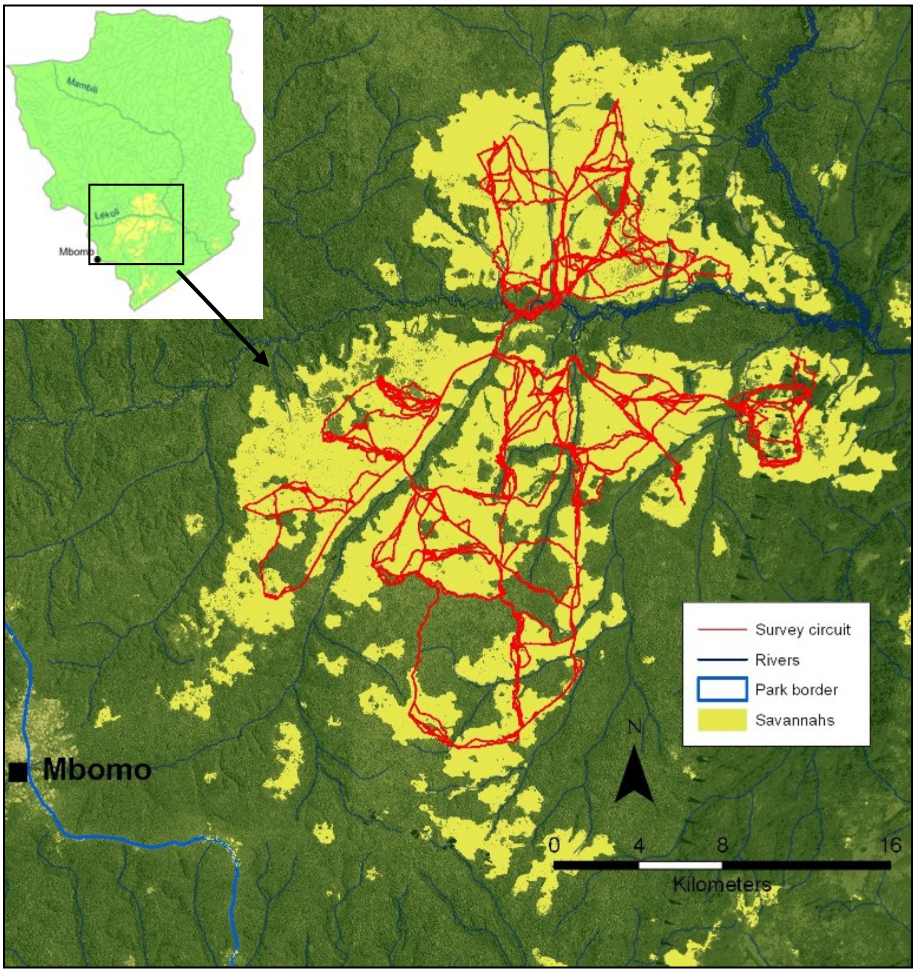


Figure 4. Map of the study area showing the survey circuit during study period Jul 2013–Mar 2014.

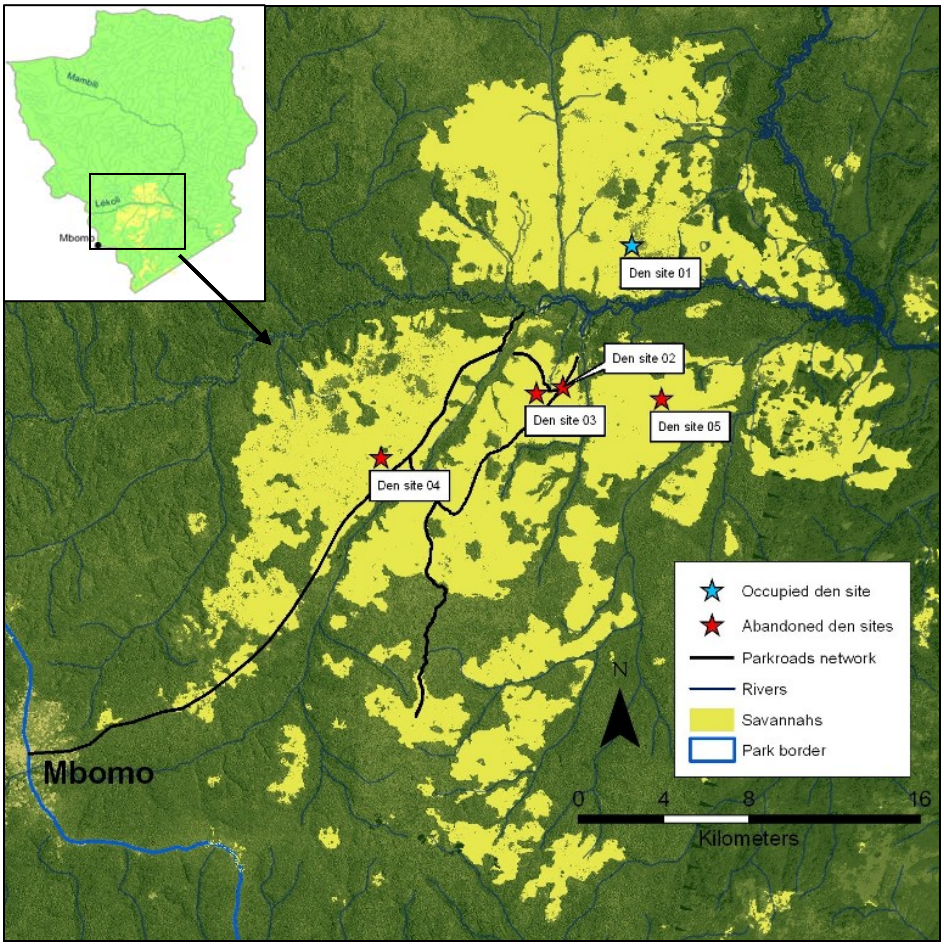


Figure 5. Map showing locations of communal den sites in the study area. The audio recorder was installed at den site 1. Den site 4 was occupied in 2008, but abandoned since 2011. The abandoned den sites 2 & 3 were discovered in 2011 and 2012 respectively (see text). The abandoned den site 5 was discovered in 2008.

Figure 6. Picture of den site 3. Signs of extensive use (circular area of bare soil) around this termite mound and an adjacent termite mound clearly identified this location as spotted hyena den site. But since no fresh tracks of adult spotted hyenas or spotted hyena cubs were seen at this location it is assumed that spotted hyenas have abandoned this den site just recently.

Figure 7. Picture of den site 1**.** Picture showing the main den of the communal den site. Note the big entrance and the circular area of bare soil around the den. Small picture: Tracks of spotted hyena cubs were seen at the entrance.

Figure 8. Back side of the main den from Figure 7. Note the large lake in the back.

Figure 9. Picture of den site 4. Tracks of spotted hyena cubs were seen on the circular area which surrounds the termite mound.

Figure 10. Pictures showing acoustic recorder and tree on which the recorder was deployed. Arrows indicate location of the recorder (left picture) and microphone (right picture) respectively.

5.3 Discussion

Spotted hyenas in the OKNP exclusively use termite mounds as communal den sites. The communal den of the clan 'North' was situated about 100 m next to a huge lake ('Mare'). During each visit of this lake herds of buffaloes, including calves, were seen. Acoustic recordings from this den site also suggested that buffaloes visited the lake during each time span of the day as vocalisations of buffaloes were often heard as background noises in the recordings. Acoustic recordings further revealed that forest buffaloes as well as elephants often walked very close to the communal den. One recording contained a prolonged sequence with sounds of hyenas attacking and hunting down a forest buffalo. In fact, it would be interesting to study the effect of the presence of this communal den to animals which visit this lake or to study to what extent spotted hyenas use this lake as hunting ground. To find communal dens in the forest-savanna was very difficult due to the high vegetation in the savannas that limited visibility. Air surveillance with small planes or drones might be therefore a more appropriate method to find communal dens in the forest-savanna mosaic. In this context, the method described in chapter 2 helps to identify core areas of clans in which intensive surveys for communal dens could be conducted with air surveillance (or by foot).

Communal dens are the centres of activities of spotted hyena clans and the protection of communal den sites is crucial for the conservation of spotted hyenas in the park. Females with cubs that are forced to abandon den sites due to human disturbance or environmental factors expose their offspring to potential dangers such as poachers, adult spotted hyenas from other clans or other large carnivores (Mills, 1990). Furthermore, in the absence of suitable other den sites, spotted hyena clans might be forced to leave their natal territory which can result in injuries or deaths during clashes with neighbouring clans (Mills, 1990). Thus, disturbance of communal den sites in the park should be avoided. In 2011, a road was built just 10 m next to a communal den. Human activities next to this den site during construction of the road have probably forced the resident clan to leave this den site. Thus, locations of communal den sites should be considered before infrastructure projects, such as roads, are implemented in the park and nearest surroundings of areas in which infrastructure projects are planned should be surveyed for communal dens in advance. The occupied den site which was discovered in 2008 was ca. 700 m away from a road, which was by that time regularly used (Bohm, 2008). Thus, a minimum distance of roads to spotted hyena den sites of about 700 m is suggested.

Acoustic monitoring aiming to determine population and clan sizes in spotted hyena populations with the help of recorded vocalisations at communal den sites seems to be a feasible method. A large number of vocalisations from adults and cubs could be recorded. However, variations within whooping bouts of adults and cubs seem to be large making it difficult to find candidate parameters for single whoops or whooping bouts on which individual identification can be based. It is therefore recommended to do an acoustic study with known individuals first to determine which parameters can be used for discrimination between individual animals.

Chapter 6: Conservation genetics of the spotted hyena in the Odzala-Kokoua National Park

6.1 Introduction

By the development of quick, non-invasive and relatively cheap genetic techniques, and the achievement of high accuracies in statistical analysis of genetic data during the last decades, population genetics has become one of the most powerful instruments for conservation (Waits, 2004; Hauffe & Sbordoni, 2009). The genetic composition of a population is typically described in terms of heterozygosities, allele frequencies and number of alleles (Frankham, Ballou & Briscoe, 2010). Populations with considerable genetic diversity are less vulnerable to changing environmental pressures and more resistant to diseases, pest and parasites (Frankham *et al.*, 2010). The main forces that change frequencies of alleles in populations are natural selection, mutation, genetic drift and gene flow (Mills, 2007). Migrations of individuals from one population to another are natural factors that allow gene flow between populations (Mills, 2007). Lack of gene flow from neighbouring populations together with a small population size could lead to inbreeding (Hedrick, 2005), loss of genetic diversity and increased risk of extinction (Lacy, 1997; Mills, 2007). Migration events, no matter how rare they may be, are of special relevance because they can maintain and substantially increase genetic variation in local populations (Mills, 2007). The severely bottlenecked and geographically isolated Scandinavian grey wolf (*Canis lupus*) population was "rescued" by the arrival of one single male immigrant, which originated from a population approximately 800km away (Ingvarsson, 2002; Vilà *et al.*, 2003). By establishing a second breeding pack and subsequently fathering six male cubs, his arrival led to an increased heterozygosity, significant outbreeding, a rapid spread of new alleles and exponential population growth in the whole population (Vilà *et al.*, 2003). Based on an analysis done by Wright (1931), the "one-migrant-per-generation rule" (OMPG rule) has emerged "as the level of gene flow sufficient to prevent the loss of alleles and minimise loss of heterozygosity within subpopulations, while still allowing divergence in allele frequencies to occur among subpopulations" (from Mills, 2007). Taking into account the various processes occurring in wild populations, a range between one and ten migrants per generation was later generally accepted as an appropriate level to avoid negative impacts arising from genetic drifts (Mills & Allendorf, 1996).

Knowledge of size and structure of a population can provide valuable information regarding its potential vulnerability for extinction. The term "minimum viable population" (MVP) is widely used as a reference to describe a population's state in which it may escape extinction probabilistically (Shaffer, 1981). MVP is regarded as a helpful instrument for managers and politicians, because it provides concrete figures that can be used in policy papers or management and action plans (Soulé & Simberloff, 1986). An often used approach to set the minimum for a viable population size is the estimation of the (genetically) effective population size (N_e). N_e is defined as the size of an ideal population which maintains the same genetic diversity (same amount of inbreeding or of random gene frequency drift) as the real population (Kimura & Crow, 1963), and is equivalent to the number of breeding animals per generation. In general, N_e is the critical population size required for a population to retain its evolutionary potential (Soulé, 1987). Since most populations do not meet the assumptions of an ideal population, such as equal genetic contribution by both sexes and constant population size over time (Creel, 1998), N_e is usually substantially lower than the actual population size (N). As a rule of thumb, the ratio of N_e to N for wildlife populations is roughly 0.2–0.3 (Frankham, 1995; Kalinowski & Waples, 2002). The size of N_e has been the subject of some debate over the past decades, with proposed sizes ranging from 50 to 5000 individuals (Franklin, 1980; Soulé, 1980; Lynch & Lande, 1998). Franklin (1980) and Soulé (1980) suggested a short-term N_e of 50 to avoid serious inbreeding depression, and a long-term N_e of 500 to maintain overall genetic variability ("50/500 rule"). In general, the 50 rule is seen as a guideline for conservation aspects and it should be avoided that population sizes fall below this threshold to avoid a possible increased risk of extinction because of genetic effects (Allendorf & Luikart, 2007). Recent advances in genetic analysis make it possible to determine N_e for a population from one set of genetic material (microsatellites) collected in the field during one time span only (Tallmon *et al.*, 2008), in contrast to previous approaches when two or more temporally spaced genetic samples were required (Waples, 1989; Berthier *et al.*, 2002).

To investigate the genetic make-up of the OKNP population, I used microsatellite profiling. Microsatellites are one of the most common genetic tools for conducting population genetic analyses, because they are very variable with a high polymorphism (Mills, 2007), making them an ideal candidate for identification of individuals within a population. Genetic analysis was used to answer the following questions:

1) What is the degree of genetic diversity in the OKNP's spotted hyena population?
2) Are spotted hyenas in the OKNP at risk of inbreeding depression?
3) Did the OKNP's spotted hyena population suffer from a recent bottleneck?
4) What is the (genetically) effective population size of the OKNP's spotted hyena population?

6.2 Methods

The mucus layer of scat samples was used for genetic analysis. This mucus layer consists of intestinal epithelium cells that contain DNA of the animal excreting the scat (East *et al.*, 2003). To obtain samples for a satisfying genetic analysis, only material from fresh hyena scats was used (Fig. 1), because it is likely that scats exposed to environmental influences might not provide material that is suitable for use in genetic analysis. The mucus layer was scraped off from the scat's surface with the flat end of a spatula and stored in a cryo-vial with 96% ethanol or 20% DMSO. Chances to find scats are highest at latrines and well-used hyena trails, and the chances to find fresh scats are highest in the early morning hours. Thus, to maximize the likelihood of finding fresh scats, latrines and well-used hyena trails in the study sites in the OKNP were regularly visited during early morning hours. DNA from mucus/faeces was extracted using a NucleoSpin Soil kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions. Seventeen spotted hyena microsatellite loci have been identified so far (Libants *et al.*, 2000; Wilhelm *et al.*, 2003). Genetic analyses were conducted at the Leibniz Institute for Zoo and Wildlife Research (Berlin, Germany). Genetic samples were collected during the two study periods: Nov 2011–Feb 2012 and Jul 2013–Mar 2014. In addition, samples collected during the study period Jan–Jun 2008 (Bohm, 2008) were also included in the analyses.

Figure 1. Spotted hyena scats samples from the OKNP. The two upper pictures show samples of fresh age from which material for genetic analysis could be obtained. Lower picture shows scat sample of older age of which no genetic material could be obtained. White colour is due to the high amount of bone powder in the scat.

Statistical analysis

Genetic diversity indices

For each locus and the whole population, allele frequencies, observed number of alleles, effective number of alleles, observed heterozygosity, expected heterozygosity and Shannon's information index were estimated using the software programs GenAlEx 6.5 (Peakall & Smouse, 2012) and GENEPOP 4.3 (Rousset, 2008). The extent of inbreeding was measured by the coefficient F_{IS} (inbreeding coefficient) (Nei, 1977) in the software FSTAT (Goudet, 2001). To test significant deviation of F_{IS} from zero bootstrap 95% CIs were calculated for overall F_{IS} and for F_{IS} for single loci using the software programs GDA (Lewis & Zaykin, 1999) and GENETIX 4.05 (Belkhir *et al.*, 2004) with 10000 replicates. Deviations from Hardy-Weinberg equilibrium (HWE) for each locus and presence of linkage disequilibrium for pairs of loci were calculated with exact tests using Markov chain methods implemented in the program GENEPOP 4.3 (Rousset, 2008) (10,000 dememorization steps, 100 batches and 1,000,000 iterations per batch). Score statistics (U tests) were used to assess heterozygote deficiency and excess for each locus and the entire population by using Markov chain methods with the same default settings. Overall deviation from HWE was calculated by using Fisher's method implemented in the software GENEPOP 4.3 (Rousset, 2008). When multiple tests were used, P-values were adjusted using sequential Bonferroni adjustment (Rice, 1989).

Bottleneck tests

A population that experienced a recent reduction of its size exhibits at selectively neutral loci a characteristic mode-shift distortion in the distribution of allele frequencies (Luikart *et al.*, 1998) and develops heterozygosity excess (Cornuet & Luikart, 1996). As a result, the number of alleles occurring at a frequency lower than 0.1 becomes less abundant than the number of alleles occurring at higher frequencies (Luikart *et al.*, 1998) and a significant number of loci show an observed heterozygosity larger than the heterozygosity expected from the observed number of alleles (Cornuet & Luikart, 1996). The population was assessed for a deficiency of the low frequency allele class by examining the overall distribution of allele frequency classes (“mode shift” test) (Luikart *et al.*, 1998). Alleles from genotyped loci were grouped into ten allele frequency classes. An approximately L-shaped distribution indicates that the population size has remained constant during the past, whereas recent bottlenecks provoke a mode shift in the distribution (Luikart *et al.*, 1998). To determine whether the population experienced a bottleneck as a result of a significant number of loci with heterozygosity excess, a “Wilcoxon sign-rank test” implemented in the software

BOTTLENECK was used (Cornuet & Luikart 1996). For this, a two-phase mutation model (TPM) with different percentages of the step-wise mutation model (SMM: 70, 80, 90%) was used. The variance was set at 12 (Piry, Luikart & Cornuet, 1999) and results were obtained from 1,000 iterations.

Genetic effective population size

For estimations of the effective population size (N_e) I used the software NeEstimator 2.01 (Do *et al.*, 2014). NeEstimator uses three single-sample estimators to estimate N_e: linkage disequilibrium (LD), heterozygote excess and molecular coancestry method respectively. NeEstimator also offers estimators based on a 'temporal method'. Here, samples from different time periods, whereas each time period corresponds to one generation, are used to estimate N_e.

Samples were collected within a relatively long time period (from 2008 to 2014), thus the assumption that samples originated from a single generation is likely violated. Thus I used different approaches to estimate N_e. Firstly, I considered all samples as having originated from one generation and estimated N_e by using all samples. Secondly, I considered samples collected in 2008 and 2011–2014 as samples from different generations and estimated N_e for each generation/study period. Thirdly, I considered samples from 2008 as generation 1 and samples from 2011–2014 as generation 2 and estimated N_e with the help of the temporal method in NeEstimator. For comparison reasons, I also calculated estimates for the effective population size using estimates for the true population size obtained through camera trapping (see chapter 2). For this, I used number of individuals (N = 81) recorded at the beginning of the camera trapping study from July 2013–March 2014. (see chapter 2).

6.3 Results

During study period Nov 2011–Feb 2012 and Jul 2013–Mar 2014 samples (one or more) from 8 and 7 respectively fresh scats were taken. During study period Jan–Jun 2008 samples (one or more) were taken from 11 fresh scats. In total, 32 samples were obtained. Of these samples, 20 samples were of sufficient quality allowing genetic analysis. During study period Jan–Jun 2008 6 animals out of 11 samples could be individually genotyped. During study period Nov 2011–Feb 2012 three animals could be individually genotyped and during study period Jul 2013–Mar 2014 six animals could be individually genotyped. From the samples collected during July 2013-Mar 2014 a sample was retrieved from an individual which was already identified and genotyped in 2008, resulting in a total number of 14 different genotyped animals.

Microsatellite analysis was based on 9 previously identified loci. Eight were previously published in Wilhelm *et al.* (2003), one (Ccroc11) is not published yet. A total of 19 different alleles could be identified (Fig. 2). Fourteen alleles are known from the Serengeti population, 5 new alleles ('private' alleles) were detected in the OKNP population (Table 1). The allelic diversity, expressed by the mean number of different alleles per locus, was 5.78 (±SE 0.57) (Table 1). The population did not show deviation from HWE ($\chi 2$ = 14.59, d.f. = 18, P = 0.69), significant heterozygote excess or deficiency (Table 1). The locus Ccroc08 had the highest number of different alleles (Table 2). The locus Ccroc10 exhibited significant deviation from HWE and deficiency of heterozygous individuals before Bonferroni adjustment, but not after (Table 2). However, the inbreeding coefficient for this locus was very high (0.43) and differed significantly from zero (CI: 0.065–0.725), suggesting that inbreeding in the population is present (Table 2) and affects this locus. Four pairs of loci (Ccroc07/Ccroc10, Ccroc10/Ccroc04, Ccroc05/Ccroc02 and Ccroc07/Ccroc04) showed significant linkage disequilibrium before Bonferroni adjustment, but only one (Ccroc07/Ccroc10) (P < 0.05) after. In comparison with the Serengeti spotted hyena population the OKNP population showed lower numbers of alleles at all loci and lower observed and expected heterozygosities at 8 loci (Table 3).

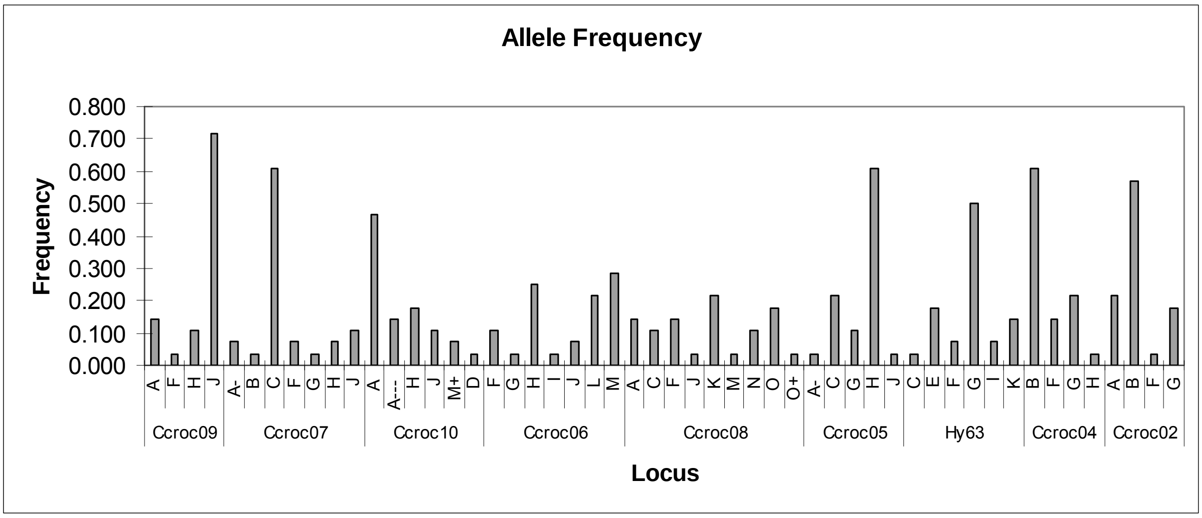


Figure 2. Figure showing frequencies of the 19 detected alleles per locus.

Table 3. Genetic diversity indices for the OKNP spotted hyena population. Private alleles = in comparison with the Serengeti population, A = mean number of different alleles per locus, A_e = mean number of effective alleles per locus, I = mean Shannon's information index, H_o = mean observed heterozygosity, H_E = mean expected heterozygosity, F_{IS} = overall Fixation index/Inbreeding coefficient, HWE = Hardy-Weinberg-Equilibrium, ht. def. = heterozygote deficiency, ht. exc. =heterozygote excess. +SE for exact tests was calculated when Markov chain methods were used.

Sample size	Different alleles observed	Private alleles	A (SE)	A_e (SE)	I (SE)	H_O (SE)	H_E (SE)	F_{IS} (95% CI)	P(HWE)	P(ht. def.)	P(ht. exc.)
14	19	5	5.78 (0.57)	3.310 (0.53)	1.343 (0.122)	0.70 (0.058)	0.67 (0.043)	-0.04 (-0.14–0.10)	0.6896	0.8443 (0.0003)	0.1564 (0.0003)

Table 4. Information on genetic diversity at nine loci in the OKNP's spotted hyena population from 14 individuals. A = number of different alleles, A_e = number of effective alleles, I = Shannon's information index, H_o = observed heterozygosity, H_E = expected heterozygosity, F_{IS} = Fixation index/Inbreeding coefficient, HWE = Hardy-Weinberg-Equilibrium, ht. def. = heterozygote deficiency, ht. exc. =heterozygote excess. Significant values ($P < 0.05$) before Bonferroni adjustment are indicated in bold. +SE for exact tests was calculated when Markov chain methods were used. For comparison, data from the Serengeti population (unpublished data) are presented in the last three columns.

OKNP										Serengeti		
Locus	A	A_e	I	H_O	H_E	F_{IS}	P(HWE)	P(ht. def.)	P(ht. exc.)	A	H_O	H_E
Ccroc02	4	2.465	1.077	0.71	0.62	-0.17	0.6477	0.904	0.2415	11	0.82	0.81
Ccroc04	4	2.292	1.030	0.64	0.58	-0.10	0.6485	0.8177	0.3437	9	0.83	0.82
Ccroc05	5	2.333	1.110	0.71	0.59	-0.21	1	0.9652 (0.0001)	0.1953 (0.0004)	10	0.90	0.84
Ccroc06	7	4.780	1.700	0.86	0.82	-0.05	0.6878 (0.0004)	0.7645 (0.0004)	0.2679 (0.0004)	14	0.88	0.86
Ccroc07	7	2.513	1.346	0.64	0.62	-0.03	0.7956 (0.0007)	0.7534 (0.0007)	0.5880 (0.0007)	16	0.92	0.91
Ccroc08	9	6.877	2.029	1.00	0.89	-0.13	0.7969 (0.0005)	1	0.1805 (0.0005)	21	0.88	0.89
Ccroc09	4	1.840	0.877	0.50	0.47	-0.06	0.4346	0.7527	0.583	10	0.81	0.78
Ccroc10	6	3.500	1.489	0.43	0.74	0.43	**0.0093 (0.0001)**	**0.0080 (0.0001)**	0.9932	13	0.88	0.86
Ccroc11	6	3.187	1.428	0.79	0.71	-0.11	0.9100 (0.0002)	0.8859 (0.0003)	0.3090 (0.0004)	17	0.91	0.89

Tests in BOTTLENECK did not detect heterozygosity excess under the two-phase mutation model ($P > 0.05$). Also, the overall distribution of allele frequency classes ('mode shift' test) showed an approximately L-shaped distribution (Fig. 3), suggesting that the population did not suffer from a recent bottleneck.

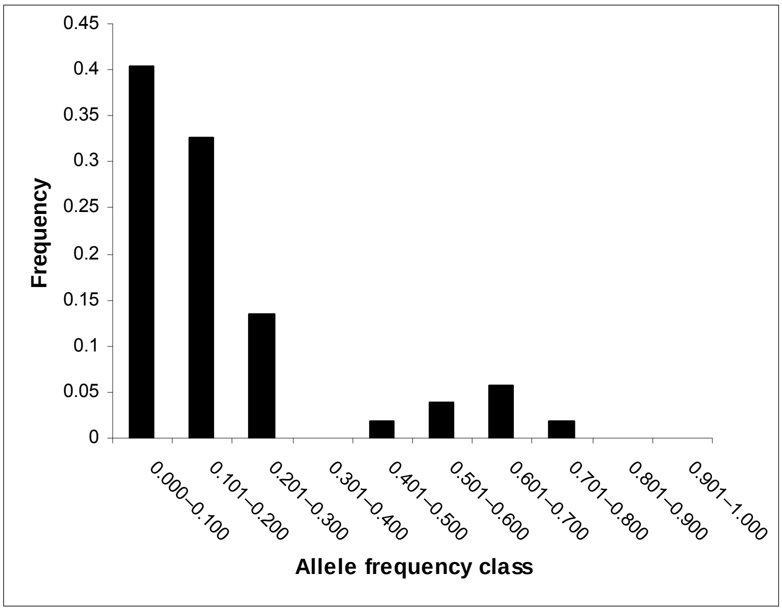


Figure 3. Distribution of the allele frequency classes from 14 genotyped individuals.

Estimates for the effective population size (N_e) ranged between 10.6 and 28.4 animals (Table 3). Consequently, the N_e/N ratio for the entire population (N = 81, incl. animals from bais, see chapter 2) was 0.14–0.35.

Estimates for N_e from genetic analysis can be compared with estimates for N_e calculated with the help of results from the camera traps census in chapter 2. Assuming a ratio of 0.2–0.3 of N_e to N, which is regarded as a rule of thumb for wildlife populations (Frankham, 1995; Kalinowski & Waples, 2002), the N_e has a size of 16.2–24.3 animals. Using the equation $N_e = 4 \cdot N_{ef} \cdot N_{em}/(N_{ef} + N_{em})$ (Mills, 2007) where N_{ef} and N_{em} refers to the numbers of effective breeding females and males respectively the number of breeding males. N_{em} can be calculated by rearranging the above equation, using the ratios of N_e/N of 0.2–0.3 and the number of 11 reproductive females (see chapter 2) identified during study period Jul 2013–Mar 2014 (see chapter 2). Consequently, the estimate for breeding males is 6.8–15.48 animals.

Table 5 Estimates for effective population sizes using different estimators and methods in the program NeEstimator. N_e = effective population size, LDM = linkage disequilibrium method, Het = Heterozygote excess method, MolCo = molecular coancestry method; na = not available, 95% confidence intervals were obtained from parametric or jackknife methods. N_e/N was calculated with estimate of the total population size (N = 81) obtained from camera trapping census (see chapter 2).

