CARNIVORE INTRA-GUILD COMPETITION IN SELATI GAME RESERVE, LIMPOPO PROVINCE, SOUTH AFRICA

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This thesis is dedicated to my late grandfather, **Wensley Brown** *(1931 - 2012),* from whom, I believe I gained my love for nature and conservation from a young age

ABSTRACT

Carnivore intra-guild interactions can be important drivers of carnivore community composition and ecosystem functioning. Large carnivores are particularly important since they occupy the highest trophic levels and can exert extensive influences on subordinate carnivores and prey species. Given Africa's rapidly expanding human population, enclosed reserves such as those found in South Africa, may become increasingly important for carnivore conservation. A major concern, however, is that the interactions and co-existence of multiple carnivores in these systems is poorly understood. Additionally, the majority of reserves in South Africa are small (< 400km^2), potentially increasing the likelihood of competition. My research aimed to provide insight into the interactions and co-existence of a multi-carnivore community within a small, enclosed reserve in South Africa (Selati Game Reserve). I tackled this task by using a combination of field techniques including camera trap surveys, ungulate transect surveys, aerial count surveys, location data collected from collared large carnivores and scat and kill site analyses. I found that carnivore-carnivore interactions, and their associated impacts, varied within the carnivore guild and that co-existence may be due to trade-offs between various risks (i.e. interference and exploitative competition) and benefits (i.e. resources such as food and space). My findings also revealed that large carnivores, such as lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*) and leopards (*Panthera pardus*) do not have homogenous effects and that site-specific research on multiple-carnivores is integral for conserving biodiversity and ecosystem dynamics. Lions were the dominant large carnivore (in terms of intra-guild predation, space use and resource use) despite being outnumbered seven to one by spotted hyaenas. Leopard occupancy was negatively influenced by lions and leopard diet overlapped almost completely (91%) with spotted hyaenas, suggesting increased kleptoparasitism of leopard kills by spotted hyaenas. While my study provides valuable insight into the complexity of carnivore intra-guild competition in a small, enclosed reserve it also highlights major research gaps and emphasises the need for ecosystem-based research throughout southern Africa to fully understand how multiple sympatric carnivores co-exist in these systems.

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TABLE OF CONTENTS

PREFACE

This thesis is structured as follows:

Chapter 1 is a general introduction that broadly describes the rationale for my study. This chapter does not introduce the data chapters, which contain their own introductions.

Chapter 2 describes the study site (Selati) in detail, as well as general methodology that is common to subsequent data chapters. Specific analytical processes are provided within each data chapter.

Chapter 3 is a data chapter that explores the abundance and density of key species on Selati Game Reserve (Selati) through a range of methods and data sets.

Chapter 4 is a data chapter that explores the occupancy (space use) and activity patterns of various carnivore species on Selati.

Chapter 5 is a data chapter that explores the diet of large carnivores (i.e. lions, leopards and spotted hyaenas) on Selati, through the combination of kill site and scat analyses.

Chapter 6 is a synthesis chapter that highlights important content covered in my thesis, points towards additional future work and touches on management implications for Selati.

Appendices include all additional information related to topics explored in the contents of my thesis.

Supplimenaty material includes supporting information that is not essential to topics explored in the contents of my thesis, but would benefit readers.

Chapter 1

GENERAL INTRODUCTION

Mbhurri – the dominant male lion on Selati Game Reserve

The mammalian order Carnivora consists of over 280 extant species, almost all of which are predators (Treves & Karanth, 2003; Karanth & Chellam, 2009). Carnivores attract a great deal of interest from conservation biologists and generally intrigue a wide range of people, not only because of the elusive and powerful image they portray, but also because of their role as predators (Sillero-Zubiri & Laurenson, 2001). Within the carnivore guild, competition can be particularly intense as carnivores are both morphologically (e.g. dental) and behaviourally (e.g. hunting strategies) adapted for killing (McDonald, 2002; Tannerfeldt, Elmhagen & Angerbjörn, 2002; Donadio & Buskirk, 2006). In many terrestrial systems, large (>20 kg) carnivores occupy the highest trophic level of the food web, which means that they have the ability to fundamentally alter the structure and function of entire ecosystems (Terborgh *et al.*, 2001; Terborgh & Estes, 2010). Even small carnivores, despite their relative rarity across landscapes, have the ability to be drivers of ecosystem processes (Gompper *et al.*, 2006). As a group, carnivores exert extensive influences on biological communities both directly, through predation and interspecific competition (i.e. interference competition), and indirectly through non-consumptive processes associated with behavioural alterations (Schmitz, Beckerman & O'Brien, 1997; Miller *et al.*, 2001; Treves & Karanth, 2003; Terborgh & Estes, 2010; Ripple *et al.*, 2014).

Generally, terrestrial ecosystems contain multiple carnivore species that not only compete for shared resources (e.g. space and food) but also pose a threat to one another (Vanak *et al.*, 2013). Studies from carnivore communities throughout Africa, Europe and North America have shown that carnivores can be adversely affected by other guild members (e.g. Mills & Mills, 1982; Karanth & Sunquist, 1995; Palomares *et al.*, 1995; Fedriani *et al.*, 2000; Vanak *et al.*, 2013). This phenomenon is known as intra-guild competition and it is an important ecological factor that can influence the structure and population dynamics of mammalian carnivores (Palomares & Caro, 1999; Linnell & Strand, 2000; Caro & Stoner, 2003). Though there are vast differences in the body sizes of carnivores, members of the carnivore guild can still compete for similar prey species, which often results in larger carnivores (e.g. lions (*Panthera leo*)) dominating smaller, competitively inferior carnivores (e.g. cheetahs (*Acinonyx jubatus*) or African wild dogs (*Lycaon pictus*); Palomares & Caro, 1999; Caro & Stoner, 2003; Sinclair, Mduma & Brashares, 2003; Radloff & Du Toit, 2004). Smaller-bodied carnivores usually suffer more from intra-guild competition, not only because larger carnivores limit their food intake and access to resource rich areas, but because larger carnivores are capable of killing smaller carnivores (Mills & Gorman, 1997; Durant, 1998; Hunter, Durant & Caro, 2007). Interspecific killing among mammalian carnivores is considered common in nature. Palomares and Caro (1999) reported that between 97 interacting pairs of carnivores, 27 actively kill other carnivores, and another 54 are susceptible to being killed. These interactions may be symmetrical (both species kill each other), asymmetrical (one species kills the other) or in some situations the adults of one species will only kill young of another species but not adults (Palomares & Caro, 1999).

The ecology of a species can be described in terms of the ‘niche’ it occupies within an environment (du Preez, 2014). Co-existence within the carnivore guild can be achieved through the segregation of three main ecological niche dimensions and these relate to temporal, spatial and resource usage (Di Bitetti *et al.*, 2010; Steinmetz, Seuaturien & Chutipong, 2013; Haidir, Macdonald & Linkie, 2018). For instance, selective predation may reduce the impact of exploitative competition (i.e. one species outcompetes another for access to prey) among carnivores, whilst variation in activity patterns (i.e. temporal) may minimise confrontation (Linnell & Strand, 2000; Caro & Stoner, 2003). Spatial segregation could possibly be the most effective method of avoiding direct competition, as it removes the potential for negative interactions (Palomares & Caro, 1999; Linnell & Strand, 2000; Caro & Stoner, 2003).

Ecological researchers have primarily focused on the interactions between carnivores and their prey and little attention has been placed on the impact that carnivores have on each other (Linnell & Strand, 2000). Our understanding of the extent and effects of carnivore intra-guild competition is heavily biased towards canids in the northern hemisphere (Ritchie & Johnson, 2009), where research has focused on the role of direct killing (Watts & Holekamp, 2008). The majority of these studies have also only examined interactions between pairs of carnivores and have completely overlooked the interactions occurring among subordinate carnivores (Owen-Smith & Mills, 2008). By doing this, these studies inadvertently assume that the behavioural decisions of subordinate carnivores are mainly a function of avoiding competition with the most dominant carnivore(s) (Owen-Smith & Mills, 2008; Vanak *et al.*, 2013). This assumption is likely to be invalid in many cases, as subordinate carnivores also compete with each other for similar resources and must simultaneously balance the risk of competition from multiple carnivore species (Vanak *et al.*, 2013). There are many looming uncertainties about how exactly intra-guild competition negatively effects carnivore populations (Watts & Holekamp, 2008; Ripple *et al.*, 2014) and a better understanding of such complex interactions (e.g. competition for food and induced behavioural changes) in multi-carnivore communities is much needed (Ritchie & Johnson, 2009; Ripple *et al.*, 2014).

Mammalian carnivores are extremely ecologically diverse and were once widespread across the entire globe, occupying all major habitat types (Barnosky *et al.*, 2004; Koch & Barnosky, 2006; Agnarsson, Kunter & May-Collado, 2010; Turvey & Fritz, 2011). Over the past two centuries, however, carnivores have suffered extensive range contractions due to the ever increasing human population (Ripple *et al.*, 2014). Consequently, carnivores are increasingly being threatened with extinction, especially in fragmented landscapes, because of their naturally low densities, relatively delayed sexual maturity, slow reproductive rates, specialized niche requirements and their inevitable conflict with humans (Purvis *et al.*, 2000; Sillero-Zubiri

& Laurenson, 2001; Hayward *et al.*, 2007b). Declines in natural prey, disease, illegal poaching, hunting and possibly increased competition within carnivore guilds have all contributed to the general decline in carnivore populations across the globe (Gese, 2001).

Large carnivores occupy extensive home ranges and require large prey populations, which means that only vast, relatively intact ecosystems can support viable populations (Sillero-Zubiri & Laurenson, 2001). When human populations expand and cultivate previously untouched habitats, large carnivores are the first to decline (Sillero-Zubiri & Laurenson, 2001; Hayward *et al.*, 2007a). As examples, brown bears (*Ursus arctos*), gray wolves (*Canus lupus*) and Eurasian lynx (*Lynx lynx*) were rapidly extirpated from the British Isles (Sillero-Zubiri & Laurenson, 2001). Black bears (*Ursus americanus*), gray wolves and cougars (*Puma concolor*) were removed from North America (Soule & Terborgh, 1999; Ripple *et al.*, 2014). Dingoes (*Canis dingo*) were eradicated from parts of Australia (Ripple *et al.*, 2014) and lions, leopards (*Panthera pardus*), African wild dogs, cheetahs and hyaenas were extirpated from South Africa (Hayward *et al.*, 2007a; Ripple *et al.*, 2014). Consequently, many conservation managers have begun reintroducing locally extirpated populations of carnivores, particularly large carnivores in an attempt to restore biodiversity and the natural integrity of ecosystems (Miller *et al.*, 2001; Terborgh *et al.*, 2001; Terborgh & Estes, 2010).

Africa supports numerous biodiversity hotspots and it is home to nearly a quarter of the world's mammal diversity (Agha *et al.*, 2018). The only intact guild of large carnivores can be found in Africa (Valkenburgh, 1988; Dalerum *et al.*, 2009) and consists of African wild dogs, cheetahs, leopards, spotted hyenas (*Crocuta crocuta*) and lions (Cozzi *et al.*, 2012). Africa, therefore, offers researchers the only opportunity to investigate the co-existence and range of interactions among large carnivores (Cozzi *et al.*, 2012). Throughout most of Africa, large carnivores are restricted to reserves or conservation areas because of human-wildlife conflict which arises due to the actual or perceived threat that free-ranging carnivores pose to livestock and/or human life (Mills, 1991; Rust & Marker, 2013). In South Africa, however, there are very few free-ranging large carnivores as most reserves are completely bound by electrified, predator-proof fencing (Hayward *et al.*, 2007b; Cozzi *et al.*, 2012). Often, these enclosed reserves, which are set aside to conserve biodiversity, are small (<400 km^2) and are unable to naturally support viable populations of large carnivores (Hayward *et al.*, 2007b; Hayward, O'Brien & Kerley, 2007c; Rostro-Garcia, Kamler & Hunter, 2015). Although large carnivore conservation in South Africa has benefited from the establishment of these small, enclosed reserves, constant monitoring and the assessment of species within the reserves is imperative as natural processes such as immigration and emigration are curtailed (Hayward *et al.*, 2007b; Rostro-Garcia *et al.*, 2015). Another important factor is that the likelihood of competition or killing among carnivore guild members within these small, enclosed reserves may increase as artificially high population densities are created due to the clumping of competing carnivores into the restricted space of the reserves (Palomares & Caro, 1999; Hayward & Kerley, 2008). Fencing protected areas can also affect ungulate species as their long-distance migrations are constrained, potentially increasing predation pressure, which could have cascading effects through the food web, especially for threatened species (Pereira, Owen-Smith & Moleón, 2014). The ways in which multiple carnivore species utilize and partition space and resources in small, enclosed reserves is currently poorly understood (Vanak *et al.*, 2013). This knowledge gap weakens the potential for conservation managers to use carnivore reintroductions to restore these ecosystems (Ritchie *et al.*, 2012).

Understanding how carnivores utilize available space and resources is important for their conservation, as it provides insight into their ecological needs (Rostro-Garcia *et al.*, 2015). Regional variation in environmental conditions and ecological communities will undeniably result in variable competitive interactions, so understanding ecological preferences throughout a carnivore's range is vital for their conservation (Rodríguez-Soto *et al.*, 2011). Given Africa's rapidly expanding human population and accelerated loss of biodiversity (Barea-Azcón *et al.*, 2007), enclosed reserves may become increasingly important for carnivore conservation (Rostro-Garcia *et al.*, 2015). Therefore, for small, enclosed reserves in South Africa to play a significant role in the conservation of carnivores, site-specific management decisions need to be made with respect to the area, density of prey and predators as well as to take into account the complex interactions among carnivores (Radloff & Du Toit, 2004; Ritchie & Johnson, 2009; Ripple, Rooney & Beschta, 2010; Rostro-Garcia *et al.*, 2015). Data on ecological communities within small, enclosed systems will help in identifying mechanisms of species declines and ultimately inform conservational decisions and provide recommendations to policy makers (Gese, 2001; Steenweg *et al.*, 2017).

Therefore, within practical limitations, my research aimed to comprehensively investigate carnivore intra-guild competition within a small, enclosed reserve in South Africa (Selati Game Reserve (Selati), Limpopo Province). Selati, which contains an almost complete guild of large carnivores (the only exception being African wild dogs) along with subordinate carnivores (Joubert & Joubert, 2015); offered the perfect opportunity for carnivore guild research to be conducted. I, therefore, aimed to provide insight into the complex interactions and co-existence of a multi-carnivore community by firstly, estimating population abundances and trends for as many carnivore and ungulate species as possible. Secondly, investigating the influences of various abiotic and biotic factors on the occupancy dynamics (i.e. space use) of carnivores. Thirdly, investigating the potential of temporal and habitat segregation among carnivores and finally to examine the dietary composition of carnivores and the potential for resource partitioning. I tackled these objectives using a combination of field techniques including camera trap surveys, ungulate transect surveys, aerial count surveys, location data collected from collared large carnivores (iridium satellite GPS/UHF/GSM collars) and finally scat and kill site analyses.

I predicted that carnivore intra-guild competition within this small, enclosed system would be more intense compared to larger, open systems as both prey and carnivore species are forced to exist within a restricted area. Additionally, I predicted that, given their size, lions would be the dominant carnivore and have the greatest impact on all other carnivores.

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Chapter 2

METHODS AND MATERIALS

A herd of breeding elephants along the Selati River in Selati Game Reserve

STUDY SITE

Selati Game Reserve (hereafter Selati) is a private, non-commercial conservancy, situated in the arid bushveld just south of the Murchinson Range and north of the Olifants River in Limpopo Province, South Africa (between 23° 54’ S and 24° 06’ S, and 30° 36’ E and 30° 55’ E; Joubert & Joubert, 2015; Fig.2.1). Selati was established in 1996 when 14 separate landowners with a collection of 16 adjoining properties united to preserve and sustain the biodiversity of the area (Dalerwa Ventures for Wildlife, 2008). The reserve is surrounded by electrified game-proof fencing and covers an area of 26 992 ha, of which approximately 25 800 ha is available to free-ranging wildlife (Joubert & Joubert, 2015). Selati’s land use can be described as private game farming, hunting (mainly trophy hunting by foreign clients) and game breeding (e.g. intensive breeding of sable antelope (*Hippotragus niger*)).

Adjacent to the north-west corner of Selati is the small town of Gravelotte and the Gravelotte Emerald Mine, whereas directly east of Selati is the community-run Marakapula Reserve, which buffers Selati from the large rural area of Namakgale (±15 km; Dalerwa Ventures for Wildlife, 2008; Fig.2.1). Phalaborwa, which borders the Kruger National Park, is the largest nearby town and is located 25 km east of Selati (Fig.2.1).

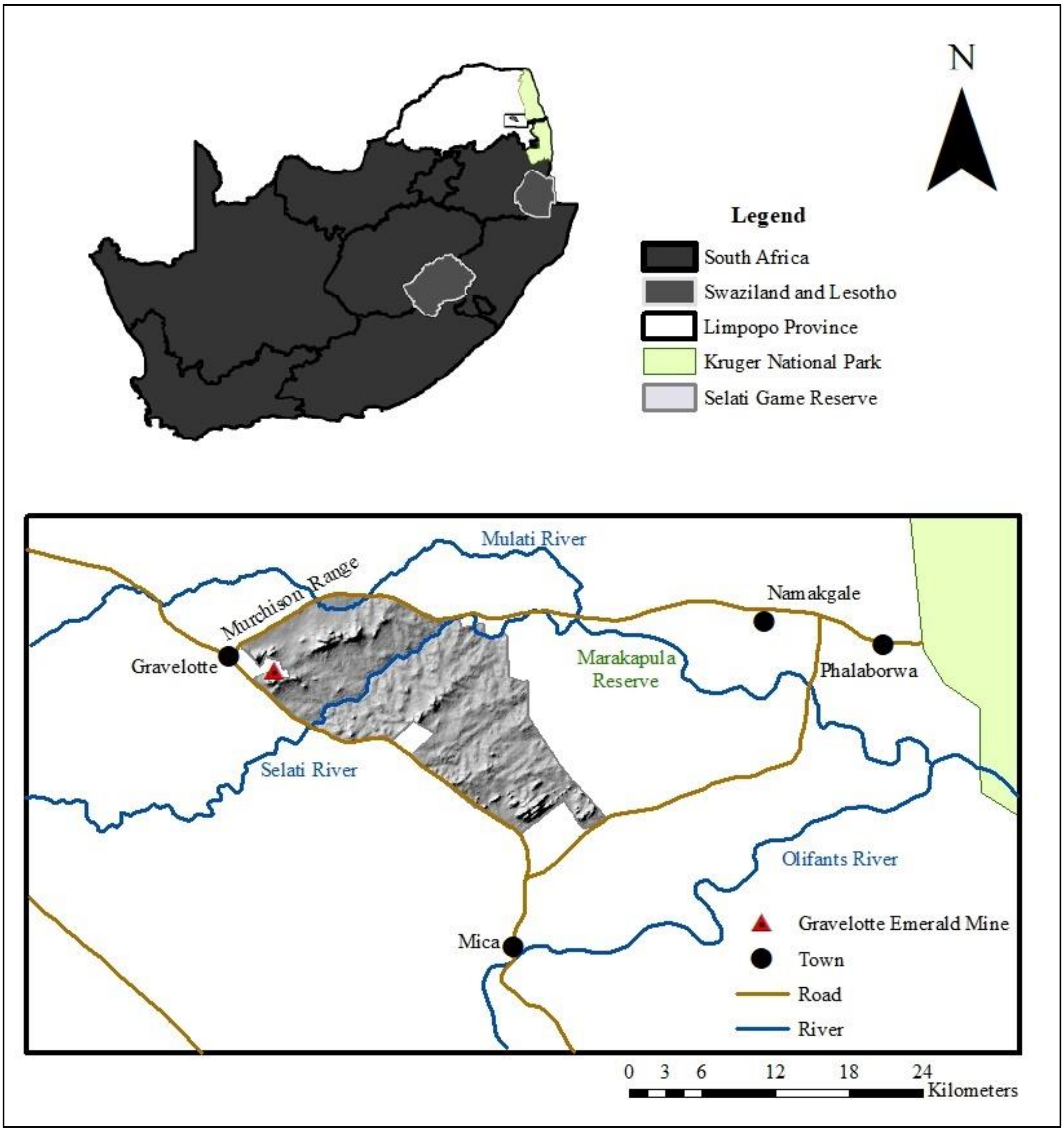

Figure 2.1: Location of Selati Game Reserve within the Limpopo Province, South Africa, highlighting important surrounding features.

General climate

Selati falls within the hot, arid steppe climate zone (BSh), which is a region that tends to have hot summers, warm to cool winters and often receives a level of precipitation below potential evapotranspiration (Kottek *et al.*, 2006). Selati receives an annual average of 530 mm of rain

(Fig.2.2), which falls mainly during summer from October to March, with a peak usually in December or January (Fig.2.3). Rainfall is unpredictable and typically occurs as thunderstorms of short durations, thus coverage is heterogeneous (Dalerwa Ventures for Wildlife, 2008).

The average daily minimum temperature in winter is 16.1ºC with the lowest average daily temperature being 10ºC in June. In summer, the average daily maximum temperature is 28.5ºC with the highest average daily temperature reaching 31ºC in January (Fig.2.4). Extreme temperatures for Selati range between a maximum of 43ºC and a minimum of 2ºC (Dalerwa Ventures for Wildlife, 2008).

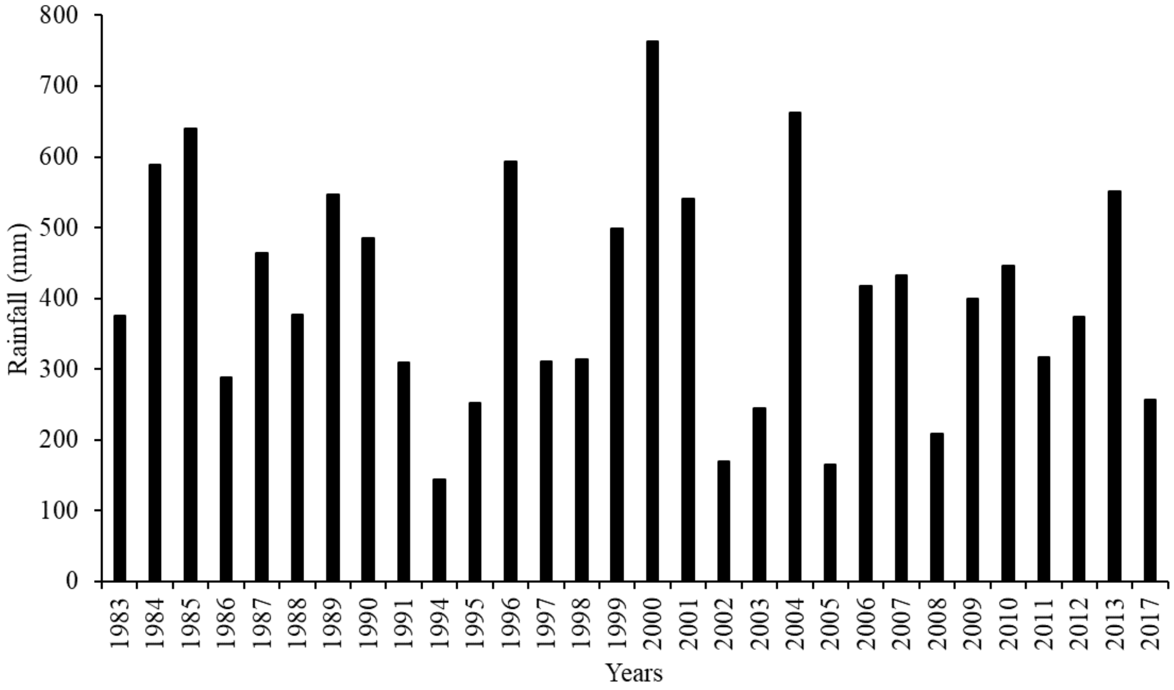

Figure 2.2: Annual rainfall (mm) at Phalaborwa, the closest weather station to Selati Game Reserve, over a 34-year period (1983-2017). Data are missing for 1992, 1993, 2014 and 2015. Data from the South African Weather Service.

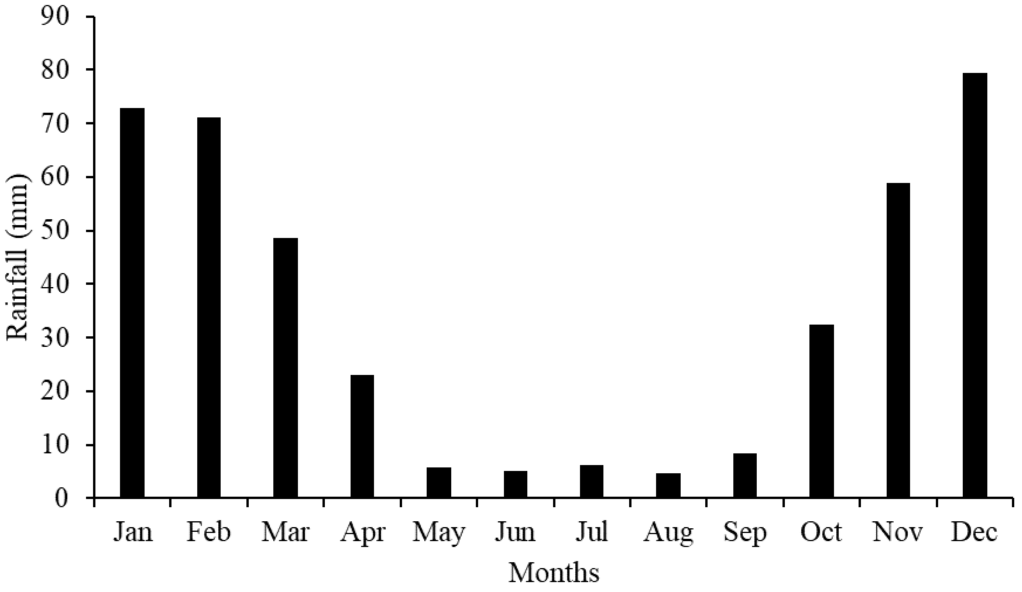

Figure 2.3: Average monthly rainfall (mm) for Phalaborwa, the closest weather station to Selati Game Reserve, over a 34-year period (1983-2017). Data missing for 1992, 1993, 2014 and 2015. Data from the South African Weather Service.

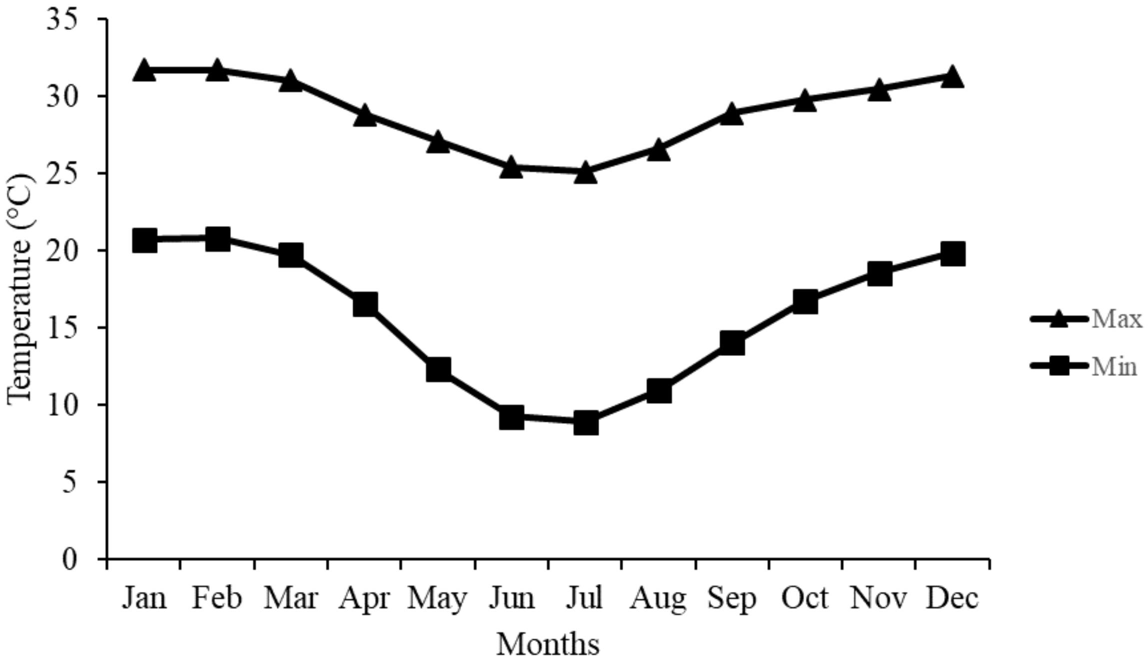

Figure 2.4: Average daily maximum and minimum temperatures for each month for Phalaborwa, the closest weather station to Selati Game Reserve, over a 34-year period (1983-2017). Data missing for 1992, 1993, 2014 and 2015. Data from the South African Weather Service.

Topography and geology

The northern section of Selati is transversed by the seasonal Selati River, which enters the reserve in the west, south of Gravelotte and exits the reserve in the northeast corner (Fig.2.5). Most of the reserve falls within the catchment area of the Selati River and lies at a mean altitude of 530 m above sea level (a.s.l.). The Selati River and other drainage lines (Fig.2.5) drain into the Olifants River, thus forming part of the greater Olifants catchment (Fig.2.1). The highest point on the reserve is found along the Ga-Mashishimale hills in the extreme south at 778.2 m a.s.l. (Fig.2.5)

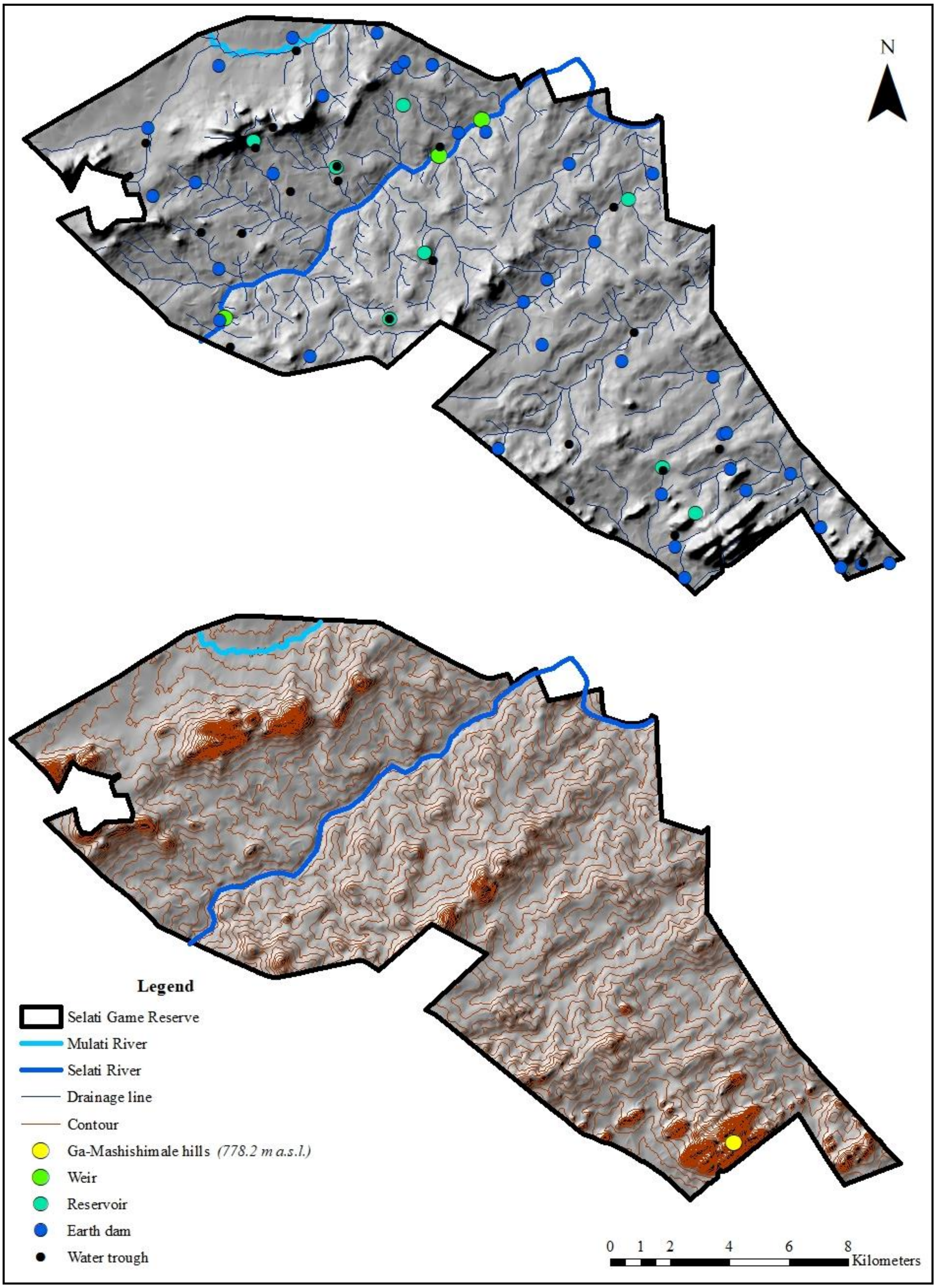

Figure 2.5: Topographical map depicting the distribution of water sources (reservoirs, earth dams and water troughs) and contours throughout Selati Game Reserve.

Throughout Selati there are 38 earth dams (or seasonal pans; Fig.2.5 & 2.6), 20 artificial water points (troughs; Fig.2.5 & 2.7), seven reservoirs (Fig.2.5) and three unequipped boreholes, seven active boreholes. The earth dams were constructed in drainage lines to capture rainwater runoff, but water levels can also be maintained by supplementing from nearby boreholes. The 20 artificial water points are distributed throughout the reserve and provide borehole water for wildlife. Six weirs have been constructed along the Selati River, three of which are broken (e.g. Fig.2.8).

Figure 2.6: Examples of two earth dams in Selati Game Reserve.

Figure 2.7: Examples of artificial water points (troughs) in Selati Game Reserve.

Figure 2.8: An example of a broken weir along the Selati River in Selati Game Reserve.

Selati lies in an area described as Ancient Granites, which have a rich and diverse geological history (Norman & Whitfield, 2006; Fig.2.9). The Murchison Greenstone belt in the north-west of the reserve is one of the volcano-sedimentary belts derived from the Archaean Kaapvaal craton and contains some of the oldest rock formations (e.g. quartz and schists) on Earth (Block *et al.*, 2013; Fig.2.9). The remainder of the reserve is made up of three different granite and pegmatite formations; the Willie, Lekkersmaak and Mashishimale gneisses. The Lekkersmaak gneiss encompasses all potassic granitoids and is dominated by quartz and feldspar, whereas the Willie gneiss is an intrusive coarse-grained pluton with predominantly muscovite and subordinate biotite rocks (Jaguin *et al.*, 2010; Fig.2.9). The Mashishimale gneiss is considered to be the most spectacular, where biotite granite protrudes on the Ga-Mashishimale hills in the south of the reserve (Fig.2.9) and provides habitat for the Lillie Cycad (*Encephalartos dyerianus*), the rarest cycad on the planet.

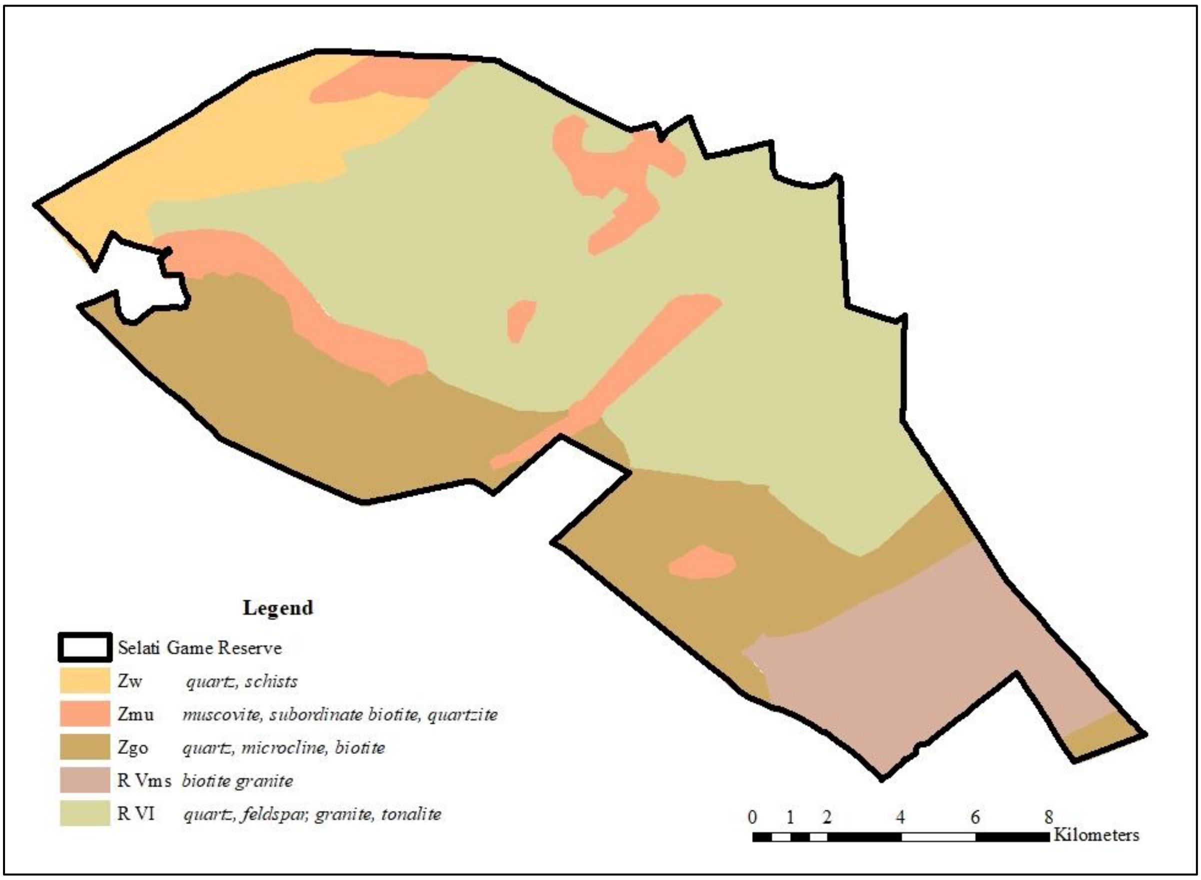

Figure 2.9: Map depicting the geology of Selati Game Reserve.

Vegetation

Selati falls within the Savanna Biome of South Africa, where the Phalaborwa-Timbavati Mopaneveld (61%) bioregion covers the largest portion of the reserve (Rutherford *et al.*, 2006; Fig.2.10). The Granite Lowveld bioregion covers a third of the reserve (33%) whereas, the Gravelotte Rocky Bushveld bioregion (6%) represents only the mountainous areas (Rutherford *et al.*, 2006; Fig.2.10).

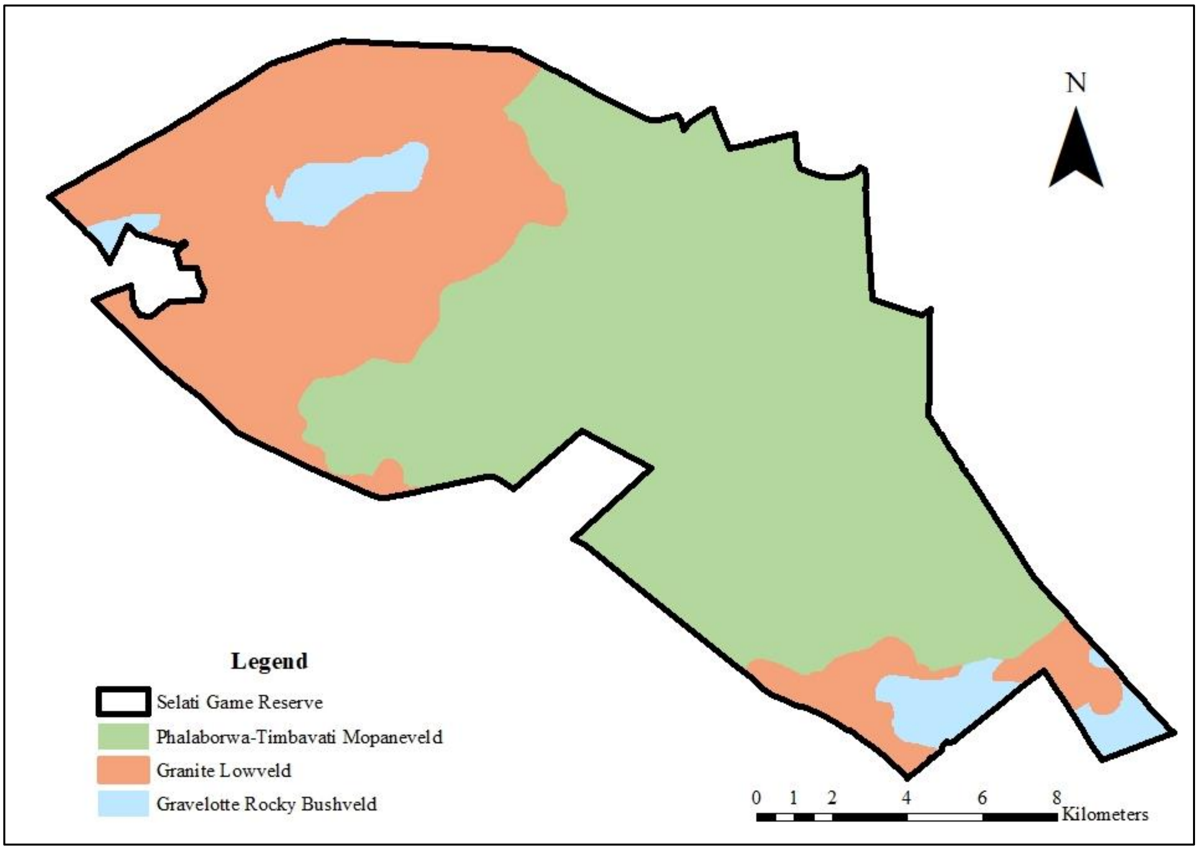

Figure 2.10: Distribution of the three main vegetation types found in Selati Game Reserve.

Phalaborwa-Timbavati Mopaneveld occurs on undulating plains between 300-600 m a.s.l. and is dominated by tree species such as red bushwillow (*Combretum apiculatum*), silver cluster-leaf (*Terminalia sericea*) and mopane (*Colophospermum mopane*; Rutherford *et al.*, 2006). A common feature of this bioregion are the large number of termite mounds. Quartz-feldspar rocks of the Makhutswi gneiss dominate this area, however, in Selati it is intruded by the Lekkersmaak granite. Sandy soils (<10% clay) prevail in the uplands, whereas clay soils tend to be found in the bottom-lands (Fig.2.11). The prevailing landtype is Fb, which is characterized by rocky or shallow soil depths limited by hard rock (Soil Classification Working Group & Macvicar, 1991; Fig.2.12). This bioregion is classed as Least Threatened in terms of conservation as only 5% has been transformed through development of human settlements and mining (Mucina & Rutherford, 2006).

Granite Lowveld is characterised by tall shrubland with few trees to moderately dense, low woodland on the deep sandy uplands where silver cluster-leaf, large-fruited bushwillow (*Combretum zeyheri*) and red bushwillow dominate (Mucina & Rutherford, 2006). The ground layer of this bioregion includes sickle grass (*Pogonarthria squarrosa*), blue seed grass (*Tricholaena monachne*) and curly leaf grass (*Eragrostis rigidior*; Rutherford *et al.*, 2006). Dense thicket to open savanna areas are dominated by knob thorn (*Senegalia nigrescens*), sicklebush (*Dichrostachys cinerea*) and brandy bush (*Grewia bicolor*). Granite Lowveld occurs at an altitude of between 250 to 700 m a.s.l., where the Makhutswi gneiss forms the major basement geology. The archaean granites and gneiss weather into sandy soils in the uplands and clay soils with high sodium content are found in the lowlands (Rutherford *et al.*, 2006; Fig.2.11). This bioregion is classified as Vulnerable in terms of conservation as more than 20% has been transformed through cultivation and settlement development (Mucina & Rutherford, 2006).

Gravelotte Rocky Bushveld is characterised by open deciduous to semi-deciduous woodland on rocky slopes and inselbergs, contrasting strongly with the surrounding plains (Mucina and Rutherford, 2006). This bioregion occurs at altitudes between 450 and 950 m a.s.l. Important tree species include; African teak (*Pterocarpus angolensis*), hook-thorn (*Senegalia caffra*), bushveld candelabra (*Euphorbia cooperi*) and red bushwillow. This bioregion is characterized by varying geology composed mainly of schist and amphibolite of the Gravelotte Group with a few quartzitic and granitic hills. Shallow, rocky soils dominate and the main landtypes are Ib, Fa, Ae and Fb (Fig.2.11 & 2.12). Landtype Ib is characterised by rocky outcrops with short, steep slopes covered with miscellaneous soils (Soil Classification Working Group & Macvicar, 1991). Landtype Ae is characterized by freely drained, red-yellow high base soils, whereas landtype Fa is classified by shallow soils with little to no lime (Soil Classification Working Group & Macvicar, 1991). The conservation of this bioregion is classified as Least Threatened as erosion is very low to moderate and only 15% has been transformed mainly through cultivation and a few settlements.

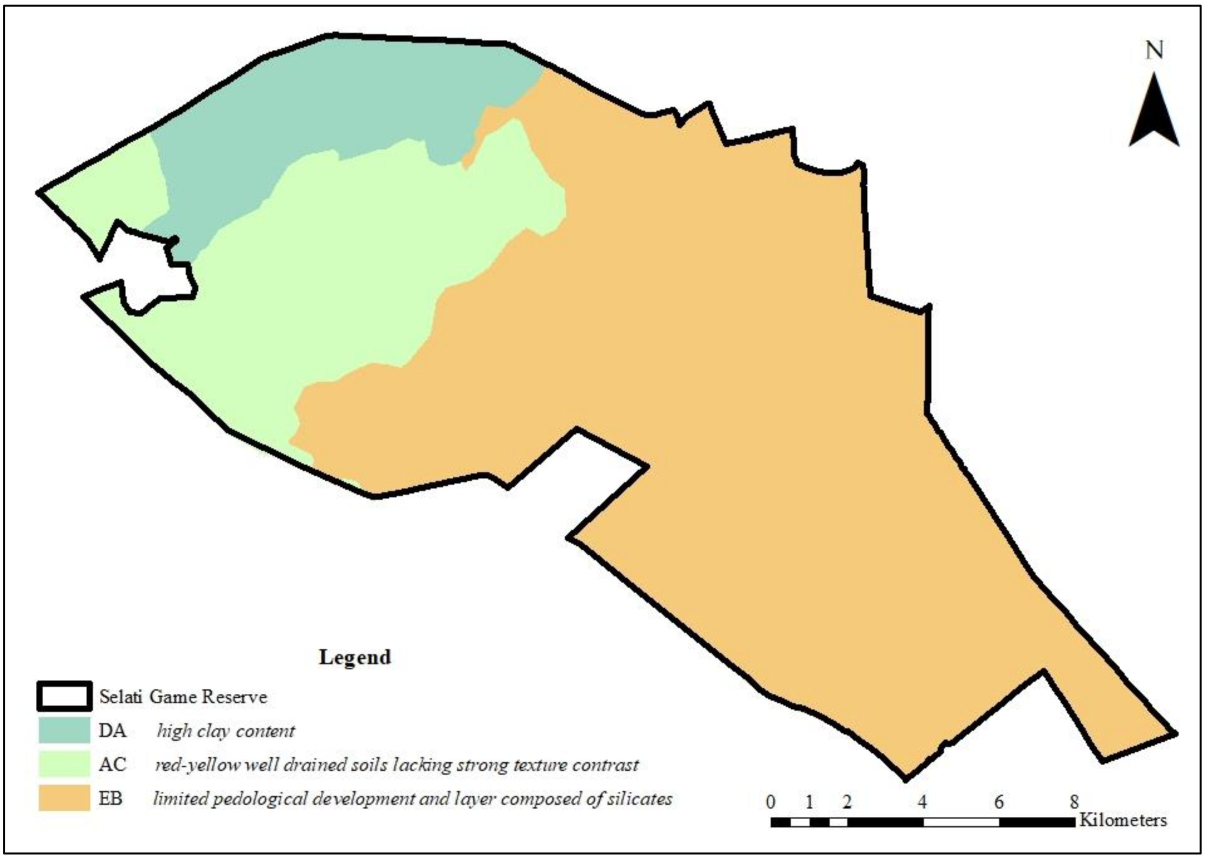

Figure 2.11: Distribution of soil types throughout Selati Game Reserve.