Sample period	n	Estimator	N_e	95% CI	N_e/N
Single-sample estimators					
2008–2014	14	LDM	19	(10.9–44.9)	0.23
		Het	17.4	na	0.21
		MolCo	28.4	na	0.35
2008	6	LDM	25.3	na	0.31
		Het	na	na	na
		MolCo	11.3	(3.1–24.8)	0.14
2011–2014	8	LDM	17.6	na	0.22
		Het	na	na	na
		MolCo	16.0	na	0.20
Temporal method					
2008–2014 'Generation 1': 2008 'Generation 2': 2011–2014	14 (6/8)	Pollak	10.6	(5.7–29.6)	0.13
		Nei/Tajima	18.5	na	0.23
		Jorde/Ryman	18.0	11.2–26.4	0.22

6.4 Discussion

Despite the enormous time spent in the field only a small number of fresh samples was found. Spotted hyenas in the park are highly nocturnal (see chapters 3, 4 & 7) and the earliest time the study area could be visited was after sunrise at 6 am. At this time, spotted hyenas activity was already low and thus fresh spotted hyena scats were difficult to find. Other methods, such as hair snares (Frantz *et al.*, 2004; Moriarty *et al.*, 2009) might therefore be more appropriate to obtain a sufficient number of samples from the OKNP's spotted hyena population. Thus, due to the low sample size, results must be interpreted with caution.

In general, the OKNP population showed lower numbers of alleles at each locus and lower heterozygosities (expected and observed) at the majority of loci in comparison to the Serengeti population. This already indicates lower genetic diversity in the OKNP population. Furthermore, the high fixation index at one locus might already indicate deleterious effects of inbreeding. One pair of loci showed significant linkage disequilibrium. In large random mating populations alleles at different loci are expected to be associated randomly, i.e. they are in equilibrium (Frankham *et al.*, 2010). Linkage disequilibrium is common in small populations due to non-random mating (Service *et al.*, 2006). Thus, the results probably just confirm that non-random mating due to low population size already occurs in the OKNP population. No population bottleneck was detected. However, the method used in the program BOTTLENECK is limited to only very recent or long-lasting reductions in effective population size (Cornuet & Luikart, 1996). Thus, bottleneck events from reductions in the population size from distant past might remain undetected.

Due to the very low sample size final conclusion on the genetically effective population size can not be drawn yet. Furthermore, estimates for effective population size of the different methods used differed a lot and in some cases reliable confidence intervals could not be obtained. However, estimates from genetic methods were similar to estimates calculated with the help of the true population size. The effective population size in wildlife populations depends on several factors. Spotted hyenas have a unique mating system in which immigrant males sire more than 90% of the cubs in a population (Engh *et al.*, 2002). Furthermore, the period after which immigrant males sire their first offspring after immigration into a clan is long. Engh *et al.* (2002) recorded a mean period of 20.8 ± 4.0 months between arrival and fathering of first cub for a clan in Kenya and East et al. (2003) recorded a period of 2.0 ± 1.4 years for clans in the Serengeti. Since males usually start to disperse from their natal clan at puberty at an age of 18–24 months (Frank, 1986b; Henschel & Skinner, 1991) their reproductive career starts at a minimum age of 3 years. Inbreeding in spotted hyena populations is rare. Of 236 cubs born in three clans in the Serengeti between 1987 and 2000, only two cubs were the result of inbreeding between daughters and fathers and inbreeding between non-dispersing natal males and their sisters or mothers was not recorded (East *et al.*, 2003). East *et al.* (2003) assume that females recognize fathers and other close relatives as kin and thus rejecting them as mates. However, the Serengeti population is sufficiently large (Hofer & Mills, 1998b) to allow constant exchange of animals between clans and, hence, avoidance of inbreeding.

The OKNP's effective population size of probably less than 30 animals might be too small to maintain genetic diversity in the OKNP's spotted hyena population in the long run and results from genetic analysis suggest that processes which can have negative impacts on the population's genetic diversity, such as inbreeding, have already occurred. Given the slow reproduction rate in spotted hyenas, a further reduction of the effective population size due to poaching (see chapter 2) or stochastic events, such as outbreaks of diseases, might have fatal consequences for the population. Further genetic monitoring of the OKNP's spotted hyena population is therefore recommended to verify or confirm already obtained results and to assess if immediate actions, such as introductions of new animals, have to be made to increase genetic diversity in the population. Given the high isolation of the OKNP's spotted hyena population, animals from candidate populations can be found only very far away. Such translocations can be very expensive, but might be inevitable to save the spotted hyena population in the OKNP. Since genetic data from this study will also be used for a continent-wide study on the genetic relatedness of spotted hyena populations, animals from candidate populations might be already available in the nearest future.

Chapter 7: Community ecology of medium and large-sized mammals in the forest-savanna mosaic of the Odzala-Kokoua National Park

7.1 Introduction

I did two camera trapping studies in the Odzala-Kokoua National Park (OKNP). The first camera trapping study was conducted from November 2011–January 2012. A second long-term camera trapping study was conducted from July 2013–March 2014. This chapter focuses only on the long-term camera trapping study in 2013 and 2014. Information on trap design and results of the short-term camera trapping study in 2011/12 are given in Appendices I and II.

Information provided in this chapter on distribution and occurrence of wildlife species in the OKNP's forest-savanna mosaic as well as on influence of habitat characteristics and human activity on trap success and behaviour of recorded species can give cues on the health status of the ecosystem and, hence, support management strategies for protection of spotted hyenas and other wildlife species in the park.

7.2 Methods

The camera trapping study was carried out from July 2013 to March 2014, spanning the complete large dry season from June to August, the large rainy season from September to November, the small dry season from December to February and one month (March) of the small rainy season. A house situated in the (not yet opened) tourist camp Mboko was used as base camp (Fig. 1). The study area was walked by foot regularly by Torsten Bohm and various field assistants, resulting in ca. 2000 km of walked survey. From time to time, a motorbike, kindly provided by the park management, was used to reach farther distances on the park’s road network. A small canoe was used to cross the Lékoli River. To reach areas which were not accessible by motorbike or during a one-day field trip, longer field trips lasting several days were done. During longer field trips, nights were spent in field camps which were built up near water courses (Fig. 1).

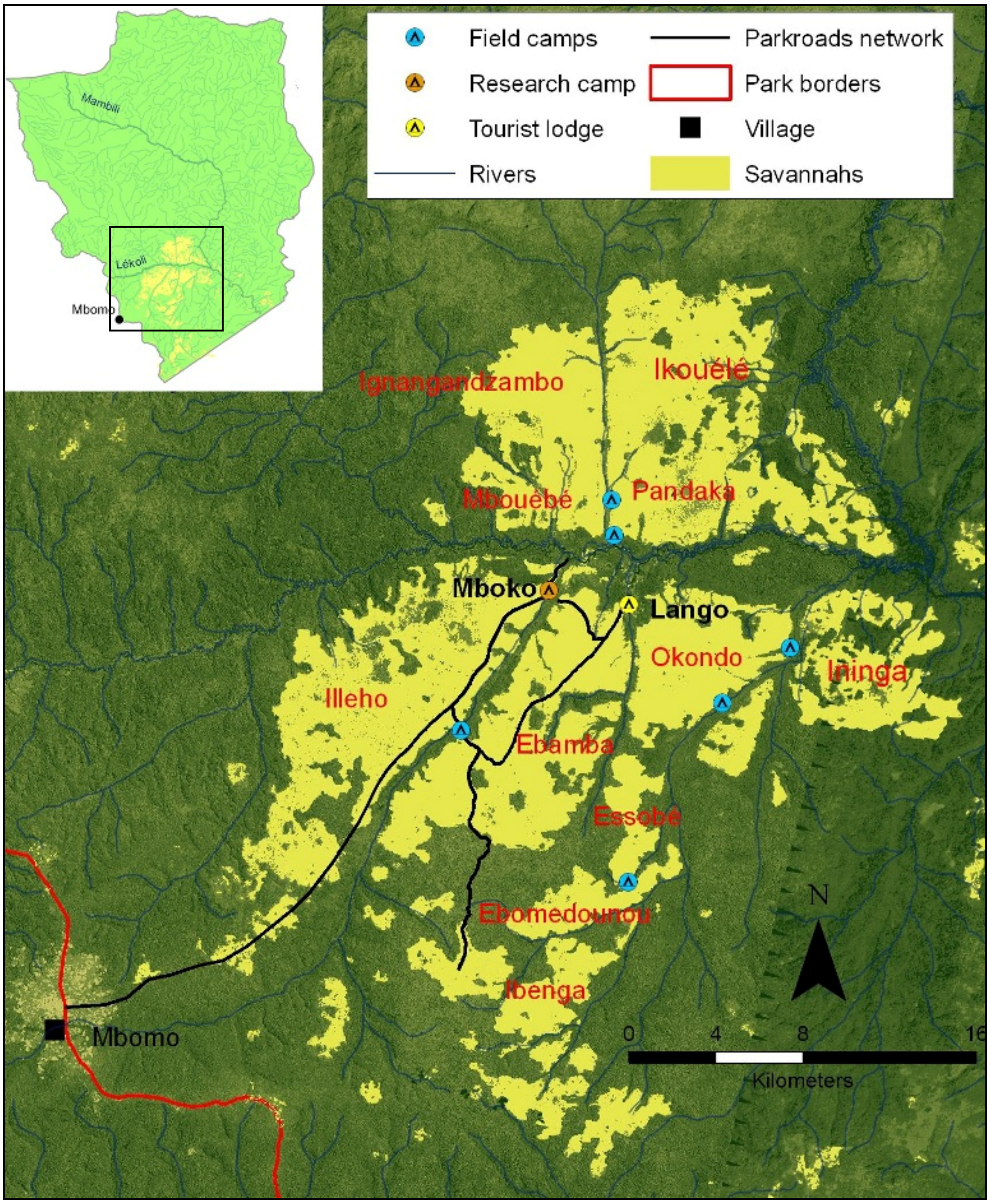


Figure 1. Map of the study area with names (red) of the different savannas in the study area, locations of tourist, research and temporary field camps.

In total, 39 trap stations were installed in the study area (Fig. 2; Table 1). Installation of 38 trap stations started in July 2013. All 38 trap stations were installed until the 20 August 2013 and operational until mid-March 2014. An additional trap station, trap station number 39 (Fig. 2) was installed on the 13 February 2014 and operational until the end of the study. Camera trap stations were deployed in each cell of a 3.5 x 3.5 km grid. Trap stations were deployed at sites where capture probabilities for spotted hyenas and other wildlife species were likely to be high. Such places were roads and wildlife trails showing signs of frequent use by either hyenas, indicated by their tracks, latrines and scats or other wildlife species. For the trap stations 1–22 same locations were used as during the camera trapping study in

2011/12 (see Appendix I). For the remaining savannas, new locations were chosen. At each trap station one Reconyx (HC500 or PC900) was installed. At several other trap stations a second camera trap from a product mixture of Bushnell Trophy Cam, Bushnell HD and Cuddeback Capture was installed. Due to the lack of additional cameras, not all trap stations could be equipped with two cameras. Thus, additional cameras were switched between trap stations during the course of the study. In total, each trap station was at least once operational with two camera traps (for one or more months).

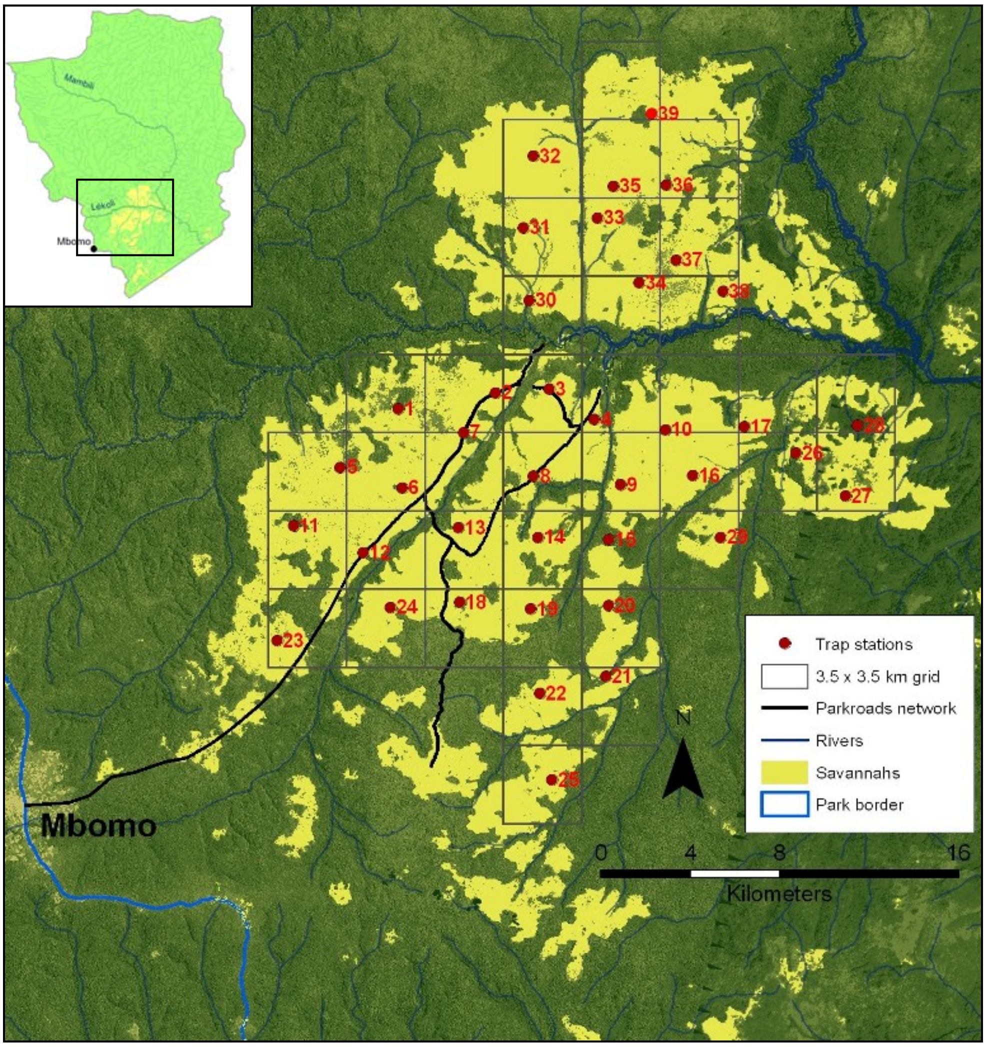


Figure 2. Map showing locations of the 39 camera trap stations. Trap station 39 was only installed for one month at the end of the study time.

Table 1. Characteristics of camera trap stations. A value of 0 indicates that trap station was situated on road or in forest or forest island. Trap station 30 was installed at the saline Mbouébé.

Trap station	Habitat	Location	Savanna	Distance to road (m)	Distance to nearest river or lake (m)	Distance to nearest forest edge or forest island (m)
1	Forest island	Wildlife trail	Illeho	3076.19	3193.15	0
2	Savanna	Road	Illeho	0	989.57	675.77
3	Savanna	Road	Ebamba	0	982.93	201.53
4	Savanna	Wildlife trail	Ebamba	285.05	604.04	313.58
5	Forest island	Wildlife trail	Illeho	3383.39	2066.29	0
6	Forest island	Wildlife trail	Illeho	826.6	1891.68	0
7	Savanna	Road	Illeho	0	1237.62	80.62
8	Savanna	Road	Ebamba	0	507.48	205.53
9	Savanna	Wildlife trail	Okondo	2996.35	741.16	217.06
10	Savanna	Wildlife trail	Okondo	3303.3	1026.27	947.51
11	Savanna	Wildlife trail	Illeho	3194.23	2945.1	117.54
12	Savanna	Road	Illeho	0	786.3	182.51
13	Savanna	Wildlife trail	Ebamba	605.99	1027.77	258.14
14	Savanna	Wildlife trail	Ebamba	2202.2	757.44	346.8
15	Forest	Wildlife trail	Okondo/Essobé	4360.29	732.91	0
16	Savanna	Wildlife trail	Okondo	5336.87	924.9	665.34
17	Savanna	Wildlife trail	Okondo	6623.73	650.06	370.5
18	Forest island	Wildlife trail	Ebamba	609.41	3716.22	0
19	Savanna	Wildlife trail	Ebamba	3281.36	1316.28	525.57
20	Savanna	Wildlife trail	Essobé	6276.75	1471.64	142.54
21	Forest	Small river	Essobé/Ebomedounou	6610.92	40.31	0
22	Savanna	Wildlife trail	Ebomedounou	4160.7	672.69	57.01
23	Savanna	Wildlife trail	Illeho	561.51	2549.64	205.55
24	Savanna	Wildlife trail	Ebamba	2277.9	1509.53	85.52
25	Savanna	Wildlife trail	Ibenga	5268.54	1197.46	524.08
26	Forest	Wildlife trail	Ininga	9177.02	541.64	0
27	Savanna	Wildlife trail	Ininga	11881.04	1755.56	318.66
28	Forest	Wildlife trail	Ininga	11598.8	63.74	0
29	Savanna	Wildlife trail	Okondo south	7976.3	1287.82	325.03
30	Forest	Wildlife trail	Mbouébé	2064.09	114.03	0
31	Savanna	Wildlife trail	Mbouébé	5289.84	1456.85	285.05
32	Savanna	Wildlife trail	Ignangandzambo	8418.37	714.25	677.46
33	Savanna	Wildlife trail	Pandaka	6130.06	599.33	405.1
34	Savanna	Wildlife trail	Pandaka	5067.23	477.86	847.49
35	Savanna	Wildlife trail	Ikouélé	7720.88	1407.29	1178.41
36	Savanna	Wildlife trail	Ikouélé	8984.65	1149.1	166.19
37	Savanna	Wildlife trail	Pandaka	6692.36	1186.3	894.92
38	Savanna	Wildlife trail	Pandaka	7015.81	746.11	459.67
39	Forest island	Wildlife trail	Ikouélé	11360.63	2136.38	0

Camera traps were housed in a security enclosure made of steel. Security enclosures and camera traps were attached with screws on trees using a portable driller approx. 3-5 m away from road or trail edges and at a height of 30–50 cm. In most cases, enclosures were additionally secured with a chain/cable lock and a padlock (Fig. 3). The vegetation in front of the cameras was cleared to avoid false camera triggers due to moving grass.

Figure 3. Picture showing camera trap in a security enclosure attached to a tree. For additional security a cable lock was wrapped around the tree and fixed to the security box. Here, additionally, a piece of wood with large nails pointing upwards was attached to the tree above the security enclosure to provide additional security.

Figures 4–6 show habitat features of the study area, such as distances of savanna and forest areas to nearest rivers and lakes as well as roads (Fig. 3–4) and distances of savanna areas to forest edges and forest islands (Fig. 5). To produce these maps I used R (R Core Team, 2015) and ArcGIS. The farthest distance of a single location inside the savannas from the nearest river or lake was ca. 4000 m (Fig. 3). Permanent lakes, so called *Mares*, (Fig 7) are situated in two savanna areas. A permanent *Mare* provides a year-round source of water in the savannas and is regularly visited by animals (Fig. 8).

Park roads, connecting the two tourist camps Lango and Mboko with each other and with the nearest village Mbomo are situated in the southern savannas sector. Five trap stations were installed on park roads.

The savannas of the study area were completely surrounded by primary rainforest and gallery forests bordering watercourses. Due to the recolonization of the savannas by the forest numerous larger and smaller forest islands, so called b*osquets*, can be found in the savannas of the OKNP (Dowsett-Lemaire, 1996) (Fig. 9). Larger forests islands cover areas of more than 3 km^2. Consequently, savanna areas were not far away from forest edges or forest islands. The farthest distance of a single location inside the savannas from the nearest forest edge or forest island was ca. 1600 m (Fig. 6).

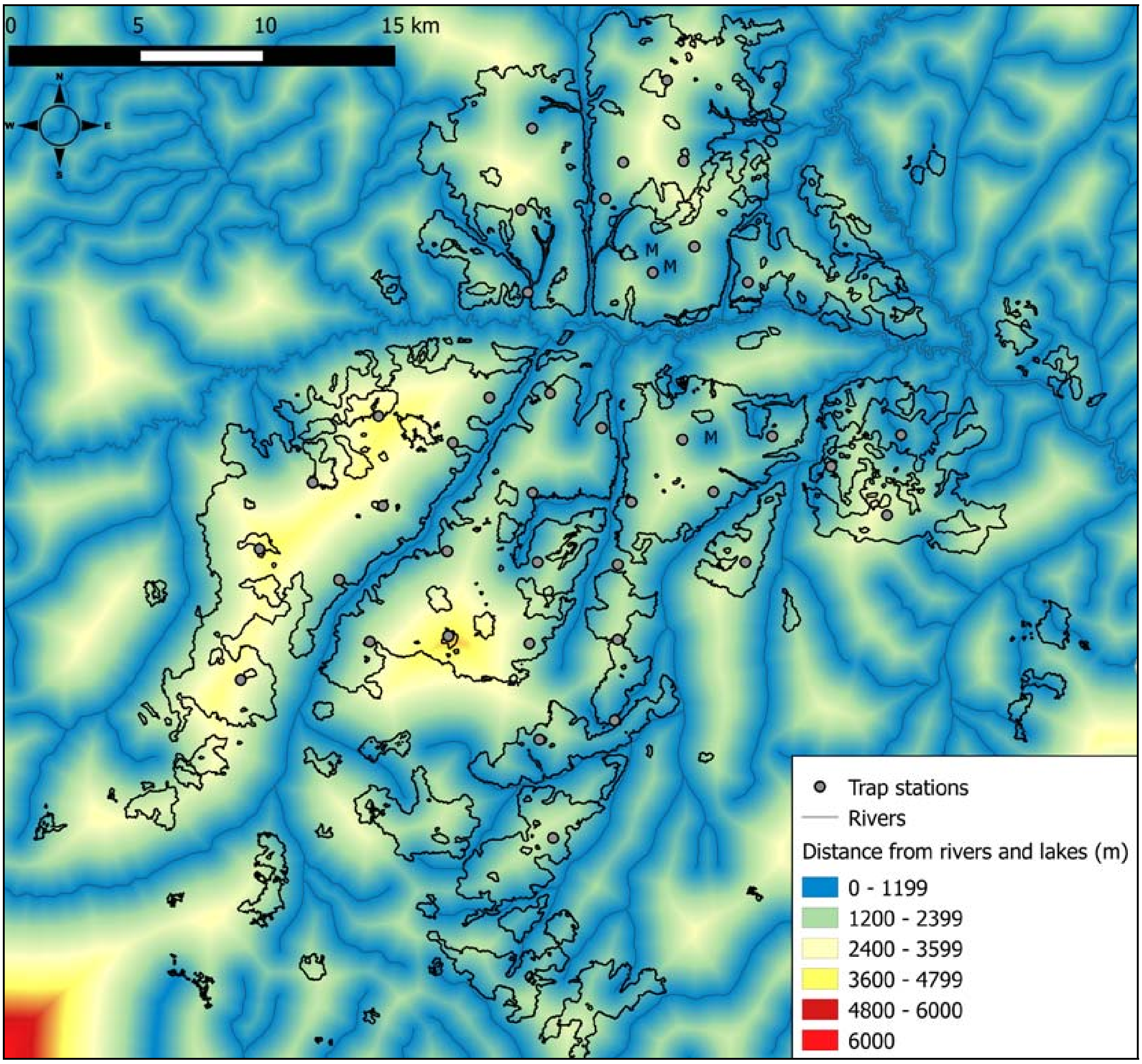


Figure 4. Map showing distances of savanna and forest areas to nearest rivers and lakes. Polygons inside savannas indicate forest islands. M indicates locations of permanent lakes ("*Mare*").

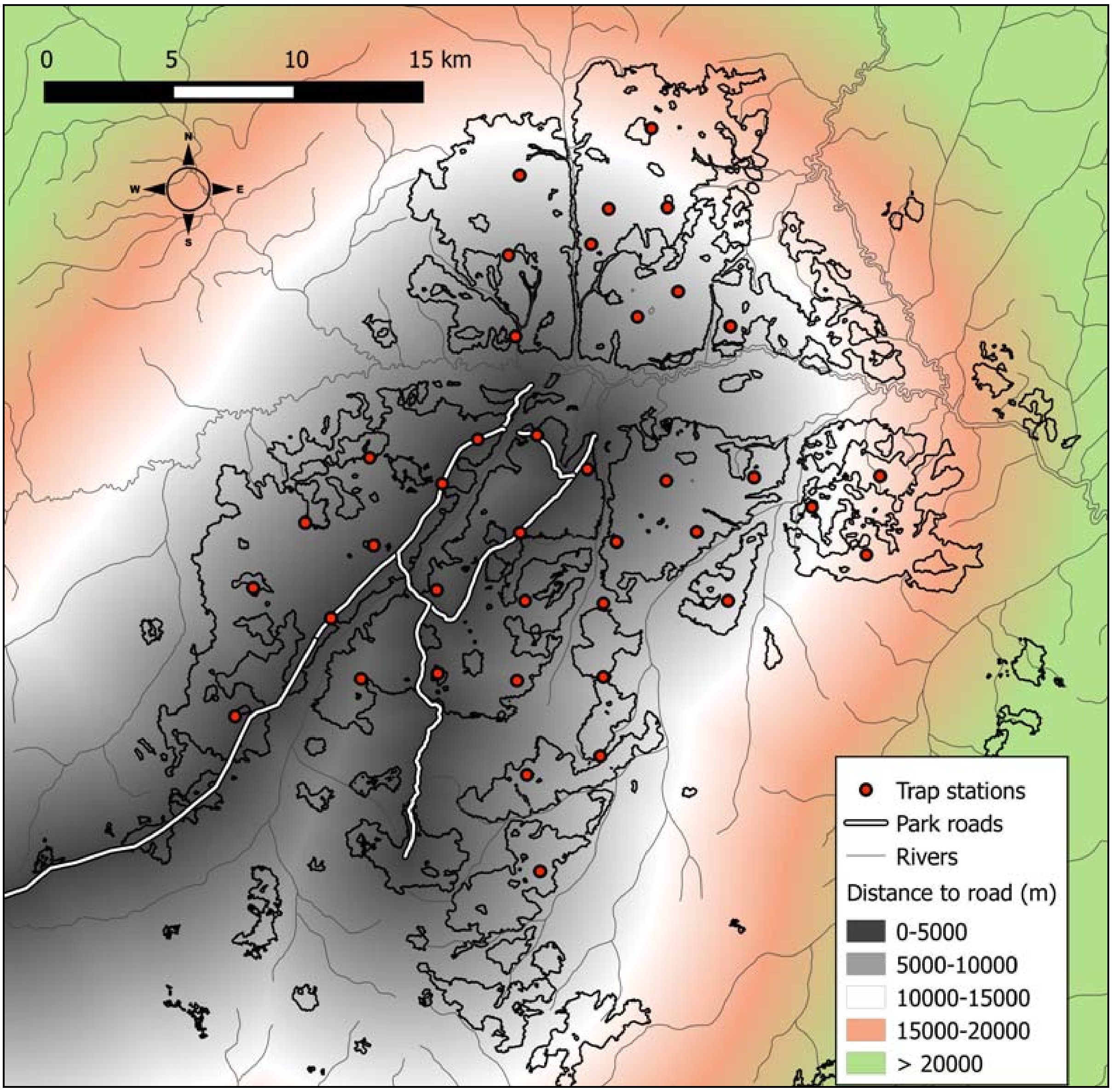


Figure 5. Map showing distances of savanna and forest areas to nearest road. Polygons inside savannas indicate forest islands.

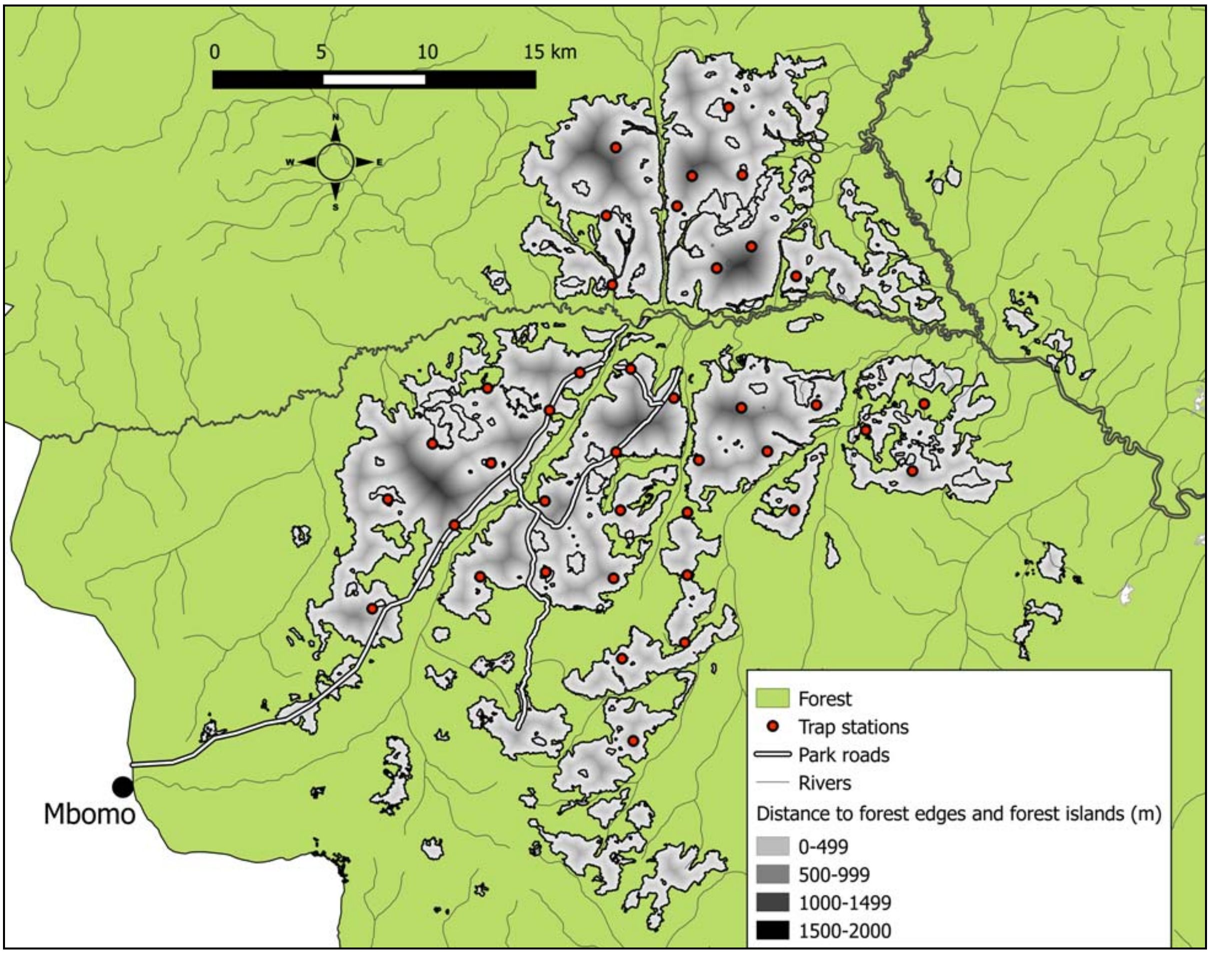


Figure 6. Map showing distances of savanna areas to nearest forest edge or forest island. Polygons inside savannas indicate forest islands.