METHODS

Reliable inferences about the ecology of mammals depends on high quality data. An optimal strategy for collecting quality data is to increase the number of repeated surveys at specific sites within the constraints of cost and time (MacKenzie & Royle, 2005). More specifically, to acquire accurate information on species occurrence, distribution and habitat selection, appropriately timed repeated surveys are important (Field, Tyre & Possingham, 2005; MacKenzie & Royle, 2005). Field *et al.*, (2005) argue that two to three repeated surveys are normally sufficient in achieving adequate statistical power. Therefore, to investigate seasonal changes in the occupancy (estimates of species presence) of both prey and carnivore species, repeated surveys (n = 4) were conducted every dry (June to August) and wet (January to March) season over a two year period (2016 to 2018). The four seasonal surveys will be referred as dry 2016, wet 2017, dry 2017 and wet 2018.

Various sampling techniques were conducted to attain different research objectives (see Chapters 3, 4 and 5). The methodology of each technique is described below and specific analytical processes will be provided within each subsequent chapter.

Camera trap survey

For modelling species' distribution or activity patterns, a systematic sampling design is recommended (Ancrenaz *et al.*, 2012), where camera traps (i.e. remotely triggered cameras) are placed randomly in relation to animal movements and the chance of them encountering one (Rovero & Zimmermann, 2016). The distance between camera trap units depends foremost on the study objective, but also on the number of camera trap units available and the area to be targeted (Rovero & Zimmermann, 2016). Importantly, when targeting multiple species, camera trap spacing should be sufficient to ensure that animals with large (~100 km^2) home ranges are sampled with adequate detection probability without cameras being too far apart, which could result in missing animals with smaller (< 50 km^2) home ranges (Rovero & Zimmermann, 2016; Appendix 2.1). Therefore, my camera trap survey followed a systematic grid structure, adapted to the local logistic constraints of Selati (Ancrenaz *et al.*, 2012). A grid cell size of 9 km^2 was chosen to effectively survey all mammalian species found on the reserve (Appendix 2.1). ArcMap 10.5.1 (ESRI, Redlands, California, USA) was used to construct a 9 km^2 grid system over the reserve (Fig.2.12).

When surveying rare or cryptic species, it is best to sample broadly as this increases the likelihood of captures (Foster & Harmsen, 2012). Therefore, from the map (Fig.2.12) grid cells that were filled by more than 50% of the reserve were chosen as areas for camera trap sites (n = 31). I used aerial photographs to randomly select potential (e.g. presence of a sturdy tree close to a road or game path) camera trap sites within each of the 31 chosen grid cells (Ancrenaz *et al.*, 2012). I ensured that sites fell within all three major vegetation types (Fig.2.12). Global Positioning System (GPS) co-ordinates of the 31 pre-selected sites were uploaded to a handheld GPS unit (Garmin GPSMap 62s) and sites were scouted on foot for exact locations. The exact location of the camera trap site was chosen based on whether there was a sturdy tree that the camera could be attached to that was in close proximity to a relatively open area (e.g. a clearing, game path or road; Kelly & Holub, 2008). A standard approach to camera trapping is to place cameras at locations that will maximise capture probability of target species (Rovero & Zimmermann, 2016). Therefore, throughout the reserve, 15 camera trap sites were placed along prominent game paths, to increase the likelihood of detecting prey species and the remaining 16 camera trap sites were placed along roads, to increase the likelihood of capturing carnivores (Karanth & Nichols, 1998; Thorn *et al.*, 2009).

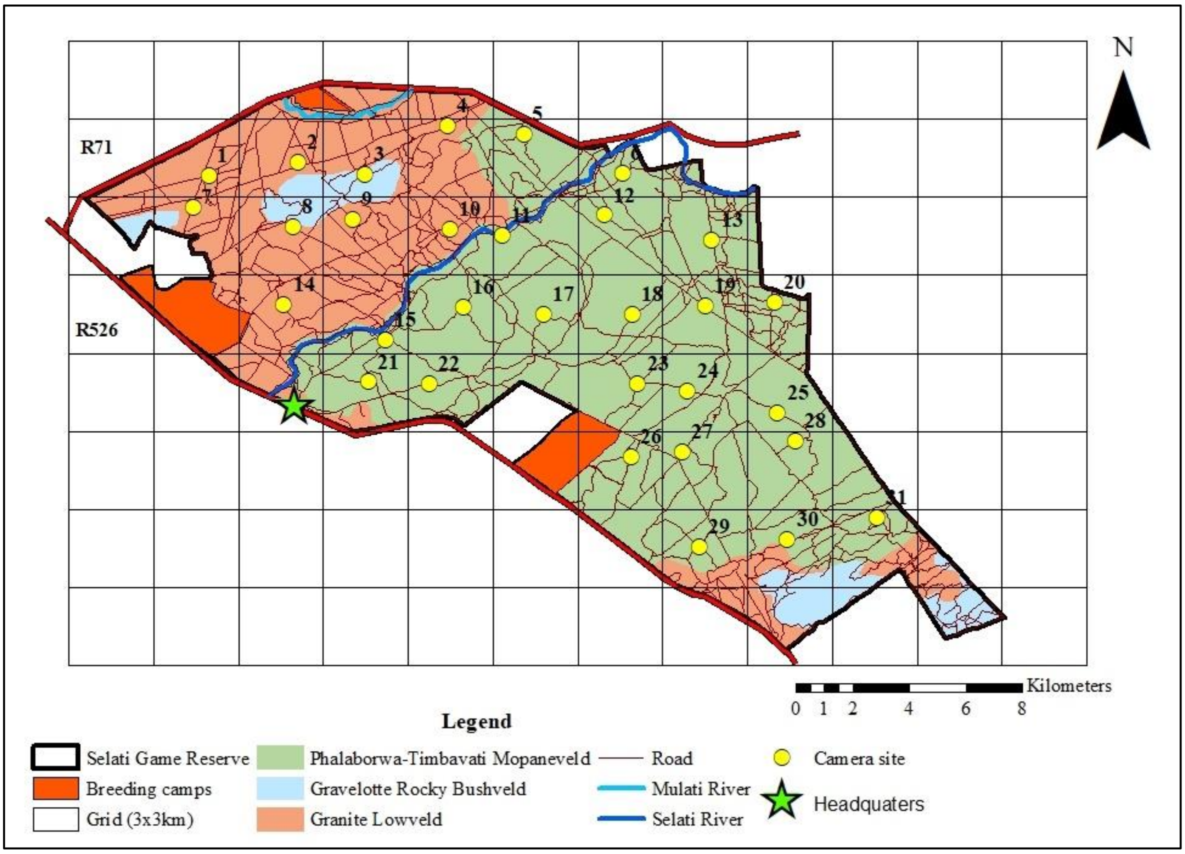

Figure 2.12: Location of the 31 sites in grids I selected to install camera traps throughout Selati Game Reserve in relation to the three major vegetation types.

To reduce bias caused by variable sensitivity (Rovero & Zimmermann, 2016), I only used Cuddeback Attack (Non Typical, Inc., Green Bay, WI, USA) cameras. The deployment of camera traps on supports followed a standardized procedure in terms of camera height, inclination and orientation (Rovero & Zimmermann, 2016). All camera traps were mounted to sturdy trees in metal casings using cable ties and wire ~45 cm above the ground. At each site, the cameras were placed parallel to the chosen clearing, game path or road. At sites where cameras needed to be higher than 45 cm, due to the surrounding environment, the cameras were angled downwards. Care was taken to ensure that the inclination of the camera at each site would result in the camera triggering for animals as small as dwarf mongooses (*Helogale parvula*) as well as for elephants (*Loxodonta africana*). The understory growth was cleared at all sites to minimise false triggering and to prevent obscured photographs. No lures were used to prevent heterogeneous capture probabilities (Foster & Harmsen, 2012).

Cuddeback Attack cameras have a passive infrared sensor that detects heat and motion and a ¼ second trigger speed, which is one of the fastest for trail cameras. The cameras required four D-cell batteries to operate and stored images on SD memory cards. Each camera was programmed to take high quality (5MP) images with the strobe flash range set at 3.3 m to reduce the risk of overexposed photographs. Cameras were active for 24 hours per day with an enforced 30 second interval between consecutive photographs. Camera trap surveys are usually conducted over short periods of time (30 to 90 days) to ensure demographic closure (no immigration or emigration) of the animals being photographed (Karanth & Nichols, 1998). I therefore, conducted each seasonal survey for 60 consecutive nights. The cameras were checked every two weeks to ensure that they were functioning correctly and to replace batteries and memory cards, as required.

Ungulate transect survey

Ungulates were counted using the line transect method (Ogutu *et al.*, 2006), whereby three random, separate transect routes, totalling 97 km were selected. The roads driven covered the majority of the reserve and passed through all three major vegetation types (Fig.2.13).

Ungulate counts were undertaken during each of the four seasonal survey periods. In each season, each transect route was driven twice, in opposite directions (north and south) over a period of six to nine days (weather dependent) by two observers in an open, four-wheel-drive vehicle at 20-25 km/hr (Hirst, 1969; Fischer & Linsenmair, 2001). Each observer was equipped with binoculars and was responsible for counting animals on opposite sides of the road. Large aggregations of ungulates (e.g. impala (*Aepyceros melampus*)) were counted by both observers to maximise accuracy (Dinerstein, 1980). All animal counts were made in the early morning between 07h00 and 11h00 in the cooler dry seasons, and between 05h30 and 09h30 in the warmer wet seasons when ungulates are most active (Dinerstein, 1980). Animals observed were counted and classified by species, sex and age (adult or juvenile). Additional information recorded included the kilometre segment, GPS co-ordinates, radial distance of the animal or herd from the road (using a Nikon 800 rangefinder) and the angle of the animal(s) from the line of movement of the vehicle.

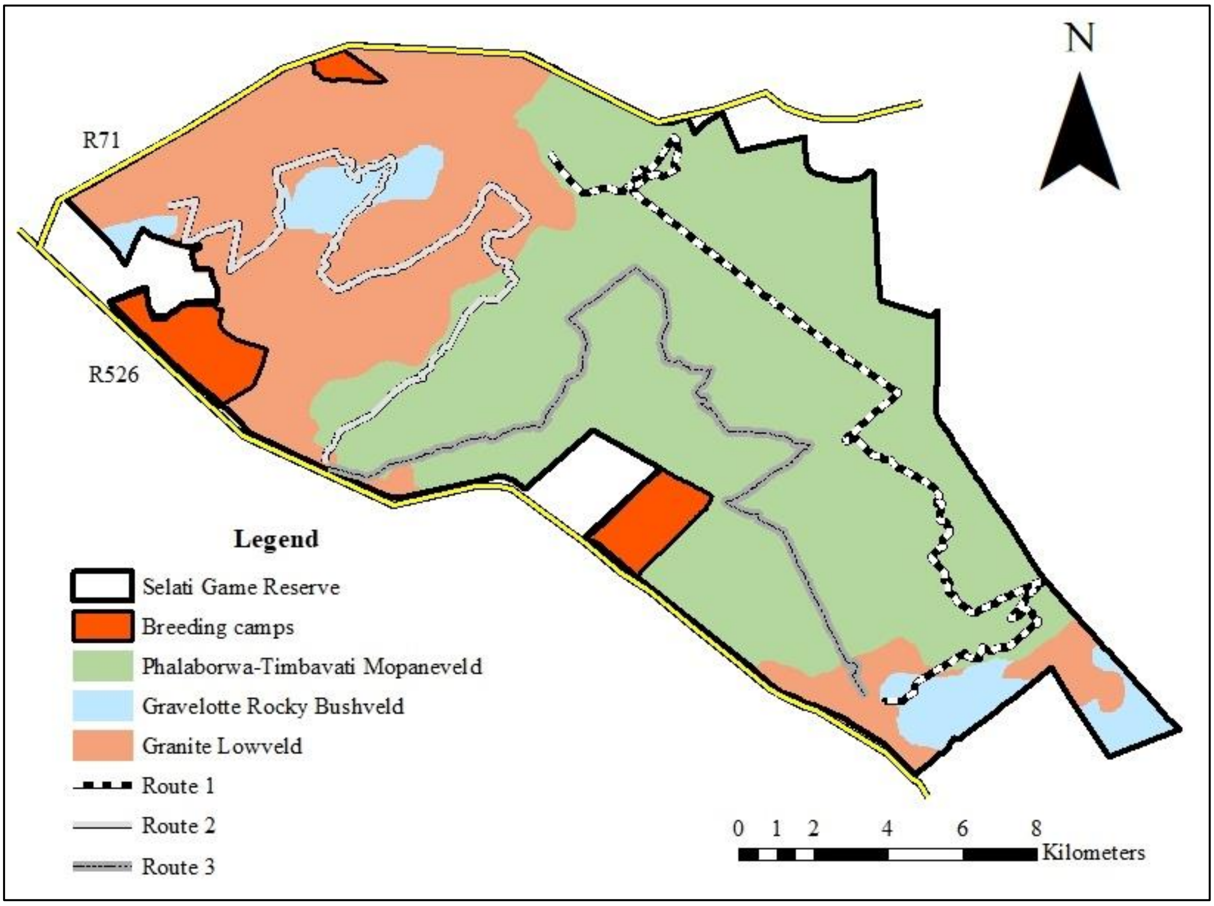

Figure 2.13: The three routes driven for the ungulate transect surveys on Selati Game Reserve.

Aerial count survey

Personnel at Selati have been conducting annual aerial counts to estimate total numbers of mammals since 2003 (except for 2013). A Bell 206 helicopter was used with a survey team consisting of a pilot, a scribe/forward observer seated next to the pilot and two rear seat observers. During the survey, all four individual were in communication. The scribe entered the GPS location, species, age, sex and total numbers of all animals observed onto a computer linked to the GPS. With the use of a GPS coupled to flight instruments, the pilot flew fixed flight lines (strips) between pre-determined points. The strip width was generally 300 m wide and flown in a north-south direction. In areas of the reserve where visibility was limited, such as over the mountains and river, narrower strip widths were searched. The actual flight path, ground speed and height above sea level were recorded every 100 m by the GPS. Depending on weather conditions, the reserve was completely surveyed within three to four days. Strips were not flown when it was raining or when there was excessive cloud cover as these conditions reduced animal sightings.

Collaring large carnivores

Capture, handling and collaring of large carnivores was done in accordance with the Animal Ethics Subcommittee of the Rhodes University Ethical Standards Committee (ethics clearance reference number: 7650848) and the Limpopo Economic Development, Environment and Tourism department (local conservation authority permit number: ZA/LP/80087).

Adults of three species of large carnivores (four lions (*Panthera leo*), four leopards (*Panthera pardus*) and four spotted hyaenas (*Crocuta crocuta*)) were fitted with iridium satellite GPS/UHF/GSM (Ultra High Frequency (UHF), Global System for Mobile communications (GSM)) collars with an integrated VHF radio transmitter (African Wildlife Tracking (AWT), Rietondale, Pretoria). Only one male cheetah (*Acinonyx jubatus*) was present on the reserve so for statistical reasons I was not able to include cheetah in my study. The collars were programmed to record the location of the animals at three-hour intervals, which was stored on the collars non-volatile memory and could be retrieved remotely from a computer-based application (AWT Tracker Version 2.0.8.133).

Various methods can be used to trap large carnivores, including free darting, baited cage traps and baited foot-loop traps (Frank, Simpson & Woodroffe, 2003). All of these methods cause minimal injury (Frank *et al.*, 2003). Boitani and Powell (2012) conducted an assessment on various methods to capture carnivores and determined that both foot-loop and cage traps are humane methods for capturing Hyaenids (e.g. spotted hyaenas) and Felids (e.g. leopards). Therefore, I used both foot-loop and cage traps initially to capture intended study animals. After numerous failed attempts with baited foot-loop traps, I only used baited cage traps to capture leopards and spotted hyaenas.

Baited cage traps

Carnivores captured in cage traps have been recorded to break their teeth or cut their mouths by biting the wire-mesh walls of the cage, thus cages with small mesh holes are superior to large mesh holes and reduce the risk of injury (Boitani & Powell, 2012). The cage trap I used was 2.2 m x 0.8 m x 0.8 m with a sliding door trap. The trap door was designed to fall past the entrance of the cage to secure the door and to allow for the easy release of any non-target animals captured from a distance. The wire-mesh walls of the cage had a small mesh size of 2.5 cm, which prevented leverage of an animal biting and thus minimized tooth breakage (Mr Joubert, pers. comm). The mesh of the cage was placed with the horizontal wire mesh welded on the inside of the cage and the vertical mesh wires on the outside of the cage, which minimized hair loss (CJ Joubert, pers. comm). Furthermore, the bait (impala meat) was hung deep inside the cage and set to only release the door once an animal was feeding (Mr Joubert, pers. comm), which prevented the door from closing on an animal.

To capture leopards, baited camera trap sites (no cage trap present) were used to identify suitable individuals for collaring. The baited camera trap sites were set up in suitable areas of the reserve where signs (tracks, scats or kills) of leopards had been recorded. Sites were selected near roads to ensure access for placing or replacing of baits and for the offloading and setting up of the cage (du Preez, Loveridge & Macdonald, 2014). Tall trees, usually a mopane with a prominent fork about 2 m above the ground, were chosen to hang baits with wire from a branch so that the lowest part of the bait was just above the fork of the tree. The bait was always covered with vegetation to reduce the chance of vultures identifying it from the air and feeding on it. I made sure that a camera trap could be set up in a tree within ± 3 m of the bait tree (du Preez *et al.*, 2014). A forked pole 3 to 4 m long, usually cut from a mopane tree, was placed perpendicular to the camera trap, against the fork of the tree and under the bait to facilitate access by leopards (du Preez *et al.*, 2014). The camera trap always faced the right side of the pole, which ensured that individual leopards could be identified from photographs captured of their right-side flanks (Fig.2.15). A mixture of intestines, stomach contents, blood and water were spread on and around the bait tree to cover our human scent but to also attract leopards (du Preez *et al.*, 2014). This mixture was also used to form scent trails from the bait tree to the road and along the road for ~1 km. Bait sites and camera trap photographs were checked every morning just after sunrise and baits were replaced when rotten (~every 5 days).

Once a suitable leopard for collaring had been photographed feeding, the cage trap was set up within ~5 m of the bait tree. The bait and pole were removed from the tree and when necessary, a fresh bait used in the cage. The cage was always set just before sunset and was often placed under bushes or covered with vegetation to blend it into the surrounding environment (McCarthy *et al.*, 2013). The camera trap used at the bait site was replaced with a RikRhino remote sensor camera trap set up on a tree facing the entrance to the cage. RikRhino cameras have multimedia messaging service capabilities (Rik Rhino Surveillance (Pty) Ltd.) and use cell phone SIM cards to send alert messages and images to the RikRhino Application. The app was installed on the cell phones of select personnel. This camera trap system allowed us to keep track (in real time) of any activity in and around the cage. This minimized the amount of time an animal spent after capture in the cage and ensured that non-target animals were released as soon as possible. If the cage trap was unsuccessful in capturing a leopard, or if the intended candidate for collaring did not return, the bait was removed from the cage and the cage was disarmed and closed the following morning before sunrise. If the cage trap was successful in capturing the intended leopard, the qualified wildlife veterinarian on standby was summoned to immobilize the animal.

Figure 2.15: Camera trap photograph of the right-side flank of a male leopard feeding at a baited site.

The same cage used to capture leopards was used to capture a spotted hyaena, following procedures used by Dheer (2016) in Kenya. No baited sites were used, but instead the baited cage trap was set up along a prominent game path close to a known active spotted hyaena den site. The baited cage was placed under bushes and trees to help blend the cage into the surrounding environment. Importantly, the floor of the cage was covered with dead grass to provide substrate continuity. Spotted hyaenas are olfactory foragers, so a mixture of intestines, stomach contents, blood and bones was thrown in and around the cage to not only attract them, but to encourage them to approach the cage to feed off the scraps. A scent trail leading to the cage from the closest road along the prominent game path was also formed to attract the spotted hyaenas. A RikRhino camera trap was set up in a tree within 3 m of the entrance to the cage so that animal movement in or around the cage could be monitored in real time. After each unsuccessful trap night, just before sunrise, the cage was disarmed, closed and the bait removed and then just before sunset the cage was reset. When the cage trap was successful in capturing a spotted hyaena, the wildlife veterinarian on standby was contacted immediately to immobilize the animal.

Free darting

I used free darting from a vehicle (Bauer & Iongh, 2005) to capture three of the four lions and two of the four spotted hyaenas. The intended animals were attracted to an appropriate area in close proximity to where they had recently been recorded using a baited call-up station (Ogutu & Dublin, 1998; Ferreira *et al.*, 2013; Tuqa *et al.*, 2014). To allow enough feeding time for the wildlife veterinarian to dart the lions and spotted hyaenas, an entire impala carcass was secured to a tree. A recording of pig squeals was used to attract lions and a recording of lions feeding off a carcass with the sounds of calling spotted hyaenas was used to attract hyaenas. The playbacks started 30 min after sunset and was played for varying periods of time through a speaker mounted on the roof of a single cab four-wheel-drive vehicle parked 20 m from the bait. The wildlife veterinarian and animal recovery team were in the back of the vehicle. A spotlight was used to scan the area approximately every 10 minutes until the target lion or spotted hyaena was feeding on the bait and could be darted by the wildlife veterinarian.

Since spotted hyaenas are known to be skittish, a transmitter dart, which can be tracked using a telemetry set and which usually remains embedded in the rump of the animal darted, was used to immobilize the two spotted hyaenas. This meant that if the darted spotted hyaena ran off before the immobilising properties of the drugs took effect, I was able to track the location of the animal. Transmitter darts reduce both time and resources required to capture wildlife (Kilpatrick, DeNicola & Ellingwood, 1996).

Free darting from a helicopter was used to immobilize the fourth lion and spotted hyaena. This took place from a Bell 206 helicopter carrying a qualified wildlife veterinarian and a spotter. The intended lioness for collaring was carrying a failing VHF collar, which meant that a ground team could search for her and relay information to the pilot. For the spotted hyaena, an area of known hyaena activity was flown until a suitable individual was identified and could be darted. All occupants in the helicopter aided in observing both the lion and spotted hyaena from the air both before and after they had been darted (Fritts *et al.*, 1997). Once darted, the helicopter retreated several hundred meters until the animal became recumbent (Ballard, Franzmann & Gardner, 1982). The location of the darted animals were relayed to a ground team, who waited nearby and monitored the animal while the helicopter landed.

The qualified wildlife veterinarian was always in charge of immobilising, monitoring and collaring animals. For darting, the wildlife veterinarian used formalised drug combinations according to species and the individual’s age and sex (e.g. Table 2.1). Once an animal had been successfully darted, the wildlife veterinarian always waited 15-20 minutes before approaching to ensure they were immobilized enough to allow safe handling. A team of three to four people always retrieved the immobilized animal with the help of a stretcher. Animals were transferred to the back of a four-wheel-drive vehicle and relocated to a suitable open area nearby, where the animal could be safely collared. Before collaring, the wildlife veterinarian removed the dart, treated the animals for any wounds, administered antibiotics and eye drops to lubricate the animals eyes. Once all procedures were completed, the wildlife veterinarian injected the animals with the reversal atipamezole (Antisedan), which accelerates the recovery process from the immobilizing drugs. A single vehicle parked 100 to 200 m away monitored the animals until fully recovered. An animal was considered fully recovered when it no longer exhibited drug influence in gait and head movements (Ballard *et al.*, 1991).

Table 2.1: Drug combinations used to immobilise and reverse one average sized adult of each species and sex (M = male, F = female and U = unknown).

Species	Sex	Immobilizing drugs		Reversal		Antibiotics
		Zoletil	Medetomidine	Yohimbine	Atipamezole	Norotrim
Lion	M	250 mg	6 mg/ml	2 ml	2 ml	15 ml
	F	150 mg	4 mg/ml	2 ml	2 ml	15 ml
Leopard	M	70 mg	4 mg/ml	1 ml	1 ml	10 ml
	F	50 mg	3 mg/ml	1 ml	1 ml	10 ml
Spotted hyaena	U	40 mg	2 mg/ml	1 ml	1 ml	5 ml

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Chapter 3

POPULATION ESTIMATES

Juvenile impala on Selati Game Reserve during the wet season of 2017

INTRODUCTION

To avoid the extinction of threatened species, preserve biodiversity and ensure adequate protection of terrestrial, freshwater and marine systems, biological indicators that accurately reflect trends in the abundance and distribution of species are crucial (Ahumada, Hurtado & Lizcano, 2013). Accordingly, basic and applied ecological research primarily revolves around studying the distribution, abundance and interactions of animals with their environment (Buckland, Anderson & Laake, 1993; Chandler & Royle, 2013). Establishing reliable population estimates (e.g. density (D) or size (N)) are essential for effective wildlife conservation management (Buckland *et al.*, 1993; Ellis & Bernard, 2005; Balme, Slotow & Hunter, 2009b). It is also important to ensure that population estimates are produced frequently enough to appropriately inform decision-making processes (Jiménez *et al.*, 2017). Constant and reliable population estimates are of particular importance for species of conservation concern, as imprecise estimates could provide a false indication of stability (Tobler & Powell, 2013), resulting in a lack of the required conservation effort (Bauer *et al.*, 2015). However, monitoring is one of the most controversial concerns when managing wildlife as obtaining reliable estimates of wild populations is often logistically difficult to achieve given funding and time limitations (Carbone *et al.*, 2001; Jiménez *et al.*, 2017; Palmer *et al.*, 2018).

Globally, accurate population estimates for multiple, sympatric species (i.e. predators and prey) are generally absent, hampering informed management and conservation initiatives (Treves, Krofel & McManus, 2016; Burgar, Burton & Fisher, 2018a). In addition, monitoring has traditionally focused on single species while management interventions are increasingly being oriented towards ecosystem functioning and population estimates of entire guilds (Ahumada *et al.*, 2013; Jiménez *et al.*, 2017). While obtaining reliable estimates for groups of species such as farmland birds or large herbivores in open systems may be achievable, estimates of cryptic and elusive vertebrate guilds is challenging (Jiménez *et al.*, 2017).

Carnivores are notoriously difficult to monitor as many are shy, solitary, nocturnal species with wide home ranges that occur at naturally low densities (Gese, 2001; Balme, Hunter & Slotow, 2009a). Direct observations or complete counts of carnivore populations are practically impossible, time-consuming and expensive (Gese, 2001; Balme *et al.*, 2009a). As a result, a number of alternative sampling techniques have been developed to provide indices of carnivore density and abundance (Seber & Schwarz, 1999). These techniques include interviewing local people, collaring individuals within the population and collecting transect data on sighting or spoor/sign encounters (Carbone *et al.*, 2001; Devens *et al.*, 2018). All have limitations. For instance, spoor and sign surveys are limited in that they require researchers with skills in both tracking and identification (Gese, 2001). Collaring of individuals is restricted to a few individuals due to the high cost involved and there is always the uncertainty about how many untagged individuals exist within the population (Karanth & Nichols, 1998; Devens *et al.*, 2018).

In the last two decades there has been a shift from labour-intensive and invasive field techniques (e.g. traditional capture-recapture) to ones that are less invasive and cost effective, such as remote sensor camera traps (Pollock *et al.*, 2002; Burton *et al.*, 2015; Rovero & Zimmermann, 2016). The use of camera trap surveys in field biology has become extremely common given that they enable concurrent detection of multiple sympatric species. This makes it a powerful tool to monitor biodiversity and populations across multiple scales (Steenweg *et al.*, 2017). Camera trap surveys can also be replicated making them efficient tools to monitor ground-dwelling terrestrial mammals over space and time (Rovero *et al.*, 2014). Camera trap surveys do have limitations as they must contend with imperfect detections of mobile species (Burton *et al.*, 2015). Recent advances in statistical analyses have, however, improved our ability to estimate population density using Bayesian spatially explicit capture-recapture (SECR) models, which account for varying detection probabilities (Chandler & Royle, 2013;

Jiménez *et al.*, 2017; Burgar *et al.*, 2018b). SECR models link abundance with location data by estimating a latent variable representing individual activity centres (Chandler & Royle, 2013). The ability of camera trap surveys to estimate the community structure of carnivores has been constrained because SECR models rely on the identification of marked individuals (Karanth & Nichols, 1998; Jiménez *et al.*, 2017). As a result, these models have predominantly been used to estimate the density of mammalian carnivores (particularly felid species) and to a lesser extent birds (Mollet *et al.*, 2015), sharks (Bradley *et al.*, 2017), amphibians (Muñoz *et al.*, 2016) and insects (Torres-Vila *et al.*, 2012).

New analytical inference-based spatial count (SC) models have been developed to estimate the density of species without individual marks, something that is common for carnivore (and ungulate) species (Chandler & Royle, 2013; Sollmann *et al.*, 2013). Generating spatial count models, however, requires complex and computationally demanding statistics with assumptions which are often difficult to verify (Palmer *et al.*, 2018). Only a handful of published papers (e.g. Sollmann *et al.*, 2013; Jiménez *et al.*, 2017; Burgar *et al.*, 2018b, 2018a; Evans & Rittenhouse, 2018) have applied SC models to field data, and these report variable degrees of convergence with other analytical models such as SECR. Although there is a need to assess the reliability of SC models, integrating this analytical technique with other modelling methods is a promising process to estimate the densities of entire animal communities or guilds (Jiménez *et al.*, 2017).

While multiple tools and analyses have been developed to monitor terrestrial carnivores, estimates of community structures (species diversity, patterns of interactions etc.) are rare (but see Ahumada *et al.*, 2013; Jiménez *et al.*, 2017). The carnivore guild can be a vital driver of ecosystem function, structure and dynamics (Jiménez *et al.*, 2017). This guild not only produces various top-down processes (e.g. trophic cascades), but also provides other ecosystem services such as seed dispersal (Jiménez *et al.*, 2017). Ungulate density has been recognized as a major driver of carnivore density both within and between species (Carbone & Gittleman, 2002). Given that at least 90 carnivore species have been listed as either threatened or endangered worldwide, understanding prey diversity and densities is therefore critical to the conservation of carnivore populations (Carbone & Gittleman, 2002).

Typically, ungulate abundance and densities are estimated using aerial total counts or ground transects in combination with distance or sightability models (Pollock *et al.*, 2002; Sollmann *et al.*, 2013). Transect sampling allows for the estimation of density of biological populations, by measuring distances from a line to objects of interest. Many terrestrial mammal species have been successfully surveyed using this method (e.g. mice, fruit bats, primates and many ungulates; Buckland *et al.*, 1993). However, an inherent drawback to both aerial and transect surveys is the substantial cost to conduct them (Pollock *et al.*, 2002).

Animal abundance can be measured as either absolute or relative abundance using camera trap surveys (Gese, 2001; Sollmann *et al.*, 2013). Absolute abundance techniques involve counts of animals leading to estimates of the number or density of animals in the population (Gese, 2001). Whereas, relative abundance does not estimate animal numbers per se, but instead produces indices of animal abundance (e.g. relative abundance index (RAI)) that can be compared over time or space (Carbone *et al.*, 2001; Gese, 2001). Photographic capture rates from camera trap surveys can be used to provide RAIs for a wide range of wildlife species. This method is less complex and not always universally applicable compared to other analytical estimation methods, but RAIs are commonly used when absolute abundance estimates are too difficult or costly to measure (Sollmann *et al.*, 2013; Palmer *et al.*, 2018).

Selati Game Reserve is a private, non-commercial reserve that focuses on breeding large mammals and trophy hunting. Rough detection probability trend analyses have previously been conducted for both large and medium-sized mammals on the reserve, but these estimates were calculated using limited data, which may bias assessments (Joubert & Joubert, 2015). The number of lions (*Panthera leo*) on Selati, however, has been carefully monitored since their reintroduction in June 2004 (Joubert & Joubert, 2015). The lion population has been artificially manipulated (e.g. relocations and female contraception) over the years and is the only large carnivore for which a definite population number is known (Joubert & Joubert, 2015).

My research objective was to assess the abundance and density of multiple, interacting mammal species (i.e. prey and particularly carnivores) through various sampling techniques and across multiple seasons in a small, enclosed protected area. I predicted that within the carnivore guild, the larger, more dominant species would supress the abundance and density of the smaller species through intra-guild competition.

METHODS

The methodology for each sampling technique and the details of the study site are described in detail in Chapter 2.

Data analyses

Camera trap survey

I used Camera Base 1.7 (Copyright 2012 Mathias Tobler) to manage all mammalian carnivore and herbivore photographs captured during each seasonal survey (i.e. dry 2016, wet 2017, dry 2017 and wet 2018). Data recorded from each photograph included survey name, date and time that the photograph was taken, camera trap site information (camera trap site number, camera trap number, GPS location, elevation (m a.s.l.), habitat type) and species present information (identification and total counts for male, female and unknown). To test whether the mammal community of Selati was adequately sampled during each seasonal survey, the average species richness was plotted against cumulative camera trap days to obtain species accumulation curves. The order in which samples were included in the curve was randomized 1000 times and results were used to derive 95% confidence intervals around the mean (Gotelli & Colwell, 2001).

For each seasonal survey, the number of active trap days (sampling effort) was calculated for each station (Rovero & Zimmermann, 2016). If cameras malfunctioned, had technical problems (e.g. no flash triggered at night, full SD card or flat batteries) or were damaged by animals (e.g. elephants (*Loxodonta africana*)) the camera trap was deemed inactive for those days. Only photographs of mammals (i.e. species of interest) were included in the analyses. To prevent repeated captures of the same species, independent capture events were defined by a 30 min interval between consecutive photographs at a camera trap site of the same species or individually identified animal (Rovero & Zimmermann, 2016). Relative abundance indices (RAI) for each species captured during each seasonal survey were computed as the number of events divided by sampling effort and multiplied by 100 (i.e. events per 100 days of camera trapping; Karanth & Nichols, 1998; Rovero *et al.*, 2014). In addition, naïve occupancy was calculated as the proportion of camera trap locations at which each species was detected, divided by the total number of camera trap locations (Rovero & Zimmermann, 2016). Although RAI and naïve occupancy can be influenced by sampling design or a species' behaviour (e.g. Sollmann *et al.*, 2013), both measures are useful for assessing species occurrence (Hedwig *et al.*, 2018). To reduce detection bias and to adequately assess the prey and carnivore populations of Selati, I standardized my sampling design by 1) only using one camera trap brand (i.e. reduce variation in detection of species) and 2) randomly placing camera trap sites along roads and game paths (i.e. reduce overestimation of carnivore species; Sollmann *et al.*, 2013). Based on the size differences amongst terrestrial mammals (Tomiya, 2013), both prey and carnivore species were categorised into four and three broad body mass categories respectively (Karanth & Sunquist, 1995; Karanth & Nichols, 1998). Prey species were categorised as small (<30 kg), medium (30-90 kg), large (90-1000 kg) and megaherbivore (>1000 kg; Krüger, Lawes & Maddock, 1999); whereas carnivore species were categorised as small (<10 kg) medium (10-20 kg) and large (>20 kg; De Cuyper *et al.*, 2019). Data were not normally distributed, so Kruskal-Wallis (non-parametric) tests were run in the R programming language (version 3.4.2, R Development Core Team, 2017) to test for the effects of season (wet and dry) on total species RAI, total prey species RAI and total carnivore species RAI. Kruskal-Wallis tests were also used to assess whether season (wet and dry) or survey (dry 2016, wet 2017, dry 2017 and wet 2018) had an effect on small, medium, large and megaherbivore prey species RAI and small, medium and large carnivore species RAI.

Spatially explicit capture-recapture

Bayesian spatially explicit capture-recapture (SECR) methods are used to model data from individually identifiable animal capture-recaptures to estimate population density and size (Efford & Fewster, 2013). Camera-trap surveys of cryptic carnivores, usually result in small sample sizes because these species are found at naturally low densities (Karanth & Nichols, 2002). Many authors suggest caution when interpreting data with small sample sizes (i.e. when the number of individual animals caught is less than 20) because they may reflect biased results (Otis *et al.*, 1978; White, 1982). Therefore, of the individually identifiable carnivores photographed (serval (*Leptailurus serval*), small-spotted genet (*Genetta genetta*), large-spotted genet (*Genetta tigrina*), African civet (*Civettictis civetta*; hereafter civet), leopard (*Panthera* *pardus*) and spotted hyaena (*Crocuta crocuta*)) only those with > 20 individual animals identified were used for SECR (i.e. leopard, spotted hyaena and civet).

Individuals were visually identified based on the position of several individually identifiable markings such as unique pelage patterns (e.g. shape, size and specific location of spots, rosettes or stripes) and facial or body scarring (Fig.3.1; Balme *et al.*, 2009a; O'Brien & Kinnaird, 2011). Although leopards, spotted hyaenas and civets are unique based on pelage patterns, these are bilaterally asymmetrical. Consequently, the photographs of these species were split into left- and right-side capture-recapture datasets, which were analysed separately. Unclear photographs of leopards, spotted hyaenas and civets either because of distance (e.g. too far or too close; Fig.3.2A) or extreme angles (e.g. moving away or towards the camera; Fig.3.2B) were discarded, as individuals could not be reliably identified.

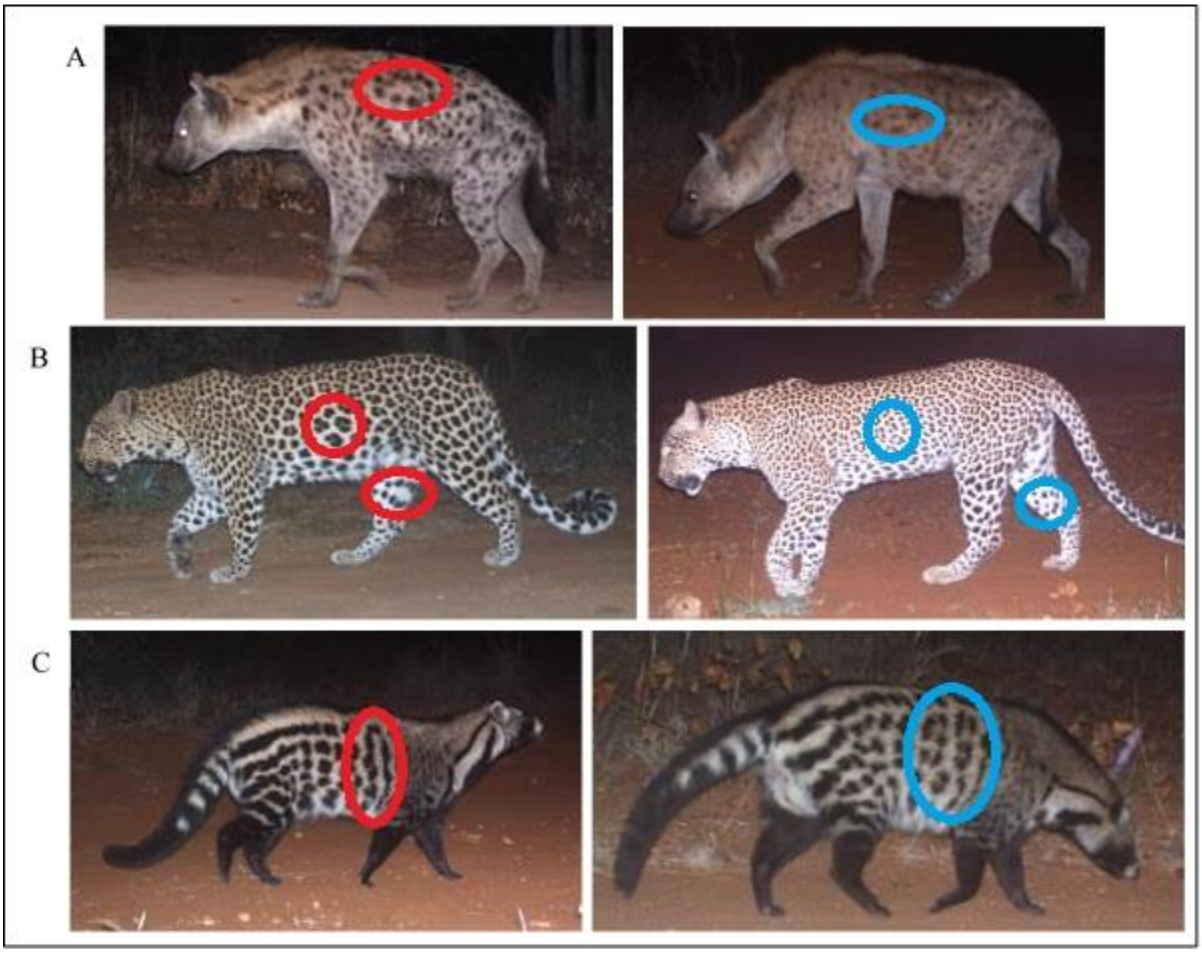

Figure 3.1: Photographs of two different individual (red and blue) spotted hyaenas (A), leopards (B) and civets (C) captured by camera traps on Selati Game Reserve, indicating how individuals could be visually identified. Identifications were based on the position of several individually identifiable markings such as unique pelage patterns and the shape, size and specific location of spots, rosettes or stripes.

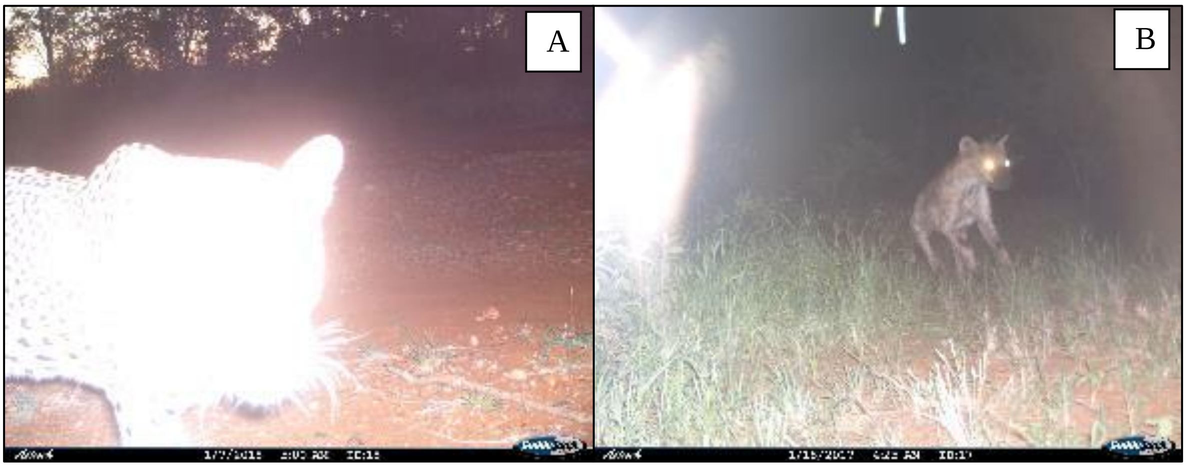

Figure 3.2: Examples of unclear photographs captured in Selati Game Reserve due to distance (e.g. being too close (A)) or angle (e.g. moving towards the camera (B)). These were removed from density estimation analyses.

I followed Heilbrun *et al.* (2003) to assign identities to leopards, spotted hyaenas and civets, whereby a photograph of an individual animal was considered an initial capture if it could not be matched to any previously identified individual. Each newly identified individual was added to the reference collection and assigned a unique identifier consisting of letters and a number (e.g. LPL01 for the first leopard identified from a left-side photograph). A photograph was considered a recapture when the individual had already been identified. For each seasonal survey, trap days were not grouped and a sampling occasion was defined as a 24-hour period (Rovero & Zimmermann, 2016).

SECR multi-session analyses were run in R using the package ‘secr’ (version 3.1) developed by Efford, Dawson & Borchers (2009) to produce full maximum likelihood population density estimates. The two primary input files required by ‘secr’ are (1) trap layout and (2) detection histories of known individuals. A trap layout file for each seasonal survey was created and contained the numbered locations and UTM coordinates of each camera trap site followed by a matrix of binary information about when cameras were active (“1”) versus inactive (“0”). The trap layout file also contained co-variate information associated with each camera trap site such as habitat type, elevation (m a.s.l.), slope (°), presence along road (“yes” or “no”), distance to the closest water source (m) and whether large predators, medium predators or small predators had been captured at each camera trap site (e.g. Appendix 3.1a). Survey-specific detections were combined into one detection history file, where each seasonal survey was given a character-valued code (survey identifier; e.g. Appendix 3.1b).

A habitat mask is required to run SECR analyses. I generated this in ‘secr’ using a specified buffer strip around each camera trap site. Various techniques can be used to determine the width of the buffer strip such as (1) mean distance from outer camera sites to reserve boundary, (2) mean maximum distance moved for animals captured on more than one occasion or (3) half this distance and the (4) mean maximum distance moved based data from radio-collars (Karanth & Nichols, 1998; Silver *et al.*, 2004). When capture-recapture data are used for animals that move across reserve boundaries (see Chapter 4), model fitting should be undertaken with a habitat mask using a buffer that is a multiple of sigma (M. Efford, author of ‘secr’, pers. comm). Therefore, I used the Root Pooled Spatial Variance (RPSV) function to determine buffer strip size for each capture-recapture dataset. RPSV is a measure of the 2-dimensional dispersion of the locations at which individual animals are detected, pooled over all individuals (Efford, 2018a).

I used the Otis *et al.* (1978) test for population closure for all species and the corresponding capture-recapture datasets. Various models with predictor variables relating to the effects of individual animals, camera trap sites, sessions (surveys) and user-defined camera trap covariates were run for each dataset. The resulting models are an approximation of what is occurring ecologically, so I evaluated suitability of contending models using Akaike’s Information Criterion (AIC; Akaike, 1974), (Symonds & Moussalli, 2011). Following the guidelines recommended by Burnham & Anderson (2004), AIC values were adjusted for small sample sizes (AICc; n/*k* is <40; n= sample size, *k* = number of parameters) to determine the best fitting model(s) for each dataset (Symonds & Moussalli, 2011). Delta AICc (△AICc) values and AICc weights were calculated for each model to explain the relative strength of each model and assess the importance of individual predictor variables (Burnham & Anderson, 2004). Low (<2) △AICc values indicate substantial support for the model, whereas values between 3 and 7 indicate considerably less support. △AICc values greater than ten suggest the model is very unlikely (Burnham & Anderson, 2004). Importantly, it is not appropriate to use AIC to compare different datasets (Burnham & Anderson, 2004).

If sampling sessions are evenly spaced in time or fall within a natural order, such as seasons (wet and dry) then multi-session analyses can be run in R to estimate the finite rate of population change (λ) using Pradel lambda models (Pradel, 1996). Both the overall and survey-specific rates of population change (λ) were calculated for each species using the capture-recapture dataset (Efford, 2018b).

Spatial count

I applied Bayesian spatial count (SC) models to unmarked individuals to estimate abundance (N) and density (D) from species detection counts (Burgar *et al.*, 2018b, 2018a; Evans & Rittenhouse, 2018). Black-backed (*Canis mesomelas*) and side-striped jackals (*Canis adustus*) were the only two unmarked species with sufficient detection data to use this analysis (Appendix 3.2). SC models are an extension of spatially explicit capture recapture (SECR) models, which consider N to be a latent variable estimated by various model variables rather than observed directly. In detail, N is estimated as a subset of the data augmentation variable M, a super-population (over-sized), which our population belongs to (Royle & Dorazio, 2012). N is estimated by summing the number of inferred activity centres, and D is calculated by dividing N by the estimated state-space, which incorporates possible activity centres for all individuals with a compelling probability of being detected by the camera traps over the survey period. The state-space is generated by buffering a distance to the grid of camera trap locations. SC models depart from SECR models in that SC models estimate the number of unmarked individuals by spatially referencing count data to infer locations of an individual activity centre (Chandler & Royle, 2013). In addition to density, SC models estimate the encounter probability of individuals at sites tallied across all occasions (λ_0), the proportion of individuals with the augmented population that occur within the sampled population (ψ) and a spatial scale or movement parameter describing the rate of decline in encounter probability with distance (σ; Chandler & Royle, 2013).