Figure 7. Lake ("*Mare*") in the savanna Okondo. Photo: Torsten Bohm

Figure 8. Herd of forest buffaloes at a lake ("Mare") in the savanna Pandaka. Photo: Torsten Bohm

Figure 9. Large forest island in the savanna in the OKNP. Photo: Torsten Bohm

Statistical analysis

Total number of trap nights was calculated as $\Sigma_{i=1} tn_i$ where i is a trap location and tn is a trap night when a camera was operational at the ith location. A period of 24 hours between 6 pm and 6 am was considered as one sampling occasions or as trap night for single trap stations respectively. The capture rate for each species was calculated as $n_i/tn_{total} \cdot 100$, where n_i is the number of independent records for this species and tn_{total} is the total number of trap nights. Consecutive photographs of different individuals of the same or different species, consecutive photographs of individuals of the same species taken more than 1 h apart and non-consecutive photos of individuals of the same species were considered as independent record. To estimate the amount of trapping effort needed to record all species in the study area I recorded the sampling occasion for each species when it was first recorded. For this, only terrestrial species were included in the analysis. In addition, I analyzed capture rates (as above) and number of species recorded for single trap stations, trap stations located in savannas and trap stations located in forests and forest islands. I used Student's t-test to analyze differences in capture rates among trap stations located in savannas and trap stations located in forests and forests islands. I used linear regression to determine if capture rate and number of species recorded per trap station is influenced by distance to forested areas.

Generalized linear model (GLM) analysis was used to construct a model describing the relationship between capture rate and habitat variables for photographed wildlife species. For this, only species with a sufficient high capture rate or species which were recorded at a sufficient number of different trap stations, were included. A quasi-Poisson distribution was assumed (using a logarithmic link function) as appropriate as it also accounts for many zeros as well as many high values (Zuur, Ieno & Smith, 2007). The following variables were included: distance of trap station to nearest river or lake, distance to forest edge or forest island and distance to road. Capture rates for each species at trap stations was used as the response variable to habitat variables. GLM was implemented in R (R Core Team, 2015).

Levels of human activity between southern and northern savannas sector are different. Currently, tourist and park staff activities are almost exclusively restricted to the southern savannas sector, thus an impact on the trap success of certain species can be assumed. To compare trap success between northern and southern savannas sectors I compared capture rates for species in each of the savannas sectors using Fisher's exact test. This test was used as some of the expected values were below 5. I included only species with a sufficient high capture rate or species which were recorded at a sufficient number of different trap stations. Due to the high number of resulting tests (n = 25), P-values were adjusted using sequential Bonferroni adjustment (Rice, 1989).

To investigate activity patterns of the recorded species I assigned independent capture events for each species to the categories dawn (05:30–06:30), day (05:31–17:29), dusk (17:30–18:30) and night (18:31–05:29). Activity levels were measured by the percentage for each category. Sunrise and sunset are around 6 am and 6 pm respectively.

In addition I compared activity patterns between 'southern' and 'northern' spotted hyenas. Results from chapter 2 suggest that spotted hyenas rarely traverse the Lékoli River. Thus I assumed, that spotted hyenas adapt their temporal activity patterns with regard to the degree of human activity in the respective savannas sectors. For analysis, I used temporal data of adult animals from the clan 'North' ('northern' spotted hyenas) and the clans 'South', 'Southwest', 'Northeast' and 'Center' ('southern' spotted hyenas) respectively. I used χ^2-test to test differences in the activity periods for both groups of hyenas.

7.3 Results

Reconyx camera traps performed well, no technical failures occurred. Several Bushnell camera traps often had technical failures and had to be removed or replaced by other camera traps. Reasons why some trap stations were not operational during the whole period were attacks by elephants or hyenas and colonization by ants/termites. Several camera traps were destroyed, detached from trees or in some cases whole trees with camera traps attached were pulled out from the ground by elephants. Elephants had no problems to detach cameras from trees, although traps were attached to trees with screws. When detached, cameras were thrown to the ground by elephants. In some cases, elephants continued to trample on camera traps, resulting in the total destruction of camera traps. In other cases, camera traps were just left on the ground; if camera traps were still operational, cameras were reattached to the same or a different tree in the nearest surroundings. However, camera traps which were additionally secured by a chain or cable lock remained at the tree. After camera traps have stopped to work elephants probably lost interest in the camera traps. In one case, a hyena destroyed one Reconyx camera trap. Here, the security enclosure was not secured with a padlock. The hyena could manage to open the security box and lift the camera out of the enclosure. This instance shows how important it is to additionally secure security boxes with a padlock.

Overall, trap stations were operational for long times, only trap stations 5, 11, 16, 21, 26, 29 and 38 were operational for about 60% or less of the time (Table 2). This was due to repeated attacks by elephants on these trap stations, or due to the fact that trap stations could only be visited after an extended period (2 or 3 months). An attack of elephants immediately after installation/visit of trap stations resulted in a longer period of non-function.

Table 2. Operating times of camera trap stations.

Trap station	Habitat	Location	First trap night	Last trap night	Total number of trap nights	# trap nights operational	Trap nights operational (%)
1	Forest island	Wildlife trail	18/07/2013	06/03/2014	233	233	100.00
2	Savanna	Road	18/07/2013	20/03/2014	247	211	85.43
3	Savanna	Wildlife trail	22/07/2013	07/03/2014	229	227	99.13
4	Savanna	Wildlife trail	19/07/2013	07/03/2014	232	155	66.81
5	Forest island	Wildlife trail	21/07/2013	06/03/2014	229	113	49.34
6	Forest island	Wildlife trail	21/07/2013	06/03/2014	229	229	100.00
7	Savanna	Road	18/07/2013	06/03/2014	233	166	71.24
8	Savanna	Road	22/07/2013	07/03/2014	229	225	98.25
9	Savanna	Wildlife trail	24/07/2013	11/03/2014	231	231	100.00
10	Savanna	Wildlife trail	24/07/2013	13/03/2014	233	233	100.00
11	Savanna	Wildlife trail	20/07/2013	09/03/2014	233	139	59.66
12	Savanna	Road	20/07/2013	09/03/2014	233	233	100.00
13	Savanna	Wildlife trail	31/07/2013	08/03/2014	221	157	71.04
14	Savanna	Wildlife trail	22/07/2013	07/03/2014	229	209	91.27
15	Forest	Wildlife trail	25/07/2013	11/03/2014	230	168	73.04
16	Savanna	Wildlife trail	24/07/2013	12/03/2014	232	147	63.36
17	Savanna	Wildlife trail	09/08/2013	13/03/2014	217	217	100.00
18	Forest island	Wildlife trail	31/07/2013	08/03/2014	221	221	100.00
19	Savanna	Wildlife trail	03/08/2013	08/03/2014	218	216	99.08
20	Savanna	Wildlife trail	03/08/2013	12/03/2014	222	158	71.17
21	Forest	Small river	04/08/2013	12/03/2014	221	137	61.99
22	Savanna	Wildlife trail	04/08/2013	11/03/2014	220	173	78.64
23	Savanna	Wildlife trail	01/08/2013	09/03/2014	221	206	93.21
24	Savanna	Wildlife trail	02/08/2013	08/03/2014	219	219	100.00
25	Savanna	Wildlife trail	04/08/2013	12/03/2014	221	169	76.47
26	Forest	Wildlife trail	10/08/2013	13/03/2014	216	84	38.89
27	Savanna	Wildlife trail	10/08/2013	13/03/2014	216	196	90.74
28	Forest	Wildlife trail	10/08/2013	13/03/2014	216	189	87.50
29	Savanna	Wildlife trail	11/08/2013	13/03/2014	215	136	63.26
30	Forest	Wildlife trail	18/08/2013	16/03/2014	211	211	100.00
31	Savanna	Wildlife trail	18/08/2013	16/03/2014	211	173	81.99
32	Savanna	Wildlife trail	18/08/2013	16/03/2014	211	211	100.00
33	Savanna	Wildlife trail	18/08/2013	17/03/2014	212	164	77.36
34	Savanna	Wildlife trail	19/08/2013	17/03/2014	211	150	71.09
35	Savanna	Wildlife trail	19/08/2013	17/03/2014	211	211	100.00
36	Savanna	Wildlife trail	19/08/2013	17/03/2014	211	211	100.00
37	Savanna	Wildlife trail	19/08/2013	17/03/2014	211	200	94.79
38	Savanna	Wildlife trail	20/08/2013	17/03/2014	210	120	57.14
39	Forest island	Wildlife trail	13/02/2014	17/03/2014	33	33	100.00
Total	-	-	-	-	8475	7081	83.55

The results of the camera trapping study are presented in Table 3. Capture success during the camera trapping study was very high, with, in total, 37 photographed terrestrial and arboreal wildlife species. All terrestrial species were photographed after 78 sampling occasions (= 2025 total trap nights) (Fig. 10). With 4005 independent records, forest elephant (*Loxodonta cyclotis*) was the most photographed wildlife species, followed by spotted hyena (2938 records), bushbuck (*Tragelaphus scriptus*) (1226 records), forest buffalo (*Syncerus caffer nanus*) (1161 records), blue duiker (*Philantomba monticola*) (1005 records) and red river hog (*Potamocheorus porcus*) (904 records). These six species alone made up 81.5 % of all the capture events. Forest elephants, spotted hyenas and forest buffaloes were photographed at all trap stations. Serval (*Leptailurus serval*) and African civet (*Civettictis civetta*) were the second-/ and third-most photographed carnivore species. In total, 13 carnivore species were photographed, including leopard (*Panthera pardus*), African golden cat (*Caracal aurata*), large grey mongoose (*Herpestes ichneumon*) and honey badger (*Mellivora capensis)*. Leopards were photographed at 13 of the 39 trap stations. Eight of the 13 trap stations where leopards were photographed were located in forests or forest islands. In total, 11 individuals could be identified with the help of camera trapping pictures. Among them were 5 adult males, 3 adult females and three cubs (Fig. 11). Results on population sizes and densities of spotted hyenas and servals are given in the chapters 2 and 4.

Six primate species, including chimpanzees (*Pan troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla*) were photographed. Among the larger terrestrial species which were not frequently captured were bongo (*Tragelaphus euryceros*) and hippopotamus (*Hippopotamus amphibious)*. Hippopotamuses are not common in the OKNP (Maisels, 1996) and spend most of their time in or near water courses, foraging only at night in open areas away from watercourses (Kingdon, 2004), which might explain the “low” capture rate for this species. Surprisingly, one hippopotamus was photographed in the savanna at trap station 38 (Fig. 12) about 500 m away from the nearest watercourses. Scars on left and right flank respectively allowed individual identification of hippopotamuses (Fig. 13): In total 5 individuals could be identified (4 at trap station 30 at the saline Mbouébé and one at trap station 38). The only larger mammal species which were not photographed were sitatunga (*Tragelaphus spekeii*) and giant pangolin (*Smutsia gigantea*).

Trap station number 26, situated in the forest, had the highest trap success (Fig. 14). Other trap stations, which were installed in forests or larger forest islands, such as trap stations 15, 28, 30 and 39, also had very high trap successes (Fig. 14). The highest number of different species, 23, was recorded at trap station 22 (Fig. 15). Mean capture rate differed significantly between trap stations located in forests and forest islands and trap stations located in savannas (Fig. 16) ($\text{t-test}_{\text{two-tailed/unequal variances}}$: $t = 2.24$, $P < 0.047$). Mean number of different species recorded differed also significantly between trap stations located in forests and forest islands and trap stations located in savannas ($\text{t-test}_{\text{Two-tailed}}$: $t = 4.21$, $P < 0.001$). There was a significant negative relationship between distance of trap stations to forest and forest islands and number of species recorded (Fig. 17) ($n = 39$; $p = 0.002$; $y = -0.007x + 15.87$; $R^2 = 0.226$), but there was no relationship between capture rate and distance to forest and forest islands ($P = 0.24$).

Table 3. Results of camera trapping study in the FSM of the Odzala-Kokoua National Park

Order	Family	Common name	Scientific name	# Captures	Capture rate*	# Trap stations**	Habitat
Artiodactyla	Bovidae	Bay duiker	*Cephalophus dorsalis*	30	0.42	7	F, S
Artiodactyla	Bovidae	Black-fronted duiker	*Cephalophus nigrifons*	25	0.35	8	F, S
Artiodactyla	Bovidae	Peter's duiker	*Cephalophus callipygus*	282	3.98	20	F, S
Artiodactyla	Bovidae	White-bellied duiker	*Cephalophus leucogaster*	19	0.27	1	F
Artiodactyla	Bovidae	Yellow-backed duiker	*Cephalophus silvicultor*	81	1.14	22	F, S
Artiodactyla	Bovidae	Blue duiker	*Philantomba monticola*	1005	14.19	18	F, S
Artiodactyla	Bovidae	Forest buffalo	*Syncerus caffer nanus*	1161	16.40	39	F, S
Artiodactyla	Bovidae	Bongo	*Tragelaphus euryceros*	25	0.35	7	F, S
Artiodactyla	Bovidae	Bushbuck	*Tragelaphus scriptus*	1226	17.31	34	F, S
Artiodactyla	Hippopotamidae	Hippopotamus	*Hippopotamus amphibius*	20	0.28	2	F, S
Artiodactyla	Suidae	Giant forest hog	*Hylochoerus meinertzhageni*	34	0.48	3	F
Artiodactyla	Suidae	Red river hog	*Potamochoerus porcus*	904	12.77	33	F, S
Artiodactyla	Tragulidae	Water chevrotain	*Hyemoschus aquaticus*	2	0.03	1	F
Carnivora	Felidae	African golden cat	*Caracal aurata*	13	0.18	6	F, S
Carnivora	Felidae	Serval	*Leptailurus serval*	285	4.02	29	F, S
Carnivora	Felidae	Leopard	*Panthera pardus*	23	0.32	13	F, S
Carnivora	Herpestidae	Marsh mongoose	*Atilax paludinosus*	200	2.82	26	F, S
Carnivora	Herpestidae	Black-footed mongoose	*Bdeogale nigripess*	7	0.10	6	F, S
Carnivora	Herpestidae	Large grey mongoose	*Herpestes ichneumon*	84	1.19	13	S
Carnivora	Herpestidae	Long-nosed mongoose	*Xenogale naso*	98	1.38	25	F, S
Carnivora	Hyaenidae	Spotted hyena	*Crocuta crocuta*	2938	41.49	39	F, S
Carnivora	Mustelidae	Honey badger	*Mellivora capensis*	1	0.01	1	F
Carnivora	Nandiniidae	African palm civet	*Nandinia binotata*	3	0.04	3	S
Carnivora	Viverridae	African civet	*Civettictis civetta*	247	3.49	27	F, S
Carnivora	Viverridae	Large-spotted genet	*Genetta maculata*	30	0.42	11	F, S
Carnivora	Viverridae	Servaline genet	*Genetta servalina*	23	0.32	6	F, S
Primates	Cercopithecidae	Agile mangabey	*Cercocebus agilis*	258	3.64	4	F, S
Primates	Cercopithecidae	Moustached monkey	*Cercopithecus cephus*	2	0.03	1	F
Primates	Cercopithecidae	White-nosed guenon	*Cercopithecus nictitans*	13	0.18	7	F, S
Primates	Cercopithecidae	Grey-cheeked mangabey	*Lophocebus albigena*	4	0.06	3	F, S
Primates	Hominidae	Western lowland gorilla	*Gorilla gorilla gorilla*	22	0.31	8	F, S
Primates	Hominidae	Chimpanzee	*Pan troglodytes*	387	5.47	17	F, S
Proboscidea	Elephantidae	Forest elephant	*Loxodonta cyclotis*	4005	56.56	39	F, S
Rodentia	Hystricidae	African brush-tailed porcupine	*Atherurus africanus*	40	0.56	11	F, S
Rodentia	Nesomyidae	African giant pouched rat	*Cricetomys gambianus*	187	2.64	17	F, S
Rodentia	Thryonomyidae	Greater cane rat	*Thryonomys swinderianus*	26	0.37	7	F, S
Tubulidentata	Orycteropodidae	Aardvark	*Orycteropus afer*	73	1.03	27	F, S
Total	-	N = 37 wildlife species	-	13783	194.65	-	-

Trap nights = 7081; * # captures/trap nights * 100; ** total number of trap stations = 39; F = Forest (islands). S = Savanna

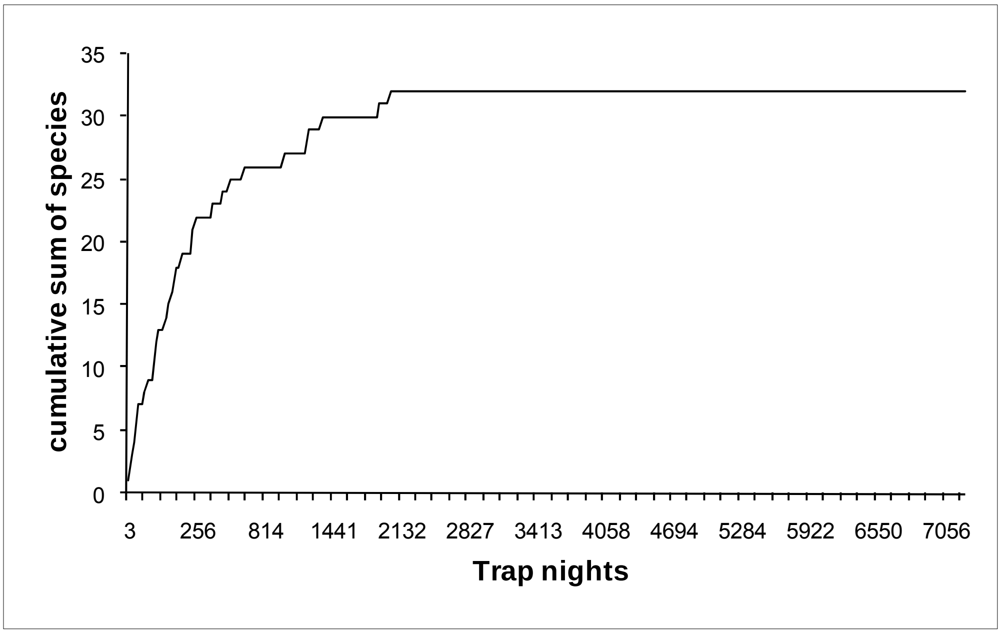


Figure 10. Cumulative number of species recorded versus trapping effort. Trapping effort (= trap nights) is expressed by the cumulative number of operational trap stations each trap night. The arboreal species African palm civet (*Nandinia binotata*), agile mangabey (*Cercocebus agilis*), grey-cheeked mangabey (*Lophocebus albigena*), moustached monkey (*Cercopithecus cephus*) and white-nosed guenon (*Cercopithecus nictitans*) were excluded. In total 32 species.

Figure 11. Camera trap picture showing two leopard cubs.

Figure 12. Camera trap picture showing hippopotamus photographed in the savanna about 500 m away from the nearest watercourse.

Figure 13. Camera trap pictures showing different "scar patterns" on left flank of different hippopotamuses which allowed individual identification.

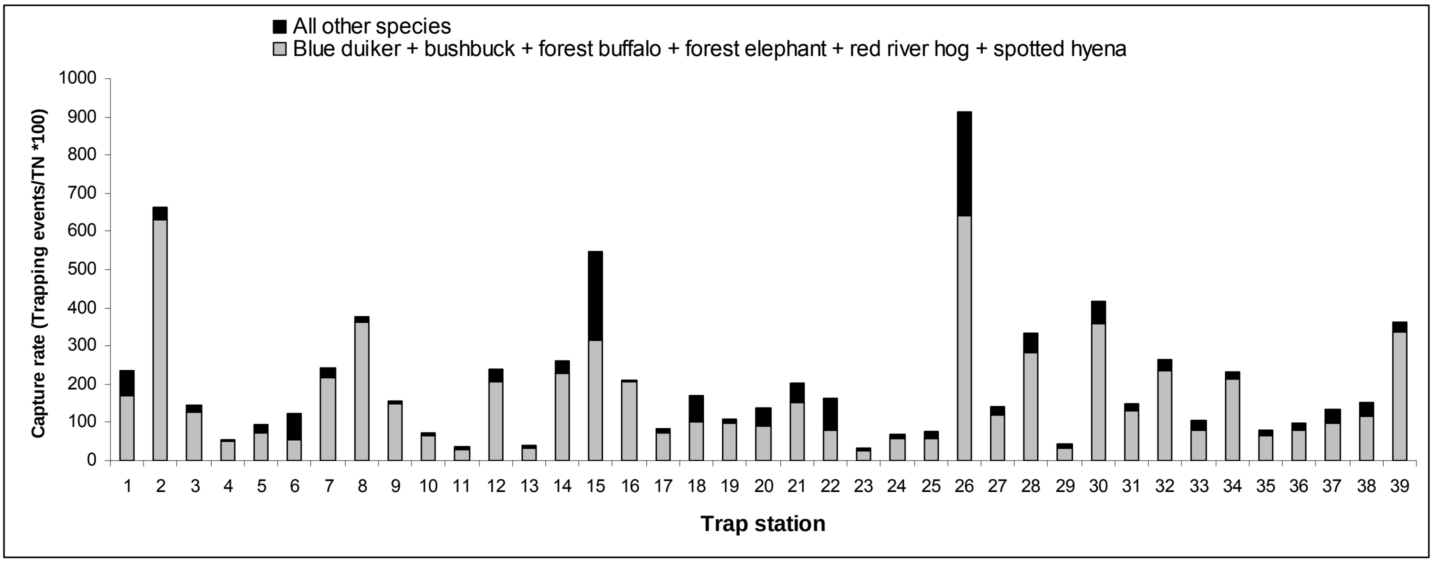


Figure 14. Trap success (capture events per 100 trap nights) for trap stations across the study site. Trap stations 1, 5, 6, 15, 18, 21, 26, 28, 30 and 39 were installed in forests and forest islands.

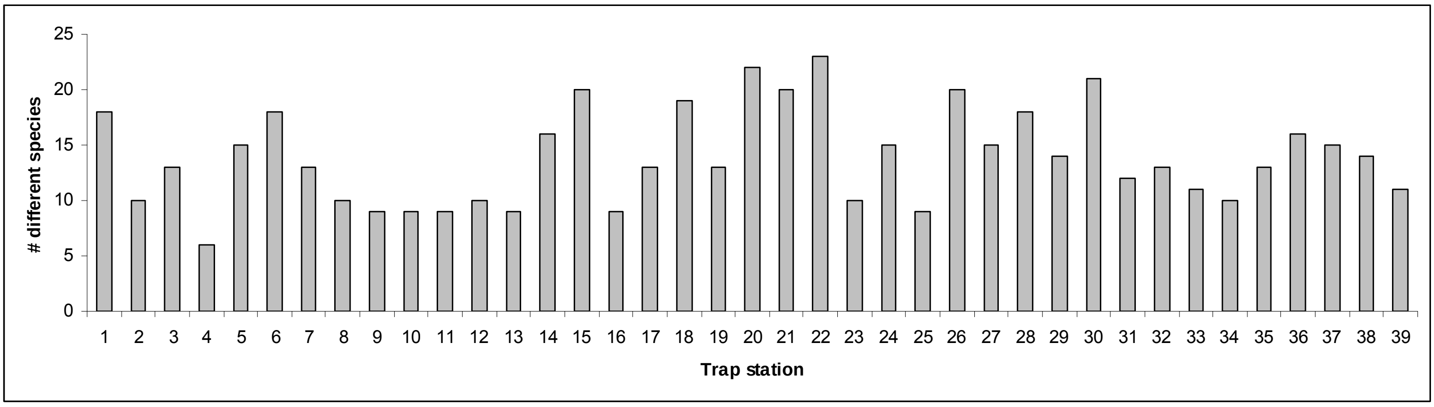


Figure 15. Number of different species recorded per trap station.

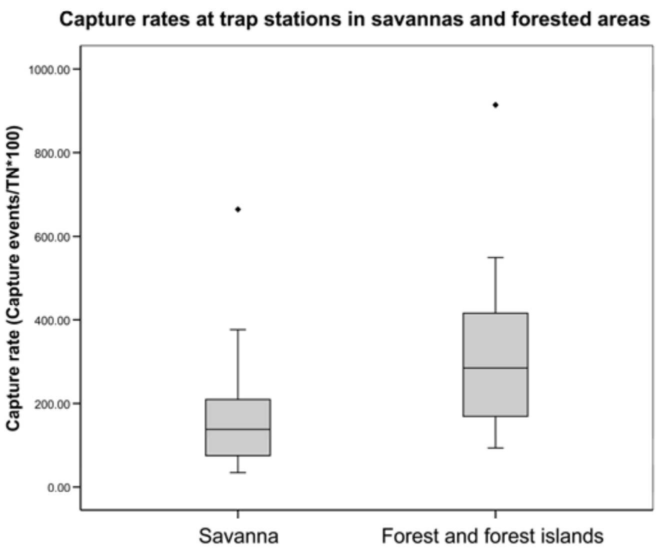


Figure 16. Comparison between capture rates of trap stations located in savannas and forested areas.

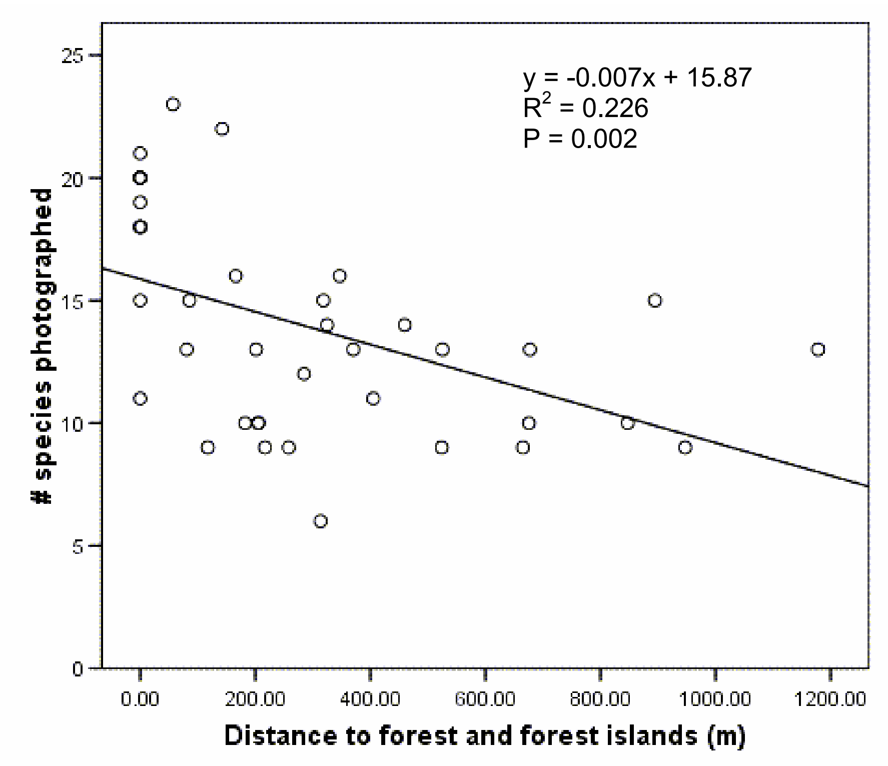


Figure 17. Number of species recorded per trap station in relation to distance to forest edge and forest islands. Circles represent trap stations.

Capture rates for, for example, forest elephant, yellow-backed duiker (*Cephalophus silvicultor*) and red river hog were positively and significantly related to distance to the nearest road (Table 4). Although regularly photographed in the savannas, these species probably avoid savanna areas near roads. Capture rates for, for example, leopard, blue duiker and Peter's duiker (*Cephalophus callipygus*) were negatively affected by distance to forest edge and forest islands, hence, showing a preference of these species for forested areas (Table 4). Capture rates for large grey mongoose, spotted hyena and marsh mongoose (*Atilax paludinosus*) was positively and significantly related to distance to forest edge and forest islands, hence showing a preference of these species for open areas (Table 4). Long-nosed mongoose (*Xenogale naso*) was the only species for which the capture rate was positively and significantly related to distance to nearest watercourse or lake.

Table 4. Results from generalized linear models for different variables. Significant results ($p < 0.05$) are given in bold. For spotted hyenas, trap station 34 which was situated very close to a communal den site was excluded.

Species	Variables					
	Distance to road		Distance to forest edge and forest islands		Distance to rivers and lakes	
	z	*P*	*z*	*P*	*z*	*P*
Aardvark	1.884	0.0679	-1.616	0.1151	-1.396	0.1716
African brush-tailed porcupine	0.994	0.3272	**-2.366**	**0.0237**	0.094	0.9256
African civet	1.746	0.0895	-1.916	0.0636	-1.354	0.1844
African giant pouched rat	-0.739	0.4649	**-2.896**	**0.0065**	1.094	0.2813
Bay duiker	0.355	0.725	**-2.4**	**0.0219**	-1.823	0.0768
Black-fronted duiker	-0.117	0.907	0.276	0.784	0.235	0.815
Blue duiker	**2.82**	**0.0079**	**-3.685**	**0.0008**	-0.26	0.7960
Bongo	1.461	0.153	-0.794	0.433	-0.787	0.437
Bushbuck	-1.666	0.1047	1.215	0.2325	-0.309	0.7588
Chimpanzee	-0.055	0.956	-0.123	0.902	-0.04	0.969
Forest buffalo	**-2.46**	**0.0190**	1.113	0.2732	-1.815	0.0782
Forest elephant	**3.237**	**0.0026**	-1.570	0.1253	-1.772	0.0850
Giant forest hog	0.728	0.4717	**-3.17**	**0.0032**	**-4.086**	**0.0002**
Greater cane rat	0.25	0.8040	-1.243	0.2220	-0.937	0.3550
Large grey mongoose	-0.31	0.7585	**3.021**	**0.0047**	-1.368	0.1801
Large-spotted genet	0.604	0.5500	0.309	0.7590	-0.384	0.7030
Long-nosed mongoose	1.086	0.2850	0.769	0.4473	**2.813**	**0.0080**
Leopard	**4.53**	**0.0001**	**-5.603**	**< 0.0001**	**-3.048**	**0.0044**
Marsh mongoose	-1.046	0.3027	**3.368**	**0.0019**	-1.550	0.1300
Peter's duiker	0.844	0.4042	**-3.74**	**0.0007**	-1.303	0.2009
Red river hog	**3.211**	**0.0028**	**-2.734**	**0.0098**	-1.512	0.1395
Spotted hyena	**-5.346**	**< 0.0001**	**2.247**	**0.0312**	**-3.428**	**0.0016**
Serval	-2.018	0.0513	0.738	0.4654	-1.412	0.1667
Western lowland gorilla	**6.099**	**< 0.0001**	**-4.155**	**0.0002**	0.875	0.3875
Yellow-backed duiker	**4.967**	**< 0.0001**	-1.180	0.2460	1.126	0.2679

Trap success for forest elephant was significantly higher in the northern savannas sector (Table 5). On the other hand, trap success for bushbuck and blue duiker was significantly higher in the southern savannas sector (Table 5). Trap success for spotted hyenas was almost equal in the two savanna sectors (Table 5).

Table 5. Comparison of capture rates for wildlife species between northern and southern savannas sectors. Significant results after Bonferroni adjustment are given in bold.

Species	Capture rates		
	Southern savannas	Northern savannas	P value
Aardvark	0.85	1.60	0.4947
African brush-tailed porcupine	0.69	0.18	1.0000
African civet	3.35	3.92	1.0000
African giant-pouched rat	3.11	1.13	0.6231
Bay duiker	0.56	0.00	1.0000
Black-fronted duiker	0.46	0.00	1.0000
Blue duiker	**17.88**	**2.38**	**0.0005**
Bongo	0.43	0.12	1.0000
Bushbuck	**21.49**	**3.92**	**0.0002**
Chimpanzee	7.04	0.42	0.0148
Forest buffalo	18.16	10.75	0.1694
Forest elephant	**45.01**	**93.59**	**< 0.0001**
Giant forest hog	0.17	1.48	0.4934
Greater cane rat	0.26	0.71	1.0000
Large grey mongoose	0.52	3.33	0.1191
Large-spotted genet	0.24	1.01	0.4934
Leopard	0.37	0.18	1.0000
Long-nosed mongoose	1.24	1.84	1.0000
Marsh mongoose	2.11	5.11	0.2788
Peter's duiker	5.15	0.24	0.0610
Red river hog	14.95	5.76	0.0573
Serval	4.17	3.56	1.0000
Spotted hyena	41.02	42.99	0.8049
Western lowland gorilla	0.31	0.30	1.0000
Yellow-backed duiker	1.20	0.95	1.0000

Apart from that, trap success at trap stations in the very south of the study area was, in general, lower. Also, only few wildlife signs, compared to other areas in the study area, were seen and wildlife trails were largely overgrown here. Trap success for forest elephants was very low in the savanna Illeho and in the northern part of the savanna Ebamba. These areas were characterized by high car traffic (Fig. 1 & 2). Moreover, forest elephants were only rarely photographed at trap stations in the very south of the study area. If forest elephants were photographed here, photographs mainly showed only solitary bulls.

Results on the daily activity patterns of photographed species are presented in Figures 18 & 19. Carnivore species which were exclusively or mainly nocturnal were, for example, large-spotted genet (*Genetta maculata*), spotted hyena and African civet (Fig. 18). Aardvark (*Orycteropus afer*), hippopotamus, forest elephant and yellow-backed duiker were also mainly nocturnal (Fig. 19). The great ape species, chimpanzee and gorilla, showed a strong diurnal activity (Fig. 19). Bushbuck, forest buffalo and serval were mainly cathemeral (Fig. 18 & 19).

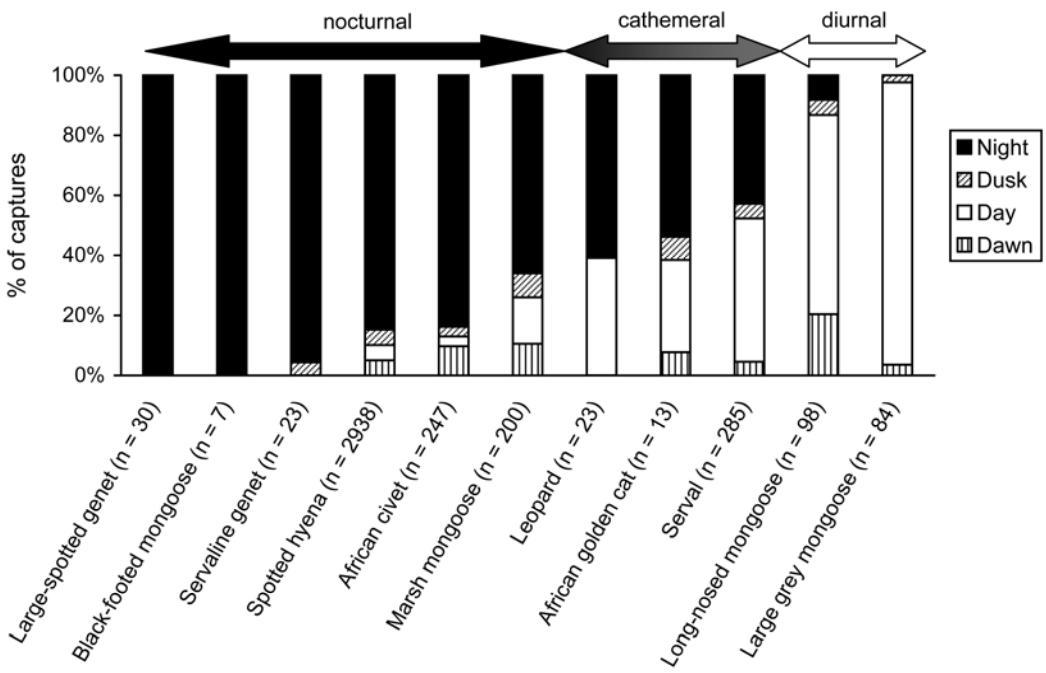


Figure 18. Daily activity patterns of carnivore species in the OKNP's FSM.

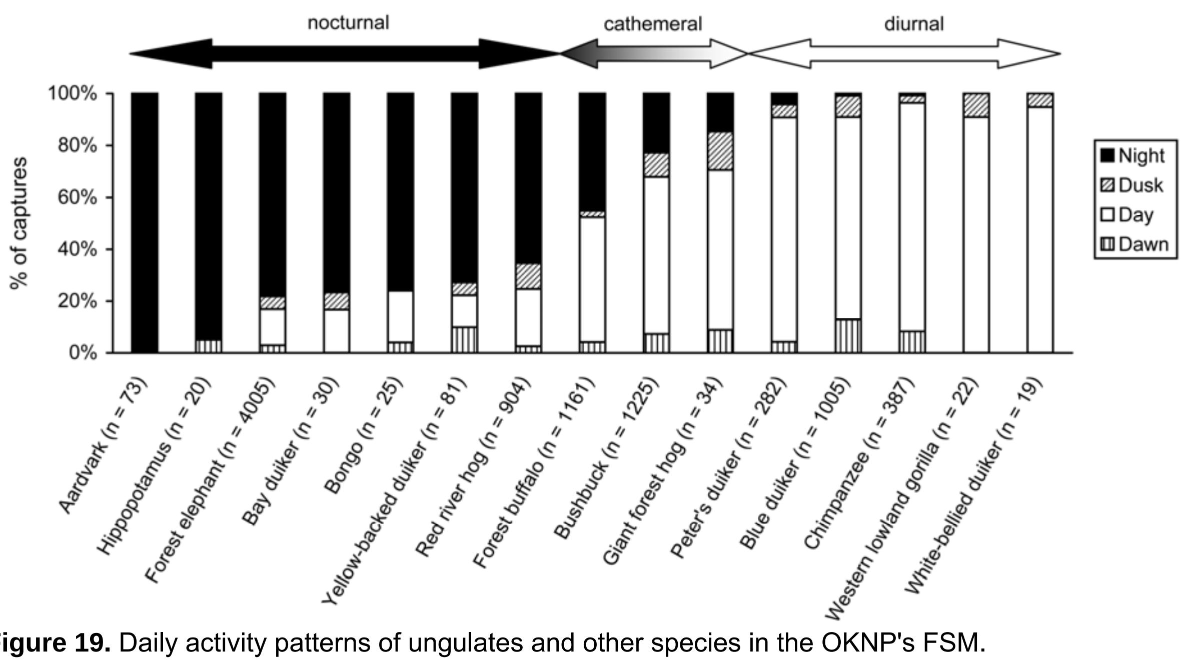


Figure 19. Daily activity patterns of ungulates and other species in the OKNP's FSM.

Adult spotted hyenas belonging to the southern clans were 88.1 % times photographed during night and 11.9 % times between dawn and dusk (Fig. 20). Adult spotted hyenas from the northern clan were photographed 77.8 % times during night and 22.2 % times between dawn and dusk (Fig. 20). The difference between 'northern' and 'southern' spotted hyenas for these activity periods was significant (χ^2-test$_{Yates}$, χ^2 = 32.55, d.f. = 1, P < 0.01), suggesting that both groups of spotted hyenas have different activity periods.

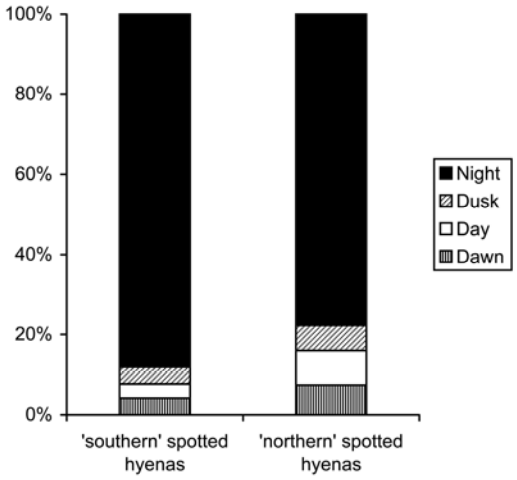


Figure 20. Comparison of daily activity patterns of 'southern' (n = 1456 capture events from 33 animals) and 'northern' (n = 544 capture events from 12 animals) spotted hyenas.

Camera traps located in the northern savannas block recorded two hyenas which showed cable snare wounds on their bodies (Fig. 21). In addition, on the 9th March 2014 I saw a spotted hyena on the road halfway between Mbomo and Mbomo (Fig. 22). The hyena was seriously limping. An analysis of the photos that were taken from this hyena revealed that this hyena suffered from a fresh flesh wound induced by a wire snare (Fig. 22).

Figure 21. Camera trap picture of a hyena with signs of cable snare injuries (circle).

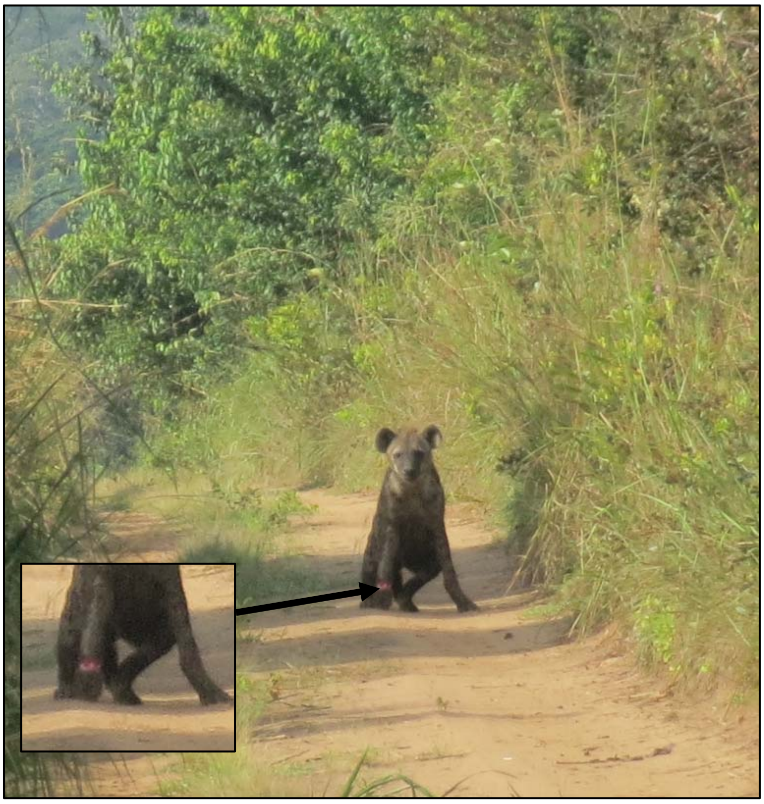


Figure 22. Picture of a spotted hyena showing signs of a cable snare wound (arrow) on the right lower foreleg (the picture was taken halfway on the road from Mbomo to Mboko). Photo: Torsten Bohm

7.4 Discussion

All terrestrial medium and large-sized mammal species, except giant pangolin and sitatunga, known to occur in the park (Maisels, 1996) were photographed during the camera trapping study. The sitatunga prefers swamp habitats (Kingdon, 2004), thus, making it difficult to record this species in open savannas or forests. The absence of giant pangolin in the records is surprising as this species was also recorded in the diet of spotted hyenas (see chapter 3). Giant pangolin was recorded during previous camera trapping studies in the bais Maya Nord, Romani and Lokoué (pers. comment African Parks) in the park's forest bloc. Giant pangolin was also recorded during my camera trapping study in Gabon (see chapter 8). The semi-arboreal white-bellied pangolin, which was also frequently recorded in the diet of spotted hyenas (see chapter 3), was also not recorded by camera traps. The vulnerability of these species to predation by spotted hyenas appears to be the main reason for their absence in the savannas and spotted hyenas probably hunt for these species in the forests.

Water chevrotain (*Hyemoschus aquaticus*) was recorded only twice at one trap station. This trap station was situated approx. 40 m away from a small river. Water chevrotains jump into waters to escape predators (Kingdon, 2004). During my camera trapping study in Gabon, water chevrotain was the second-most photographed ungulate species and was also recorded in the savannas (see chapter 8). Like pangolins, water chevrotains also probably avoid open savannas and forests in the OKNP to avoid predation by spotted hyenas. Bushbuck, forest buffalo and red river hog were the most frequently photographed larger ungulate species. These species were also the most frequently recorded prey species in the diet of spotted hyenas (see chapter 3). Spotted hyenas are known to prey on the most abundant ungulate species (Mills, 1990; Hayward, 2006). The high occurrence of these species in the diet of spotted hyenas as well as their high capture rates during the camera trapping study might therefore indicate that these species occur in high abundances in the park's FSM.

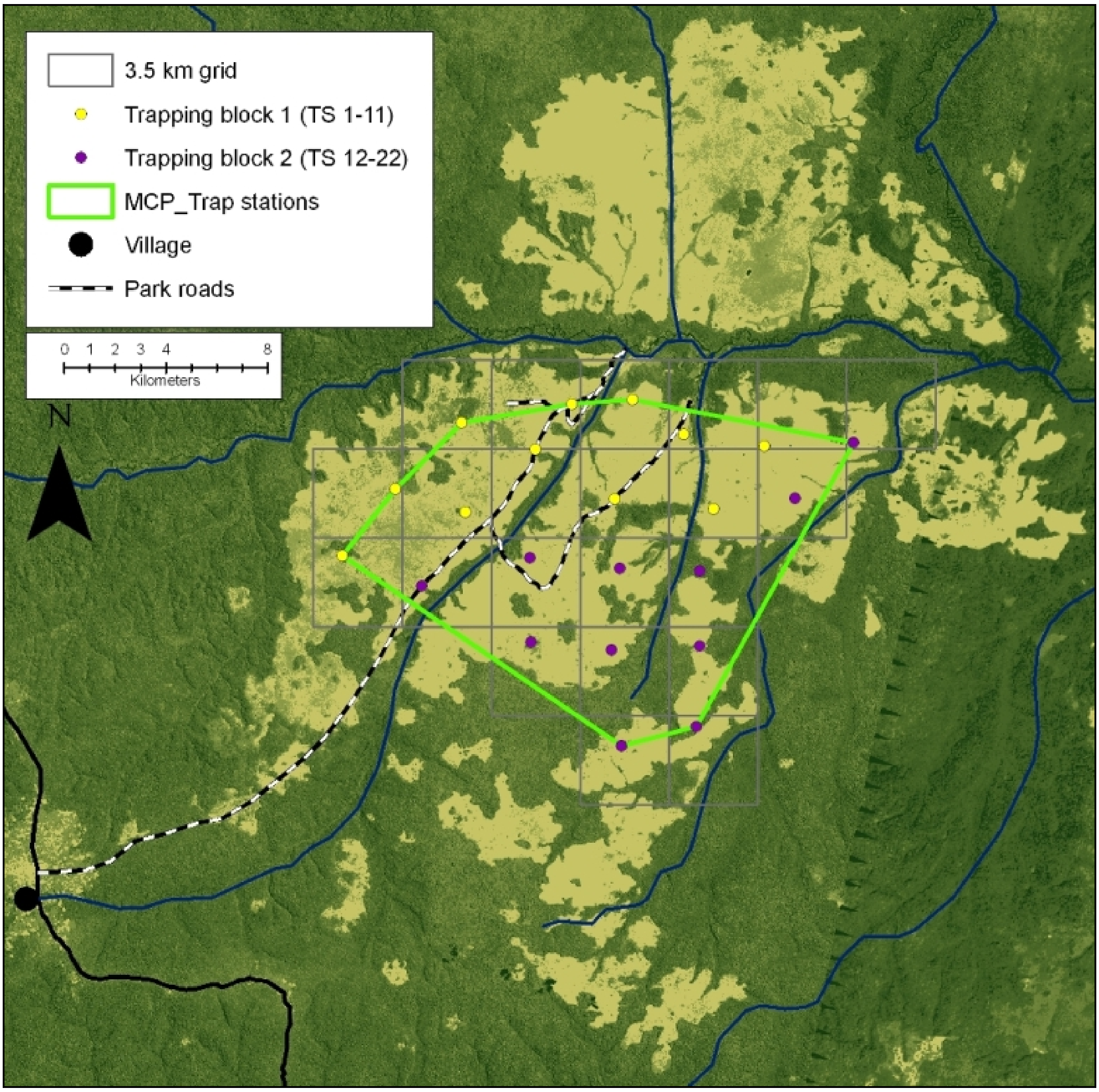
The high trap success in forests and forests islands is not surprising as camera traps also photographed species here which predominantly or exclusively occur in forests, such as smaller carnivores and monkey species. However, some of these species were also occasionally recorded in savannas and the trap station which recorded the highest number of different species was also located outside forested areas (but just ca. 60 m). However, as the results demonstrated, camera traps located farther away from forested areas recorded, in general, smaller numbers of different species, showing that a large number of species need forested areas, which provide shelter and food, in close proximity. This was also confirmed by results from generalized linear models, which showed that certain species, such as blue duiker, can only be found in close proximity to forested areas.

Results showed that human activities had an influence on the distribution of mammal species in the FSM. This was particularly true for forest elephants: Firstly, the significantly higher trap success for forest elephants in the northern savannas sector showed that forest elephants avoid areas with high human activity. Secondly, forest elephants strongly avoided areas near roads. Thus, future infrastructure projects, such as roads, in the northern savannas sector should be well thought through and planned. Roads and other infrastructure measures potentially cause stress by hindering movements between feeding sites and, thus, will likely have a negative impact on the distribution and well-being of forest elephants there. In particular, it should be avoided that roads lead to the interruption of the large elephant boulevards which are already in use for many generations and traverse the northern savannas to connect distant forest areas. However, currently, it appears that the northern savannas sector remains the only undisturbed refuge of open habitat for forest elephants - and probably other wildlife species too - in the park.

It is known that the wildlife trails on which trap stations 20 (savanna Essobé) and 25 (savanna Ibenga) were installed, were extensively used by poachers ("poacher trails") in the past (pers. information research assistants; Henschel, 2007; Bohm, 2012). While still one poacher was filmed by camera traps and other signs of poaching were recorded in this area (see Appendix I) (Bohm, 2012) in 2012, no significant poaching signs were recorded in this area during this study. However, very little wildlife activity was recorded by the camera traps in the savanna Ibenga and the very south of the savanna Illeho. Additionally, only few signs of wildlife were recorded during walks in these areas. Furthermore, wildlife trails were largely overgrown here, suggesting that either wildlife in this area has not yet fully recovered from disturbances in the past or that poaching is still present here. Sufficiently protected, savannas in this area and further south could provide more than 100 km^2 of suitable habitat for spotted hyenas and other wildlife species. A camera trapping study in this area could reveal important information on the occurrence of spotted hyenas and other wildlife species as well as information on poaching in this area. Since also spotted hyenas with cable snare wounds were photographed by camera traps and seen in the field, it can be assumed that poaching with wire snares has a negative impact on the OKNP's spotted hyena population (see chapter 2). The nearest villages are just 15–30 km away from the park's FSM. Poachers probably use areas in the nearest surroundings of their villages as hunting territories and also occasionally travel deep into the park (Vanwijnsberghe, 1996; Gami, 2000). A sufficient protection of the park's FSM and surrounding forests is therefore crucial to enhance the survival chances of the OKNP's spotted hyena population.

Spotted hyenas are known to modify their temporal activity with regard to the occurrence and degree of human activities (Boydston *et al.*, 2003). In general, spotted hyenas in the park are highly nocturnal. In the southern savannas sector, a region in which almost all of the tourist and park staff activity is concentrated, spotted hyenas are even 'more nocturnal'. This modification in the behaviour is likely due to human activity rather than due to the activity patterns of their prey species (see chapter 3).

Appendix I. Camera trapping design during camera trapping study from November 2011 to January 2012. Trap stations in trapping block one were operational from 17/11/2011 to 20/12/2011. Trap stations in trapping block two were operational from 17/12/2011 to 20/01/2012. The size of the trapping polygon (MCP) was 167 km^2.



Appendix II. Results from camera trapping study November 2011 to January 2012

Order	Family	Common name	Scientific name	# Captures*	Capture rate**	# Trap stations***	Habitat
Artiodactyla	Bovidae	Black-fronted duiker	*Cephalophus nigrifons*	2	0.29	1	F
Artiodactyla	Bovidae	Blue duiker	*Philantomba monticola*	53	7.82	7	F, S
Artiodactyla	Bovidae	Peter's duiker	*Cephalophus callipygus*	22	3.24	5	F
Artiodactyla	Bovidae	Yellow-backed duiker	*Cephalophus silvicultor*	5	0.74	3	F, S
Artiodactyla	Bovidae	Bushbuck	*Tragelaphus scriptus*	92	13.57	16	F, S
Artiodactyla	Bovidae	Forest buffalo	*Syncerus caffer nanus*	114	16.81	17	F, S
Artiodactyla	Suidae	Red river hog	*Potamochoerus porcus*	26	3.83	7	F, S
Carnivora	Felidae	Leopard	*Panthera pardus*	7	1.03	5	F, S
Carnivora	Felidae	Serval	*Leptailurus serval*	32	4.72	8	F, S
Carnivora	Herpestidae	Large grey mongoose	*Herpestes ichneumon*	4	0.59	3	S
Carnivora	Herpestidae	Long-nosed mongoose	*Xenogale naso*	8	1.18	4	F, S
Carnivora	Herpestidae	Marsh mongoose	*Atilax paludinosus*	26	3.83	11	F, S
Carnivora	Hyaenidae	Spotted hyena	*Crocuta crocuta*	434	64.01	21	F, S
Carnivora	Nandiniidae	African palm civet	*Nandinia binotata*	1	0.15	1	F
Carnivora	Viverridae	African civet	*Civettictis civetta*	27	3.98	7	F, S
Carnivora	Viverridae	Large-spotted genet	*Genetta maculata*	2	0.29	2	S
Carnivora	Viverridae	Servaline genet	*Genetta servalina*	9	1.33	4	F, S
Primates	Hominidae	Chimpanzee	*Pan troglodytes*	12	1.77	4	F, S
Primates	Cercopithecidae	Agile mangabey	*Cercocebus agilis*	1	0.15	1	F
Proboscidea	Elephantidae	Forest elephant	*Loxodonta cyclotis*	165	24.34	17	F, S
Rodentia	Hystricidae	African brush-tailed porcupine	*Atherurus africanus*	29	4.28	5	F, S
Rodentia	Nesomyidae	African giant pouched rat	*Cricetomys gambianus*	15	2.21	4	F, S
Rodentia	Thryonomyidae	Greater cane rat	*Thryonomys swinderianus*	24	3.54	3	S
Tubulidentata	Orycteropodidae	Aardvark	*Orycteropus afer*	5	0.74	4	F, S
-	-	Poacher	-	1	0.15	1	F
Total	-	n = 24 wildlife species + hunter		1116	164.60	-	-

* "independent capture event" = (1) consecutive photographs of different individuals of the same or different species, (2) consecutive photographs of individuals of the same species taken more than 0.5 h apart and (3) nonconsecutive photos of individuals of the same species

** # captures/trap nights (678) * 100

*** total number of trap stations = 22

F = Forest, S = Savanna

Chapter 8: Status of spotted hyenas and other wildlife species in three regions of the Batéké Plateaux in southeast Gabon

8.1 Introduction

Until the late 1940ies, the vast forest-savanna mosaics that cover large areas of the Republic of Congo (hereafter: Congo) and the Gabon were once a stronghold for spotted hyenas (*Crocuta crocuta*) (Malbrant & Maclatchy, 1949) (Fig. 1). Since then, the distribution range of spotted hyenas in both countries has dramatically declined, resulting in only one remaining population inhabiting the Odzala-Kokoua National Park (OKNP) in the north of the Congo (Henschel, 2009) (Fig. 1). This range loss was likely related to the depletion of potential prey base and in some instances the result of eradication programmes initiated by cattle ranch owners (Henschel, 2006, 2009).

Within the last decades, individual spotted hyenas have been recorded at different localities within the Congo Basin. Single spotted hyenas were recorded by camera traps deep inside rainforest habitat in the early 2000s in the Ivindo National Park, Gabon and the Noubalé-Ndoki National Park, Congo (Henschel & Ray, 2003). Just recently, one single spotted hyenas was photographed by camera traps in the Noubalé-Ndoki National Park again (Gessner *et al.*, 2013). More tragic cases occurred in Gabon and Equatorial Guinea: A young adult spotted hyena (between 3–6 years old) was killed by a car near a village on the south-eastern side of Rio Muni in Equatorial Guinea in 1991 and one spotted hyena was killed by a mob of scared people in the town of Koulamoutou in Gabon around 2004 (pers. comment P Henschel) (Fig. 1). More promising and recent records were recorded in Gabon again: In 2008, hyena spoors were discovered in a forest-savanna mosaic approximately 30 km north-west of the Batéké Plateaux National Park (BPNP) (Bout *et al.*, 2010). These spoors belonged to four individuals (Bout *et al.*, 2010). More tracks of spotted hyenas were recorded near the town of Léconi in 2009 (pers. comment P. Henschel), just less than 100 km away from the previous location (pers. comment P. Henschel).

All the above described events about individuals found either dead or recorded just once within short time periods suggest that these spotted hyenas were not remnants of local resident populations, but in fact, probably just represented unsuccessful dispersal events from the spotted hyena population in the OKNP. However, the findings of Bout *et al.* (2010) were promising as their findings also included a set of tracks which was likely left by a group of three individuals, including maybe a juvenile. This area is connected by an expanding network of public and logging roads, of which a considerable amount have been abandoned (Laporte *et al.*, 2007). Spotted hyenas show preferences for roads when travelling (Sillero Zubiri & Gottelli, 1992; Bohm, 2008), thus they are likely to use these roads. However, for the establishment of a new reproductive clan, a group of related adult females has to emigrate into a vacant area or a clan with no adult females (Höner *et al.*, 2005; Holekamp *et al.*, 2010). Until now, this was only reported twice (Holekamp *et al.*, 1993; Höner *et al.*, 2005).

In 2011 I visited the area where Bout *et al.* (2010) made their findings to investigate if spotted hyenas are present in this area (or recently were). To obtain results on the status of spotted hyenas I conducted reconnaissance surveys in three study areas and one camera trapping study in one study area.

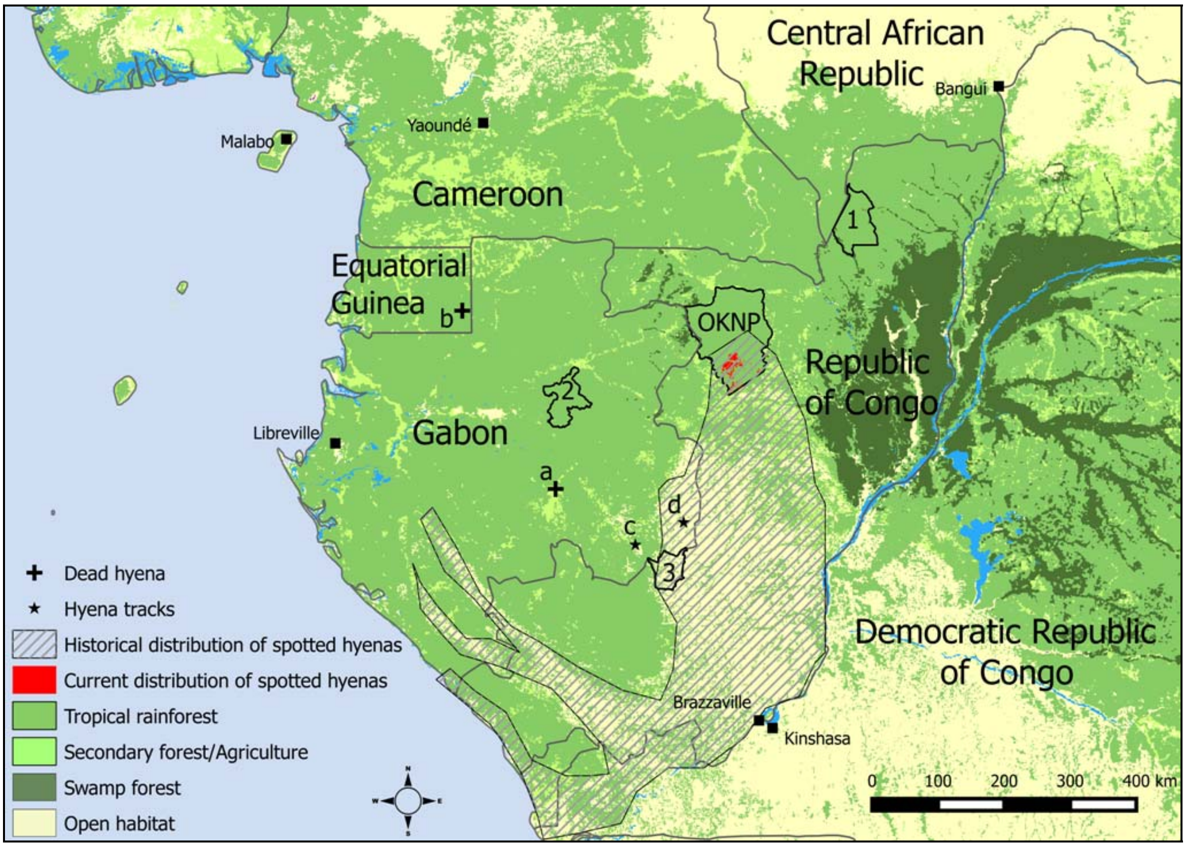


Figure 1. Historical distribution (modified from Henschel, 2009), recent records and current distribution of spotted hyenas in the Congo Basin. OKNP = Odzala-Kokoua National Park. Spotted hyenas were photographed by camera traps at locations 1 (Noubalé-Ndoki National Park) and 2 (Ivindo National Park). One hyena was killed by villagers near location a (town Koulamoutou). One hyena was killed by a car at location b (Rio Muni in Equatorial Guinea). Hyena tracks were recorded at locations c (forest-savanna mosaic south of Franceville) and d (near town Léconi). See text for details. 3 = Batéké Plateaux National Park. The only remaining spotted hyena population today can be found in the small forest-savanna mosaic inside the Odzala-Kokoua National Park (red area).