SC models were run using JAGS (ver 4.2.0; Plummer, 2003), interfacing through R by means of the *rjags* package (Plummer, 2016). SC parameters were estimated using Markov Chain Monte Carlo (MCMC) sampling in a hierarchical Bayesian modelling framework (Chandler & Royle, 2013). This requires specification of an upper limit (M) to a uniform prior distribution on abundance (N), which should be large enough such that the probability that $N=M$ is effectively 0 (Chandler & Royle, 2013). In all models, M was set to 200, well above the expected population size of all species.

Previous studies (e.g. Jiménez *et al.*, 2017; Burgar *et al.*, 2018b, 2018a; Evans & Rittenhouse, 2018) have concluded that the accuracy of SC model estimates is low without incorporating additional information. Thus, for all models, I specified a λ_0 prior with a uniform distribution between 0 and 10 and a ψ prior having a beta distribution with shape and scale set to 1. For the informative σ priors, I assumed a gamma distribution with the shape and spread changing based on the home range sizes for each species (Chandler & Royle, 2013; Jiménez *et al.*, 2017). Home range estimates for black-backed (2-17.8 km^2; Fuller *et al.*, 1989; Kaunda, 2001; Loveridge & Macdonald, 2002; Kamler *et al.*, 2012) and side-striped jackals (2-12.24 km^2; Fuller *et al.*, 1989; Rhodes *et al.*, 1998; Loveridge & Macdonald, 2002) were taken from previous studies conducted in similar environments (Jiménez *et al.*, 2017). The home range of σ was calculated following Chandler and Royle (2013) and assuming a chi-square distribution with 2 degrees of freedom: black-backed jackal (30:50) and side-striped jackal (30:58, Supplementary material 1).

I ran three chains of the JAGS model for 100,000 iterations with a burn in of 50,000 (after an adaptive phase of 1,000) and I did not thin the posterior distribution. MCMC chain convergence was assessed by visually examining trace plots for each parameter (Supplementary material 1). I calculated the Gelman-Rubin statistic $\hat{R}$ using the *coda* package (Plummer *et al.*, 2006), where values < 1.1 indicated convergence.

To test the validity of the SC model estimates for black-backed and side-striped jackals, I fitted Bayesian SC models to marked carnivore species (leopard, spotted hyaena and civet) and compared the results with Bayesian single-season SECR (similar to multi-season SECR analyses described above) models. Both analyses were run with detection data collected during the third seasonal survey (dry 2017; Evans & Rittenhouse, 2018). I also fitted SC models to lion detection data from the third survey and compared these results to the known population size. Sparse detection data can potentially produce biased low estimates for both SECR and SC analyses (Chandler & Royle, 2013; Burgar *et al.*, 2018b). Thus, the third seasonal survey was selected for the comparative analyses as most of the species concerned had the highest recapture rates. For comparative purposes, I calculated the difference between the density estimates of the two analyses as a percentage.

All SC models were run as described above, except that home range estimates for lion, leopard and spotted hyaenas were derived from minimum convex polygons created from GPS telemetry location data collected from the study area (see Chapter 4). African civet home range sizes were taken from the literature (3-5 km^2; Swanepoel *et al.*, 2016).

Ungulate transect survey

Although most ungulate species known to occur on the reserve were recorded during each survey, only species (n=10) that were likely to be encountered across all four surveys (Ellis & Bernard, 2005) and which are known to be important prey species for large carnivores on the reserve were included in my analyses (Vanak *et al.*, 2013). These included: blue wildebeest (*Connochaetes taurinus*), common duiker (*Sylvicapra grimmia*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), plains zebra (*Equus quagga*), steenbok (*Raphicerus campestris*), warthog (*Phacochoerus africanus*) and waterbuck (*Kobus ellipsiprymnus*).

I used DISTANCE 7.2 (Thomas *et al.*, 2010) to analyse the data from the line transect surveys. To reliably estimate relative density, DISTANCE requires a minimum of 60 observations per object/animal per survey (Buckland *et al.*, 1993). To satisfy this requirement, all individual observations recorded for the selected ungulates were combined in each survey. An overall density of ungulates per square kilometre and an overall ungulate population size estimate was obtained from which the relative density and population size of individual ungulate species was calculated using the species-specific contribution (frequency of occurrence).

My data were analysed following Buckland, Anderson & Laake (1993) by first examining histograms of the perpendicular distance versus count frequency data for each seasonal survey to determine an appropriate truncation of outlier distances to improve estimation of the detection function. Secondly, various models (e.g. uniform-cosine, uniform-simple polynomial, half normal-cosine, half normal-hermite, hazard rate-cosine, hazard rate-simple polynomial, negative exponential-cosine, negative exponential-simple polynomial) were run and the best-fit model was chosen based on a combination of low AIC score, low variance and a non-significant chi-square goodness-of-fit value (Focardi, Isotti & Tinelli, 2002).

Aerial count survey

I provide a summary of the aerial counts conducted during my study (2016-2018), as statistical parameters could not be computed from the single observations recorded.

Lion population estimates

Since their reintroduction in 2004, the lion population on Selati has been carefully monitored by various research groups using VHS collars, telemetry and direct observations (Joubert & Joubert, 2015). To compare the SECR and SC density estimates for the other carnivore species on the reserve, the lion density was estimated using adults only. The density of lions was calculated as the number of individuals/100km^2 and was estimated using home range data derived from minimum convex polygons created from GPS telemetry location data (see Chapter 4).

RESULTS

Camera trap survey

The 31 camera trap sites during each of the four camera trapping surveys covered an area of 144.27 km^2, with a mean (± SD) inter-site distance of 1.95 km (± 0.54 km). Although each seasonal camera trapping survey ran for 60 consecutive days, camera trap effort (number of active trapping days) varied across the seasonal surveys because cameras either malfunctioned or were removed or damaged by animals (Table 3.1). The average number (± SD) of active trapping days was 1773 ± 38 (range from 1709 (wet 2017) to 1805 (dry 2016; Table 3.1). The average number of animal images captured was 3520 ± 363 and ranged from 3010 (wet 2018) to 4031 (wet 2017; Table 3.1). Total number of mammal events ranged from 1937 (wet 2018) to 3250 (dry 2017). The first (dry 2017) and last (wet 2018) seasonal surveys had the fewest mammal events with 1957 and 1937 respectively (Table 3.1). Overall, I photographed 40 mammal species of which 25 were prey species and 15 were carnivores (Table 3.1). The species accumulation curves from all four seasonal surveys increased steeply initially but then reached a plateau (Appendix 3.3), which indicates that sampling effort was sufficient to capture a good portion of species in the community.

The number of events, the proportion of total events and the relative abundance index (RAI) for all mammal species recorded from each seasonal surveys is shown in Appendix 3.2. Although the combination of the most commonly captured mammal species, based on RAI values (> 6), varied across the seasonal surveys, impala was always the most common, followed by either plains zebra, warthog or kudu (Appendix 3.2). Other common species captured included common duiker, giraffe, blue wildebeest and spotted hyaena (Appendix 3.2). The most frequently captured carnivore across the seasonal surveys was the spotted hyaena followed by either black-backed jackal or side-striped jackal (Appendix 3.2). The least common species, which were only captured once or twice throughout my study were cheetah (*Acinonyx jubatus*; dry 2016), Meller's mongoose (*Rhynchogale melleri*; dry 2017), dwarf mongoose (*Helogale parvula*; wet 2018) and the tree squirrel (*Paraxerus cepapi*; wet 2018).

Table 3.1: Summary data for the four seasonal camera trap surveys conducted on Selati Game Reserve, Limpopo, South Africa.

	Dry 2016 (8th June to 7th August 2016)		**Wet 2017** (5th Jan to 7th March 2017)		**Dry 2017** (1st June to 2nd August 2017)		**Wet 2018** (5th January to 7th March 2018)		**All sessions**	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
No. active trapping days	1805		1709		1780		1799		7093	
Total no. animal images captured	3458		4031		3583		3010		14082	
Total no. events	1957		3196		3250		1937		10340	
Total prey events	1653	*100*	2948	*100*	2816	*100*	1745	*100*	9162	*100*
Small prey (<30 kg)	279	*16.88*	332	*11.26*	406	*14.42*	334	*19.14*	1351	*14.75*
Medium prey (30-90 kg)	576	*34.85*	1511	*51.26*	1299	*46.13*	757	*43.38*	4143	*45.22*
Large prey (>90 kg)	534	*32.30*	735	*24.93*	751	*26.67*	437	*25.04*	2457	*26.82*
Megaherbivores (>1000 kg)	264	*15.97*	370	*12.55*	360	*12.78*	217	*12.44*	1211	*13.21*
Total carnivore events	304	*100*	248	*100*	434	*100*	192	*100*	1176	*100*
Small carnivore (<10 kg)	18	*5.92*	23	*9.27*	31	*7.14*	13	*6.77*	85	*7.22*
Medium carnivore (10-20 kg)	118	*38.82*	98	*39.52*	191	*44.01*	81	*42..19*	488	*41.50*
Large carnivore (>20 kg)	168	55.26	127	*51.21*	212	*48.85*	98	*51.04*	603	*51.28*
Total mammal species	36		35		37		36		40	
Total prey species	23		24		24		23		25	
Total carnivore species	13		11		13		13		15	

I found that season (wet and dry) had no effect on total species RAI (K–W $\chi^2 = 0.6$, df= 1, P = 0.44), total prey species RAI (K–W $\chi^2 = 0.6$, df= 1, P = 0.44) or total carnivore species RAI (K–W $\chi^2 = 2.4$, df = 1, P = 0.12). Further, neither season (wet and dry) nor survey (dry 2016, wet 2017, dry 2017 and wet 2018) had an effect on the RAI of small, medium, large or megaherbivore prey species (all $P \geq 0.72$; Table 3.2). Additionally, no seasonal or survey effects were found for the RAI of small carnivore, medium carnivore or large carnivore species (all $P \geq 0.34$; Table 3.2).

Table 3.2: The effect of season (wet and dry) and survey (dry 2016, wet 2017, dry 2017 and wet 2018) on the relative abundance indices (RAI) of the prey and carnivore body mass categories.

	season statistics (wet and dry)			**survey statistics (dry 2016, wet 2017, dry 2017 and wet 2018)**		
RAI	**K–W χ^2**	**df**	**P -value**	**K–W χ^2**	**df**	**P-value**
small prey species	0.21	1	0.98	0.04	3	0.84
medium prey species	0.41	1	0.94	0.01	3	0.92
large prey species	0.00	1	0.92	0.13	3	0.72
megaherbivore species	0.01	1	0.92	0.34	3	0.72
small carnivore species	0.00	1	1.00	1.18	3	0.76
medium carnivore species	0.90	1	0.34	1.24	3	0.74
large carnivore species	0.00	1	0.94	2.10	3	0.55

Spatially explicit capture-recapture

My analysis for population closure based on the left-side datasets for leopard and spotted hyaena across all four seasonal surveys (sessions) supported the assumption that the populations were closed ($P > 0.05$; Table 3.3). Closure tests for the right-side dataset for leopards produced multiple warnings due to small sample size (Otis *et al.*, 1978; Efford *et al.*,

2009) and was therefore excluded from further analyses. For spotted hyaenas, based on data for the right-side, I rejected the population closure assumption for the first (dry 2016, P = 0.01) and last (wet 2018, P = 0.03) seasonal surveys (Table 3.3). These data were, therefore, also excluded from further analyses. Although both the left- and right-side datasets for civets supported the assumption of population closure (Table 3.3). Further analyses for civet were based on only the right-side dataset as more individuals were identified, making for more robust estimates.

Table 3.3: Results of the Otis test (Otis *et al.* 1978) for population closure in each seasonal survey using left-side data for both leopard and spotted hyaena and right-side data for spotted hyaena.

	Leopard		**Spotted hyaena**				**Civet**			
	left-side		**left-side**		**right-side**		**left-side**		**right-side**	
Survey	**Z**	**P**	**Z**	**P**	**Z**	**P**	**Z**	**P**	**Z**	**P**
dry 2016	-0.89	0.17	-0.52	0.30	-2.44	0.01*	-0.55	0.29	0.55	0.71
wet 2017	0.07	0.53	0.79	0.78	-0.75	0.23	-1.56	0.06	-0.33	0.37
dry 2017	0.80	0.79	-1.39	0.08	2.37	0.99	1.12	0.87	0.61	0.73
wet 2018	-0.60	0.28	1.11	0.87	-1.95	0.03*	0.06	0.52	1.16	0.88

* signifies a significant result and rejection of population closure

The buffer strip widths, as determined by the RSVP function, to create habitat masks for each species capture dataset (Fig.3.3) were 4597 m for leopard left-side data, 3662 m for spotted hyaena left-side data and 2455 m for civet right-side data.

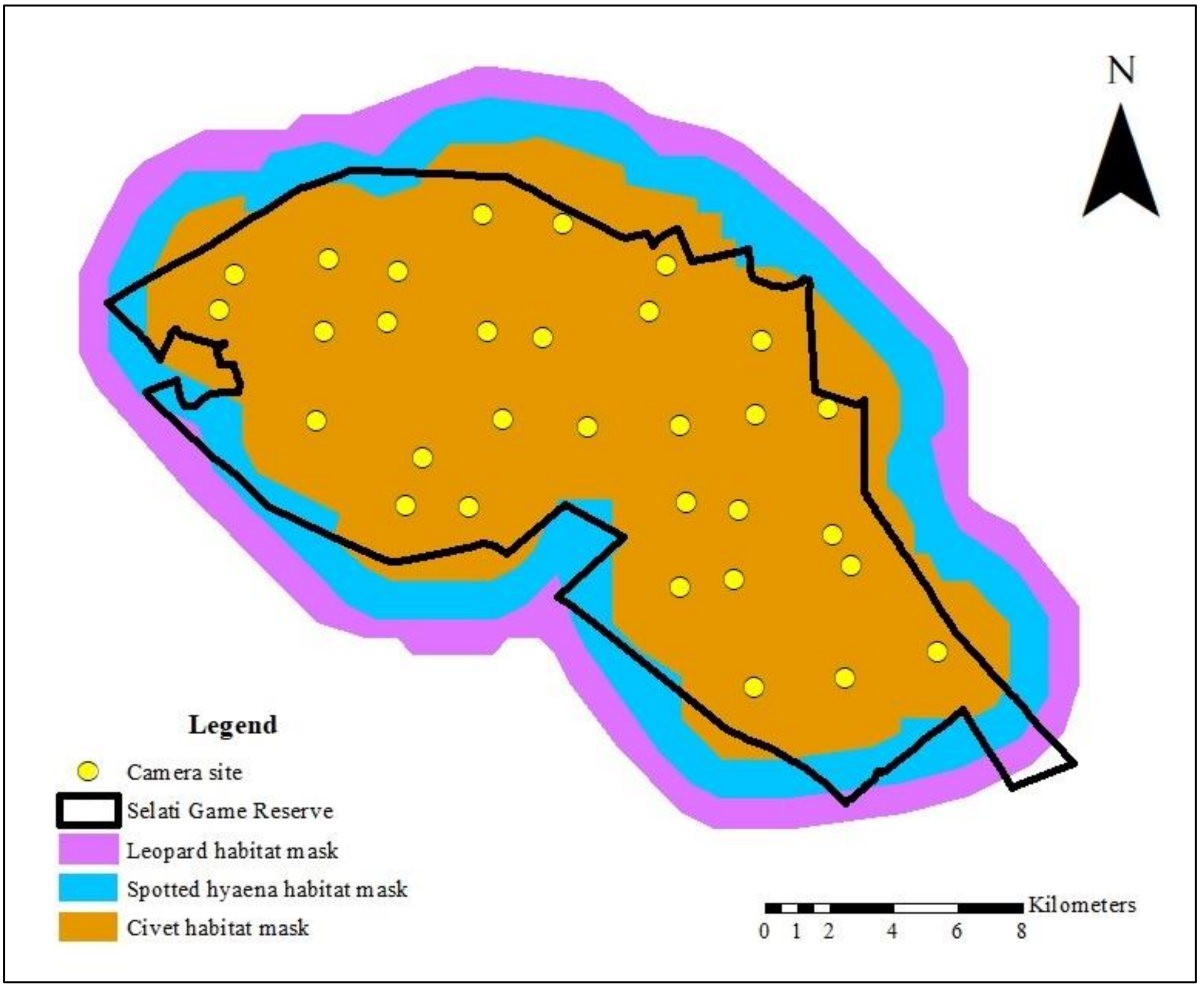

Figure 3.3: A map depicting the buffer strips created around the camera trap sites used as the habitat mask for density estimates in 'secr' for leopards (4597 m), spotted hyaenas (3662 m) and civets (2455 m) in Selati Game Reserve.

Leopards

For the left-side leopard data, the 'road + bk' model, which included a road covariate and an individual animal site-specific learned response variable (bk), performed the best with an AIC weighting of 0.94 (Table 3.4). This can be interpreted as a 94% likelihood that the 'road + bk' model was the most important model. Additionally, this model was the only model that scored a low (<2) △AICc value (Table 3.4), which also supports the contention that it is the best approximating model. The 'road + k' model, which includes a road covariate and site learned response variable ('k'), had a △AICc value of 5.33 (Table 3.4), meaning that although it is less likely to be the best approximating model, it should not be discounted. The AICc weighting for this model ('road + k') was, however, only 0.06 (Table 3.4), meaning it only had a 6% chance of being correct and was therefore ignored. All of the remaining models (e.g. 'bk', Table x) had △AICc values greater than 10 and AICc weighting values of 0, indicating that they were extremely unlikely to be the best approximating models and were therefore also ignored (Table 3.4). The left-side density estimate (± SE) for the best performing model ('road + bk') for leopard was 3.28 individuals/100 km^2 ± 0.91 $x10^{-4}$ (Table 3.4). The expected leopard population size (± SE) for the best fitting model was estimated to be 18.83 ± 4.40 individuals, with a range of between 9 and 27 individuals.

I estimated the overall finite rate of population change (λ) for leopards to be 0.79, which indicates that the population was declining over the entire sampling period (2016-2018). The session-specific rate of population change from survey one (dry 2016) to survey two (wet 2017; $\lambda = 1.03$), and from survey two to survey three (dry 2017; $\lambda = 0.98$) was stable. However, between survey three and four (wet 2018; $\lambda = 0.34$) the leopard population decreased by 66% (Appendix 3.4).

Table 3.4: Results of the left-side maximum likelihood SECR analyses for the best performing models for leopards. The 'Model' column depicts which predictor variable was used in the analyses where the remaining columns describe the associated density estimate (expressed as number of leopards per 100 km^2), standard error (SE $x10^{-4}$), 95% confidence interval (95% CI) and the four Akaike Information Criterion (AIC) values.

Model	Density (100 km^2)	SE	95% CI	AIC	AICc	△AICc	AICc weight
road + bk[a]	3.28	0.91	1.92 – 5.58	739.16	741.66	0	0.94
road + k[b]	4.97	2.18	2.18 – 13.10	744.50	747.00	5.33	0.06
Bk	3.36	0.94	1.96 – 5.76	750.13	751.73	10.07	0.00

a: individual animal site-specific learned response variable

b: site learned response variable

Spotted hyaenas

For the left-side spotted hyaena data, the model that included a road covariate and an individual animal site-specific learned response variable (bk), performed the best with an AIC weighting of 1 (‘road + bk’; Table 3.5). This can be interpreted as a 100% likelihood that the road model was the most important model. Additionally, the road and site-specific learned response (‘road + bk’) model was the only model for the spotted hyaena data that scored a low (<2) △AICc value (Table 3.5), which also supports the contention that it is the best performing model. The remaining models (e.g. ‘road + K’ and ‘road’, Table 3.5) not only had △AICc values greater than 10, meaning that they were extremely unlikely to be the best approximating models, but that they also had AICc weightings of zero, meaning they were extremely unimportant. Therefore, all other models, except for the ‘road + bk’ model, were ignored (Table 3.5). The left-side density estimate for the best performing model (‘road + bk’) for spotted hyaena was 12.52 individuals/100 $km^2 \pm 1.61 \times 10^{-4}$ (Table 3.5). The expected population size for the best fitting model (road) was estimated at 50.34 ± 6.47 individuals, with a range of between 39 and 64 individuals.

According to the overall finite rate of population change, the spotted hyaena population remained fairly stable over the entire sampling period ($\lambda = 0.93$). The session-specific rate of population change for spotted hyaenas suggested that the population decreased from survey one (dry 2016) to survey two (wet 2017; $\lambda = 0.67$), then increased from survey two to survey three (dry 2017; $\lambda = 1.42$) and then decreased again between survey three and four (wet 2018; $\lambda = 0.75$; Appendix 3.4).

Table 3.5: Results of the left-side maximum likelihood SECR analyses for the best performing models for spotted hyaenas. The 'Model' column depicts which predictor variable was used in the analyses where the remaining columns describe the associated density estimate (expressed as number of spotted hyaenas per 100 km^2), standard error (SE x10^{-4}), 95% confidence interval (95% CI) and the four Akaike Information Criterion (AIC) values.

Model	**Density (100 km^2)**	**SE**	**95% CI**	**AIC**	**AICc**	**△AICc**	**AICc weight**
road + bk[a]	12.52	1.61	8.20 - 12.49	2409.95	2410.52	0	1
road + K[c]	12.82	1.67	9.95 - 16.52	2420.43	2421.00	10.48	0
road	11.46	1.35	9.10 - 14.43	2458.13	2458.51	47.99	0

a: individual animal site-specific learned response variable

c: site transient response variable

Civet

For the left-side civet data, the model that included the presence or absence of medium sized predators as a covariate and a site-specific learned response variable ('bk + medium predators'), was the best performing model with an AICc weighting of 1 (Table 3.6). This can be interpreted as a 100% likelihood that the model was the most essential. The remaining models (e.g. 'bk + small predators' and 'small predators') had weightings of zero and AICc values greater than 10, indicating that they were irrelevant. Therefore, I only considered the model incorporating the presence of medium sized predators and a site-specific learned response in further analyses. The left-side density estimate for the best performing model was 5.26 individuals/100 km^2 ± 1.37 x10^{-4} (Table 3.6). The expected population size for civet from the best fitting model (medium predators) was estimated at 21.73 individuals, with a range of between 13 and 36 individuals.

According to the overall finite rate of population change, the civet population remained fairly stable over the entire sampling period ($\lambda = 0.98$). The session-specific rate of population change for civet reveals that the population increased from survey one (dry 2016) to survey two (wet

2017; $\lambda = 1.41$), then increased from survey two to survey three (dry 2017; $\lambda = 1.6$) and then drastically decreased between survey three and four (wet 2018; $\lambda = 0.28$; Appendix 3.4).

Table 3.6: Results of the right-side maximum likelihood SECR analyses for the best performing models for civets. The 'Model' column depicts which predictor variable was used in the analyses where the remaining columns describe the associated density estimate (expressed as number of civets per 100 km^2), standard error (SE x10^{-4}), 95% confidence interval (95% CI) and the four Akaike Information Criterion (AIC) values.

Model	**Density (100 km^2)**	**SE**	**95% CI**	**AIC**	**AICc**	**△AICc**	**AICc weight**
bk[a] + medium predators	8.96	2.54	5.20 – 15.44	986.34	988.01	0	0.98
bk + small predators	9.78	2.88	5.55 – 17.21	994.64	996.31	8.30	0.02
Bk	9.86	2.90	5.61 – 17.34	1031.80	1032.88	44.87	0

a: individual animal site-specific learned response

Spatial count

For all my models and parameters, the Gelman-Rubin statistic $\hat{R}$ was always < 1.1, which indicated convergence of the MCMC chains on each run. The total number of events recorded for black-backed jackals differed across all four seasonal surveys (range: 32-86; Table 3.7). The first dry seasonal survey (2016) recorded the lowest number of events, whereas the second dry seasonal survey (2017) recorded the highest (Table 3.7).

Table 3.7: Spatial count posterior summaries for black-backed jackals sampled in Selati Game Reserve during four seasonal surveys from June 2016 to March 2018. Parameter values are presented as the mean and standard deviation (SD). Parameters include density (D), population size (N), baseline capture probability (λ_0), an inclusion probability in the augmented data set for unmarked individuals (ψ) and a Gaussian scale parameter for the distance function (σ).

	Dry 2016 (32)		**Wet 2017 (46)**		**Dry 2017 (86)**		**Wet 2018 (48)**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
D	26.10	12.84	6.46	3.90	11.34	5.05	7.72	4.03
N	85.32	42.08	21.10	12.76	37.08	16.51	25.24	13.17
λ_0	0.04	0.02	0.84	1.53	0.54	0.35	0.55	0.97
ψ	0.43	0.21	0.1	0.07	0.19	0.09	0.13	0.07
σ	0.59	0.01	0.53	0.10	0.46	0.08	0.21	0.09

* Value in brackets indicates the number of detections for each seasonal survey

Interestingly, the total number of events for side-striped jackals during both the dry season surveys was 43, whereas for both wet season surveys the number of events was only nine (Table 3.8).

Table 3.8: Spatial count posterior summaries for side-striped jackals sampled in Selati Game Reserve during four seasonal surveys from June 2016 to March 2018. Parameter values are presented as the mean and standard deviation (SD). Parameters include density (D), population size (N), baseline capture probability (λ_0), an inclusion probability in the augmented data set for unmarked individuals (ψ) and a Gaussian scale parameter for the distance function (σ).

	Dry 2016 (43)		**Wet 2017 (9)**		**Dry 2017 (43)**		**Wet 2018 (9)**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
D	10.92	5.51	6.81	5.52	14.31	7.25	5.81	5.88
N	35.68	18.03	22.27	18.03	46.78	23.69	19.00	19.21
λ_0	0.21	0.16	0.40	0.92	0.36	0.76	1.21	2.10
ψ	0.18	0.09	0.12	0.10	0.24	0.12	0.10	0.10
σ	0.48	0.08	0.46	0.83	0.42	0.08	0.48	0.09

- Value in brackets indicates the number of detections for each seasonal survey

SC median densities (individuals/100 km^2 (SD)) varied across the four seasonal surveys for both black-backed (6.46 (3.90) – 26.10 (12.84)) and side-striped (5.81 (5.88) – 14.31 (7.25)) jackals (Table 3.7 and 3.8). The density estimates between the two analyses (SC and SECR) varied for civet (6.94%), leopard (20.78%) and spotted hyaena (70%; Table 3.9). Comparing the SC estimate to the known lion population density produced the least amount of difference (5.23%), despite the lion population only having 11 detections (Table 3.9). My verifications suggest that the SC models produced biased towards lower density estimates for species with small detection datasets (leopards) and biased towards high density estimates when detection datasets were larger (civet; Table 3.9). The complete opposite was the case for spotted hyaenas, which had the largest detection dataset but an extremely biased estimate to a low density (Table 3.9). The SC model for spotted hyaenas estimated a much smaller population size (12.63) than the actual number of individuals (39) that were identified for the SECR analyses (Table 3.9).

Table 3.9: Spatial count (SC) posterior summaries and spatially explicit capture-recapture (SECR) estimates for civet, lion, leopard and spotted hyaena in Selati Game Reserve during the third seasonal survey (dry 2017). Parameter values for SC and SECR are presented as the mean and standard deviation (SD) or standard error (SE). Parameters for SC include density (D), population size (N), baseline capture probability (λ_0), an inclusion probability in the augmented data set for unmarked individuals (ψ) and a Gaussian scale parameter for the distance function (σ). Parameter values for SECR include density (D), population size (N) and number of individuals identified (n). The final column (% diff) indicates the percentage difference between the density estimates of the two analyses.

Civet

SC analyses (53)			**SECR analyses**			**% diff**
	Mean	**SD**		**Mean**	**SE**	
D	19.01	8.26	D	17.69	8.55	6.94%
N	62.14	33.40	N	53.96	26.20	
λ_0	0.49	0.23	n	18		
ψ	0.31	0.17				
σ	0.34	0.05				

Lion

SC analyses (11)			**Known**		**% diff**
	Mean	**SD**			
D	1.45	3.9	D	1.53	5.23%
N	4.73	12.98	N	5	
λ_0	0.02	0.01			
ψ	0.03	0.07			
σ	3.17	0.32			

Leopard

SC analyses (34)			**SECR analyses**			**% diff**
	Mean	**SD**		**Mean**	**SE**	
D	3.08	1.43	D	4.46	2.44	20.78%
N	14.56	6.78	N	18.87	10.33	
λ_0	0.06	0.03	n	9		
ψ	0.08	0.04				
σ	1.53	0.13				

Spotted hyaena

SC analyses (140)			**SECR analyses**			**% diff**
	Mean	**SD**		**Mean**	**SE**	
D	3.20	0.69	D	10.51	2.11	70%
N	12.63	2.72	N	42.27	8.47	
λ_0	0.28	0.05	n	32		
ψ	0.07	0.22				
σ	1.27	0.28				

- Value in brackets indicates the number of detections for each seasonal survey

Ungulate transect survey

Mean time spent in the field per seasonal survey was 2.8 ± 0.4 (SD) hours. Across all four seasonal surveys the best fit model incorporated truncating the largest 5% of distances and either a negative exponential-simple polynomial (dry 2016 and wet 2017) or negative exponential-cosine (dry 2017 and wet 2018) key estimator (Table 3.10). Total ungulate density estimates (D ± SE) per km^2 were 88.16 ± 14.86, 65.46 ± 15.45, 51.58 ± 18.66 and 143.57 ± 28.82 for the seasons dry 2016, wet 2017, dry 2017 and wet 2018 respectively (Table 3.10). The coefficient of variation (%) for each seasonal survey ranged from 16.85 to 36.18% and the effective strip width ranged from 75.50 to 100.45 m (Appendix 3.5).

Ungulate densities of the 10 most important species varied considerably between the ungulate surveys (Table 3.10). As for the camera trap survey, impala was always the most abundant and contributed two thirds or more of the total ungulate density in each survey (Table 3.10). In the last seasonal survey (wet 2018) I estimated there were more than 10 000 impala on the reserve (Table 3.10), which is highly unrealistic. Aside from impala; kudu, blue wildebeest, giraffe and plains zebra were the most abundant ungulates (Table 3.10). Of the five most abundant species identified across the seasonal ungulate transect surveys, kudu and plains zebra were the only two species that constantly increased (Table 3.10). By contrast, the abundance of the remaining three species (impala, blue wildebeest and giraffe) all fluctuated and experienced both increases and decreases across the study period (Table 3.10).

Aerial count survey

The data from the aerial surveys conducted in the years that overlapped with my study (2016 – 2018) identified 21 prey species and only five carnivore species (Appendix 3.6). Impala were always the most abundant species while giraffe, kudu, plains zebra and blue wildebeest were the other most abundant species across the years (Appendix 3.6). The population trends of the five most abundant species fluctuated across the three years with all species increasing and decreasing (Appendix 3.6).

Lion population estimates

Over the duration of the study, the lion population increased from five adults in 2016 to a total of seven in 2017 after two cubs were born (Fig.3.4). In 2018, three more cubs were born, increasing the total number to 10 (Fig.3.4). The adult lion density was estimated at 1.53 individuals/100 km^2.

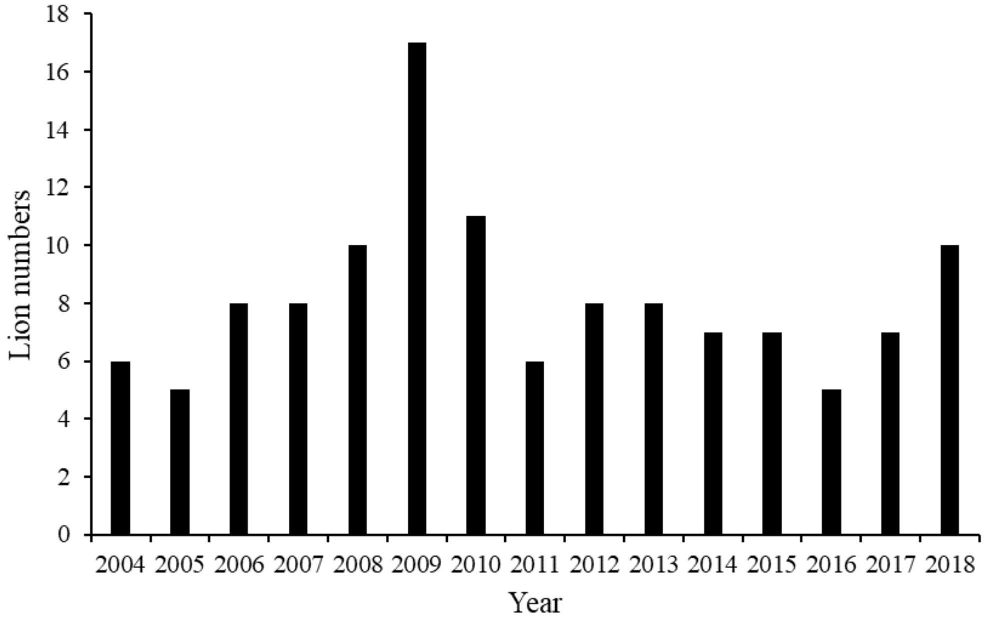

Figure 3.4: Lion population numbers in Selati Game Reserve since their reintroduction in June 2004.

Table 3.10: Population estimates for the 10 most common species recorded during ungulate transect surveys in Selati Game Reserve. Estimates include relative density (D), population size (N) and species-specific contribution (*%*) to the total group.

	Dry 2016			**Wet 2017**			**Dry 2017**			**Wet 2018**		
Species	**D**	**N**	***%***	**D**	**N**	***%***	**D**	**N**	***%***	**D**	**N**	***%***
Blue wildebeest	3.16	307	*3.59*	0.7	68	*1.08*	2.56	248	*4.96*	8.5	825	*5.92*
Common duiker	0.51	49	*0.58*	0.42	41	*0.65*	0.4	39	*0.78*	0.77	75	*0.54*
Giraffe	8.06	782	*9.14*	2.96	287	*4.52*	2.56	248	*4.96*	5.51	534	*3.84*
Impala	66.73	6473	*75.69*	54.34	5271	*83.01*	33.83	3281	*65.58*	111.4	10805	*77.59*
Kudu	1.22	119	*1.39*	1.83	178	*2.8*	3.36	326	*6.51*	7.34	712	*5.11*
Nyala	2.35	228	*2.66*	0	0	*0*	0.96	93	*1.86*	0.1	9	*0.07*
Plains zebra	1.22	119	*1.39*	1.55	150	*2.37*	2.96	287	*5.74*	4.06	394	*2.83*
Steenbok	0.51	49	*0.58*	0.21	20	*0.32*	0.56	54	*1.09*	0.48	47	*0.34*
Warthog	2.65	257	*3.01*	1.55	150	*2.37*	2.56	248	*4.96*	3.28	319	*2.29*
Waterbuck	1.73	168	*1.97*	1.9	184	*2.9*	1.84	178	*3.57*	2.13	206	*1.48*
Total	**88.16**	**8552**	***100***	**65.46**	**6350**	***100***	**51.58**	**5003**	***100***	**143.57**	**13926**	***100***

DISCUSSION

Reliable methods to estimate species richness, abundance and density are important for managers and conservationists as they provide key data to make the right decisions for wildlife management and conservation (Barea-Azcón *et al.*, 2007). My study advances our understanding of conducting multiple camera trap, aerial total count and ungulate transect surveys to effectively monitor wildlife population trends in an enclosed reserve. In terms of species richness, the camera trap surveys identified 40 mammalian species (24 prey and 16 carnivores) while the aerial counts identified 26 (21 prey and 5 carnivores) and the ungulate transect survey was restricted, finding 10 predominantly medium and large-sized prey species. Despite the population estimates for ungulates being variable between the sampling techniques, the five most abundant species were always impala, kudu, blue wildebeest, giraffe and plains zebra. The three techniques all showed that over the study period, ungulate populations fluctuated in terms of abundance (relative and absolute). This is to be expected as wildlife populations fluctuate naturally over time due to demographic stochasticity (random births and deaths; Bjørnstad & Grenfell, 2001). Predation, which I will explore in Chapter 5, is another possibility but so is hunting and the harvesting of animals (see Supplementary material 2 for figures for Selati). Well monitored hunting is of vital importance for conservation throughout Africa, especially in areas which may be unsuitable for alternative wildlife-based land uses such as photographic ecotourism (Lindsey, Roulet & Romañach, 2007). Both trophy hunting, through the provision of economic incentives and subsistence hunting, through the provision of staff rations for example, can promote the acceptance of conservation objectives for wildlife areas such as Selati (Lindsey *et al.*, 2007).

Despite the potential for bias between relative abundance indices (RAIs) and true measures of absolute abundance, RAIs are commonly used to draw inferences about the ecology of unmarked mammals (Sollmann *et al.*, 2013). Especially because only a small portion of the animals photographed by camera traps are individually identifiable (Carbone *et al.*, 2001). Palmer *et al.* (2018) found that RAIs derived from systematic camera trap surveys could provide reliable indices of relative abundance for multiple species. My study supports this contention and the incorporation of RAIs for both prey and carnivore species into additional analyses (e.g. carnivore occupancy (Chapter 4) and diet (Chapter 5)) allow me to gain insight into the mammalian community structure and dynamics of Selati, with particular focus on carnivore intra-guild interactions.

Ungulate estimates from the transect survey were not only restricted to 10 medium and large-sized prey species (with only one small prey species), but also highly over estimated species numbers, especially for impala during the final seasonal survey (wet 2018). This was most likely because impala were always the most frequently observed species on the reserve, skewing the results as line transect surveys do not account for undetected animals (Bårdsen & Fox, 2006). A number of other variables such as animal behaviour, observer effectiveness, environmental conditions and topography can affect the detection of species (Bårdsen & Fox, 2006). Although it is impossible to keep all of these variables constant during a survey, I minimised their effects by using two observers and models that meet the requirements of pooling, model robustness and 'shape criterion' stipulated by Burnham, Anderson & Laake (1980). To achieve more reliable ungulate estimates from transect surveys, greater sampling effort could be incorporated, as I only used three replicate transect routes (Bårdsen & Fox, 2006).

Even though the aerial count data produced more reliable results for a wider range of ungulates, compared to the ungulate transect survey, these counts were restricted to once a year due to financial constraints. Although aerial counts are popular amongst wildlife managers and a suitable means for Selati to monitor their wildlife over time, the RAIs were more appropriate for further analyses (e.g. occupancy modelling) as they incorporated a much broader spectrum of species and could be generated for each seasonal survey.

In terms of monitoring carnivore species, the camera trap survey was the only technique to accurately identify the wide range of mammalian carnivores present on the reserve. Sampling design can play a major role in camera trap surveys (Pollock *et al.*, 2002; Sollmann *et al.*, 2013) and a potential research constraint of my project was that the cameras might have been spaced too far apart to gain reliable estimates of the smaller sized carnivore species (e.g. serval and African wildcat (*Felis silvestris lybica*)). Conversely, reliable estimates from camera trap surveys may have been unattainable for smaller sized carnivores because their population sizes were too small (Otis *et al.*, 1978; White, 1982; Efford, Dawson & Borchers, 2009).

Systematic camera trap sampling of individually identifiable species, along with spatially explicit capture-recapture models, typically give the most accurate estimate of density (Carbone *et al.*, 2001). Based on my analyses, I was able to estimate the density (individuals/100 km^2 ± SE) of civet (5.26 ± 1.37), leopard (3.28 ± 0.91) and spotted hyaena (12.52 ± 1.61). Running seasonal camera trap surveys allowed me to determine the finite rate of change for these carnivore populations, which is of fundamental importance in assessing population status. The overall population trends for civet and spotted hyaena were stable, whereas the leopard population decreased. In fact, most leopard populations in South Africa are declining (Mann *et al.*, 2018). Since their reintroduction onto Selati in 2004, the lion population has been continuously monitored and managed. With the exception of two adult female lionesses being removed in 2016, the adult lion population has remained stable over the duration of the study (2016 – 2018) and was estimated to occur at a density of 1.53 individuals/100 km^2.

A lion density of 1.53 individuals/100 km^2 in Selati falls at the low end of the density range for lions in southern Africa. In Welgevonden Private Game Reserve (Limpopo) lions were estimated to occur at 4.55 individuals/100 km^2, whereas in Pilansberg National Park (North West) and Karongwe Game Reserve (Limpopo) lion densities were estimated at 7.89 and 8.86 individuals/100 km^2 respectively (Miller & Funston, 2014). In the Greater Makalali Private Game Reserve (Limpopo) lion densities are even higher at 9.36 individuals/100 km^2 (Miller & Funston, 2014).

Within the Limpopo Province of South Africa, the leopard density of Selati (3.28 individuals/100 km^2) is comparable to the 3.9 leopards/100 km^2 on Atherstone Nature Reserve (Mann *et al.*, 2018). On commercial game and livestock farms, however, leopard densities are slightly higher at 6.59 individuals/100 km^2 (Swanepoel, Somers & Dalerum, 2015). The highest density ever recorded for leopard is from the Soutpansberg Mountains at 10.7 individuals/100 km^2 (Chase Grey, Kent & Hill, 2013). The only other large carnivores present on the Soutpansberg Mountains were unknown densities of brown hyaena (*Parahyaena brunnea*) and spotted hyaena (Chase Grey *et al.*, 2013). These results lead me to suspect that the presence of competing sympatric carnivores could be negatively affecting leopard populations within protected areas, which I will explore in the next two chapters. Anthropogenic mortality (e.g. illegal killing for their skin, retaliatory killing by farmers, road kill) has, however, been associated with the nationwide decline of leopard populations in South Africa (Mann *et al.*, 2018).

In the Kruger National Park (Limpopo Province) spotted hyaena densities are estimated to be the highest in South Africa, falling between 2 and 20 individuals/100 km^2 (Hunnicutt *et al.*, 2016). In Phinda Private Game Reserve (KwaZulu-Natal), the spotted hyaena population continuously increased from 2007 to 2014, where their density was estimated at 8.8 individuals/100 km^2 in 2014. In Mkhuzu Game Reserve (KwaZulu-Natal), however, the spotted hyaena population declined from 12.1 individuals/100 km^2 in 2008 to 7.2 individuals/100 km^2 in 2015 (Hunnicutt *et al.*, 2016). In Selati, the spotted hyaena population has been stable for the past three years (2016-2018) and estimated at 12.52 individuals/100 km^2, which is currently one of the highest recorded for South Africa.

Civet in Selati were estimated at 5.26 individuals/100 km^2, which is similar to the estimate of 6.42 individuals/100 km^2 on Welgevonden Private Game Reserve that also had lions present (Swanepoel *et al.*, 2016). Interestingly, civet density from a protected area without lions (Lapalala Wilderness, Limpopo) was much higher at 14.11 individuals/100 km^2 (Swanepoel *et al.*, 2016), which potentially supports my prediction that larger carnivores are supressing the abundance of smaller, less dominant carnivores in Selati. Other areas in Limpopo also had similar estimates of civet populations such as 10.1 individuals/100 km^2 in Mogalakwena Game Reserve and 14.18 individuals/100 km^2 at Moyo Conservation Project reserve (Swanepoel *et al.*, 2016).

These estimates for carnivores rely on individual identification of animals, for which camera trapping is limited to species with individual markings (e.g. coat patterns; Sollmann, 2018). Newly developed spatial count (SC) models have tried to overcome this limitation by using spatial correlation on counts across camera trap detectors to estimate the density of species with unmarked individuals (Chandler & Royle, 2013). SC models allowed me to estimate the densities of black-backed jackals (between 6.46 and 26.10 individuals/100 km^2) and side-striped jackals (between 5.81 and 14.31 individuals/100 km^2)

Black-backed jackal estimates for South Africa vary from 34–40 individuals/100 km^2 in the Drakensburg Mountains (KwaZulu-Natal) to as low as 2 individuals/100 km^2 on game farms in the Free State and Northern Cape where they are actively managed (Klare *et al.*, 2010; Minnie *et al.*, 2016). On Benfontein Game Reserve (Northern Cape), where large carnivores were extirpated prior to 1990, the black-backed jackal density was estimated to be 32.5 individuals/100 km^2 (Kamler *et al.*, 2012), which is higher than in Selati where large carnivores are present. This is not unexpected, as population densities of subordinate carnivores are often negatively related to the density of sympatric large carnivores (particularly lions) because of both exploitative and interference intra-guild competition (du Preez, 2014), supporting my prediction.

My study provides the first density estimate for side-striped jackal in South Africa. The only previous density estimates for this species are from commercial farmlands in western Zimbabwe and Niokolo-Koba National Park in Senegal (Camacho *et al.*, 2016). Estimates from Zimbabwe ranged from 50 to 80 individuals/100 km^2, whereas side-striped jackals were much lower in Senegal at 7 individuals/100 km^2 (Camacho *et al.*, 2016). Although, both jackal species are present throughout much of sub-Saharan Africa, in the arid regions of South Africa, the side-striped jackal is replaced by the black-backed jackal and in North Africa side-striped jackals are replaced by the African golden wolf (*Canis anthus lupaster*; Camacho *et al.*, 2016; Minnie *et al.*, 2016). Side-striped jackals, however, seem to be expanding their range in South Africa and are known to occur in the Lowveld (e.g. Selati) where black-backed jackal numbers appear to be suppressed (Camacho *et al.*, 2016). My SC results support these observations, as black-backed jackal numbers in Selati were lower than elsewhere in South Africa. Additionally, while side-striped jackal density estimates for Selati are lower than those for Zimbabwe, where the species is not being replaced by black-backed jackals, they are similar to the estimates in Senegal, where the species is being replaced by African golden wolf (Camacho *et al.*, 2016).

As with the large carnivore species, the black-backed and side-striped jackal populations of Selati may be influenced by the density and composition of both carnivore and prey communities on reserves (Camacho *et al.*, 2016). For example, although large apex carnivores may facilitate scavenging opportunities for the two jackal species (increased local densities), they may also increase the risk of predation and interspecific competition (decreased local densities; Brassine & Parker, 2012). I will assess both of these ecological scenarios in the following two chapters.

SC density estimates are sensitive to sampling design and detection data density and can be inaccurate (Chandler & Royle, 2013; Burgar *et al.*, 2018a). Verification of my SC estimates are in line with Burgar *et al.* (2018) in that when detection data are small, density estimates may be biased negatively (low). The complete opposite occurred for spotted hyaena, as despite having the most detections, the SC models produced biased low density estimates. Although spotted hyaenas are flexible hunters that can cooperatively take down large prey items (e.g. buffalo (*Syncerus caffer caffer*)) or steal carcasses from other carnivores, they spend up to 75% of their time foraging alone for small prey items (Holekamp *et al.*, 1997). Analysing the spotted hyaena photographs I captured supports this statement as the majority of the photographs were of lone individuals. However, spotted hyaenas are a social species, which means that a single camera trap would have captured a larger number of individuals over the survey periods, compared to the solitary leopard, civet or black-backed jackal that live as monogamously mated pairs.

There is no doubt that SC models require refinement (Burgar *et al.*, 2018a), potentially with respect to animal life-history as identified in my verification analyses, but the other techniques I used (e.g. ungulate transect survey and aerial total counts) were not precise either. Camera traps can operate continuously for multiple years with little effort, whereas other techniques are time-consuming and expensive. Camera traps along with SECR and SC models provide the potential to monitor multiple species over time and space at low costs (Burgar *et al.*, 2018b). SC models have the power to provide insight into the population numbers of understudied and non-individually identifiable species, such as the side-striped jackal.

Realistically, the lack of monitoring often reflects a lack of conservation effort (Bauer *et al.*, 2015). I demonstrate that a systematic, non-baited camera trap survey conducted over time (i.e. several seasons) is an effective method to monitor populations of multiple medium to large-sized terrestrial mammals. Wildlife populations may fluctuate for various reasons and so need to be monitored frequently, as understanding the threats to carnivores at the species level is vital to the development of effective conservation strategies.

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Chapter 4

SPATIAL UTILISATION

A male leopard captured on a camera trap allogrooming

INTRODUCTION

Scientists and reserve managers are tasked with the challenge of monitoring biodiversity and ecosystem integrity (Manley *et al.*, 2004). It is impossible to monitor all species within a reserve, or to develop appropriate management and conservation objectives by focusing on only one species at a time (Franklin, 1993). In an era of tightening budgets, managers and researchers typically compromise by carefully selecting a small set of individual species to monitor that arguably represent the integrity of the entire ecosystem (Simberloff, 1998; Manley *et al.*, 2004).

Southern Africa is a biodiversity hotspot, where the mammalian carnivore guild is an important group of animals for economic-driven operations (e.g. ecotourism and trophy hunting) and for maintaining the structure and function of entire ecosystems (e.g. through trophic cascades and seed dispersal; Lindsey, Roulet & Romañach, 2007; Owen-Smith & Mills, 2008). The influence of exploitation and interference competition among carnivore guild members and their prey are vital components of functional terrestrial ecosystems (Dalerum *et al.*, 2008). Thus, conservation of the carnivore guild is arguably more important than the conservation of other individual species (Woodroffe & Ginsberg, 2005).

Despite decades of conservation efforts, carnivores across the globe continue to suffer from population declines, which are exacerbated by an ever-increasing human population (Ripple *et al.*, 2014). Innate biological traits (e.g. specialised niche requirements) of terrestrial carnivores put them at high risk of extinction (Sillero-Zubiri & Laurenson, 2001). Monitoring carnivores, particularly large (> 20 kg) carnivores is notoriously difficult because of their predominantly nocturnal habits, secretive behaviour, low densities and extensive spatial requirements (Balme, Slotow & Hunter, 2010). Camera traps have become an increasingly important tool to collect data important for conservation purposes and have improved our ability to study the temporal and spatial patterns of rare carnivores (Lynam *et al.*, 2013). Camera traps are non-invasive, affordable and can be deployed over vast areas to collect continuous detection/non-detection data on multiple species (Rovero & Zimmermann, 2016). Time stamps of captured animal photographs can provide accounts of activity patterns amenable to investigating ecological processes such as whether potentially competing carnivores temporally overlap or avoid one another (Karanth & Sunquist, 1995; Lynam *et al.*, 2013).

Carnivores are morphologically and behaviourally adapted to kill, which strengthens the effects of interspecific competition in this guild (Palomares & Caro, 1999). Interference competition (i.e. aggressive interactions for shared resources) can lead to intra-guild predation (often the killed competitor is not consumed) or to temporal and/or spatial partitioning (Schuette *et al.*, 2013). In addition, factors affecting carnivore survival and co-existence are often interrelated, making multifaceted research approaches vital to collect data that enable conservation (Winterbach *et al.*, 2013).

Various fields of ecology use occupancy, or the probability of a species occupying a specific area, as a parameter to address ecological hypotheses concerning species distributions (e.g. Monadjem, 1997) and habitat associations (e.g. Rovero *et al.*, 2013). Occupancy models were originally designed for sedentary animals and are based on the assumption of population closure (i.e. no immigration or emigration) during the sampling period (Miller, Dugelby & Foreman, 2001; Betts *et al.*, 2008; Bled, Nichols & Altwegg, 2013). Dynamic occupancy models, however, have been developed for mobile species to account for imperfect detections and population dynamics, such as colonisation and local extinction (MacKenzie & Royle, 2005; Bled *et al.*, 2013; Rovero & Zimmermann, 2016). These dynamic models do not require species to be individually identifiable of species and can provide valuable information on the influence of environmental and other variables on species distributions, through the examination of detection/non-detection data (MacKenzie & Royle, 2005; Bled *et al.*, 2013).

Space use of sympatric carnivores can be influenced by both biotic and abiotic factors (Ramesh *et al.*, 2012). For example, the risk of predation or interference competition can significantly alter the spatial distribution of a carnivore (Fortin *et al.*, 2005). In many cases, parameters associated with intra-guild relationships (i.e. biotic factors) have a greater influence on carnivore occupancy than environmental factors (i.e. abiotic factors; Schuette *et al.*, 2013; Wang *et al.*, 2018). The occupancy of a species can vary over time and space (Buckland, Anderson & Laake, 1993), which is why reliable occupancy estimates require data replicated both spatially and temporally (MacKenzie & Royle, 2005; Bailey *et al.*, 2007).

Carnivores evolved and adapted to the interactions with guild members within large, heterogeneous ecosystems where they roamed freely (Creel, Spong & Creel, 2001). In South Africa, there are very few free ranging carnivores as populations are restricted to predominantly small, isolated, enclosed reserves (Hayward *et al.*, 2007a, 2007b; Rostro-García, Kamler & Hunter, 2015). Although predator-proof fences effectively reduce human-wildlife conflict in South Africa, they also influence the utilisation of space and resources within communities (Packer *et al.*, 2013). Within confined small, enclosed systems intra-guild competition between wide-ranging large carnivores could be particularly intense as these species share similar resources and spatial requirements (Palomares & Caro, 1999). Habitat selection of carnivores is central to their ecology and may facilitate co-existence within the guild (Pettorelli *et al.*, 2010). Thus, analysing the spatial distributions of carnivores within reserves can provide valuable insights into key resource requirements (Lindsey *et al.*, 2011). Enclosed reserves need careful assessment in this regard, to investigate whether managers are providing adequate resources to allow the co-existence of multiple carnivores (Marker *et al.*, 2008).

Global Positioning Satellite (GPS) collars are one of the most important tools available to study carnivore ecology. These devices provide relocation data that can be used to answer questions about space use (i.e. home ranges), interspecific relationships and behaviours that are otherwise difficult to obtain (Karanth, Funston & Sanderson, 2010). Despite their high cost, GPS collars are also particularly important for collecting reliable data on elusive large carnivores (Karanth *et al.*, 2010).

The majority of studies examining intra-guild competition focus on the interactions between pairs of species and ignore interactions occurring among subordinate carnivores (Vanak *et al.*, 2013). My research objectives were therefore to use camera trap surveys and individual GPS collared carnivores (e.g. lions (*Panthera leo*), leopards (*Panthera pardus*) and spotted hyaenas (*Crocuta crocuta*)) to determine and compare activity patterns, habitat selection and occupancy dynamics of multiple carnivores in a small, enclosed reserve (Selati Game Reserve). I predicted that large carnivores (i.e. biotic factors) would have the greatest influence on the occupancy dynamics of the smaller, subordinate carnivores. I also predicted that small- (< 10 kg) and medium-sized (10–20 kg) carnivores would select habitats and have activity patterns that overlap the least with larger carnivores. Within the large carnivore guild, I predicted that lions (being the largest members of the guild) would be the dominant species and negatively influence the space use, habitat selection and activity patterns of both spotted hyaenas and leopards.

METHODS

The methodology for each sampling technique and the details of the study site are described in detail in Chapter 2.

Data analyses

Camera trap survey

Multi-season occupancy models

I used the single-species, multi-season dynamic occupancy model of MacKenzie *et al.* (2003) to analyse probability of occurrence trends in medium- (black-backed jackal (*Canis mesomelas*), side-striped jackal (*Canis adustus*), honey badger (*Mellivora capensis*) and African civet (*Civettictis civetta*; here after civet)) and large-sized (lion, leopard and spotted hyaena) carnivores. Dynamic occupancy models provide estimates of initial occupancy (ψ), site colonization (γ), local extinction (ε) rates (i.e. changes in occupancy between primary sampling periods) and detection probability ((*p)* the probability that a species will be detected if it is truly present; MacKenzie *et al.*, 2003; Schuette *et al.*, 2013). Covariates (e.g. abiotic and biotic) were included in my occupancy models to prevent biased estimates and identify factors that most strongly affected the spatial patterns and occupancy dynamics of each species (MacKenzie *et al.*, 2003; Bled *et al.*, 2013; Schuette *et al.*, 2013).

I defined five abiotic site covariates (vegetation type, elevation (m), slope (°), road and distance to water (m)) and four (one abiotic and three biotic) key categories of survey-specific site covariates (rainfall (mm), human activity (RAI), sympatric carnivore relative abundances (RAI) and prey relative abundances (RAI); Table 4.1). Vegetation type, elevation, slope and distance to closest water source were assigned to each camera trap site using topographical maps of Selati in ArcGIS (version 10.5.1; ESRI, Redlands, California, USA). A riverine vegetation type was added to the vegetation map of Selati (see Chapter 2) as it represents lush strips of vegetation along rivers or drainage lines that contrast with the neighbouring savanna landscape (Fig.4.1; Monadjem & Reside, 2008). I accounted for the placement of camera traps along roads using the categorical variable (yes or no). Relative carnivore abundances (RAI) at each camera trap site for each seasonal survey were individually determined for large carnivores (lions, leopards and spotted hyaenas). I allocated relative abundances of the remaining carnivore species as either medium- or small-sized carnivores according to their body mass (see Chapter 3). I also allocated prey species relative abundance (RAI) to each camera trap site during each seasonal survey according to body mass as either small, medium or large (Krüger, Lawes & Maddock, 1999). Due to the large range of values present, all continuous survey-specific site covariate values were scaled into standardized z-scores (Harihar & Pandav, 2012; Bruggeman *et al.*, 2016). Variance inflation factors (VIF; Neter *et al.*, 1996) were calculated to quantify multicollinearity among site covariates and excluded those with a VIF > 3 (Wang *et al.*, 2018).

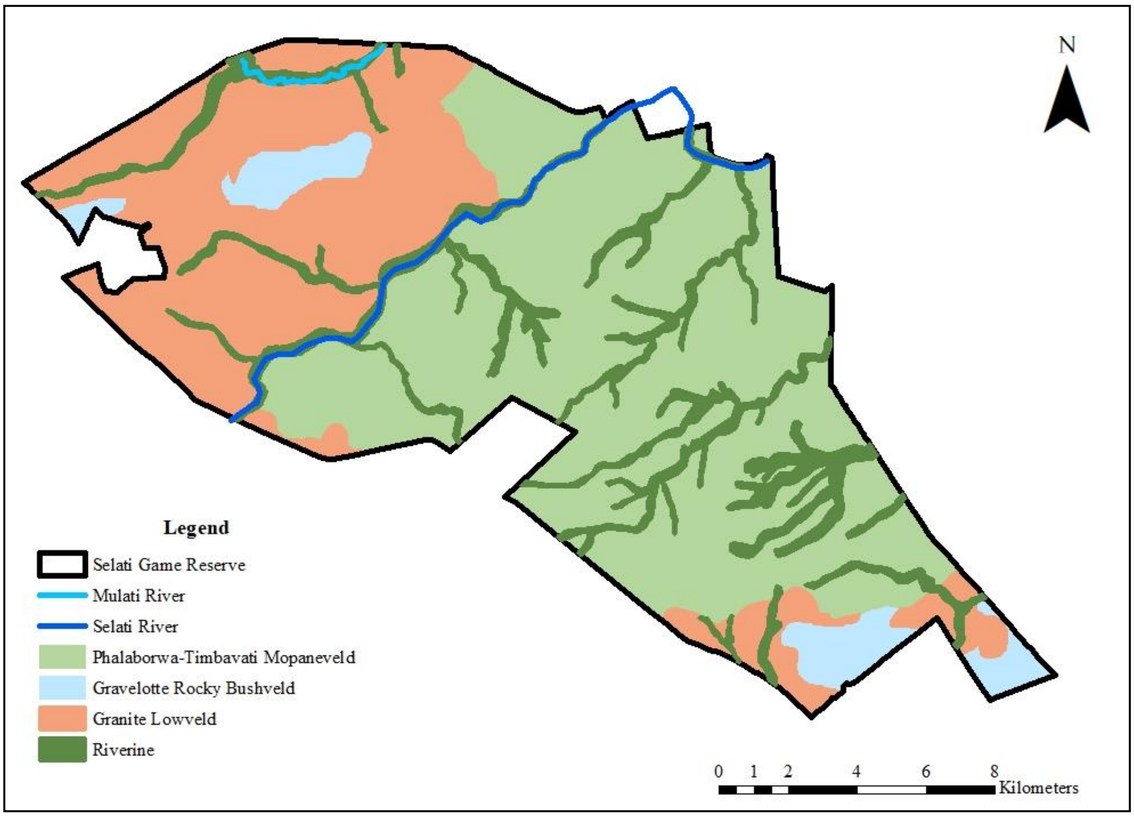


Figure 4.1: Distribution of the three main vegetation types found in Selati Game Reserve including riverine vegetation.

Table 4.1: Definitions of site and survey-specific site covariates used in modelling factors related to the occupancy dynamics of carnivores in Selati Game Reserve.

Covariate level	Name	Description	Source
site covariate	vegetation	Categorical, 3 land-cover classes: Granite (Granite Lowveld), Mopaneveld (Phalaborwa-Timbavati Mopaneveld), Bushveld (Gravelotte Rocky Bushveld) and Riverine	Extracted from topographical maps of Selati Game Reserve (Refer to Chapter 2)
	slope	Numeric, angle of the slope in degrees	
	elevation	Numeric, meters above sea level	Camera trap data (Refer to Chapter 3)
	road	Categorical variable denoting if the camera trap site was along a road (‘yes’ or ‘no’)	
	water	Numeric, distance in meters to the nearest water source	Extracted from topographical maps of Selati Game Reserve (Refer to Chapter 2)
survey-specific site covariate	rainfall	Numeric, rainfall (mm) recorded for the area of the camera trap site	Camera trap data (Refer to Chapter 3)
	lion	Numeric, relative abundance (RAI) of lion	
	leopard	Numeric, relative abundance (RAI) of leopard	
	hyaena	Numeric, relative abundance (RAI) of spotted hyaena	
	mpred	Numeric, relative abundance (RAI) of medium carnivores	
	spred	Numeric, relative abundance (RAI) of small carnivores	
	lprey	Numeric, relative abundance (RAI) of large prey species	
	mprey	Numeric, relative abundance (RAI) of medium prey species	
	sprey	Numeric, relative abundance (RAI) of small prey species	
	human	Numeric, relative abundance (RAI) of human activity	
	mpredno_	Numeric, relative abundance (RAI) of medium carnivores without the relative abundance of the model species	
	spredno_	Numeric, relative abundance (RAI) of small carnivores without the relative abundance of the model species	

Unique detection histories consisting of 1s (detection) and 0s (non-detection) were created for carnivores with sufficient recaptures for each seasonal survey (dry 2016, wet 2017, dry 2017, wet 2018). The unique detection histories reflected the presence or absence of each carnivore at each camera trap site on each occasion (maximum value ‘1’ per 24 hr period) for each survey (Appendix 4.1a). Original unique detection history datasets (n occasions = 61) for each carnivore and seasonal survey were collapsed into data subsets by merging the occasions into intervals of between five to 10 day sampling occasions (Appendix 4.1b). This was deemed appropriate as it reduced each carnivore’s dataset into manageable sizes for computational purposes and accurately represented the rarity of the study species (Erb, McShea & Guralnick, 2012; Sollmann, 2018). A global occupancy model (most complex) that included all ecologically relevant covariates was applied to the subsets of data for each carnivore and tested for goodness-of-fit (MacKenzie & Bailey, 2004). The subset data for each carnivore that had the closest over dispersion statistic (ĉ) to 1 (extreme values over (> 3) or under 1 (< 0.90) indicate poor fit of the data) and an insignificant chi-square probability ($\chi^2 p > 0.05$), was chosen for further occupancy analyses (Mazerolle, 2017). This showed maximum model fit without over compressing the statistical power of the data (Burnham & Anderson, 2004; MacKenzie & Bailey, 2004).

For each carnivore, only combinations of covariates that could affect the four parameters (ψ, γ, ε, p) and that presented ecologically reasonable hypotheses were included (McDonald *et al.*, 2016). With such a large number of covariates, the set of candidate models that I might have examined was vast (Schuette *et al.*, 2013). Therefore, I used a stepwise procedure following Dugger, Anthony & Andrews, (2011), whereby the first step was to model detection probabilities by investigating additive combinations of both site and survey-specific site covariates while treating the other three parameters as constant (i.e. intercept only). I retained the best detection probability model for each carnivore to use in subsequent analyses of factors affecting ψ, γ and ε. The second step was to compare a set of nine models that combined site covariates that I hypothesized might affect initial occupancy (ψ) and 11 survey-specific covariates I hypothesized could influence site colonisation (γ) and extinction (ε). This resulted in an *a priori* set of a maximum 99 models (9 combinations of variables potentially influencing ψ x 11 variables potentially influencing γ and ε) for each carnivore. Although this model set was not exhaustive, it was appropriate to evaluate the influence of various combinations of biotic and abiotic variables based on my hypotheses (Schuette *et al.*, 2013). The package 'unmarked' (Fiske & Chandler, 2011) was used to fit models and to estimate covariate coefficients for each parameter in R (version 3.5.1, R Development Core Team, 2017).

For model selection, the over dispersion statistic ($\hat{c}$) estimated from the global model for each carnivore was used to compute quasi-likelihood information criteria (QAICc: for small sample sizes) by scaling the log-likelihood of each model, for each carnivore, by its corresponding $\hat{c}$ value (Mazerolle, 2017). In the case of moderate underdispersion (i.e. $\hat{c} > 0.90$), the value of $\hat{c}$ was set to 1 when calculating QAICc (Mazerolle, 2017). The R package 'AICcmodavg' was used for all model selection computations (Mazerolle, 2017).

The best-approximating models for each carnivore were selected using the lowest $\triangle$QAICc scores (< 2) and highest QAICc weights ($w > 0.10$; Burnham & Anderson, 2004). I compared the influence of abiotic and biotic variables on occupancy (ψ), changes in occupancy (γ, ε) and detection probability (p). I summed QAICc weights for all models containing abiotic and biotic variables with $w > 0.10$ and QAICc < 2 for the three body size classes (large, medium and small). I drew conclusions about strength of evidence of relationships between covariates and parameters ($\psi, \gamma, \varepsilon, p$) based on 95% confidence intervals (CIs) of coefficients and the direction of relationships. I considered 95% CIs not containing zero, to indicate strong evidence of relationships, 95% CIs that contained zero, but not centred on zero to indicate medium strength and CIs containing zero to indicate weak evidence of relationships (i.e. uninformative covariates; Arnold, 2010).

Spatial partitioning by vegetation type

To assess potential differences in the occupancies of carnivores in various vegetation types (i.e. spatial partitioning), I estimated carnivore occupancies across the four vegetation types. To allow for the direct comparison of effects across the carnivore species, I applied the same broad model to all carnivores. The model included vegetation type (with the four categories) as the only independent variable for initial occupancy (ψ), local colonisation (γ) and extinction (ε; Schuette *et al.*, 2013). For detection probability (p), each carnivore's respective top detection probability covariates were used in an effort to reduce the likelihood that the observation process masked the ecological process of interest (response to vegetation type; Schuette *et al.*, 2013).

Temporal partitioning

To analyse differences in activity patterns of large, medium and small sized carnivores, I assigned independent capture events for each carnivore species to each hour of the day (00:00 – 23:00). I defined activity as nocturnal (mostly active between 18:00-06:00), diurnal (mostly active between 06:00-18:00), crepuscular (mostly active during twilight (04:00-07:00 and 17:00-20:00 (valid for both wet and dry season in Limpopo Province)) and cathemeral (irregular activity throughout the day and night; Lynam *et al.*, 2013). To quantify overlap between the activity patterns of all carnivores, I used statistical methodology developed by Ridout & Linkie (2009). For this, each carnivores activity pattern was first estimated separately using kernel density estimates which fits a smooth, circular curve to the times recorded from species capture events where peaks in the curve resemble peaks in animal activity (Ridout & Linkie, 2009). In a second step, I calculated a measure of overlap between two focal carnivore distributions following Ridout & Linkie (2009) who recommend the coefficient of overlap, $\triangle_{1}$, for small sample sizes ($n = < 75$) and which is defined as the area under both density curves. The coefficient of overlap varies from 0, indicating no overlap, to 1, indicating complete overlap. I undertook these analyses using the package ‘overlap’ in R.

Collared large carnivores

Home range and core area estimates

I calculated home ranges using relocation data (GPS locations) collected from collared large carnivores (see Chapter 2). I downloaded each carnivore’s relocation data remotely from the African Wildlife Tracking (AWT, Rietondale, Pretoria, South Africa) computer-based application.

An animal’s home range and core area, which is used more intensely, can be estimated by using an accumulation of 95% and 50% of their GPS fixes respectively (White & Garrott, 1990). The kernel utilisation distribution (UD) technique has received considerable attention since its introduction in 1989 (Worton, 1989). This home range estimator has been integrated into many computer and statistical packages (Worton, 1989, 1995; Seaman & Powell, 1996; Laver & Kelly, 2008). Kernel UD’s use probability density estimations to calculate how much time an animal spends in any one place. This method involves assigning a kernel (a bivariate probability density) over each GPS location in a sample and then superimposing a rectangular grid over all kernels. A density estimator is produced for each grid intersection. A kernel density estimator is then calculated across the entire grid by using density estimates from each intersection (Seaman & Powell, 1996). Observations that are close to the GPS location of interest will contribute more to the density estimation than locations that are further away. Therefore, areas with higher concentrations of GPS locations will have higher density estimates, and vice versa (Seaman & Powell, 1996). Contour lines or isopleths connecting areas of equal density allow for home range estimates to be made. I calculated home ranges (95% UD) and core areas (50% UD) for each collared individual using the package 'adehabitatHR' in R.

Home range overlap

At a coarse spatial scale (i.e. the entire study site), I determined the extent of overlap in home ranges and core areas between collared large carnivores using the volume of intersection (VI) index (Fieberg & Kochanny, 2005; Vanak *et al.*, 2013). The simplest statistical methods for quantifying home range overlap only incorporate the spatial area of individual home ranges and ignore relative probability of use (i.e. UD; Fieberg & Kochanny, 2005). The VI index uses UD estimates of two species and ranges from zero (two home ranges with no overlap) to one (two home ranges with the same UD; Fieberg & Kochanny, 2005).

Habitat use

My assessment of spatial partitioning amongst collared large carnivores was limited to two datasets because of the timing of collar deployment. I used data collected between 22 September and 26 November 2016 and between 19 July and 20 November 2017 when location data overlapped for at least one individual from each species (i.e. lion, leopard and spotted hyaena). To test whether large carnivores as a group selected specific vegetation types, I carried out a compositional analysis using the package 'adehabitatHS' in R. I assessed the proportion of vegetation type selected for by all three large carnivores in comparison to the proportion of each vegetation type available within the reserve. I then used Ivlev's electivity index to investigate whether large carnivores used the vegetation types in accordance to their availability in the study site (Krebs, 1989).

RESULTS

Camera trap survey

Multi-season occupancy models

Without collapsing the capture data, 752 unique detections (maximum value '1' per sampling occasion) were recorded from 15 carnivore species across the four camera trap surveys (Table 4.2). The total number of unique detections for each carnivore ranged from one (dwarf mongoose (*Helogale parvula*) and Meller's mongoose (*Rhynchogale melleri*)) to 216 (spotted hyaena; Table 4.2). Models for species with < 28 unique detections did not converge (i.e. data indicated lack of fit) and were thus excluded from occupancy analyses. Although the number of unique detections for civet was relatively high (n = 110; Table 4.2), there was a lack of fit in the data (Appendix 4.2) and these were also excluded from my occupancy analyses.

Table 4.2: Total number of unique detections (maximum value '1' per sampling occasion) from each species best-fit global occupancy model. Data came from all four seasonal camera trap surveys in Selati Game Reserve.

Carnivore species	Body size	# unique detections
African wildcat (*Felis silvestris lybica*)*	Small	30
Dwarf mongoose (*Helogale parvula*)	Small	1
Meller's mongoose (*Rhynchogale melleri*)	Small	1
Serval (*Leptailurus serval*)	Small	8
Small-spotted genet (*Genetta genetta*)	Small	21
Large-spotted genet (*Genetta tigrina*)	Small	4
African civet (*Civettictis civetta*)	Medium	110
Black-backed jackal (*Canis mesomelas*)*	Medium	134
Caracal (*Caracal caracal*)	Medium	9
Honey badger (*Mellivora capensis*)*	Medium	28
Side-striped jackal (*Canis adustus*)*	Medium	80
Cheetah (*Acinonyx jubatus*)	Large	2
Leopard (*Panthera pardus*)*	Large	71
Lion (*Panthera leo*)*	Large	36
Spotted hyaena (*Crocuta crocuta*)*	Large	216

* Indicates species analysed with occupancy models

The number of variables influencing patterns of occupancy in well-supported models (QAICc <2; $w > 0.10$) ranged from five to 11 (Table 4.3). Leopard occupancy was influenced by 11 variables, side-striped jackal by eight, three species by seven variables (lion, black-backed jackal and honey badger), African wildcat by six and spotted hyaena by five (Table 4.3).

Summing model weights across all carnivores, it was evident that unique combinations of abiotic factors influenced occupancies (Table 4.3). Presence of camera traps along a road had the strongest influence on occupancy for large carnivores ($\Sigma w = 1.03$), whereas distance to the closest water source was strongest for medium-sized carnivores ($\Sigma w = 1.67$; Table 4.3). Occupancies of African wildcats (the only small carnivore with sufficient data for occupancy modelling) were negatively influenced by the steepness of slope (Table 4.3).

Detection probabilities for medium-sized carnivores and African wildcats were mainly influenced by biotic factors, particularly the presence of large carnivores (Table 4.3). Lions were associated with decreased detection probabilities of black-backed jackals and African wildcats, whereas leopards had increased detection probabilities of these smaller carnivores. Lions increased detection probabilities of side-striped jackals and leopards decreased detection probabilities of honey badgers (Table 4.3). Spotted hyaenas only negatively influenced the detection probabilities of black-backed jackals and African wildcats (Table 4.3). By comparison, large carnivore detection probabilities were strongly associated with abiotic factors rather than biotic ones (Table 4.3). Presence of camera traps along a road was strongly associated with all three species' probability of being detected (Table 4.3). Lions were the only species whose detection probability was not associated with any biotic variables (Table 4.3).

Biotic factors had the strongest influences on the spatial patterns (colonisation or extinction) of all carnivores (Table 4.3). Seasonal changes in medium-sized prey (and large-sized prey for lion) triggered medium to weak changes in space use patterns of large-sized carnivores (Table 4.3). Within the large carnivore guild, spatial patterns of leopards were influenced by spotted hyaenas, and to a lesser extent lions (Table 4.3). Spatial patterns of medium-sized carnivores and African wildcats were influenced the most by seasonal changes in the presence of lions (Table 4.3).

Table 4.3: QAICc weights (*w*) for abiotic and biotic variables for well-supported models ($w > 0.10$, QAIC < 2; Appendix 4.3) for each carnivore species. The direction of the relationship for variables from the best fit models are indicated in parentheses.

			Large carnivore					**Medium carnivore**					**Small carnivore**	
Par.	**type**	**covariate**	**lion**	**hyaena**	**leopard**	Σw_{cov}	Σw_{type}	**ssj**	**bbj**	**badger**	Σw_{cov}	Σw_{type}	**wildcat**	Σw_{type}
ψ	**Abiotic**	road		0.78^{a}	0.25	1.03	**1.94**			0.20^{b}	0.2	**2.28**		**0.69**
		elevation	0.30(-)^{a}		0.15	0.45		0.28		0.13	0.41			
		slope	0.18		0.28^{b}	0.46					0		0.69(-)^{a}	
		water				0		0.60(-)*	0.88(-)^{a}	0.19	1.67			
γ, ε	**Abiotic**	rainfall			0.15	0.15	**0.15**				0	**0**		**0**
											0			
	Biotic	lion			0.14	0.14	**1.96**	0.28	0.88 γ(-)^{a}		1.16	**2.13**	0.69^{b}	**0.69**
		leopard				0				0.17	0.17			
		hyaena			0.28γ(.)^{a}ε(+)*	0.28					0			
		mprednobadger				0				0.20^{b}	0.20			
		lprey	0.30^{b}			0.30					0			
		mprey	0.13	0.78 ε(+)^{a}	0.15	1.06		0.60 ε(+)*			0.60			
		human	0.18			0.18					0			
p	**Abiotic**	water				0	**2.44**	0.60(+)*			0.60	**3.16**		**0.69**
		rainfall				0		0.60(+)*	0.88(-)*		1.48			
		road	0.30*	0.78*	0.28*	1.36			0.88*	0.20*	1.08		0.69*	
		vegetation		0.78(+)*		0.78					0			
		slope	0.30(+)*			0.30					0			
	Biotic	human				0	**1.62**	0.60(+)*			0.60	**4.04**		**2.07**
		lion			0.28^{b}	0.28		0.60(+)*	0.88(-)*		1.48		0.69(-)*	
		leopard		0.78(+)*		0.78			0.88(+)*	0.20(-)*	1.08		0.69(+)*	
		hyaena			0.28(+)*	0.28			0.88(-)*		0.88		0.69(-)^{a}	
		lprey			0.28(+)^{a}	0.28					0			

Species abbreviations: lion (African lion), hyaena (spotted hyaena), ssj (side-striped jackal), bbj (black-backed jackal), badger (honey badger).

Covariates: for definitions refer to Table 4.1.

Σw_{cov} is the sum of the model weights for the well-supported models containing each covariate across the large- and medium-sized carnivore species. Σw_{type} is the sum of the weights for models with covariates classified as abiotic or biotic variables for each parameter across the large- and medium-sized carnivores.

*Indicates a strong effect (CI estimates do not overlap 0).

^{a} indicates a medium effect (CI estimates overlap 0, but are not centred on 0).

^{b} indicates a weak effect (CI estimates overlap 0 and centred on 0).

Spatial partitioning by vegetation type

Broad vegetation type occupancy models (vegetation type set as the only variable to describe effects on ψ,γ and ε), revealed minimal evidence for spatial partitioning amongst carnivores in Selati (Fig.4.2). The steep rocky slopes of the Gravelotte Rocky Bushveld (Bushveld) showed zero utilization by carnivores, whereas the other three vegetation types were used evenly (Fig.4.2A). Large carnivores occurred at high rates across all three vegetation types (Fig.4.2 B). Medium-sized carnivores occurred at the highest rates in the moderately dense woodland areas of the Granite Lowveld (Granite) and in the undulating plains of Phalaborwa-Timbavati Mopaneveld (Mopaneveld: Fig.4.2C). The riverine vegetation was utilized the least by medium-sized carnivores compared with any other carnivore group (Fig.4.2C). African wildcats, which were the only small carnivore analysed (Fig.4.2D), occurred at extremely low rates in the Granite vegetation and at high rates in Mopaneveld and riverine.

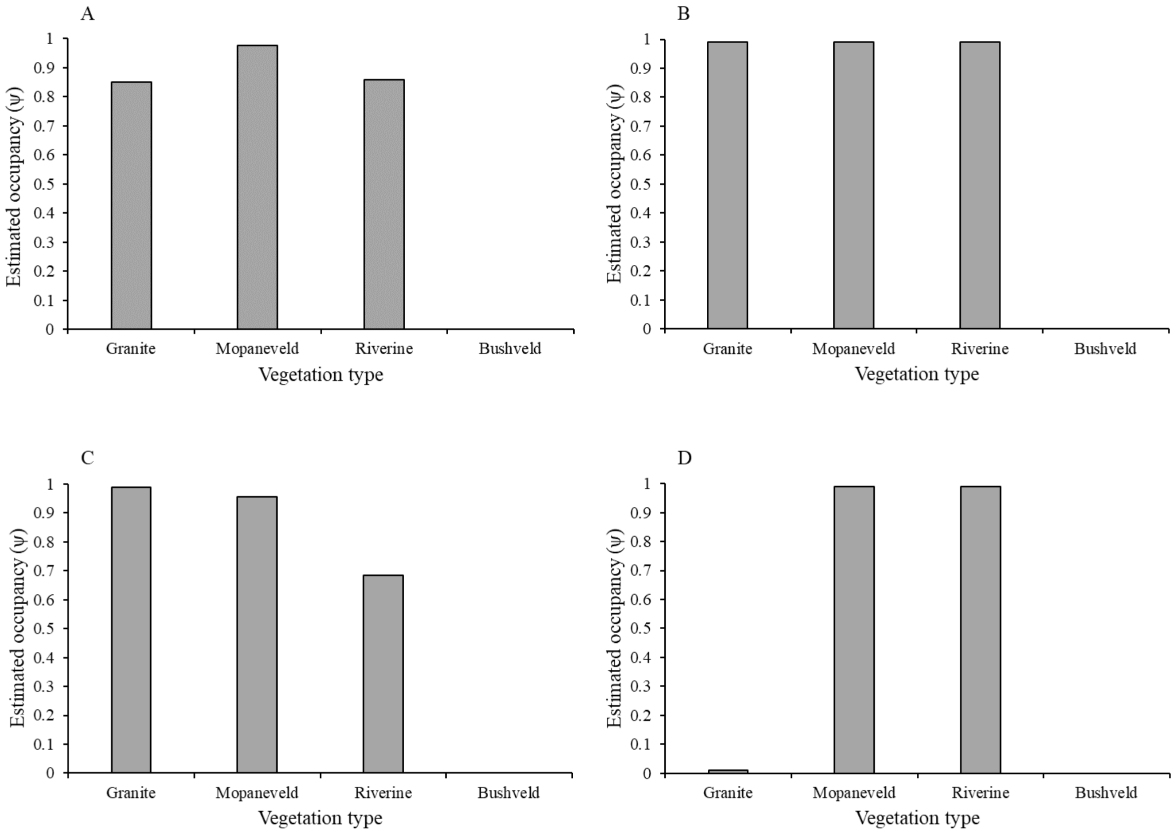
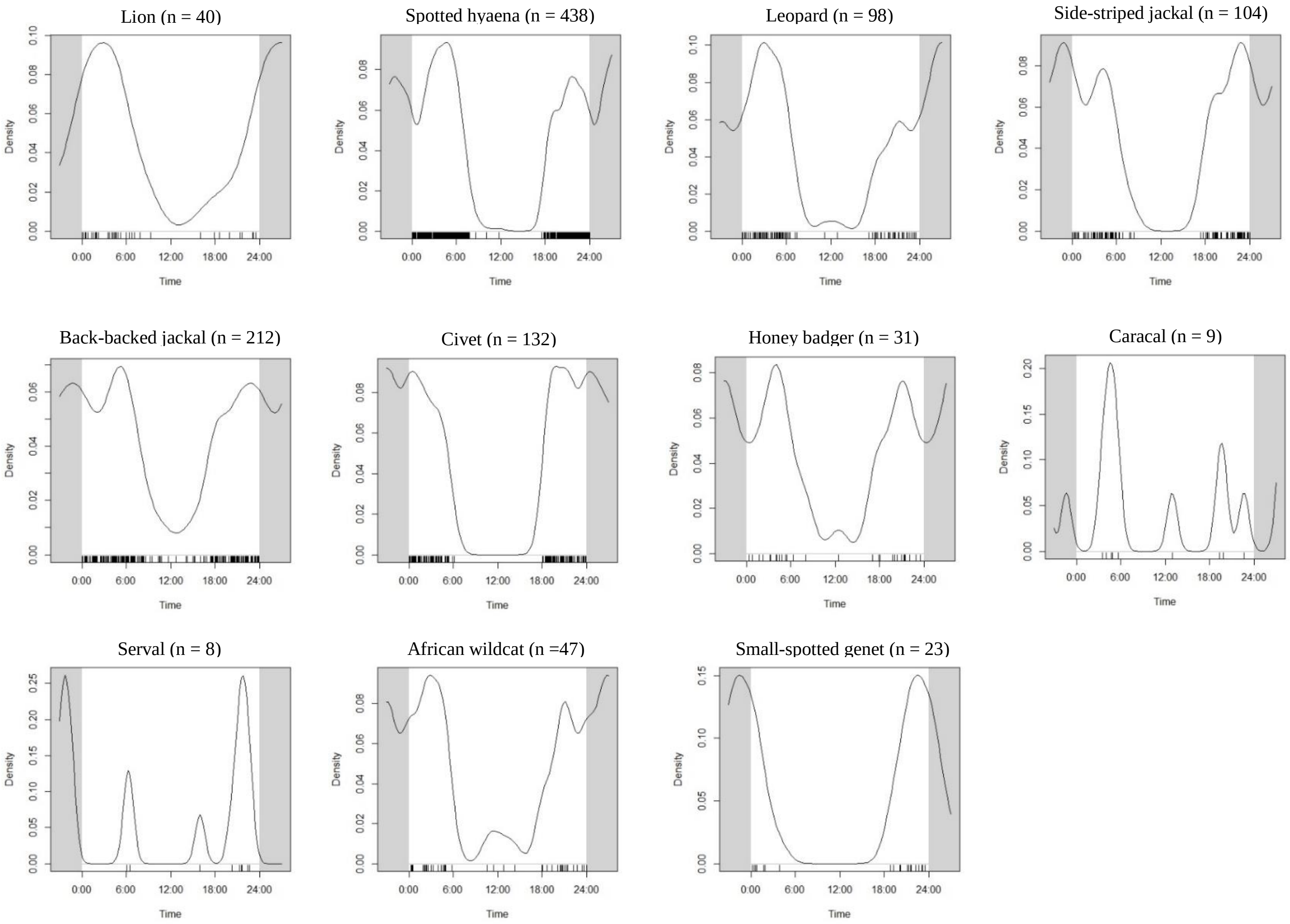


Figure 4.2: Graphs illustrating the mean estimated occupancies for each vegetation type, averaged across all carnivore species (A), large-sized carnivores (B), medium-sized carnivores (C) and the estimated occupancies for African wildcat (small-sized carnivore (D)) in Selati Game Reserve.

Temporal partitioning

Sufficient data enabled activity pattern analyses for 11 carnivore species (Fig.4.3). Caracal (n = 9) and serval (n = 8) had the fewest detections while spotted hyaena (n = 438) and black-backed jackal (n = 212) had the most (Fig. 4.3). Based on the limited data, caracal and serval were cathemeral and had activity peaks throughout the day and night (Fig. 4.3). Genets and civets were nocturnal, whereas lions, spotted hyaenas, leopards, side-striped jackals, black-backed jackals, honey badger and African wildcat were nocturnal with crepuscular peaks (Fig. 4.3). No carnivore exhibited a diurnal activity pattern (Fig. 4.3).

Of 55 pairs of sympatric focal carnivore species, I found 11 with an extremely high degree of daily activity overlap (estimated overlap coefficients ≥ 0.85) and 21 with a moderately high degree of overlap (estimated overlap coefficients ≥ 0.80; Table 4.4). Large carnivore activity patterns overlapped the most with one another, whereas small carnivore activity patterns overlapped the least with one another (Table 4.4). In fact, small carnivore activity patterns had the lowest degree of overlap with all other carnivores. Across all pairs of sympatric carnivores, except for African wildcat and small-spotted genet (*Genetta genetta*), activity patterns overlapped the least with lions (Table 4.4). Carnivore species with the highest degree of daily overlap were spotted hyaenas and leopards (estimated overlap coefficient = 0.90).



Lion (n = 40)

Spotted hyaena (n = 438)

Leopard (n = 98)

Side-striped jackal (n = 104)

Back-backed jackal (n = 212)

Civet (n = 132)

Honey badger (n = 31)

Caracal (n = 9)

Serval (n = 8)

African wildcat (n =47)

Small-spotted genet (n = 23)

Figure 4.3: Activity density estimates of daily activity patterns of carnivores (from large (top left) to small (bottom right)) in Selati Game Reserve. Solid lines represent kernel-density estimates and the short vertical lines above the x-axis indicate the times of individual photographs.

Table 4.4: Estimates of activity pattern overlap ($\triangle_1$) between carnivore species (1 = indicates identical activity) recorded in Selati Game Reserve, with approximate 95% bootstrap confidence intervals in parentheses.

	Large carnivore			**Medium carnivore**					**Small carnivore**		
Carnivore species	**Lion**	**Spotted hyaena**	**Leopard**	**Side-striped jackal**	**Black-backed jackal**	**Civet**	**Honey badger**	**Caracal**	**Serval**	**African wildcat**	**Small-spotted genet**
Lion	-	0.81 (0.71, 0.89)	0.87 (0.76, 0.96)	0.76 (0.64, 0.88)	0.8 (0.68,0.91)	0.70 (0.58, 0.83)	0.77 (0.62, 0.91)	0.52 (0.29, 0.74)	0.35 (0.17, 0.53)	0.79 (0.66, 0.91)	0.80 (0.62, 0.97)
Spotted hyaena		-	0.90 (0.83, 0.95)	0.89 (0.81, 0.95)	0.83 (0.78, 0.88)	0.81 (0.74, 0.87)	0.87 (0.76, 0.96)	0.6 (0.36, 0.82)	0.45 (0.27, 0.62)	0.84 (0.75, 0.91)	0.62 (0.49, 0.74)
Leopard			-	0.84 (0.74, 0.93)	0.83 (0.74, 0.91)	0.77 (0.70, 0.86)	0.85 (0.71, 0.95)	0.58 (0.35, 0.80)	0.40 (0.22, 0.57)	0.87 (0.76, 0.95)	0.57 (0.42, 0.72)
Side-striped jackal				-	0.83 (0.75, 0.90)	0.87 (0.79, 0.93)	0.88 (0.75, 0.98)	0.55 (0.31, 0.80)	0.45 (0.26, 0.63)	0.84 (0.73, 0.92)	0.68 (0.53, 0.82)
Black-backed jackal					-	0.72 (0.60, 0.82)	0.89 (0.77, 0.99)	0.53 (0.30, 0.75)	0.45 (0.25, 0.64)	0.79 (0.70, 0.88)	0.56 (0.43, 0.69)
Civet						-	0.77 (0.64, 0.89)	0.53 (0.29, 0.79)	0.41 (0.22, 0.59)	0.85 (0.73, 0.94)	0.76 (0.60, 0.89)
Honey badger							-	0.57 (0.34, 0.80)	0.44 (0.24, 0.65)	0.85 (0.71, 0.96)	0.58 (0.40, 0.76)
Caracal								-	0.31 (0.06, 0.57)	0.57 (0.33, 0.80)	0.36 (0.11, 0.63)
Serval									-	0.38 (0.20, 0.57)	0.50 (0.29, 0.71)
African wildcat										-	0.65 (0.48, 0.81)
Small-spotted genet											-

Collared large carnivores

Home range and core area estimates

AWT collars had variable success across the three collared large carnivore species. Collars worked best for lions, with an average working duration of 481 days, whereas collars on leopards worked for an average of 127 days (Table 4.5). Spotted hyaena collars only had an average working duration of 93 days (Table 4.5). One leopard and spotted hyaena collar both failed to record GPS fixes after deployment (Table 4.5).

Table 4.5: Summary of collared adult large carnivores on Selati Game Reserve.

Species	**Name**	**Sex**	**GSM**	**Date collared**	**GPS data until**	**# of days**	**# of fixes**	**Method of collaring**
Lion								
	Mburri	M	1733	09/09/16	05/01/18	484	5361	Free dart
	Dela	M	2019	29/05/17	03/10/18	493	3711	Free dart
	Matumi	F	2020	29/04/17	04/12/18	585	4172	Free dart
	Mfuti	F	1734	16/09/16	11/09/17	361	15036*	Free dart
average						*481*		
Leopard								
	LM1	M	1735	16/09/16	26/11/16	72	954	Baited cage
	LF1	F	1737	22/09/16	05/06/17	257	3695	Baited cage
	LF2	F	2012	08/06/17	04/12/17	180	1130	Baited cage
	LF3	F	1739	15/06/17	-	0	0	Baited cage
average						*127*		
Spotted hyaena								
	SH1	U	1736	16/09/16	06/05/17	233	3166	Free dart
	SH2	U	1738	02/05/17	14/05/17	13	83	Baited cage
	SH3	U	2011	19/07/17	20/11/17	125	214	Transmitter dart
	SH4	U	1736	15/07/17	-	0	0	Transmitter dart
average						*93*		

* only collar to record a GPS hourly instead of every three hours

As expected, the largest home ranges were used by lions, especially Dela (315.30 km^2) who used a large portion of neighbouring game farms (Table 4.6; Fig.4.4 A). Female lions only used areas within Selati (Fig.4.4 B). The only collared male leopard (LM1) had an extremely large home range (187.27 km^2). Three months after being collared he moved out of Selati, after which his collar failed to record GPS fixes (Fig.4.4 C; Table 4.6). The two female leopards exhibited remarkably different home ranges with LF2 having a home range (75.31 km^2) twice the size of LF1 (31.87 km^2; Fig.4.4 C; Table 4.6). LF2 used game farm areas to the northeast of Selati whereas LF1 remained within the reserve boundary (Fig.4.4 C). Spotted hyaenas had the smallest home ranges, with all three animals having similar home range sizes and using areas only within Selati (Table 4.6; Fig.4.4 D).

Table 4.6: The home range (km^2; 95% UD) and core area (km^2; 50% UD) for each collared adult large carnivore in Selati Game Reserve.

Species	**Animal ID**	**Sex**	**Home range area (km^2)**	**Core area (km^2)**
Lion	Mburri	M	196.93	33.41
	Dela	M	315.30	81.66
	Matumi	F	132.49	17.22
	Mfuti	F	105.26	18.96
Leopard	LM1	M	184.27	23.20
	LF1	F	31.87	10.30
	LF2	F	75.31	13.11
Spotted hyaena	SH1	U	33.93	7.27
	SH2	U	29.28	4.55
	SH3	U	35.86	5.66

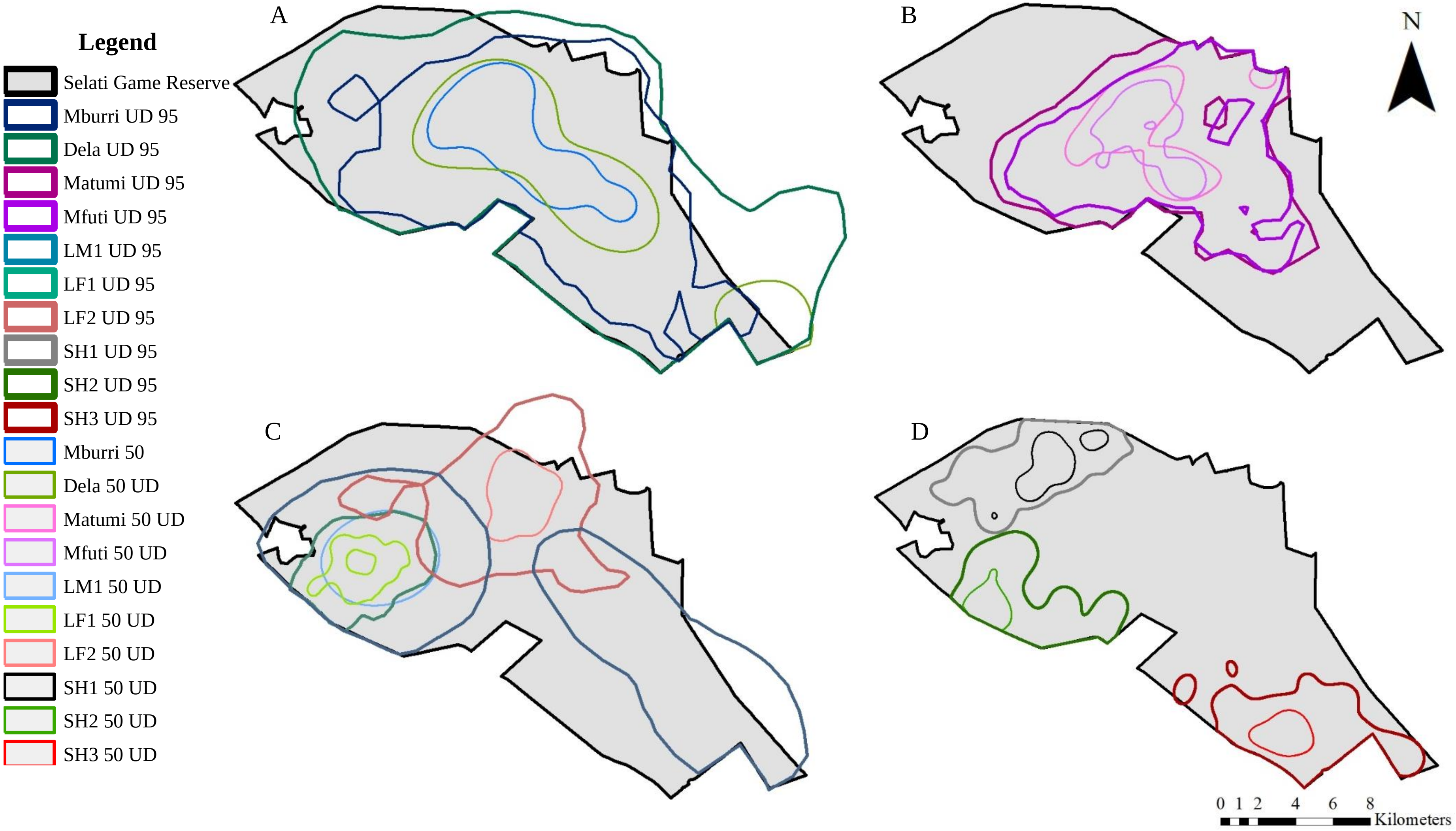


Figure 4.4: The home ranges (95% Kernel utilisation distribution) and core areas (50% Kernel utilisation distribution) for collared male (A) and female (B) lions, leopards (C) and spotted hyaenas (D).