8.2 Methods

Reconnaissance surveys in Mopia, Ranch de la Lékabi and Batéké Plateaux National Park

The two study areas Mopia and Ranch de la Lékabi were situated south and north of Franceville respectively (Fig. 2 & 3). They consisted of mosaics of forests and savannas.

These forest-savanna-mosaics (hereafter FSM) are partly separated from the rolling savannas of the Batéké Plateaux in the east and south-east by dense rainforest which cover most of Gabon (Fig. 1).

Study area 1 - Mopia - (Fig. 2) was situated approx. 30 km south of Franceville and approximately 8 km south of the village Mopia. The FSM in this area had an extent of roughly 250 km^2. The study area had a size of 147 km^2. Natural borders of the study areas were the Ogooué river to the west and the Ndjoumou river to the east respectively. The savannas of the study area were separated by a road which connects Franceville with Boumango in the south into a smaller western and a larger eastern part. Two smaller villages are situated along this road and lie therefore directly within the borders of the study area. Numerous arms of the Ogooué as well as the Ndjoumou run through the savannas of the study area, thus dividing the study area into smaller savannas. Human encroachment as well as hunting is high in this area. Furthermore, the savannas are regularly burnt here to enhance visibility during hunting trips. This study area was chosen due to the findings of spotted hyena spoors on the road traversing the FSM (*Bout et al.,* 2010).

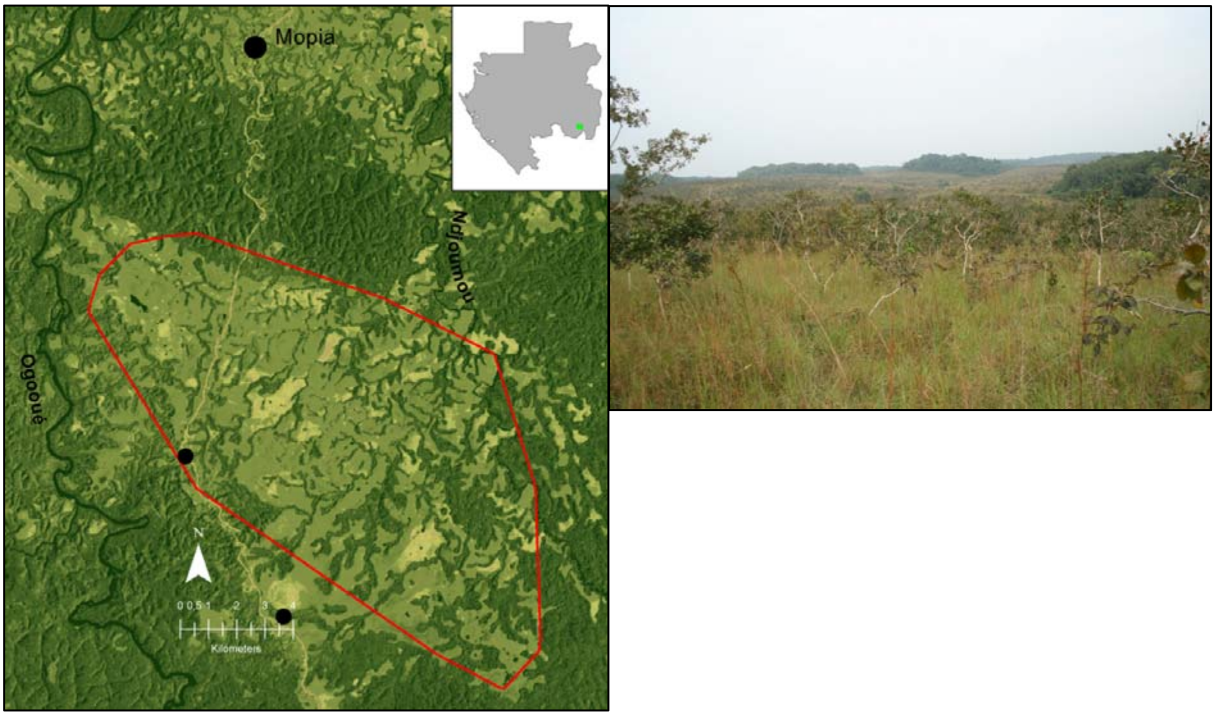


Figure 2. Map of the study area Mopia (red polygon). Black circles indicate villages which are connected by a road. Photo on the right shows landscape of the study area. Savannas = light green, forests = dark green. Photo: Torsten Bohm

Study area 2 - Ranch de la Lékabi (hereafter Lékabi) - (Fig. 3) was situated approx. 20 km north of Franceville. The study area, with a size of approx. 212 km^2 was situated in the southern part of Lékabi. The study area was bordered by the Ogooué river to the west and the Lékabi river to the north. The Lékabi river runs from northwest to southeast and also borders the ranch at its the eastern side. To the south, the ranch is separated from the surrounding savannas by a road. Numerous arms of the Ogooué as well as the Lékabi run through the savannas of the study area, thus dividing the study area into smaller savannas, especially in the western part of the ranch (Fig. 3). A settlement which is inhabited by the "*conservateur*" of the ranch and ranch workers was situated in the central part of the southern savanna area. This settlement is surrounded by cultivated land, incl. fruit plantations (e.g. pineapples). The nearest larger village is Okoloville which is situated south-east of the ranch. Two smaller villages (not shown in the map) are situated along the road at the southern border of the ranch. Hunting is strictly prohibited in the ranch, although no efforts are made, e.g. through law enforcement, to protect the ranch's wildlife from poaching.

The ranch belongs to the family of the president of Gabon and was used as a ranch for cattle farming in former years. By now, the number of cattle has dropped from more than 3000 to just a small herd of about 20 animals (pers. comm. N. Bout; pers. observation). By the time the study was conducted, plans were underway to restock the ranch with 500 cattle (pers. comm. N. Bout) within the following months. To facilitate cattle farming, various roads were built throughout the ranch's area by the owner. This study area was chosen due to reports by local villagers about an animal which has killed ten of their dogs. These incidents were reported to the "*conservateur*" of the BPNP who asserted subsequently that the animal in question which has killed the dogs was a spotted hyena.

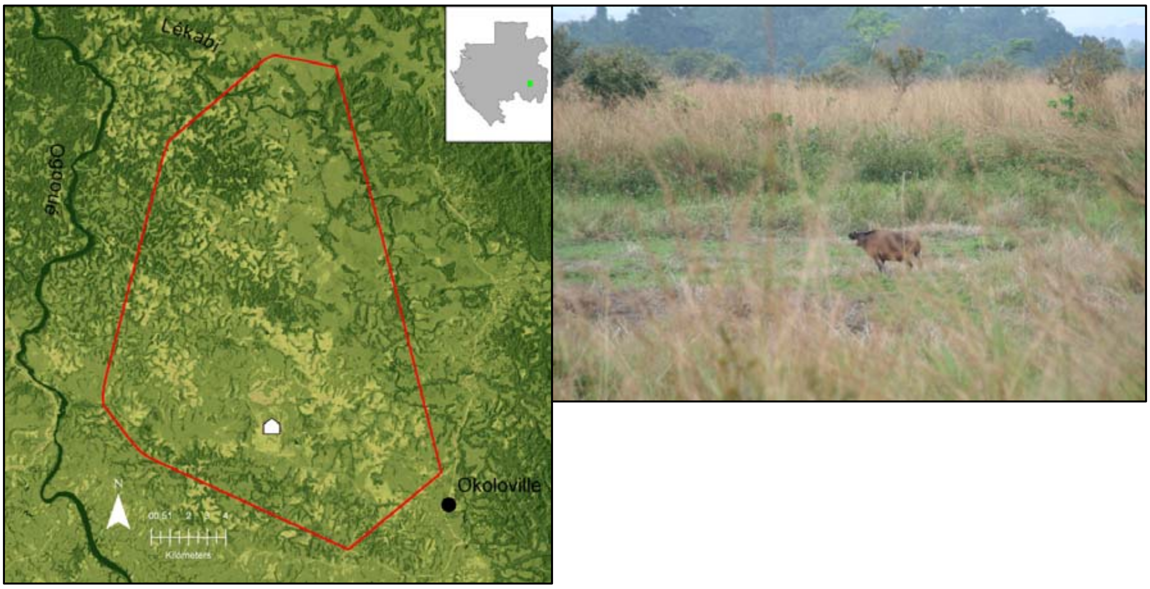


Figure 3. Map of Lékabi study area. Red polygon indicates study area. House indicates settlement with houses of the "*conservateur*" and ranch workers and fruit plantations. Right picture shows a forest buffalo which was photographed in the study area. Photo: Torsten Bohm

In study area 3 - Batéké Plateaux National Park (hereafter BPNP) - (Fig. 4 & 5) two surveys were conducted, one in the northwest and one in the northeast of the park respectively. Unusual large carnivore tracks, resembling spotted hyena tracks were seen here in 2009 (pers. comment N Bout). The park was established in 2002 and covers an area of 2,034 km^2. The park consists of rolling savannas with gallery forests bordering watercourses in valleys. On the hilltops, especially in the north-eastern part of the park, the vegetation consists mainly of vast grasslands, without bushes or trees (Fig. 5). The park is regularly patrolled by ecoguards, but poaching is locally high. Gangs of Congolese poachers regularly infiltrate the park at the eastern boundary of the park (pers. comment N. Bout) which simultaneously represents the national border between Congo and Gabon (Fig. 4). The BPNP harbours a rich wildlife (Bout, 2006). Species which predominantly occur in the savannas are side-striped jackal (*Canis adustus*) and Grimm's duiker (*Sylvicapra grimmia*), locally known as Ntsa. The Grimm's duiker, also known as bush or common duiker, is locally endangered and strictly protected under Gabonese law (République Gabonaise, 1994).

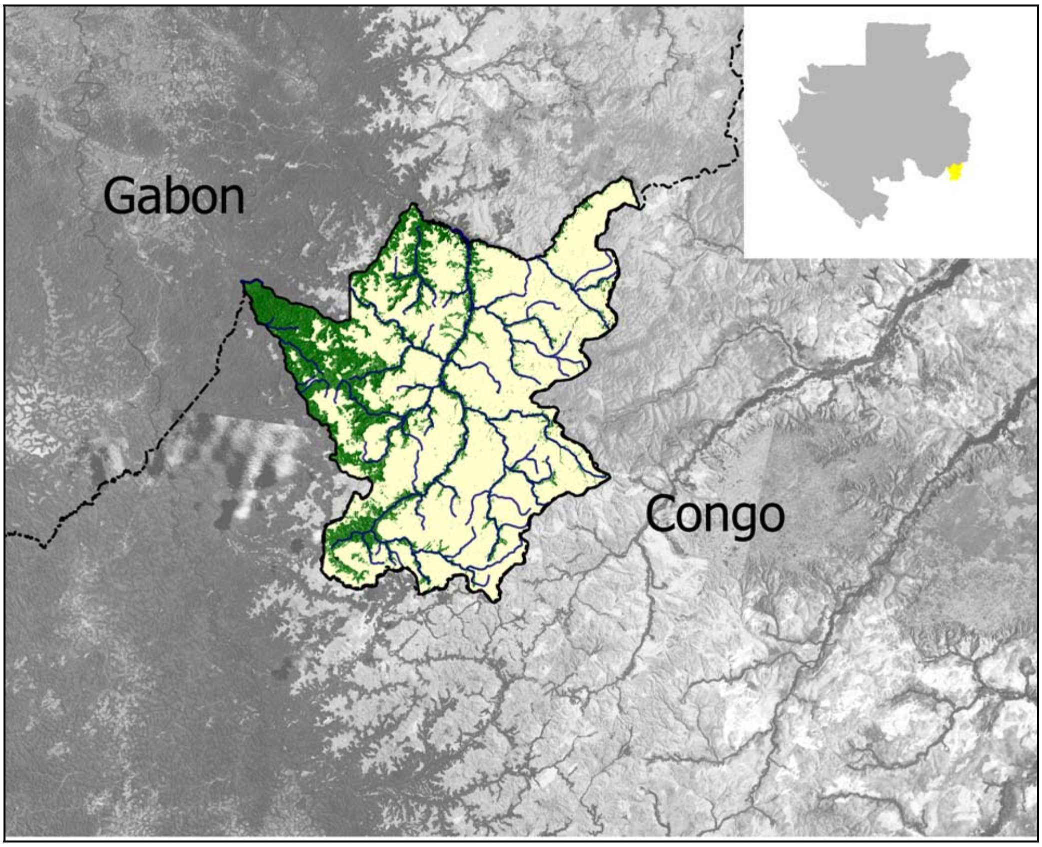


Figure 4. Map of the Batéké Plateaux National Park. Green areas = rainforest, yellow areas = savannas, blue lines = rivers.

Figure 5. Photos of the BPNP. Right photo: north-eastern part of the BPNP. Photos: Torsten Bohm

Data collection during reconnaissance surveys

The study areas were surveyed by foot by Torsten Bohm and two Gabonese assistants (one tracker, one porter). Field work in Mopia was conducted from June 10th to June 19th (10 days); field work in Lékabi was conducted from July 6th to July 17th (12 days) and field work in the BPNP was conducted from 29th July to 11th August. A stationary camp was prepared for each night during field work. At the very next morning the camp was taken down and a new camp was installed at another location at the same day. In certain cases, a camp was left on the spot for the same day and the surrounding areas were surveyed with only “light” baggage.

During walks, prominent game trails, such as buffalo trails or elephant “boulevards”, were followed. Such larger game trails are extensively used by larger carnivores such as spotted hyenas (Bohm, 2008). In addition, these game trails often lead to features, such as marshes, lakes and “bais” (forest clearings) which are known to attract larger carnivores as well as their prey species. Therefore, during field studies, these features were also visited and surveyed for spoors. If possible, roads in the study area were walked as well. Spotted hyenas as well as other larger carnivores show preferences for roads when travelling (Bohm, 2010; Sillero-Zubiri & Gottelli, 1992), thus they are likely to use these roads. In Lékabi, an extensive network of roads existed. This network was extensively used during field work. However, many of these roads were in a bad condition, i.e. overgrown by vegetation. During field work, it was aimed to survey as many savannas as possible. However, for the survey, predominantly savannas were chosen which were situated farthest away from human settlements. During field work it was necessary to traverse many forests since savannas in the study areas were not directly linked with each other. Therefore, a substantial part of the surveyed area incorporated also forest habitat. During the walks, the exact location was recorded every 50 meters with the help of the GPS receiver’s “tracklog” function to record the exact survey circuit. During walks GPS locations of signs from potential spotted hyena prey animals, larger and smaller carnivores as well as hunting found in the field were stored in a handheld GPS navigator (Garmin GPSMap® 60CSx). If necessary, further relevant information were recorded in a fieldbook. GPS locations of the following signs were recorded:

- direct observations of larger mammals (number of animals, group size)
- dung from ungulates, incl. age (fresh, recent or old)
- tracks of potential prey species and carnivores (If well preserved tracks from middle-sized or large-sized carnivores were found, measurements of the tracks were also taken.)
- carnivore scats, incl. age (fresh, recent or old) and African civet (*Civettictis civetta*) latrines (only Lékabi); if possible measurements of the width at the thickest spot of the scat were also taken
- regurgitations from large carnivores
- poaching signs (type of sign, e.g. empty cartridge shell, poacher camp)
- other relevant signs (e.g. feeding signs of great apes)
- tracks and dung from forest elephants (*Loxodonta cyclotis*) (only in Lékabi and BPNP)

In case if scats and regurgitations from larger carnivores were found, a quick examination of the hairs found in the scats was done in the field in order to determine the prey animals eaten. Because the rainy season has just passed, only fresh dung and spoors from ungulates were recorded during Mopia field study. Since it can be assumed that ungulate densities are different during rainy and dry seasons, recordings of all dung signs could lead to diametric results. Prior to and during field studies, villagers and other persons were interviewed about their knowledge on spotted hyena occurrence in the respective areas.

Camera trapping study in Mopia

In addition I conducted a camera trapping study in the study area Mopia from the 9th September to the 1st November 2011. Trap stations were deployed in two trapping blocks (Fig. 6). Twelve trap stations were deployed in trapping block 1 at the beginning of the study and left in this block for four weeks. All trap stations were installed within four days. After installation of all trap stations in block 1, a quick survey was done in trapping block 2 to find suitable places for trap stations. During this survey two trap stations were already installed in trapping block 2. After four weeks trap stations from trapping block 1 were transferred to trapping block 2 and left here for further four weeks. In total, 24 trap stations were deployed. One trap station was stolen, so that only data from 23 trap stations could be used for analysis. Trap stations were deployed in a 3.5 x 3.5 km grid and placed along wildlife trails and roads. At each trap station one Reconyx HC500 and either one Bushnell Trophy Cam 2009 or Bushnell Trophy Cam 2010 was deployed. Reconyx were programmed to take 5 pictures per trigger event without interval between trigger events. Bushnell Trophy Cams were programmed to take three pictures per trigger event with the smallest interval between trigger events (for Bushnell Trophy Cams ca. 5–6 s). The size of the trapping polygon was 168.5 km² (Fig. 6). The total amount of trapping nights (6 pm–6 am) (sum of trap nights trap stations were operating) was 624.

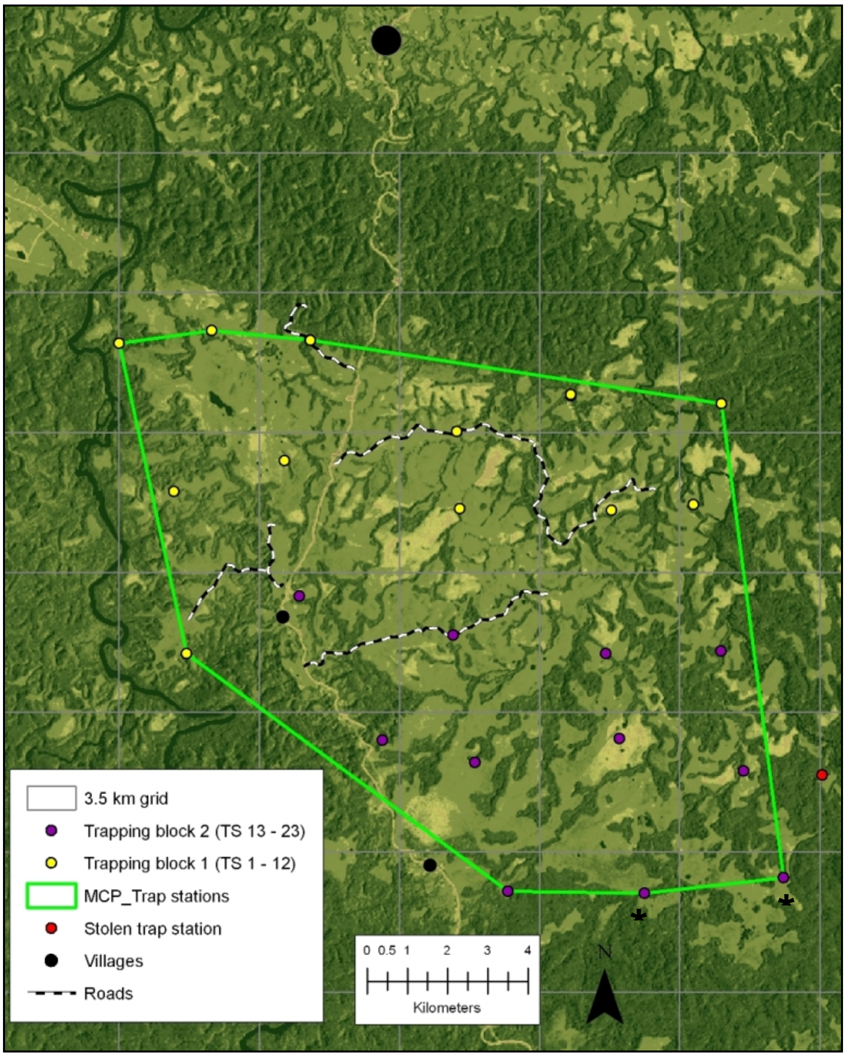


Figure 6. Map showing locations of the trapping blocks and camera trap stations in the study area Mopia. Asterisks indicate that these two trap stations were installed shortly after installation of all trap stations in trapping block 1.

8.3 Results

Reconnaissance surveys

In Mopia, a total distance of 150 km was walked (Fig. 7). During this time seven stationary camps were established and a total area of 147 km^2 was covered. During the walks, no signs of spotted hyena presence were recorded. Signs of larger carnivores - two scats and two regurgitations - were found on four occasions. One scat was very fresh, probably less than one hour old. This scat was very big and could have also been deposited by a spotted hyena, although the scat lacked the typical features of hyena scat, such as size, white colour and clearly visible lobes. Thus, it is assumed that this scat, as well as the other scat and the regurgitations, were likely deposited by a leopard (*Panthera pardus*). The scats could be easily identified as large carnivore scats due to their size and their containing prey remains, i.e. hairs and larger (> 1 cm) bone pieces. The other scat was several days old and was found on a big tree trunk crossing a river in a forest. Spotted hyenas are known to regurgitate a large proportion of undigested prey remains (Sillero-Zubiri & Gottelli 1992). However, leopards are also known to regurgitate undigested prey remains (pers. comm. P. Henschel). Since no hyena signs could be found in the study area, it is assumed that the collected regurgitations were from leopards. For diet analysis, only one scat and the two regurgitations were examined. The samples contained remains of three different mammal species: unidentified "red duiker", forest buffalo (*Syncerus caffer nanus*) and African brush-tailed porcupine (*Atherurus africanus*). In addition, one regurgitation contained a completely preserved duiker’s hoof.

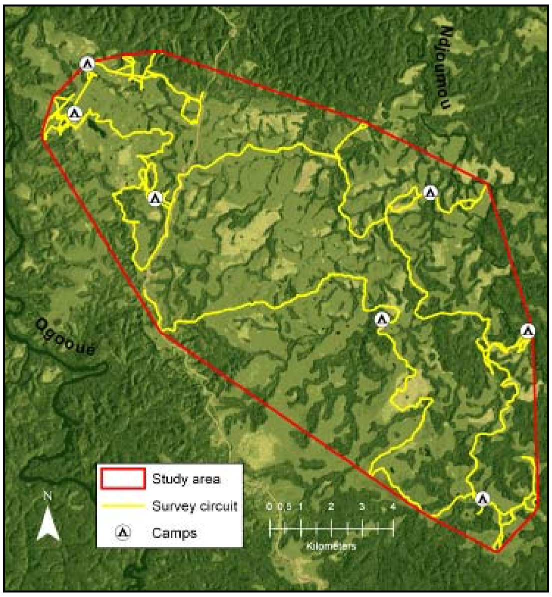


Figure 7. Map of the study area Mopia, showing the survey circuit and the stationary camp sites. The survey started at the road at the north-western border of the study area and ended ca. 4 km south of the starting point. The western savanna section was surveyed first.

Table 1 gives an overview of the wildlife / poaching signs recorded during this survey. By far the most signs were from forest buffalo, followed by “antelopes”, red river hog (*Potamochoerus porcus*) and small carnivores. The encounter rates (No. of signs and direct observations / km distance walked) for these species were 0.680, 0.280, 0.213 and 0.187

signs/km respectively. Poaching signs were recorded on 19 occasions (Figure 8, Table 2). Fifteen of these signs consisted of "cutting signs", i.e. visible signs of cuts from a machete on vegetation, mostly along wildlife/hunter trails. During the study time two gun shots (the second shot followed the first shot after about two minutes) were heard in the western savanna part at about 6:00 pm on the 11th of June. My two assistants identified the gun shots as ammunition for hunting large mammal species such as buffaloes or elephants. One empty cartridge shell was found as well. According to my assistants the empty cartridge shell belongs to ammunition which can be used to hunt smaller animals, such as birds. During a later visit of the study site a cable snare with the remains of a red river hog was found in dense forest near one of the two villages in the study area (Fig. 9). Larger mammal species were observed on eight occasions (Table 3). Among the observed mammals were bushbuck (*Tragelaphus scriptus*), forest buffalo, forest elephant, blue duiker (*Cephalophus monticola*) and yellow-backed duiker (*C. silvicultor*).

Table 1. Encounter rates of mammal and poaching signs during field survey in Mopia. Signs include fresh spoors and dung from buffalo, "antelopes" and red river hogs. In case of red river hog also their conspicuous digging signs and nests were recorded. Signs for small carnivores include only scats, as no spoors from smaller carnivores could be recorded.

Species name	Scientific name	Total # signs (incl. direct observations)	Distance (km)	Encounter rate (# signs / 150)
Forest buffalo	*Syncerus caffer nanus*	102	150	0.680
"Antelopes" (incl. all duiker species, water chevrotain and bushbuck) [a)]	*Cephalophus spec., Philantomba monticola, Tragelaphus scriptus, Hyemoschus aquaticus*	42	150	0.280
Red river hog	*Potamochoerus porcus*	32	150	0.213
Small carnivores (serval, African golden cat, mongooses, domestic cat, domestic dog) [b)]	*Leptailurus serval, Caracal aurata, Felis silvestris catus, Canis lupus familiaris*	28	150	0.187
Poacher	-	19	150	0.127
Leopard	*Panthera pardus*	4	150	0.027
Monkeys	-	2	150	0.013
Gorilla [c)]	*Gorilla gorilla gorilla*	1	150	0.007

[a)] Dung from "antelopes" were not divided into dung from smaller, medium-sized or larger "antelopes".

[b)] Domestic dogs and cats are included as it is possible that some of the recorded scats from smaller carnivores could have originated from domestic cats and dogs. However, although regularly seen, GPS locations of spoors from domestic cats and domestic dogs were not recorded by the field team.

[c)] Feeding signs on a tree fruit. According to research assistants, these feeding signs originated from gorillas.

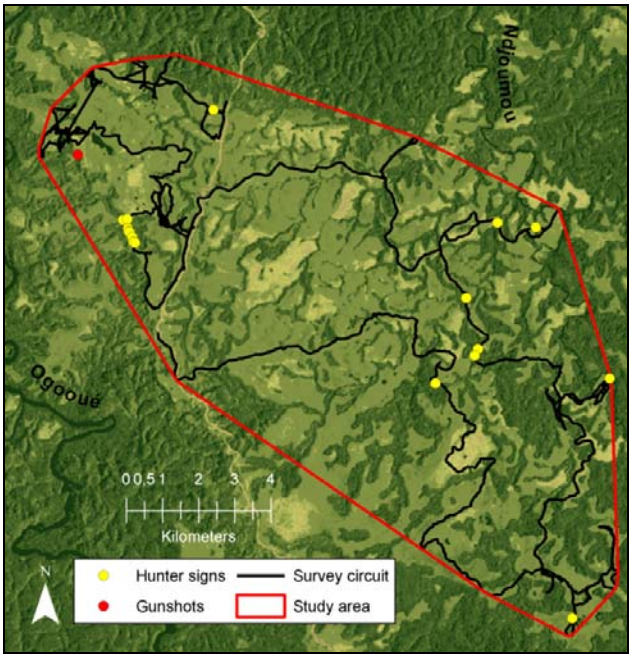


Figure 8. Map showing locations of poaching signs.

Table 2. List of poaching signs recorded in Mopia study area.

Poaching sign	# signs
"Cutting signs" [a)]	15
Gunshots	2
Empty cartridge shells	1
Footprint	1
Total	19

[a)] cutting signs from machete on vegetation along wildlife/hunter trails

Figure 9. Photo taken in a forest near a village in the study site Mopia showing cable snare with remains of a red river hog. Photo: Torsten Bohm.

Table 3. List of larger mammal species observed in Mopia.

Species	# observations	# individuals	group size(s)
Bushbuck	3	3	1
Forest elephant	2	5	1, 4
Forest buffalo	1	1	1
Blue duiker	1	1	1
Yellow-backed duiker	1	1	1

Wildlife was concentrated in the north-western and the south-eastern part of the study area (see Fig. 10–11). Only few signs of ungulates were found in the north-eastern part of the study area. Apart from that, five elephants were observed in a large *bai* at the Ndjoumou in the north-east of the study area (Fig. 12).

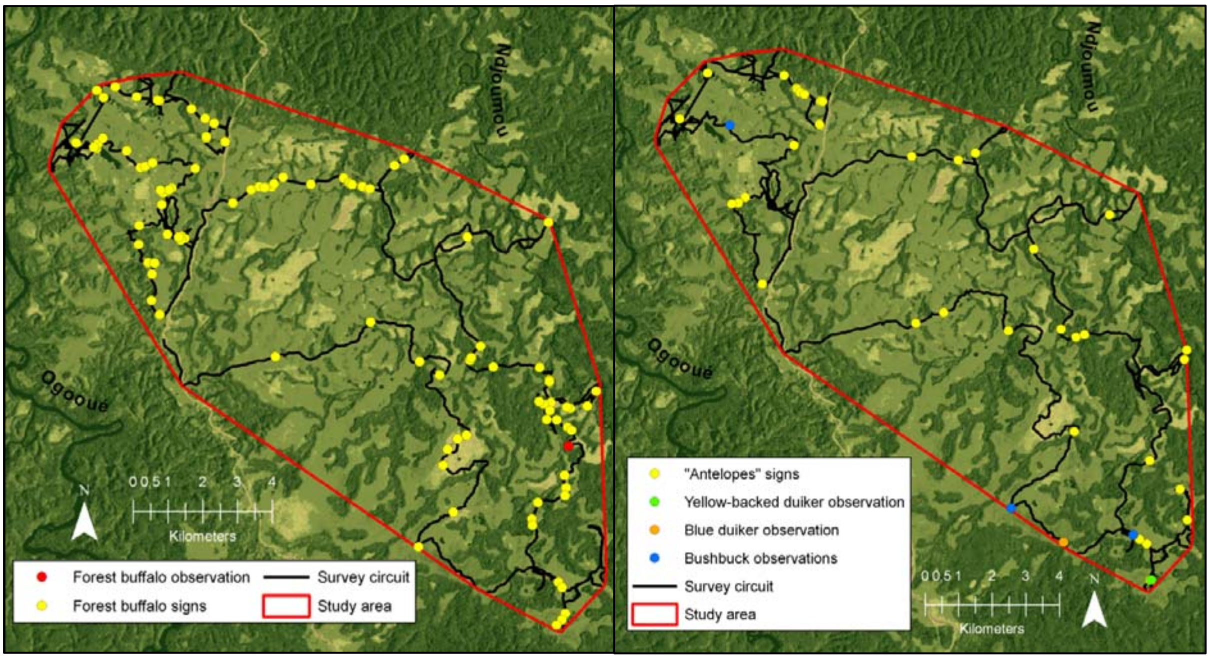


Figure 10. Maps showing locations of forest buffalo (left) and "antelopes" signs (right).