Home range overlap

Collared large carnivore home ranges overlapped little with each other (Table 4.7). Leopards generally overlapped more with lions than with spotted hyaenas, whereas spotted hyaenas generally overlapped more with leopards than lions (Table 4.7). Lions had considerable overlap among themselves whereas leopards had minimal overlap and spotted hyaenas had nearly no overlap (Table 4.7). Regarding core areas, collared large carnivores had minor overlap with each other (Table 4.8).

Table 4.7: Volume of intersection indicating overlap (zero = no overlap, 1 = complete overlap) amongst the home ranges (95% Kernel utilisation distribution) of the collared large carnivores in Selati Game Reserve.

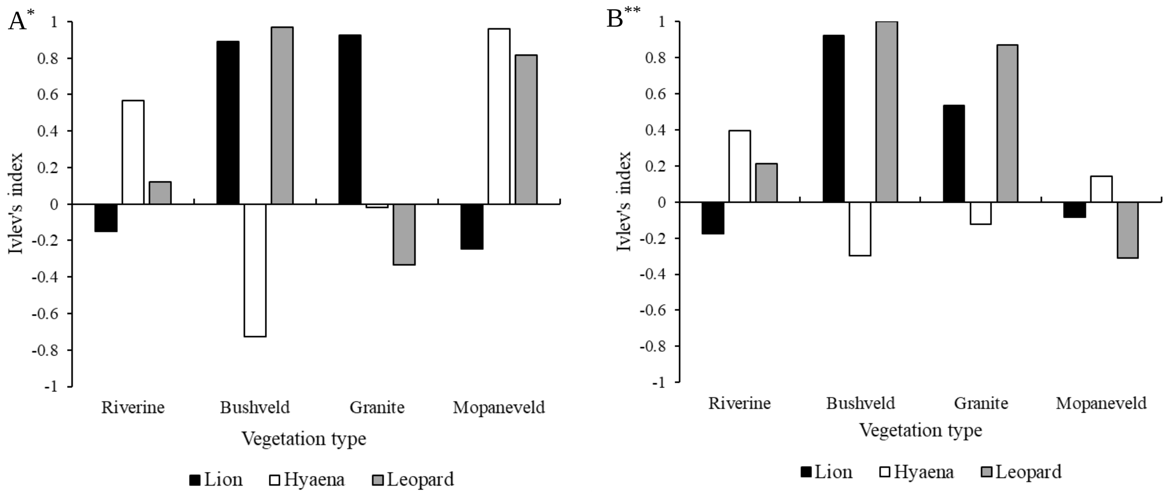
	Lion	**Spotted hyaena**	**Leopard**
Lion	0.34 ± 0.16	0.12 ± 0.06	0.24 ± 0.06
Spotted hyaena		0.03 ± 0.05	0.12 ± 0.09
Leopard			0.18 ± 0.17

Table 4.8: Volume of intersection indicating overlap (zero = no overlap, 1 = complete overlap) amongst the core areas (50% Kernel utilisation distribution) of large carnivores collared in Selati Game Reserve.

	Lion	**Spotted hyaena**	**Leopard**
Lion	0.07 ± 0.07	0.03 ± 0.02	0.05 ± 0.03
Spotted hyaena		0.003 ± 0.005	0.02 ± 0.02
Leopard			0.05± 0.05

Habitat use

Large carnivores exhibited no significant vegetation type preferences within the reserve during 2016 ($\lambda = 0.17$, $P = 0.11$) or 2017 ($\lambda = 0.32$, $P = 0.26$). Ivlev's electivity index revealed evidence for spatial partitioning amongst large carnivore species as spotted hyaenas always avoided areas (Bushveld and Granite) preferred by lions and vice versa (Fig.4.5). Leopards preferred the dense riverine (Riverine) vegetation less than the spotted hyaenas did (Fig.4.5), but always preferred the rocky slopes of the Gravelotte Rocky Bushveld (Bushveld) more than lions (Fig.4.5). In 2016, lions preferred the moderately dense woodland areas of the Granite Lowveld (Granite) whereas the leopards avoided it.



* overlapping large carnivore collar data collected in 2016 (22/09/16 – 26/11/16) for Mburri, Mfuti, LM1, LF1 and SH1

** overlapping large carnivore collar data collected in 2017 (19/07/17 – 20/11/17) for all lions, LF2 and SH3

Figure 4.5: Vegetation selection by lions, leopards and spotted hyaenas (hyaena) within Selati Game Reserve based on Ivlev's index. Values > 0 indicate a vegetation type used more than available (preferred) and values < 0 indicate a vegetation type used less than available (avoidance).

DISCUSSION

Some of the most complex terrestrial carnivore communities are found in African savannas, where morphological, behavioural and life history adaptations have minimised the cost of interspecific competition (especially for subordinate competitors) and promoted co-existence through resource partitioning (Fedriani *et al.*, 2000; Owen-Smith & Mills, 2008). Carnivore communities in most of South Africa's protected areas resemble those found throughout sub-Saharan Africa, where multiple species (~15) co-exist (Schuette *et al.*, 2013). A major difference, however, is that in South Africa, many protected areas are fenced, minimising anthropogenic pressures (Hayward *et al.*, 2007a, 2007b) but potentially increasing carnivore intra-guild competition (Palomares & Caro, 1999; Hayward & Kerley, 2008).

In the large (~1000 km^2), open system of Kenya's Rift Valley, anthropogenic pressures had the strongest influences on the occupancy dynamics of medium- and large-sized carnivores (Schuette *et al.*, 2013). In Selati, human presence had a minimal influence on carnivore occupancy dynamics. Instead, the presence of large carnivores (particularly lions) strongly influenced medium-sized carnivores, whereas the presence of prey species and placement of cameras along roads were important factors for the large carnivores. Throughout most of Africa's savanna systems, lions and spotted hyaenas are the largest and often most abundant carnivores (Périquet, Fritz & Revilla, 2015). Consequently, these two large carnivores can have profound effects on smaller carnivores through either exploitative (i.e. indirect negative effects due to shared resources, usually food) or interference competition (i.e. direct aggression for resources; Vance, 1984; Périquet *et al.*, 2015). Such effects can include behavioural responses, changes in activity patterns or space and habitat use, declines in population size through predation or intraspecific killing and in extreme cases local extinction (Creel *et al.*, 2001; Fortin *et al.*, 2005; Hayward & Kerley, 2008). I found some support for interference competition and changes in spatial distributions within the large carnivore guild of Selati. For example, leopards were the only species whose occupancy dynamics were negatively influenced by the presence of the more dominant lions and spotted hyaenas.

Spatial partitioning can promote the co-existence of sympatric carnivores when the ecological niche of competitors differs from one another (Périquet *et al.*, 2015). This is an important aspect of biological diversity as various biotic and abiotic factors may affect the competitive ability of different species (Orians & Wittenberger, 1991). My results show that each carnivore species had a unique combination of abiotic variables influencing their initial occupancies, which could support the spatial niche partitioning hypothesis (Schuette *et al.*, 2013). This hypothesis refers to the process by which natural selection drives competitively inferior carnivores to use space within the environment differently to escape competition and facilitate co-existence (Durant, 2000; Broekhuis *et al.*, 2013). In most systems, however, the situation is multifaceted as co-existence can concurrently produce varying costs (e.g. predation) and benefits (e.g. facilitation) for species (Périquet *et al.*, 2015). Although I found support for interference competition, which is the direct negative effect resulting from aggression between species, there was also evidence against this ecological top-down force. For example, lions and spotted hyaenas negatively influenced the detection probability of black-backed jackals and African wildcats, but leopards had a positive effect. In addition, lions positively influenced the detection probability of side-striped jackals. These results contradict the ecological theory of mesopredator release (Gehrt & Prange, 2007; Ritchie & Johnson, 2009). This theory posits that large carnivores assist in limiting the populations of mesopredators (i.e. medium-sized carnivores) through opportunistic intra-guild predation or through predation risk avoidance whereby mesopredators avoid areas frequented by larger carnivores (Gehrt & Prange, 2007; Lloyd, 2007). Carnivore intra-guild avoidance could be a variation of the “predation risk effect” usually described for predator-prey interactions, where herbivores need to balance demands for resources (i.e. food and space) and safety (MacArthur & Pianka, 1966; Lima & Dill, 1990). Therefore, the risks posed by the lions and spotted hyaenas in Selati may have outweighed the benefits of access to resources for some species such as leopards, black-backed jackals and African wildcats. Conversely, the benefits of resources (e.g. increased carrion) for black-backed jackals and African wildcats potentially overshadowed any risks posed by leopards.

Side-striped jackals occur throughout the moist savanna regions of tropical Africa (Macdonald, Loveridge & Atkinson, 2004), but are adaptable in their habitat use and are expanding their range into the semi-arid regions of South Africa where black-backed jackal numbers appear to be suppressed (e.g. Selati; Camacho *et al.*, 2016). Despite their larger size, side-striped jackals are usually displaced by the aggressive behaviours of black-backed jackals (Loveridge & Macdonald, 2002). The aggressive traits of black-backed jackals have been associated with the greater tendency of this species to risk feeding alongside lions and spotted hyaenas (Estes, 1967, 1991). A completely different situation may be occurring in Selati, as my results suggest that lions and spotted hyaenas are negatively influencing black-backed jackals but lions appear to be positively influencing side-striped jackals. Perhaps in the small, enclosed system of Selati, the risk of interference competition from black-backed jackals is greater than that of lions for side-striped jackals. However, information on side-striped jackals in South Africa is extremely limited and my study highlights the need for future research to focus on this species, especially its relationship with other sympatric carnivores. While my results partially support my hypothesis that large carnivores have the greatest influence on the smaller, less dominant carnivores, they also reveal that such a generalization does not necessarily hold for all of the species considered. I believe that the complexity of carnivore-carnivore relationships in African savannas is likely one of the main drivers of such variability.

Few published studies, most of which were conducted in open savanna systems, have evaluated the spatio-temporal use of habitat (vegetation) amongst carnivores (see Périquet *et al.*, 2015). This is an important mechanism proposed for co-existence (Périquet *et al.*, 2015) and is necessary for understanding how carnivores can be maintained within small, enclosed reserves. Temporal niche partitioning is an advantageous evolutionary strategy adopted by subordinate carnivores to avoid the potentially negative influences of dominant competitors (Fedriani *et al.*, 2000; Hayward & Slotow, 2009). All carnivores analysed in Selati were nocturnal to at least some extent. Activity patterns of the smaller carnivores overlapped the least with all carnivores but particularly with those of the lions, supporting my prediction that temporal partitioning promotes co-existence (*sensu* Ridout & Linkie, 2009; Schuette *et al.*, 2013). The extensive activity overlap between large carnivore guild members, however, does not promote temporal partitioning and co-existence. Carnivore activity patterns are not only influenced by the restrictions imposed by competitors but can also be influenced by environmental conditions such as temperature (Hayward & Slotow, 2009; Schuette *et al.*, 2013). In extreme environments, such as the semi-arid ecosystem of Selati, carnivores likely adopt nocturnal habits to escape the intense heat (~31ºC; see Chapter 2) during the day (Penido *et al.*, 2017). Spatial avoidance and the use of different areas by competitively inferior carnivores in Selati could also be promoting co-existence (Périquet *et al.*, 2015), particularly for the large carnivore guild, and this should be the focus of future research.

Occupancies of carnivores in relation to the vegetation types of Selati showed minimal evidence of spatial partitioning, whereas the selection of vegetation by the collared large carnivores showed stronger evidence of spatial partitioning. For example, spotted hyaenas always avoided areas preferred by lions. Leopards, however, showed minimal evidence of avoiding habitats preferred by lions and spotted hyaenas and used a wide range of habitats. Leopards are described as being catholic in their use of habitat and to have highly adaptable hunting and feeding behaviours (Hayward *et al.*, 2006). Leopards are, however, considered competitively subordinate to lions and spotted hyaenas (Palomares & Caro, 1999) and often avoid areas of increased presence of competing carnivores, which present a potential threat to them or their kills (Balme, Hunter & Slotow, 2007; Cupples *et al.*, 2011). In Phinda Private Game Reserve, which is also a small, enclosed reserve in South Africa, leopards lost more kills to spotted hyaenas than lions even though both dominant carnivores occurred at relatively low densities (Balme *et al.*, 2007). In Selati, when leopards and lions preferred the same vegetation type, the preference of leopards was always stronger, whereas with spotted hyaenas the preference of leopards was always weaker. Additionally, leopard home ranges and core areas overlapped the least with spotted hyaenas compared to lions. These results could potentially be because of kleptoparasitism and the much higher densities of spotted hyaenas (12.52 individuals/100 km^2) compared to lions (1.53 individuals/100 km^2) on Selati. I could not empirically test this theory, as observational data on these species in Selati were not available. Nevertheless, a recent study by Balme *et al.* (2017) in Sabi Sand Game Reserve, South Africa found that leopard distribution (no avoidance) and abundance (stable population) were not affected by interference competition with lions despite interspecific killing and kleptoparasitism. Balme *et al.* (2017) only considered interactions between lions and leopards and did not incorporate spotted hyaenas in their assessment. Furthermore, Sabi Sands Game Reserve is open (no boundary fence) to surrounding game reserves (Manyeleti Game Reserve and Kruger National Park), allowing animals to roam freely over more than 22 000 km^2 (Balme *et al.*, 2017), which could minimise the influence of competition. My results support those of Balme *et al.* (2017) in that leopards in Selati were unaffected by the relatively low density of lions, but seemed to be influenced by the higher density of spotted hyaenas. Prey abundance is vital to the co-existence of large carnivores (Périquet *et al.*, 2015; Balme *et al.*, 2017) and in highly productive ecosystems such as Selati where large and medium prey species are abundant, spotted hyaenas are capable of attaining high densities (i.e. form large clans) which may explain the negative impact on leopards (Périquet *et al.*, 2015).

Lions and spotted hyaenas have wide habitat tolerances, but spotted hyaenas are considered to be more generalist in their habitat requirements (Périquet *et al.*, 2015). Spotted hyaenas do not require vegetation cover while hunting, whereas the hunting tactics of lions require vegetation and terrain that facilitates concealment to catch prey (Davidson *et al.*, 2012; Périquet *et al.*, 2015). This could explain why the lions in Selati preferred the steeper, rocky slopes of the Gravelotte Rocky Bushveld and the moderately dense woodland vegetation of the Granite Lowveld, while the spotted hyaenas avoided these areas and preferred the undulating plains of the Phalaborwa-Timbavati Mopaneveld and lush strips of riverine vegetation. Previous studies on the habitat use of sympatric lions and spotted hyaenas have shown that both species favour dense woodland habitats (e.g. Broekhuis *et al.*, 2013), or thicket vegetation with high densities of impala (e.g. Mills & Biggs, 1993) or that their occupancy patterns in open mixed-use landscapes are similar (e.g. Schuette *et al.*, 2013). My study is the first account of the habitat selection of simultaneously collared lions and spotted hyaenas and I found completely different results. Despite their higher density, spotted hyaenas always avoided areas preferred by the lions. The majority of the studies on interactions between lions and spotted hyaenas (and carnivores in general) have been conducted in large open systems (>1000 km^2), but interactions within closed savanna ecosystems are likely to differ (Périquet *et al.*, 2015), as highlighted by my data. Périquet *et al.* (2015) theorized that in small, enclosed reserves, strong lion populations would outcompete spotted hyaenas and cause local population declines. I have found no evidence for spotted hyaena population decline in Selati (see Chapter 3). This could be because when prey availability is high, spotted hyaena clan sizes tend to increase while their home ranges decrease. This enables spotted hyaenas to tolerate competition with lions, as they are more capable of protecting their kills or aggressively take over lion kills (Périquet *et al.*, 2015). My study supports this scenario as spotted hyaena densities were high and their home ranges were relatively small (~32 km^2). Male lions are a major cause of spotted hyaena mortality, whereas there is little evidence of spotted hyaenas killing lions (but see Schaller, 1972; Loveridge *et al.*, 2007). Spotted hyaenas are therefore, considered subordinate to male lions and the fear or predation risk of the two large home ranged male lions in Selati could potentially be the cause of the habitat selection differences between the two species. The impact of exploitation competition is likely to play an important role in shaping the carnivore community (Loveridge *et al.*, 2007) of Selati. I will investigate this in the next chapter.

My results demonstrate the importance of collecting empirical information on the spatio-temporal partitioning of multiple carnivores in a small, enclosed reserve, which represents a conservational gap in South Africa. Focusing on pairs of carnivores and overlooking the interactions of subordinate carnivores could lead to inappropriate conservation and management actions and prevent the protection of biodiversity and ecosystem health. Future research needs to be aimed at improving our understanding of carnivore-carnivore interactions and how these relationships influence ecosystem functioning, particularly in small, enclosed systems.

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Chapter 5

DIETARY COMPOSITION

An adult spotted hyaena

INTRODUCTION

Large mammalian carnivores such as lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*) and leopards (*Panthera pardus*) can regulate ecological interactions and maintain terrestrial ecosystem health (Ritchie & Johnson, 2009; Pitman, Swanepoel & Ramsay, 2012). As keystone species (Power *et al.*, 1996; Elbroch & Wittmer, 2012), large carnivores can influence lower trophic levels by affecting the density of subordinate carnivores and natural prey through direct (interference competition, predation or killing) or indirect (exploitative competition, trophic cascades) interactions (Case & Gilpin, 1974; Elbroch & Wittmer, 2012). Large carnivores even have the potential to influence plant communities by supressing the effects of ungulates on vegetation (Messier, 1994; Hobbs, 1996; Augustine & McNaughton, 1998).

Carnivores exhibit morphological (e.g. dental) and behavioural (e.g. hunting strategies) adaptations that reflect competition in various forms (McDonald, 2002; Tannerfeldt, Elmhagen & Angerbjörn, 2002; Donadio & Buskirk, 2006). The most extreme form of competition between species is killing (i.e. interference competition), which is increasingly recognised as one of the most important factors structuring carnivore communities (Durant, 2000; Caro & Stoner, 2003; Donadio & Buskirk, 2006; Di Bitetti *et al.*, 2010; Broekhuis *et al.*, 2013). For instance, species diversity can be limited by interference competition as the number of carnivores that can potentially co-exist in an ecosystem is restricted by their similarity in ecological niches (Morin, 1999; Di Bitetti *et al.*, 2010). Carnivores run the risk of being killed by sympatric carnivores and if the victim is consumed, the phenomenon is referred to as intra-guild predation (Lindström, Brainerd & Overskaug, 1995; Palomares & Caro, 1999). Often the killed competitor is not consumed and thus referred to as interspecific killing (Palomares & Caro, 1999; Schuette *et al.*, 2013).

Competition theory proposes that carnivores should kill sympatric guild members when benefits overshadow costs or risks (Donadio & Buskirk, 2006). Benefits may include the freeing of resources that otherwise would be used by the competitor that is killed, whereas risks may include injuries and costs may include energy expenditure (Case & Gilpin, 1974). Carnivores with lower competitive abilities can be highly affected by interference and exploitative competition, which have been credited as playing a major role in limiting their abundance and space use (Laurenson, 1995; Lindström *et al.*, 1995). Competition for food has been acknowledged as a key factor triggering intra-guild predation and interspecific killing (Palomares & Caro, 1999), as extensive dietary overlap often motivates aggression among carnivores (Mills & Biggs, 1993; Palomares & Caro, 1999). Prey abundance within an ecosystem can be important in determining carnivore species richness, as selective predation and ecological separation could possibly facilitate their co-existence (Karanth & Sunquist, 1995a). Theoretical models of intra-guild predation and interspecific killing predict that carnivore co-existence arises when the subordinate carnivore (i.e. victim) is superior at exploitative competition for shared resources (i.e. prey), but that the killer gains significantly from the consumption or killing of the subordinate (Palomares & Caro, 1999). Therefore, a trade-off may exist between a species' success in either exploitative or interference competition (Vanak & Gompper, 2009).

Carnivores can obtain food through predation, scavenging (i.e. feeding on carrion) or kleptoparasitism (i.e. the displacement of other carnivores from their kills through superiority in size or numbers; Honer *et al.*, 2002; Pereira, Owen-Smith & Moleón, 2014). Spotted hyaenas and lions are Africa's top two carnivores (i.e. largest and most numerous) and their interactions with one another can be intense, as their diets tend to overlap extensively (Owen-Smith & Mills, 2008; Pereira *et al.*, 2014). Lions have frequently been recorded killing spotted hyaenas, but spotted hyaenas have seldom been recorded killing lions and when they have it has mainly been cubs (Palomares & Caro, 1999; Pereira *et al.*, 2014). Both large carnivores scavenge from one another, but in areas where spotted hyaenas are more abundant, lions are said to scavenge more regularly from spotted hyaenas than vice versa (Pereira *et al.*, 2014). This is usually because the presence of at least one male lion provides lions with a substantial advantage (Kruuk, 1972). Competitive interactions such as these may result in subordinate carnivores, such as spotted hyaenas, altering their foraging strategies and diet composition (Périquet *et al.*, 2015b).

As an opportunistic and competitively inferior large carnivore, leopards have been recorded exploiting an incredibly wide variety of prey, ranging from rodents to adult eland (*Tragelaphus oryx*; Hayward *et al.*, 2006). Their wide dietary breadth and prey size variation could reflect the level of intra-guild competition leopards face throughout their range, and may be a means to minimize competition (du Preez *et al.*, 2017). For example, in India, leopards were found to switch from a rodent dominated diet to an increased consumption of larger prey species following the extirpation of the local tiger (*Panthera tigris)* population (Mondal *et al.*, 2011). This suggests that leopards may be particularly vulnerable to exploitative competition and alter their behavioural ecology in relation to the level of intra-guild competition (du Preez *et al.*, 2017). Therefore, carnivore competition may force species to occupy niches in which they are less efficient, potentially affecting their survival (du Preez *et al.*, 2017).

In Africa, high levels of human-carnivore conflict, particularly in areas adjacent to protected areas, leads to human-induced carnivore mortality (Woodroffe & Frank, 2005; Balme, Slotow & Hunter, 2010). These actions have been shown to be one of the most important factors causing the local extinction of large carnivores (Watts & Holekamp, 2008; Balme, Slotow & Hunter, 2009). During the early 20th century, the agricultural and economic development of South Africa led to the local extinction of many carnivores in all but the most uninhabitable areas (Hayward *et al.*, 2007; Devineau *et al.*, 2010). Over the past two decades, however, the conversion of uneconomical pastoral land into enclosed protected areas has led to the reintroduction of locally extirpated wildlife populations throughout South Africa (Hayward *et* *al.*, 2007). Large carnivore reintroductions have been of particular importance because not only are they major tourist drawcards (i.e. economic incentives), but they also have the potential to restore ecosystem structure and function (Lindsey, Roulet & Romañach, 2007; Owen-Smith & Mills, 2008). Though these enclosed reserves often reduce the potential for human-carnivore conflict and mortality, these systems are often small (< 400 km^2), which may increase the likelihood of carnivore intra-guild competition (Palomares & Caro, 1999; Packer *et al.*, 2013). The conservation of viable large carnivore populations, which is not naturally attainable in these small, enclosed reserves, is essential to ecosystem health (Hayward *et al.*, 2007; Rostro-García, Kamler & Hunter, 2015). Effective conservation strategies are therefore needed to ensure the viability of carnivores in South Africa, but such strategies cannot be developed without understanding how carnivores affect each other or their prey in small reserves (Périquet, Fritz & Revilla, 2015a). Predation also constitutes an important feature of the biotic environment of wild ungulates (Hirst, 1969). Human pressure and fencing of protected areas can also affect ungulate species as their long-distance migrations are constrained (Pereira *et al.*, 2014). This increases the predation pressure on prey populations, which could have cascading effects throughout the food web, especially for threatened species (Pereira *et al.*, 2014). Regional variation in ecological community structures (i.e. species richness and abundance) and resulting interactions are inevitable, so understanding the ecological preferences and interactions of carnivores throughout their range is vital (Rodríguez-Soto *et al.*, 2011).

Hunting habits and prey selection of carnivores is best studied through continuous observations (Mills, 1992), but these methods are labour-intensive, time-consuming and, in moderately dense, woodland savanna landscapes, logistically unrealistic (Schaller, 1972; Silvestre, Novelli & Bogliani, 2000; Radloff & Du Toit, 2004). Carnivores are also naturally scarce, making direct surveys difficult (Davison *et al.*, 2002). Recent advances in Global

Positing System (GPS) technology has allowed for the non-invasive analyses of carnivore kill sites which, along with non-invasive, cost efficient scat analyses, can be used to effectively determine the dietary composition of multiple sympatric carnivores (Floyd, Mech & Jordan, 1978).

My aim for this chapter was to examine the dietary overlap among carnivores in a small, enclosed reserve (Selati Game Reserve) through the analysis of a combination of kill site and scat data. I predicted that within the large carnivore guild, lions and spotted hyaenas would have the highest dietary overlap, as both species would preferentially select for the most abundant medium (30-90 kg) and large (90-1000 kg) prey species. I further predicted that leopards would consume the widest variety of prey, potentially minimising their dietary overlap with the dominant lions and spotted hyaenas because of exploitation competition. I also predicted that small- (<10 kg) and medium-sized (10-20 kg) carnivores would suffer the most from intra-guild predation and that their dietary composition would overlap the most with leopards.

METHODS

The details of the study site are described in detail in Chapter 2.

Small mammal trapping

Small mammal (e.g. rodents) species are often difficult to identify in carnivore scats because reference material is not available (Breuer, 2005). The small mammal community of Selati is understudied, meaning not all potential food items for carnivores such as caracals (*Caracal*

caracal) and leopards are known. Consequently, reference material for small mammal species were missing and the diet of such carnivores could not be accurately assessed. To address this data gap, I undertook small mammal trapping (Authorized by the Animal Ethics Subcommittee of the Rhodes University Ethical Standards Committee; ethics clearance reference number: RU-LAD-16-09-002).

Sherman traps (7.5 x 9 x 23 cm), baited with peanut butter and rolled oats (Kerley, 1992; Avenant, Watson & Schulze, 2008), were used to trap small mammals between 12 February and 2 March 2018. A trapping station was established in each of the three major vegetation types of Selati (Fig.5.1), where three trap lines of at least 100 m apart were set up with 15 traps each, spaced 15 to 20 m apart for three nights (Gurnell & Flowerdew, 1990). Most species of small mammals are nocturnal or crepuscular, so traps were set at dusk (17h30) and checked and removed at dawn (05h30; Barnett & Dutton, 1995). Thus, animals spent as little time as possible in the traps to reduce mortalities (Barnett & Dutton, 1995). All traps were set under vegetation to hide them and to provide thermal insulation (Gurnell & Flowerdew, 1990; Barnett & Dutton, 1995).

If a trap captured an animal, I used the plastic bag technique to extract animals from the traps (Gurnell & Flowerdew, 1990). Animals were handled as little as possible and I wore thick leather gloves to avoid exposure to viral or bacterial diseases (Barnett & Dutton, 1995). To remove a captured animal from a trap, the trap was placed inside an adequately sized zip-lock bag, after which the trap was opened and the animal gently shaken out (Barnett & Dutton, 1995). Once the animal was in the bag, the trap was removed and the animal gently manoeuvred into a corner (Barnett & Dutton, 1995). Each captured animal was identified to species if possible, sexed, weighed and a hair sample clipped for capture-recapture purposes and to produce hair slides to add to the Rhodes University mammal reference collection. All captured animals were released at the point of capture and traps were cleaned before re-use.

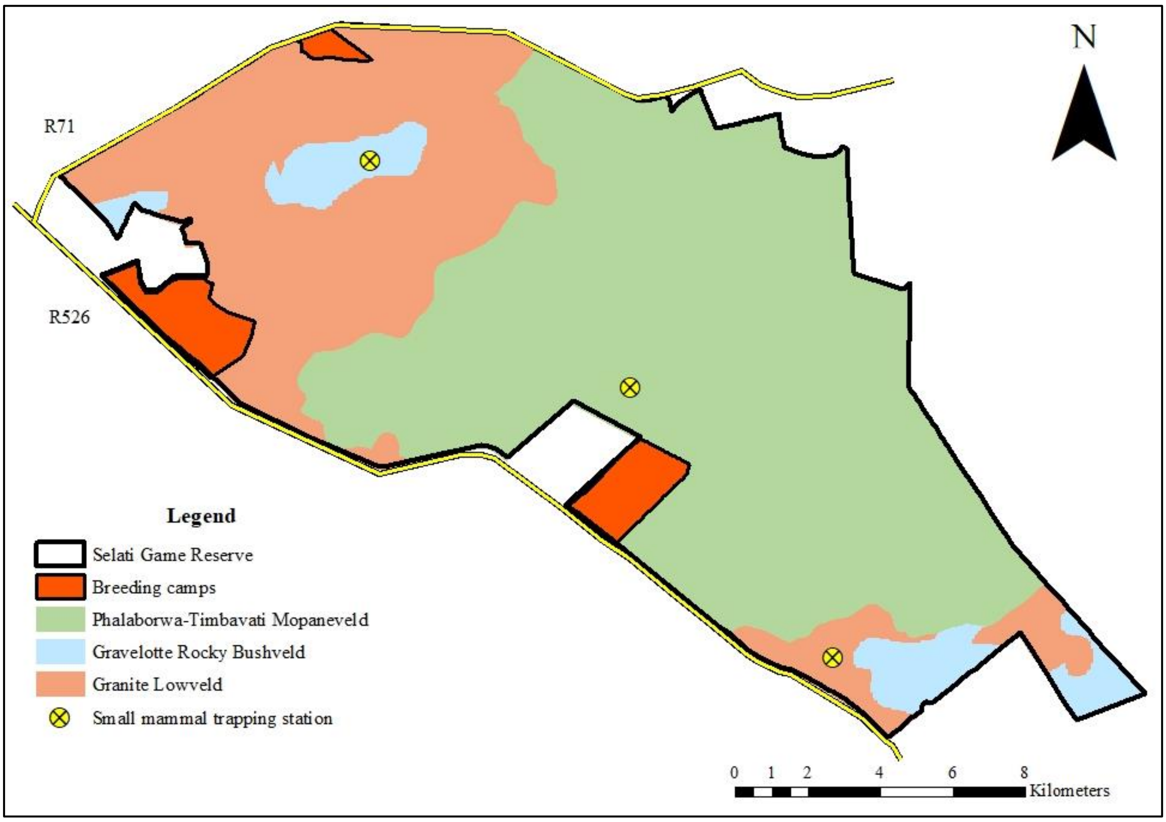


Figure 5.1: Positioning of the small mammal trap grids within Selati Game Reserve.

Large carnivore diet composition

Carnivore scat collection

Carnivore scat samples were collected opportunistically while either driving or walking between June 2016 and July 2018. Carnivore scats can be reliably identified to species level using diagnostic characteristics such as size, shape and smell (Davison *et al.*, 2002; Stuart & Stuart, 2003). Scats were stored in air-tight zip-lock bags labelled with species ID, date and GPS co-ordinates and frozen before processing in the laboratory at Rhodes University.

Each frozen scat sample was placed in a nylon stocking tied at both ends (Klare, Kamler &

MacDonald, 2011a). The stockings were placed into beakers of water in a hot water bath (± 45^{0}C) and left to soak and soften for up to 48 hours. Once soft, scats were removed and carefully washed and strained under running water and through a 1 mm wire mesh sieve to trap remains (e.g. hair, bones, and teeth) and remove all faecal matter (Karanth & Sunquist, 1995b). Remains from each scat were placed into plastic containers lined with paper towel and allowed to air-dry for ~36 hours. Once dry, all remains were stored in labelled plastic bags.

Cross sections of mammalian hair found in the scats were prepared following the method of Douglas (1989), whereby a random selection of between 10 and 20 hairs (ensuring that all hair types present in the scat were included) from each scat was placed into the front section of a disposable plastic pipette (Reynolds & Aebischer, 1991). Melted paraffin wax (Paraplast Plus, Sherwood Medical Co., St Louis, Missouri, USA) was drawn into the pipette, which was then dipped into a beaker of crushed ice to solidify the wax. The front end of the pipette was cut into several thin cross sections (1-2 mm thick) with a surgical blade. These sections were secured onto labelled microscope slides using drops of melted paraffin wax.

Hair samples for each scat sample were identified to species level by comparing the prepared slides to the Rhodes University mammal hair reference collection (n = 90) of all potential prey species found in Selati (Karanth & Sunquist, 1995b; Spaulding, Krausman & Ballard, 2000). I verified all species identifications at least twice to ensure accuracy (Williams *et al.*, 2018). Rodents and mongooses are difficult to identify to species and were therefore classified to Order and Family respectively (Martins *et al.*, 2011; Williams *et al.*, 2018). Birds were classified to their class (Martins *et al.*, 2011) and if hair samples could not be classified to species or order, they were recorded as unidentified (Klare *et al.*, 2010).

Lion and leopard kill sites

Relocation data from collared carnivores can be used to collect valuable information on their diet and prey selection through the GPS cluster method (Anderson & Lindzey, 2003). This method has been used with success for multiple carnivores including cougars (*Puma concolor*; Anderson & Lindzey, 2003), wolves (*Canis lupus*; Sand *et al.*, 2005; Webb, Hebblewhite & Merrill, 2008), lynx (*Lynx lynx*; Mejlgaard *et al.*, 2013), tigers (Athreya *et al.*, 2013), cheetahs (*Acinonyx jubatus*; Hubel *et al.*, 2016), snow leopards (*Panthera unica*; Shehzad *et al.*, 2012), lions (Tambling *et al.*, 2010) and leopards (Martins *et al.*, 2011).

Spotted hyaenas are efficient hunters and scavengers and it is not possible to assess whether prey remains found at their GPS clusters have been scavenged or killed (Périquet *et al.*, 2015b). Hence, I only considered kill site data for lions and leopards. During each seasonal fieldtrip (see Chapter 2), I downloaded relocation data (i.e. GPS fixes) remotely from the AWT computer-based application for a maximum period of three months for lions and leopards. I plotted the relocation data in ArcMap 10.5.1 (ESRI, Redlands, California, USA) to identify GPS clusters and potential kill sites. I defined a GPS cluster as more than two consecutive locations within 100 m of each other over a 16-hr period (Anderson & Lindzey, 2003; Martins *et al.*, 2011). Once I had identified potential kill clusters, I uploaded the co-ordinates onto a hand-held GPS unit (Garmin GPSMap 62s) and investigated each cluster on foot. GPS locations can be inaccurate (Webb *et al.*, 2008) and kill remains can be scattered around the points of the GPS cluster, so I searched an area of ~20 m around each point for prey remains (Tambling *et al.*, 2010). Potential predation events were identified from the presence of prey stomach contents (Fig.5.2A), hair, teeth, bones (Fig.5.2B) or hooves (Tambling *et al.*, 2010). These items were used to identify prey species and, whenever possible, to record the age (juvenile (small dependent calf or lamb) or adult (fully grown, reproductive animal); Davidson *et al.*, 2012) and sex (Tambling *et al.*, 2010) of the prey item. I also recorded the actual location of each kill. Direct observations or the opportunistic location of lion and leopard kills in the field were also recorded (prey species, age, sex and GPS location).

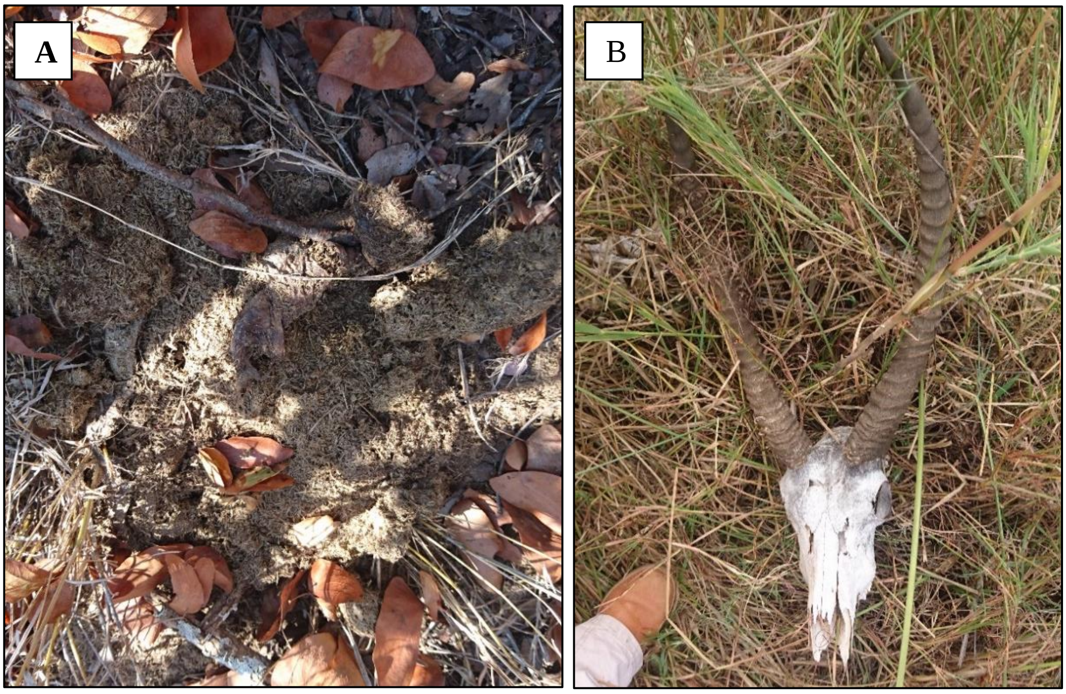


Figure 5.2: Examples of potential prey remains (A – stomach contents; B – adult male waterbuck (*Kobus ellipsiprymnus*) skull) found at large carnivore GPS clusters/potential kill sites.

Data analyses

Small mammal trapping

No statistical analyses were necessary as I only conducted a single mammal trap survey to identify potential food items (and create hair reference material) for carnivores such as caracal and leopard.

Large carnivore diet composition

Scat analyses are an indirect method of describing diet and are therefore inherently biased (Klare, Kamler & Macdonald, 2011b). Two broad categories of scat analyses have been developed and include qualitative methods in which frequency of prey species occurrence is determined and quantitative methods that take into account the mass of the prey consumed (e.g. biomass calculations; Klare *et al.*, 2011). Using the wrong method for intended species and data could lead to imprecise biological conclusions (Klare *et al.*, 2011b). For example, spotted hyaenas are efficient hunters and scavengers who can regurgitate variable portions of excess hair and (or) skin from eaten prey (Kruuk, 1972; Bearder, 1977). Hairs found in their scats are therefore better considered an indication of the frequency with which they feed on each species (Bearder, 1977; Silvestre *et al.*, 2000). Thus, for comparative purposes, the importance of each food item found in the scat samples of each large carnivore was expressed only in terms of frequency of occurrence (FO; Silvestre *et al.*, 2000).

Trites and Joy (2005) calculated that a minimum of 59 scats is required to broadly describe the diet of a carnivore at a specific site. Therefore, I constructed species accumulation curves in the R programming language (version 3.5.1, R Development Core Team, 2017) to test whether my sample sizes were adequate (Wentworth, Tambling & Kerley, 2011). Spotted hyaena and leopard curves reached asymptotes, indicating that I collected a sufficient number of scats for these two species. However, insufficient lion scats were collected (Appendix 5.1). Qualitative scat analyses tend to overestimate smaller prey species (Floyd *et al.*, 1978), while kill site data tends to be biased towards larger prey species (Hayward *et al.*, 2006). To compensate for the small lion scat sample size and the biases of the two data collection methods, I chose to include both methods in determining the diet composition of large carnivores on Selati, to ensure that the majority of each carnivores prey species were assessed in my analyses (Hayward *et al.*, 2006).

Overall diet composition for each species was calculated as FO, which is calculated as a percentage, using the number of times a food item was encountered as a function of the total number of occurrences of all food items found (Loveridge & Macdonald, 2003; Klare *et al.*, 2011b; Périquet *et al.*, 2015b). Reducing the large number of prey species consumed into categories allows for the simplification of descriptions and comparisons of diet (Trites & Joy, 2005). Therefore, prey species were assigned to one of four size categories: small (<30 kg), medium (30-90 kg), large (90-1000 kg; Krüger, Lawes & Maddock, 1999) and 'others'. Species occurring in low proportions in the diets of large carnivores or species for which reliable population numbers were not available; viz. Cape porcupine (*Hystrix africaeaustralis*), chacma baboon (*Papio ursinus*), rock hyrax (*Procavia capensis*), scrub hare (*Lepus saxatilis*), vervet monkey (*Chlorocebus pygerythrus*), side-striped jackal (*Canis adustus*), small-spotted genet (*Genetta genetta*), mongooses, rodents and birds were grouped into a category named 'other' (Appendix 5.2a; Périquet *et al.*, 2015b; Périquet, Fritz & Revilla, 2015a).

The age or size of food items killed or scavenged by carnivores cannot be determined from scat samples. I recognized the potential limitation of direct body size inference due to the uncertainty of the actual size of consumed prey. However, du Preez *et al.* (2017) stated that intraspecific prey size differences are not crucial to determining niche separation between carnivores, as adults and juveniles of the same species are likely to associate spatio-temporally (see Estes, 1991). Even though carnivores may hunt different size classes of the same species, incidents of carnivore interactions and conflict could still arise, as there may be little spatial separation in actual predation behaviour and events when consuming the same prey (du Preez *et al.*, 2017)**.** Therefore, the potential ecological separation between carnivores to reduce competition can still be tested without including data on the actual size of individuals consumed (du Preez *et al.*, 2017).

I assessed prey preference for each carnivore using Jacobs' selection index, $D = r - p/((r + p)-(2rp))$, which takes into account the proportion of scats containing a particular prey species (r) and the proportional abundance (derived from aerial counts) of the prey species killed ((p); Jacobs, 1974). Jacobs index ranges between -1 (highly avoided), 0 (used in proportion to availability) and +1 (highly selected) and minimises the biases associated with small sample size, rare food items and non-linearity in proportional use over time (Krebs, 1989). I used Levin's index (B) to determine dietary breadth (i.e. uniformity) for lions, spotted hyaenas and leopards. To compare the dietary overlap of lions, spotted hyaenas and leopards I used Pianka's index (O), which ranges from 0 (no overlap) to 1 (complete overlap; Pianka, 1974). Dietary overlap was considered biologically significant when the value exceeded 0.60 (Navia, Mejía-Falla & Giraldo, 2007).

Insufficient numbers of small- and medium sized carnivore scats were collected to conduct reliable analyses. Nevertheless, to get an indication of what the smaller sized carnivores may be feeding on, I grouped these species as 'other carnivores' and compared their food items to those of the large carnivores.

RESULTS

Small mammal trapping

I trapped and identified five Rodentia species (fat mouse (*Steatomys pratensis*), Natal multimammate mouse (*Mastomys natalensis*), pouched mouse (*Saccostomus campestris*), lowveld gerbil (*Gerbilliscus leucogaster*; Fig.5.3) and highveld gerbil (*Gerbilliscus brantsii*)) from the entire small mammal trap survey. I collected hair from each species and created reference slides to add to the Rhodes University mammal hair reference collection.

Figure 5.3: A lowveld gerbil captured during the small mammal trap survey in Selati Game Reserve.

Large carnivore diet composition

In total, I identified 23 prey species (in addition to rodents and birds) from large carnivore scats and kill sites (Appendix 5.2a). Lions fed on 11 food items (from 22 scats and 95 kill sites), spotted hyaenas fed on 16 (from 78 scats) while leopards fed on the most with 18 food items recorded (52 scats and 22 kill sites; Appendix 5.2a). Only five prey species were common to all three large carnivores (Appendix 5.2a) and, in order of importance, these were impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), warthog (*Phacochoerus africanus*) and bushpig (*Potamochoerus larvatus*; Appendix 5.2b).

Lions and spotted hyaenas completely avoided small prey species (D = -1) whereas leopards had a high preference for small prey (D = 0.89; Fig.5.4). Medium prey species were avoided by lions (D = -0.60), whereas spotted hyaenas (D = 0.04) and leopards used medium sized prey in accordance to their availability in Selati (D = 0.18; Fig.5.4). Leopards (D = -0.71) avoided large prey species while lions (*D* = 0.61) preferentially selected for them and spotted hyaenas (*D* = -0.006) selected for them in accordance to their availability (Fig.5.4).

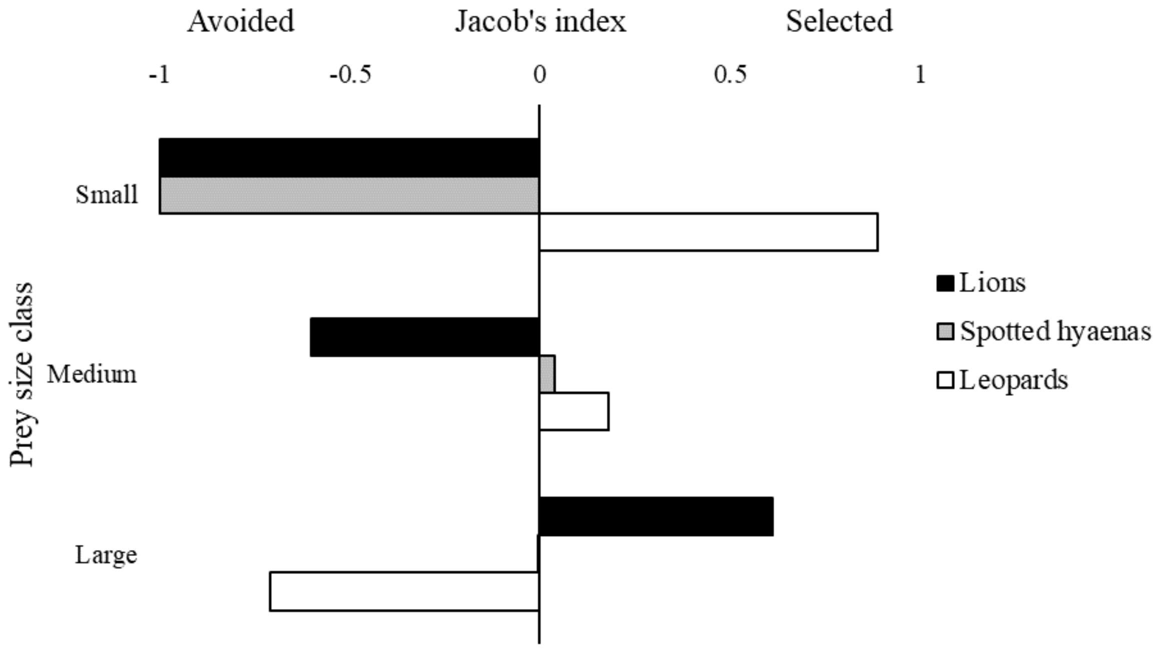


Figure 5.4: Jacob’s selection indices for prey size classes consumed by lions (black bars), spotted hyaenas (grey bars) and leopards (white bars) in Selati Game Reserve.