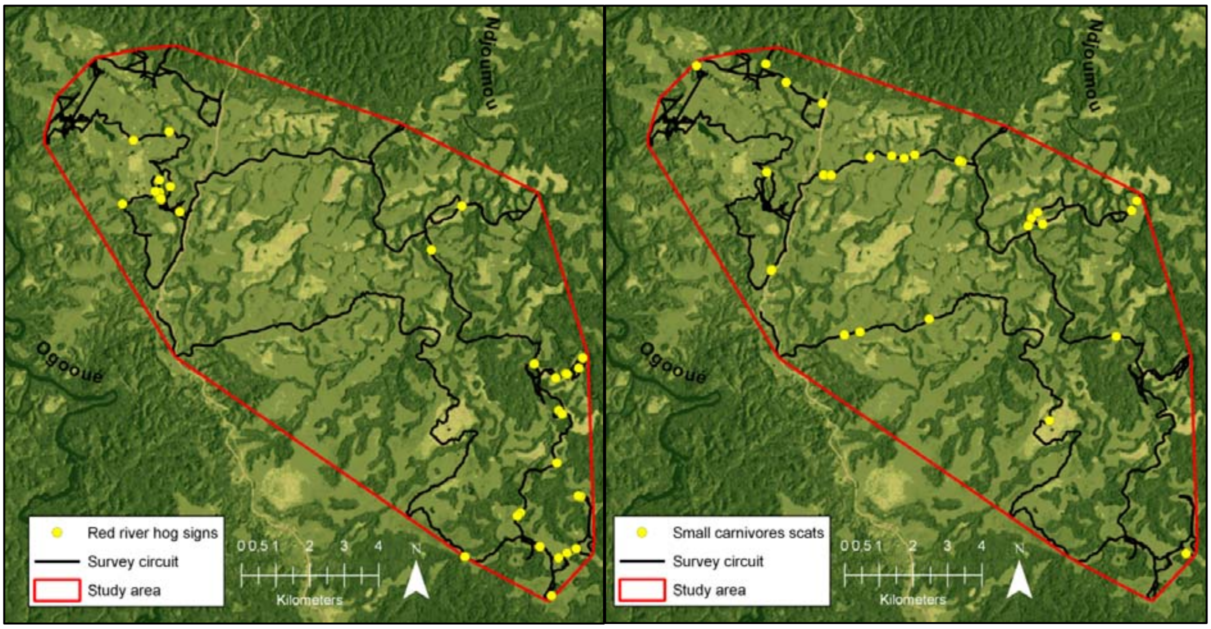


Figure 11. Map showing locations of red river hog signs (left) and small carnivores scats (right).

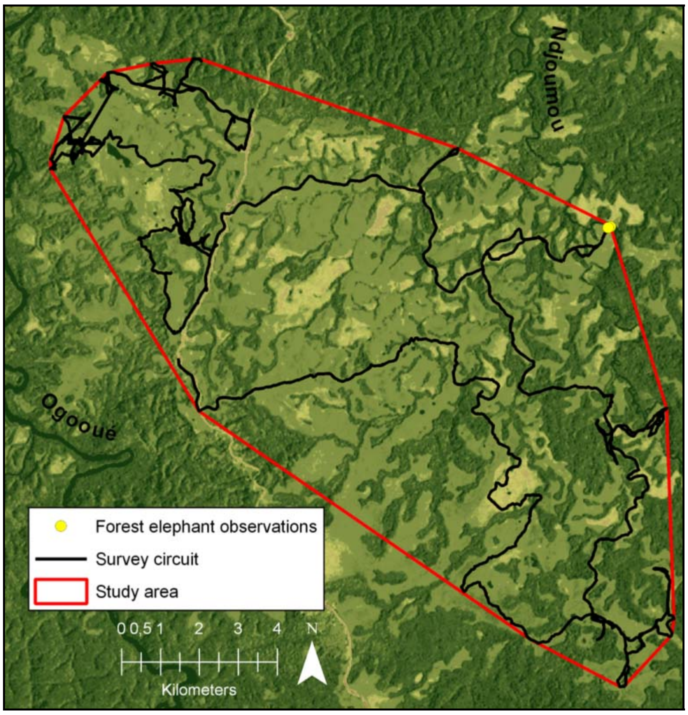


Figure 12. Map showing location of the bai where elephants were observed.

Talks with villagers revealed no significant information on the presence of spotted hyenas. One village chief from a small village stated that he has not seen spotted hyena spoors for more than ten years now. Another villager stated that it is possible to see spotted hyenas in the savannas when the savannas are burnt. However, I imitated whoop calls of spotted hyenas during talks with villagers and none of the villagers could recognize the whoop calls, suggesting that they have never heard these calls before.

In the study area Lékabi a total distance of 212 km was walked (Fig. 13). During this study nine stationary camps were established; once the house of the guardian next to the entrance of the ranch at the southern border was used as camp site (Fig. 13). A total area of 314 km^2 was covered during the study time. As in Mopia, no signs of spotted hyena presence were recorded. Five leopard scats were found in the study area. The five scats were several days old and contained prey remains of "red duikers", red river hog and African brush-tailed porcupine.

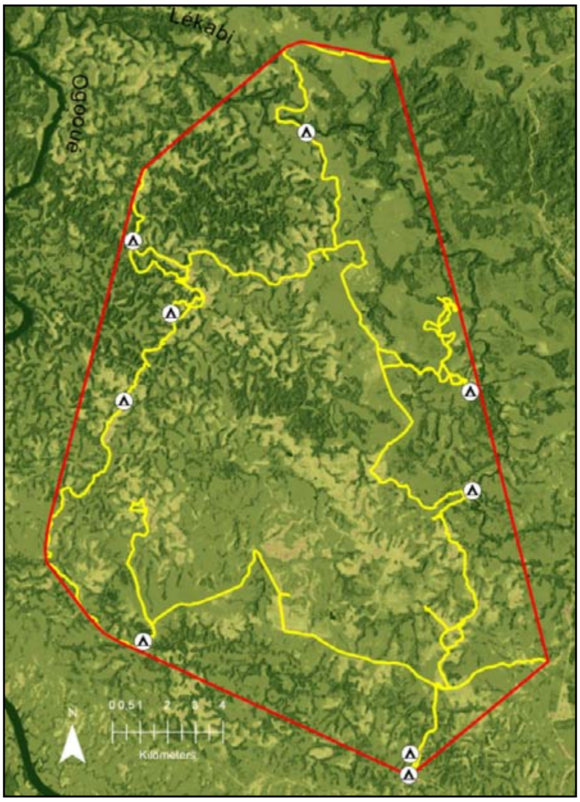


Figure 13. Map of the Lékabi study area, showing the survey circuit and the stationary camps. The most southern camp indicates the house of the guardian. The survey started at the road at the southern border of the study area. The eastern part of the survey area was surveyed first.

The most frequent signs were from forest buffalo, followed by forest elephant, small carnivores and “antelopes” (Table 4). The encounter rates (No. of signs and direct observations / km distance walked) for these species were 0.929, 0.769, 0.519 and 0.0.245 signs/km respectively. Only a small proportion of ungulate dung found in the field was of fresh or recent age (Table 5). In total, only 9 fresh elephant dung piles, representing 6.3 % of all elephant dung piles, were found.

Poaching signs were recorded 43 times (Fig. 14, Table 6). In addition, we met hunters on two occasions (one single hunter/ one group of two hunters) on the main road which connects the entrance of the ranch with the settlement for the “*conservateur*”. These people were identified as hunters as they carried guns. One poacher camp was found in a forest in the north of the study area (Fig. 15). We found a dead owl in the camp (Fig. 15). But it can not be said if the hunters which used the camp have killed the owl. Apart from that, large parts of the savannas in the south-western part of the study area were burnt by hunters.

Table 4. Encounter rates of mammal and poaching signs during field survey in Lékabi. Signs include fresh spoors and dung from forest elephants, buffalo, "antelopes" and red river hogs. In case of red river hog also their conspicuous digging signs and nests were recorded.

Species name	Scientific name	Total # signs (incl. direct observations)	Distance (km)	Encounter rate (# signs / 212)
Forest buffalo	*Syncerus caffer nanus*	197	212	0.929
Forest elephant	*Loxodonta cyclotis*	163	212	0.769
Small carnivores (serval, African golden cat, mongooses, domestic cat, domestic dog) [a)]	*Leptailurus serval, Caracal aurata, Felis silvestris catus Canis lupus familiaris*	110 [b)]	212	0.519
"Antelopes" (incl. all duiker species, water chevrotain and bushbuck) [c)]	*Cephalophus spec., Philantomba monticola, Tragelaphus scriptus, Hyemoschus aquaticus*	52	212	0.245
Poacher	-	43	212	0.203
Red River Hog	*Potamochoerus porcus*	23	212	0.108
African civet	*Civettictis civetta*	16 [d)]	212	0.075
Monkeys	-	7	212	0.033
Leopard	*Panthera pardus*	5	212	0.024

[a)] incl. 104 scats, 4 tracks from middle-sized felids (African golden cat or serval), one unidentified small carnivore track and one direct observation of a marsh mongoose

[b)] Domestic dogs and cats are included as it is possible that some of the recorded scats from smaller carnivores could have originated from domestic cats and dogs. However, although regularly seen, GPS locations of tracks from domestic dogs were not recorded by the field team. Tracks from domestic cats were not found.

[c)] Dung from "antelopes" were not divided into dung from smaller, medium-sized or larger "antelopes".

[d)] includes 5 latrines and 11 single scat findings

Table 5. Proportion of old, recent and fresh ungulate dung piles found in the field.

Species	# signs (dung and spoors)	# spoors / dung	# old / recent / fresh dung % old / recent / fresh dung
Forest buffalo	194	37 / 157	112 / 19 / 26 71.3 / 12.1 / 16.6
Forest elephant	163	19 / 144	129 / 6 / 9 89.6 / 4.2 / 6.3
"Antelopes"	51	28 / 23	18 / 2 / 1 85.7 / 9.5 / 4.8
Red river hog	23	4 / 19	11 / 4 / 4 57.9 / 21.1 / 21.1

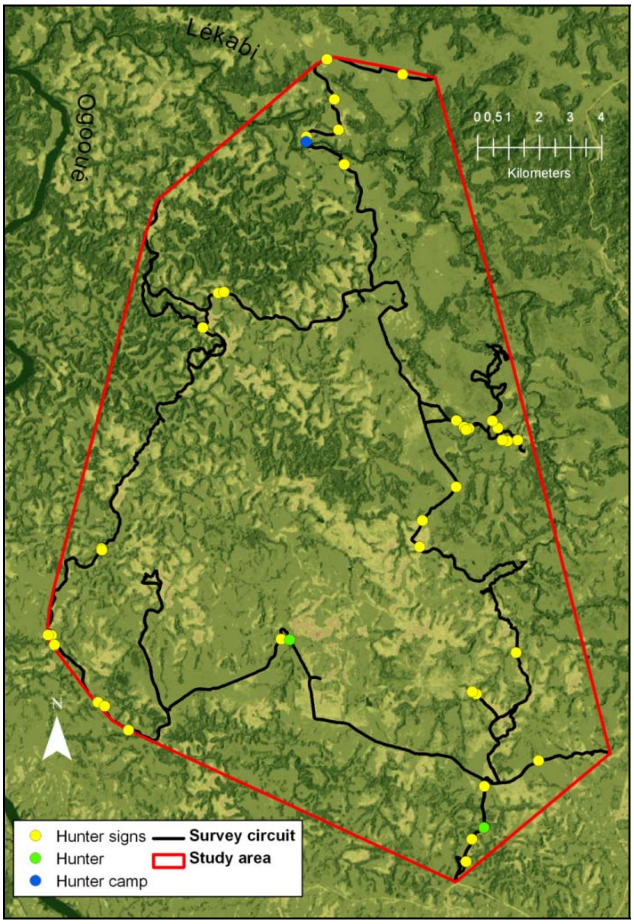


Figure 14. Map showing locations of poaching signs.

Table 6. List of poaching signs detected in the study area Lékabi.

Poaching sign	# signs
"Cutting signs" [a)]	23
Empty cartridge shells	15
Hunter [b)]	3
Footprint	1
Poacher camp	1
Total	43

[a)] cutting signs from machete on vegetation along wildlife/hunter trails

[b)] one single hunter / a group of two young hunters

Figure 15. Poacher camp in a forest in the Lékabi study area. Small picture: Photo of dead owl found in the poacher camp. Photos: Torsten Bohm

Larger mammal species were observed on five occasions (Table 7). Among the observed mammals were forest buffalo, water chevrotain (*Hyemoschus aquaticus*) and marsh mongoose (*Atilax paludinosus*).

Table 7. List of larger mammal species observed during the study time.

Species	# observations	# individuals	group size(s)
Forest buffalo	3	3	1
Water chevrotain	1	1	1
Marsh mongoose	1	1	1

An important finding of the survey in Lékabi was the high occurrence of small carnivore scats (Fig. 16). The majority of these scats were found on roads. Ten of these scats were very fresh. The majority of these scats were likely from mongooses or medium-sized “wild” felids, since tracks from domestic dogs were only found on the main road and no tracks from domestic cats were found in the study area. Apart from that, four sets of tracks from middle-sized felids were found in the study area. The individual paw prints had a maximum length and width of ca. 4 to 4.5 cm and were likely left by a serval or an African golden cat (*Caracal aurata*). A set of tracks from an unidentified small carnivore (marsh mongoose?) was found in one swampy area.

In addition, several scats and latrines from African civets were found (Fig. 16). The latrines and scats could be easily identified as civet latrines and scats as they always contained large amounts of prey remains from millipedes. In addition, the diameters of the scats were always very large (up to 3.9 cm) and often contained completely preserved big tree nuts and had seeds on their surface.

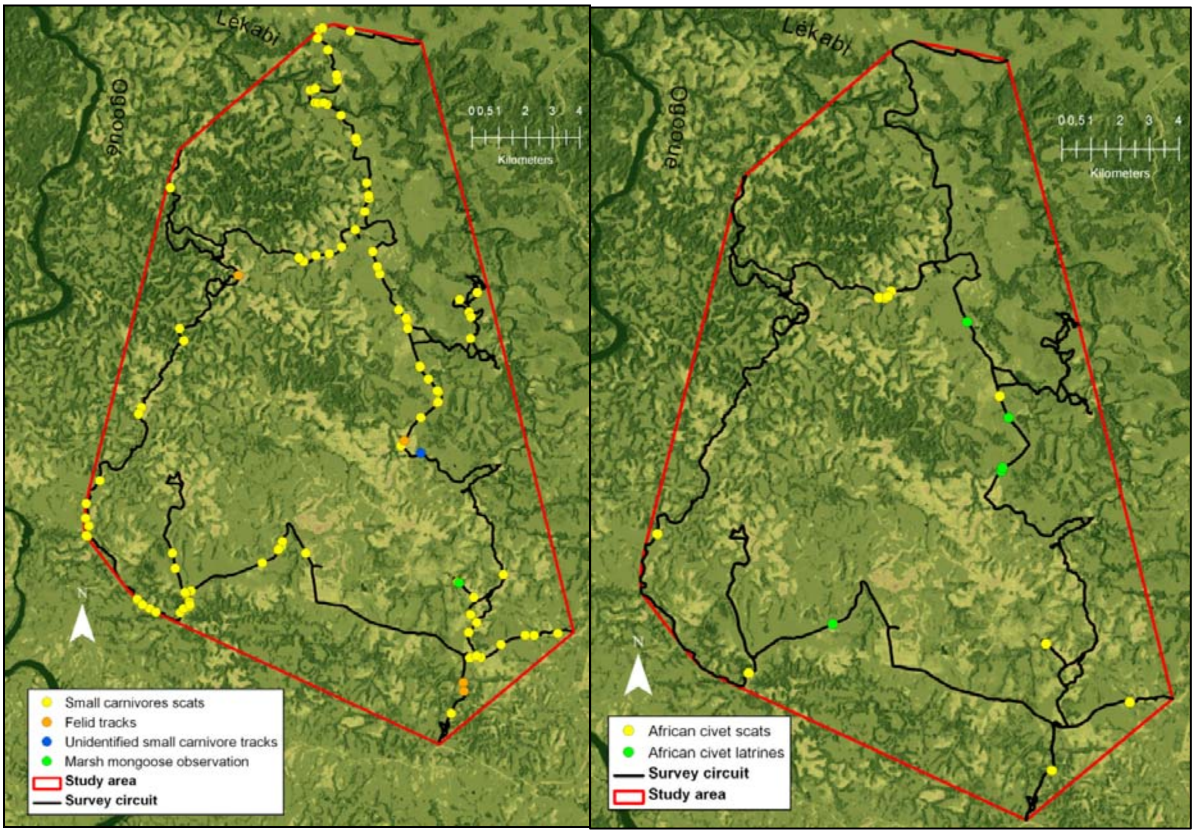


Figure 16. Map showing locations of small carnivores signs (left) and locations of African civet scats and latrines (right).

Signs of ungulates were regularly seen along the entire survey circuit with the exception of the south-western, south-central and most northern part of the study area (Fig. 17 & 18).

During talks with villagers in Okoloville and a small settlement along the road at the southern border of the ranch, villagers stated that they neither have heard the conspicuous whoop calls of spotted hyenas, nor that they have seen a spotted hyena or their tracks yet. During the morning of the 17th of July two villagers visited the guardian of the ranch. At this time we lived in the guardian's house. After the visitors have heard that we conduct a study about spotted hyenas, they suddenly mentioned that they have seen a set of spotted hyena tracks on the road to Okoloville. After showing them a document with different carnivore tracks, incl. tracks from lion (*Panthera leo*), leopard, African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*), one man pointed on the correct spotted hyena track on the paper. However, I asked him if he could outline the size of the tracks he has seen for me. He outlined the length of the track with his fingers and it was clear from the beginning that the tracks he has seen were not left from a spotted hyena. After a short discussion I decided to follow the man to the spot where he has seen the tracks. At our arrival only a few tracks of domestic dogs were found.

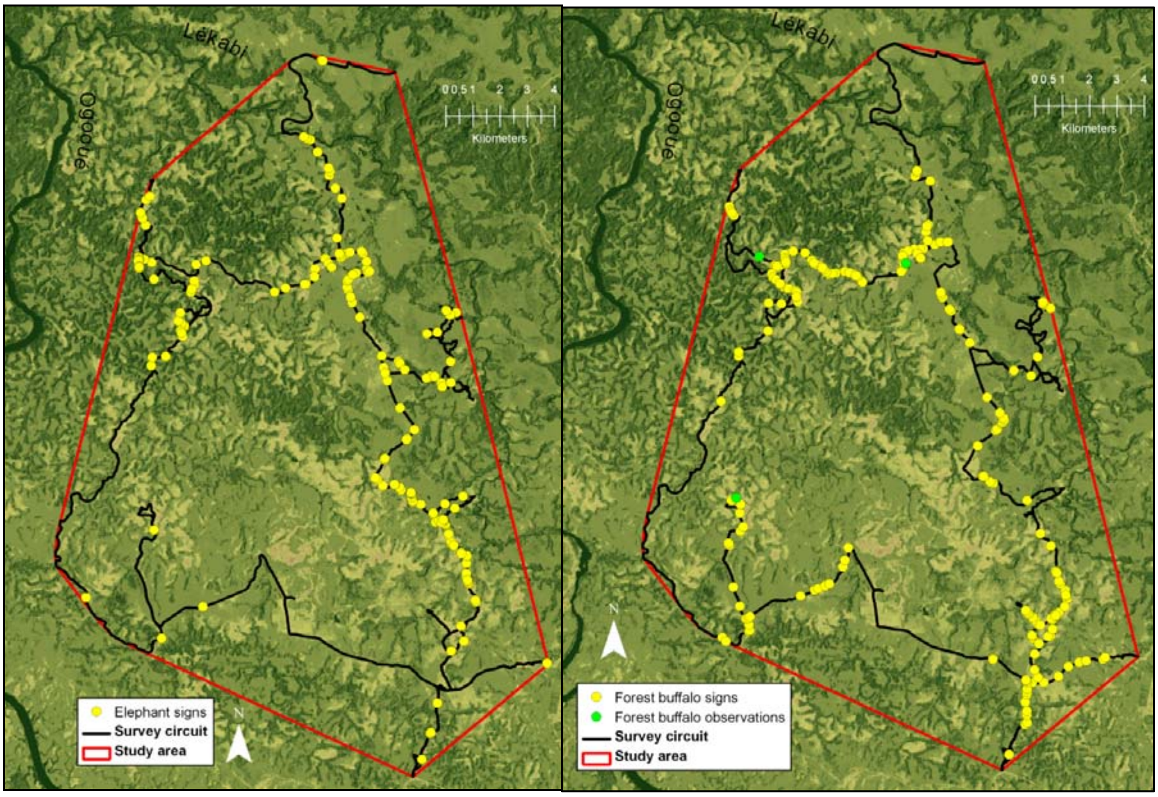


Figure 17. Maps showing locations of forest elephant (left) and forest buffalo (right) signs.

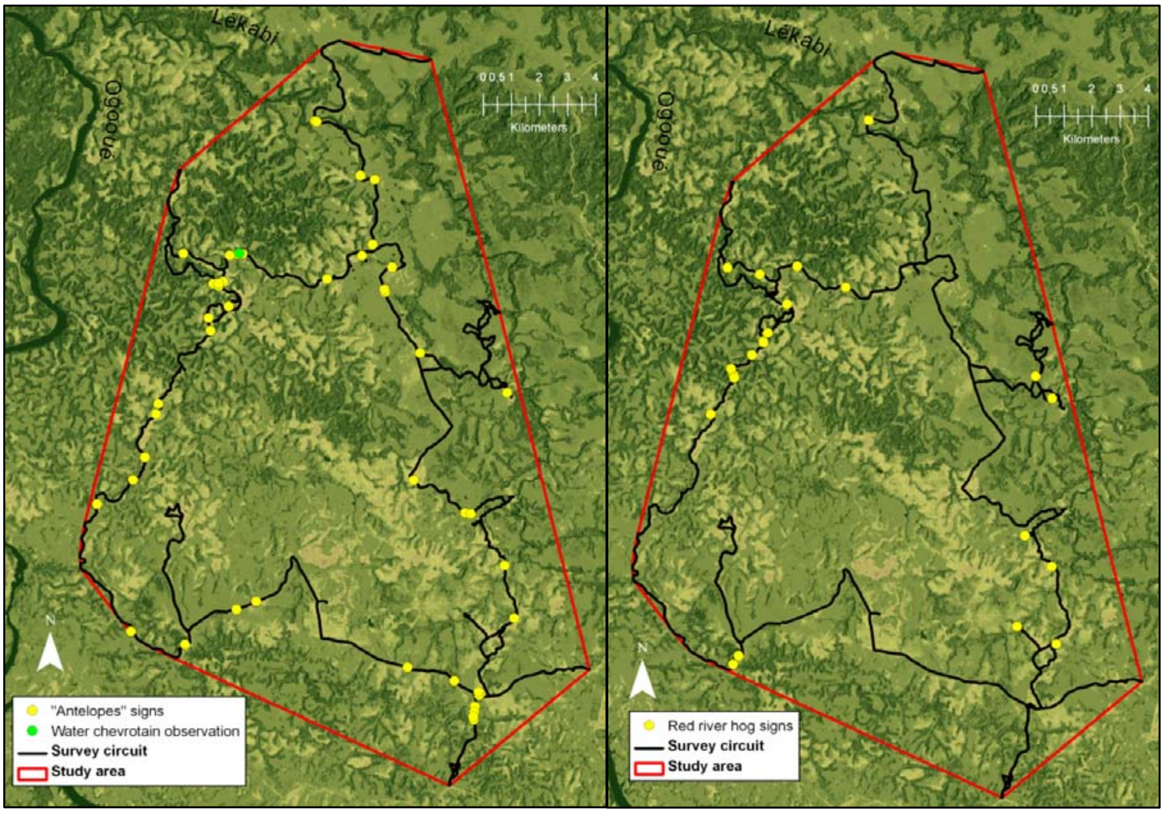


Figure 18. Maps showing locations of "antelopes" (left) and red river hog (right) signs.

In the Batéké Plateaux National Park, a total of 184 km (88 km in the north-western area and 96 km in the north-eastern area) was walked (Fig. 19). As in Mopia and Lékabi, no signs of spotted hyena presence were detected. Signs of red river hog, followed by forest elephant, forest buffalo and "antelopes" were recorded most (Table 8). Signs of aardvarks (*Orycteropus afer*) were also regularly found (Table 8). Wildlife signs where mostly found in the valleys whereas on the hilltops wildlife signs were rare (Fig. 20–23). Poaching signs were recorded 22 times (Table 9), but only in the north-eastern part (Fig. 24). The north-western part was situated close to the camps of PPG (Projet Protection des Gorilles) and poachers likely avoid this area. Sand roads which were likely used by poachers were found in the north-eastern part. Several larger mammal species were observed directly, among them Grimm's duikers, which were seen seven times and often on the hilltops, yellow-backed duiker and forest buffalo (Table 10).

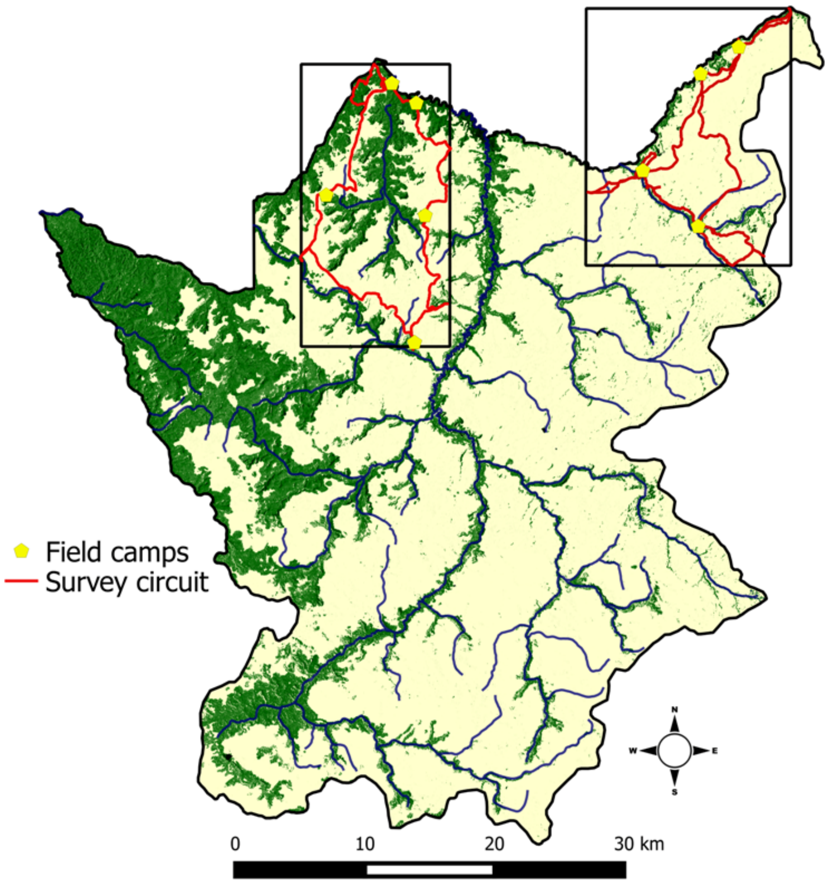


Figure 19. Map of the BPNP study area, showing the survey circuits and stationary camps.

Table 8. Encounter rates of mammal species and poaching signs during field surveys in the Batéké Plateaux National Park. Signs include fresh spoors and dung from forest elephants, buffalo, “antelopes” and red river hogs. In case of red river hog also their conspicuous digging signs and nests were recorded. Other species of interest, such as aardvark and jackal are also included. For aardvark, their conspicuous burrows, digging signs and tracks were recorded.

Species name	Scientific name	Total # signs (incl. direct observations)	Distance (km)	Encounter rate (# signs / 184
Red river hog	*Potamochoerus porcus*	248	184	1.348
Forest elephant	*Loxodonta cyclotis*	216	184	1.174
Forest buffalo	*Syncerus caffer nanus*	180	184	0.978
"Antelopes" (all duiker species, incl. Grimm's duiker, water chevrotain and bushbuck) [c)]	*Cephalophus spec., Tragelaphus scriptus, Hyemoschus aquaticus, Sylvicapra grimmia*	152	184	0.826
Aardvark	*Oryteropus afer*	34	184	0.185
Poaching signs	-	22	184	0.120
Side-striped jackal	*Canis adustus*	11	184	0.060
Monkeys	-	5	184	0.027
Leopard	*Panthera pardus*	5	184	0.027
Mongooses	-	4	184	0.022
Small felids (serval, African golden cat)	*Leptailurus serval* *Caracal aurata*	2	184	0.011
African civet	*Civettictis civetta*	2	184	0.011

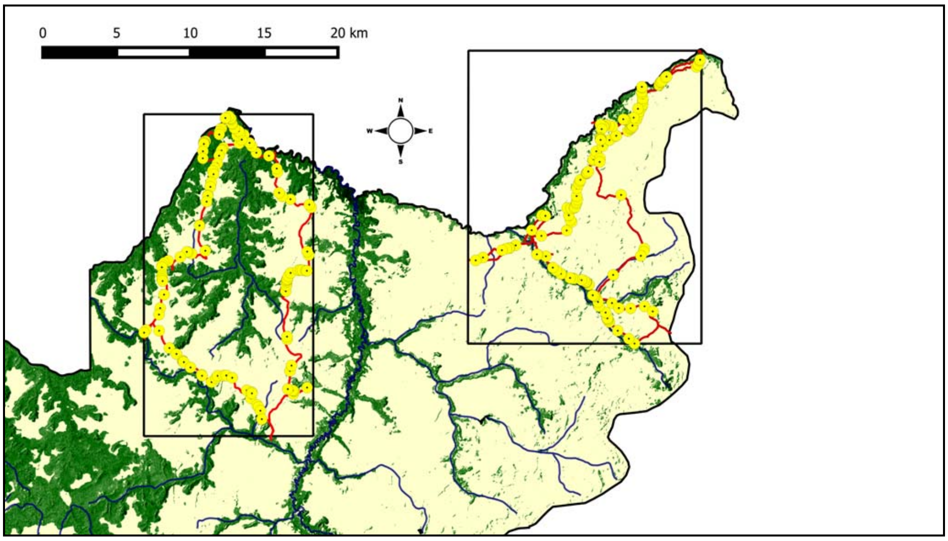


Figure 20. Map showing locations of red river hog signs.

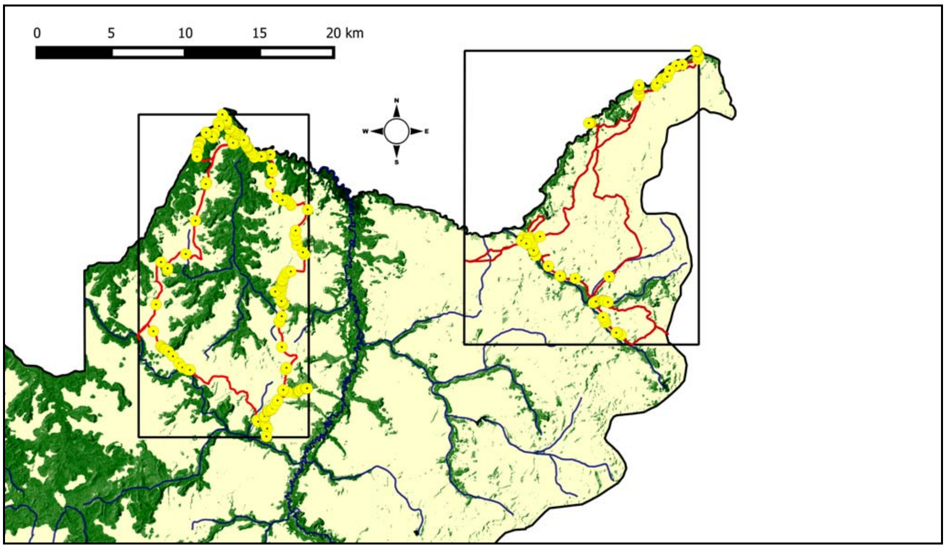


Figure 21. Map showing locations of forest elephant signs.

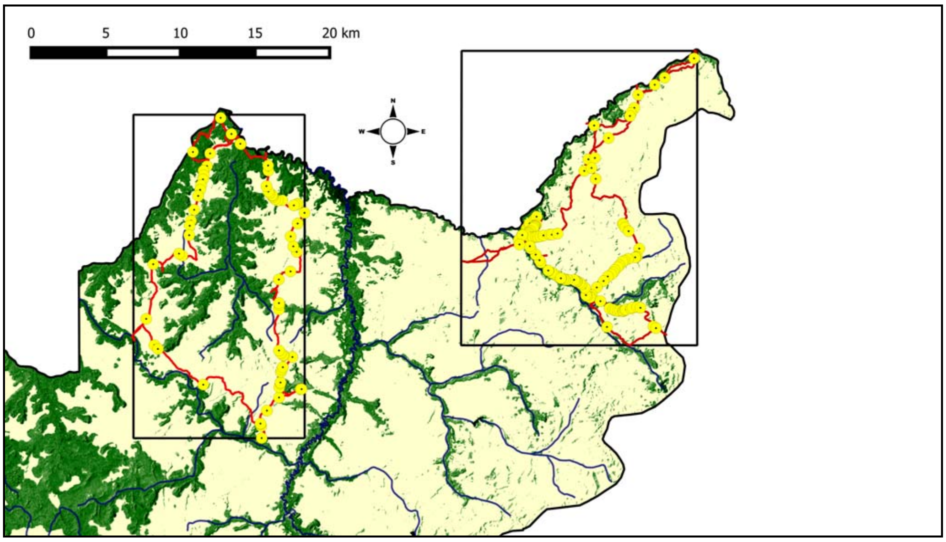


Figure 22. Map showing locations of forest buffalo signs.

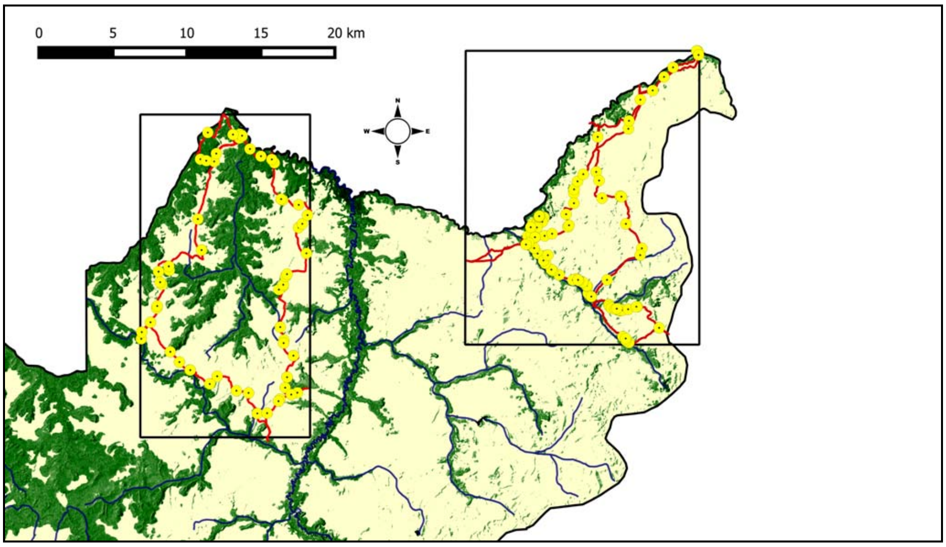


Figure 23. Map showing locations of "antelopes" signs.

Table 9. Overview of poaching signs detected in the BPNP.

Poaching sign	# signs
"Cutting signs" [a)]	9
Markings [b)]	1
Footprints	2
Garbage	1
Burnt savanna areas	2
Roads [c)]	7
Total	22

[a)] cutting signs from machete on vegetation along wildlife/hunter trails

[b)] Markings on trees made by poachers to inform other poachers

[b)] Especially in the north-eastern part where savanna vegetation consists only of small grass without trees (see Figure 4), some roads were visible. Due to the proximity to the Congolese border it can be assumed that these roads were used by Congolese poachers with their pick-ups.

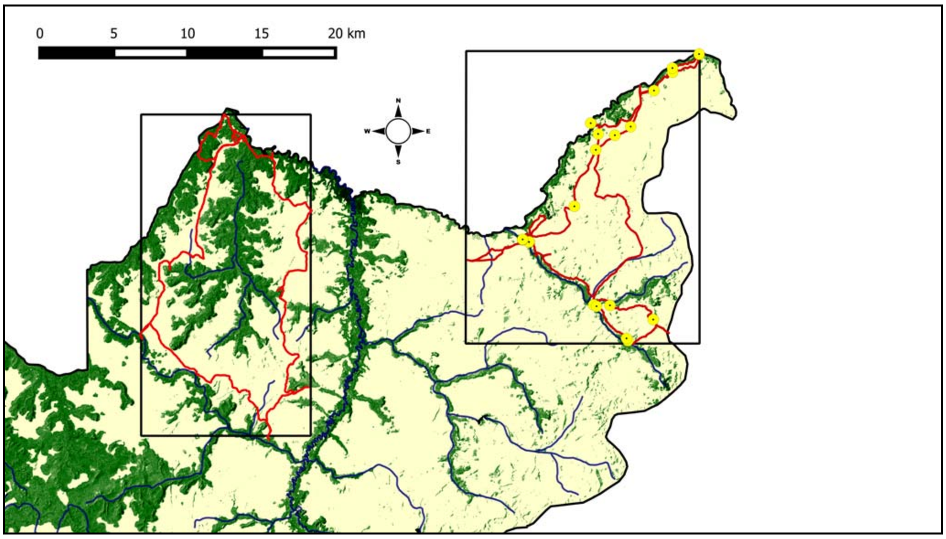


Figure 24. Map showing locations of poaching signs.

Table 10. List of larger mammal species observed in the BPNP.

Species	# observations	# individuals	group size(s)
Grimm's duiker	7	9	1, 3[a]
Bushbuck	2	2	1
Red river hog	1	1	1
Forest buffalo	1	3	3
Blue duiker	1	1	1
African civet	1	1	1
Yellow-backed duiker	1	1	1

[a)] Group contained 2 adults and one sub-adult, probably one male following a female with subadult

Camera trapping study in Mopia

Twenty-four wildlife species were photographed during the camera trapping study (Table 11). Forest elephant was the most photographed wildlife species with 139 independent captures. Forest elephant was photographed at 12 different trap stations (Table 11). The trapping success for other wildlife species was considerably lower. Larger ungulates occurring in the study area, such as red river hog, forest buffalo, yellow-backed duiker and bushbuck, were photographed 37, 12, 8 and 7 times respectively. Nine different carnivore species belonging to three different families were photographed (Table 11). Marsh mongoose was with 19 independent captures the most photographed carnivore species. Servals (*Leptailurus serval*) were photographed 11 times. In total, four different individuals could be identified, among them was a melanistic serval (Fig. 25). Six different duiker species were photographed with blue duiker (*Philantomba monticola*) being the most photographed duiker species. Three hunters, carrying guns and cooking utensils, were photographed at one trap station.

Table 11. Results of the camera trapping study in the study area Mopia.

Order	Family	Common name	Scientific name	# Captures *	Capture rate**	# Trap stations***	Habitat
Artiodactyla	Bovidae	Bay duiker	*Cephalophus dorsalis*	1	0.16	1	F
Artiodactyla	Bovidae	Black-fronted duiker	*Cephalophus nigrifons*	4	0.64	2	S
Artiodactyla	Bovidae	Blue duiker	*Philantomba monticola*	10	1.60	6	F, S
Artiodactyla	Bovidae	Ogilby's duiker	*Cephalophus ogilbyi crusalbum*	9	1.44	3	F
Artiodactyla	Bovidae	Peter's duiker	*Cephalophus callipygus*	1	0.16	1	F
Artiodactyla	Bovidae	Yellow-backed duiker	*Cephalophus silvicultor*	8	1.28	5	F, S
Artiodactyla	Bovidae	Bushbuck	*Tragelaphus scriptus*	7	1.12	4	F, S
Artiodactyla	Bovidae	Forest buffalo	*Syncerus caffer nanus*	12	1.92	5	F, S
Artiodactyla	Suidae	Red river hog	*Potamochoerus porcus*	37	5.93	5	F, S
Artiodactyla	Tragulidae	Water chevrotain	*Hyemoschus aquaticus*	17	2.72	6	F, S
Carnivora	Felidae	Leopard	*Panthera pardus*	3	0.48	2	S
Carnivora	Felidae	Serval	*Leptailurus serval*	11	1.76	5	S
Carnivora	Herpestidae	Black-footed mongoose	*Bdeogale nigripes*	1	0.16	1	F
Carnivora	Herpestidae	Large grey mongoose	*Herpestes ichneumon*	10	1.60	4	S
Carnivora	Herpestidae	Long-nosed mongoose	*Herpestes naso*	2	0.32	2	F
Carnivora	Herpestidae	Marsh mongoose	*Atilax paludinosus*	19	3.04	6	S
Carnivora	Viverridae	African civet	*Civettictis civetta*	7	1.12	3	F, S
Carnivora	Viverridae	Large-spotted genet	*Genetta maculata*	18	2.88	10	F, S
Carnivora	Viverridae	Servaline genet	*Genetta servalina*	8	1.28	4	F
Pholidota	Manidae	Giant pangolin	*Smutsia gigantea*	4	0.64	2	F
Pholidota	Manidae	White-bellied pangolin	*Manis tricuspis*	1	0.16	1	S
Primates	Hominidae	Chimpanzee	*Pan troglodytes*	15	2.40	1	F
Proboscidea	Elephantidae	Forest elephant	*Loxodonta cyclotis*	139	22.28	12	F, S
Rodentia	Hystricidae	African brush-tailed porcupine	*Atherurus africanus*	8	1.28	3	F, S
Rodentia	Nesomyidae	African giant pouched rat	*Cricetomys gambianus*	10	1.60	3	F, S
-	-	Hunter	-	3	0.48	1	F
Total		N = 24 wildlife species + hunter		365	58.49	-	-

* "independent capture event" = (1) consecutive photographs of different individuals of the same or different species, (2) consecutive photographs of individuals of the same species taken more than 0.5 h apart and (3) nonconsecutive photos of individuals of the same species

** # captures/trap nights (624) * 100

*** total number of trap stations = 23

Figure 25. Melanistic serval photographed by camera traps in Mopia.

8.4 Discussion

Spotted hyenas are large carnivores that live in groups, so called clans, and inhabit territories with well-defined borders (Mills, 1990; Henschel & Skinner, 1991). Territories are regularly marked by clan members at latrines and pasting sites (Kruuk, 1972; Mills, 1990). Latrines are sites within or at the borders of a clan's territories, where clan members regularly defecate (Bearder & Randall, 1979). Spotted hyenas leave conspicuous white, large droppings at latrines which can be easily identified in the field (Bohm, 2008). Spotted hyenas use a wide repertoire of vocalisations (East & Hofer, 1991a, 1991b), including the well-known whoop call which can be heard up to a distance of 5 km (East & Hofer, 1991a). During the field studies in Mopia, Lékabi and the BPNP respectively neither latrines, tracks nor vocalisations were recorded, indicating that spotted hyena populations are not present in either of the study areas. Bout *et al.* (2010) recorded spotted hyena spoors in Mopia in July 2008 and January 2009 respectively. The recorded spoors in 2009 comprised footprints of three individuals (two adults, one juvenile). The spoors recorded by Bout *et al.* (2010) in January 2009 suggest that they could have belonged to individuals that belonged to a clan since also spoors from a juvenile spotted hyena were recorded. Juvenile spotted hyenas begin to accompany adults on foraging trips at an age of seven months (Mills, 1990). Foraging trips involving juveniles can be quite extensive: Mills (1990) observed a seven-month-old cub which accompanied a group of adults for 29 km in the Kalahari ecosystem. However, normally, foraging trips with cubs are not this extensive (Mills, 1990). The spotted hyena population in the OKNP in the north of Republic of Congo is situated about 250–300 km away from the three study areas. Although spotted hyenas can travel up to 80 km per night on foraging trips and often do not visit their den sites for many days (Mills, 1990), it remains a mystery if the observed hyena spoors in 2009 in Mopia were really left by a group of spotted hyenas from the OKNP. It is also possible that these spoors were left by a group of spotted hyenas that either inhabited this area or an area nearby. However, since no spotted hyena signs were recorded during the field studies, it can be assumed that spotted hyenas do not live in the three study areas. Furthermore, none of the interviewed villagers have ever heard the conspicuous spotted hyena whoop calls or seen spotted hyena latrines in the recent past. This indicates that spotted hyenas were never common in this area. Spotted hyenas are highly vulnerable to snaring and snaring is the most important mortality factor for spotted hyenas in the Serengeti (Hofer *et al.*, 1993). Although hunting with guns is the preferred hunting method by villagers surrounding the study areas, snaring with illegal metal snares also occurs from time to time (pers. comm. villagers and research assistant) and snares were also found in one of the study areas. My two research assistants also said that hunters shoot on everything and do not hesitate to kill larger or smaller carnivores. In addition, the savannas in Mopia and Lékabi are highly frequented by humans and burnt by hunters on a regular basis. This massive human disturbance could be the reason why spotted hyenas are not present in this area anymore or why spotted hyenas left this area respectively, probably a long time ago. (In Lékabi, I think, spotted hyenas were mistakenly blamed for the killings of the village dogs and I believe that spotted hyenas were never present in this area.)

The OKNP in the Republic of Congo harbours probably the largest population of forest buffaloes in the Congo Basin (East, 1999). Forest buffalo was also the most frequent prey found in scat samples from spotted hyenas in the OKNP (see chapter 3). The continuous disappearance of forest buffaloes from open habitats in Congo and Gabon during the last decades (East, 1999) appears to be the main reason for the simultaneous disappearance of spotted hyenas in these areas (Henschel, 2009). Thus, a large population of forest buffaloes is potentially required to support viable populations of spotted hyenas in the Congo Basin. Many buffalo signs were detected in Mopia, but often only single buffalo dung piles were found, indicating that this area is not inhabited by larger groups of buffaloes. For instance, in the OKNP, large groups containing 50 to 100 animals can be regularly seen (Bohm, 2008; Chamberlan *et al.*, 1998). Additionally, villagers in Mopia regularly hunt forest buffaloes - also during the non-hunting season (pers. comment research assistants) - suggesting that hunting pressure on forest buffaloes is high here.

Results from camera trapping study confirm the results obtained from reconnaissance surveys. In general, capture success for wildlife species in Mopia was low. The camera trapping study in Mopia can be compared well with the camera trapping study I did in the OKNP from November 2011–January 2012 (see Appendices I–II in chapter 7). During this study in the OKNP I used the same sampling protocol as in Mopia: camera trapping was conducted in two sampling blocks, whereas each sampling block was operational for ca. four weeks and consisted of eleven trap stations and the trapping polygon had, with 167 km^2, also a similar size. Overall trapping success in the OKNP was about three times higher than in Mopia and larger ungulate species such as forest buffalo and bushbuck were frequently photographed (see Appendix II in chapter 7).

In conclusion, population numbers of potential spotted hyena prey species, such as forest buffalo, in Mopia and Lékabi are probably to low to support healthy spotted hyena populations. Furthermore, both areas are characterized by high levels of human encroachment and hunting. In case of a return of spotted hyenas in these areas, spotted hyenas would be in direct competition with hunters for food and confronted with a human population which is hostile to large carnivores. Some of the elderly villagers still had knowledge about spotted hyenas, but knowledge about spotted hyenas among the young villagers was poor. However, knowledge was limited to the common prejudices and spotted hyenas were considered as "*méchant*" (evil) and coward scavengers. If spotted hyenas would return into this area they would probably face the same fate as the spotted hyena that was killed by a mob of scared people in the village of Koulamoutou in 2004, or they would be killed by a villager with a rifle and a fast right hand.

With the BPNP, a sufficient large area of protected habitat which can sustain healthy numbers of forest buffaloes and other potential spotted hyena prey species is situated just nearby. Poaching in the park is still very high (pers. comment N. Bout) and poaching is carried out with guns and wire snares. Provided that effective law enforcement measures are implemented, the park could sustain a healthy spotted hyena population. The protection of the last spotted hyena population in the OKNP is of high priority. Establishment of other spotted hyena populations in suitable open habitats in Central Africa is crucial in order to enhance the survival chances for spotted hyenas in Central Africa, whereas the OKNP population could help to repopulate these areas. “Natural translocations” through the provision and protection of wildlife corridors are recommended for this purpose. The vast forest-savanna mosaics of the BPNP are suitable as prime habitats for spotted hyenas and until the middle of the 20th century these habitats were inhabited by spotted hyenas (Malbrant & Maclatchy, 1949). By protecting wildlife corridors and establishing more protected areas within the huge area of forest-savanna mosaics inhabited by low density of humans (CIESIN & CIAT, 2005), long distance movements and exchange of spotted hyenas could be supported.

Chapter 9: General discussion

The purpose of the present study was to collect basic information on the status and ecology of the spotted hyena (*Crocuta crocuta*) in the Odzala-Kokoua National Park (OKNP). The OKNP represents the last refuge for this species in the Central African Congo Basin. The study focused on

1) estimation of population abundance and density, parameters which represent important information for status assessment and management strategies,
2) investigation of the diet, which gives information about the prey base needed to be secured for the persistence of this keystone predator in the OKNP (and in other potential suitable habitats in Central Africa),
3) investigation of den sites and characteristics, which gives important baseline information for better protection of these key locations which are crucial for the reproductive success in the population, and
4) investigation of the genetic diversity, which gives a cue about the threats the population is facing due to its small size and high isolation.

In addition, I applied and developed novel methods which give insights into compositions and sizes of clans in spotted hyena populations.

I also collected basic information on the serval (*Leptailurus serval*) population in the OKNP. The serval has been received only little scientific attention so far. In fact, this study provided the first robust population size and density estimate of this medium-sized carnivore in its Central African distribution range. Moreover, I collected basic information on the ecology of the mammal community in the OKNP's forest-savanna mosaic with the help of camera traps and I proved that spotted hyenas are not present in southeast Gabon.

9.1 Methodological considerations

Overall, the non-invasive tools that I have used (scat analysis, camera trapping and acoustic monitoring) proved to be very effective for studying ecology and status of spotted hyenas (and other animals) in the park. An important aspect of this study was the use of professional camera traps. Reconyx camera traps are very pricey but were crucial for the success of this study. With their short trigger time of 0.2 s and their ability to continuously record pictures without intervals, thousands of high quality pictures could be obtained with which it was possible to determine not only spotted hyena groups, but also sex of recorded individuals. The high masculinisation of female spotted hyenas makes it difficult to determine sex of individual spotted hyenas. However, with the help of Reconyx camera traps, often dozens of high quality close up pictures for individual spotted hyenas were available, with which it was possible to determine sex. Thus, future studies wishing to determine population sizes of spotted hyenas should aim to use only professional camera traps such as Reconyx. A further important aspect of this study was the long duration of the second camera trapping study. As spotted hyenas regularly forage outside their territories for prolonged periods, very short camera trapping studies might fail to record all individuals in the study area.

Furthermore, camera traps allowed to determine fates of individual spotted hyenas, making camera traps a powerful tool for monitoring of demographic parameters in spotted hyena populations.

Camera trapping with Reconyx camera traps also proved to be very effective for studying influence of human disturbance and habitat characteristics on the mammal community in the park's forest-savanna mosaic. In addition, camera traps provided valuable information on temporal activity patterns of spotted hyenas' main prey species in the park and, hence, gave insights into the foraging ecology of spotted hyenas. Furthermore, since camera traps also produced pictures of poachers as well as of animals suffering from cable snare wounds they could also be used for investigating poaching levels in the study areas.

Several hundreds of scats were collected during the study periods. However, among them were also many scats which contained only bone powder or many very old scats which contained no hairs anymore. In addition, it was important that I also collected spotted hyena regurgitations. Spotted hyena regurgitations provided additional information on important prey species, such as pangolins, whose remains are difficult to detect in scat samples. Furthermore, regurgitations allowed to some extent also determination of age of the consumed prey species as regurgitations often contained completely preserved prey remains such as horns and hooves from which the age of the consumed prey species could be assessed. Scats mostly only contained prey hairs, or sometimes small pieces of other prey remains, from which it was virtually impossible to determine the age of prey species. In general, spotted hyena regurgitations are an important additional source of information and should be generally included in studies aiming to determine diet of spotted hyenas. Regurgitations are also easy to find along roads and spotted hyena trails. Also, regurgitations found in the study area always contained spotted hyena hairs, making them undisputable as having originated from spotted hyenas.

Unfortunately, it was difficult to find very fresh scats for genetic analysis. Due to the spotted hyenas' nocturnal activity in the park, scats are deposited during the night and, thus, were already too old for collection when study area could be first visited during morning hours. Therefore, others methods, such as hair traps, might be more appropriate for obtaining high quality samples for genetic analysis.

Acoustic recorders worked very well and provided hundreds of records of spotted hyena whooping bouts. Studying spotted hyena populations and compositions of single clans by discriminating between individuals by features of their vocalisations appears to be a feasible method. However, more research needs to be done to find candidate parameters which allow individual discrimination. I used recorders which autonomously recorded sounds over a long period. The acoustic recorders that I have used can also be operated with car batteries. The high capacities of car batteries could operate a single recorder for many weeks or even months, making this methodology highly convenient in studies of spotted hyena populations in which not enough manpower is available or in which the study area includes remote areas that can not be visited on a regular base.

9.2 Management implications for spotted hyenas in the Odzala-Kokoua National Park and recommendations for follow-up studies

The spotted hyena population in the OKNP is critically endangered. With probably just 69 remaining individuals, the population is on the verge of extinction. Urgent conservation actions are needed to preserve the population for the future. Complete eradication of poaching in and near areas which spotted hyenas inhabit in the park is necessary to achieve this goal. Surveys in areas which could not be surveyed during this study, such as the savannas situated in the very south of the park, need to be conducted to get a more comprehensive picture on spotted hyena numbers and distribution in the park. More samples for genetic analysis are needed to get more robust results on the genetic make-up of the population. Due to the small population size, introduction of new individuals might be inevitable. Animals from candidate populations can be found with the help of genetic data that were collected during this study. New individuals can boost population growth and at the same time bring new genetic material into the population. Establishment of a second population in the Batéké Plateaux might be necessary for the long-term conservation of this species in the Congo Basin. The Batéké Plateaux National Park in southeast Gabon is a sufficiently large protected area that could potentially support viable populations of spotted hyenas and their main prey species. However, well-protected wildlife corridors are needed to support dispersal of spotted hyenas from the OKNP into other suitable habitats. Large carnivores, such as spotted hyenas have great ecological value to the ecosystems they inhabit. Thus, their disappearance from the OKNP's forest-savanna mosaic can have a broad array of consequences for this ecosystem. The preservation of this precious last spotted hyena population in the Congo Basin should be pursued as priority conservation goal by the current park management and an action plan, for which data from this study can be used, should be developed to save this unique and precious spotted hyena population from extinction.

Summary

The spotted hyena (*Crocuta crocuta*) is a social large carnivore that lives in groups, so called clans. The spotted hyena is the most abundant large carnivore in Africa and inhabits a wide range of habitats in sub-Saharan Africa. Due to their unique social system, in which females play the dominant role, spotted hyenas have become popular research objects. Like other large carnivores in Africa the spotted hyena is threatened by habitat loss and direct conflict with humans. As a result, many spotted hyena populations are now rapidly declining, even in protected areas. Whereas spotted hyenas have been well studied in eastern and southern Africa, nothing is known about their ecology and conservation status in Central Africa.

Most of Central Africa is covered by the tropical rainforests of the Congo Basin. The Batéké Plateaux area, covering almost two-thirds of the Republic of Congo and extending into neighbouring Gabon, is the remnant of an ancient large savanna ecosystem which once covered most of the Congo Basin. Until the 1940ies large social carnivores such as spotted hyenas, African wild dogs (*Lycaon pictus*) and lions (*Panthera leo*) were once widespread in the savannas of the Batéké Plateaux. A dramatic decline occurred during the second half of the 20th century resulting in the complete extinction of lions and African wild dogs and the nearby extinction of spotted hyenas. Today, spotted hyenas can only be found in the small forest-savanna mosaic of the Odzala-Kokoua National Park (OKNP), situated in the northwest of the Republic of Congo. The spotted hyena population in the OKNP represents the only remaining spotted hyena population in the Batéké Plateaux and the Congo Basin. In order to support successful conservation strategies accurate monitoring of this population is necessary.

The present dissertation investigated population status and ecology of the spotted hyena in the OKNP. I also collected basic information on population size and density of servals (*Leptailurus serval*) in the OKNP. In addition, I used data from camera trapping to provide basic information on the distribution and occurrence of other wildlife species in the OKNP's FSM, which can support management strategies for spotted hyenas. Furthermore, I investigated the situation for spotted hyenas and other wildlife species in three regions in southeast Gabon. In chapter 2 I estimated spotted hyena population size as well as trends in the population size based on data from camera trapping studies. I conducted camera trapping studies in the park's forest-savanna mosaic from November 2011 to February 2012 and July 2013 to March 2014. In addition, I used data from a camera trapping study which was conducted by the park management in forested areas outside the park's forest-savanna mosaic between December 2012 and May 2013. I was able to identify sex, age and clan memberships of recorded individuals from camera traps pictures. Clans and clan membership were determined by analysing spotted hyena groups recorded by camera traps. By the end of March 2014 I observed 69 individuals, among them 50 adults, 11 subadults

and 8 cubs. Five clans, including 52 individuals, inhabited the park's forest-savanna mosaic. Nine individuals, including 5 adults and 4 subadults, were only recorded in forest clearings in the park's forest bloc. Further 8 individuals were identified as transients with no affiliations to either of the identified clans in the forest-savanna mosaic. Population density was estimated as 6.42 individuals / 100 km^2. Camera traps showed pictures of spotted hyenas with cable snare wounds. Almost 50 % of individuals which were recorded during the first camera trapping study in the park's forest savanna mosaic were not recorded during the second camera trapping study. In addition, 11 individuals have likely died during the course of the second camera trapping study. The spotted hyena population in the OKNP is now at the verge of extinction and poaching with illegal wire snares is probably the main reason for that. Unless this problem can not be solved immediately, extinction of this highly precious spotted hyena population might be imminent within the nearest future. Furthermore, the high isolation of this last remaining spotted hyena population in the Congo Basin makes it highly vulnerable to stochastic factors, such as outbreaks of diseases, and processes which can have negative impacts on the population's genetic diversity, such as inbreeding.

In chapter 3 I analysed the diet of the spotted hyena in the OKNP. For this, I collected spotted hyena scats and regurgitations in the park's forest-savanna mosaic. Diet was determined by analysis of prey hairs and remains in 402 scats and regurgitations. Twenty-six different prey species were identified in the diet, with forest buffalo (*Syncerus caffer nanus*) accounting for 25.2 % of all prey items identified, followed by red river hog (*Potamocherus porcus*) (17.5 %) and bushbuck (*Tragelaphus scriptus*) (16.4 %). These three dominant prey species in the diet predominantly occur in the park's forest-savanna mosaic. The data suggested that the long-term survival of spotted hyenas in the OKNP will likely depend on the abundance of these prey species. In addition, I estimated overlaps of temporal activity patterns between spotted hyenas and their main prey species through the coefficient Δ with data from the camera trapping study conducted from July 2013 to March 2014. The average Δ across spotted hyenas' main prey species was 0.65 (±SE 0.10). Despite its importance in the prey, there was little overlap between the highly nocturnal spotted hyena and their largest prey species, the cathemeral forest buffalo, suggesting that spotted hyenas invest high levels of energy searching for food.

In chapter 4 I analysed population density and activity patterns of servals in the OKNP. For this, I used data from the camera trapping study conducted from July 2013 to March 2014. I recorded 51 individuals, among them were four kittens, four subadults and 43 adults. Almost two-thirds of the individuals recorded belonged to the servaline morph, which has a pattern mutation of small 'freckled' spots. Using spatially explicit capture-recapture methods the serval density in the park's forest-savanna mosaic was estimated as 11.20–11.72 individuals per 100 km^2. Male servals were largely nocturnal whereas female servals were mainly diurnal with a peak in the morning hours. Differences in capture rates and activity patterns between male and female servals were likely related to the occurrence of spotted hyenas. Spotted hyenas were highly nocturnal and, consequently, had a higher overlap in activity patterns with male servals. Despite its wide distribution in Africa, the serval has received only very little scientific attention so far. This study provided the first robust density estimates for this medium-sized carnivore in Central Africa.

In chapter 5 I analysed den site selection of spotted hyenas in the park and the applicability of acoustic monitoring to determine number of individuals within a clan. For this, I placed acoustic recorders at a communal den site. Recorders were operational from mid-October 2013 to end of February and produced 907 hours of recordings. For analysis, whooping bouts of spotted hyenas were used. In total, 223 whooping bouts of sufficient quality were recorded at the communal den. One-hundred-and-forty-one whooping bouts were identified as whooping bouts from adults and 92 whooping bouts were identified as whooping bouts from cubs. To discriminate between individuals by features of their vocalisations, acoustic parameters of whoops and whooping bouts were measured. First results showed that variations within whooping bouts of adults and cubs is large. This makes it difficult to find candidate parameters for single whoops or whooping bouts on which individual identification can be based. It is therefore recommended to do an acoustic study with known individuals first to determine which parameters can be used for identification of individuals.