Of the six most abundant prey species (impala, kudu, blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), waterbuck and warthog) on Selati (see Appendix 5.2b), lions preferentially selected four species (kudu, waterbuck, blue wildebeest and warthog), spotted hyaenas two (waterbuck and warthog) and leopards one (warthog; Fig.5.5). Despite the relative rarity of prey species such as tsessebe (*Damaliscus lunatus*), mountain reedbuck (*Redunca fulvorufula*) and Sharpe’s grysbok (*Raphicerus sharpei*) in Selati (FO < 0.10%; Appendix 5.2b), lions preferentially selected for tsessebe and leopards preferentially selected for the latter two (Fig.5.5).

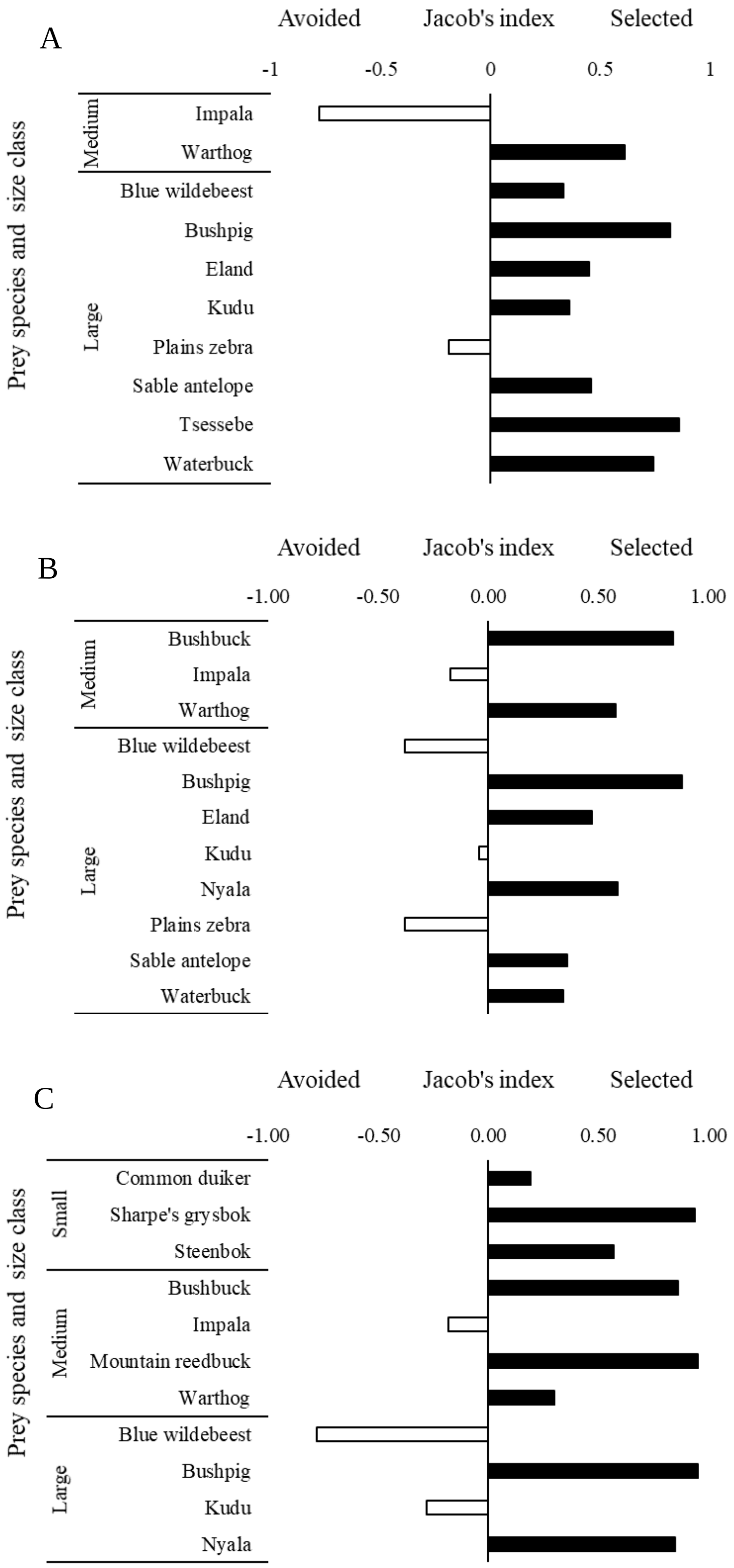
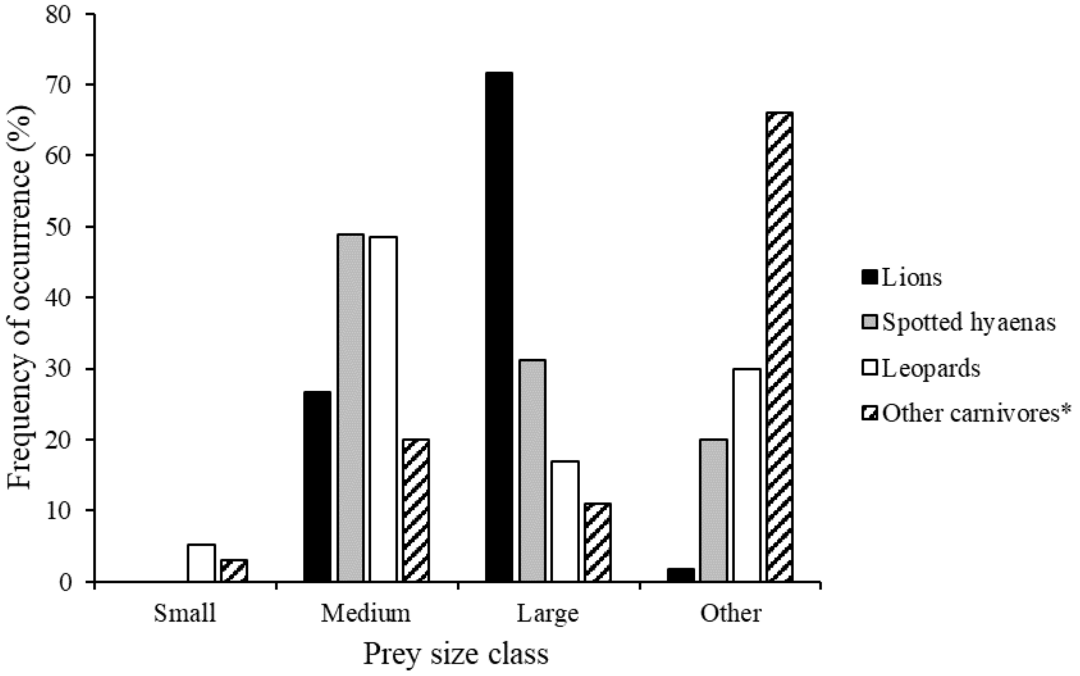


Figure 5.5: Jacob's selection indices for species consumed by lions (A), spotted hyaenas (B) and leopards (C) in Selati Game Reserve. Black bars indicate preference and white bars indicate avoidance.

The diet of the lions contained predominantly large prey (71%), whereas for spotted hyaenas and leopards, medium prey species (~48%) were more important (Fig.5.6). Food items classified as 'other' accounted for ~1% of the diet of lions, whereas for spotted hyaenas and leopards it accounted for 20 and 30%, respectively (Fig.5.6). This category was also the most important for small- and medium sized carnivores (66%; Fig.5.6) and consisted predominantly of rodents and mongooses (Appendix 5.2c). Similarly, leopards and spotted hyaenas also consumed these items the most within the 'other' category (Appendix 5.2c). Besides the presence of mongoose, leopards were the only carnivore found to consume other carnivores (side-striped jackal and small-spotted genet; Appendix 5.2c).



*Other carnivores include serval, caracal, black-backed jackal, side-striped jackal and civet

Figure 5.6: Diet composition in prey size classes for lions, spotted hyaenas, leopards and the group of small- and medium-sized carnivores.

Dietary niche breadths were similar amongst the three large carnivores, with lions exhibiting a slightly broader breadth ($B = 5.96$), followed by spotted hyaenas ($B = 5.51$) and then leopards ($B = 5.13$; Table 5.1). Dietary overlap between spotted hyaenas and leopards was the greatest and biologically significant (i.e. $O > 0.60$) for both prey species ($O = 0.91$; Table 5.1) and prey size class ($O = 0.96$; Table 5.2). Dietary composition overlapped the least between lions and leopards and was not considered biological significant for either prey species ($O = 0.43$; Table 5.1) or prey size class ($O = 0.56$; Table 5.2). Small- and medium-sized carnivores (other) overlapped the most with leopards ($O = 0.63$ & 0.76), followed by spotted hyaenas ($O = 0.42$ & 0.62) and finally lions ($O = 0.21$ & 0.27; Table 5.1 & 5.2).

Table 5.1: Dietary breadth (Levin's index) and overlap (Pianka's index) for lions, spotted hyaenas, leopards and other carnivores according to prey species.

Species	Pianka's index (*O*)				Levin's index (*B*)
	Lions	Spotted hyaenas	Leopards	Other*	
Lions	-	0.65	0.43	0.21	5.96
Spotted hyaenas		-	0.91	0.42	5.51
Leopards			-	0.63	5.13
Other				-	3.76

*Other carnivores include serval, caracal, black-backed jackal, side-striped jackal and civet

Table 5.2: Dietary overlap (Pianka's index; *O*) for lions, spotted hyaenas and leopards according to prey size class.

Species	Lions	Spotted hyaenas	Leopards	Other*
Lions	-	0.76	0.56	0.27
Spotted hyaenas		-	0.96	0.62
Leopards			-	0.76
Other				-

*Other carnivores include serval, caracal, black-backed jackal, side-striped jackal and civet

DISCUSSION

Dietary overlap among carnivores is commonly used to assess the potential for competition (Donadio & Buskirk, 2006). Both interference and exploitative competition can occur among sympatric carnivores when the same prey species are preferentially selected in greater proportions than available in the environment (Durant, 2000; Caro & Stoner, 2003; Donadio & Buskirk, 2006). In these circumstances, competition theory predicts that larger carnivores will have a competitive advantage over smaller carnivores (Hayward & Kerley, 2008), which may include intra-guild predation or killing (du Preez *et al.*, 2017). Prey size distributions and densities within an ecosystem can either enhance or reduce competition, and in areas where suitably sized prey are not limited, selective predation is thought to facilitate large carnivore co-existence (Karanth & Sunquist, 1995a; du Preez *et al.*, 2017). My results support this contention because, large carnivore guild members in Selati preferentially selected for varying combinations of small, medium and large prey.

Contrary to my predictions, lions and spotted hyaenas did not exhibit the highest dietary overlap. Instead, spotted hyaenas and leopards showed almost complete overlap (91%). Dietary overlap between lions and spotted hyaenas was still considered biologically significant and conformed with the values reported in other studies (overlap > 65%; Hayward, 2006). This high degree of overlap among the large carnivores of Selati suggests that there is strong potential for exploitation competition (Périquet *et al.*, 2015a), particularly between the spotted hyaenas and leopards. Exploitative competition can be inferred where dominant carnivores kleptoparasitise from subordinates, but this phenomenon cannot easily be accounted for in carnivore communities, especially in areas such as Selati where continuous observations are logistically challenging (Vanak & Gompper, 2009). It is therefore impossible to determine to what extent this activity contributes to the dietary composition of carnivores in Selati. In Phinda Private Game Reserve (Phinda), which is also a small enclosed South African reserve like

Selati, leopards suffered higher rates of kleptoparasitism from spotted hyaenas compared to lions despite both dominant carnivores having relatively low densities (Balme, Hunter & Slotow, 2007). The much higher densities of spotted hyaenas (12.52 individuals/100 km^2) compared to lions (1.53 individuals/100 km^2) on Selati, coupled with the potential of increased kleptoparasitism could partially explain the almost complete dietary overlap of spotted hyaenas and leopards.

Additionally, when the dietary niche breadth of sympatric competitors are alike, as I found to be the case among large carnivores in Selati, the species that can survive at the lowest resource density has the potential to outcompete others (Odden, Wegge & Fredriksen, 2010). Within the large carnivore guild, sympatric carnivores are known to scavenge from one another (i.e. consume food left by another species with no confrontation) or from animals that have died from natural causes (Périquet *et al.*, 2015a). Spotted hyaenas are probably the species that gain the most from this feeding strategy as they can access nourishment from skin and bones, whereas lions and leopards are more dependent on meat remains at a carcass (Périquet *et al.*, 2015a).

Consistent with my second prediction, leopards consumed the greatest number of food items (n=18) in Selati. Additionally, I identified leopards as the only large carnivore to preferentially kill small prey, which could be attributed to their inability to continually defend their kills from kleptoparasitism and not necessarily their hunting abilities (du Preez *et al.*, 2017). Smaller prey items may be more energetically profitable for leopards as they can be consumed instantly or cached in vegetation (Henschel, Abernethy & White, 2005; du Preez *et al.*, 2017). du Preez *et al.* (2017) predicted that under minimal competitive pressure (e.g. interference and exploitative) leopards may select for larger prey. Studies conducted on leopards and tigers in India, revealed how recovering tiger populations forced leopards to switch to smaller, suboptimal prey such as rodents (Harihar, Pandav & Goyal, 2011; Mondal *et al.*, 2011).

Increased exploitative and interfere competition among the two carnivores was also linked to leopard population decline (Harihar, Pandav & Goyal, 2011; Mondal *et al.*, 2011). The leopard's ability to hunt a wide variety of prey may reduce their risk of encounters with spotted hyaenas and lions (Mondal *et al.*, 2011; Harihar & Pandav, 2012; du Preez *et al.*, 2017). Therefore, the dietary composition of leopards, along with evidence of their population declining (see Chapter 3) in Selati, could potentially be attributed to intra-guild competition with the lions and spotted hyaenas.

In Selati, I found spotted hyaenas to be generalist foragers that fed on a wide range of prey species (n = 16), which is consistent with prior studies (see Kruuk, 1972; Mills, 1990). Spotted hyaenas did not consistently consume prey relative to their availability, which has also been reported in other studies researching their feeding ecology (e.g. Honer *et al.*, 2002; Wentworth, Tambling & Kerley, 2011; Périquet *et al.*, 2015b). All studies, including my research, showed site-specific dietary composition for spotted hyaenas (Périquet *et al.*, 2015b). Lions, on the other hand, always seem to favour the same three or four species in savanna ecosystems (i.e. wildebeest, warthog and kudu as prey; Mills, 1991; Power, 2002), which was no different for lions in Selati. Honer *et al.* (2002) suggest that spotted hyaenas have preferences for prey species that are relatively easier to hunt, such as juveniles because they are smaller. In Selati, I found that spotted hyaenas predominantly consumed medium prey, which would be easier to kill than large prey (Périquet *et al.*, 2015a). I based spotted hyaena dietary composition entirely on scat analyses, which meant I could not discern what proportion of their diet was hunted, scavenged or comprised juveniles. Therefore, the dietary overlap among lions and spotted hyaenas may be lower if these two species are preying on different age classes (Hayward, 2006; Périquet *et al.*, 2015a).

Lions are much larger than spotted hyaenas and, within small, enclosed reserves, where lions are not actively managed and reach high densities, it is possible for lions to outcompete spotted hyaenas causing localised declines (du Preez *et al.*, 2017). Lions on Selati are actively managed (e.g. through translocations and contraception) and have an adult population density (1.53 individuals/100 km^2) that falls on the low end of the range for this species in southern Africa (Miller & Funston, 2014). Besides a few permitted hunts (see Supplementary material 2) spotted hyaenas have not been actively managed and have reached an estimated density of 12.52 individuals/100 km^2, which is amongst the highest recorded for South Africa. Despite spotted hyaenas outnumbering lions nearly seven fold in Selati, interspecific killing of three spotted hyaenas by lions was recorded between 2016 and 2017 (see Supplementary material 2). Spotted hyaenas did not kill any adult lions or cubs. Périquet *et al.* (2015a) state that the presence of an adult male lion at a kill always allows lions to outcompete spotted hyaenas. Competition for food and the presence of two wide-ranging male lions in Selati could explain the spotted hyaena killings. When prey abundance is high, exploitative competition is said to be limited and spotted hyaenas are able to reach higher densities, forming larger foraging groups over smaller home ranges (as seen in Selati), which could have negative impacts on lions (Périquet *et al.*, 2015a). In Selati, however, the higher spotted hyaena densities seem to be affecting the declining leopard population more than the lion population. My study reiterates the complexity of carnivore guild interactions and emphasises the need for multi-carnivore research.

I found dietary overlap between lions and leopards to be limited which supports the findings of Balme *et al.* (2017) where lions predominantly targeted large prey and leopards small to medium prey. Though Balme *et al.* (2017) found lions to account for 20% of leopard mortalities in Phinda, this form of competition was compensatory as the leopard population was regarded as stable. No evidence for interspecific killing or predation on leopards from lions or between spotted hyaenas and leopards was found on Selati, but should not be ruled out as a possible cause for the declining leopard population. My results show that lions are potentially the most dominant carnivore on Selati and that the availability of suitably sized prey could be enabling resource partitioning between the large carnivores, facilitating their co-existence (Balme *et al.*, 2017).

Interspecific competition and predation by large-sized carnivores has emerged as an important limiting factor for small- and medium-sized carnivores (Hayward et al. 2006; Caro & Stoner 2003). My results support this statement and my final prediction, as the diets of spotted hyaenas, leopards and other carnivores (small- and medium-sized) all contained the presence of mongooses (FO > 6%). Additionally, side-striped jackal hair was found in the scats of leopards which, along with other small carnivores, is considered a common occurrence (Kruuk, 1972; Schaller, 1972). The presence of large prey species in the diets of small- and medium-sized carnivores is most likely due to the consumption of carrion (Pereira *et al.*, 2014). These results show the potential for risk-benefit trade-offs occurring among medium-sized carnivores in Selati that may be attributed to their ability to co-exist with dominant carnivores (Vanak & Gompper, 2009).

Throughout southern Africa, as identified in Selati, carnivores show varying patterns of prey selection (Linnell & Strand, 2000). Changes in the composition of carnivore communities mediated by aggressive interactions may have knock-on effects on prey species of conservation or management interest (Henke & Bryant, 1999). For instance, in Selati, lions and leopards preferentially selected for tsessebe and mountain reedbuck, despite their low population abundances. Throughout their range over the past two decades, mountain reedbuck have suffered extreme population declines resulting in this species being listed as Endangered (Taylor *et al.*, 2016). Reasons as to why mountain reedbuck populations have drastically declined are unknown, but it is suspected that higher predation rates from increased abundances of large- and medium-sized carnivores in areas that lack ecosystem based management are a major factor (Taylor *et al.*, 2016). The low abundance of mountain reedbuck in Selati could therefore be attributed to predation, not because of increased densities of leopard (the only carnivores recorded to prey on mountain reedbuck), but because interference and exploitative competition have forced leopards to be opportunistic and prey on a wider range of species.

Tsessebe are listed as vulnerable in southern Africa, and although the population seems stable, threats such as poaching surrounding protected areas and increased drought frequency, brought about by climate change are intensifying (Nel *et al.*, 2016). Besides predation, unnaturally high competition from other grazers due to high stocking rates in enclosed reserves, have also been listed as a threat to this species (Nel *et al.*, 2016). This could be a reason for this species low abundance in Selati as densities of other grazers (e.g. blue wildebeest (260 animals/100km^2), impala (1270 animals/100 km^2) and plains zebras (199 animals/100 km^2)) are relatively high, especially impala. Wildlife managers across southern Africa are encouraged to continue establishing and monitoring threatened prey species throughout their natural range, because in protected areas where prey populations are forced to be resident, predation can easily eliminate prey species with low abundances (Power, 2002).

In Selati, impala was the most frequently consumed prey by spotted hyaenas and leopards and third after kudu and waterbuck for lions. In accordance with their abundance (~50% of entire prey population), however, impala were under-selected. My results are similar to those found in Phinda (Hunter, 1998) and Madjuma Lion Reserve, Limpopo Province where lions under-selected impala despite their availability (Power, 2002). This occurrence has been attributed to the extreme alertness and superior vigilance behaviour of impala (Mooring & Dennis, 1999). Monitoring prey species can be important for ecosystem health, especially for a species such as impala, which are destructive, highly selective mixed feeders that have the ability to alter the composition of vegetation to the detriment of other ungulates, such as tsessebe (Wentzel, Bothma & van Rooyen, 1991; Nel *et al.*, 2016). Although Selati personnel removed ~1600 impala between 2016 and 2017 (see Supplementary material 2), an aerial count survey conducted in 2018 estimated the population at ~3600 individuals (Appendix 3.6). Therefore, for ecological reasons, Selati management should continue monitoring and controlling the impala population, as the large carnivore guild seems to be unable to do so.

My study demonstrates the importance of monitoring multiple prey and carnivore species within an enclosed system. The full implications of carnivore intra-guild competition, particularly aggressive interactions in small, enclosed reserves throughout southern Africa are largely unknown. Additionally, interactions among carnivores and their interactions with prey species, are flexible and subject to variation depending on several site-specific circumstances (e.g. composition of prey and carnivore communities or presence of fences), which is why community based research is encouraged across all protected reserves in southern Africa.

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Chapter 6

SYNTHESIS

Matumi's three cubs

Over the past century, carnivore intra-guild competition has been recognised by wildlife scientists as a vital component of animal community structures (St-Pierre, Ouellet & Crête, 2006) and ecosystem functioning (Vanak *et al.*, 2013). Additionally, conservational efforts have shown how large, apex carnivores can be particularly important to these processes because of their role in driving trophic cascades (Berger, Gese & Berger, 2008; Terborgh & Estes, 2010) and their top-down competitive effects on sympatric carnivores (Linnell & Strand, 2000; Ritchie & Johnson, 2009). As a result of these strengthening conservational efforts, people across the globe have changed their perception of carnivores purely being vermin (Sillero-Zubiri & Laurenson, 2001). This change in attitude, however, may not be taking place among local communities living near free-ranging wild carnivores who suffer from human-carnivore conflict (i.e. actual or perceived threat posed to livestock and humans; Sillero-Zubiri & Laurenson, 2001). Throughout Africa, carnivores frequently spill over the edges of unfenced protected areas and come into conflict with humans which sometimes results in a hostile relationship between local communities and conservation agencies (Sillero-Zubiri & Laurenson, 2001). In these areas, community based conservation (e.g. educate and involve local communities) is essential to ensure the co-existence between humans and carnivores (Sillero-Zubiri & Laurenson, 2001).

In South Africa, all protected areas containing dangerous carnivores (e.g. lions (*Panthera leo*)) have to be bound by electrified predator-proof fencing, which reduces human-carnivore conflict (Hayward *et al.*, 2009). Often these protected areas are small (< 400 km^2) and unable to naturally conserve viable populations of large carnivores (Hayward, O'Brien & Kerley, 2007), which due to their size and trophic positions, require extensive home ranges and large prey populations (Sillero-Zubiri & Laurenson, 2001; Woodroffe & Frank, 2005). As I found in my study, predator-proof fences do not always provide effective barriers to carnivores (Woodroffe, Hedges & Durant, 2014), as both lions and leopards (*Panthera pardus*) had home ranges encompassing game farms outside of Selati (see Chapter 4). This is usually due to the challenges of appropriate fence design, location of required fences (e.g. mountainous regions or across rivers), construction and maintenance (Woodroffe *et al.*, 2014). Species such warthog (*Phacochoerus africanus*) and porcupine (*Hystrix africeaustralis*), which are skilled at digging under fences can cause frequent and widespread damage making maintenance costly (Du Plessis *et al.*, 2018). The nationwide decline of leopards in South Africa has partly been attributed to anthropogenic mortality, which includes the illegal killing of leopards for their skin or retaliatory killing by farmers (Mann *et al.*, 2018). Other carnivores such as black-backed jackals (*Canis mesomelas*) and caracals (*Caracal caracal*) also suffer extensive losses from retaliatory killing by South African farmers (Bergman *et al.*, 2013), primarily due to financial losses inflicted by predation on livestock (Du Plessis *et al.*, 2018). Even though fences may reduce human-carnivore conflict in South Africa, wildlife managers still have to deal with the difficulty of deciding what action to take when carnivores leave the confines of protected areas (Mills, 1991). Conservation strategies aimed at changing the perspectives and attitudes of farmers and illegal hunters towards carnivores may be just as important for the protection of carnivores in fenced areas as it is in unfenced areas.

A balance between the beneficial and harmful effects of fencing wildlife populations is needed to conserve biodiversity globally (Woodroffe *et al.*, 2014). For example, lions have been found to reach higher densities in fenced areas compared to unfenced areas (Miller *et al.*, 2013). This could have detrimental effects on sympatric carnivores and herbivores in small, enclosed reserves due to increased predation, which could be linked to changes in vegetation and other ecosystem components if management programs are not implemented (Woodroffe *et al.*, 2014). A major concern highlighted throughout my study was that the implications of small, enclosed reserves on the ecology of carnivores has not been adequately studied in South Africa (Hayward *et al.*, 2009). The over-abundance of large carnivores within small, enclosed reserves needs further attention as changes in their population dynamics may significantly disrupt ecosystem structure, function and services through interactions associated with increased intra-guild competition (Périquet, Fritz & Revilla, 2015). For example, in Selati, lions are the only actively managed large carnivore and are kept at a relatively low density, whereas spotted hyaenas (*Crocuta crocuta*) which are not managed were recorded to have one of the highest densities in South Africa. Despite spotted hyaenas outnumbering lions seven to one, I found that lions (due to their size and the presence of two dominant males) outcompeted spotted hyaenas in terms of intra-guild predation (see Chapter 5), space use (see Chapter 4) and potentially resource use (see Chapter 5). Leopards were recorded at a relatively low density and were the only large carnivore with a declining population in Selati. This could potentially be attributed to increased intra-guild competition as lions negatively influenced their occupancy dynamics and their diet almost completely overlapped (91%) with spotted hyaenas, which might be due to increased kleptoparasitism from the large spotted hyaena population. The large carnivore guild had varying influences on subordinate medium- and small-sized carnivores through risk-benefit trade-offs (Schuette *et al.*, 2013; Vanak *et al.*, 2013) as I found evidence for predation and resource facilitation (i.e. carrion). This shows that assemblages of dominant carnivores cannot simply be assumed to have homogenous effects on carnivore communities in Africa and that maintaining intact guilds of carnivores is important for ecosystem functioning (Estes *et al.*, 2011; Vanak *et al.*, 2013). My study provides valuable insight into the complexity of carnivore-carnivore interactions in a small, enclosed reserve and how there are gaps in our understanding of intra-guild competition (e.g. extent of kleptoparasitism and interspecific killing, segregation in selection of prey species age classes and spatio-temporal segregation). The real challenge for future research is to investigate how different carnivores co-exist in the presence of these complex interactions, as the co-existence of different carnivore guild members across varying landscapes is integral for biodiversity and ecosystem dynamics (Linnell & Strand, 2000; Périquet *et al.*, 2015).

At the beginning of my research there was only one male cheetah (*Acinonyx jubatus*) on the reserve, so this species was excluded from my study for statistical reasons. In April 2018, once the majority of my fieldwork was completed, an additional female cheetah was released onto Selati and by August 2018, she had seven cubs. Spotted hyaenas killed all seven cubs several weeks later. This was not unexpected as lions and spotted hyaenas are the two main competitors of cheetahs and severely affect cheetah offspring survival through predation (Durant, 2000). The adult lion population in Selati will soon double with the maturation of five cubs, three of which are males. Along with the already high spotted hyaena population, the increasing lion population (especially of competitively dominant males) could have detrimental implications on subordinate carnivores (Périquet *et al.*, 2015). Increasing competition pressure between lions and spotted hyaenas has been attributed to the decline and local extinction of subordinate carnivores, such as African wild dogs (*Lycaon pictus*) in small, enclosed protected areas (Creel & Creel, 1996; Durant, 1998). The only way to minimise these potential effects and maintain viable populations of multiple-carnivores within Selati and other small protected areas would be to intensively manage all carnivore populations (Packer *et al.*, 2013; Périquet *et al.*, 2015). Managing prey species is also imperative as the availability of appropriately sized prey can affect the intraspecific variation and density of carnivores (Carbone & Gittleman, 2002; Woodroffe & Ginsberg, 2005). Management interventions for over-abundant carnivores can include translocations, fertility control and regulated trophy hunting (Lindsey, Roulet & Romañach, 2007; Hayward *et al.*, 2009). Many privately owned reserves in South Africa depend on the economic benefits of trophy hunting or ecotourism (Licht, Slotow & Millspaugh, 2008). Income from tightly managed trophy hunting can provide incentives for management, conservation and reintroductions of both carnivore and prey species (Lindsey *et al.*, 2007). In parts of South Africa, the recovery of bontebok (*Damaliscus dorcas*), black wildebeest (*Connochaetes gnu*) and Cape mountain zebra (*Equus zebra*) were facilitated by trophy hunting on private reserves (Lindsey *et al.*, 2007).

Worldwide, range fragmentation due to the ever-expanding human population has led to the decline and local extinction of many large carnivore populations (Bruinderink *et al.*, 2003; Ripple *et al.*, 2014). This is because numerous carnivore populations are genetically isolated (Slotow & Hunter, 2005) and inbreeding can cause measurable reductions in reproductive rates and disease resistance (Sodhi, Brook & Bradshaw, 2009). Metapopulation management strategies, which involve the linking of isolated populations of carnivores (or ungulates) through continuous translocations, have become a major focus of conservation across landscapes such as South Africa that are highly modified by human activity (Wegmann *et al.*, 2014). These strategies have been successful in protecting endangered carnivores such as African wild dogs and cheetahs (van Dyk & Slotow, 2003; Lindsey, du Toit & Mills, 2005; Dolrenry *et al.*, 2014). These strategies could be implemented in the conservation of multiple species and could even help protect carnivore and ungulate populations in heavily disturbed areas (Bothma, 2002; Dolrenry *et al.*, 2014).

Human-mediated climate change also represents a potentially devastating sleeping giant in terms of future biodiversity loss (Sodhi *et al.*, 2009). According to future biodiversity scenarios, by 2050, Africa is predicted to be among the continents with the largest habitat and biodiversity losses (Visconti *et al.*, 2011). In this scenario, protected areas such as the ones found in South Africa are expected to play a crucial role in conserving biodiversity (Wegmann *et al.*, 2014). Protecting large carnivore populations is essential to ecosystem health, but this cannot be guaranteed without fully understanding the complex interactions of multiple sympatric carnivores (Périquet *et al.*, 2015; Gompper *et al.*, 2016). As my study highlights, the outcomes of intra-guild competition, such as cascading ecological impacts are likely to vary with resource availability (e.g. structure and abundance of prey), habitat structure and carnivore community composition. Therefore, to better understand the effects of intra-guild competition and carnivore co-existence, site-specific ecosystem-based research is needed in small, enclosed reserves across southern Africa.

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APPENDICES

Appendix 2.1: List of mammalian species found in Selati Game Reserve. Each species average home range size (km^2) across southern Africa is given. Based on average adult weight prey species (small prey (<30 kg), medium prey (30-90 kg), large prey (90-1000 kg) and megaherbivore (>1000 kg)) and carnivore species (small carnivore (<10 kg), medium carnivore (10-20 kg) and large carnivore (>20 kg)) were divided into size classes.

Species	Home range size (km^2)	Carnivore size class	Prey size class
Order Primates			
Chacma baboon (*Papio ursinus*)	27		small
Vervet monkey (*Chlorocebus pygerythrus*)	1.76		small
Order Carnivora			
African civet (*Civettictis civetta*)	4-11	medium	
African wildcat (*Felis silvestris lybica*)	6-10	small	
Banded mongoose (*Mungos mungo*)	2	small	
Black-backed jackal (*Canis mesomelas*)	2-18	medium	
Cape clawless otter (*Aonyx capensis*)	2-5	medium	
Caracal (*Caracal caracal*)	5-48	medium	
Cheetah (*Acinonyx jubatus*)	102-438	large	
Dwarf mongoose (*Helogale parvula*)	0.45	small	
Honey badger (*Mellivora capensis*)	120 - 540	medium	
Large-spotted genet (*Genetta tigrina*)	3 - 6	small	
Leopard (*Panthera pardus*)	31-75*	large	
Lion (*Panthera leo*)	105-315*	large	
Marsh mongoose (*Atilax paludinosus*)	2	small	
Meller’s mongoose (*Rhynchogale melleri*)			
Serval (*Leptailurus serval*)	5-60	small	
Side-striped jackal (*Canis adustus*)	2-13	medium	

Slender mongoose (*Galerella sanguinea*)	0.21-0.60	small	
Small-spotted genet (*Genetta genetta*)	0.34-0.75	small	
Spotted hyaena (*Crocuta crocuta*)	29-36*	large	
Order Tubulidentata			
Aardvark (*Orycteropus afer*)	10-30		medium
Order Hyracoidea			
Rock hyrax (*Procavia capensis*)	-		small
Order Lagomorpha			
Scrub hare (*Lepus saxatilis*)	0.04-0.20		small
Order Rodentia			
Bushveld gerbil (*Tatera leucogaster*)	-		small
Cape porcupine (*Hystrix africaeaustralis*)	-		small
Common mole rat (*Cryptomys hottentotus*)	-		small
Fat mouse (*Steatomys pratensis*)	-		small
Highveld gerbil (*Tatera brantsii*)	-		small
Mountain ground squirrel (*Xerus princeps*)	-		small
Natal multimammate mouse (*Mastomys natalensis*)	-		small
Pouched mouse (*Saccostomus campestris*)	-		small
Tree squirrel (*Paraxerus cepapi*)	-		small
Order Artiodactyla			
Blue wildebeest (*Connochaetes taurinus*)			large
Bushbuck (*Tragelaphus scriptus*)	0.13-0.33		medium
Bushpig (*Potamochoerus larvatus*)	3-10		large
Common duiker (*Sylvicapra grimmia*)	0.03-0.17		small
Eland (*Tragelaphus oryx*)	50-200		large
Giraffe (*Giraffa camelopardus*)	7-11		megaherbivore

Impala (*Aepyceros melampus*)	0.80-5	medium
Klipspringer (*Oreotragus oreotragus*)	-	small
Kudu (*Tragelaphus strepsiceros*)	8-24	large
Mountain reedbuck (*Redunca fulvorufula*)	0.08-0.76	medium
Nyala (*Tragelaphus angasii*)	0.15-3.60	large
Sable antelope (*Hippotragus niger*)	38-118	large
Sharpe's grysbok (*Raphicerus sharpei*)	-	small
Southern reedbuck (*Redunca arundinum*)	0.74-1.20	medium
Steenbok (*Rhaphicerus campestris*)	0.62	small
Tsessebe (*Damaliscus lunatus*)	2 - 3	large
Warthog (*Phacochoerus africanus*)	0.62-3.30	medium
Waterbuck (*Kobus ellipsiprymnus*)	2-6	large
Order Perissodactyla		
Black rhinoceros (*Diceros bicornis*)	20	megaherbivore
Plains zebra (*Equus quagga*)	80-600	large
White rhinoceros (*Ceratotherium simum*)	12-52	megaherbivore
Order Proboscoidea		
African elephant (*Loxodonta africana*)	52-240	megaherbivore

*Home rage estimates from collared individuals in Selati Game Reserve

Appendix 3.1a: An example of the format for a trap layout file used in the ‘secr’ package to estimate density. The table shows the numbered locations (trap ID) and UTM coordinates (X, Y) of each camera trap site. The numbers 1 – 10 represent occasions, where “1” indicates that the camera was active on that particular occasion. Co-variate information associated with each camera trap site: habitat type, elevation (m a.s.l.), slope, road, distance to closest water source (distance to water) and whether large predators, medium predators or small predators were captured; are given.

trap ID	**X**	**Y**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**habitat type**	**m a.s.l.**	**slope**	**road**	**distance to water**	**large predator**	**medium predator**	**small predator**
C1	261428	7350906	1	1	1	1	1	1	1	1	1	1	Granite	513	2.3	no	524.26	yes	yes	yes
C2	264310	7351403	1	1	1	1	1	1	1	1	1	1	Granite	521	5.2	yes	1200.24	yes	yes	no
C3	266489	7351022	1	1	1	1	1	1	1	1	1	1	Bushveld	548	7.1	yes	741.24	no	no	no
C4	269117	7352796	1	1	1	1	1	1	1	1	1	1	Granite	520	2.9	yes	1014.24	yes	yes	no
C5	271592	7352498	1	1	1	1	1	1	1	1	1	1	Mopane	482	3.6	yes	210.74	yes	yes	yes
C6	274797	7351192	1	1	1	1	1	1	1	1	1	1	Mopane	452	1.0	yes	1784.95	yes	yes	no
C7	260928	7349794	1	1	1	1	1	1	1	1	1	1	Granite	530	0.0	no	742.21	yes	yes	no
C8	264189	7349145	1	1	1	1	1	1	1	1	1	1	Granite	473	5.9	yes	1025.56	yes	no	no
C9	266111	7349433	1	1	1	1	1	1	1	1	1	1	Granite	514	2.9	no	540.98	yes	yes	no
C10	269246	7349143	1	1	1	1	1	1	1	1	1	1	Granite	489	3.2	no	1085.27	no	yes	no
C11	270940	7348971	1	1	1	1	1	1	1	1	1	1	Mopane	453	4.0	no	1135.02	no	yes	no
C12	274249	7349743	1	1	1	1	1	1	1	1	1	1	Mopane	473	6.5	yes	1176.97	yes	yes	no
C13	277727	7348877	1	1	1	1	1	1	1	1	1	1	Mopane	455	3.2	no	1087.49	yes	no	no
C14	263928	7346383	1	1	1	1	1	1	1	1	1	1	Granite	494	0.0	no	702.7	no	yes	no
C15	267239	7345216	1	1	1	1	1	1	1	1	1	1	Mopane	472	3.0	no	2528.24	no	no	no
C16	269716	7346402	1	1	1	1	1	1	1	1	1	1	Mopane	504	3.2	yes	1762.65	yes	yes	yes
C17	272323	7346193	1	1	1	1	1	1	1	1	1	1	Mopane	497	2.9	yes	925.2	yes	yes	yes
C18	275190	7346228	1	1	1	1	1	1	1	1	1	1	Mopane	508	5.2	yes	938.94	yes	no	no
C19	277549	7346562	1	1	1	1	1	1	1	1	1	1	Mopane	491	1.0	yes	615.74	yes	yes	yes
C20	279802	7346754	1	1	1	1	1	1	1	1	1	1	Mopane	486	5.1	no	2354.39	yes	no	no
C21	266705	7343765	1	1	1	1	1	1	1	1	1	1	Mopane	517	0.0	yes	1203.63	yes	no	no
C22	268657	7343694	1	1	1	1	1	1	1	1	1	1	Mopane	505	0.0	no	1317.41	yes	no	no

Appendix 3.1b: An example of the detection histories file format used in the 'secr' package to estimate density. The table shows the character value-code (survey ID) for each season along with the survey-specific detections of individual animals (animal ID) and the associated occasion and camera trap site (trap ID).

survey ID	animal ID	occasion	trap ID
S1	LPL18	52	C6
S1	LPL19	16	C8
S1	LPL20	44	C9
S1	LPL21	28	C18
S1	LPL21	41	C12
S1	LPL22	39	C13
S1	LPL22	54	C20
S1	LPL23	19	C16
S1	LPL24	11	C31
S1	LPL24	23	C22
S1	LPL25	52	C22
S1	LPL26	45	C24
S1	LPL27	28	C29
S2	LPL20	58	C8
S2	LPL22	21	C12
S2	LPL22	46	C18
S2	LPL24	59	C29
S2	LPL26	57	C24
S2	LPL27	16	C24
S2	LPL29	16	C19
S2	LPL32	18	C12
S2	LPL33	51	C10
S2	LPL42	31	C21
S2	LPL42	38	C16
S2	LPL43	48	C17
S2	LPL44	48	C17
S2	LPL45	14	C25
S2	LPL45	28	C29
S2	LPL45	32	C29
S2	LPL45	38	C24
S2	LPL45	48	C24
S3	LPL20	29	C8
S3	LPL20	31	C8
S3	LPL20	34	C8
S3	LPL29	4	C12
S3	LPL29	4	C14
S3	LPL29	13	C12
S3	LPL29	53	C6
S3	LPL30	4	C7
S3	LPL31	10	C7
S3	LPL32	8	C12
S3	LPL32	36	C29
S3	LPL32	46	C16
S3	LPL33	17	C14
S3	LPL33	25	C19
S3	LPL35	27	C19
S3	LPL35	55	C19

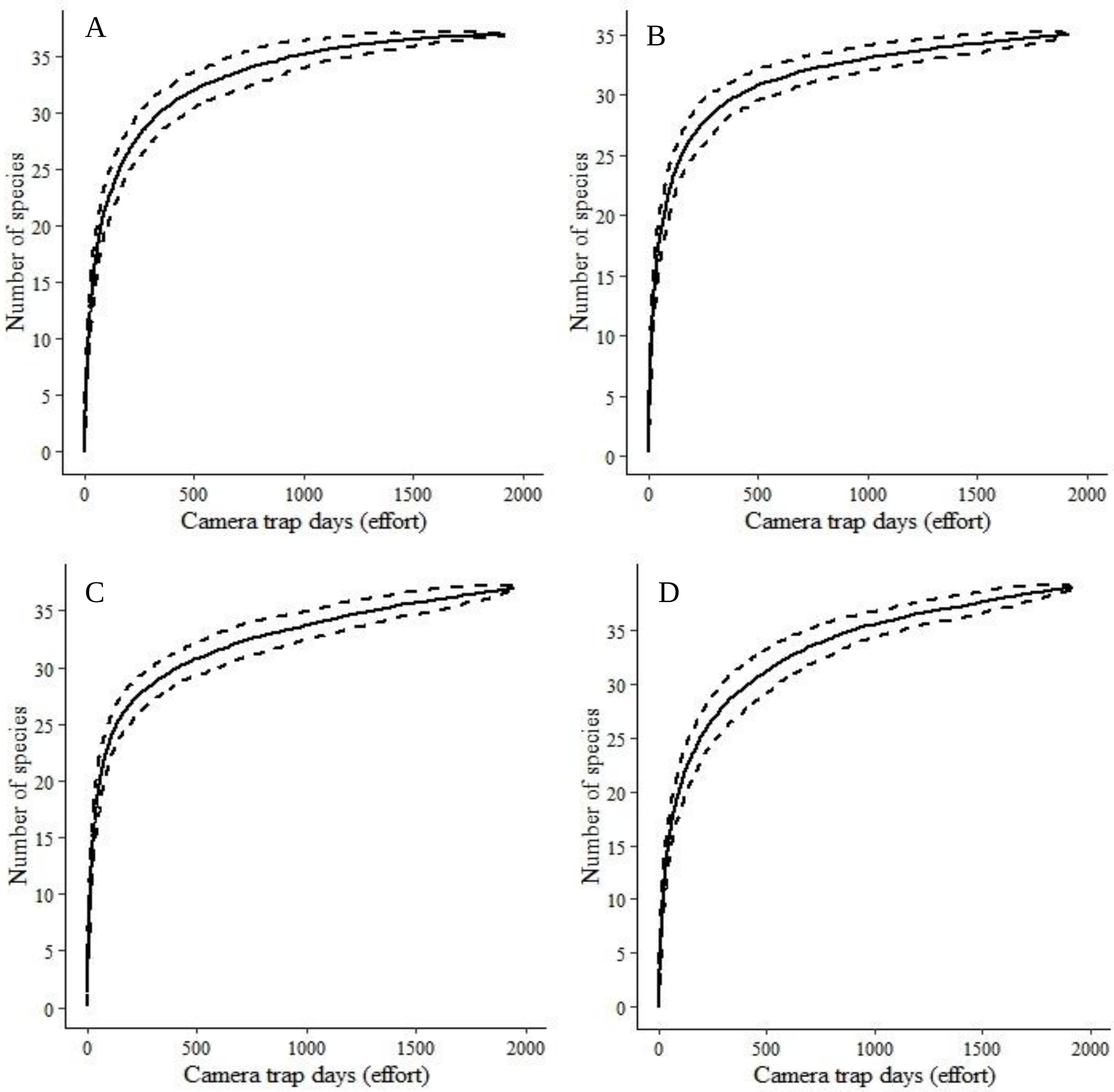
Appendix 3.2: Checklist of mammal species photographed during the four seasonal camera trap surveys (dry 2016, wet 2017, dry 2017 and wet 2018) in Selati Game Reserve, Limpopo Province, South Africa. Mammalian species are categorised into body size classes for both prey and carnivore species, reporting raw indices of abundances: number of events (n), species percentage of total events (Spp.%), relative abundance index (RAI) and naïve occupancy (n.o).