During three field studies between 2008 to 2014 I could find five spotted hyena communal den sites in the park's forest-savanna mosaic. In 2008 and 2013, I could find occupied den sites. The other three den sites were already abandoned by the time they were discovered. Termite mounds in the savannas served as communal den sites. A characteristic large termite mound with a varying number of large entrances served as main den. Several smaller dens could be found in the nearest surroundings of this main den. These smaller dens were smaller termite mounds with only one entrance and served probably as short-term shelter for cubs. Burrows in the termite mounds were likely excavated by aardvarks (*Orycteropus afer*) and giant pangolins (*Smutsia gigantea*). One communal den site was found just 10 meters next to a park road. By the time this den site was discovered signs of recent use were found. Since this road was just built recently it is likely that spotted hyenas have abandoned this den site during construction of this road. Communal dens are the centres of activities of spotted hyena clans and the protection of communal den sites is crucial for the conservation of spotted hyenas in the park. Females with cubs that are forced to abandon den sites due to human disturbance expose their offspring to potential dangers such as poachers, adult spotted hyenas from other clans or other large carnivores. Disturbance of communal den sites should therefore be avoided. Thus, it is recommended to do further surveys in the park's forest-savanna mosaic in order to find spotted hyena communal den sites. In the future, locations of these communal den sites should be considered before infrastructure projects, such as roads, are implemented or nearest surroundings of areas in which infrastructure projects are planned should be surveyed for communal dens in advance respectively.

In chapter 6 I analysed the genetic diversity in the spotted hyena population. Furthermore, genetic analysis was done to check if the OKNP's spotted hyena population has gone through a bottleneck in the recent past and if deleterious genetic processes, such as inbreeding, have already occurred in the population. Genetic material was obtained from fresh scat samples which were collected between 2008 and 2014. To investigate the genetic make-up, I used microsatellite profiling. In total, 20 samples were of sufficient quality allowing genetic analysis, resulting in a total number of 14 different genotyped animals. A total of 19 different alleles on nine different loci could be identified. The population did not show deviation from Hardy-Weinberg-Equilibrium (HWE), significant heterozygote excess or deficiency. One locus exhibited significant deviation from HWE. The inbreeding coefficient for this locus was also very high, suggesting that inbreeding in the population is present and affects this locus. One pair of loci showed significant linkage disequilibrium. In comparison with the Serengeti spotted hyena population, the OKNP population showed lower numbers of alleles at all loci and lower observed and expected heterozygosities at eight loci. Tests for bottleneck events showed that the population did not suffer from a recent bottleneck. In addition, I estimated genetic effective population size (N_e) from genetic data. Estimates for N_e ranged between 10.6 and 28.4 animals. Unfortunately, the small sample size of only 14 genotyped individuals does not allow to draw final conclusions on the genetic make-up of the OKNP's spotted hyena population. But, given the small population size this very small sample size might be already a good indicator of the population's genetic make-up. According to the results, the population appears to already be suffering from low genetic diversity and inbreeding. Lack of influx of new individuals from other populations due to the high isolation of the OKNP's population is probably the main reason for that. Introduction of new individuals into the population might therefore be necessary in order to bring new genetic material into the population.

In chapter 7, I analysed data from the long-term camera trapping study I conducted in the OKNP from July 2013 to March 2014. I analysed trap success and temporal activity patterns for recorded wildlife species as well as influence of habitat characteristics and human activities on the mammal community in the park's forest-savanna mosaic. In total, 37 wildlife species were recorded. All terrestrial species were photographed after 78 sampling occasions (= 2025 total trap nights). Forest elephant (*Loxodonta cyclotis*) was the most photographed wildlife species, followed by spotted hyena, bushbuck, forest buffalo, blue

duiker (*Philantomba monticola*) and red river hog. In total, 13 carnivore species were photographed, including leopard (*Panthera pardus*), African golden cat (*Caracal aurata*), large grey mongoose (*Herpestes ichneumon*) and honey badger (*Mellivora capensis*). Trap stations which were installed in forested areas had very high trap successes. Trap stations located in forested areas also recorded more different species than trap stations located in savannas. There was a significant negative relationship between distance of trap stations to forested areas and number of different species recorded. In addition, certain species, such as blue duiker and Peter's duiker (*Cephalophus callipygus*), showed a strong preference for areas situated in close proximity to forests. Carnivore species which were exclusively or mainly nocturnal were, for example, large-spotted genet (*Genetta maculata*), spotted hyena and African civet (*Civettictis civetta*). Aardvark, hippopotamus (*Hippopotamus amphibicus*), forest elephant and yellow-backed duiker (*Cephalophus silvicultor*) were also mainly nocturnal. The great ape species, chimpanzee (*Pan troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla*), showed a strong diurnal activity. Bushbuck and forest buffalo were mainly cathemeral. The Lékoli river divides the park's forest-savanna mosaic into a southern and a northern savannas sector. Currently, tourist and park staff activity is restricted to the southern savannas sector. I compared capture rates between these two savanna sectors for different wildlife species as well as temporal activity patterns of spotted hyena clans inhabiting the northern savannas sector and spotted hyena clans inhabiting the southern savannas sector to find out if tourist and park staff activity has an influence on distribution and temporal activity of wildlife species. Trap success for forest elephant was significantly higher in the northern savannas sector. Trap success for spotted hyenas was almost equal in the two savanna sectors. However, adult spotted hyenas in the southern savannas sector were significantly more active during night than adult spotted hyenas from the northern savannas sector. This suggests that spotted hyenas modify their temporal activity with regard to the occurrence and degree of human activities in the park's forest-savanna mosaic. The increasing tourist activities likely also have an influence on the distribution of forest elephants. Besides being less often photographed in the southern savannas sector, forest elephants also avoided areas in close proximity to roads. In addition, trap success for forest elephants as well as other larger wildlife species was very low in the very south of the study area. This area was closest to the park border and villages surrounding the park, suggesting that larger wildlife species avoid this area due to increased levels of poaching. In this context, it appears that the northern savannas sector with its lower human activity remains the only undisturbed refuge of open habitat for elephants in the OKNP and any future infrastructure projects, such as roads, should be well thought through and planned before they will be implemented.

In chapter 8, I analysed data I have collected in south-eastern Gabon in 2011. Spotted hyena spoors were discovered here in 2008 in a forest-savanna mosaic south of the town Franceville. To verify if spotted hyenas are present I did a reconnaissance survey and a camera trapping study in this area. In addition, I did reconnaissance surveys in two other areas, including the Batéké Plateaux National Park. During the studies no signs of presence of spotted hyenas were detected, suggesting that spoors seen here in 2008 have likely originated from spotted hyenas that have dispersed from the OKNP which is situated about 250 km away. Furthermore, poaching levels and levels of human encroachment was very high in the three surveyed areas. The data also suggested that abundance of potential spotted hyena prey species, such as forest buffalo and bushbuck, is scarce in the surveyed area. However, with its vast savannas, the Batéké Plateaux National Park could, if properly managed, potentially support healthy populations of spotted hyenas and their main prey species. The camera trapping study recoded a variety of wildlife species, among them was a melanistic (black) serval. However, trap success for servals was too low to determine population size and density but the records suggested that servals can persist in the highly degraded forest-savanna mosaics in this region.

Zusammenfassung

Die Tüpfelhyäne (*Crocuta crocuta*) ist ein Großkarnivor mit einem ausgeprägten Sozialverhalten. Sie ist der häufigste Großkarnivor in Afrika und bewohnt ein breites Spektrum an Habitaten in Gebieten Afrikas südlich der Sahara. Aufgrund ihres einzigartigen Sozialverhaltens, in welchem Weibchen die dominante Rolle übernehmen, sind Tüpfelhyänen über die Jahre zu einem beliebten Forschungsobjekt avanciert. Ebenso wie andere Großkarnivoren Afrikas ist auch die Tüpfelhyäne durch Habitatverlust und direkte Konflikte mit Menschen bedroht. Aufgrund dessen schwinden in vielen Gebieten Tüpfelhyänenpopulation rapide, sogar in geschützten Gebieten. Tüpfelhyänen wurden bisher ausgiebig im südlichen und östlichen Afrika untersucht. Über Tüpfelhyänen in Zentralafrika ist bisher aber weitgehend so gut wie nichts bekannt.

Ein Großteil von Zentralafrika ist vom tropischen Regenwald des Kongobeckens bedeckt. Das Batéké Plateaux-Gebiet, welches nahezu zwei Drittel der Republik Kongo bedeckt und sich bis ins benachbarte Gabun erstreckt, ist das Überbleibsel eines ehemaligen riesigen Savannen-Ökosystems welches einst den Großteil des Kongobeckens bedeckte. Bis hinein in die 1940er waren soziale Großkarnivoren, wie zum Beispiel Tüpfelhyäne, Löwe (*Panthera leo*) und Afrikanischer Wildhund (*Lycaon pictus*) in den Savannen der Batéké Plateaux weit verbreitet. Ein dramatischer Rückgang ereignete sich in der zweiten Hälfte des 20. Jahrhunderts. Dieser hatte die komplette Ausrottung von Löwen und Afrikanischen Wildhunden und die annähernde Ausrottung von Tüpfelhyänen zur Folge. Heutzutage bewohnen Tüpfelhyänen in den Batéké Plateaux nur noch ein kleines Wald-Savannen-Mosaik innerhalb des Odzala-Kokoua Nationalparks (OKN) im Nordwesten der Republik Kongo. Die Population im OKN ist die letzte verbliebene Tüpfelhyänen-Population im Kongobecken. Um erfolgreiche Strategien zum Schutz der letzten Tüpfelhyänen im OKN zu gewährleisten, ist ein bestmögliches Monitoring vonnöten.

In der vorliegenden Dissertation untersuchte ich die Ökologie und den Populationsstatus der Tüpfelhyänen im OKN. Zusätzlich sammelte ich Informationen über die Populationsgröße und -dichte von Servalen (*Leptailurus serval*) im OKN. Des weiteren nutzte ich Kamerafallendaten um Aussagen über die Verbreitung und das Vorkommen von weiteren Wildtierarten im Wald-Savannen-Mosaik des OKN zu machen. Daraus abgeleitete Informationen können Managementstrategien zum Schütz von Tüpfelhyänen im OKN wirkungsvoll unterstützen. Darüber hinaus untersuchte ich die Situation für Tüpfelhyänen und andere Wildtierarten in drei Regionen im Südosten Gabuns. In Kapitel 2 schätze ich sowohl die Populationsgröße der Tüpfelhyänenpopulation als auch eingetretene Veränderungen in der Populationsgröße. Beide Parameter wurden mithilfe von Kamerafallen untersucht. In den Zeiträumen November 2011 bis Februar 2012 und Juli 2013 bis März 2014 führte ich dafür Kamerafallenstudien im Wald-Savannen-Mosaik des OKNs durch. Zusätzlich nutzte ich

Daten welche mir von der Parkverwaltung zu einer von ihr in bewaldeten Gebieten des Parks durchgeführten Kamerafallenstudie (Dezember 2012 bis Mai 2013) zur Verfügung gestellt wurden. Mithilfe von Kamerafallenbildern konnte ich das Geschlecht, Alter und die Zugehörigkeit von Individuen zu einzelnen Clans bestimmen. Die Zugehörigkeit zu einzelnen Clans konnte mithilfe von in Gruppen fotografierten Tüpfelhyänen bestimmt werden. Zum Ende der zweiten Kamerafallenstudie (März 2014) konnte ich eine Populationsgröße von 69 Tieren beobachten. Darunter waren 50 Adulte, 11 Subadulte und 8 Welpen. Fünf Clans, mit insgesamt 52 Tieren, bewohnten das Wald-Savannen-Mosaik im Park. Neun weitere Tiere (5 Adulte und 4 Subadulte), wurden nur in Waldlichtungen im dichten Waldblock des Parks und außerhalb des Wald-Savannen-Mosaiks aufgenommen. Weitere 8 Tiere wurden als Nomaden identifiziert, welche keine Zugehörigkeit zu einem ansässigen Clan im Wald-Savannen-Mosaik hatten. Die Populationsdichte wurde auf 6.42 Individuen / 100 km^2 geschätzt. Kamerafallen fotografierten auch Tüpfelhyänen mit Kabelschlingenverletzungen. Beinahe 50 % der Tiere welche während der ersten Kamerafallenstudie im Wald-Savannen-Mosaik fotografiert wurden, wurden nicht während der zweiten Kamerafallenstudie fotografiert. Darüber hinaus sind wahrscheinlich elf Tiere im Verlauf der zweiten Kamerafallenstudie gestorben. Die Tüpfelhyänenpopulation im OKN steht am Rande der Ausrottung. Illegale Wilderei mit Kabelschlingen ist wahrscheinlich der Hauptgrund dafür. Sofern dieses Problem nicht umgehend gelöst werden kann, ist die baldige Ausrottung dieser kostbaren Tüpfelhyänenpopulation die Folge. Die weitgehende Isolation der Tüpfelhyänenpopulation im OKN birgt eine weitere Gefahr in sich. Denn dadurch ist sie besonders anfällig gegenüber stochastischen Ereignissen, wie zum Beispiel Krankheitsausbrüche, und Prozessen, wie zum Beispiel Inzucht, welche negative Auswirkungen auf die genetische Vielfalt der Population haben.

In Kapitel 3 analysierte ich das Nahrungsspektrum der Tüpfelhyänen im OKN. Dafür sammelte ich Kotproben und erbrochene Haarballen von Tüpfelhyänen im Wald-Savannen-Mosaik des OKN. Zur Bestimmung des Beutespektrums untersuchte ich die in den Proben gefundenen Beutetierhaare und sonstigen Beutetierbestandteile. Die Analyse beruhte insgesamt auf 402 Kotproben und erbrochenen Haarballen. Sechsundzwanzig verschiedene Beutetiere wurden identifiziert, wobei 25.2 % der identifizierten Beutetierbestandteile auf Rotbüffel (*Syncerus caffer nanus*) entfielen, gefolgt von Rotem Pinselohrschwein (*Potamochoerus porcus*) (17.5 %) und Buschbock (*Tragelaphus scriptus*) (16.4 %). Diese drei das Nahrungsspektrum der Tüpfelhyänen dominierenden Beutetiere kommen vorwiegend im Wald-Savannen-Mosaik vor. Aufgrund der Daten ließ sich sagen, dass die Überlebensfähigkeit der Tüpfelhyänen im OKN vom Vorkommen und der Häufigkeit dieser Beutetiere im Park abhängig ist. Zusätzlich untersuchte ich Überlappungen in den zeitlichen Aktivitätsmustern zwischen Tüpfelhyänen und ihren wichtigsten Beutetieren mithilfe des

Koeffizienten Δ. Zur Bestimmung der Aktivitätsmuster wurden Daten aus der Kamerafallenstudie von Juli 2013 bis März 2014 herangezogen. Die durchschnittliche Überlappung Δ der Aktivitätsmuster von Tüpfelhyänen und ihrer wichtigsten Beutetiere betrug 0.65 (±SE 0.10). Trotz der großen Wichtigkeit im Nahrungsspektrum der Tüpfelhyänen, gab es nur wenig Überlappung in den Aktivitätsmustern von Tüpfelhyänen, welche hochgradig nachtaktiv waren, und Rotbüffeln, welche vorwiegend kathemeral waren. Das lässt vermuten, dass Tüpfelhyänen große Mengen an Energie auf der Suche nach Nahrung im OKN aufbringen müssen.

In Kapitel 4 analysierte ich Populationsdichte und zeitliche Aktivitätsmuster von Servalen im OKN. Dafür benutze ich Daten, welche mit der Kamerafallenstudie von Juli 2013 bis März 2014 gesammelt wurden. Insgesamt konnte ich 51 Individuen identifizieren, darunter waren 43 Adulte, 4 Subadulte und 4 Servalbabys. Beinahe zwei Drittel aller Individuen waren Tiere der servalinen Morphe. Tiere dieser Morphe haben eine Tüpfelung mit sehr kleinen Flecken. Mithilfe von räumlich-expliziten Fang-Wiederfang-Modellen schätzte ich die Servaldichte im Wald-Savannen-Mosaik auf 11.20–11.72 Individuen / 100 km². Männliche Servale waren hauptsächlich nachtaktiv, wohingegen weibliche Servale hauptsächlich tagaktiv waren, mit einem Peak in den Morgenstunden. Die Unterschiede in den Fangraten und zeitlichen Aktivitätsmustern zwischen weiblichen und männlichen Servalen hingen wahrscheinlich mit dem Vorkommen von Tüpfelhyänen in den Savannen zusammen. Tüpfelhyänen waren fast ausschließlich nachtaktiv. Infolgedessen hatten auch männliche Servale eine höhere Überlappung im zeitlichen Aktivitätsmuster mit Tüpfelhyänen. Trotz ihrer weiträumigen Verbreitung in Afrika haben Servale bisher nur wenig Aufmerksamkeit von wissenschaftlicher Seite her bekommen. Mit dieser Studie war es mir möglich, erste aussagekräftige Schätzungen zur Populationsdichte dieses mittelgroßen Räubers in Zentralafrika zu gewinnen.

In Kapitel 5 untersuchte ich die Bauten von Tüpfelhyänen im Park und die Anwendbarkeit von akustischem Monitoring zur Bestimmung von Individuen in einem Clan. Dafür installierte ich akustische Aufnahmegeräte ("Rekorder") bei einem kommunalen Zentralbau eines Tüpfelhyänenclans im Wald-Savannen-Mosaik des Parks. Die Rekorder waren aktiv von Mitte Oktober 2013 bis Ende Februar 2014 und lieferten insgesamt 907 Stunden an Aufnahmen. Für die Analyse nutzte ich "whooping bouts" von Tüpfelhyänen. Insgesamt wurden 223 whooping bouts von zufriedenstellender Qualität am Zentralbau aufgenommen. 141 wurden als whooping bouts von Adulten identifiziert und 92 wurden als whooping bouts von Welpen identifiziert. Um Individuen anhand von Merkmalen in den Vokalisationen zu unterscheiden, wurden akustische Parameter einzelner whoops und whooping bouts untersucht. Erste Ergebnisse deuten darauf hin, dass die Variation innerhalb der whooping bouts von Adulten und Welpen sehr groß ist. Das macht es schwierig geeignete Parameter für einzelne whoops und whooping bouts zu finden, mit deren Hilfe eine individuelle Unterscheidung erfolgen kann. Daher ist es wahrscheinlich eher von Vorteil zunächst eine akustische Studie zu machen, bei der zunächst verschiedene whoops von bekannten Tieren aufgenommen werden. Aufgrund dieser Aufnahmen könnten dann die charakteristischen Parameter bestimmt werden.

Während dreier Feldstudien zwischen 2008 und 2014 konnte ich fünf kommunale Zentralbauten im Wald-Savannen-Mosaik des Parks finden. In 2008 und 2013 konnte ich je einen besetzen Zentralbau finden. Die anderen drei Zentralbauten waren bereits verlassen. Termitenhügel in den Savannen dienen den Tüpfelhyänen als Zentralbauten. Ein charakteristischer großer Termitenhügel mit mehreren Eingängen diente jeweils als Hauptbau. Zahlreiche kleinere Bauten befanden sich in der nächsten Umgebung dieses Hauptbaus. Die kleineren Bauten waren jeweils kleinere Termitenhügel mit nur einem Eingang und dienten Welpen wahrscheinlich als Kurzzeit-Unterschlupf. Die Höhlen in den Termitenhügeln wurden wahrscheinlich von Erdferkeln (*Orycteropus afer*) oder Riesenschuppentieren (*Smutsia gigantea*) gegraben. Ein Zentralbau befand sich nur 10 m entfernt von einer Parkstraße. Als der Bau entdeckt wurde, wurden auch Anzeichen entdeckt, welche darauf schließen ließen, dass der Bau noch vor gar nicht allzu langer Zeit besetzt war. Da die Straße erst kurz vorher erbaut wurde, ist es wahrscheinlich, dass die Tüpfelhyänen den Bau aufgrund der mit der Konstruktion der Straße einhergehenden menschlichen Aktivitäten in der Nähe des Baus verließen. Kommunale Zentralbauten repräsentieren das soziale Aktivitätszentrum eines Tüpfelhyänenclans. Der Schutz von Zentralbauten ist daher von entscheidender Bedeutung, um den Schutz von Tüpfelhyänen im Park zu gewährleisten. Weibchen mit Welpen, welche gezwungen sind aufgrund von menschlichen Aktivitäten den Zentralbau zu verlassen, setzen ihre Jungtiere potentiellen Gefahrenquellen, wie zum Beispiel Wilderern, adulten Tüpfelhyänen von anderen Clans oder anderen Großraubtieren, aus. Störungen von kommunalen Zentralbauten sollten deshalb vermieden werden. Deshalb ist es ratsam eine genaue Erfassung sämtlicher Kommunalbauten im Wald-Savannen-Mosaik durchzuführen. Zukünftig sollten Standorte von Zentralbauten bei der Umsetzung von Infrastrukturmaßnahmen, wie zum Beispiel Straßen, berücksichtigt werden bzw. sollten vor Umsetzung solcher Maßnahmen die betreffenden Gebiete vorher untersucht werden, um auszuschließen, dass Zentralbauten durch Infrastrukturmaßnahmen gefährdet werden.

In Kapitel 6 analysierte ich die genetische Vielfalt der Tüpfelhyänenpopulation. Zusätzlich wurden genetische Analysen durchgeführt, um herauszufinden, ob die Population in der jüngsten Vergangenheit durch einen Bottleneck gegangen ist und ob bereits schädliche genetische Prozesse, wie zum Beispiel Inzucht, in der Population vorkommen. Genetisches Material wurde aus frischen Kotproben gewonnen, welche zwischen 2008 und

2014 gesammelt wurden. Microsatelliten-Analyse wurde zur Untersuchung der genetischen Zusammensetzung durchgeführt. Insgesamt waren 20 der gesammelten Proben von ausreichender Qualität. Anhand der 20 Proben konnten 14 verschiedene Tiere genotypisiert werden. Insgesamt wurden 19 Allele an neun verschiedenen Loci identifiziert. Die Population zeigte keine Abweichung vom Hardy-Weinberg-Gleichgewicht (HWG). Ebenfalls wurden kein Heterozygoten-Überschuss und kein Heterozygoten-Defizit festgestellt. Ein Locus zeigte eine signifikante Abweichung vom HWG. Der Inzucht-Koeffizient für diesen Locus war ebenfalls sehr hoch. Dies ließ vermuten, dass Inzucht in der Population bereits vorhanden ist und diesen Locus betrifft. Ein Loci-Paar zeigte ein signifikantes Kopplungsungleichgewicht (*linkage disequilibrium*). Im Vergleich mit der Serengeti-Tüpfelhyänenpopulation wies die Population im OKN eine geringere Anzahl von Allelen an allen Loci, sowie geringere erwartete und beobachtetet Heterozygotien an acht Loci auf. Bottleneck-Tests zeigten, dass die Population in der jüngsten Vergangenheit nicht durch einen Bottleneck ging. Zusätzlich schätze ich die genetische effektive Populationsgröße (N_e) mithilfe von genetischen Daten. Schätzungen für (N_e) reichten von 10.6 bis 28.4 Tieren. Bedauerlicherweise lies die kleine Stichprobengröße von nur 14 genotypisierten Tieren keine ausreichende Schlussfolgerung zu. Aber wenn man die bereits sehr kleine Populationsgröße berücksichtigt, könnten die Ergebnisse aus dieser geringen Probenanzahl bereits ein guter Indikator für die genetische Vielfalt in der Population sein. Unter Berücksichtigung der Resultate ist anzunehmen, dass die Population bereits an geringer genetischer Vielfalt und Inzucht leidet. Das Nichtvorkommen von Einwanderung neuer Individuen aufgrund der hohen Isolation der Population ist wahrscheinlich der Hauptgrund dafür. Einführung von neuen Individuen mag daher sinnvoll sein, um neues genetisches Material in die Population einzubringen.

In Kapitel 7 analysierte ich Kamerafallendaten der Langzeit-Kamerafallenstudie von Juli 2013 bis März 2014. Ich untersuchte sowohl Fangerfolge und zeitliche Aktivitätsmuster für die verschiedenen detektierten Wildtierarten als auch den Einfluss von Habitatmerkmalen und menschlichen Aktivitäten auf die Artengemeinschaft im Wald-Savannen-Mosaik des OKN. Insgesamt wurden 37 Wildtierarten fotografiert. Alle terrestrischen Tierarten wurden bereits nach 78 Gesamtfallentagen (= 2025 Fallennächte) detektiert. Waldelefant, (*Loxodonta cyclotis*) war die am häufigsten fotografierte Tierart, gefolgt von Tüpfelhyäne, Buschbock, Rotbüffel, Blauducker (*Philantomba monticola*) und Rotem Pinselohrschwein. Insgesamt wurden 13 Raubtierarten fotografiert, inklusive Leopard (*Panthera pardus*), Afrikanische Goldkatze (*Caracal aurata*), Ichneumon und (*Herpestes ichneumon*) und Honigdachs (*Mellivora capensis*). In Waldgebieten installierte Kamerafallenstationen hatten höhere Fangerfolge und zeichneten ebenfalls mehr Tierarten auf als Kamerafallenstationen, welche in den Savannen installiert wurden. Es gab einen signifikant negativen Zusammenhang zwischen der Distanz von Kamerafallenstationen zu Waldgebieten und der

Anzahl detektierter Tierarten. Darüber hinaus zeigten bestimmte Tierarten, wie zum Beispiel Blauducker und Petersducker (*Cephalophus callipygus*), eine starke Präferenz für Gebiete in unmittelbarer Nähe von Waldgebieten. Raubtiere welche ausschließlich oder zum Großteil nachtaktiv waren, waren, zum Beispiel, Großfleck-Ginsterkatze (*Genetta maculata*), Tüpfelhyäne und Afrikanische Zibetkatze (*Civettictis civetta*). Erdferkel, Nilpferd (*Hippopotamus amphibicus*), Waldelefant und Gelbrückenducker (*Cephalophus silvicultor*) waren ebenfalls hauptsächlich nachtaktiv. Die zwei im Park vorkommenden Menschenaffen Westlicher Flachlandgorilla (*Gorilla gorilla gorilla*) und Schimpanse (*Pan troglodytes*) waren sehr stark tagaktiv. Buschbock und Rotbüffel waren hauptsächlich kathemeral. Der Lékoli-Fluss teilt das Wald-Savannen-Mosaik des Parks in einen südlichen und einen nördlichen Savannensektor. Derzeit beschränken sich die Aktivitäten von Touristen und Parkpersonal auf den südlichen Savannensektor. Um herauszufinden, ob Touristen- und Parkpersonalaktivitäten einen Einfluss auf die Verbreitung von Wildtieren haben, verglich ich die Fangraten von Tierarten in den beiden Savannensektoren. Zusätzlich verglich ich das zeitliche Aktivitätsmuster von im nördlichen Savannensektor lebenden Tüpfelhyänen mit dem Aktivitätsmuster von im südlichen Savannensektor lebenden Tüpfelhyänen. Der Fangerfolg für Waldelefanten war im nördlichen Savannensektor signifikant höher. Fangerfolg für Tüpfelhyänen war in beiden Savannensektoren in etwa gleich groß. Allerdings waren adulte Tüpfelhyänen im südlichen Savannensektor signifikant häufiger nachtaktiv als adulte Tüpfelhyänen im nördlichen Savannensektor. Das ließ vermuten, dass Tüpfelhyänen im Park ihr Aktivitätsmuster an das Vorkommen und den Grad menschlicher Aktivitäten im Wald-Savannen-Mosaik anpassen. Die steigenden touristischen Aktivitäten haben wahrscheinlich auch einen Einfluss auf die Verbreitung der Waldelefanten im Park. Nicht nur wurden Waldelefanten im südlichen Savannensektor weniger oft fotografiert, sondern sie vermieden auch Gebiete in unmittelbarer Nähe von Straßen. Zusätzlich war sowohl der Fangerfolg von Waldelefanten als auch der Fangerfolg von anderen großen Wildtierarten im südlichsten Teil des Studiengebietes sehr gering. Dieses Gebiet befand sich am nächsten zu den Parkgrenzen und den Dörfern welche an den Park angrenzen. Dies ließ vermuten, dass Wildtierarten den äußersten Süden des Wald-Savannen-Mosaiks aufgrund des dortigen höheren Ausmaßes an Wilderei vermeiden. In diesem Zusammenhang liegt die Vermutung nahe, dass der nördliche Savannensektor aufgrund der geringeren menschlichen Aktivitäten hier als einziges verbliebenes nicht bewaldetes Rückzugsgebiet für Waldelefanten im Park fungiert. Jedwede Infrastrukturmaßnahmen hier, wie zum Beispiel Straßen, sollten daher gut durchdacht und geplant sein.

In Kapitel 8 analysierte ich Daten welche ich in 2011 im Südosten Gabuns gesammelt habe. Pfotenabdrücke von Tüpfelhyänen wurden hier in 2008 in einem Wald-Savannen-Mosaik südlich der Stadt Franceville entdeckt. Um zu überprüfen ob Tüpfelhyänen (noch) präsent sind unternahm ich ein *reconnaissance survey* und eine Kamerafallenstudie in diesem Gebiet. Zusätzlich unternahm ich *reconnaissance surveys* in zwei weiteren Gebieten, unter anderem im Batéké Plateaux Nationalpark. Während der Studien wurden keine Zeichen gefunden, welche auf eine Präsenz von Tüpfelhyänen hinwiesen. Deshalb ist anzunehmen, dass die Pfotenabdrücke die in diesem Gebiet gefunden wurden von Tüpfelhyänen hinterlassen wurden, welche aus dem 250 km entfernten OKN stammen und hierhin eingewandert waren. Darüber hinaus zeichneten sich die drei untersuchten Gebiete durch einen hohen Grad an Wilderei und menschlicher Beeinflussung aus. Die Daten deuteten auch daraufhin, dass die Abundanz von potentiellen Beutetieren von Tüpfelhyänen, wie zum Beispiel Buschbock und Rotbüffel, in den drei Gebieten eher gering ist. Allerdings könnte der Batéké Plateaux Nationalpark mit seinen riesigen Savannen aber, falls richtig gemanagt, potentiell gesunde Beutetierpopulationen und mithin auch gesunde Tüpfelhyänenpopulationen beherbergen. Während der Kamerafallenstudie wurde eine Vielzahl von Wildtierarten fotografiert, darunter auch ein melanistischer (schwarzer) Serval. Leider war der Fangerfolg für Servale zu gering, um genauere Schätzungen zu Populationsgröße und -dichte durchführen zu können. Anzunehmen ist aber, dass gesunde Servalpopulationen in diesen hochgradig von Menschen beeinflussten Wald-Savannen-Mosaiken überleben können.

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