Species	**Dry 2016**				**Wet 2017**				**Dry 2017**				**Wet 2018**			
	n	**Spp.%**	**RAI**	**n.o**	**n**	**Spp.%**	**RAI**	**n.o**	**n**	**Spp.%**	**RAI**	**n.o**	**n**	**Spp.%**	**RAI**	**n.o**
Small prey (< 30 kg)																
Cape porcupine (*Hystrix africaeaustralis*)	17	0.87%	0.94	0.32	24	0.75%	1.40	0.23	37	1.15%	2.08	0.16	8	0.41%	0.44	0.22
Common duiker (*Sylvicapra grimmia*)	85	4.34%	4.71	0.81	146	4.57%	8.54	0.77	222	6.89%	12.47	0.77	144	7.43%	8.09	0.84
Chacma baboon (*Papio ursinus*)	39	1.99%	2.16	0.52	84	2.63%	4.92	0.52	57	1.77%	3.20	0.45	48	2.48%	2.67	0.74
Klipspringer (*Oreotragus oreotragus*)	-		-		3	0.09%	0.18	0.03	1	0.03%	0.06	0.03	-		-	
Scrub hare (*Lepus saxatilis*)	77	3.93%	4.27	0.42	16	0.50%	0.94	0.26	49	1.52%	2.75	0.42	99	5.11%	5.56	0.42
Sharpe’s grysbok (*Raphicerus sharpei*)	2	0.10%	0.11	0.03	7	0.22%	0.41	0.13	3	0.09%	0.17	0.06	3	0.15%	0.17	0.10
Steenbok (*Raphicerus campestris*)	55	2.81%	3.05	0.58	49	1.53%	2.87	0.55	35	1.09%	1.97	0.45	29	1.50%	1.63	0.48
Tree squirrel (*Paraxerus cepapi*)	-		-		-		-		-		-		1	0.05%	0.06	0.03
Vervet monkey (*Chlorocebus pygerythrus*)	4	0.20%	0.22	0.10	3	0.09%	0.18	0.10	2	0.06%	0.11	0.03	3	0.15%	0.17	0.09
Medium prey (30-90 kg)																
Aardvark (*Orycteropus afer*)	23	1.18%	1.27	0.32	30	0.94%	1.76	0.58	29	0.90%	1.63	0.32	21	1.08%	1.18	0.48
Bushbuck (*Tragelaphus scriptus*)	8	0.41%	0.44	0.06	1	0.03%	0.06	0.03	2	0.06%	0.11	0.03	1	0.05%	0.06	0.03
Impala (*Aepyceros melampus*)	411	21.00%	22.77	1	1198	37.48%	70.10	1	1126	34.94%	63.26	1	623	32.16%	35.00	1
Warthog (*Phacochoerus africanus*)	134	6.85%	7.42	0.90	282	8.82%	16.50	0.84	142	4.41%	7.98	0.68	112	5.78%	6.29	0.81

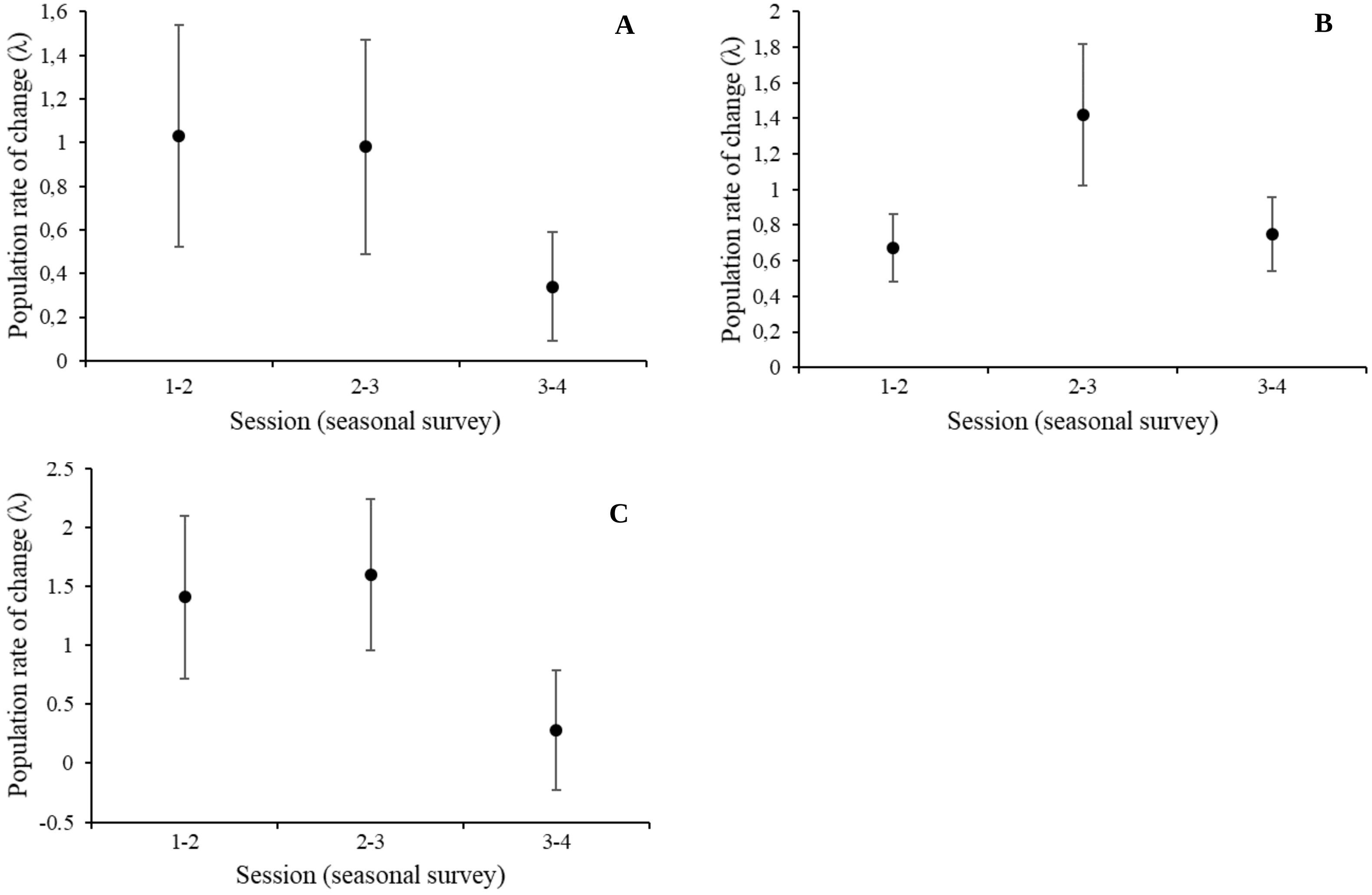
Large prey (90-1000 kg)																
Blue wildebeest (*Connochaetes taurinus*)	140	7.15%	7.76	0.87	149	4.66%	8.72	0.77	165	5.12%	9.27	0.81	108	5.58%	6.07	0.71
Bushpig (*Potamochoerus larvatus*)	3	0.15%	0.17	0.06	2	0.06%	0.12	0.06	1	0.03%	0.06	0.03	4	0.21%	0.22	0.06
Eland (*Tragelaphus oryx*)	7	0.36%	0.39	0.10	55	1.72%	3.22	0.23	20	0.62%	1.12	0.13	12	0.62%	0.67	0.26
Kudu (*Tragelaphus strepsiceros*)	140	7.15%	7.76	0.84	152	4.76%	8.89	0.87	249	7.73%	13.99	0.94	115	5.94%	6.46	0.81
Plains zebra (*Equus quagga*)	188	9.61%	10.42	0.90	268	8.39%	15.75	0.87	234	7.26%	13.15	0.74	145	7.49%	8.15	0.84
Nyala (*Tragelaphus angasii*)	4	0.20%	0.22	0.06	14	0.44%	0.82	0.10	12	0.37%	0.67	0.16	4	0.21%	0.22	0.13
Sable antelope (*Hippotragus niger*)	14	0.72%	0.78	0.13	9	0.28%	0.53	0.26	16	0.50%	0.90	0.16	10	0.52%	0.56	0.16
Waterbuck (*Kobus ellipsiprymnus*)	38	1.94%	2.11	0.35	86	2.69%	5.03	0.58	54	1.68%	3.03	0.42	39	2.01%	2.19	0.45
Megaherbivore (> 1000 kg)																
African elephant (*Loxodonta africana*)	49	2.50%	2.71	0.65	81	2.53%	4.75	0.71	87	2.70%	4.89	0.77	30	1.55%	1.69	0.52
Black rhinoceros (*Diceros bicornis*)	8	0.41%	0.44	0.23	12	0.38%	0.70	0.29	8	0.25%	0.45	0.13	7	0.36%	0.39	0.23
Giraffe (*Giraffa camelopardalis*)	167	8.53%	9.25	0.94	216	6.76%	12.64	0.87	198	6.14%	11.12	1	115	5.94%	6.46	0.77
White rhinoceros (*Ceratotherium simum*)	40	2.04%	2.22	0.35	61	1.91%	3.57	0.32	67	2.08%	3.76	0.45	65	3.36%	3.65	0.45
Small carnivore (< 10 kg)																
African wildcat (*Felis silvestris lybica*)	10	0.51%	0.55	0.19	17	0.53%	0.99	0.10	15	0.47%	0.85	0.16	5	0.26%	0.28	0.13
Dwarf mongoose (*Helogale parvula*)	-		-		-		-		-		-		1	0.05%	0.06	0.03
Meller's mongoose (*Rhynchogale melleri*)	-		-		-		-		1	0.03%	0.06	0.03	-		-	
Serval (*Leptailurus serval*)	2	0.10%	0.11	0.03	5	0.16%	0.29	0.26	1	0.03%	0.06	0.03	-		-	

Small-spotted genet (*Genetta genetta*)	5	0.26%	0.28	0.03	1	0.03%	0.06	0.03	13	0.40%	0.73	0.16	4	0.21%	0.22	0.10
Large-spotted genet (*Genetta tigrina*)	1	0.05%	0.06	0.03	-		-		1	0.03%	0.06	0.03	2	0.10%	0.11	0.06
Medium carnivore (10-20 kg)																
African civet (*Civettictis civetta*)	29	1.48%	1.61	0.35	34	1.06%	1.99	0.19	53	1.64%	2.98	0.35	16	0.83%	0.89	0.26
Black-backed jackal (*Canis mesomelas*)	32	1.64%	1.77	0.45	46	1.44%	2.69	0.26	86	2.67%	4.83	0.39	48	2.48%	2.67	0.29
Caracal (*Caracal caracal*)	4	0.20%	0.22	0.10	1	0.03%	0.06	0.03	2	0.06%	0.11	0.03	2	0.10%	0.11	0.29
Honey badger (*Mellivora capensis*)	10	0.51%	0.55	0.19	8	0.25%	0.47	0.19	7	0.22%	0.39	0.19	6	0.31%	0.33	0.03
Side-striped jackal (*Canis adustus*)	43	2.20%	2.38	0.32	9	0.28%	0.53	0.13	43	1.33%	2.42	0.32	9	0.46%	0.51	0.16
Large carnivore (> 20 kg)																
Cheetah (*Acinonyx jubatus*)	2	0.10%	0.11	0.03	-		-		-		-		-		-	
Leopard (*Panthera pardus*)	17	0.87%	0.94	0.42	36	1.13%	2.11	0.35	34	1.05%	1.91	0.35	11	0.57%	0.61	0.19
Lion (*Panthera leo*)	11	0.56%	0.61	0.19	12	0.38%	0.70	0.29	11	0.34%	0.62	0.19	6	0.31%	0.33	0.13
Spotted hyaena (*Crocuta crocuta*)	138	7.05%	7.65	0.74	79	2.47%	4.62	0.61	140	4.34%	7.87	0.61	81	4.18%	4.55	0.68

Appendix 3.3: Species accumulation curves (solid lines) and 95% confidence intervals (dashed lines) for the mammal community of Selati Game Reserve, Limpopo Province, South Africa detected by camera trapping across four seasonal surveys (dry 2016 (A), wet 2017 (B), dry 2017 (C) and wet 2018 (D)).



Appendix 3.4: Outcomes of the survey-specific rates of population change (λ) for leopard left-side data (A), spotted hyaena left-side data (B) and civet right-side data (C). Pradel lambda models were used to estimate the rate of population change (λ).



Appendix 3.5: The outcomes of the best-fit model for the seasonal ungulate transect survey analyses conducted in DISTANCE from data collected in Selati Game Reserve, Limpopo Province, South Africa. Parameters given are relative density (Density (D)), population size (Number of animals N)), standard error (SE), coefficient of variation (% CV) and the 95% confidence intervals (95% CI).

Survey	Best-fit model	Goodness-of-fit (χ^2)	Effective strip width	Parameter	D/N	SE	% CV	95% CI
Dry 2016	Negative exponential-simple polynomial	P = 0.15	75.50	Density	88.16	14.86	16.85	63.24 – 122.90
				Number of animals	8552	1441.30	16.85	6134 - 11922
Wet 2017	Negative exponential-simple polynomial	P = 0.12	83.55	Density	65.46	15.45	23.61	40.269 - 106.41
				Number of animals	6350	1499.10	23.61	3906 - 10322
Dry 2017	Negative exponential-cosine	P = 0.15	82.02	Density	51.58	18.66	36.18	20.720 - 128.38
				Number of animals	5003	1809.90	36.18	2010 - 12453
Wet 2018	Negative exponential-cosine	P = 0.17	100.45	Density	143.57	28.82	20.08	95.168 - 216.59
				Number of animals	13926	2796.30	20.08	9231 - 21009

Appendix 3.6: Total counts of mammalian species from aerial surveys conducted in Selati Game Reserve, Limpopo Province, South Africa from 2003 to 2018 (except for 2013). Values in brackets indicate the species-specific percentage contribution of the total number of species counted.

Species	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2014**	**2015**	**2016**	**2017**	**2018**
Small prey (<30 kg)															
Common duiker (*Sylvicapra grimmia*)	70	17	57	79	54	12	44	16	55	61	41	90	108 *(1.34)*	44 *(0.76)*	53 *(0.82)*
Klipspringer (*Oreotragus oreotragus*)	16	14	3	7	10	8	15	2	7	6	7	15	21 *(0.26)*	2 *(0.03)*	5 *(0.08)*
Sharpe’s grysbok (*Raphicerus sharpei*)	12	15	9	2	2	2	3	1	5	8	1	8	16 *(0.20)*	2 *(0.03)*	0
Steenbok (*Raphicerus campestris*)	21	26	14	25	21	7	14	9	26	28	18	48	30 *(0.37)*	23 *(0.40)*	30 *(0.46)*
Medium prey (30-90 kg)															
Bushbuck (*Tragelaphus scriptus*)	38	36	47	47	46	15	9	1	17	13	19	9	13 *(0.16)*	9 *(0.16)*	1 *(0.02)*
Common reedbuck (*Redunca arundinum*)	1	-	3	-	12	2	-	-	13	14	12	1	0	0	0
Impala (*Aepyceros melampus*)	339	2224	4013	3695	4660	4101	2922	2274	2804	3653	3778	3785	4007 *(49.80)*	2675 *(46.33)*	3605 *(55.44)*
Mountain reedbuck (*Redunca fulvorufula*)	7	23	5	5	8	19	10	7	18	18	13	17	6 *(0.07)*	2 *(0.03)*	9 *(0.14)*
Warthog (*Phacochoerus africanus*)	869	641	442	426	708	222	139	195	266	298	288	327	335 *(4.16)*	201 *(3.48)*	129 *(1.98)*
Large prey (90-1000 kg)															
Blue wildebeest (*Connochaetes taurinus*)	623	603	776	460	456	633	531	497	606	695	675	813	717 *(8.91)*	809 *(14.01)*	592 *(9.10)*
Bushpig (*Potamochoerus larvatus*)	14	-	5	6	-	-	9	-	13	3	6	4	8 *(0.10)*	8 *(0.14)*	1 *(0.02)*
Eland (*Tragelaphus oryx*)	188	207	222	226	219	213	131	92	84	94	58	41	70 *(0.87)*	52 *(0.90)*	64 *(0.98)*
Kudu (*Tragelaphus strepsiceros*)	866	957	1140	1020	1250	557	477	506	634	691	782	1041	1006 *(12.50)*	678 *(11.74)*	765 *(11.77)*

Nyala	91	71	119	119	106	68	33	40	41	39	51	61	61	53	22
(*Tragelaphus angasii*)													*(0.76)*	*(0.92)*	*(0.34)*
Plains zebra	388	354	469	334	355	383	301	422	435	481	484	671	648	483	485
(*Equus quagga*)													*(8.05)*	*(8.37)*	*(7.46)*
Red hartebeest	2	4	-	5	-	-	-	-	-	-	-	-	-	-	-
(*Alcelaphus buselaphus*)															
Sable antelope	149	62	16	16	14	8	9	2	4	9	6	14	31	49	39
(*Hippotragus niger*)													*(0.39)*	*(0.85)*	*(0.60)*
Tsessebe	11	13	-	-	10	-	-	-	7	6	-	3	4	5	4
(*Damaliscus lunatus*)													*(0.05)*	*(0.09)*	*(0.06)*
Waterbuck	492	283	461	583	487	352	353	350	375	427	355	301	399	200	184
(*Kobus ellipsiprymnus*)													*(4.96)*	*(3.46)*	*(2.82)*
Megaherbivore prey (>1000 kg)															
African elephant	72	87	84	75	67	71	61	75	84	87	115	112	102	114	115
(*Loxodonta africana*)													*(1.27)*	*(1.97)*	*(1.77)*
Black rhinoceros	-	-	-	-	-	-	-	-	13	7	11	9	13	10	14
(*Diceros bicornis*)													*(0.16)*	*(0.17)*	*(0.22)*
Known black rhino									13	10	13	14	14	15	15
Giraffe	207	197	255	251	265	226	315	244	268	321	329	303	354	253	312
(*Giraffa camelopardalis*)													*(4.40)*	*(4.38)*	*(4.80)*
White rhinoceros	45	53	51	49	60	58	66	58	69	65	74	101	78	67	54
(*Ceratotherium simum*)													*(0.97)*	*(1.16)*	*(0.83)*
Known white rhino											74	80	78	74	78
Medium carnivore (10-20 kg)															
Black-backed jackal	5	2	10	-	-	-	5	5	5	3	2	2	1	7	12
(*Canis mesomelas*)													*(0.01)*	*(0.12)*	*(0.18)*
Honey badger	-	-	2	-	-	-	-	-	-	-	2	1	3	1	0
(*Mellivora capensis*)													*(0.03)*	*(0.02)*	

Large carnivore (>20 kg)															
Cheetah (*Acinonyx jubatus*)	4	-	-	3	-	3	2	-	-	-	1	-	0	0	0
Leopard (*Panthera pardus*)	-	-	-	1	1	5	7	2	1	4	2	1	1 *(0.01)*	14 *(0.24)*	1 *(0.02)*
Lion (*Panthera leo*)	-	-	-	2	3	-	15	-	2	2	-	-	3 *(0.03)*	1 *(0.02)*	0
Spotted hyaena (*Crocuta crocuta*)	5	3	-	1	-	1	7	-	4	5	7	4	11 *(0.14)*	12 *(0.21)*	6 *(0.09)*
Total	**4535**	**5892**	**8203**	**7437**	**8814**	**6966**	**5478**	**4798**	**5869**	**7048**	**7224**	**7876**	**8013**	**5774**	**6595**

Appendix 4.1a: Example of a unique detection history file for spotted hyaenas captured during the first seasonal camera trap survey (dry 2016) at Selati Game Reserve. Numbers C1-C31 represent each camera trap site where numbers 1- 26 represent sampling occasions and "1" signifies that an animal was present and "0" signifies that an animal was absent.

Site	**Occasions**																									
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
C1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C2	0	1	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	1	0	0
C3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C4	0	1	0	0	0	1	1	0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1
C5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
C7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
C8	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
C14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
C17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C21	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
C22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0
C25	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
C29	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	1	0	0
C30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C31	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 4.1b: An example of a spotted hyaena unique detections subset of data after being collapsed into intervals of 10-day sampling occasions. Numbers C1-C31 represent each camera trap site where numbers 1.1- 4.6 represent the 10-day sampling occasions for each seasonal survey (dry2016:1, wet2017:2, dry2017:3, wet2018:4). “1” signifies that spotted hyaenas were present and “0” signifies that spotted hyaenas were absent during the 10-day interval.

Site	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4	3.5	3.6	4.1	4.2	4.3	4.4	4.5	4.6
C1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C2	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	1
C3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C4	1	1	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1
C5	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
C6	0	1	0	0	0	1	1	0	0	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1
C7	0	1	1	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
C8	1	0	0	1	1	1	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0
C9	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
C10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C12	0	0	1	0	1	1	0	1	1	0	0	0	1	0	1	1	1	1	0	1	0	1	0	1
C13	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C14	0	0	0	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0
C15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C16	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
C17	0	1	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0
C18	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0
C19	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	1	0	0
C20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
C21	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	0	0
C22	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
C23	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
C24	0	1	1	0	1	1	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	1	1	0
C25	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
C26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C27	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C28	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
C29	1	1	1	1	0	1	0	1	0	0	0	1	1	0	1	1	1	1	0	1	0	1	1	1
C30	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1
C31	0	1	0	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0

Appendix 4.1a: Example of a unique detection history file for spotted hyaenas captured during the first seasonal camera trap survey (dry 2016) at Selati Game Reserve. Numbers C1-C31 represent each camera trap site where numbers 1- 26 represent sampling occasions and “1” signifies that an animal was present and “0” signifies that an animal was absent.

Site	**Occasions**																									
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
C1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C2	0	1	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	1	0	0
C3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C4	0	1	0	0	0	1	1	0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1
C5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
C7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
C8	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
C14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
C17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C21	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
C22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0
C25	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
C29	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	1	0	0
C30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C31	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 4.1b: An example of a spotted hyaena unique detections subset of data after being collapsed into intervals of 10-day sampling occasions. Numbers C1-C31 represent each camera trap site where numbers 1.1- 4.6 represent the 10-day sampling occasions for each seasonal survey (dry2016:1, wet2017:2, dry2017:3, wet2018:4). “1” signifies that spotted hyaenas were present and “0” signifies that spotted hyaenas were absent during the 10-day interval.

Site	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4	3.5	3.6	4.1	4.2	4.3	4.4	4.5	4.6
C1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C2	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	1
C3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C4	1	1	1	0	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1
C5	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
C6	0	1	0	0	0	1	1	0	0	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1
C7	0	1	1	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
C8	1	0	0	1	1	1	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0
C9	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
C10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C12	0	0	1	0	1	1	0	1	1	0	0	0	1	0	1	1	1	1	0	1	0	1	0	1
C13	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C14	0	0	0	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0
C15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C16	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
C17	0	1	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0
C18	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0
C19	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	1	0	0
C20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
C21	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	0	0
C22	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
C23	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
C24	0	1	1	0	1	1	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	1	1	0
C25	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
C26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C27	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C28	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
C29	1	1	1	1	0	1	0	1	0	0	0	1	1	0	1	1	1	1	0	1	0	1	1	1
C30	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1
C31	0	1	0	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0

Appendix 4.2: Goodness-of-fit results from the chi-square probability (χ^2p) and over dispersion statistic (ĉ) for the global model for each suitable carnivore species, using different collapsing day periods. For each species, environmental and biologically important covariates were set for initial occupancy (ψ), colonisation (γ), extinction (ε) and detection (*p*). The sample period was limited to 54, 56 or 60 days depending on whether it was a multiple of the sampling occasion length and all 31 camera trap stations were included. The best fit model for each species is italicised in bold and was used to run the dynamic occupancy models.

Lion

Collapsing period	**No. of periods**	**χ^2p**	**ĉ**
5 day sampling period	12	0.03	3.1
6 day sampling period	***10***	***0.12***	***1.03***
7 day sampling occasions	8	0.76	0.78
8 day sampling occasions	7	0.78	0.77
9 day sampling occasions	6	0.03	2.96
10 day sampling occasions	6	0.77	0.81

Spotted hyaena

Collapsing period	**No. of periods**	**χ^2p**	**ĉ**
5 day sampling occasions	12	0.70	0.91
6 day sampling occasions	10	0	19.04
7 day sampling occasions	***8***	***0.20***	***1.06***
8 day sampling occasions	7	0.71	095
9 day sampling occasions	6	0.61	0.97
10 day sampling occasions	6	0.56	0.98

Leopard

Collapsing period	**No. of periods**	**χ^2 p**	**ĉ**
5 day sampling period	***12***	***0.22***	***1.22***
6 day sampling occasions	10	0.35	0.98
7 day sampling occasions	8	0.95	0.57
8 day sampling occasions	7	0.96	0.60
9 day sampling occasions	6	0.89	0.77
10 day sampling occasions	6	0.92	0.75

Side-striped jackal

Collapsing period	**No. of periods**	**χ^2 p**	**ĉ**
5 day sampling occasions	12	0.56	0.87
6 day sampling occasions	10	0.53	0.90
7 day sampling occasions	8	0.21	1.17
8 day sampling occasions	***7***	***0.35***	***1.06***
9 day sampling occasions	6	0.47	0.98
10 day sampling occasions	6	0.21	1.13

Black-backed jackal

Collapsing period	**No. of periods**	**χ^2 p**	**ĉ**
5 day sampling occasions	12	0	20.76
6 day sampling occasions	10	0.98	0.68
7 day sampling occasions	***8***	***0.41***	***1.03***
8 day sampling occasions	7	0.96	0.75
9 day sampling occasions	6	0.98	0.74
10 day sampling occasions	6	0.82	0.86

African civet: $p > 0.05$ indicated lack of fit

Collapsing period	**No. of periods**	**χ^2 p**	**$\hat{c}$**
5 day sampling occasions	12	0	6.8
6 day sampling occasions	10	0	2
7 day sampling occasions	8	0	7.4
8 day sampling occasions	7	0	2.7
9 day sampling occasions	6	0.001	1.59
10 day sampling occasions	6	0.001	1.62

Honey badger

Collapsing period	**No. of periods**	**χ^2 p**	**$\hat{c}$**
5 day sampling occasions	12	0.98	0.07
6 day sampling occasions	10	0.94	0.15
7 day sampling occasions	8	0.09	1.73
8 day sampling occasions	7	0.95	0.34
9 day sampling occasions	***6***	***0.13***	***1.31***
10 day sampling occasions	6	0.14	1.39

African wildcat

Collapsing period	**No. of periods**	**χ^2 p**	**$\hat{c}$**
5 day sampling occasions	12	0.69	0.69
6 day sampling occasions	10	0.79	0.69
7 day sampling occasions	***8***	***0.53***	***0.92***
8 day sampling occasions	7	0.89	0.55
9 day sampling occasions	6	0.76	0.79
10 day sampling occasions	6	0.78	0.78

Appendix 4.3: Below are the dynamic occupancy results for the best fit models for each carnivore species

Lion

Table 4.3.1: Top ranked models for lions in Selati Game Reserve, using quasi-likelihood information criterion for small sample size (QAICc), ΔQAICc difference in QAICc between each model and top ranking model, QAICcwt cum.wt, and K the number of parameters.

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**	**Cum.wt**	**LL**
ψ(elevation)γ(lprey) ε(lprey)*p*(road+slope)	10	252.56	0	0.30	0.30	-118.31
ψ(slope)γ(human) ε(human)*p*(road+slope)	10	253.52	1.03	0.18	0.48	-118.82
ψ(slope)γ(lprey)ε(lprey) *p*(road+slope)	10	254.03	1.57	0.14	0.62	-119.09
ψ(elevation)γ(mprey) ε(mprey)*p*(road+slope)	10	254.20	1.75	0.13	0.75	-119.19
ψ(elevation)γ(human)ε(human) *p*(road+slope)	10	254.36	1.92	0.12	0.86	-119.27
ψ(water+elevation)γ(lprey) ε(lprey)*p*(road+slope)	11	256.65	4.03	0.04	0.90	-117.88

Table 4.3.2: Model averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model (table x3) from the analysis examining factors related to the occupancy dynamics of lion in Selati Game Reserve. Bold estimates indicate that there was a strong association between the covariate and lion occupancy (CIs do not overlap zero). Italicised estimates indicate an intermediate strength of evidence (CIs contain zero but are not centred on zero).

Parameter covariate	**Initial occupancy probability (ψ)**	**Colonisation probability (γ)**	**Local extinction probability (ε)**	**Detection probability (*p*)**
Intercept	*32.16 (-2.48, 66.81)*	-27.2 (-450.58, 396.21)	*-30.1 (-111.71, 51.52)*	**-5.58 (-7.15, -4.01)**
elevation	*-0.06 (-0.13, 0.005)*			
lprey		-15.8 (-396.59, 364.98)	14.2 (-24.18, 52.51)	
road				**2.72 (1.19, 4.25)**
slope				**0.20 (0.02, 0.38)**

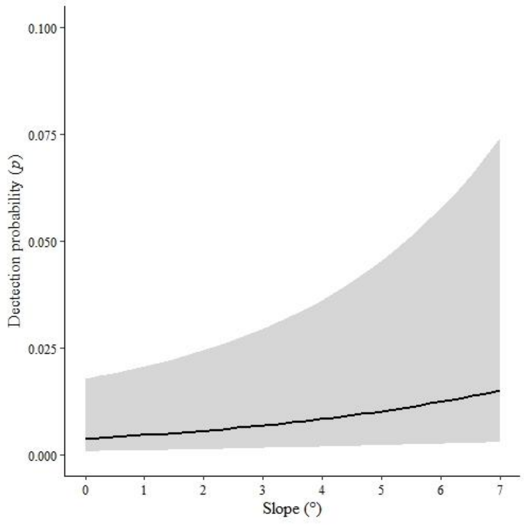


Figure 4.3.1: Probability of detecting lions in Selati Game Reserve related to slope (°). Grey ribbons depict upper and lower 95% confidence intervals.

Spotted hyaena

Table 4.3.3: Top ranked models for spotted hyaenas in Selati Game Reserve, using quasi-likelihood information criterion for small sample size (QAICc), ΔQAICc difference in QAICc between each model and top ranking model, QAICcwt cum.wt, and K the number of parameters.

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**	**Cum.wt**	**LL**
ψ(road)γ(mprey)ε(mprey) *p*(road+leopard+vegetation)	12	888.87	0	0.78	0.78	-423.77
ψ(road)γ(spred)ε(spred) *p*(road+leopard+vegetation)	12	892.33	3.46	0.14	0.92	-425.50

Table 4.3.4: Model averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model (table x3) from the analysis examining factors related to the occupancy dynamics of spotted hyaena in Selati Game Reserve. Bold estimates indicate that there was a strong association between the covariate and spotted hyaena occupancy (CIs do not overlap zero). Italicised estimates indicate an intermediate strength of evidence (CIs contain zero but are not centred on zero).

Parameter covariate	**Initial occupancy probability (ψ)**	**Colonisation probability (γ)**	**Local extinction probability (ε)**	**Detection probability (*p*)**
Intercept	*0.66 (-0.57, 1.88)*	*-0.69 (-2.10, 0.72)*	*-1.91 (-3.25, -0.57)*	**-3.83 (-5.35, -2.32)**
road	7.96 (-36.48, 52.39)			**1.15 (0.68, 1.61)**
mprey		0.32 (-0.60, 1.25)	*1.29 (-0.09, 2.66)*	
leopard				**0.25 (0.03, 0.48)**
Vegetation Granite				**2.96 (1.47, 4.45)**
Vegetation Mopaneveld				**2.01 (0.56, 3.47)**

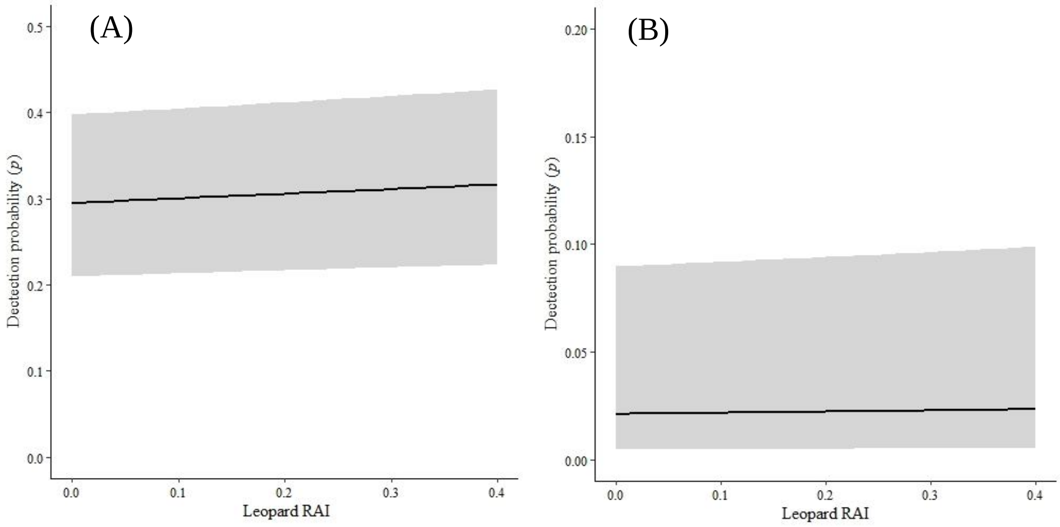


Figure 4.3.2: Probability of detecting spotted hyaenas in Selati Game Reserve related to (A) leopard relative abundance (RAI) in Mopaneveld vegetation and (B) leopard abundance in Granite vegetation. Grey ribbons depict upper and lower 95% confidence intervals.

Leopard

Table 4.3.5: Top ranked models for leopards in Selati Game Reserve, using quasi-likelihood information criterion for small sample size (QAICc), ΔQAICc difference in QAICc between each model and top ranking model, QAICcwt cum.wt, and K the number of parameters.

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**	**Cum.wt**	**LL**
ψ(slope)γ(hyaena) ε(hyaena)*p*(road+lion+hyaena+lprey)	12	457.88	0	0.28	0.28	-208.27
ψ(road)γ(hyaena) ε(hyaena)*p*(road+lion+hyaena+lprey)	12	458.08	0.20	0.25	0.53	-208.37
ψ(elevation)γ(rainfall)ε(rainfall) *p*(road+lion+hyaena+lprey)	12	459.07	1.19	0.15	0.69	-208.87
ψ(slope)γ(mprey) ε(mprey)*p*(road+lion+hyaena+lprey)	12	459.15	1.28	0.15	0.84	-208.91
ψ(road)γ(lion) ε(lion)*p*(road+lion+hyaena+lprey)	12	459.32	1.45	0.14	0.97	-208.99
ψ(vegetation)γ(hyaena) ε(hyaena)*p*(road+leopard)	13	462.43	4.55	0.03	1.00	-207.51

Table 4.3.6: Model averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model (table x3) from the analysis examining factors related to the occupancy dynamics of leopard in Selati Game Reserve. Bold estimates indicate that there was a strong association between the covariate and leopard occupancy (CIs do not overlap zero). Italicised estimates indicate an intermediate strength of evidence (CIs contain zero but are not centred on zero).

Parameter covariate	**Initial occupancy probability (ψ)**	**Colonisation probability (γ)**	**Local extinction probability (ε)**	**Detection probability (*p*)**
Intercept	*2.29 (-0.08, 4.66)*	*-33.8 (-150.14, 82.63)*	**-1.29 (-2.33, -0.25)**	**-3.65 (-4.33, -2.97)**
slope	-0.28(-0.80, 0.23)			
hyaena		*55.9 (-136.5, 248.40)*	**0.62 (0.37, 1.60)**	**0.31 (0.07, 0.55)**
road				**1.52 (0.79, 2.4)**
lion				-0.10 (-0.40, 0.20)
lprey				*0.21 (-0.02, 0.45)*

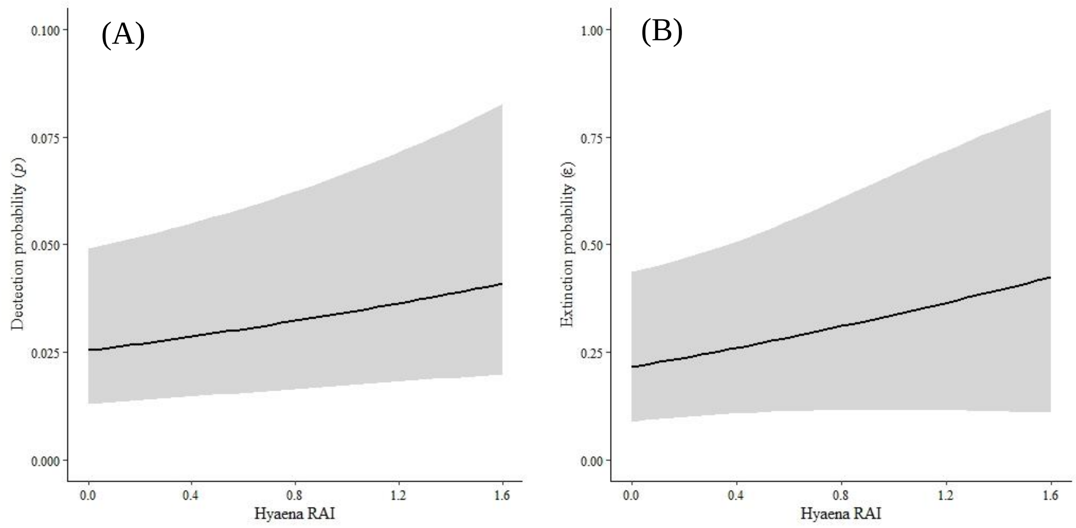


Figure 4.3.3: Probability of detecting leopards in Selati Game Reserve related to (A) spotted hyaena (hyaena) relative abundance (RAI) and the extinction probability of leopards related to (B) spotted hyaena (hyaena) relative abundance (RAI). Grey ribbons depict upper and lower 95% confidence intervals.

Side-striped jackal

Table 4.3.7: Top ranked models for side-striped jackals in Selati Game Reserve, using quasi-likelihood information criterion for small sample size (QAICc), ΔQAICc difference in QAICc between each model and top ranking model, QAICcwt cum.wt, and K the number of parameters.

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**	**Cum.wt**
ψ(water)γ(mprey)ε(mprey) *p*(water+rainfall+human+lion)	12	336.14	0.00	0.60	0.54
ψ(water)γ(spred)ε(spred) *p*(water+rainfall+human+lion)	12	337.66	1.53	0.28	0.89
ψ(water)γ(lion)ε(lion) *p*(water+rainfall+human+lion)	12	339.78	3.32	0.11	1.00

Table 4.3.8: Model averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model (table x3) from the analysis examining factors related to the occupancy dynamics of side-striped jackal in Selati Game Reserve. Bold estimates indicate that there was a strong association between the covariate and side-striped jackal occupancy (CIs do not overlap zero). Italicised estimates indicate an intermediate strength of evidence (CIs contain zero but are not centred on zero).

Parameter covariate	**Initial occupancy probability (ψ)**	**Colonisation probability (γ)**	**Local extinction probability (ε)**	**Detection probability (*p*)**
Intercept	*6.80 (-3.84, -1.31)*	**-2.58 (-3.84, -1.31)**	*-0.20 (-1.27, 0.87)*	**-3.25 (-4.26, -2.25)**
water	**-0.006 (-0.01, -0.001)**			**0.002 (0.001, 0.003)**
rainfall				**0.59 (0.25, 0.94)**
human				**0.70 (0.17, 1.23)**
lion				**0.48 (0.06, 0.89)**
mprey		-0.48 (-2.01, 1.06)	**2.14 (0.002, 4.27)**	

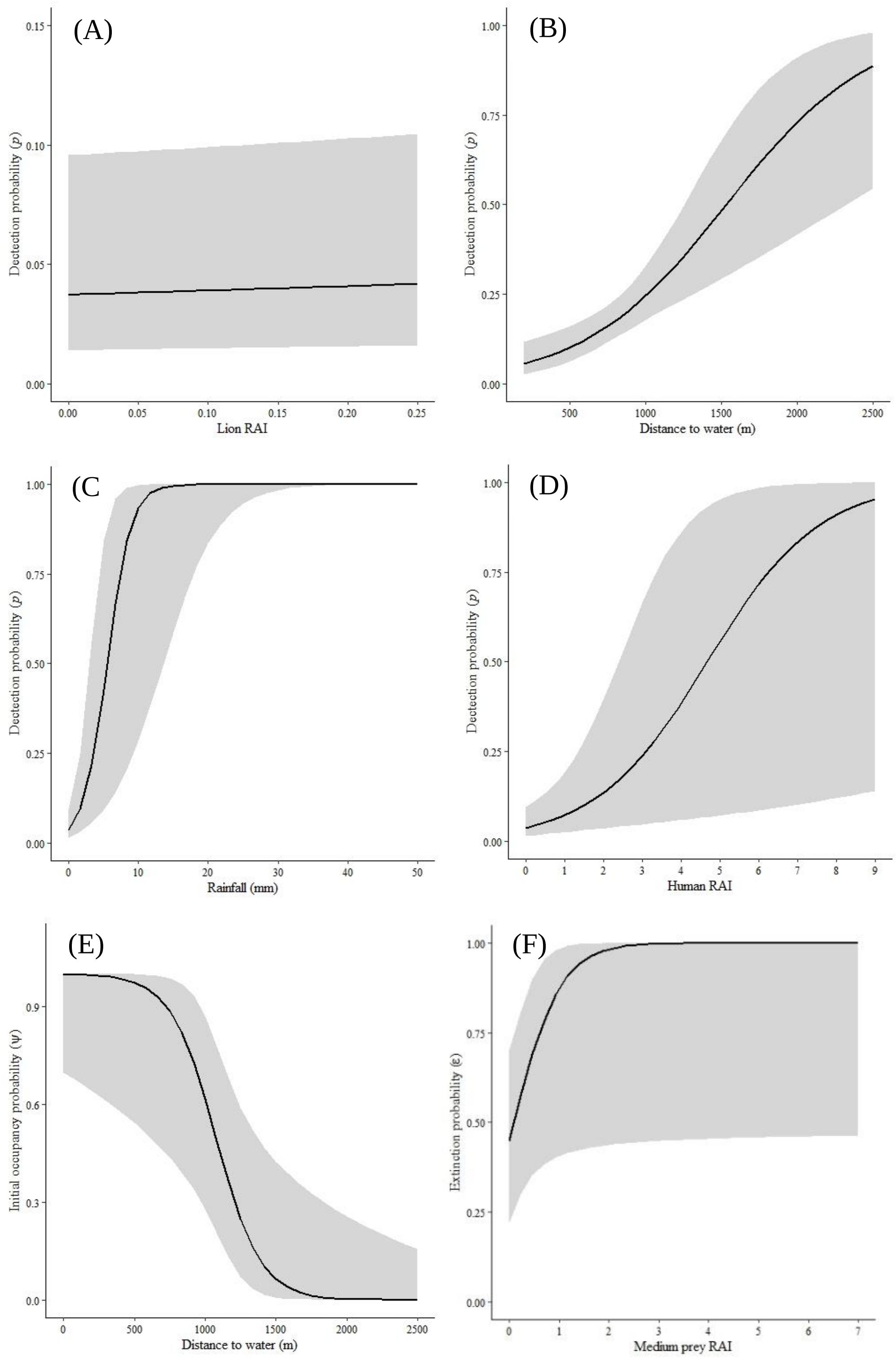


Figure 4.3.4: Probability of detecting side-striped jackals in Selati Game Reserve related to (A) lion relative abundance (RAI), (B) distance to the closest water source (m), (C) rainfall (mm) and (D) human relative abundance (RAI). The initial occupancy probability of side-striped jackals related to distance of water and the extinction probability of leopards related to (F) medium prey relative abundance (RAI). Grey ribbons depict upper and lower 95% confidence intervals.

Black-backed jackal

Table 4.3.9: Top ranked models for black-backed jackals in Selati Game Reserve, using quasi-likelihood information criterion for small sample size (QAICc), ΔQAICc difference in QAICc between each model and top ranking model, QAICcwt cum.wt, and K the number of parameters.

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**	**Cum.wt**
ψ(water)γ(lion)ε(lion) *p*(road+rainfall+leopard+lion+hyaena)	13	521.07	0.00	0.88	0.88
ψ(water)γ(sprey)ε(sprey) *p*(road+rainfall+leopard+lion+hyaena)	13	524	4.68	0.09	0.97

Table 4.3.10: Model averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model (table x3) from the analysis examining factors related to the occupancy dynamics of black-backed jackal in Selati Game Reserve. Bold estimates indicate that there was a strong association between the covariate and black-backed jackal occupancy (CIs do not overlap zero). Italicised estimates indicate an intermediate strength of evidence (CIs contain zero but are not centred on zero).

Parameter covariate	**Initial occupancy probability (ψ)**	**Colonisation probability (γ)**	**Local extinction probability (ε)**	**Detection probability (*p*)**
Intercept	*2.28 (-0.34, 4.89)*	**-1.613 (-2.55, -0.67)**	2.0 (-20.08, 24.08)	**2.07 (-2.62, -1.52)**
water	*-0.002 (-0.004, 0.0007)*			
lion		*-0.44 (-1.82, 0.95)*	7.2 (-44.37, 58.76)	**-0.42 (-0.83, -0.004)**
leopard				**0.46 (0.18, 0.74)**
road				**1.50 (0.86, 2.14)**
hyaena				**-0.40 (-0.74, -0.06)**
rainfall				**-0.32 (-0.56, -0.08)**

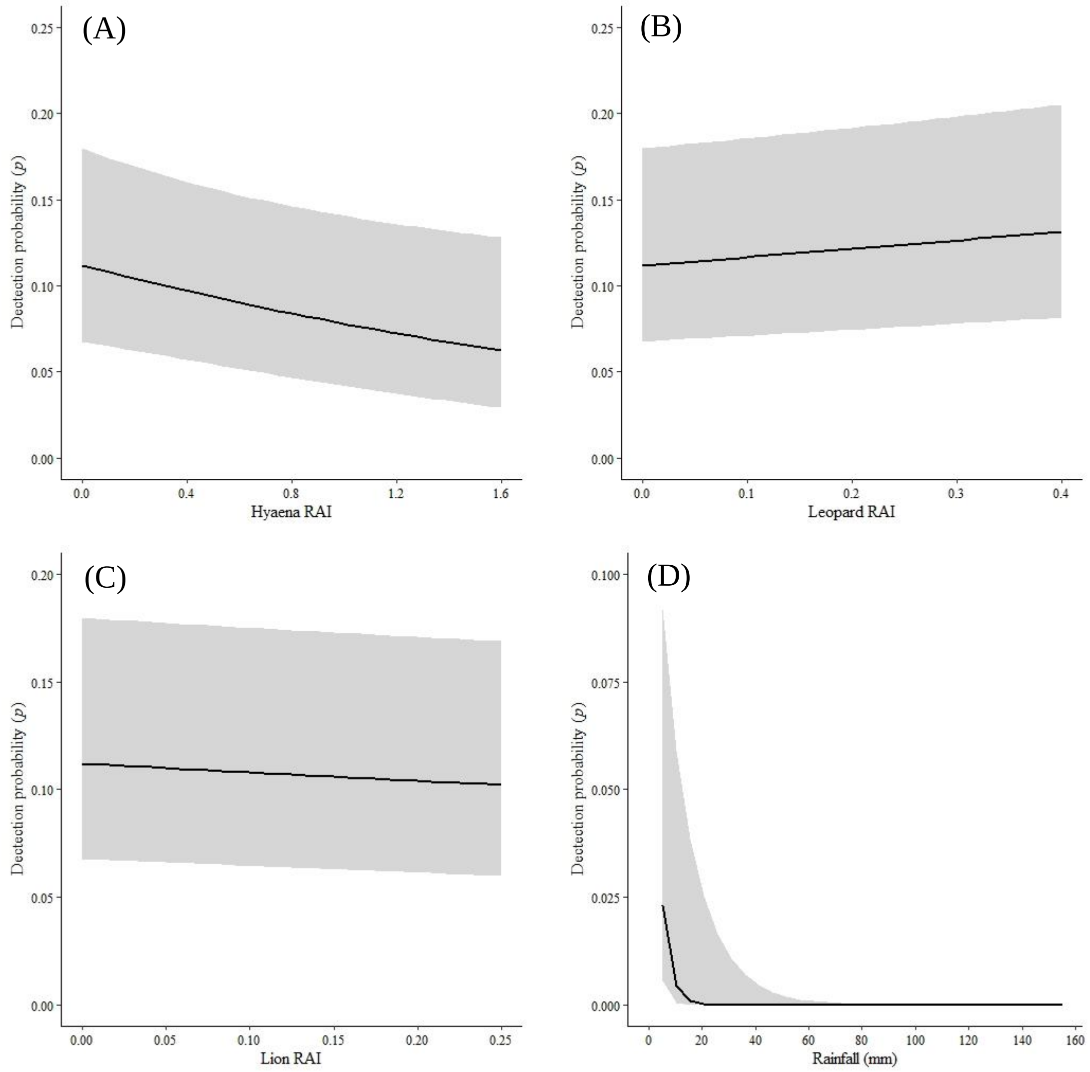


Figure 4.3.5: Probability of detecting black-backed jackals in Selati Game Reserve related to (A) spotted hyaena (hyaena) relative abundance (RAI), (B) leopard relative abundance (RAI), (C) lion relative abundance (RAI) and (D) rainfall (mm).

Honey badger

Table 4.3.11: Top ranked models for honey badgers in Selati Game Reserve, using quasi-likelihood information criterion for small sample size (QAICc), ΔQAICc difference in QAICc between each model and top ranking model, QAICcwt cum.wt, and K the number of parameters.

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**	**Cum.wt**
ψ(road)γ(mprednobadger) ε(mprednobadger)*p*(road+leopard)	10	169.57	0.00	0.20	0.20
ψ(water)γ(mprednobadger) ε(mprednobadger)*p*(road+leopard)	10	169.61	0.04	0.19	0.39
ψ(water)γ(leopard)ε(leopard) *p*(road+leopard)	10	169.91	0.34	0.17	0.56
ψ(.)γ(.)ε(.)*p*(road+leopard)	9	170.30	0.73	0.14	0.69
ψ(elevation)γ(mprednobadger) ε(mprednobadger)*p*(road+leopard)	10	170.40	0.83	0.13	0.82
ψ(road)γ(rainfall)ε(rainfall) *p*(road+leopard)	10	171.08	1.51	0.09	0.91

Table 4.3.12: Model averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model (table x3) from the analysis examining factors related to the occupancy dynamics of honey badger in Selati Game Reserve. Bold estimates indicate that there was a strong association between the covariate and honey badger occupancy (CIs do not overlap zero). Italicised estimates indicate an intermediate strength of evidence (CIs contain zero but are not centred on zero).

Parameter covariate	**Initial occupancy probability (ψ)**	**Colonisation probability (γ)**	**Local extinction probability (ε)**	**Detection probability (*p*)**
Intercept	6.16 (-91.005, 103.32)	-12.84 (-206.59, 180.90)	-9.06 (-146.20, 128.09)	**-4.29 (-5.29, -3.30)**
road	-6.42 (-103.60, 90.75)			**2.25 (1.16, 3.33)**
mprednpbadger		5.53 (-226.93, 238.00)	-12.96 (-231.07, 205.15)	
leopard				**-0.76 (-1.51, -0.005)**

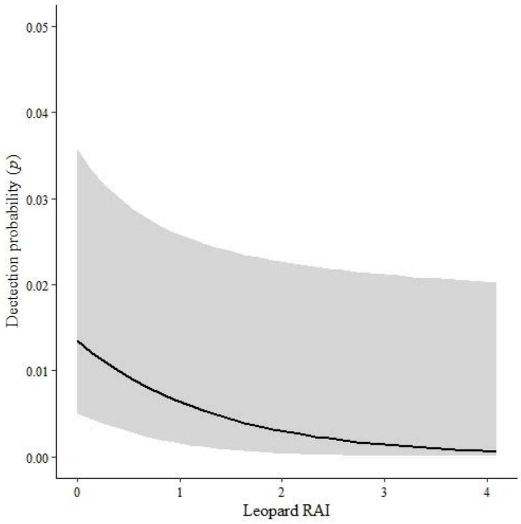


Figure 4.3.6: Probability of detecting honey badgers in Selati Game Reserve related to leopard relative abundance (RAI).

African wildcat

Table 4.3.13: Top ranked models for African wildcats in Selati Game Reserve, using quasi-likelihood information criterion for small sample size (QAICc), ΔQAICc difference in QAICc between each model and top ranking model, QAICcwt cum.wt, and K the number of parameters.

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**	**Cum.wt**	**LL**
ψ(slope)γ(lion)ε(lion) *p*(road+leopard+lion+hyaena)	11	216.47	0.00	0.69	0.69	-87.57
ψ(slope)γ(leopard)ε(leopard) *p*(road+leopard+lion+hyaena)	11	218.52	2.05	0.25	0.94	-88.59

Table 4.3.14: Model averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model (table x3) from the analysis examining factors related to the occupancy dynamics of African wildcat in Selati Game Reserve. Bold estimates indicate that there was a strong association between the covariate and African wildcat occupancy (CIs do not overlap zero). Italicised estimates indicate an intermediate strength of evidence (CIs contain zero but are not centred on zero).

Parameter covariate	**Initial occupancy probability (ψ)**	**Colonisation probability (γ)**	**Local extinction probability (ε)**	**Detection probability (*p*)**
Intercept	6.34(-3.60, 16.29)	-3.71(-18.41, 10.98)	2.05(-19.77, 23.88)	**-5.21(-6.83, -3.58)**
slope	*-2.04(-5.29, 1.21)*			
lion		-4.03(-38.32, 30.26)	7.38(-43.57, 58.32)	**-1.46(-2.69, -0.22)**
road				**3.74(2.09, 5.39)**
leopard				**0.67(0.17, 1.18)**
hyaena				*-0.41(-0.84, 0.02)*

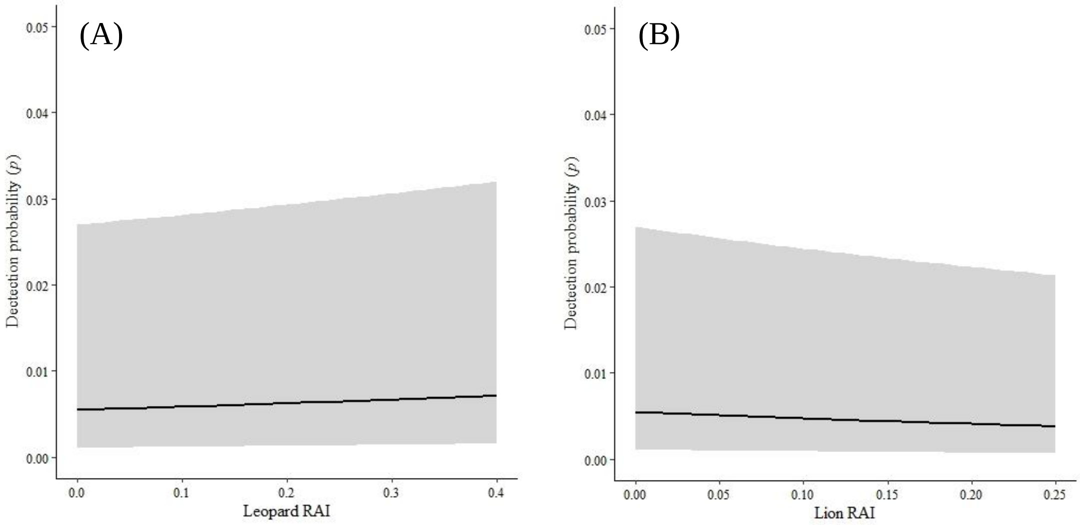
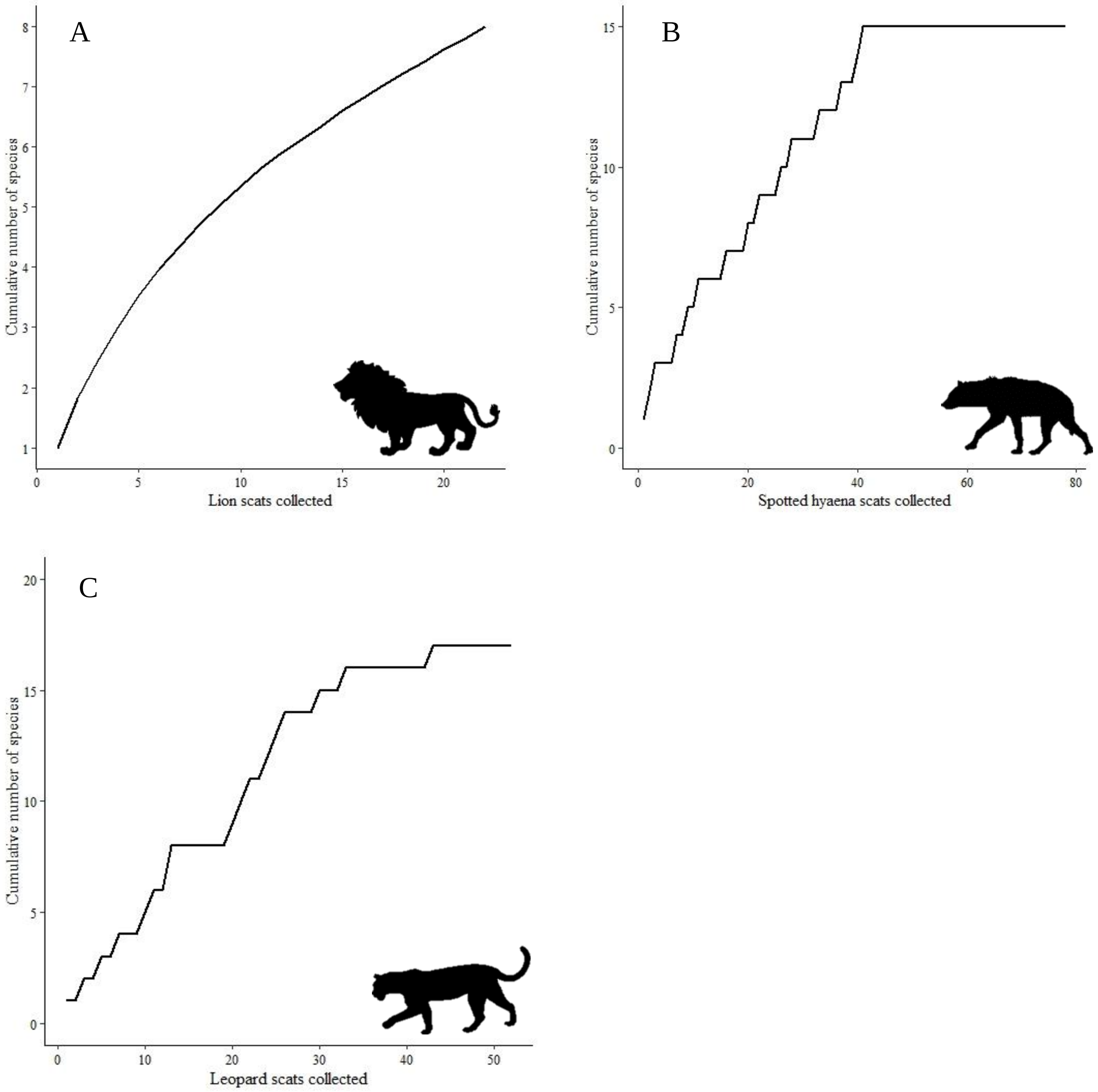


Figure 4.3.7: Probability of detecting African wildcats in Selati Game Reserve related to (A) leopard and (B) lion relative abundance (RAI).

Appendix 5.1: Species accumulation curves for lion (A), spotted hyaena (B) and leopard (C) scat samples in Selati Game Reserve, Limpopo Province, South Africa.



Appendix 5.2a: Food items identified in large carnivore scats and at kill sites in Selati Game Reserve. Number in parenthesis give the sample size.

Food items	**Lions**		**Spotted hyaenas**	**Leopards**	
	scats (22)	**kills (68)**	**scats (78)**	**scats (52)**	**kills (22)**
Small prey (<30 kg)					
Common duiker (*Sylvicapra grimmia*)				1	
Sharpe’s grysbok (*Raphicerus sharpei*)				1	1
Steenbok (*Raphicerus campestris*)					1
Medium prey (30-90 kg)					
Bushbuck (*Tragelaphus scriptus*)			1	1	
Impala (*Aepyceros melampus*)	6	10	34	18	12
Mountain reedbuck (*Redunca fulvorufula*)				2	
Warthog (*Phacochoerus africanus*)	7	8	9	3	1
Large prey (90-1000 kg)					
Blue wildebeest (*Connochaetes taurinus*)	1	13	4		1
Bushpig (*Potamochoerus larvatus*)	1		1	2	
Eland (*Tragelaphus oryx*)	1	2	2		
Kudu (*Tragelaphus strepsiceros*)	3	25	9	3	2
Nyala (*Tragelaphus angasii*)			2	1	4
Plains zebra (*Equus quagga*)	1		3		
Sable antelope (*Hippotragus niger*)		2	1		
Tsessebe (*Damaliscus lunatus*)		1			
Waterbuck (*Kobus ellipsiprymnus*)	2	25	6		
Other					
Cape porcupine (*Hystrix africaeaustralis*)		2	3		
Chacma baboon (*Papio ursinus*)			2	1	
Rock hyrax (*Procavia capensis*)				1	
Scrub hare (*Lepus saxatilis*)				1	
Vervet monkey (*Chlorocebus pygerythrus*)				1	
Side-striped jackal (*Canis adustus*)				1	
Small-spotted genet (*Genetta genetta*)				1	
Mongoose			7	5	
Rodent			3	12	
Bird			3		

Appendix 5.2b: Diet composition from scats and kill sites combined given as the total number (n) and frequency of occurrence (FO) for each food item for each large carnivore in Selati Game Reserve. Prey species average abundance over the study period (2016-2018) from aerial counts (n) and their frequency of occurrence (FO) are given.

Food items	**Prey species**		**Lions**		**Spotted hyaenas**		**Leopards**	
	n	**FO**	**n**	**FO**	**n**	**FO**	**n**	**FO**
Small prey (<30 kg)								
Common duiker (*Sylvicapra grimmia*)	68	1.01%					1	1.30%
Sharpe's grysbok (*Raphicerus sharpei*)	6	0.09%					2	2.60%
Steenbok (*Raphicerus campestris*)	28	0.41%					1	1.30%
Medium prey (30-90 kg)								
Bushbuck (*Tragelaphus scriptus*)	8	0.11%			1	1.11%	1	1.30%
Impala (*Aepyceros melampus*)	3429	50.62%	16	13.78%	34	37.78%	30	38.96%
Mountain reedbuck (*Redunca fulvorufula*)	6	0.08%					2	2.60%
Warthog (*Phacochoerus africanus*)	222	3.27%	15	12.93%	9	10.00%	4	5.19%
Large prey (90-1000 kg)								
Blue wildebeest (*Connochaetes taurinus*)	706	10.42%	14	12.07%	4	4.44%	1	1.30%
Bushpig (*Potamochoerus larvatus*)	6	0.08%	1	0.86%	1	1.11%	2	2.60%
Eland (*Tragelaphus oryx*)	62	0.92%	2	2.59%	2	2.22%		
Kudu (*Tragelaphus strepsiceros*)	816	12.05%	28	24.14%	9	10.00%	5	6.49%
Nyala (*Tragelaphus angasii*)	45	0.67%			2	2.22%	5	6.49%
Plains zebra (*Equus quagga*)	539	7.95%	7	6.03%	3	3.33%		

Sable antelope (*Hippotragus niger*)	40	0.59%	2	1.72%	1	1.11%		
Tsessebe (*Damaliscus lunatus*)	4	0.06%	1	0.86%				
Waterbuck (*Kobus ellipsiprymnus*)	261	3.85%	27	23.28%	6	6.67%		
Other								
Cape porcupine (*Hystrix africaeaustralis*)			2	1.72%	3	3.33%		
Chacma baboon (*Papio ursinus*)					2	2.22%	1	1.30%
Rock hyrax (*Procavia capensis*)							1	1.30%
Scrub hare (*Lepus saxatilis*)							1	1.30%
Vervet monkey (*Chlorocebus pygerythrus*)							1	1.30%
Side-striped jackal (*Canis adustus*)							1	1.30%
Small-spotted genet (*Genetta genetta*)							1	1.30%
Mongoose					7	7.78%	5	6.49%
Rodent					3	3.33%	12	15.58%
Bird					3	3.33%		

Appendix 5.2c: Diet composition from scats as the total number (n) and frequency of occurrence (FO) for each food item for small- and medium-sized carnivores (other carnivores) in Selati Game Reserve.

Food items	**Other carnivores***	
	scats (31)	**FO**
Small prey (<30 kg)		
Klipspringer (*Oreotragus oreotragus*)	1	2.86%
Medium prey (30-90 kg)		
Bushbuck (*Tragelaphus scriptus*)	1	2.86%
Impala (*Aepyceros melampus*)	5	14.29%
Warthog (*Phacochoerus africanus*)	1	2.86%
Large prey (90-1000 kg)		
Eland (*Tragelaphus oryx*)	1	2.86%
Kudu (*Tragelaphus strepsiceros*)	1	2.86%
Waterbuck (*Kobus ellipsiprymnus*)	2	5.71%
Other		
Chacma baboon (*Papio ursinus*)	1	2.86%
Mongoose	6	17.14%
Rodent	16	45.71%

* Other carnivores include serval, caracal, black-backed jackal, side-striped jackal and civet

SUPPLEMENTARY MATERIAL

Supplementary material 1

1) *SC model*

```
{
 sigma ~ dgamma(30,50) # black-backed jackal
 # sigma ~ dgamma(30,58) # side-striped jackal
 # sigma ~ dgamma(40,110) # civet
 # sigma ~ dgamma(100,31) # lion
 # sigma ~ dgamma(164,100) # leopard
 # sigma ~ dgamma(1965,1500) # spotted hyaena
 lam0 ~ dunif(0,10)
 psi ~ dbeta(1,1)
 for(i in 1:M) {
 z[i] ~ dbern(psi)
 s[i,1] ~ dunif(xlim[1], xlim[2])
 s[i,2] ~ dunif(ylim[1], ylim[2])
 for(j in 1:J) {
 distsq[i,j] <- (s[i,1] - X[j,1])^2 + (s[i,2] - X[j,2])^2
 lam[i,j] <- lam0 * exp(-distsq[i,j] / (2*sigma^2)) * z[i]
 }
 }
 for(j in 1:J) {
 bigLambda[j] <- sum(lam[,j])
 for(k in 1:K) {
 n[j,k] ~ dpois(bigLambda[j])
 }
 }
 N <- sum(z[])
 D <- N/area
 }
 ",file="bbj_dry2016_J.txt")
```

2) *Home range size and calculations for the σ priors*

Home range size estimates for lion (n=4), leopard (n=2) and spotted hyaena (n=3) were derived from minimum convex polygons created from GPS telemetry location data collected from the study area (lion: 2016-2018, leopard: 2016-2017; spotted hyaena: 2016-2017; refer to Chapter 4). Black-backed jackal, side-striped jackal and civet home range sizes were taken from the literature from studies conducted in similar environments. The home range of σ was calculated following Chandler & Royle (2013) and assuming a chi-square distribution with 2 degrees of freedom.

Black-backed jackal

```
#home range estimates from literature: 2 – 17.8 km^2

sqrt(2/pi)/sqrt(5.99) = 0.33 km

sqrt(17.8/pi)/sqrt(5.99) = 0.97 km

# we want a prior with most of the density between:

0.33 and 0.97

# Gamma(30,50) covers this

qgamma(c(0.001,0.5,0.999),30,50) # 0.3173834 0.5933467 0.9960723
```

Side-striped jackal

```
#home range estimates from literature: 2 – 13 km^2

sqrt(2/pi)/sqrt(5.99) = 0.33 km

sqrt(13/pi)/sqrt(5.99) = 0.83 km

# we want a prior with most of the density between:

0.33 and 0.83

# Gamma(30,58) covers this

qgamma(c(0.001,0.5,0.999),30,58) # 0.2736064 0.5115057 0.8586830
```

Civet
#home range estimates from literature: 2 – 5 km^2

sqrt(3/pi)/sqrt(5.99) = 0.40 km

sqrt(5/pi)/sqrt(5.99) = 0.50 km

we want a prior with most of the density between:

0.40 and 0.50

Gamma(40,110) covers this

qgamma(c(0.001,0.5,0.999),40,110) # 0.2114540 0.3606106 0.5674510

Lion
#home range estimates from telemetry data: 105 - 315 km^2

sqrt(105/pi)/sqrt(5.99) = 2.36 km

sqrt(315/pi)/sqrt(5.99) = 4.09 km

we want a prior with most of the density between:

2.36 and 4.09

Gamma(100,31) covers this

qgamma(c(0.001,0.5,0.999),100,31) # 2.320045 3.215060 4.315170

Leopard
#home range estimates from telemetry data: 30 - 75 km^2

sqrt(31/pi)/sqrt(5.99) = 1.28 km

sqrt(75/pi)/sqrt(5.99) = 1.99 km

we want a prior with most of the density between:

1.28 and 1.99

Gamma(164,100) covers this

qgamma(c(0.001,0.5,0.999),164,100) # 1.272559 1.636668 2.064389

Spotted hyaena
#home range estimates from telemetry data: 29 - 36 km^2

sqrt(29/pi)/sqrt(5.99) = 1.24 km

sqrt(36/pi)/sqrt(5.99) = 1.38 km

we want a prior with most of the density between:

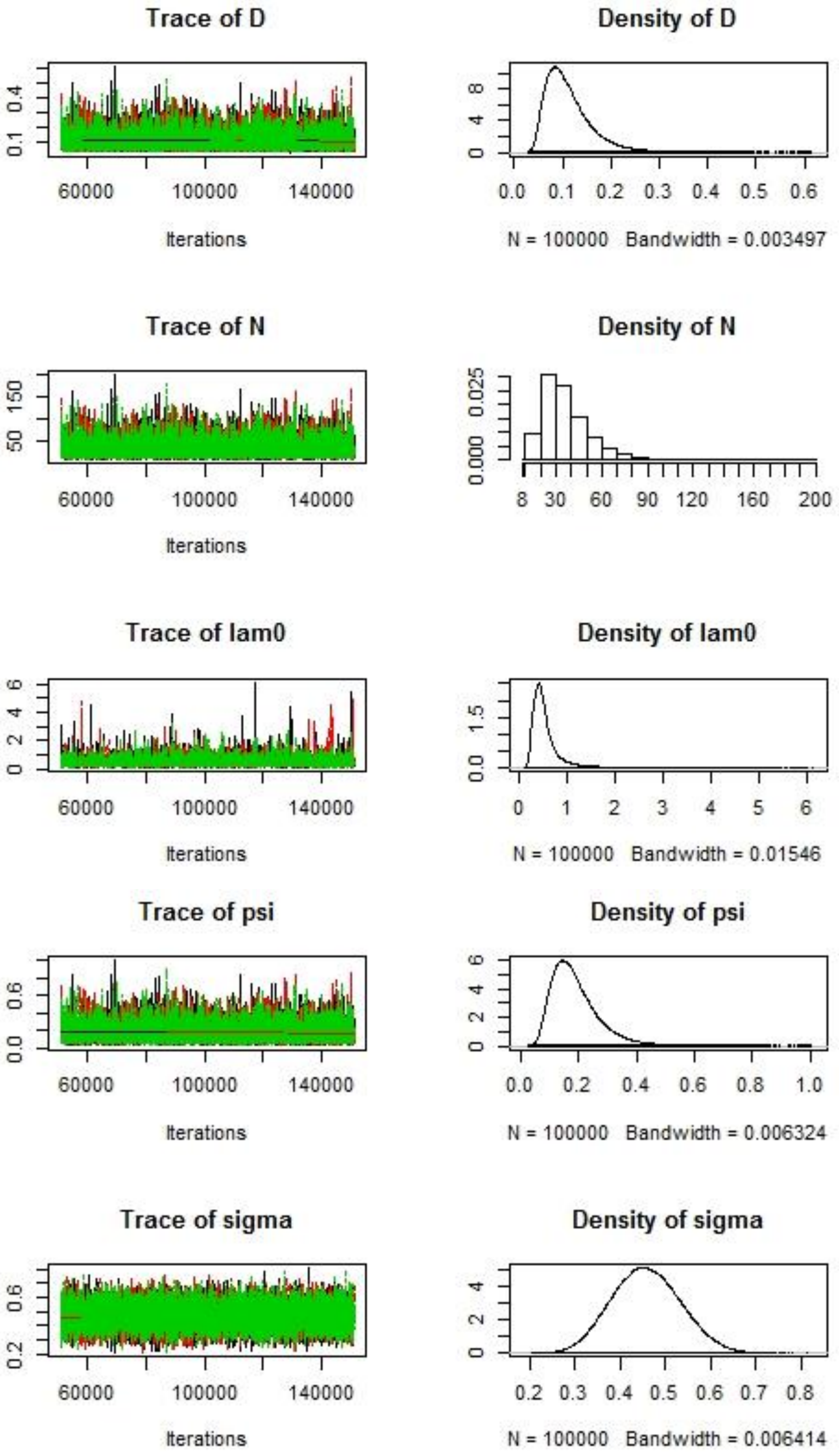
1.24 and 1.38

Gamma(1965,1500) covers this

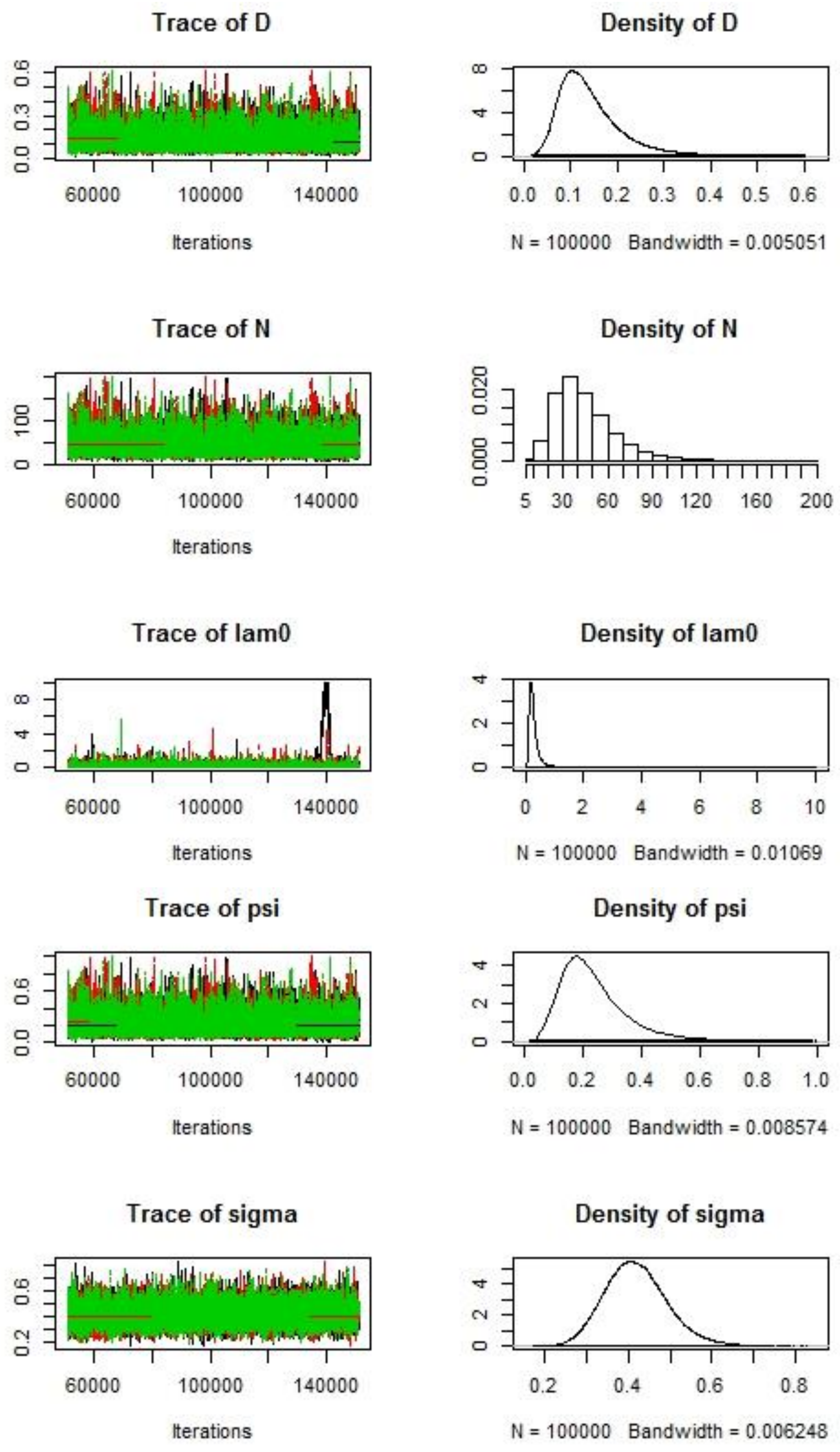
qgamma(c(0.001,0.5,0.999), 1965,1500) # 1.220573 1.309778 1.403226

Markov Chain Monte Carla Traceplots and Posterior Probability Histograms for the dry 2017 survey for each species, where M was set at 200, density (D) is individuals per km^2 and σ (sigma) is in 10 km units

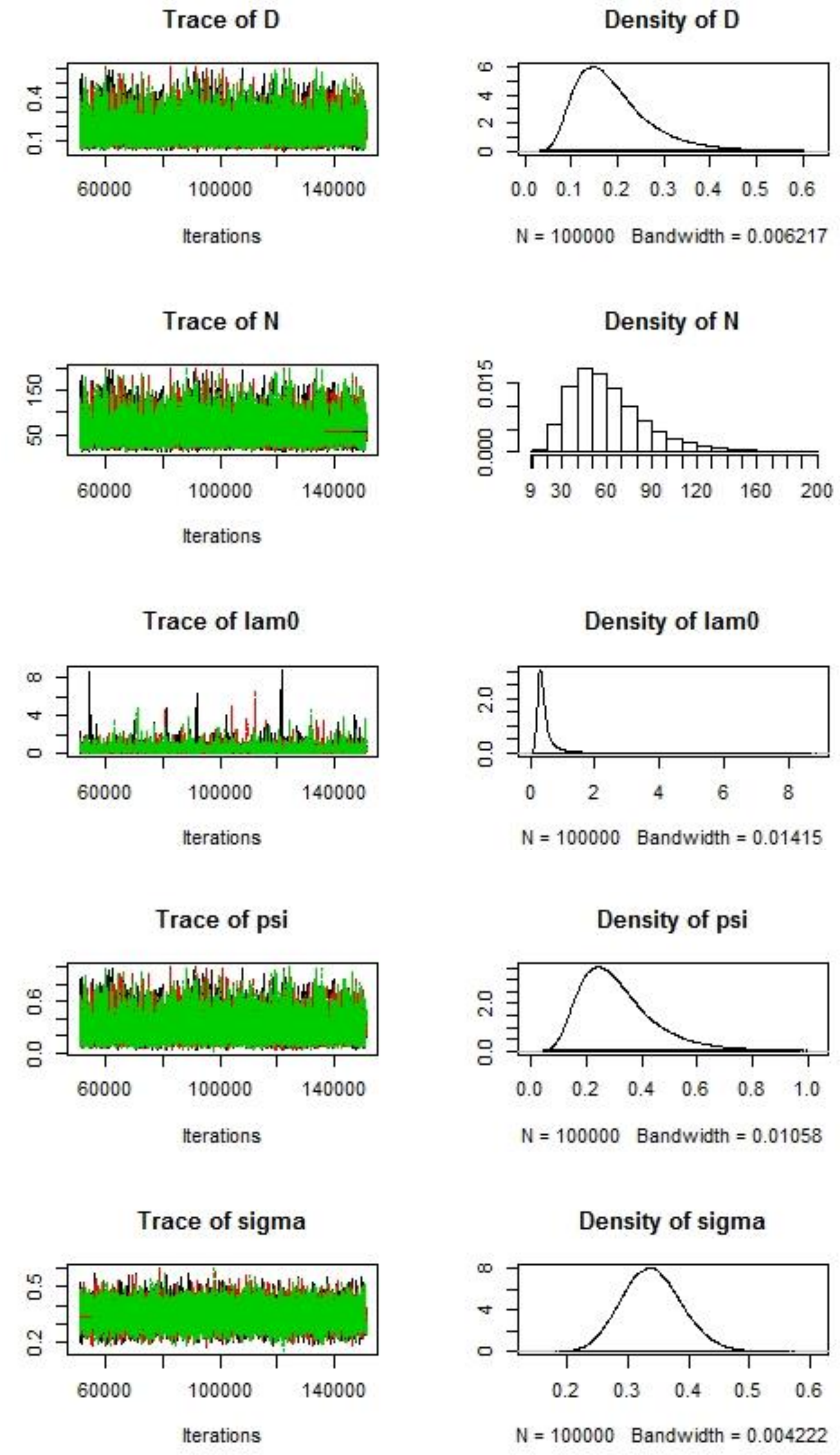
Black-backed jackal



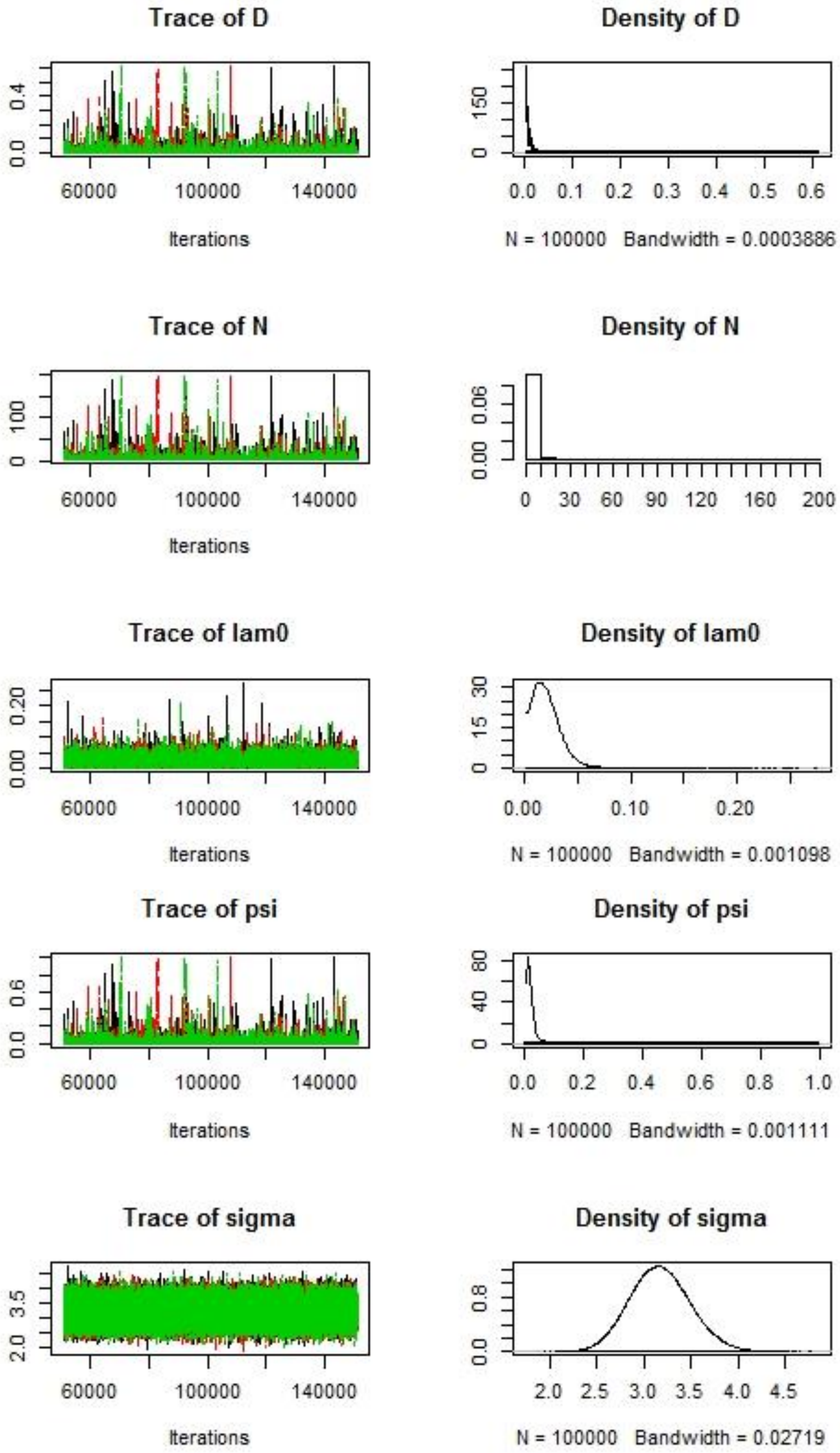
Side-striped jackal



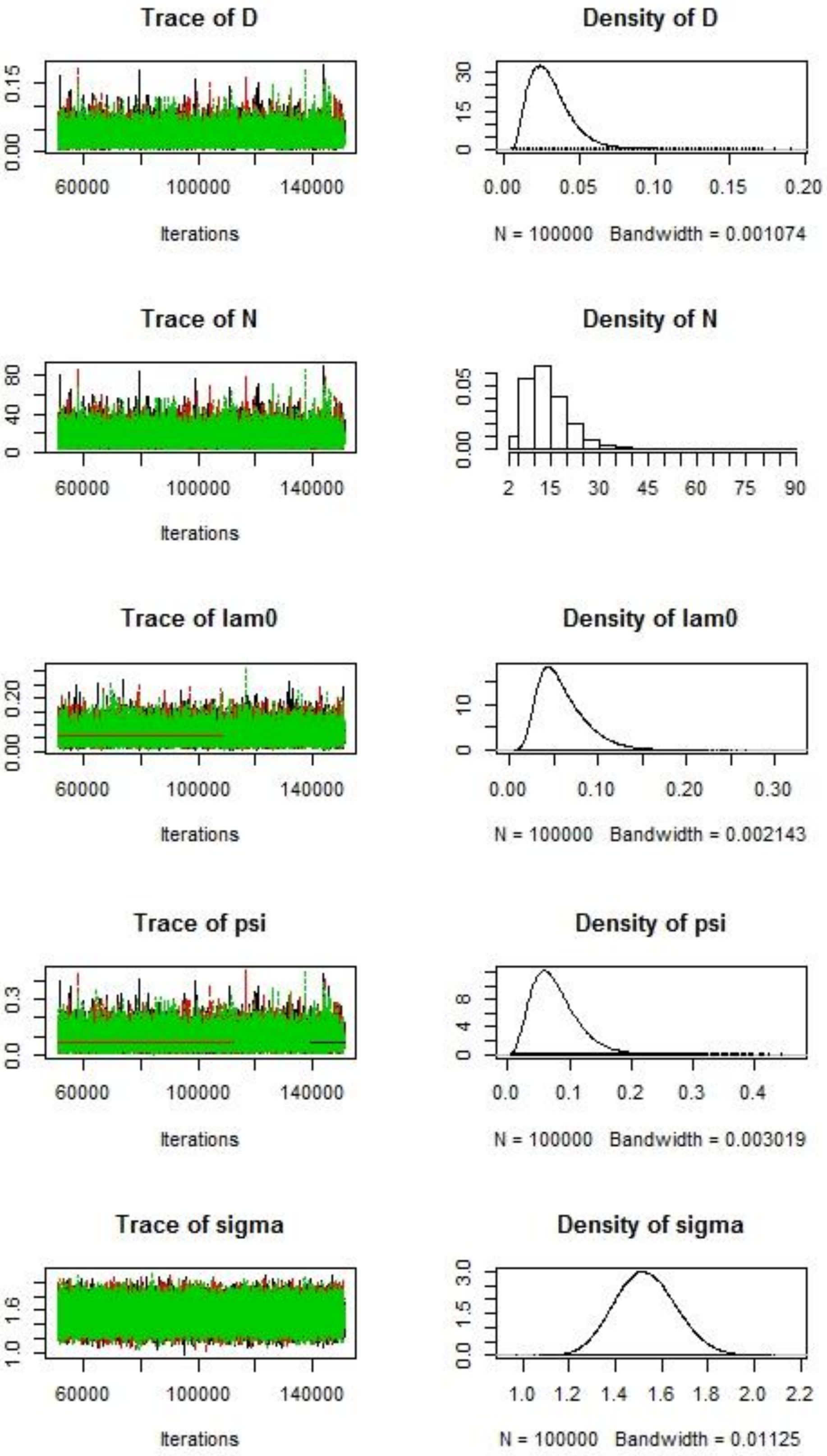
African Civet



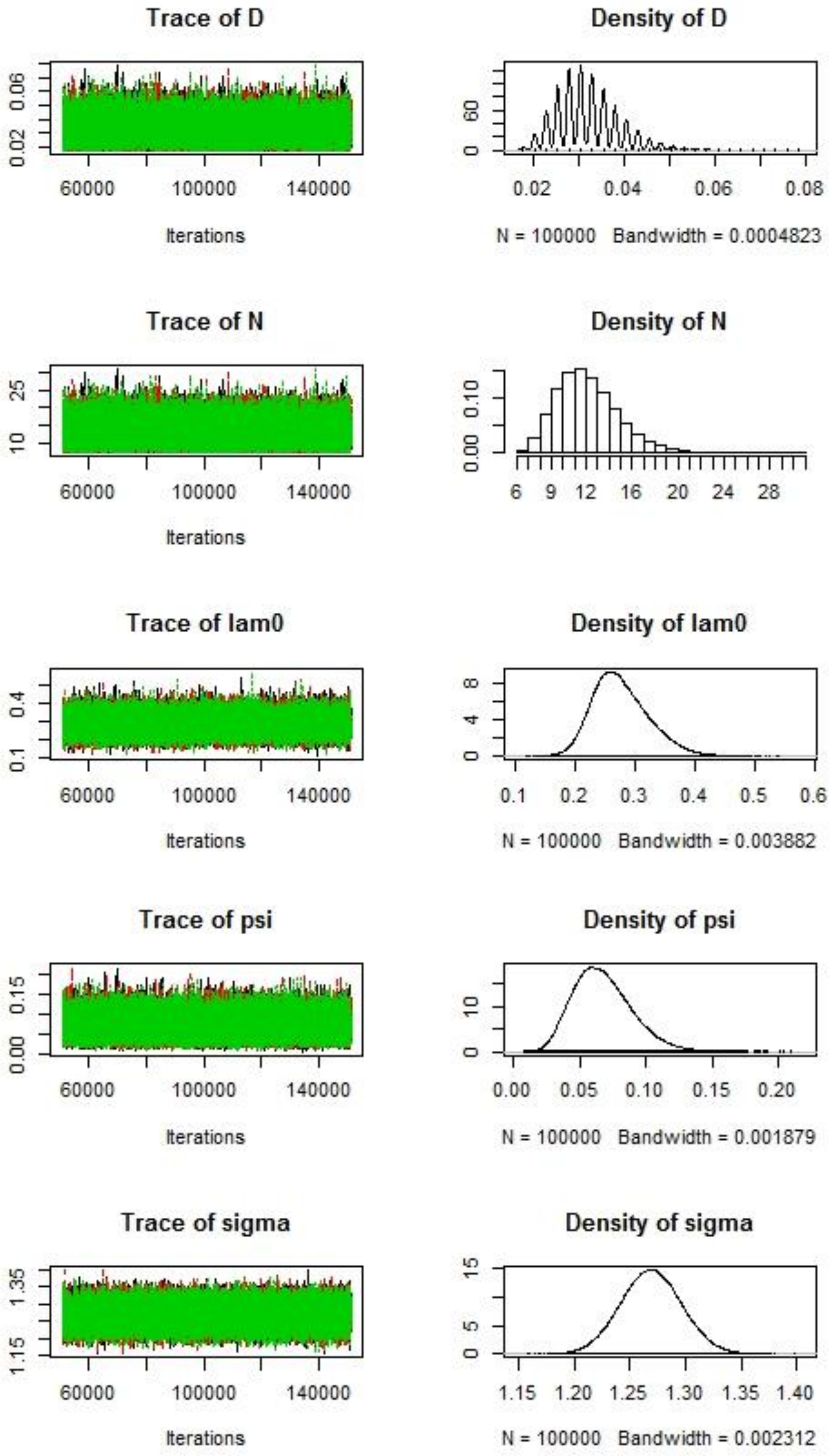
Lion


Trace of D
0.0
0.4
60000
100000
140000
Iterations
Density of D
0
150
0.0
0.1
0.2
0.3
0.4
0.5
0.6
N = 100000 Bandwidth = 0.0003886
Trace of N
0
100
60000
100000
140000
Iterations
Density of N
0.00
0.06
0
30
60
90
120
160
200
Trace of lam0
0.00
0.20
60000
100000
140000
Iterations
Density of lam0
0
15
30
0.00
0.10
0.20
N = 100000 Bandwidth = 0.001098
Trace of psi
0.0
0.6
60000
100000
140000
Iterations
Density of psi
0
40
80
0.0
0.2
0.4
0.6
0.8
1.0
N = 100000 Bandwidth = 0.001111
Trace of sigma
2.0
3.5
60000
100000
140000
Iterations
Density of sigma
0.0
0.8
2.0
2.5
3.0
3.5
4.0
4.5
N = 100000 Bandwidth = 0.02719

Leopard


Trace of D
0.00
0.15
60000
100000
140000
Iterations
Density of D
0
15
30
0.00
0.05
0.10
0.15
0.20
N = 100000 Bandwidth = 0.001074
Trace of N
0
40
80
60000
100000
140000
Iterations
Density of N
0.00
0.05
2
15
30
45
60
75
90
Trace of lam0
0.00
0.20
60000
100000
140000
Iterations
Density of lam0
0
10
0.00
0.10
0.20
0.30
N = 100000 Bandwidth = 0.002143
Trace of psi
0.0
0.3
60000
100000
140000
Iterations
Density of psi
0
4
8
0.0
0.1
0.2
0.3
0.4
N = 100000 Bandwidth = 0.003019
Trace of sigma
1.0
1.6
60000
100000
140000
Iterations
Density of sigma
0.0
1.5
3.0
1.0
1.2
1.4
1.6
1.8
2.0
2.2
N = 100000 Bandwidth = 0.01125

Spotted hyaena



Supplementary material 2:

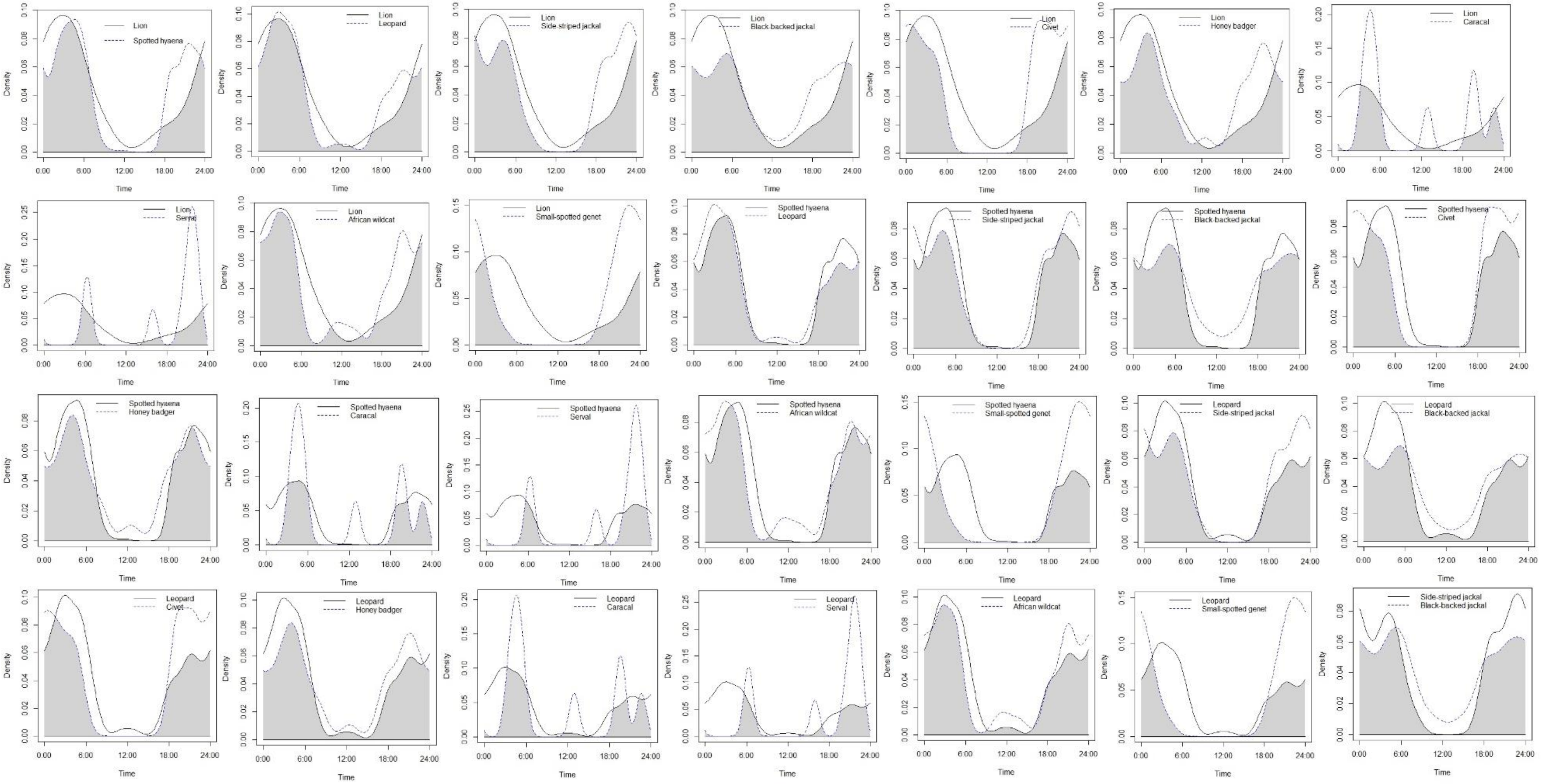
Table a: Total number of species harvested from Selati Game Reserve, Limpopo Province, South Africa, in 2016 and 2017.

	Blue wildebeest	Eland	Giraffe	Impala	Kudu	Nyala	Rhino	Sable	Warthog	Waterbuck	Zebra	Spotted hyaena
2016	148	1	16	554	35	2	12	22	17	15	35	2
2017	18	9	20	1071	46	18	1	34	14	8	12	3

Table b: The break down of harvested species during 2017 on Selati Game Reserve, Limpopo Province, South Africa.

	Blue wildebeest	Eland	Giraffe	Impala	Kudu	Nyala	Rhino	Sable	Warthog	Waterbuck	Zebra	Spotted hyaena
Staff rations				38					4			
Hunting	13	3	5	210	21	3			8	8	10	2
Sales								29				
Natural causes	5		5	14	25	15	1	5	2		2	1
Culling		6	10	793								
Road kill												

Supplementary material 3: Kernel density estimates of daily activity patterns and overlap amongst pairs of focal carnivore species (from large vs large (top left) to small vs small (bottom right on next page)) captured on camera traps across all four seasonal surveys conducted in Selati Game Reserve. The overlap coefficient is the shaded area under the two carnivore density estimates.



Supplimentary material 3 continued: