UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

Drivers of leopard population dynamics in the Kruger National Park, South Africa

by

Nakedi Walter Maputla

Submitted in partial fulfillment of requirements for the degree of

Doctor of Philosophy

(Zoology)

In the Faculty of Natural and Agricultural Sciences

Department of Zoology and Entomology

University of Pretoria

Pretoria

South Africa

August 2014

Drivers of leopard population dynamics in the Kruger National Park, South Africa

by

Nakedi Walter Maputla

Mammal Research Institute (MRI), Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa

SUPERVISORS:

Doctor Sam M. Ferreira

Scientific Services, South African National Parks (SANPARKS), Skukuza, 1350 South Africa

Professor Christian T. Chimimba

Mammal Research Institute (MRI) and DTS-NRF Centre of Excellence for Invasion Biology (CIB), Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa

Declaration

I, **Nakedi Walter Maputla** declare that this thesis which I hereby submit for the degree of Doctor of Philosophy in Zoology at the University of Pretoria is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature: N. Map ………………………………………………………………

Date: 15 August 2014 ………………………………………………………………

Disclaimer

This thesis consists of a series of chapters that have been prepared as stand-alone manuscripts, some of which were/have been submitted for publication. It is therefore possible that some unavoidable repetition may occur between chapters.

Thesis Abstract

In the Kruger National Park (KNP), South Africa, five of the six extant members of the large carnivore guild: lions, *Panthera leo*, spotted hyaenas, *Crocuta crocuta*, leopards, *P. pardus*, cheetahs, *Acynonyx jubatus*, and wild dogs, *Lycaon pictus*, are sympatric. *A priori* and *posteriori* deductions dictate that lions maintain a balance in the top-down processes in the KNP ecosystem including population abundances and behaviour of the subordinate predators. The recent discovery of the extrinsic disease, bovine tuberculosis (bTB) caused by a bacterium *Mycobacterium bovis*, in lions suggests that potentially, lion population may decline. Further deductions dictate that the leopard population whereas at individual level may be affected, does not appear to be challenged by the disease. This presupposes that the balance in the top-down processes will potentially be affected. By specifically assessing how this change may affect the leopard population, two mechanisms, which in the context of the KNP are contradictory were invoked. The first mechanism is the meso-predator release hypothesis, which predicts that should the lion population decline, the leopard population would increase as a consequence. The second mechanism, niche packing hypothesis, predicts that the leopard population will not experience a change as a result of the lion population declining; it argues that leopards and lions have co-evolved and as a result have developed conflict avoidance life history, morphological and ecological patterns. Consequently, the thesis set out to investigate if these mechanisms were in effect in the KNP by: (i) designing a robust method to estimate leopard abundances; (ii) estimating leopard abundances throughout the KNP; (iii) comparing leopard abundances with abundances of other members of the large carnivore guild; and (iv) assessing how leopard movements responded to indices of resource distribution and models that predicted space use by lions. Results revealed that leopards responded to resource distribution more than in response to other carnivores and especially lions as was predicted.

Accordingly, niche packing theory was selected over meso-predator release theory on the grounds that at population level leopards, at least as far as the KNP is concerned, are not affected by other carnivores. This study therefore, has direct implications on the large carnivore management in KNP. The present study suggests that the leopard population is mainly driven by resources and secondarily by lions. That means in the absence of factors such as human-induced effects, and diseases that are likely to threaten their resource base and them as a result, leopard population is likely to self-regulate in KNP.

Key words: leopard, lion, spotted hyaena, bovine tuberculosis, meso-predator, niche packing, abundance, competition, Kruger National Park

Acknowledgements

I thank my supervisors, Dr Sam Ferreira and Prof Chris Chimimba for their support, guidance, and patience during the process of conducting this work. I thank KCS Pacific Foundation, Nancy-Carroll Draper Foundation, Wildlife and Environment Society of Southern Africa, Karl Meyer Stiftung, and Peter and Charmian Corne for funding this study. I thank the SATIB Trust providing field clothes. I am indebted to my colleagues at African Wildlife Foundation. Special thanks to Patrick Bergin, Helen Gichohi, Simon Munthali, Philip Muruthi, Craig Sholley, Gregg Mitchell, Joanna Elliot, Kathleen Fitzgerald, Harry van der Linde, Christina Rollin, Kurt Redenbo, Stephen Ham, Kate Gersh, Kathleen Garrigan, Christine Meek, Christina van Winkle, Nadia Mitchem, Amy Rizzoto, Daniel McGahey, Elizabeth Opee, David Williams, Paul Thomson, Annika Vieira, Rose Mayienda, Michael Maina, and Nnzumbeni Tshikalange. I am grateful to the South African National Parks Board (SANParks) for granting permission to conduct this study and for logistical and financial support. I thank SANParks Scientific Services, Veterinary Wildlife Services and Nature Conservation for providing support at different stages of this study. The following people from SANParks were helpful during the study: Markus Hofmeyr, Peter Buss, Danny Govender, Johan Malan, Marius Kruger, Izak Smit, Pauli Viljoen, Hendrik Sithole, Adolf Manganyi, Joel Tleane, Reinhardt Scholtz, Laurence Kruger, Thomas Ramabulana, Stephen Midzi, Rendani Nethengwe, Marius Renke, Agnes Mukondeleli, Albert Smith, Cross Muchocho, Phindile Makhuvele, Joe Nkuna, Johann Oelofse, Rob Thomson, Evans Mkansi, Richard Sowry, Neels van Wyk, Steven Whitfield, Rodney Landela, Karien Keet, Thomas Mbokota, Tinyiko Chauke, Don English, and Louis Olivier. I am thankful to the Timbavati Private Nature Reserve management for granting permission for collar deployment especially Jacques Brits and Almero Bosch. I thank the University of Pretoria for financial support. I am grateful to the following people for their

assistance at the University of Pretoria’s Department of Zoology and Entomology: Human Buirski, Christian Pirk, Armanda Bastos, and Ingrid Vis. The following students were very helpful, one way or another: Mohlamatsane Mokhatla, Rolanda Julius, Anja Le Grange, Asiashu Lithole, Claude Moshobane, Ayesha Hassim, Lydia Belton, Oscar Mohale, and Andrew Davies. I thank the Singita Group and all the staff at Singita Kruger National Park for support at the beginning of this study. I thank Paul Levy and Michael Goldberg of Makanyi for support and for allowing us to work on their property. I am grateful for the time shared with colleagues at Makanyi: Jeremy Kemp-Symonds, Mark Jack Freeman, Dave Jackaman, Lukson Ndlovu, Rebecca Dicks, Holly Siddons, and Christina Hansen. I thank the management of the following concessions within the Kruger National Park: Tinga, Jock, Shishangeni, and Rhino Walking Safaris. Special thanks to the following people who took their time to visit the study site: Ellie, Edwin, Charmian and Peter Corne, Christine Hemrick, David and Karie Thomson, Patrick Bergin, Helen Gichohi, Craig Sholley, Kathleen Fitzgerald and her husband Scott, Stephen Ham, Wayne Safro, Harry and Claudia van der Linde, Karen Vickers, Kim Laxton, Mrs Anderson, Hazel and Julian Judelman, Natasha Constant and Rik van Laarhoven. The following game guards worked with me during the course of the study: The Late Ozias Cubayi (rest in peace Baba), Kaizer Mathebula, Onicah Ndlovu, Mofat Mambane, Mr Rikhombe, and Veli Ndlovu. I am indebted to the following volunteers and interns: Michael Gallagher, Kim Laxton, Mark Freeman, Susan Shane, Molly Shane, and Lars Sund. The following students provided much needed companionship and ears for bouncing off ideas: Nkabeng Maruping (thanks for reading through my chapters), the Late Kevin Deenadayalan (rest in peace brother), Lisa Lerm (thanks for helping me with T-Locoh), Samantha Mabuza, Thabang Sibiya, Tertia Strydom, Faith Jumbi, Manqhai Kraai, Nokubonga Mgqatsa, Nozipho Tyagana, Sindiso Chamane, Katlego Makutulela, Noah Konaite, and Trevor Nkuna. I thank Leigh-Ann Woolley and Ryan Taylor for the great times we had in Satara. I thank my friends, Leana Pool and Nicki de Villiers for their support. Lastly, I thank Sibo Mpakanyiswa and our little man Lethabo; I thank mom (Mapula), dad (Tlabo) and my siblings Sele, Mashilo, Mphee and Tumelo for all their support.

Dedication

To my family

Table of Contents

List of figures

List of tables

Chapter 1. General introduction

Introduction

Leopards, *Panthera pardus*, are adaptable and have the widest distribution of all large cats (Bertram 1999). Worldwide, they are found in Africa, the Middle East, the Far East, Republics of the former USSR, but not the arctic tundra (Figure 1.1) (Bothma & Walker 1999). In Africa, leopards inhabit approximately 40 countries while effectively occupying all habitat types except the un-vegetated sand dunes (Grimbeek 1991; Bailey 1993; Bothma & Walker 1999; Marker & Dickman 2005; Skinner & Chimimba 2005). Leopards have a flexible diet, which is complemented by their solitary lifestyle, hunting, and feeding behaviour. Their diet includes a wide variety of prey including invertebrates, rodents, hyraxes, ungulates as large as elands and other carnivores (Grimbeek 1991; Bailey 1993; Karanth & Sunquist 1995; Cowlishaw 1997; Bertram 1999; Sinclair *et al.* 2003; Hayward *et al.* 2006; Steyn & Funston 2006; Ott *et al.* 2007; Owen-Smith & Mills 2008). Their ability to adapt and persist where other predators don't, has led to leopards becoming one of the most persecuted of the large cats through high hunting quotas (Nowell & Jackson 2006, Packer *et al.* 2011), retaliatory killing (Balme *et al.* 2009; McManus *et al.* 2014), and illegal hunting (Balme *et al.* 2010). Consequently, the conservation status of leopards is classified as near threatened (NT) in the IUCN's Red List of Threatened Species (IUCN 2008). However, the Amur Leopard, *P. pardus orientalis*, a subspecies from south-western Russia and formerly in China and Korean Peninsula is classified as critically endangered (CR) (Jackson & Nowell 2006).

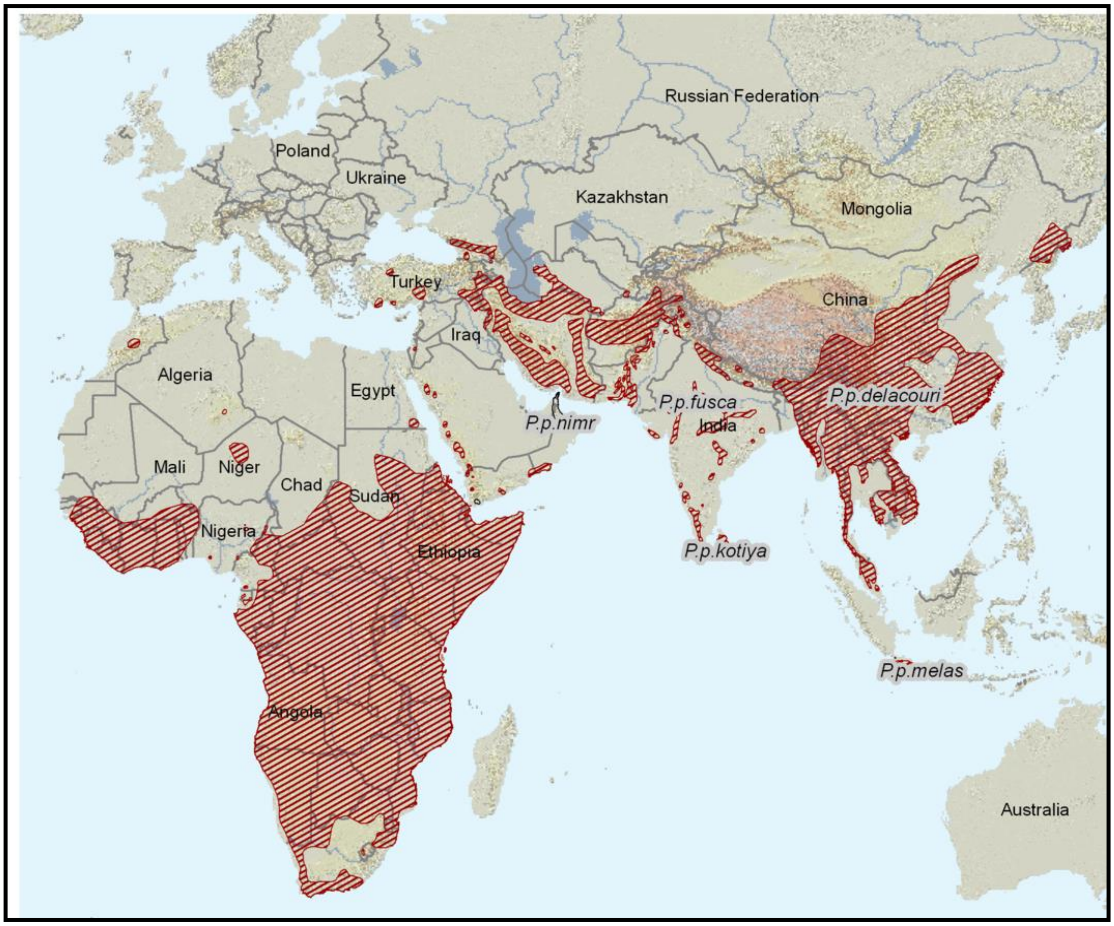


Figure 1.1. Global distribution map of leopards, *Panthera pardus* (IUCN Red List of Threatened Species Version 2011.1. <www.iucnredlist.org>)

Leopards in South Africa have variable home range sizes depending on the sex, prey availability and the terrain they inhabit (Bailey 1993). These ranging patterns are attributed to the heterogeneous nature of the South African landscape, driven by rainfall. As a result, leopards from arid regions, due to the scarcity of prey, tend to have larger home ranges than leopards from mesic areas (Bothma *et al.* 1997). Male leopards generally have large home ranges that overlap two or more female home ranges (Grimbeek 1991; Bailey 1993; Bothma *et al.* 1997; Marker & Dickman 2005).

In South Africa, leopards persist both in and outside protected areas. Outside protected areas, they have to contend with anthropogenic activities including land transformation, habitat fragmentation, and retaliatory killings by livestock and game farmers (Balme *et al.* 2009; McManus *et al.* 2014). To persist, leopards live in refuges, where their survival is hampered by poor dispersal success, which leads to poor gene flow. In addition, populations in these refuges are small. In an event of stochastic occurrences such as disease, they run a risk of facing local extinctions. Protected areas on the other hand provide sanctuaries in which leopards can persist away from anthropogenic influences. Despite this, animals that are in protected areas face various stressors, which may jeopardise their persistence.

In the Kruger National Park (KNP), the effects of extrinsic diseases on the large carnivore guild are largely unknown (Ferreira & Funston 2010). While ecosystems are known to respond gradually to changes that occur over long periods of time, diseases may cause drastic shifts in community structure (Scheffer *et al.* 2001; Bengis *et al.* 2003; Smith *et al.* 2009). This is especially true when keystone species are directly affected by the disease to a point where their numbers crash (Smith *et al.* 2009; Riordan *et al.* 2007). In such instances, the consequences are top-down or bottom-up cascading effects, which have both positive and negative effects on other species (predators and prey) along the food chain (Menge *et al.* 2002; Kissui & Packer 2004; Škalodouvá *et al.* 2007). When the affected taxa are predators, occurrence called the meso-predator release may be experienced (Prugh *et al.* 2009; Ritchie & Johnson 2009; Russell *et al.* 2009). Meso-predator release hypothesis predicts that in a given ecosystem, a collapse in top predator population abundances may trigger a sharp rise in abundances of competitively inferior predators. For example, in West Africa, declines in lion (*Panthera leo*) and leopard abundances strongly correlated with a sharp increase olive baboon (*Papio anubis*) abundances, which in turn closely correlated with declines in small mammal and ungulate abundances (Ripple *et al.* 2014). Interference with top-down processes is a cause for concern in conservation biology because, while some species' population numbers may flourish, other species' population numbers may decline or even experience local extinctions (Kissui & Packer 2004). In such instances, for example, as in the meso-predator release scenario, shifts in ecosystem processes may lead to a collapse of the ecosystem (Ritchie & Johnson 2009). If it is the case of meso-predator release, this predicts that if lion population in the KNP were to decrease, leopard population would increase; suggesting therefore that leopard abundances are a function of lion abundances.

Equally, but in the opposite direction, are the predictions of the niche packing hypothesis (Pianka 1974). Niche packing theory states that species that compete for the same resources in an ecosystem for a long time, co-evolve in such a way that co-existence is enhanced while competition is reduced (Pianka 1974). Several studies have assessed this form of ecological separation and found compelling evidence of niche separation in nature. Examples of this include: (i) diet separations as illustrated by Owen-Smith & Mills (2008), by suggesting that whereas there was overlap in the large carnivore diet, each carnivore species had its own preferred prey species; (ii) character displacement including size variation, and morphological changes that lead to different methods of acquiring food (Dayan & Simberloff 1998); and (iii) separation in the timing of food acquisition (Meiri *et al*. 2005). If niche-packing is in effect, that means at population level, leopards should not be affected negatively by larger predators.

Large carnivore guild in the KNP includes lions, spotted hyaenas (*Crocuta crocuta*), leopards, cheetahs (*Acinonyx jubatus*), and wild dogs (*Lycaon pictus*). All these species are sympatric and often, aggressive interactions among them persist, leading to the cheetah and wild dog being rare (Mills & Funston 2003; Marnewick *et al.* 2014). On the whole, there is a clear pattern on diet preferences among them (Owen-Smith & Mills 2008). Leopard diet in the KNP is dominated by impala (*Aepyceros melampus*) (Bailey 1993), with 76% of recorded kills; and overall small and medium size ungulates accounting for 92% of recorded kills (Hayward *et al.* 2006; Owen-Smith & Mills 2008). Impala in the KNP are known to forage in risky environments, which include dense woody vegetation, during the day; thus placing them at risk of predation (Burkepile *et al.* 2013).

Bovine tuberculosis (bTB) was introduced into the KNP ecosystem between 1950 and 1960 from infected cattle to Cape buffalo (*Syncerus caffer*) (Michel *et al.* 2006). The buffalo is, as such, the maintenance host (Caron *et al.* 2003), although in time, the disease spilled over to other species (Keet *et al.* 1996). The lion, top predator in the KNP ecosystem, is thought to be directly affected by the disease, although the negative impacts of the disease cannot be fully substantiated (Ferreira & Funston 2010, Maruping 2014). Negative effects of bTB on leopards, at population level have since been refuted (Caron *et al*. 2003), on account of leopard behaviour and majority of leopard prey species testing negative for the disease. This consequently led to concerns that this situation may trigger meso-predator release mechanism in leopards (van Helden & Uys 2009).

Aims and key questions

The aim of this study was to investigate the drivers of leopard population dynamics in the KNP ecosystem as a result of the indirect effects of bTB. The results would in turn form a basis for management to make informed decisions on conservation interventions and in the drafting of the large carnivore management plan in the KNP. The project was based on three predictions. The first prediction relates to the meso-predator release hypothesis. It was based on the premise that if meso-predator release mechanisms were in effect, leopard abundances would be high where lion abundances were low and *vice versa*. The second prediction revolved around the niche packing theory. If niche packing were indeed prevalent among the large carnivore guild in the KNP, variations in leopard numbers across the KNP would respond to variables other than lion and spotted hyaena (*Crocuta crocuta*) abundances. The last prediction was based on the premise that leopards were primarily resource-driven and that the influence of lions on their movement behaviour was secondary.

Accordingly, key questions, which also formed chapters for this thesis were: (i) What trapping design and survey effort produce the most robust estimates of a known leopard population?; (ii) What is the estimated population size of leopards in the KNP?; (iii) How do leopard population estimates compare with population estimates for lion and hyena in KNP?; and (iv) How does leopard movement behaviour predicted from individual space use models overlap with indices of resource distributions and movement patterns predicted for lions?

Study area

The Kruger National Park is located in the north-east border of South Africa and Moçambique, between 22°25’ - 25°32’ S and 30°50’ - 32°02’ E (Fig. 1.2). The park has a north to south orientation, spanning almost 400 kilometres in length, but with variable width distances giving it an average width of approximately 65 kilometres. The eastern boundary of the park is lined by the Lebombo Mountains. Two main river systems dissect the park in west-east direction, the Limpopo system in the north and the Nkomati system in the South. These systems comprise six main rivers, namely: (i) Crocodile, Sabi, and Sand in the south; (ii) Olifants and Letaba in the centre; and (iii) Luvuvhu and Limpopo (which forms the northern boundary) in the north. The geology of the park is divided longitudinally into granite formations in the west and mostly basalts in the east (Joubert 1986). This has a direct influence on the main soil types, where in the west, the soils are mainly sandy and light in colour, while in the eastern half is dominated by dark clay soils. The park can be divided into 35 landscapes that were identified based on geomorphology, climate, soil, vegetation patterns, and to an extent associated fauna (Gertenbach 1983). The park has a dry tropical climate which has induced deciduous savannahs (Venter & Gertenbach 1986). There is a decreasing rainfall gradient as one moves from south to north ranging from 740 mm in the south and approximately 440 mm in the north (Gertenbach 1980). In addition, Gertenbach (1980) identified two rainfall cycles, the wet and dry cycles, which differ by about 26%, with each cycle lasting for up to 10 years. There are 14 major vegetation assemblages, which are strongly correlated with rainfall patterns, identified for the park (Venter & Gertenbach 1986).

The park has a diverse range of faunal species (Joubert 2012). There are primitive life forms such as viruses, bacteria and protozoans, which together with invertebrates that act as endo- and ecto-parasites play an important role in the population dynamics of faunal species inhabiting the park (Joubert 2012). Invertebrates found in the park include insects, arachnids, scorpions, crustaceans and acarians (Joubert 2012). The vertebrates include fish, amphibians, reptiles, birds, and mammals. Herbivore distribution follows vegetation assemblages, which mirrors the 35 landscapes in the park (Gertenbach 1983). There carnivores are represented by lions, leopards, spotted hyaenas, cheetahs, and wild dogs (Mills & Funston 1993).

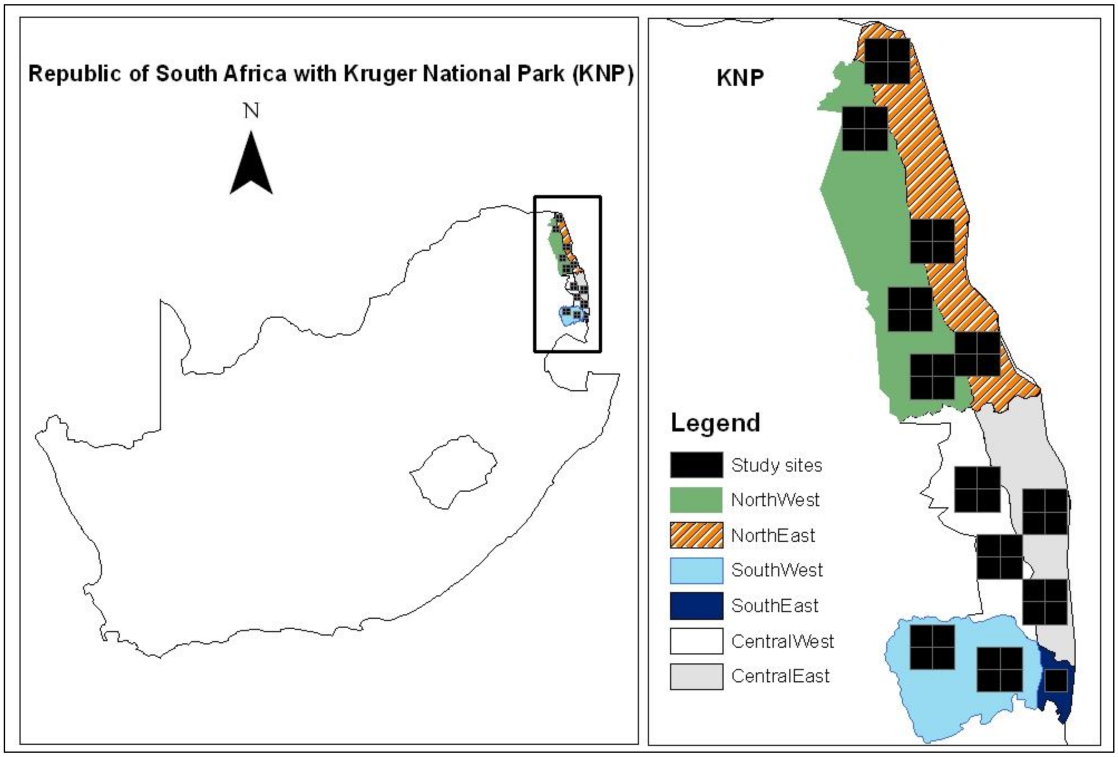


Figure 1.2. Map of the Kruger National Park divided into six zones following Ferreira & Funston (2010). The descriptions of the shaded areas are as follows: NorthWest – Low bTB prevalence (0-5%) and low prey biomass (643 kg/km^2); NorthEast – Low bTB prevalence (0-5%) and medium prey biomass (1068 kg/km^2); CentralWest – Medium bTB prevalence (15-24%) and high prey biomass (1396 kg/km^2); CentralEast – Medium bTB prevalence (15-24%) and very high prey biomass (2749 kg/km^2); SouthWest – High bTB prevalence (40-60%) and high prey biomass (1976 kg/km^2); SouthEast – High bTB (40-60%) and very high prey biomass (2412 kg/km^2).

Approach

The thesis is divided into six chapters, four of which are aimed at addressing the main research questions alluded to above. The first step of the study focused on designing a robust technique to estimate leopard abundances. Using the results of the pilot study, focus then shifted to estimating the leopard population for the whole of KNP. Following the estimation of leopard abundances the project tested the meso-predator release and niche packing hypotheses by comparing leopard abundances with estimates for lion and spotted hyaena in the park. The study then assessed space use by leopards relative to indices of resource distributions and investigated if lion movement behaviour were a factor in how leopards navigated the landscape. Below is the outline of the thesis broken down into four chapters according to the key questions as well as the sixth chapter, which summarizes the project outcomes:

Chapter 2. Calibrating a camera trap based biased mark-recapture sampling design to survey the leopard population in the Kruger National Park, South Africa

For this chapter, I used the biased survey to estimate leopard abundances on the N’wanetsi concession in the KNP using motion sensitive camera-traps. The method is biased because cameras were placed in areas of known leopard activity based on local knowledge of leopard activity. The aim of this part of the study was to design and test a technique of estimating accurate and precise leopard abundances by: (i) defining how individual trapping success varied with time; (ii) determining the effort to achieve an asymptote in new individuals captured; (iii) identifying the effort at which precision of population estimates stabilized; and (iv) establishing the abundance of leopards in the study area. This study formed the basis for consequent photographic survey for the whole KNP.

Chapter 3. A camera-trap based photographic survey reveals robust leopard population abundances in the Kruger National Park, South Africa.

After successfully completing the calibration phase, KNP was divided into six zones following Ferreira and Funston (2010). Fourteen sites with area sizes ranging from 198 km^2 – 400 km^2 were selected throughout KNP for the camera-trap photographic survey (Fig. 1.2). The cameras were left to run for approximately 45 days to satisfy the assumptions of population closure. Specific aim of this chapter was to estimate leopard abundances in the KNP. The chapter formed a basis for the next chapter where leopard estimates were compared with lion and spotted hyaena estimates.

Chapter 4. Comparing regional abundances of large carnivores in the Kruger National Park, South Africa

This chapter investigated the meso-predator release and niche packing hypotheses. The study used spatially explicit large carnivore abundances to investigate how leopards compared with lion and spotted hyaena abundances throughout KNP. Leopard abundances were guided by the results of Chapter 3, while lion and spotted hyaena abundances in the KNP were obtained from call surveys that were implemented between 2005 and 2009 (Ferreira & Funston 2010). The chapter was based on the premise that there was either evidence of meso-predator release or niche packing as predicted by numerical comparisons between leopards and other large carnivores.

Chapter 5. Spatial and temporal separation between lions and leopards in the Kruger National Park and the Timbavati Private Nature Reserve, South Africa

The focus of this chapter was based on collar data from two study areas, the KNP and the Timbavati Private Nature Reserve (TPNR). The KNP study area included seven leopards comprising four females and three males; and one lion pride in the southern section of the park. The TPNR study site comprised a pride, a single nomadic young male lion, and a male leopard. Data on indices of leopard resources were obtained from water distribution model, Digital Terrain Model, woody cover percentage, and Enhanced Vegetation Index (CSIR Meraka, 2013). In addition, the relationship between GPS fixes and distances to roads and streams were measured because leopards are known to use roads and areas near streams frequently. Lion data were transformed into landscapes of activity based on hulls that were frequently visited, but with short durations of stay and hulls that were less frequently visited, but with long duration of stay. The specific aim of this chapter was to investigate if leopard movement behaviour in KNP and TPNR was primarily driven by resource distribution or by how lions used the landscape.

Chapter 6. Synthesis, recommendations and conclusions

The final chapter learned synthesis of the main findings of the present study, knowledge gaps, opportunities, final conclusions and recommendations. The essence of this chapter is to examine the findings from this research and explore the links with major topics in Conservation Biology, Community Ecology, and Landscape Ecology by invoking: (i) the significance of disease as a major player in shaping ecosystem processes; (ii) revisiting two theories relating to co-existence in sympatric species, namely niche packing and meso-predator release hypotheses; and (iii) landscape use and movement behaviour. This chapter also explores and recommends the applicability of this study in informing the adaptive management strategy adopted by the management at KNP for their use in the development and implementation of the large carnivore management programme.

References

Bailey, T.N. 1993. *The African leopard. Ecology and behaviour of a solitary felid.* New York: Columbia University Press.

Balme, G., Slotow, R., & Hunter, L. 2009. Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation,* **142:** 2681-2690.

Balme, G., Slotow, R., & Hunter, L. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation* **doi:** 10.111/j.1469-1795.2009.00342.x

Bertram, B.C.B. 1999. Leopard. In: *The Encyclopaedia of Mammals,* 44-48. Ed: D.W. Macdonald. Oxford: Andromeda Oxford Limited.

Bengis, R.G., Grant, R. & de Vos, V. 2003. Wildlife diseases and veterinary controls: A savanna ecosystem perspective. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity.* Eds: J.T. du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington, DC, USA.

Bothma, J. du P., Knight, M.H., Le Riche, E.A.N. & van Hensbergen, H.J. 1997. Range size of southern Kalahari leopards. *South African Journal of Wildlife Research,* **27:** 94-99.

Bothma, J. du P. & Walker, C. 1999. *Larger carnivores of the African Savannas.* Pretoria, van Schaik.

Burkepile, D.E., Burns, C.E., Tambling, C.J., Amendola, E., Buis, G.M., Govender, N., Nelson, V., Thompson, D.I., Zinn, A.D., & Smith, M.D. 2013. Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. *Ecosphere,* **4:** 139. http://dx.doi.org/10.1890/ES13-0078.1.

Caron, A., Cross, P.C., & du Toit, J.T. 2003. Ecological implications of bovine tuberculosis in African buffalo herds. *Ecological Applications,* **13:** 1338-1345.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour,* **53:** 667-686.

Dayan, T. & Simberloff, D. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Reviews*, **28:** 99-124.

Ferreira, S.M., & Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in the Kruger National Park, South Africa. *Wildlife Research,* **37:** 1-13.

Gertenbach, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe-African Protected Area Conservation and Science,* **23:** 35-43.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe-African Protected Area Conservation and Science,* **26:** 9-121.

Grimbeek, A.M. 1992. The ecology of the leopard (*Panthera pardus*) in the Waterberg. MSc Thesis, University of Pretoria.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, **270:** 298-313.

Joubert, S. 2012. *The Kruger National Park: A History, Prehistory – 1994. Volume II*. 2nd Edn. High Branching (Pty) Ltd, Johannesburg, RSA.

Karanth, K.U. & Sunquist, M.E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology*, **64:**439-450.

Keet, D.F., Kriek, N.P.J., Penrith, M.-L., Michel, A. & Huchzermeyer, H. 1996. Tuberculosis in buffaloes (*Syncerus caffer*) in the Kruger National Park. Spread of the disease to other species. *Onderstepoort Journal of Veterinary Research*, **63:** 239-244.

Kissui, B.M., & Packer, C. 2004. Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London*, **271:** 1867-1874.

Marker, L.L. & Dickman, A.J. 2005. Factors affecting leopard (*Panthera pardus*) spatial ecology, with reference to Namibian farmlands. *South African Journal of Wildlife Research*, **35:** 105-115.

Marnewick, K., Ferreira, S.M., Grange, S., Watermeyer, J., Maputla, N., & Davies-Mostert, H.T. 2014. Evaluating the status of African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist-based photographic surveys in the Kruger National Park. *PloS ONE*, **9:** e86265.doi:10.1371/journal.pone.0086265.

Maruping, N.T. 2014. Drivers and consequences of bovine tuberculosis in lions of the Kruger National Park, South Africa. DTech. Thesis, Tshwane University of Technology.

McManus, J.S., Dickman, A.J., Gaynor, D., Smuts, B.H. & Macdonald, D.W. 2014. Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. *Oryx*, **doi:** 10.1017/S0030605313001610.

Meiri, S., Dayan, T., & Simberloff, D. 2005. Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology*, **86:** 1432-1440.

Menge, B.A. Olson, A.M, & Dahloff, E.P. 2002. Environmental stress, bottom-up effects, and community dynamics: integrating molecular-physiological and ecological approaches. *Integrative and Comparative Biology*, **42:** 892-908.

Michel, A.L., Bengis, R.G., Keet, D.F., Hofmeyr, M., De Klerk, L.M., Cross, P.C., Jolles, A.E., Cooper, D., Whyte, I.J., Buss, P., Godfroid, J. 2006. Wildlife tuberculosis in South African conservation areas: implications and challenges. *Veterinary Microbiology*, **112:** 91-100.

Mills, M.G.L. & Funston , P.J. 2003. Large carnivores and savannah heterogeneity. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds: J.T. du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington, DC, USA.

Nowell, K. & Jackson, P. 2006. Wild Cats, Survey and Conservation Action Plan. IUCN/SSC Cat specialist group. IUCN.

Ott, T., Kerley, G.I.H. & Boshoff, A.F. 2006. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology*, **42:** 31-37.

Owen-Smith, N. & Mills, M.G.L. 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, **77:** 173-183.

Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology*, **25:** 142-53.

Pianka, E.R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Science USA*, **71:** 2141-2145.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. 2009. The rise of the mesopredator. *BioScience*, **59:** 779-791.

Radloff, F.G.T. & du Toit, J.T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology*, **73:** 410-423.

Renwick, A.R., White, P.C.L. & Bengis, R.G. 2007. Bovine tuberculosis in southern African wildlife: a multi-species host-pathogen system. *Epidemiology and Infection*, **135:** 529-540.

Riordan, P., Hudson, P. & Albon, S. 2007. Do parasites matter? Infectious diseases and the conservation of host populations. In: *Key Topics in Conservation Biology*. Eds. D. Macdonald and K. Service. Blackwell Publishing, UK.

Ripple, W.J., Estes, J.A, Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D, & Wirsing, A.J. 2014. Status and ecological effects of the world's largest carnivores. *Science*, **343:** 1241484. doi:1126/science.1241848.

Ritchie, E.G. & Johnson, C.N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12:** 982-998.

Russell, J.C., Lecomte, V., Dumont, Y. & Le Corre, M. 2009. Intraguild predation and mesopredator release effect on long-lived prey. *Ecological Modelling,* **220:** 1098-1104.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., & Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature*, **413:** 591-596.

Sinclair, A.R.E., Mduma, S., & Brashares J.S. 2003. Patterns of predation in a diverse predator-prey system. *Nature,* **245:** 288-290.

Škaloudová, B., Zemek, R., & Křivan, V. 2007. The effect of predation risk on an acarine system. *Animal Behaviour*, **74:** 813-821.

Skinner, J.D. & Chimimba, C.T. 2005. *The Mammals of the Southern African Subregion*, 3rd edn., Cambridge University Press, Cambridge.

Smith, K.F., Behrens, M.D., Sax, D.F. 2009. Local scale effects of disease on biodiversity. *EcoHealth.* Electronic publication, Springer New York, ISSN 1612-9210.

Steyn, V. & Funston, P.J. 2006. Land-use and socio-spatial organisation of female leopards in a semi-arid wooded savanna, Botswana. *South African Journal of Wildlife Research*, **39:** 126-132.

van Helden, P. & Uys, P. 2009. Modelling predator-predator population dynamics in the context of BTB. *Disease Risk Assessment Workshop Report: African Lion (Panthera leo) Bovine Tuberculosis.* Eds. Keet, D.F., Davies-Mostert, H., Bengis, R.G., Funston, P., Buss, P., Hofmeyr, M., Ferreira, S., Lane, E., Miller, P. & Daly, B.G. Conservation Breeding.

Venter, F.J. & Gertenbach, W.P.D. 1986. A cursory review of the climate and vegetation of the Kruger National Park. *Koedoe-African Protected Area Conservation and Science,* **29:** 139-148.

Chapter 2. Calibrating a camera-trap based biased mark-recapture sampling design to survey the leopard population in the Kruger National Park, South Africa

*Nakedi W. Maputla[a,b], Christian T. Chimimba[b], Sam M. Ferreira[c]

*Corresponding author

a) *African Wildlife Foundation (AWF), AWF Conservation Centre, Ngong Road, Karen, P.O. Box 310, 00502, Nairobi, Kenya*
Email: nwmaputla@zoology.up.ac.za

b) *Mammal Research Institute (MRI) and DST-NRF Centre of Excellence for Invasion Biology (CIB), Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028, South Africa*
Email: ctchimimba@zoology.up.ac.za

c) *Scientific Services, South African National Parks (SANPARKS), Skukuza, 1350, South Africa*
Email: sam.ferreira@sanparks.org

This chapter was published in *African Journal of Ecology* under the following full citation:

Maputla, N.W., Chimimba, C.T., & Ferreira, S.M. 2013. Calibrating a camera trap-based biased mark-recapture sampling design to survey the leopard population in the N'wanetsi concession, Kruger National Park, South Africa. *African Journal of Ecology*, **51:** 422-430.

Abstract

Estimating large carnivore abundance can be a challenging undertaking. A biased leopard population survey was conducted at the N'wanetsi concession in the Kruger National Park using motion sensitive camera traps from April to August 2008. Effort included 88 trapping occasions and 586 trap days. It yielded 24 leopard photographs, comprising 14 adults, 11 males and 3 females. The capture rate was determined to be 24.4 trap days per leopard. Estimates of population abundance stabilized at approximately 500 trap days. Precision of population estimates began to stabilize after 378 trap days. We estimated that there were 19 leopards in an area of 150 km^2 (SE = 4.55; CI = 15-35; $P = 0.013$). Leopard density was estimated at 12.7 (95% CI: 9.3-24) leopards for every 100 km^2. We recommend that the method we employed be used to survey the leopard population in the Kruger National Park and surrounding areas.

Introduction

Estimating population abundances for solitary and secretive carnivore species with extensive home ranges poses challenges caused by sampling design and the suitability of methods (Karanth & Nichols 2000; Carbone & Gittleman 2002). Indirect methods use signs such as kills and scats to estimate population abundance (Karanth & Sunquist 1995; Owen-Smith & Mills 2008; Marker *et al.* 2003; Ott *et al.* 2006), habitat assessments (Daly *et al*. 2005), prey availability (Karanth & Sunquist 1995; Carbone & Gittleman 2002; Bailey 1993) and pug marks (Stephens *et al.* 2006). Sometimes researchers conduct interviews with local people to carry out inventories (Tobler *et al.* 2008). However, such indices carry assumptions about the relationship between population size of a species and index values related to species local population structure such as demography, density, and other trends.

Direct methods of estimating large carnivore abundances use formal survey designs, such as, call-up stations where a recording of a prey species, e.g., buffalo calf in distress, is played repeatedly using an amplifier and speakers to attract large carnivores (e.g. Mills *et al.* 2001; Ferreira & Funston 2010) or mark-recapture techniques using cameras that detect movement (Karanth & Nichols 1998; Balme *et al.* 2009). Data collected using these methods may be good for population monitoring, given enough time and resources (Harris 1986); however, sometimes they are found to be unreliable (Karanth & Nichols 1998; Tobler *et al.* 2008). For species with natural markings, the use of camera traps may provide valuable answers to such challenges and, in some instances, natural markings may not even be necessary to establish animal abundance from photographs

(Rowcliffe *et al.* 2008). The use of camera traps may be particularly suitable for surveying secretive carnivores for which signs are hard to find (Karanth & Nichols 2000).

Estimating leopard (*Panthera pardus*) abundance epitomizes these challenges. Passive detection of individually recognizable animals through camera traps allows the use of mark and recapture techniques to estimate population abundance (Nichols 1992; Kauffmann *et al.* 1997; Karanth & Nichols 2000; Efford *et al.* 2004; Marnewick *et al.* 2008). Abundance can be estimated with a narrow margin of error, if detection probability is high and camera shyness is low (Wegge *et al*. 2004). Such camera trap based mark-recapture studies have been used to estimate tiger numbers in Asia (Karanth & Nichols 1998), defined carnivore communities in Namibia (Kauffmann *et al.* 1997, Stein *et al.* 2008), and provided cheetah population estimates in South Africa (Marnewick *et al.* 2006; Marnewick *et al.* 2008).

Even so, camera trap based mark-recapture approaches are seldom used following standardized methods, thus often overlooking camera performance and efficiency (Kelly 2008). This may result in varying surveying efforts (Henschel & Ray 2003; Tobler *et al.* 2008); effort here implying the duration of camera deployment. This may be caused by site-specific characteristics that make standardisation of methods inapplicable across a large geographical space with varying landscape features (White *et al.* 1978; Harris 1986; Agresti 1994; Kéry & Schmidt 2003; Efford *et al.* 2004). Researchers thus need to accommodate changes across time and space to account for variability when they conduct this type of work.

Estimating population size with acceptable accuracy and precision is a key challenge for field ecologists (Harris 1986; Mills *et al.* 2001; Efford *et al.* 2004; Ferreira & Funston 2010). Attaining precision is mainly affected by incomplete detection (White *et al.* 1978; Aebischer 1986; Harris 1986; Agresti 1994; Thompson 2002; Kéry & Schmidt 2003; Efford *et al.* 2004), trapping design (Nichols 1992, Karanth & Nichols 2000), and effort (Karanth & Nichols 2000). For secretive carnivores like leopards, researchers can use biased sampling anticipating the likely activity hotspots (Karanth & Nichols 1998), attractant sampling like luring individuals to a trapping site (Henschel & Ray 2003), systematic sampling (Efford *et al.* 2004, Wegge *et al.* 2004, Kauffmann *et al.* 2007) and complete random sampling (Maffei *et al.* 2004) or combinations of these. Several authors favoured biased sampling (Karanth & Nichols 1998; Jackson *et al.* 2006; Marnewick *et al.* 2006; Marnewick *et al.* 2008), but seldom checked the sampling effort to obtain estimates with robust precision. This carries some value, since the detection of trends are dependent on precision of estimates (Harris 1986), but effort has cost and efficiency implications.

In this study, we assessed these trade-offs using biased sampling of leopards as a case study. We aimed to assess the efficiency of cameras placed in a biased sample design to estimate leopard population sizes by (1) defining how individual leopard trapping success varied with time; (2) determining the effort to achieve an asymptote in new individuals captured; (3) identifying the effort at which precision of population estimates stabilize; and (4) establishing the abundance of leopards in the study area. We make recommendations on the sample design to estimate leopard abundances for a large area such as the Kruger National Park.

Materials and methods

Study area

The study was carried out at the N’wanetsi Concession, which covers 15,000 hectares in the south central part of South Africa’s Kruger National Park (KNP) on the border with Mozambique (Fig. 2.1). The study area is in the subtropical semi-arid zone aligning with the Lebombo Mountains and has a mean annual rainfall of 514.6 mm (data from 1966 – 1999). There are marked differences in temperature between seasons with temperatures exceeding 40°C in the summer and as low as 0.2°C during winter. Two ephemeral rivers, the N’wanetsi and the Sweni, dissect the concession. The most dominant vegetation types are *Acacia – Sclerocarya* savanna woodland in the west of the Lebombo Mountains and the mixed *Combretum* woodland in the east, as well as in the mountains.

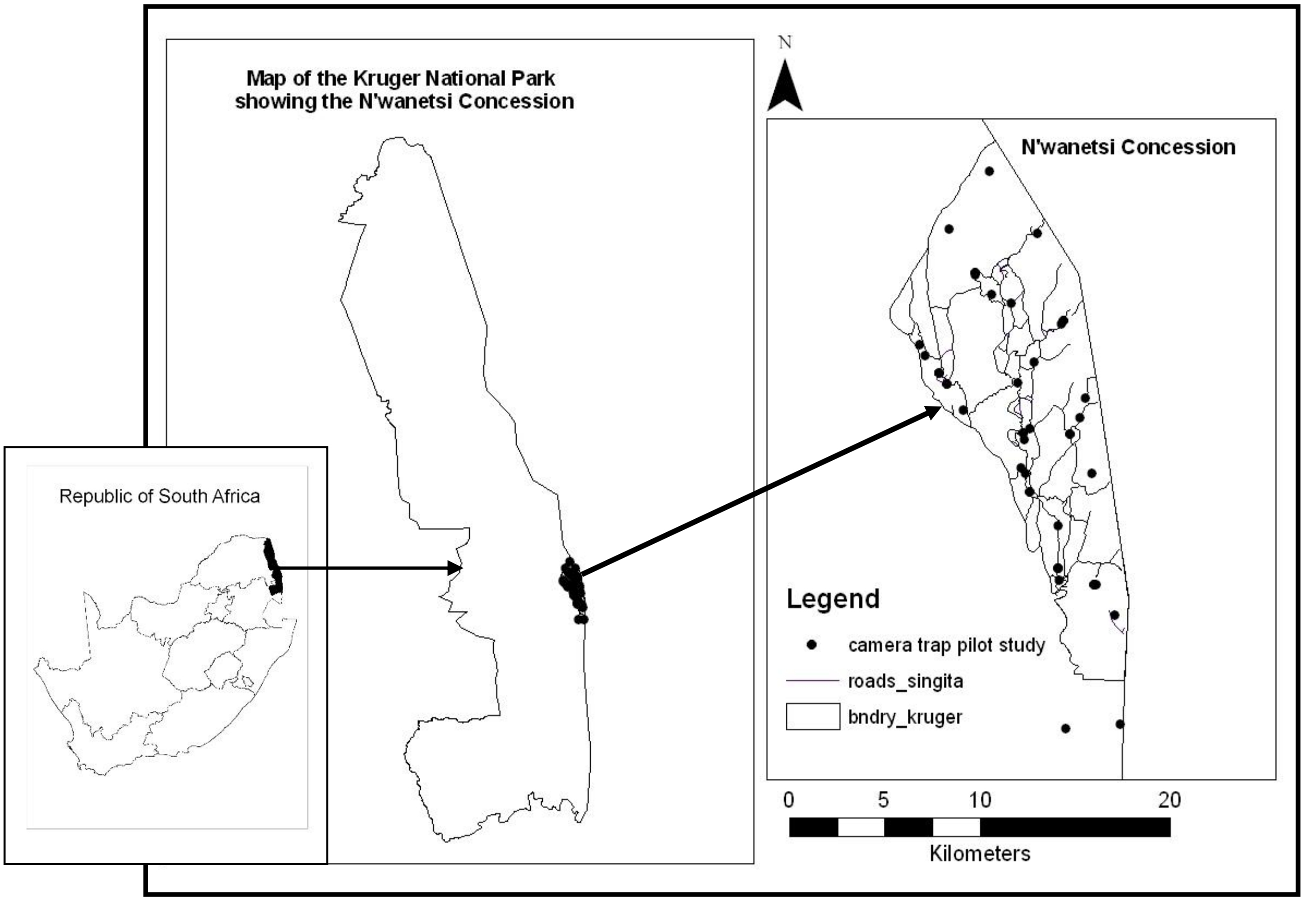


Figure 2.1. Map of the Republic of South Africa (inset) and the Kruger National Park with the study area, the N’wanetsi concession.

Data collection

We used a biased sampling design (see Karanth & Nichols 1998) and placed nine Cuddeback® EXcite™ C2000 digital cameras and one Reconyx™ RM 45 camera in areas of known leopard activity based on the advice of the N'wanetsi Concession's guides: game trails leading toward water points, drainage lines and ridges in the Lebombo Mountains were focal points. An infra-red transmitter triggered a camera if the beam was broken by a moving object. Cameras also recorded times and dates when photographs were taken. A one minute delay period between photographs was imposed on each camera to counter the effects of large herds of animals moving in the area. We placed the cameras in close proximity to the roads for logistical reasons. In the beginning of the study we had 10 working cameras, but as the survey continued two cameras malfunctioned. The cameras captured leopard pictures over four sessions between April and August during 2008 (Fig. 2.1). For each sampling session (22 days of 24 hour length), some traps were shifted to accommodate some logistical constraints. However, traps covered the same study area in a similar biased sample design i.e., traps were placed in areas of known or expected leopard activity. We pooled trapping sessions to give a total of 88 occasions.

To protect cameras from elephants, rhinos and hyenas, we placed them inside steel casings, made to fit the cameras. Casings were fixed to drop poles and lodged firmly in the ground. We also sprayed the casings with pepper spray to further protect them from being uprooted by elephants or rhinos. We did not have inclinations to believe that the use of pepper spray would have an effect on leopard activity around the traps as the cameras were not necessarily placed in the middle of the path, but out of the way so as not to interfere with animal movements. To upload photographs onto a laptop computer we visited camera stations any day after the third day of being placed or being checked.

Cameras that malfunctioned were excluded from the survey, but their data up to the day of malfunction were used. To overcome the inevitable inconsistencies caused by periods of not trapping in between surveys and camera malfunctions, each camera was allocated to a trap day. A trap day was defined as a camera active for a 24 hour period. Our data thus comprised 586 trap days.

Data analysis

Identification - After uploading leopard pictures to the computer, we used the unique spot patterns on the flanks, legs, and face to identify and allocate an identity number to each individual. For this study, we used only one camera per station, which meant only one flank at a time was captured. To compensate for this discrepancy, we used images that were provided by visitors and guides at the N'wanetsi concession to verify the identity of each individual. In cases where there were no supplementary images, we used only the right flank to identify individuals because 90% of the images were on the right flanks.

Captures and non-captures were recorded as "1's" and "0's", respectively to create a capture history for each leopard in the form of a matrix. The matrix was imported into program CAPTURE (White *et al.* 1978; Rextad & Burnham 1991) for analysis.

Cumulative new individuals and capture rates - To define how individual trapping success varied with time we plotted the cumulative number of captures against time. The capture rate was calculated by dividing increase in effort, which refers to the number of trap days, by the number of leopard photographs during the survey period. In addition, we ran 100 simulations that rearranged capture events for all the captures to explore the stabilisation of capturing new individuals with increasing effort.

We used the generalized accumulation curve ($y = ax^b$) to evaluate how leopard numbers increased as more individuals were captured (Flather 1996). Desirable effort was achieved when the number of new leopards increased by less than 10% per unit increase in effort (Flather 1996; Thompson et al. 2003; Wegge *et al.* 2004).

To evaluate whether we observed all the leopards in the study site, we plotted the number of leopards *versus* the number of individuals as more and more captures were recorded in the survey. To account for individuals that we may have missed in the survey we used Estimate S 8.2.0. (Colwell 2006) to :1) generate data using jackknife and bootstrap methods; 2) generate abundance based coverage estimator (ACE), which uses information based on individuals that were captured on 10 or less occasions and incidence based coverage estimator (ICE), which uses information on leopards that were captured in ten or less camera trap stations (Lee & Chao 1994); and 3) fit the Michaelis-Menton equation (MM) based on the Mao Tau's curve for leopards observed (Lobs) to predict the number of leopards where the curve levelled off.

Population estimates and precision - We used program CAPTURE to estimate leopard abundance. CAPTURE uses mark-recapture methods to estimate population densities and abundance, by testing for population closure and assuming that all animals have equal opportunity of being captured. Test for population closure after 88 occasions yielded a z-score of -3.28 ($P < 0.05$) rejecting the assumption that the population was closed. However, given that there were no observed deaths or introductions during the survey, we assumed that the population was closed (Otis *et al.* 1978). Furthermore, CAPTURE has several models that account for the variability brought about by time, behaviour, heterogeneity and a combination of the three (Otis *et al.* 1978, Karanth & Nichols 2000, Wang & Macdonald 2009). For each occasion parameter estimates were generated under a model that best fit the data (see Otis *et al.* 1978). In this case, parameter estimates were generated under the assumptions of model M_h, which was the best-fit model for the analysis. We used the Jackknife estimator to estimate leopard capture probabilities (P) and population size (N).

To identify the effort at which the values and precision of population estimates stabilised, we recalculated estimates for each simulation and plotted values and precision against effort. Desirable precision of estimates was achieved when the variance was consistently less than 10% with increasing effort.

For each level of effort we calculated abundance to generate a time series of increased survey effort. We then calculated the coefficient of variance (CV) in abundance indices at each increasing measure of effort. Again, we used the generalised accumulation curve and defined the desirable effort to estimate abundance when the CV changed by less than 10% with increasing effort (Flather 1996).

Results

Defining how individual trapping success varied with time

The 586 trap day effort yielded 24 leopard photographs of 14 individual adult leopards, resulting in a capture rate of 24.4 trap days per adult leopard capture. Of the 14 individuals, five were re-captures. One individual was captured five times while two were captured three times and two twice (Fig. 2.2A). There were eleven males and three females.

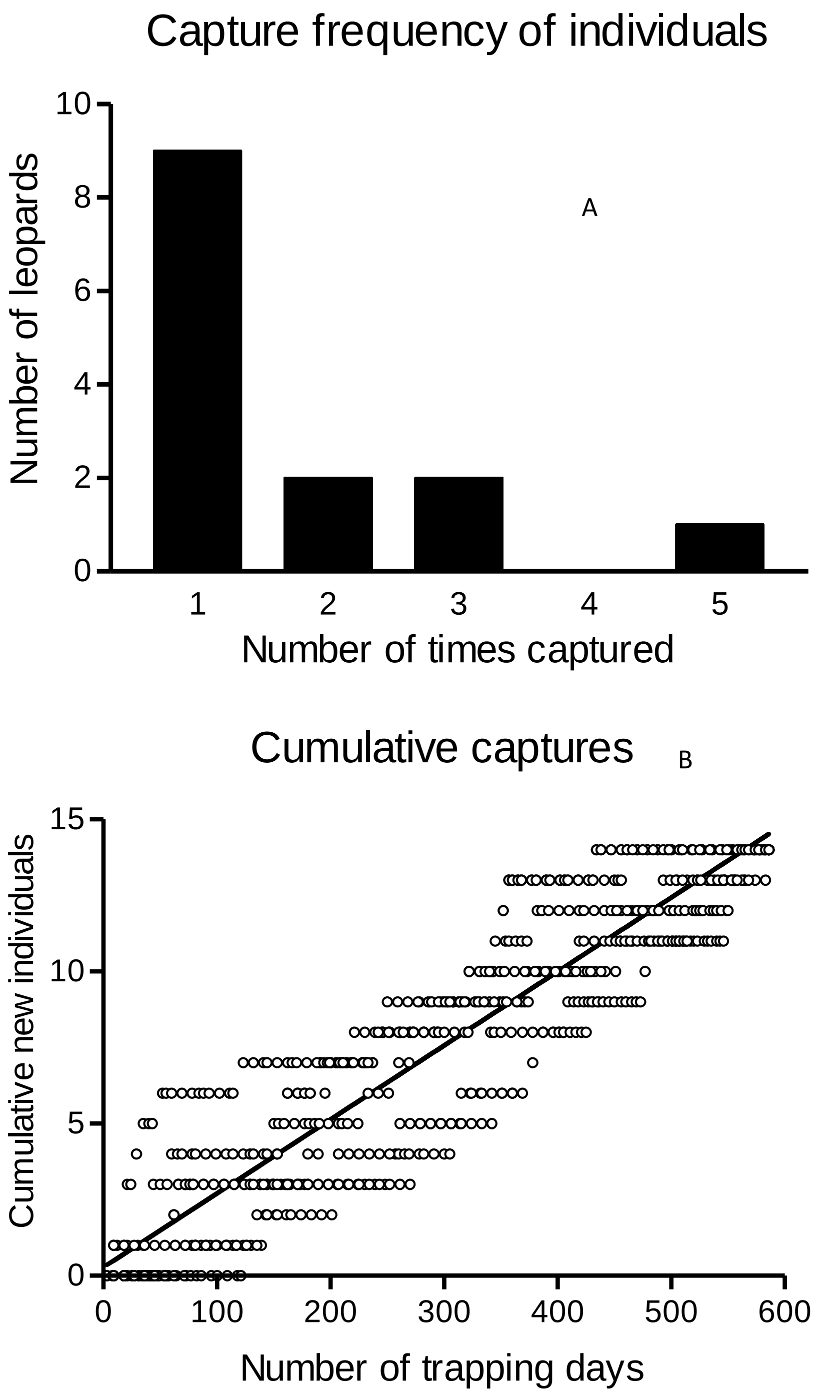


Figure 2.2. A) Capture frequencies for leopards in the N'wanetsi Kruger National Park concession during the period April - August 2008. B) Cumulative number of individual leopards with increasing effort following capture simulations (100 iterations).

Achieving an asymptote in new individuals captured

Cumulative number of captures increased with effort. New individuals continued to be encountered as the number of trapping days increased and did not reach and asymptote (Fig. 2.2B). Mean number of leopards observed Lobs (Mao Tau) was 14 (95% CI = 8.88-19.12) (Fig. 2.3). An asymptote was not reached with regards to the values we would get for an infinite number of randomizations following Mao Chang Xuan including the upper and lower confidence intervals. An asymptote also was not reached for jackknife, bootstrap, ACE, and ICE estimators (Fig. 2.3). The fitted MM continued to increase, albeit negligibly, with the increasing number of new captures (Fig. 2.3).

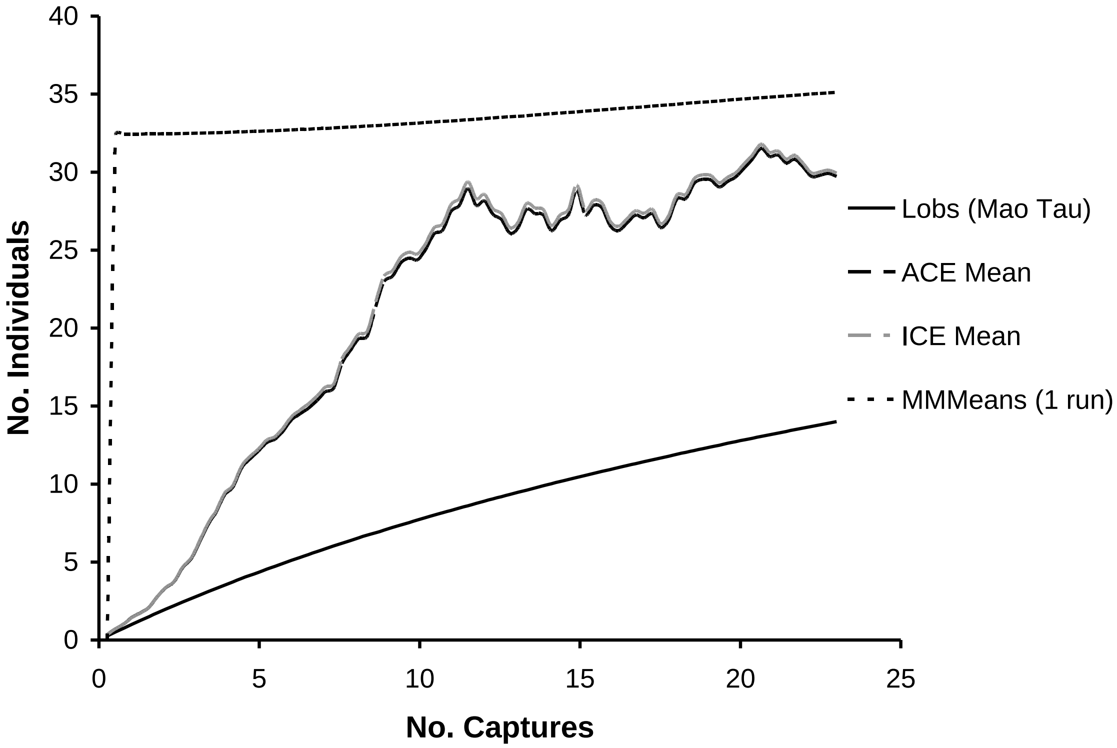


Figure 2.3. Graph output from EstimateS for accumulation curves with abundance estimators namely leopards observed (Lobs), abundance based coverage estimator (ACE) incidence based coverage estimator (ICE) and the Michaelis-Menton mean estimator (MMMeans).

Effort at which precision of population estimates began to stabilize

Population estimates stabilised after 500 trap days (Fig. 2.4A). At 378 trap days the precision of population estimates began to stabilise (Fig. 2.4B). Accuracy of population estimates was validated by visual presentation of stabilisation of standard error with increasing effort (Fig. 2.4C). In the final 208 trap days and 47 trapping occasions the variance recorded scores of < 1.00 on average, a marked change from the variance scores of $\geq$ 20 in 23 occasions at the beginning of the survey (Fig. 2.4B). After 88 occasions, the probability of leopard capture was estimated at 0.013 and population was estimated at 19 individuals (SE = 4.55; 95% CI = 15 – 35).

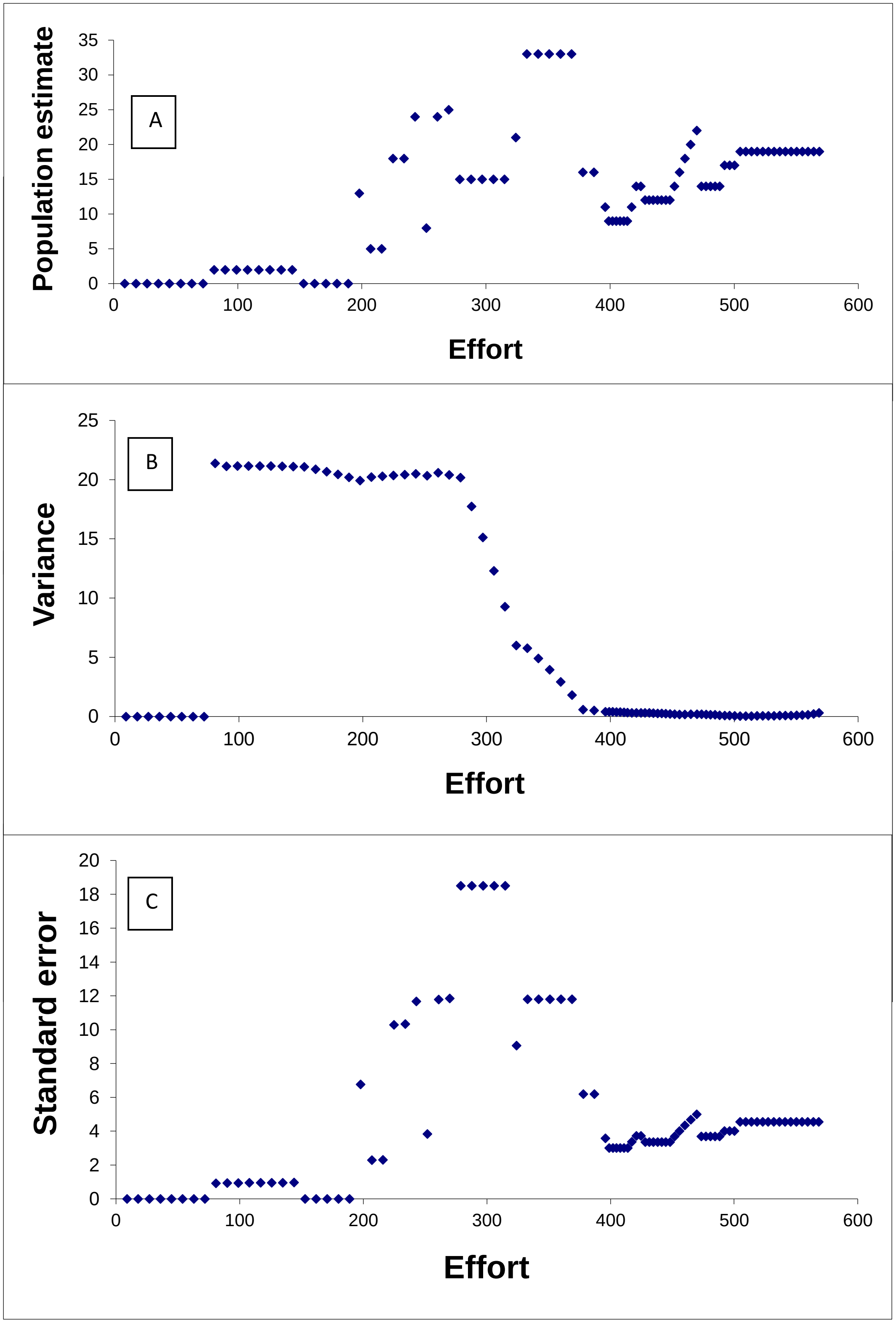


Figure 2.4. A) Changes in leopard population estimates at the N'wanetsi concession of the Kruger National Park with increasing effort. B) A plot depicting variance in population estimates for the N'wanetsi concession of the Kruger National Park leopards with increasing effort. C) Standard error of the population estimate plotted against effort from the photographic surveys in the N'wanetsi concession of the Kruger National Park.

Discussion

Attempts to validate robust leopard population estimates in South Africa's Kruger National Park have been minimal (but see Bailey, 1993), due to several challenges including resources and time needed for such a study. A lack of standardised methods to conduct leopard population surveys further exacerbated the challenge. The use of camera traps may eliminate some of these challenges, because cameras are non-invasive tools that have provided reliable information for researchers and wildlife managers in other places (Karanth, 1998). Studies involving camera trapping designs include short- and long-term population monitoring (Karanth *et al.* 2006; Sharma & Jhala 2011), ecological and temporal partitioning of large carnivores (Romero-Muñoz *et al.* 2010) and species inventories (Tobler *et al.* 2008). In southern Africa, several studies monitored and estimated population numbers for cheetah (Marnewick *et al.* 2006; Marnewick *et al.* 2008), leopards (Balme *et al.* 2009 a, b; Balme *et al.* 2010), and provided species inventories (Stein *et al.* 2008). We are aware of two studies (Wang & MacDonald 2009; Sharma & Jhala 2011) that included explicit evaluation of sampling effort to obtain statistically robust leopard population estimates.

In our study we focused on addressing these shortcomings. Leopards are secretive and solitary (Bailey, 1993; Skinner & Chimimba, 2005) and use a variety of landscapes (Bothma & Bothma, 2005). Both these factors may induce variance in the effort needed to obtain robust population estimates. Our results suggest that ~ 500 trap days are required to achieve stabilisation of population estimates and precision thereof. This requirement is in accordance with that noted by Wang & Macdonald (2009).

We noted two potential anomalies. First, the number of new individuals added to the population did not stabilize with increasing effort (Fig. 2.3). Individual accumulation curves showed little sign of reaching an asymptote with increasing number of leopards being captured. After 20 leopards captured, the number of unique leopards continued to increase. Similarly, bootstrap and jackknife estimate means kept on rising without showing signs of levelling out, suggesting that we would continue to have new individuals coming into the system with increasing effort. In contrast, abundance estimators, particularly ACE and ICE, were not as sensitive and fluctuated after 10 captures. The Michaelis-Menton mean estimator reached an asymptote at approximately 33 captured leopards even though there is subtle indication that it is increasing as more individuals are captured. While this estimator (originally designed for enzyme catalysed reactions) rises rapidly, raising questions about its biological plausibility in this context, it gives the data a structure and an indication of where one would expect to have captured all the individuals in the study area.

A second anomaly associated with population structure and make-up also arose. We captured more males than females (at a ratio of 4:1), a marked disparity in captures. This is surprising given that leopards in the savannah ecosystems have average home ranges of 16 km^2 (Skinner & Chimimba 2005). In addition, males generally occupy territories overlapping two to four female territories (Bailey 1993). Unlike lions where sexual dimorphism is distinct, in leopards, especially between males of approximately two years of age, it may not always be possible to differentiate the sexes (Balme *et al.* 2012).

We revisited the photographs for verification according to the recommendations by Balme *et al.* (2012) and found our assessment to be correct. The captured individuals were identified and their sex and age determined according to suggestions provided in Balme *et al.* (2012). Despite this, based on the current knowledge of leopard behaviour and ecology, we should have noted more females than males. Given that two of the females known to the guides at the time of the survey in the concession were not captured, several factors may contribute to this anomaly including: 1) the sampling design is heavily biased towards male preferred paths; 2) females are not well-represented, suggesting that the study population is different from other studied leopard populations; 3) there are hidden factors that may be contributing negatively to females; 4) the cameras were set too far apart outside the females' home ranges; 5) the males that we captured were dispersing individuals in search of a new home); and 6) the present data may just be a snap shot of a population in transition from one state to another. Similar findings were reported for cheetahs (Marnewick *et al.* 2006; Marnewick *et al.* 2008; Chapman & Balme 2010.

Regarding camera shyness, a study on the response of tigers to camera traps found that some animals had a tendency to avoid camera stations, especially after the first exposure to the camera (Wegge *et al.* 2004). This is unlikely in our study as several leopards were captured on two or more occasions (Fig. 2.2). Even so, we anticipated variability in individual capture probabilities, because the model also may account for differences in home ranges, land use patterns and social hierarchy (Otis *et al.* 1978). This was confirmed when model M_h was consistently selected as the best fit during simulations.

We did not consider the use of baits and lures in the present study because we anticipated model M_h which accommodates differential capture probabilities (Otis *et al.* 1978; White *et al.* 1978). Baits and lures may homogenize capture probabilities (Thorn *et al.* 2009), but their application carries trade-offs. Camera traps need to be serviced more often to ensure bait and lures are still attractive. It is, however, acknowledged that using an attractant during the survey could slow down target species and thus improve picture quality (P.J. Funston *pers. comm*). Improvement of capture probabilities has been tested for brown hyaenas, *Hyaena brunnea* (Thorn *et al.* 2009). Small mammal capture studies typically use bait (Ferreira & van Aarde 2000) and in associated mark-recapture studies models favouring heterogeneity in individual capture probabilities provide best fit to observed data (Wang & MacDonald 2009). Studies using lures from other species had similar results (Quy *et al.* 2008). We thus anticipate that bait and lures are not likely to homogenize leopard capture probabilities and are, therefore, unlikely to result in selection of less complex capture models when estimating population sizes and variance in our study.

Our study suggests that there are 15 to 35 individuals (19 being the likely estimate) in a 150 km^2 area of the N'wanetsi concession of the Kruger National Park. That translates to a density of 12.7 (95% CI: 9.3-24.0) leopards per 100 km^2, within the range of densities noted for several studies across South Africa in areas of comparable prey densities (Chapman & Balme 2010).

The biased sampling by camera traps of leopards at the N'wanetsi concession has highlighted that: 1) even with increased effort we would continue to encounter new individuals; 2) stabilisation of population estimates should be anticipated at ~ 500 trap days; and 3) precision of population estimate should stabilise after ~ 380 trap days.

We successfully used camera traps to estimate leopard population abundance in the N'wanetsi concession. This study provides standard steps to follow in order to successfully survey 2.2 million hectare Kruger National Park for leopards. We acknowledge that given the magnitude of the Kruger National Park, there are different landscapes, vegetation types, precipitation, soil types, and prey densities. We expect that regardless of these causes of variation, there should be game paths, drainage lines, management roads and other features that to a degree resemble those of our pilot study. This should enable us to successfully survey the rest of the park. The study also provides much needed baseline data for leopards in the N'wanetsi section of the Kruger Park, and future monitoring efforts can be used against this established benchmark.

Lastly we have three recommendations, namely: (A) based on our results, camera traps, if used effectively, provide reliable data to answer questions relating to population structure; (B) by targeting sites that resemble the specific sites where cameras were deployed in the N'wanetsi concession elsewhere in the Kruger National Park, we would likely be in a position to successfully capture leopards; and (C) the use of advice from the locals would help in capturing individuals that are known to use a specific site.

References

Aebischer, N.J. 1986. Estimating the proportion on uncatchable animals in a population by double-sampling. *Biometrics*, **42:** 973-979.

Agresti, A. 1994. Simple capture-recapture models permitting unequal catchability and variable sampling effort. *Biometrics*, **50:** 494-500.

Bailey, T.N. 1993. *The African leopard. Ecology and behavior of a solitary felid.* New York: Columbia University Press.

Balme, G.A., Hunter, L.T.B., Slotow, R. 2009. Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, **73:** 431-443.

Balme, G.A., Slotow, R. & Hunter, L.T.B. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, **13:** 315-323.

Balme, G.A., Hunter, L.T.B., Goodman, P., Ferguson, J.C., Craigie, J. & Slotow, R. 2010. An adaptive management approach to trophy hunting of leopards (*Panthera pardus*): a case study from KwaZulu-Natal, South Africa.

Balme, G.A., Hunter, L. & Braczkowski, A.R. 2012. Applicability of age-based hunting regulations for African leopards. *PloS One*, **7:** e35209.doi:10.1371/journal.pone.0035209.

Carbone, C. & Gittleman, J.L. 2002. A common rule for scaling carnivore density. *Science*, 295, 2273-2276.

Chapman, S. & Balme, G. 2010. An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research*, **40:** 114-120.

Colwell, R.K. 2006. *EstimateS: Statistical estimation of species richness and shared species from samples.* Version 8.2.0. User's guide and application published at: http://purl.oclc.org/estimates.

Daly, B., Power, J., Camacho, G., Traylor-Holzer, K., Barber, S., Catterall, S., Fletcher, P., Martins, Q., Martins, N., Owen, C., Thal, T., & Friedmann, Y. 2005. Leopard (*Panthera pardus)* PHVA Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG South Africa. Endangered Wildlife Trust.

Efford, M.G., Dawson, D.K., & Robbins, C.S. 2004. Density: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation,* **27:** 217-228.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in the Kruger National Park, South Africa. *Wildlife Research* **37:** 1-13.

Ferreira, S.M. & van Aarde, R.J. 2000. Maintaining biodiversity through intermediate disturbances: evidence from rodents colonizing rehabilitating coastal dunes. *African Journal of Ecology,* **38:** 286-294.

Flather, C.H. 1996. Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. *Journal of Biodiversity,* **23:** 155-68.

Harris, R.B. 1986. Reliability of trend lines obtained from variable counts. *Journal of Wildlife Management,* **50:** 165-171.

Henschel, P. & Ray, J. 2003. *Leopards in African rainforests: Survey and monitoring techniques.* Wildlife Conservation Society, Global Carnivore Program.

Jackson, R.M., Roe, J.D., Wangchuk, R. & Hunter, D.O. 2006. Estimating snow leopard population abundance using photography and capture recapture techniques. *Wildlife Society Bulletin,* 34: 772-781.

Karanth, K.U. & Sunquist, M.E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. J*ournal of Animal Ecology,* **64:** 439-450.

Karanth, K.U. & Nichols, J.D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology,* **79:** 2852-2861.

Karanth, K.U. & Nichols, J.D. 2000. *Monitoring tigers and their prey: a manual for researchers, managers and conservationists in tropical Asia.* Centre for Wildlife studies, Karnataka, India.

Karanth, K.U., Nichols, J.D., Kumar, N.S. & Hines, J.E 2006.Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology*, **87:** 2925-2937.

Kauffmann, M.J., Sanjayan, M., Lowenstein, J., Nelson, A., Jeo, R.M. & Crooks, K.R. 1997. Remote camera-trap methods and analyses reveal impacts of rangeland management on Namibian carnivore communities. *Oryx*, **41:** 70-78.

Kelly, M.J. 2008. Design, evaluate, refine: camera trap studies for illusive species. *Animal Conservation*, **11:** 182-184.

Kéry, M. & Schmidt, H. 2003. Monitoring programs need to take into account imperfect species detectability. *Basic Applied Ecology,* **5:** 65-73.

Lee, S.-M. & Chao, A. 1994. Estimating population size via sample size coverage for closed capture-recapture models. *Biometrics*, **50:** 88-97.

Maffei, L., Cuéllar, E. & Noss, A. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology (Lond),* **262:** 295-304.

Marker, L.L., Mills, M.G.L. & Macdonald, D.W. 2003. Factors influencing perceptions and tolerance toward cheetahs (*Acinonyx jubatus*) on Namibian farmlands. *Conservation Biology,* **17:** 1-9.

Marnewick, K., Bothma, J. du P., & Verdoon, G.H. 2006. Using camera-trapping to investigate the use of a tree as a scent-marking post by cheetahs in the Thabazimbi district. *South African Journal of Wildlife Research,* **36:** 139-145.

Marnewick, K., Funston, P.J., & Karanth, K.U. 2008. Evaluating camera trapping as a method for estimating cheetah abundance in ranching areas. *South African Journal of Wildlife Research,* **38:** 59-65.

Mills, M.G.L., Juritz, J.M., & Zucchini, W. 2001. Estimating the size of spotted hyena (*Crocuta crocuta*) population through playback recordings allowing for non-response. *Animal Conservation,* **4:** 335-343.

Nichols, J.D. 1992. Capture-Recapture Models. *BioScience,* **42:** 94-102.

Otis, D.L., Burnham, K.P., White, G.C., & Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monograms,* **62:** 3-135.

Ott, T., Kerley, G.I.H. & Boshoff, A.F. 2006. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology,* **42:** 31-37.

Owen-Smith, N. & Mills, M.G.L. 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, **77:** 173-183.

Quy, R.J., Watkins, R.W., Lambert, M.S. & Cowan, D.P. 2008. Validating census methods to measure changes in house mouse populations. *Pest Management Science,* **65:** 275-282.

Rextad, E. & Burnham, K.P. 1991. *User's guide for interactive Program CAPTURE.* Fort Collins: Colorado Cooperative Fish and Wildlife Unit.

Romero-Muñoz, A., Maffei, L., Cuéllar, E. & Noss, A.J. 2010. Temporal separation between jaguar and puma in the dry forests of southern Bolivia. *Journal of Tropical Ecology*, **26:** 303-311.

Rowcliffe, J.M., Field, J., Turvey, S.T., Carbone, C. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology,* **45:** 1228-1236.

Sharma, K.R. & Jhala, Y.V. 2011. Monitoring tiger populations using intensive search in a capture-recapture framework. *Population Ecology,* **53:** 373-381.

Skinner, J.D. & Chimimba, C.T. 2005. *The Mammals of the southern African subregion*, 3rd edn., Cambridge University Press, Cambridge.

Stein, A.B., Fuller, T.K. & Marker. L.L. 2008. Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in north central Namibia. *Biodiversity Conservation,* **17:** 3579-3587.

Stephens, P.A., Zaumyslova, O.YU., Miquelle, D.G., Myslenkov, A.I. & Hayward, G.D. 2006. Estimating population density from indirect sign: track counts and the Formozov-Malyshev-Pereleshin formula. *Animal Conservation,* **9:** 339-348.

Thompson, W.L. 2002. Towards reliable bird surveys: Accounting for individuals present but not detected. *The Auk,* **119:** 18-25.

Thompson, G.G., Withers, P.C., Pianka, E.R. & Thompson, S.A. 2003. Assessing biodiversity with species accumulation curves; inventories of small reptiles by pit-trapping in Western Australia. *Australian Ecology,* **28:** 361-383.

Thorn, M., Scott, D.M., Green, M., Bateman, P.W. & Cameron, E.Z. 2009. Estimating brown hyaena occupancy using baited camera traps. *South African Journal of Wildlife Research,* **39:** 1-10.

Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R., & Powell, G. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation,* **11:** 169-178.

Wang, S.W. & Macdonald, D.W. 2009. The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation,* **142:** 606-613.

Wegge, P., Pokheral, C., Pd., & Jnawali, S.R. 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Biological Conservation,* **7:** 251-256.

White, G.C., Burnham, K.P, Otis, D.L., & Anderson, D.R. 1978. *User's manual for program CAPTURE*. Utah State University Press, Logan, Utah 84322.

Chapter 3. A camera-trap based photographic survey reveals robust leopard population abundances in the Kruger National Park, South Africa

This chapter is formatted for submission to *Wildlife Research*

*Nakedi W. Maputla[a,b], Christian T. Chimimba[b], Sam M. Ferreira[c]

*Corresponding author

a) *African Wildlife Foundation (AWF), AWF Conservation Centre, Ngong Road, Karen, P.O. Box 310, 00502, Nairobi, Kenya*
Email: nwmaputla@zoology.up.ac.za

b) *Mammal Research Institute (MRI) and DST-NRF Centre of Excellence for Invasion Biology (CIB), Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028, South Africa*
Email: ctchimimba@zoology.up.ac.za

c) *Scientific Services, South African National Parks (SANPARKS), Skukuza, 1350, South Africa*
Email: sam.ferreira@sanparks.org

Running title: Camera-trap based photographic survey

Abstract

The leopard is an important species as part of the large carnivore guild in Kruger National Park (KNP), South Africa. The guild as a whole has been exposed to an emerging disease, bovine tuberculosis (bTB), the consequences of which were not detectable for at least one guild member at the population scale. The disease has far-reaching conservation implications, which notionally have a potential to alter ecosystem processes in KNP; thus extenuating the significance of knowing population abundances of species of concern. We used camera-traps to establish leopard population estimates by conducting photographic surveys at 15 study sites across KNP from March to August during 2008 and over a two-year period from February 2010 to December 2011 in the study area. We aimed to evaluate how abundance estimates changed over time between six zones of different prey biomass as well as prevalence of bTB within prey as indicated by prevalence measured in buffalo. Leopard population estimates were obtained using classical capture recapture analysis and through spatially explicit capture recapture methods. Power analysis was used to infer the amount of effort it would take to detect changes in the leopard population structure and the amount of time it would take to detect changes. Population estimates using photo mark-recapture revealed that 2188 (95% CI: 1633-2862) adult leopards lived during 2008-2011 in KNP. Fewer leopards live in the central than in the northern and southern regions of the park. These differences do not associate with bTB prevalence in prey or prey biomass. In addition, historical densities at selected sites were comparable to estimates at the same site during the present study. Power analysis revealed that optimal leopard population surveys can be carried out twice over six years allowing detection of a 2% change in abundances. Our robust regional estimates suggest that leopard abundances in KNP has varied nondirectionally in the past 40 years, but factors other than prey biomass and prevalence of bTB in prey could influence regional variance.

Keywords: abundance, effort, camera-trap, photographic survey, Kruger National Park, density, trends, South Africa

Introduction

Large carnivores including lion, *Panthera leo*, spotted hyaena, *Crocuta crocuta*, leopards, *P. pardus*, cheetah, *Acynonyx jubatus*, and wild dog, *Lycaon pictus* are important species in African ecosystems because of their novel and unique prey preferences (Hayward *et al.* 2007). They play a role in top-down regulation of ecosystem structure (Kissui & Packer 2004) and consequently indirectly influence other processes such as patch dynamics (De Roos *et al.* 1998). In some instances, they occur in low densities and isolated populations. In such cases, large carnivores may be prone to extinction caused by stochastic events (Gros *et al.* 1996; De Roos *et al.* 1998).

Threats to large carnivores abound both within and beyond protected areas. Outside protected areas, extinction risks are exacerbated by human persecution (Balme *et al*. 2009a) and other anthropogenic activities such as poaching (Balme *et al.* 2009b). Some of these threats also spill over into protected areas (Balme *et al.* 2009b; Packer *et al.* 2011) where population persistence is driven by factors such as reserve size (Balme *et al.* 2010), prey availability (Bailey 1993), habitat suitability (Pulliam *et al.* 1992) and wildlife management (Hayward et al. 2007). For instance, managers of small protected areas use meta-population management models to create corridors to facilitate dispersal or physically move animals between reserves where the use of corridors is not viable (Davies-Mostert *et al*. 2009; Lindsey *et al.* 2011; Potgieter *et al.* 2012). This is assumed to ensure persistence of functional populations (Diamond 1975) although surprises abound because of stochasticity associated with small population sizes (e.g., Tambling *et al.* 2013).

Within large protected areas, however, population persistence is resilient due to heterogeneity and complexity of ecosystems (Woodroffe & Ginsberg 1998). Such scale buffers against chance or rare events. For instance, the lion disease outbreaks in the large ecosystem of the Serengeti re-organized the population and predator-prey dynamics (Holdo *et al.* 2009) but never threatened lions or its prey. Within another large protected area in southern Africa, an emerging disease challenged the heterogeneous and complex ecosystems of the Kruger National Park (KNP) (Keet *et al.* 1996; Pickett *et al.* 2003). Bovine tuberculosis (bTB) infected buffalo was noted during the 1960s in KNP (Rodwell *et al.* 2001). Several carnivore species have since been noted with infections as well as infections of their prey since then (Keet *et al.* 1996).

Concerns associated with emergent bTB predicted declines for dominant large carnivore guild members; i.e., lion, directly associated with bTB mediated health compromises (Keet *et al.* 1996). Lions, however, have remained relatively stable (Ferreira & Funston 2010). Changes in leopard populations, if any, may, however, be a consequence of direct influence of bTB on leopards themselves given that a suite of leopard prey item species have been noted with bTB (Keet *et al.* 1996; Renwick *et al.* 2007). Thus, conservation implications of this study hinge upon the *a priori* predictions surrounding the effects of bTB on KNP wildlife. We first estimate the leopard population size in KNP and then evaluate how this changed over time. We then attempt to address the question of how leopard population densities associate with varying prey biomass and bTB prevalence in different zones within KNP.

Materials and methods

Study area

The study was conducted in the Kruger National Park (KNP), South Africa, located in the north-east border of South Africa and Moçambique, between 22°25’ - 25°32’ south and 30°50’ - 32°02’ east (Fig. 3.1). The park has a north to south orientation, spanning almost 400 km in length, but with variable east-west distances with an average of approximately 65 km. The eastern boundary of the park is lined by the Lebombo Mountains and the border with Moçambique’s Limpopo National Park for most of the north-eastern boundary and Zimbabwe in the northern-most corner. Two main river systems dissect the park in west-east direction, the Limpopo River system in the north and the Nkomati River system in the South. These river systems comprise seven main rivers, namely: a) Crocodile, Sabi, and Sand in the south; b) Olifants and Letaba in the centre; and c) Luvuvhu and Limpopo (which forms the northern boundary) in the north.

Region	Site	Cameras	Effort	Captures	2008					2010												2011											
					A	M	J	J	A	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
North west	Punda Maria	43	847	32									■	■	■																		
5499km^2	Woodlands/Shangoni	39	1239	20										■	■	■																	
	Phalaborwa	35	918	16													■	■															
North East	Pafuri	46	2060	35							■	■	■																				
4372km^2	Shingwedzi/Vlakteplaas	42	1616	42										■	■																		
	Letaba	40	1576	32												■	■	■															
Central West	Kingfischer Spruit	33	1485	19																■	■												
2654km^2	Tshokwane	24	648	4																												■	■
Central East	Houtboschrand	35	1637	24														■	■														
2919km^2	N'wanetsi	9	569	14	■	■	■	■	■																								
	Lower Sabie	30	586	11																		■	■	■									
South West	Skukuza	25	468	18																			■	■	■								
3161km^2	Pretoriuskop	31	825	22																				■	■								
	Malelane	32	1029	28																									■	■			
South East 400km^2	Crocodile Bridge	31	513	9																						■	■						

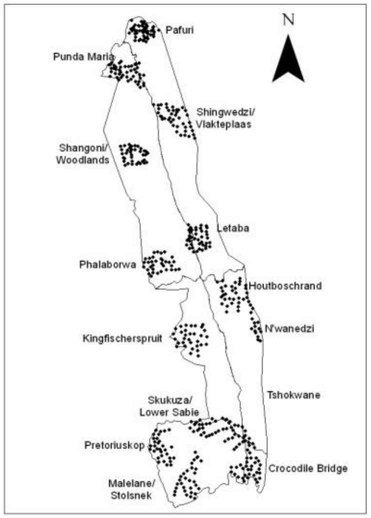


Figure 3.1. Summary of trap sites, cameras deployed, trapping days (effort) and number of leopards captured on camera at 15 trapping configurations distributed throughout Kruger National Park, South Africa. We also illustrate the time during which camera traps were active and their placement localities.

The geology of the park is divided longitudinally into granite formations in the west and mostly basalts in the east (Joubert 1986). This has a direct influence on the main soil types, where in the west, the soils are mainly sandy and light in colour, while the eastern half is dominated by dark clay soils. The park can be divided into 35 landscapes that were identified based on geomorphology, climate, soil, vegetation patterns, and to an extent, associated fauna (Gertenbach 1983). The park has a dry tropical climate which has induced deciduous savannahs (Venter & Gertenbach 1986). There is a decreasing rainfall gradient from south to north ranging from 740 mm in the south and approximately 440 mm in the north (Gertenbach 1980). In addition, Gertenbach (1980) identified two rainfall cycles, the wet and dry cycles, which differ by about 26%, with each cycle lasting for up to 10 years. There are 14 major vegetation assemblages, which are strongly correlated with rainfall patterns, identified for the park (Venter & Gertenbach 1986).

Study sites were selected to accommodate previously selected sites by Ferreira & Funston (2010) by stratifying KNP into six zones based on bTB prevalence and prey biomass (Fig. 3.1). Procedure for quantifying bTB prevalence and prey biomass are described in Rodwell *et al.* (2001) and Ferreira & Funston (2010). There were two zones in each of the three main regions of KNP. These regions are: (i) Southern region, which includes an area of the park south of the Sabie River; (ii) Central region, which covers an area between the Sabie River in the south and the Olifants River in the north; and (iii) Northern region, covering an area north of the Olifants River.

Camera placement and leopard identification

The biased camera placement techniques following Maputla *et al.* (2013) were used to conduct KNP-wide photographic survey between February 2010 and December 2011. Fourteen sites with area sizes ranging from 71 km^2 – 363 km^2 were selected throughout KNP for the survey (Fig. 3.1). Two hundred E-Z Cam™ camera-traps from Wildview® were used to survey leopards in these study sites resulting in 24 to 50 camera stations at each study site. Camera-traps were partitioned into two batches of 100 camera-traps each to survey two study sites simultaneously. Two camera-traps per station, placed on both sides of a game path (Karanth & Nichols 1998) captured both flanks of a passing animal and were placed for 45 days and set to capture three images separated by one second after each shot. Camera-traps were placed between 2 km and 7 km apart on game paths, management roads, dry river beds, and drainage lines following recommendations by Maputla *et al.* (2013). At the end of sampling, camera-traps were removed and the pictures uploaded onto a computer for analysis. Camera-traps were then deployed at the next study site.

Leopard pictures were extracted from cameras and stored in a computer and spot patterns used to identify and assign a number to each individual leopard. Photographed leopards were assigned age and sex following recommendations by Balme *et al.* (2012). Capture histories of each leopard were recorded as 1 for capture and 0 for non-capture with increasing effort in a capture matrix to prepare for analysis. Effort or trap day was regarded as the number of active camera-traps per occasion represented by a 24-hour day. Only adult and sub-adult leopards were used in the analysis because it was not always possible to determine the age of pictured leopards as suggested by Balme *et al.* (2012). Sollmann *et al.* (2011) noted that there were variable capture probabilities for male and female jaguars, *P. onca*. Consequently, both sexes were pooled and later analysed separately.

Data analysis

Presently, several studies have outlined the bias inherent in the use of classical closed population capture-recapture models to estimate abundances. These studies note factors relating to how vaguely the conventional methods capture biological reality including that: (i) classical methods often overestimate the actual density of the studied population (Sollmann *et al.* 2011); (ii) the methods don't account for edge effects associated with the uncertainty of the home range of the studied animal, thus not accounting for the fact that all animals in the study area do not have the same exposure to be captured (Efford *et al.* 2009; Efford & Fewster 2013); (iii) often the studied population is a subset of a continuous population over a large area (Efford *et al.* 2009); and (iv) the effects of capture probabilities were seldom accounted for by the trapping process (Efford *et al.* 2013). Similar inconsistences were observed in the population estimate studies of large cats (Sollmann *et al.* 2011). Spatially explicit capture recapture analysis (SECR) on the other hand, account for these limitations (Borchers & Efford 2008; Foster & Harmsen 2011). As a result, we used traditional closed population capture recapture models and the now widely used SECR methods to analyse the data. The number of trap days for each study site was determined by adding the total number of days that each camera remained active in each study site, signifying effort per camera station.

Closed population models - Matrices of binary data outlining capture histories of each individual were analysed using the program Capture (Otis *et al.* 1978; White *et al.* 1978; Rextad & Burnham 1991). The analysis accounted for variations caused by time (M_t), heterogeneity (M_h), behaviour (M_b) and a combination of these (M_{bh}, M_{tb}, and M_{tbh}). Akaike Information Criterion (AIC) scores were used to select the most suitable model that best described the data. Population estimate for each of the six zones was estimated by including the total area of each zone in the analysis. Density was calculated for each study site using the boundary strip method (Otis *et al.* 1978; Karanth & Nichols 1998) and adding a boundary strip to the area covered by traps to define an effective sampling area. We calculated the mean maximum distance moved (MMDM) for each study site to calculate the boundary strip. Boundary strip width (BSW) was calculated as half MMDM and it was added to the minimum convex polygon depicting the sampled area.

SECR - We ran the analysis through program Density 5.0 (Efford 2012). The occasions and the camera trap locations where each individual leopard was captured were recorded. Density estimates were based on maximum likelihood model that assumed that capture probabilities of individuals follow the Poisson principles (Borchers & Efford 2008; Efford & Fewster 2013). Effort included the number of days that the camera remained active.

We extrapolated density estimate for each of the six zones by generating 60 000 random numbers > 0, but < 1 from the study site population estimates based on results from capture recapture analysis. Final density estimates were represented as the median from the 60 000 random numbers, while the lower and upper confidence intervals were calculated from the lower and upper percentiles and then multiplied by 0.025 and 0.975, respectively. Following this, leopard abundance estimates within each zone were calculated as the product of the density estimate and the size of each zone. Finally, we ran general linear models to investigate how leopard population estimate in each zone associated with prey biomass and bTB.

The influence of effort - Due to the size of KNP and the variation in sizes of study sites, resultant capture probability was plotted against effective area sampled based on closed population models, effort (defined as the number of trap days per study site), population abundance and density estimates. This was done in an attempt to account for variable effort throughout the study period.

Detecting trends - We estimated the coefficient of variation from the standard deviation of population estimates by running 60 000 bootstrap permutations for the total population size and then dividing the standard deviation by the median. We were interested in trade-offs between the frequency of sampling required and the amount of time it would take to detect 2% and 5% increase in abundance and *vice versa* using power analysis (Gerrodette 1987). By convention, in mark-recapture studies, the coefficient of variation (CV) is proportional to the square root of population estimate (Gerrodette 1987). In order to avoid type I and type II errors, data were analysed at the $\alpha = 0.05$ and at the $\beta = 0.2$ using two-tailed tests. Thus, we used the inequality equation suggested by Gerrodette (1987) to define detection of trends in population structure over time with Power = 0.8. We calculated an effective rate of change per interval following Gerrodette (1987) as well as the total change by the time rate of change is detected.

Results

Total area directly covered by camera trapping sites amounted to 2837.3 km^2, approximately 14% of KNP (Fig. 3.1). Across Kruger, capture probability was low; 0.02 captures/trap day (Table 3.1). The survey yielded 326 leopard captures during 14962 trapping days. Of these, 151 were males, 128 females while the remaining 47 leopard photographs were either obscure or too difficult to determine the sex of the individuals. Leopard capture probability associated negatively with trapping effort ($F_{1; 14} = 14.16$; $n = 13$; $P < 0.01$). However, there was poor support for the association between capture probability and effective trapping area, population abundance and density estimates.

Table 3.1. Summary of population estimates derived from leopard images captured at study sites in the Kruger National Park, South Africa using camera trap configurations. Summarized are the results from Program CAPTURE and provide support for the most likely model that account for resulting variations in capture probabilities (Otis *et al.* 1978). M_h – accounts for the variation caused by individual differences leopards, M_0 – accounts for no effect by any variable, M_{bh} – accounts for the variation caused by leopard behaviour and individual differences, M_{tbh} – accounts for variation caused by time, behaviour and individual differences. Closure tests reveal whether the population under study behaves as closed or not; assumptions of population closure are supported when the test statistic is not statistically significant. We also provide estimates of capture probability at each study site. N is the population estimate derived from the best model. LCL – lower 95% confidence limit. UCL – upper 95% confidence limit. Numbers in parentheses are probability estimates.

Trapping Site	Closure Test	Capture Probability	Model	N	LCL	UCL
Punda Maria	-2.34 (0.01)	0.03	M_h (1.00)	16	14	32
Woodlands Shangoni	-0.31 (0.38)	0.02	M_{bh} (1.00)	21	17	36
Phalaborwa	-0.74 (0.23)	0.02	M_0 (1.00)	21	13	57
Pafuri	-0.97 (0.17)	0.01	M_0 (1.00)	34	24	65
Shingwedzi Vlakteplaas	-1.91 (0.03)	0.01	M_0 (1.00)	38	26	68
Letaba	-0.81 (0.21)	0.02	M_0 (1.00)	37	27	65
Kingfischerspruit	2.11 (0.98)	0.01	M_h (1.00)	30	19	62
Tshokwane	6.00 (1.00)	0.02	M_{tbh} (1.00)	5	5	79
Houtboschrand	-1.74 (0.04)	0.01	M_h (1.00)	14	11	29
N'wanetsi	-3.28 (0.013)	-	M_h (0.99)	19	14	36
Lower Sabie	-0.56 (0.29)	0.02	M_0 (1.00)	23	12	75
Skukuza	-3.38 (0.00)	0.03	M_0 (1.00)	22	18	38
Pretoriuskop	-2.6 (0.01)	0.01	M_h (1.00)	103	68	165
Malelane	-1.49 (0.07)	0.02	M_0 (1.00)	37	28	66
Crocodile Bridge	0.18 (0.57)	0.03	M_h (1.00)	8	7	27

Classical capture recapture analysis - Assumptions of population closure associated with estimating female abundances did not support captures for Shingwedzi, Tshokwane and Lower Sabie study sites (Table 3.2). At seven of the study sites, M_h was chosen as the most suitable model, with M_0 as the most suitable at the remaining sites. As second suitable model M_h ($n = 7$) also dominated with five sites having M_0 and two sites having M_b as the second most suitable model. Estimates for the number of females at a particular site ranged from 1 (95% CI: 1-1) to 24 (95% CI: 12-59) female leopards at the Crocodile Bridge and Pretoriuskop study sites, respectively. For the males, all populations were closed (Table 3.3). Models M_h and M_{bh} were the most suitable models based on AIC scores each at three study sites. The lowest male estimate was recorded for the Crocodile Bridge study site at 4 (95% CI: 4-22), while the highest estimate was recorded for the Lower Sabie study site at 18 (95% CI: 9-54) (Table 3.3).

Table 3.3. Summary of population estimates derived from male leopard images captured at study sites in the Kruger National Park, South Africa using camera trap configurations. Summarized are the results from Program CAPTURE and provide support for the most likely model that account for resulting variations in capture probabilities (Otis *et al.* 1978). M_h – accounts for the variation caused by individual differences leopards, M_0 – accounts for no effect by any variable, M_{bh} – accounts for the variation caused by leopard behaviour and individual differences, M_{tbh} – accounts for variation caused by time, behaviour and individual differences. Closure tests reveal whether the population under study behaves as closed or not; assumptions of population closure are supported when the test statistic is not significant. We also provide estimates of capture probability at each study site. N is the population estimate derived from the best model. LCL – lower 95% confidence limit. UCL – upper 95% confidence limit. Numbers in parentheses are probability estimates.

Trapping Site	Closure Test	Capture Probability	Model	N	LCL	UCL
Punda Maria	-2.45 (0.01)	0.02	M_0 (1.00)	8 2.12	7	16
Woodlands Shangoni	-1.35 (0.09)	0.03	M_{bh} (1.00)	7 3.02	7	24
Phalaborwa	-0.65 (0.26)	0.02	M_h (1.00)	10 3.58	8	26
Pafuri	-0.66 (0.25)	0.02	M_0 (1.00)	12 3.59	10	28
Shingwedzi Vlakteplaas	-1.92 (0.08	0.02	M_0 (1.00)	13 3.68	11	29
Letaba	-1.03 (0.15)	0.04	M_{bh} (1.00)	6 2.60	6	21
Kingfischerspruit	1.4 (0.92)	0.02	M_{bh} (1.00)	13 4.52	9	31
Tshokwane	-	-	-	-	-	-
Houtboschrand	-0.62 (0.27)	0.02	M_h (1.00)	5 2.59	5	22
N'wanetsi	0.45 (0.67)	0.01	M_{bh} (1.00)	15 4.49	12	32
Lower Sabie	-0.56 (0.29)	0.01	M_h (1.00)	18 10.28	9	54
Skukuza	-1.95 (0.03)	0.03	M_0 (1.00)	9 3.00	9	27
Pretoriuskop	-1.65 (0.05)	0.01	M_0 (1.00)	28 16.60	15	93
Malelane	-1.30 (0.10)	0.03	M_0 (1.00)	13 3.57	11	29
Crocodile Bridge	0.99 (0.84)	0.02	M_0 (1.00)	4 2.62	4	22

When we pooled all captures, only Tshokwane could not be assumed to be closed (Tables 3.1, 3.2 & 3.3). The null model (M_0) and heuristic model (M_h) were selected as the most appropriate models that best explained the data. Two other models were selected at two separate sites: Tshokwane (M_{tbh} – suggesting that a combination of time, behaviour and random events influenced the observed patterns, which is not an ideal situation to estimate abundance) and Shangoni (M_{bh}; M_{tbh} – suggesting that either a combination of behaviour and chance events or a combination of time, behaviour, and chance events influenced leopard capturing). The population estimates at each of the study sites ranged from 5 (95% CI = 5-79) for the Tshokwane study site to 103 (95% CI = 68-165) for the Pretoriuskop study site.

Leopard distances between captures of the same leopard allowed us to estimate the effective area sampled at each site using the MMDM method (Karanth & Nichols 2008). At three study sites (Pafuri, Tshokwane and Nwanedzi) there were no recaptures, with the longest mean distance moved between captures being 17.99 km at Lower Sabie. By adding estimated boundary strip widths to the area covered by a specific trapping configuration at a study site, we estimated effective sampling areas ranging from 92 km^2 (Crocodile Bridge) to 975 km^2 (Lower Sabie). Site-specific leopard densities ranged from 0.02 leopards/km^2 to 0.5 lepards/km^2 (Table 3.4).

SECR - Leopard population density estimates obtained from the different study sites differed slightly with density estimates from classical methods (Table 3.4). The most noteworthy results were observed in the Pretoriuskop study site, which had a very high density estimate when traditional methods (0.5; 95% CI: 0.33-0.8) were used, but SECR suggested a smaller density estimate (0.3; 95% CI: 0.01-13.18), but with wider error margins.

Table 3.4. Density estimates of leopards at trapping sites in the Kruger National Park, South Africa. We used the mean maximum distance moved estimated for recaptured leopards and defined the effective area sampled by adding a boundary strip width equal to half the mean maximum distance moved (MMDM). *N* refers to the number of individuals used to calculate the MMDM. The values in parentheses are the estimated standard error for the MMDM and Effective Area Sampled. The values in parentheses in the Density column are the 95% confidence intervals. We also used the spatially explicit capture-recapture (SECR) analysis to estimate density. Similarly, numbers in parentheses are the 95% confidence intervals.

Trapping Site	**Area (km^2)**	***N***	**Mean maximum distance moved (km)**	**Boundary strip width (km)**	**Effective Area Sampled (km^2)**	**Density MMDM (n.km^{-2})**	**Density SECR (n.km^{-2})**
Punda Maria	240	12	0.58 (0.38)	0.29 (0.19)	258 (11)	0.062 (0.054-0.124)	0.071 (0.034-0.15)
Woodlands Shangoni	204	5	4.18 (2.86)	2.09 (1.43)	333 (93)	0.063 (0.051-0.108)	0.1 (0.046-0.23)
Phalaborwa	238	3	7.37 (3.68)	3.68 (1.84)	629 (164)	0.033 (0.021-0.091)	0.077 (0.027-0.22)
Pafuri	140	7	-	-	140	0.243 (0.171-0.464)	0.15 (0.073-0.29)
Shingwedzi/ Vlakteplaas	215	5	6.12 (3.48)	3.48 (3.06)	487 (239)	0.078 (0.053-0.140)	0.13 (0.06-0.29)
Letaba	231	9	1.08 (0.66)	0.54 (0.33)	265 (19)	0.14 (0.102-0.245)	0.121 (0.066-0.22)
Kingfischerspruit	363	4	5.76 (2.43)	2.88 (1.22)	595 (105)	0.05 (0.032-0.104)	0.084 (0.038-0.19)
Tshokwane	234	-	-	-	234	0.021 (0.017-0.338)	-
Houtboschrand	471	6	9.57 (5.54)	4.78 (2.77)	946 (302)	0.015 (0.012-0.031)	0.04 (0.018-0.075)
N'wanetsi	150	-	-	-	150	0.127 (0.093-0.240)	-
Lower Sabie	155	2	17.99 (-)	9 (-)	975 (-)	0.024 (0.012-0.077)	0.07 (0.025-0.20)
Skukuza	93	16	2.06 (0.99)	1.03 (0.5)	140 (21)	0.157 (0.129-0.271)	0.1 (0.06-0.17)
Pretoriuskop	206	10	0 (-)	0 (-)	206 (-)	0.5 (0.330-0.801)	0.3 (0.01-13.18)
Malelane	210	31	1.29 (0.96)	0.64 (0.48)	258 (27)	0.144 (0.109-0.256)	0.083 (0.054-0.13)
Crocodile Bridge	71	3	1.12 (1.12)	0.56 (0.56)	92 (19)	0.087 (0.076-0.295)	0.044 (0.014-0.138)

Zone-specific estimates - These site-specific leopard densities provide the basis for estimates of population sizes within the six defined zones. The North-East zone had the highest leopard population estimate of 661 (95% CI: 521-1114) and density estimate of 0.15 (95% CI: 0.11-0.28) leopards/km^2 with the South-East Zone the lowest estimate of 35 (95% CI: 31-117) and density estimate of 0.09 (95% CI: 0.08-0.3) leopards/km^2. We estimated that 2188 (95% CI: 1633-2862) mostly adult leopards lived in KNP during the survey.

Zone-specific leopard density estimates during the present study did not associate with either prey biomass ($F_{1,4} = 0.24$; $n = 6$; $P = 0.80$) or bTB prevalence in prey ($F_{1,4} = 1.25$; $n = 6$; $P = 0.38$). Multivariate models including both these variables also failed to explain variance in density ($F_{2,4} = 0.50$; $n = 6$; $P = 0.65$).

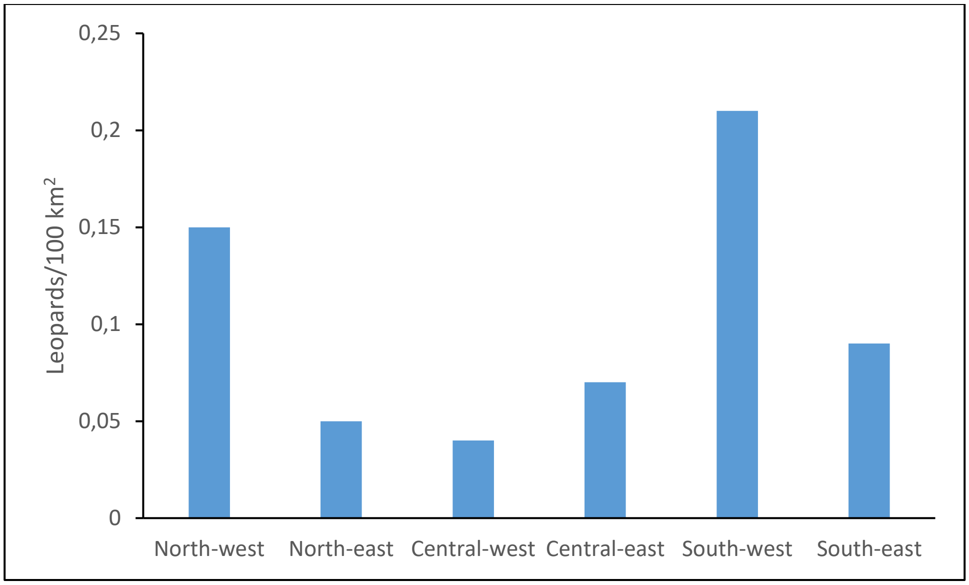


Figure 3.2. Leopard densities in each of the six pre biomass/bovine tuberculosis (bTB) zones in the Kruger National Park, South Africa. The zones were delineated according to prey biomass and bTB prevalence.

Trends - Only one study provided leopard estimates (Bailey 1993), but focused on the south-western region of KNP that largely overlapped with our South-West Zone. Exponential growth rate (0.9% per annum) based on density estimates during 1974 and 2012 includes zero in the 95% confidence intervals (-3.1% to 0.9%). Leopard populations were similar in 2012 to 1974 at least within the South-West Zone.

Power analysis revealed that with four surveys every seven years, we would detect a 2% decline in the leopard population. By the time changes are detected, it will be after 21 years and the population would have changed by -34%. In contrast, to detect a 5% decline it would take two surveys in six years and by that time there would have been a total percentage change of -27% (Table 3.5). To detect a 2% increase in the leopard population with five years in between surveys, it would take nine surveys and 40 years before a change is detected. Again, with five years in between surveys, we would need 6 surveys for every five years and it would take 25 years to detect a change. By that time the total change will be 239% (Table 3.5).

Table 3.5. Effects of different survey intervals on the frequency of surveys required to detect -2%, -5%, 2%, and 5% decline and increase in leopard population size in the Kruger National Park, South Africa. Included is the number of years to detecting a trend as well as the total change.

Detecting a 2% decline				Detecting a 5% decline			
Years between surveys (*i*)	Number of surveys required (*n*)	Years to detection $[i(n-1)]$	Total % change* $[(1+r)^{i(n-1)}-1]$	Years between surveys (*i*)	Number of surveys required (*n*)	Years to detection $[i(n-1)]$	Total % change* $[(1+r)^{i(n-1)}-1]$
1	15	14	-24.6%	1	8	7	-30.2%
2	10	18	-30.5%	2	5	8	-33.7%
3	7	18	-30.5%	3	4	9	-37.0%
4	6	20	-33.2%	4	4	12	-46.0%
5	5	20	-33.2%	5	3	10	-40.1%
6	5	24	-38.4%	6	2	6	-26.5%
7	4	21	-34.6%	7	2	7	-30.2%
8	4	24	-38.4%	8	2	8	-33.7%
9	4	27	-42.0%	9	2	9	-37.0%
10	4	30	-45.5%	10	2	10	-40.1%

Detecting a 2% increase				Detecting a 5% increase			
Years between surveys (*i*)	Number of surveys required (*n*)	Years to detection $[i(n-1)]$	Total % change* $[(1+r)^{i(n-1)}-1]$	Years between surveys (*i*)	Number of surveys required (*n*)	Years to detection $[i(n-1)]$	Total % change* $[(1+r)^{i(n-1)}-1]$
1	22	21	51.6%	1	13	12	79.6%
2	15	28	74.1%	2	9	16	118.3%
3	12	33	92.2%	3	7	18	140.7%
4	10	36	104.0%	4	6	20	165.3%
5	9	40	120.8%	5	6	25	238.6%
6	8	42	129.7%	6	5	24	222.5%
7	8	49	163.9%	7	5	28	292.0%
8	7	48	158.7%	8	5	32	376.5%
9	7	54	191.3%	9	5	36	479.2%
10	6	50	169.2%	10	4	30	332.2%

Discussion

Our estimate of the leopard abundances suggest that a robust leopard population persisted in KNP between 2008 and December 2011. There was no marked variation between density estimates from conventional methods and SECR. In addition, the process of estimating leopard abundances brought to light four noteworthy assertions, namely: a) that the biased leopard sampling method using camera-trap photographic surveys is an efficient way of estimating the leopard population abundance in KNP; b) that whereas prey density is noted as an important variable (Bailey 1993), it is not the sole variable driving leopard population abundances; and c) that the effects of bTB at population level are not clear when using the available data.

Analysis of the amount of effort applied in the different study sites suggests that there were significant differences between study sites. This can be attributed to interferences from runaway fires, floods, and large mammals including lions, spotted hyaenas and elephants. Despite this inconsistency in effort, there was not enough evidence to suggest that leopard capture probabilities were negatively affected. Effort in each of the study sites exceeded the conventional cut-off effort of 450-500 trap days. Additionally, results obtained here concur with the findings of Maputla *et al.* (2013), which showed that an asymptote may be achieved at approximately 400 trap days within a representative study site in their study area in the KNP. Thus in spite of the disparity in effort, we were able to capture most leopards that could be captured in each study site.

The estimated leopard population size is markedly higher than the historical estimate of 700 leopards (Bailey 1993). A close look at density scores at the study sites by Bailey (1993) however, show remarkable similarities with the estimates obtained in the present study. This similarity in density estimates suggests that the leopard population in the overlapping study sites has been consistent for the past 40 years. This suggests that the use of extrapolators in the past may have undermined leopard population abundances in KNP. Whereas the two studies used different methods to estimate leopard abundances, Bailey's (1993) study is a very important baseline.

Leopard density estimates from this study were similar to leopard population estimates from elsewhere. At study site level, most KNP density estimates were comparable and different to leopard densities from elsewhere in southern Africa. In the Phinda Private Nature Reserve, KwaZulu-Natal Province, South Africa, Balme *et al.* (2010) estimated 6 leopards.km^{-2}. In north-central Namibia, a study site markedly different from the current study site, Stein *et al.* (2011) estimated 4 leopards.100km^{-2} outside protected areas and 1 leopard.100km^{-2} in protected areas. Thus our leopard population estimates fall within the estimated leopard abundances in southern Africa.

While there was no sufficient evidence to suggest significant differences between the six bTB prevalence/prey biomass zones in terms of leopard captures, southern KNP had the highest estimate for leopard abundances in KNP. Incidentally, this zone received a considerably lower amount of effort than the north-east region (a difference of $\geq$ 2000 trap days). In addition, the south-west zone stands out from the other zones for three reasons:

a) the two landscapes, the Malelane Mountain Bushveld and the Thickets of the Sabie & Crocodile rivers that yielded the most captures are well-represented in the zone; b) the granitic soils, which yielded 179 leopard captures cover most of the zone; and c) annual rainfall, which shows a positive correlation with leopard captures, is highest in this zone.

In contrast, the south-east zone had the lowest leopard population abundance estimate of 8 leopards. Understandably, the zone occupies by far the smallest area (90 km^2) of the six zones. As such, the estimate of 8 leopards is justifiable considering the size of the study site (71 km^2). The two northern-most zones were second and third in leopard abundance estimates.

The two zones in the central region had leopard estimates of below 100. Given that the topology there is different to the rest of the park may be supportive of the observed data. Although the prey biomass is high, it is possible that the bulk of the biomass referred to is not accessible to leopards, but trapped in the large-bodied herbivores that prefer open savanna to thick bushveld. Consequently, leopard population densities were lower in this region than in other regions of the park.

The disparity in the ratio between male and female captures may be indicative of behavioural differences and navigation within the landscape. A similar pattern was observed in Maputla *et al.* (2013) and Martins & Harris (2013). Bailey (1993) noted that one was likely to see more males than females in his study sites, but managed to capture more females than males in the cage traps. Similarly, Maputla (*unpublished data*) captured slightly more females, than males in their cage traps in KNP. It could be argued that while there may be more females than males in a landscape, their movement patterns vary extensively, i.e., males may be displaying bold personalities by walking on game paths, dry river beds, and management roads while females did so sparingly. Additional studies could reflect on what the drivers of this variation might be.

Results from the photographic surveys suggested that a different method may be necessary to explain the demographic characteristics of the leopard population in KNP. Leopards in general start moving around after independence from their mothers. This may have limited the number of photographs of young leopards. Thus, unless there was a photograph of a female with a young or sub-adult cub, there was no occasion in which a cub or sub-adult was captured on their own. Bailey (1993) found similar trends to what we observed during this study.

The use of power analysis to detect trends (Gerrodette 1987) has enabled us to optimise the number of surveys and the number of years it would take to detect changes in population abundances. Based on the results, we propose that the leopard population be surveyed twice every six years if a change of -2% were to be detected (Table 3.5). This means resources, time, and effort can be directed elsewhere in between surveys.

In conclusion, the results in this study suggest that while leopard population abundance in KNP may not associate with bTB prevalence, prey biomass alone is insufficient to explain the differences in leopard population abundances in the bTB/prey biomass zones. Similarities in density estimates between historical and recent studies suggest that the leopard abundances were consistent for the past four decades. We suggest that the leopard population in KNP be monitored two times every six years as that will be the likely time that trends will be detected. Furthermore, for future surveys, we suggest the use of public participation by encouraging tourists to provide photographs and localities of leopards they encounter. This may have far-reaching benefits including public awareness; reduced amount of time spent in the field; and reduced financial costs.

References

Bailey, T.N. 1993. The African Leopard: ecology and behaviour of a solitary felid. Columbia University Press, New York, USA.

Balme, G.A., Hunter, L.T.B., Slotow, R. 2009. Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, **73:** 431-443.

Balme, G.A., Slotow, R. & Hunter, L.T.B. 2009. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, **13:** 315-323.

Balme, G.A., Hunter, L.T.B., Goodman, P., Ferguson, J.C., Craigie, J. & Slotow, R. 2010. An adaptive management approach to trophy hunting of leopards (*Panthera pardus*): a case study from KwaZulu-Natal, South Africa. In: Macdonald DW, Loveridge A, Eds. *Biology and Conservation of Wild Felids.* Oxford (UK): Oxford University Press. Pp 341-352.

Balme, G.A., Hunter, L. & Braczkowski, A.R. 2012. Applicability of age-based hunting regulations for African leopards. *PloS One,* **7:** e35209.doi:10.1371/journal.pone.0035209.

Borchers, D.L. & Efford, M.G. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, **64:** 377-385.

Davies-Mostert, H.T., Mills, M.G.L. & Macdonald, D.W. 2009. South Africa’s wild dog *Lycaon pictus* metapopulation management programme. In: The reintroduction of top-order predators. Eds M.W. Hayward & M.J. Sommers, pp 10-42. Blackwell Publishing, Oxford, UK.

De Roos, A.M., McCauley, E. & Wilson, W.G. 1998. Pattern formation and the spatial scale of interaction between predators and their prey. *Theoretical Population Biology,* **53:** 108-130.

Diamond, J.M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation,* **7:** 129-146.

Efford, M.G., Dawson, D.K. & Borchers, D.L. 2009. Population density estimated from locations of individuals on a passive detector array. *Ecology,* **90:** 2676-2682.

Efford, M.G. 2012. Density 5.0: software for spatially explicit capture-recapture. Department of Mathematics and Statistics, University of Otago, Dunedin, New Zealand. http://www.otago.ac.nz/density.

Efford, M.G., Borchers, D.L. & Mowat, G. 2013. Varying effort in capture-recapture studies. *Methods in Ecology and Evolution,* **4:** 629-636.

Efford, M.G. & Fewster, M.F. 2013. Estimating population size by spatially explicit capture-recapture. *Oikos,* **122:** 918-928.

Epps, C.W., Wasser, S.K., Keim, J.L, Mutayoba, B.M. & Brashares, J.S. 2013. Quantifying a past and present connectivity illuminates a rapidly changing landscape for the African elephant. *Molecular Ecology,* **22:** 1574-1588.

Ferreira, S.M. & Van Aarde, R.J. 2009. Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. *South African Journal of Wildlife Research,* **39:** 181-191.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildlife Research,* **37:** 194-206.

Foster, R.J. & Harmsen, B.J. 2011. A critique of density estimation from camera-trap data. *Journal of Wildlife Management,* **76:** 224-236.

Gerrodette, T. 1987. A power analysis for detecting trends. *Ecology,* **68:** 1364–1372.

Gertenbach, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe-African Protected Area Conservation and Science,* **23:** 35-43.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe-African Protected Area Conservation and Science,* **26:** 9-121.

Gros, P.M., Kelly, M.J. & Caro, T.M. 1996. Estimating carnivore densities for conservation purposes. *Oikos,* **77:** 197-207.

Hayward, M.W., O'Brien, J. & Kerley, G.I.H. 2007. Carrying capacity of large African predators: Predictions and tests. *Biological Conservation,* **139:** 219-229.

Holdo, R.M., Holt, R.D. & Fryxell, J.M. 2009. Grazers, browsers, and fire influence the extend and spatial pattern of tree cover in the Serengeti. *Ecological Applications,* **19:** 95-109.

Joubert, S.C.J. 1986. The Kruger National Park – An Introduction. *Koedoe-African Protected Area Conservation and Science,* **29:** 1-11.

Karanth, K.U. & Nichols, J.D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology,* **79(8):** 2852-2861.

Keet, D.F., Kriek, N.P.J., Penrith, M.-L., Michel, A. & Huchzermeyer, H. 1996. Tuberculosis in buffaloes (*Syncerus caffer*) in the Kruger National Park. Spread of the disease to other species. *Onderstepoort Journal of Veterinary Research,* **63:** 239-244.

Kissui, B.M. & Packer, C. 2004. Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society B,* **24:** 200-210.

Lindsey, P.A., Tambling, C.J., Brummer, R., Davies-Mostert, H.T., Hayward, M.W., Marnewick, K.A. & Parker, D.M. 2011. Minimum prey and area requirements of cheetahs: implications for reintroductions and management of the species as a managed metapopulation. *Oryx,* **45:** 587-599.

Maputla, N.W., Chimimba, C.T., & Ferreira, S.M. 2013. Calibrating a camera trap-based biased mark-recapture sampling design to survey the leopard population in the N'wanetsi concession, Kruger National Park, South Africa. *African Journal of Ecology,* **51:** 422-430.

Marnewick, K., Ferreira, S.M., Grange, S., Watermeyer, J., Maputla, N. & Davies-Mostert, H.T. 2014. Evaluating the status of African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist based photographic surveys in the Kruger National Park. *PloS One.* **9:** e86265. **doi: 10**.1371/journal.pone.0086265.

Martins, Q. & Harris, S. 2013. Movement activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *African Journal of Ecology,* **51:** 571-579.

Mills, M.G.L., Juritz, J.M. & Zucchini, W. 2001. Estimating the size of spotted hyaena (*Crocuta crocuta*) populations through playback recordings allowing for non-response. *Animal Conservation,* **4:** 335-343.

Nowell, K. & Jackson, P. 1996. *Status Survey and Conservation Action Plan: Wild Cats.* The Burlington Press, Cambridge, U.K.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, **62:** 3-135.

Pickett, S.T.A., Cadenasso, M.L. & Benning, T.L. 2003. Biotic and abiotic determinants of savanna heterogeneity at a multiple spatiotemporal scales. In: *The Kruger experience: Ecology and management of a savanna heterogeneity*. Eds J.T. Du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington DC, USA.

Potgieter, K.R., Whittington-Jones, B., Gusset, M., Mills, M.G.L. & Davies-Mostert, H.T. 2012. *The South African wild dog metapopulation compendium.* http://www.wagsa.org.za/pdf/Metapopulation%20compendium.pdf; accessed 12/08/2014.

Pulliam, H.R., Dunning Jr, J.B & Liu, J. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications*, **2:** 165-177.

Renwick, A.R., White, P.C.L. & Bengis, R.G. 2007. Bovine tuberculosis in southern African wildlife: a multi-species host-pathogen system. *Epidemiology and Infection,* **135:** 529-540.

Rextad, E. & Burnham, K.P. (1991) *User's Guide for Interactive Program CAPTURE*. Colorado State University, Fort Collins, Colorado, USA.

Rodwell, T.C., Kriek, N.P., Bengis, R.G., Whyte, I.J., Viljoen, P.C, de Vos, V. & Boyce, W.M. 2001. Prevalence of bovine tuberculosis in African buffalo at Kruger National Park. *Journal of Wildlife Diseases*, **37:** 258-264.

Skinner, J.D. & Chimimba, C.T. 2005. *The Mammals of the southern African subregion*, 3rd edn., Cambridge University Press, Cambridge.

Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T.A., Tôrres, N.M. &

Silveira, L. 2011. Improving density estimates for illusive carnivores: accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biological Conservation,* **144:** 1017-1024.

Tambling, C.J., Ferreira, S.M., Adendorff, J. & Kerley, G.I.H. 2013. Lessons from management interventions: consequences for lion-buffalo interactions. *South African Journal of Wildlife Research,* **43:** 1-11.

Venter, F.J. & Gertenbach, W.P.D. 1986. A cursory review of the climate and vegetation of the Kruger National Park. *Koedoe-African Protected Area Conservation and Science,* **29:** 139-148.

White, G.C., Burnham, K.P., Otis, D.L. & Anderson , D.R. 1978. *User's Manual for Program CAPTURE,* Utah State University Press, Logan, Utah, USA.

Woodroffe, R. & Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. *Science,* **280:** 2126-2128.

Zu Ermgassen, P.S.E., Spalding, M.D., Blake, B., Coen, L.D., Dumbauld, B., Geiger, S., Grabowski, J.H., Grizzle, R., Luckenbach, M., McGraw, K., Rodney, W., Ruesink, J.L., Powers, S.P. & Brumbaugh, R. 2013. Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. *Proceedings of the Royal Society B,* **279:** 3393-3400.

Chapter 4. Comparing regional abundances of large carnivores in the Kruger National Park, South Africa: inferences on leopard abundance

This chapter is formatted for submission to *Animal Conservation*

*Nakedi W. Maputla[a,b], Christian T. Chimimba[b], Sam M. Ferreira[c],

*Corresponding author

a) *African Wildlife Foundation (AWF), AWF Conservation Centre, Ngong Road, Karen,*
P.O. Box 310, 00502, Nairobi, Kenya
Email: nwmaputla@zoology.up.ac.za

b) *Mammal Research Institute (MRI) and DST-NRF Centre of Excellence for Invasion Biology (CIB), Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa*
Email: ctchimimba@zoology.up.ac.za

c) *Scientific Services, South African National Parks (SANPARKS), Skukuza, 1350 South Africa*
Email: sam.ferreira@sanparks.org

Running title: Comparison of large carnivore abundances

Abstract

Relatively intact African reserves are characterised by co-existence of large carnivores. Several stressors such as the effects of diseases and associated ecological cascades may derail co-existence. Niche packing predicts that in a complex ecosystem, negative associations of co-existing taxa with each other may not be apparent because of co-evolved attributes that minimise competition – the effect of past evolutionary interactions. In contrast, meso-predator release suggests that top predators supress abundances of smaller predators – the effect of present species interactions. Five large carnivore species: lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), leopards (*P. pardus*), cheetahs (*Acynonyx jubatus*), and wild dogs (*Lycaon pictus*) live in Kruger National Park (KNP), South Africa. Niche packing predicted no relationships between abundances of these species, while meso-predator release predicted that leopard abundances would be high in areas where lions and spotted hyaenas are low. Regional variation in leopard abundances did not associate with abundances of any other large carnivore. Past competitive interactions drive co-existence with little evidence of other carnivores suppressing abundance of leopards. Cascading effects of emerging diseases such as bovine tuberculosis (bTB) is thus an unlikely driver of large carnivore guild dynamics in KNP.

Keywords: niche packing, meso-predator release, disease, Kruger National Park, large carnivores, leopard, South Africa

Introduction

Protected areas provide refuges to wildlife species that would otherwise be unable to persist elsewhere. Within intact heterogeneous and complex protected areas, predation is a key process driving top-down processes (Kissui & Packer 2004). Predation is resource-driven and as a consequence large carnivores respond to the abundances of prey species, their sizes and the degree of vulnerability to predation apart from the significant role played by landscape features, rainfall and vegetation (Sinclair 2003; Owen-Smith & Mills 2008b).

In African protected areas, several large carnivore species live sympatrically. Co-existence may be facilitated when smaller carnivores and their diet are nested within those of the larger predators (Rosenzweig 1966; Gittleman 1985). This predicts that if the abundance of a larger carnivore is reduced then smaller ones should increase – the meso-predator release mechanism (Johnson *et al*. 2007). Alternatively, niche packing (Pianka 1974) is a product of evolutionary refinement caused by co-evolution among competing taxa (Diamond 1975; Roughgarden 1975; Roughgarden 1983). This results in temporal separation (Meiri *et al*. 2005), size variation and character displacement as a result of diet partitioning (Rosenzweig 1966; Gittleman 1985; Dayan & Simberloff 1998), and numerical variation in density (Robinson & Redford 1986). Evaluating the effects of past competition has proved challenging (Connor & Simberloff 1979; Connell 1980) and assertions waned as additional evidence outlining the importance of keystone species, environmental processes and history in shaping community structure were invoked (Tanner et al. 1994; Tanner *et al.* 1996; Owen-Smith & Mills 2008).

These two contrasting mechanisms of coexistence within large carnivore guilds predict different outcomes in response to emerging stressors. For instance, in Kruger National Park (KNP), South Africa, five members of the large carnivore guild: lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), leopards (*P. pardus*), cheetahs (*Acynonyx jubatus*) and wild dogs (*Lycaon pictus*) coexist. The emergence of bovine tuberculosis (*Mycobacterium bovis*) (bTB) in lions (Keet *et al.* 1996) is a stressor potentially leading to declines in lion abundances. The evolutionary niche packing mechanism predicts little consequences for abundances of the other carnivores, while the meso-predator release mechanism predicts increases.

The meso-predator release mechanism has been speculated as a driver of leopard abundances in KNP (Van Helden & Uys 2009). Using data collected from KNP through several methods including camera-trap facilitated photographic surveys (leopards), call-up surveys (lions and spotted hyaenas), public participation photographic surveys (cheetahs and wild dogs), and aerial surveys (herbivores), we investigated evidence of evolutionary niche packing and meso-predator release mechanisms associated with leopard abundances using spatially explicit abundance estimates of the large carnivore guild.

Materials and methods

Study area

The Kruger National Park is a stretch of land occupying 19495 km^2 in the north-east corner of South Africa (22°25’ - 25°32’ S; 30°50’ - 32°02’ E) (Fig. 4.1). Its north-south orientation spans ≈ 400 km in length with an average width of ≈ 65 km. Physical features of KNP include: a) the Lebombo Mountains, which line most of the eastern boundary of the park; and b) two main river systems running in an easterly direction namely, the nKomati system comprising the Crocodile, Sabi, and Sand Rivers in the south and the Limpopo system comprising the Olifants, Letaba, Limpopo and Luvuvhu Rivers in the north. The Sabi River in the south and the Olifants River in the north divide the park into the south, central and northern regions. The Limpopo and the Crocodile Rivers mark the northern and southern boundaries of the park, respectively. Other features include the longitudinal dissection of the park into granitic soil types in the west and the basaltic soil types in the east (Joubert 1986), 35 landscapes, which are aligned to different faunal species (Gertenbach 1983), a dry tropical climate with induced deciduous savannas comprising 14 major vegetation assemblages associated with the north-south increasing rainfall gradient ranging from 440 mm to 740 mm (Gertenbach 1980; Venter & Gertenbach 1986).

Kruger was divided into six zones as dictated by the two major soil types and the two main rivers, the Sabi in the south and the Olifants in central Kruger such that each of the three regions comprised two zones (Ferreira & Funston 2010). In addition, each zone had different prey biomass and bTB prevalence in buffalo (Fig. 4.1).

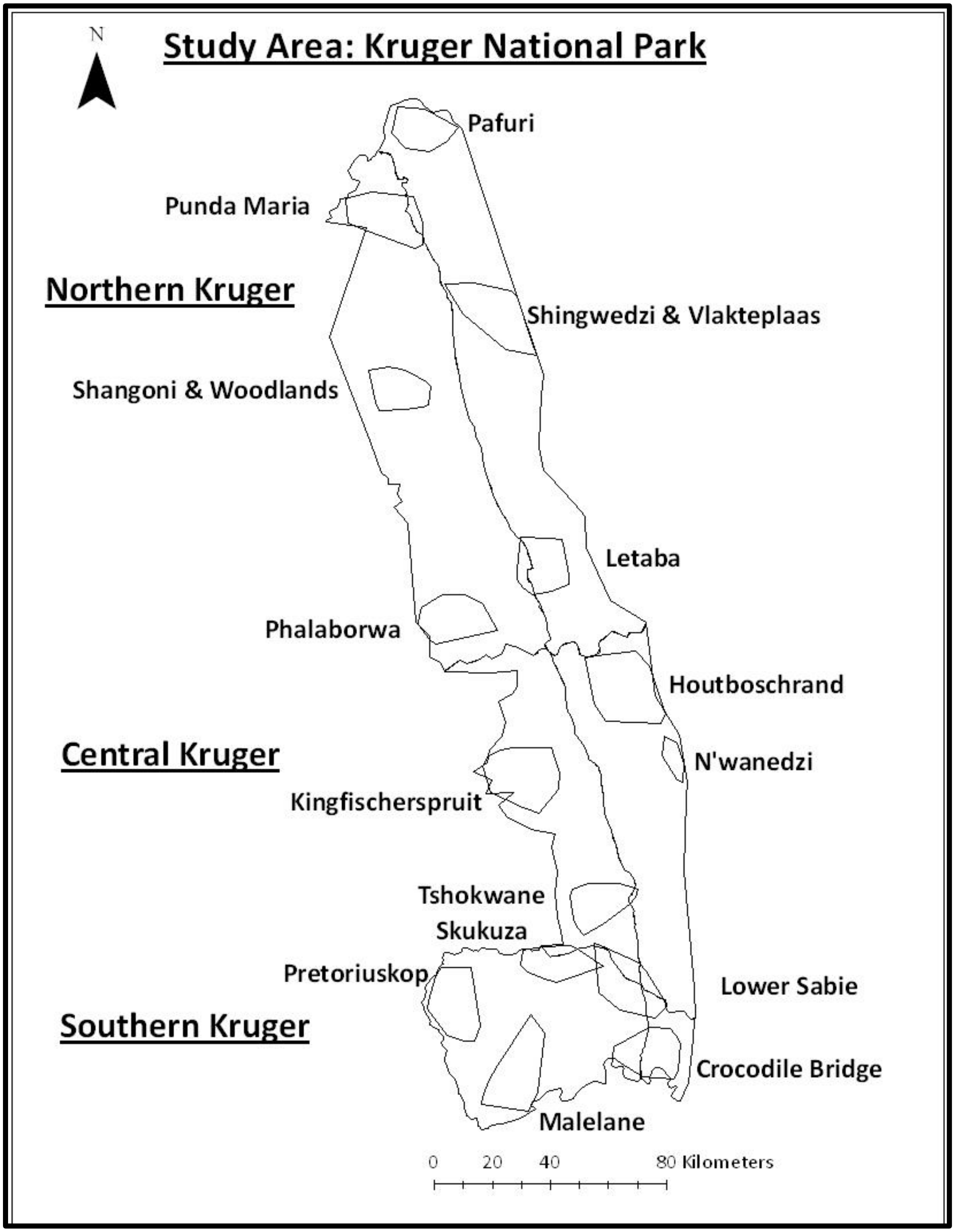


Figure 4.1. Map of the study area, Kruger National Park, South Africa, with the minimum convex polygons of the study sites, the six bovine tuberculosis and prey biomass delineated zones, and the three major regions of the park.

.

Data collection

Leopard abundance estimates for 14 study sites and six bTB/prey biomass zones where obtained from a camera-trap based mark-recapture KNP-wide photographic survey conducted in 2008 and from February 2010 to December 2011 (Chapter 3). Datasets for lions and spotted hyaenas were obtained from the South African National Parks' (SANParks) biological data archives. These data were collected using call-up stations where vocals of a prey animal in distress were played over a loud speaker to attract lions and spotted hyaenas. Methods outlining this survey technique are described in Ferreira & Funston (2010) and Funston & Ferreira (*unpublished data*). Lion surveys were conducted during the winters of 2005 and 2006, while the spotted hyaena surveys occurred during the winter of 2008. Additionally, regional estimates of lion abundances were obtained from Ferreira & Funston (2010). We used ArcGIS 10 (ESRI, Redlands, CA, USA) to extract the locations and response data from call-stations for lions and spotted hyaenas within the effective sampling areas as dictated by the leopard photographic surveys. We adapted the population estimate (N) in the study site j from Ferreira & Funston (2010) to have:

$$N_j = \frac{A_T \sum_{s=1} fs}{n\bar{A}P}$$ for lion and spotted hyaena population estimates.

Where A_T is the total size of the effective sampling area from the leopard photographic surveys, n is the number of call-up stations in the study site, $\sum_{s=1} f_s$ are the total number of lions or spotted hyaenas in a group, P is the probability that either lions or spotted hyaenas would respond, and A is the effective area sampled by a station. For lions we used $\bar{A} = 57.7$ km^2 and for hyaenas we used $\bar{A} = 32.21$km^2 as suggested by Ferreira & Funston (2010) and Funston & Ferreira (*unpublished data*). For the probability that the lions would respond, we took an average for lions with cubs and lions without cubs from Ferreira & Funston (2010). For the probability that spotted hyaena would respond we used P = 0.61 as suggested by Mills *et al.* (2001) and Funston & Ferreira (*unpublished data*).

Estimates for the smaller members of the guild, the cheetah and wild dog, were obtained from KNP-wide photographic surveys using public participation (Marnewick *et al.* 2014). Unlike leopards, lions and spotted hyaenas, abundances for the cheetahs and wild dogs were calculated for the three regions owing to the constraints associated with sampling methods and the biology of study animals.

We used ArcGIS 10 (ESRI, Redlands, CA, USA) to divide KNP into six zones according to prey biomass and bTB prevalence (Ferreira & Funston 2010). We obtained information on herbivore counts from SANParks' archives based on the 2008, 2010 and 2011 herbivore censuses. The censuses were conducted using a fixed-wing light aircraft and the counting methods are outlined in Kruger *et al*. (2008). Owen-Smith & Mills (2008) noted that leopards in KNP preferred prey species that weighed below 170 kg. Accordingly, impala (*Aepyceros malempus*), kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymus*), steenbok (*Raphicerus campestris*), common ostrich (*Struthio camelus*), and warthog (*Phacochoerus africanus*) were used in the biomass estimation. We followed Jolly's method (Jolly 1969) of estimating population abundances and densities from quadrants with unequal transect lengths to estimate abundance and density of each leopard prey species as described in Krebs (1989). $D = \frac{Total\ units\ counted}{Total\ area\ searched}$, where D was the prey population density for the area sampled. To calculate the variance for sampling with replacement we used the following equation:
$Var(X) = \frac{N^2}{n(n-1)}[\sum x^2 + R^2 \sum z^2 - 2R \sum xz]$; where X was the estimated prey species abundance, N was the number of possible aerial transects in the study area, n was the number of transects used in the survey, x was the total number of dungs counted and z was the area covered by a given transect (Krebs 1989; Zar 1999). Subsequently 95% confidence intervals were calculated as $X \pm t_{.025}(standard\ error)$.

Biomass for each prey species within a particular study site was estimated as the product of density and the conventional female body mass of that species (Bothma *et al.* 2006). We then calculated the total leopard prey biomass for each study site to be the sum of prey biomass estimated for prey species recorded in that study site. Finally, within each study site we divided the resultant biomass estimate by the effective area sampled for leopard abundance estimates so that we had biomass in kg/km^2 (Ferreira & Funston 2010).

Data analysis

We plotted leopard population estimates against prey biomass, lion population estimates and hyaena population estimates in each of the study sites (Fig. 4.1). We ran multiple regression analyses using generalised linear model. Consequently, we ran model selection under GLM to assess the model that best fitted the data using prey biomass, lion population estimate and spotted hyaena population estimate as descriptor variables. The sample size of the analysis was very small. To account for this in model selection, we used Akaike Information Criterion for small sample sizes (Hooper *et al.* 2008).

Similarly we ran multiple regression analysis through GLM to explain the variation in leopard population estimates in the six zones (Fig. 4.1). We ran model selection to investigate the likelihood of predictor variables including prey biomass, and population estimates of lions, and hyaenas explaining the variation in leopard population estimates among the six zones in KNP.

Finally, we compared leopard estimates to all the major carnivores in KNP's three main regions, namely: north central and south. The aim of this analysis was to assess how leopards fared numerically in comparison to the other carnivores currently living in KNP.

Results

Study sites - The best model predicting the relationship between leopard abundances among the study sites included the interaction between the three predictor variables namely prey biomass, lion abundances and spotted hyaena abundances (Table 4.1). At regional level, examination of the multiple regression analysis revealed a positive relationship between leopard abundances and spotted hyaenas with 53% of the variation explained (Fig. 4.2b). There was a negative linear relationship between leopard abundance estimates and the three predictor variables, but with poor support (Fig. 4.2a). Overall, the study site that had the most influence was Pretoriuskop, with a leopard population estimate of 103 (95% CI = 68-165) and a density estimate of 0.5 leopards.km^{-2} (95% CI = 0.3-0.8; Table 4.2). To illustrate the importance of the Pretoriuskop study site; and using prey biomass as a predictor variable, only 8% of the variation in leopards could be explained; however, removal of the study site from the analysis resulted in 24% of the variation in leopards being explained. In addition, there was a 79% change in the slope (b = -0.037 to -0.029) and a reduction in standard error (42.3%).

Table 4.1. Summary for model selection statistics for the General Linear Models (GLM) analysing the probability of explaining variations in leopard abundances in each of the study sites in the Kruger National Park (KNP), South Africa. The variables selected for this study were prey biomass, lion abundance and spotted hyaena abundance. Models were ranked according to Akaike weights (w_i) following Akaike Information Criterion for small samples (AICc). Presented are also the number of parameters (K), the log likelihood and the Delta (Δ_i) - differences between AICc's and the smallest AICc.

Rank	Model	*K*	log likelihood	AICc	Δ_i	w_i
1	(Prey + Lion + Hyaena)^2	6	-58.92	122.84	-8.14	0.277
2	Prey * Hyaena + Lion	4	-58.99	130.98	0.00	0.240
3	Prey * Lion * Hyaena	7	-58.53	127.06	-3.92	0.215
4	Prey + I(Prey^2)) + Lion + I(Lion^2) + Hyaena + I(Hyaena^2))	6	-58.83	122.66	-8.32	0.209
5	Prey * Lion + Hyaena	4	-59.71	132.42	1.44	0.031
6	Lion * Hyaena + Prey	4	-59.555	132.11	1.13	0.016
7	Prey + Lion + Hyaena	3	-59.715	127.43	-3.55	0.009
8	poly(Prey, 2) + Lion + Hyaena	4	-59.23	131.46	0.48	0.003

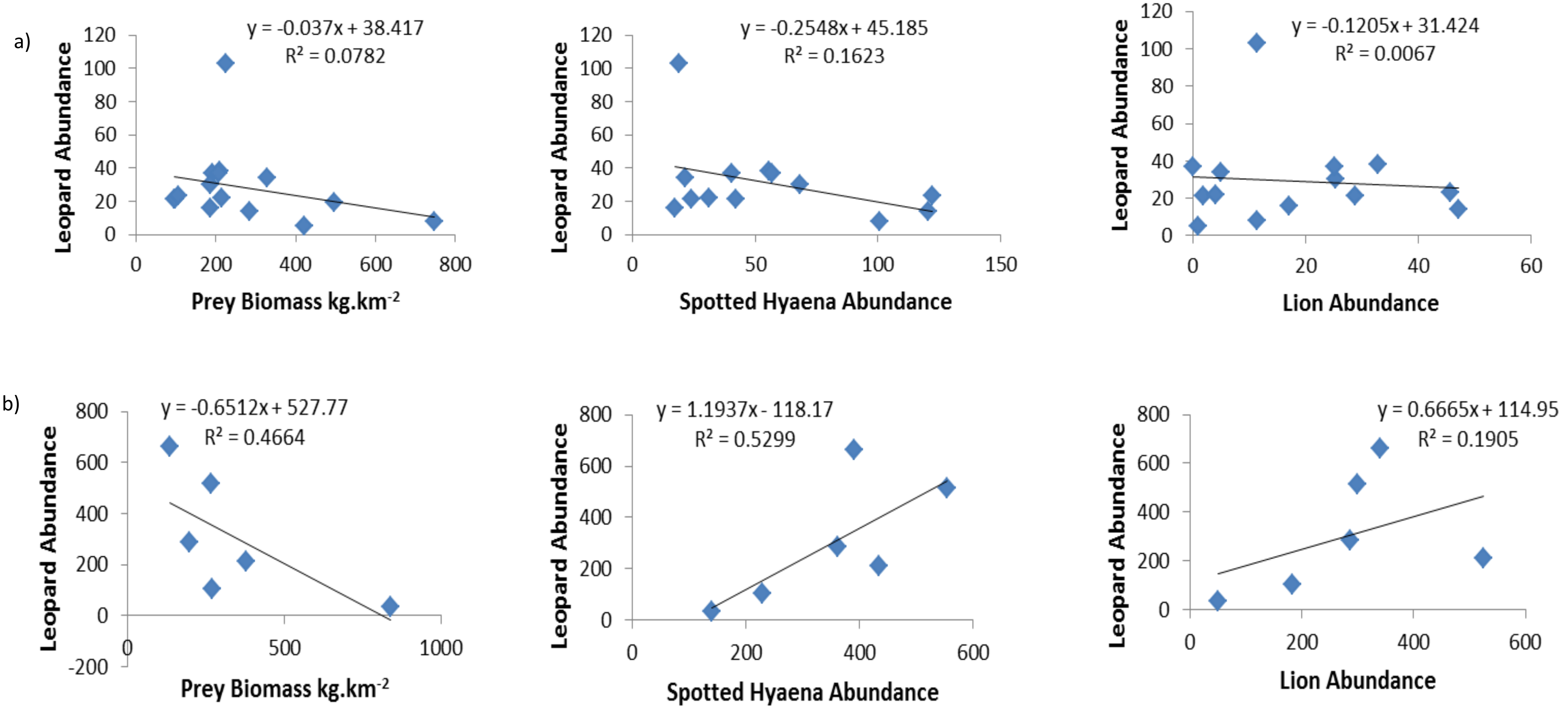


Figure 4.2. Linear regression plots depicting how leopard population estimates associated with prey biomass, spotted hyaena and lion population estimates in the Kruger National Park, South Africa between 2005 and 2011: a) Shows association by study site and b) shows regional associations.

Table 4.2. Study sites including study area, site-specific prey biomass estimated from leopard preferred prey and abundance estimates for leopards, lions and spotted hyaenas in the Kruger National Park, South Africa. Numbers in parentheses are confidence limits.

Study Site	**Area (km^2)**	**Prey Biomass ($kg.km^{-2}$)**	**Leopard Estimate**	**Leopard Density**	**Lion Estimate**	**Lion Density**	**Hyaena Estimate**	**Hyaena Density**
Pafuri	140	329 (177.1-480.8)	34 (24-65)	0.062 (0.054-0.124)	5 (± 8)	0.04	21 (± 95)	0.15
Shingwedzi & Vlakteplaas	487	209.5 (124-294.8)	38 (26-68)	0.063 (0.051-0.108)	33 (± 25)	0.07	56 (± 46)	0.11
Letaba	265	192.9 (-1.9-387.8)	37 (27-67)	0.14 (0.102-0.245)	0 (± 4)	0.00	40 (± 164)	0.15
Punda Maria	258	187.7 (50.4-324.9)	16 (14-32)	0.243 (0.171-0.464)	17 (± 18)	0.07	18 (± 27)	0.07
Shangoni & Woodlands	333	95.3 (-17.4-207.9)	21 (17-36)	0.078 (0.053-0.140)	29 (± 28)	0.09	42 (± 172)	0.13
Phalaborwa	629	99.7 (6.6-192.7)	21 (13-57)	0.033 (0.021-0.091)	2 (± 4)	0.00	24 (± 24)	0.04
Houtboschrand	946	285.6 (159.3-411.9)	14 (29-Nov)	0.015 (0.012-0.031)	47 (± 39)	0.05	120 (± 74)	0.13
N'wanedzi	150	496.9 -	19 (14-36)	0.127 (0.093-0.240)	-	-	-	-
Kingfischerspruit	595	187.0 (43.7-330.3)	30 (19-62)	0.05 (0.032-0.104)	25 (± 27)	0.04	68 (± 56)	0.11
Tshokwane	234	420.6 (167.4-673.9))	5 (5-79)	0.021 (0.017-0.338)	1 (± 5)	0.00	-	-
Skukuza	140	215.3 (-847.9-1278.6)	22 (18-38)	0.157 (0.129-0.271)	4 (± 8)	0.03	31 (± 22)	0.22
Lower Sabie	975	107.8 (62.8-152.7)	23 (12-75)	0.024 (0.012-0.077)	46 (± 33)	0.05	122 (± 58)	0.13
Pretoriuskop	206	226 (80.2-371.8))	103 (68-165)	0.5 (0.330-0.801)	11 (± 12)	0.06	19 (± 14)	0.09
Malelane	258	206.6 (91.9-321.2)	37 (28-66)	0.144 (0.109-0.256)	25 (± 22)	0.10	57 (± 64)	0.22
Crocodile Bridge	92	748.3 (-142.2-1638.8)	8 (27-Jul)	0.087 (0.076-0.295)	11 (± 11)	0.06	100 (± 391)	0.53

bTB/prey biomass zones - The best model predicting the relationship between leopard abundances in the six bTB/prey biomass zones included prey biomass, lion abundance, spotted hyaena abundance and the interaction between prey biomass and lion abundance (Table 4.3). Throughout the park, leopard abundance decreased with increasing prey biomass albeit with poor support (46.64%; Fig. 4.2b). This was in contrast with lion abundances, which increased with increasing prey biomass (see Ferreira & Funston 2010). Contrary to observations on the individual study sites, leopard abundances increased with increasing spotted hyaena abundances with 53% of the variation explained by a linear model (Fig. 4.2b). Whereas leopard abundances increased with increasing lion, only 19% of the variation in leopard abundances could be explained (Fig. 4.2b). Leopard density was highest in the south-west zone with 21 (95% CI = 15-35) leopards/100km^2, while spotted hyaena density of 31±78 hyaenas/ 100km^2 (Table 4.4) corresponded with the south-east zone, which had the highest prey biomass of 838 (95% CI = 380-1296) kg/km^2.

Table 4.3. Summary for model selection statistics for the General Linear Models analysing the probability of explaining variations in leopard abundances in the six bTB/prey biomass zones in the Kruger National Park (KNP), South Africa. The variables selected for this study were prey biomass, lion abundance and spotted hyaena abundance. Models were ranked according to Akaike weights (w_i) following Akaike Information Criterion for small samples (AICc). Presented are also the number of parameters (K), the log likelihood and the Delta (Δ_i) -differences between AICc's and the smallest AICc.

Rank	**Model**	***K***	**log likelihood**	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
1	Prey*Lion+Hyaena	4	-34.08	81.16	0	0.413
2	Prey * Hyaena + Lion	4	-34.395	81.79	0.63	0.302
3	(Prey, 2) + Lion + Hyaena)	4	-34.54	82.08	0.92	0.261
4	Prey + Lion + Hyaena	3	-39.71	87.42	6.26	0.018
5	Lion * Hyaena + Prey	4	-39.085	91.17	10.01	0.003
6	poly(Lion, 2) + Prey + Hyaena	4	-39.5	92.00	10.84	0.002
7	poly(Hyaena, 2) + Prey + Lion)	4	-39.51	92.02	10.86	0.002

Table 4.4. Regional population estimates for the large carnivores from the Kruger National Park (KNP), South Africa. Prey biomass was adjusted to the leopard preferred prey following Owen-Smith & Mills (2008). Leopard estimates were obtained from Chapter 3; lion estimates were taken directly from Ferreira & Funston (2010); and spotted hyaena estimates were calculated from surveys conducted in the KNP during 2008. N denotes the number of animals that either responded to the call-up stations (lions and spotted hyaenas) or were captured in the mark-recapture photographic surveys (leopards).

				Leopard			**Lion** (Ferreira & Funston 2010)			**Spotted hyaena**		
Region	**bTB prevalence (%)**	**Prey biomass (kg/km^2)**	**Area (km^2)**	**N**	***Estimate***	**Density .km^{-2}**	**N**	***Estimate***	**Density .km^{-2}**	**N**	***Estimate***	**Density .km^{-2}**
Northern KNP	North-west 0-5	134 (90-342)	6810	45	661 (521-1114)	0.15 (0.11-0.28)	58	340 (280-400)	0.05 (0.04–0.059)	35	391 (216-566)	0.06 (±1.02)
	North-east 0-5	196 (143-249)	3442	55	286 (247-509)	0.05 (0.04-0.11)	45	286 (239-333)	0.083 (0.069–0.097)	62	362 (200-524)	0.11 (±0.31)
Southern KNP	Central-west 15-24	270 (143-397)	2502	23	103 (68-550)	0.04 (0.02-0.22)	27	183 (137-230)	0.073 (0.055–0.092)	38	230 (126-335)	0.09 (±0.60)
	Central-east 15-24	378 (179-577)	3016	31	212 (156-383)	0.07 (0.05-0.14)	18	525 (353-698)	0.17 (0.11–0.23)	51	435 (232-638)	0.14 (±0.29)
	South-west 40-60	265 (83-447)	3675	77	515 (366-993)	0.21 (0.15-0.35)	70	299 (255-344)	0.081 (0.069–0.094)	77	554 (304-804)	0.15 (±0.18)
	South-east 40-60	838 (380-1296)	460	6	35 (31-117)	0.09 (0.08-0.3)	14	51 (34-68)	0.11 (0.075–0.149)	18	140 (-19-299)	0.31 (±0.78)

Regions - There were marked differences between the three largest predators namely leopards, spotted hyaenas, and lions; and smaller, less abundant cheetahs and wild dogs (Table 4.5). Leopard estimates were highest (947; 95% CI: 786-1623) in the northern region of the park where prey biomass was lowest (165; 95% CI: 233-591). Interestingly, in the central region of KNP, where there was an increase in prey biomass (324; 95% CI: 322-947), leopard abundances where relatively low (315; 95% CI: 224-933), while lion and spotted hyaena abundances were high. Even so, leopard abundance was still markedly higher than cheetah and wild dog abundances.

Table 4.5. Numerical comparisons of the large carnivore guild in the Kruger National Park, South Africa. Prey biomass has been adjusted to the leopard preferred prey (Owen-Smith & Mills 2008). References for the estimated abundances are in parenthesis; bTB refers to bovine tuberculosis. Values in parentheses are the naïve density estimates obtained by dividing carnivore abundance estimates by the size of the study area.

bTB Prevalence	**Area** (km^2)	**Prey biomass** (kg/km^2)	**Leopards**	**Lions** (Ferreira & Funston 2010)	**Hyenas**	**Wild dogs** (Marnewick et al. 2014)	**Cheetahs** (Marnewick et al. 2014)
Low	10252	165 (233-591)	947 (786-1623)	626 (519-733)	753 (416-1090)	24 (19-29)	No data
Medium	5518	324 (322-974)	315 (224-933)	708 (490-928)	665 (358-973)	23 (20-27)	137 (83-191)
High	4135	1103 (463-1743)	550 (397-1110)	350 (289-412)	694 (285-1103)	89 (87-91)	236 (174-298)

Discussion

Leopard abundances were not influenced by lion abundances, spotted hyaena abundances and prey biomass. In addition, the marked numerical superiority of leopards to both the cheetah and wild dog abundances suggest that the two smaller carnivores did not play a role in the observed variation in leopard abundances throughout KNP. This was however, expected as previous studies in KNP suggest that leopards, in addition to having had a different response to the historical management practices, were tolerant of broader ecological conditions than cheetahs and wild dogs (Bailey 1993; Mills & Funston 2003).

Although there was poor statistical support for the relationships between leopards and the predictor variables, a further assessment of the results presented two contrasting views. Firstly, at the study site level, leopard abundance declined with increasing prey biomass, lion abundances and hyaena abundances. On the other hand, at bTB/prey biomass zone level, leopard abundance decreased with increasing prey biomass but increased with increasing lion and hyaena abundances. Furthermore, we noted as an anomaly, a tendency for leopard abundances to decrease with increasing prey biomass at the study site and bTB/prey biomass zone levels. At park-wide scale, the relationship between leopard abundances and prey biomass did not reveal any pattern.

There are two possible reasons for the contrasting associations between leopard abundances with lion and spotted hyaena abundances (Fig. 4.2) at the two spatial scales. Firstly, the observed anomaly may be a result of differences in sample sizes (13 study sites as opposed to six KNP zones) and overall, of small sample sizes. Secondly, we asked the question of scale; study site level specific differences observed for the three carnivore species were not accounted for when extrapolations for zone specific abundance estimates were calculated. The zones being significantly larger than the study sites, should be more heterogeneous in terms of distribution of prey species and other environmental factors. Even so, this anomaly is unlikely to change the outcomes of the study because of poor statistical support. Furthermore, the observed trends showed no discernable pattern when regional estimates were invoked (Table 4.5). Similarly, it is plausible that the observed association between leopard abundances and prey biomass may not be an active player because biomass estimates may be above the threshold of leopard dietary requirements. Mills & Funston (2003) argued that on average, carnivores in KNP have at their disposal 1,750 kg/km^2 of prey biomass annually. As such, this makes the negative relationship between leopards and prey biomass trivial.

Accordingly, our results support assumptions of the niche packing hypothesis, while challenging assumptions of the mesopredator release hypothesis in the context of KNP. Niche packing assumes several conditions in order to be justified. Firstly, the ecosystem has to be complex. Complex ecosystems associate with large reserves. Taxa involved must have a history of evolutionary interactions leading to the extant observed patterns. Indeed, KNP represents a complex ecosystem represented by a substantial measure of heterogeneity (Rogers 2003, Venter *et al.* 2003). In addition, leopards in Africa coexisted with other large carnivores for a very long time. This is further supported by the findings by Owen-Smith & Mills (2008) that leopard diet was not nested within those of lions and hyaenas as suggested elsewhere (see Gittleman 1985). In India, Harihar *et al.* (2008) found that leopards tended to relocate to the edges of the reserve away from the centres, upon the re-introduction of tigers to a reserve. This was unlikely in our case for three reasons. Firstly, the Indian study was in a forest setting. Forests are not known for being as heterogeneous as the savannahs are. Secondly, it appears that their study site was much smaller than the KNP study, thus not supported by the assumptions of niche packing. Thirdly, their study area was devoid of tigers for an extended period of time. This takes away from the evolutionary refinement of *within* and *between* species life history patterns suggested by Pianka (1974). The scenario is as such different to the KNP study where leopards coexisted with lions and spotted hyaenas for a very long time.

Meso-predator release hypothesis predicted that leopard abundances in KNP should be low where lion abundances and spotted hyaena abundances were high; and be high where lion abundances and spotted hyaena abundances were low. Our current data by not showing discernible association between leopard abundances and lion and hyaena abundances, weaken the speculations of meso-predator release being a driver of leopard abundances in KNP. This may be because KNP ecosystem is both strongly bottom-up and top-down driven. Smit (2011) showed a robust relationship between herbivores and good quality food availability in KNP. In addition, Owen-Smith & Mills (2006) noted that whereas predation could not easily be disentangled as a by-product of past management practices in the park, herbivore population dynamics were largely bottom-up driven. The two statements argue for strong bottom-up effects in KNP ecosystem. Indeed, on the other hand, carnivores and especially lions in KNP play a significant role regulating abundances of certain herbivore species as a result of fluctuating prey species abundances in response to environmental conditions (Owen-Smith & Mills 2008b); thus arguing for a strong top-down regulation of ecosystem processes in KNP. To be realised, meso-predator release phenomenon requires strong top-down regulated ecosystems even though bottom-up processes should still be taken into account (Elmhagen & Rushton 2007; Ritchie & Johnson 2009) especially when anthropogenic activities are not taken into consideration; of which KNP is not. The emergence of bTB as a stressor may weaken such strong top-down processes by leading to a decline in lion abundance and consequently allowing for an increase in leopard abundances (Van Helden & Uys 2009). This postulate has since been refuted as Ferreira & Funston (2010) who noted that lion population abundances in KNP had been consistent for the past 30 years. Even so, our data suggest that even if the lion population were to decline, the consequences of such an event would not affect leopard abundances. Our results therefore, suggest that the KNP ecosystem is strongly skewed towards bottom-up processes, which presently overshadows top-down processes for this predator guild.

Currently, leopard abundances maybe driven by factors other than those suggested in this study or a combination of these and other factors. Other plausible variables that could explain leopard population abundances, but were not considered in this study are intraspecific interactions, leopard-specific diseases – other than bTB, and hunting success of leopards. Indeed, Bailey (1993) found strong relationships between hunting success in leopards and the propensity to starve to death. On the other hand, he noted that the hunting success was also very high. This eliminates hunting success as a possible driver. Michel *et al.* (2006) noted that leopards being a solitary species are unlikely to suffer population level impact of diseases such as bTB; thus eliminating disease as another possible driver. This leaves intraspecific interactions. The extent of intraspecific interactions for leopards in KNP has not been fully investigated. To this end, it is possible that for the KNP leopard population, a host of several variables need to be taken into account as drivers of leopard abundances.

Conclusion

Our data weaken postulations that a meso-predator release phenomenon triggered by a decline in lion and hyaena abundance is likely to be observed in the KNP leopard population. Our results suggest that observed patterns are as a result of millions of years of co-evolution among large carnivores, leading to the observed trends. Presently, there is no sufficient evidence to suggest declines in lion abundances as a result of a stressor, bTB in the park, but across the park, lions occur in variable numbers. Our data showed that this event would not have an influence on leopard abundance. We postulate that prey biomass in KNP is higher than the required threshold for leopards for its effects to be observed. The present study suggests that leopard life history patterns and intraspecific interactions between leopards may be driving variations in leopard abundances in KNP. The observed patterns support the theory of niche packing in KNP.

References

Bailey, T.N. 1993. *The African Leopard: ecology and behaviour of a solitary felid.* Columbia University Press, New York, USA.

Bengis, R.G., Grant, R. & de Vos, V. 2003. Wildlife diseases and veterinary controls: A savanna ecosystem perspective. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity.* Eds: J.T. du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington, DC, USA.

Bothma, J., du P., van Rooyen, N. & du Toit, J.G. 2002. Antelope and other smaller herbivores. In: *Game Ranch Management.* Ed. J. du P. Bothma. Van Schaik Publishers, Pretoria, R.S.A.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos,* **35:** 131-138.

Connor, E.F., & Simberloff, D. 1979. The assembly of species communities: chance or competition? *Ecology*, **60** 1132-1140.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W. & Schmid, B. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa’s large carnivores. *Ecology*, **93:** 2590-2599.

Dayan, T., & Simberloff, D. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Reviews,* **28:** 99-124.

Diamond, J.M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, **7:** 129-146.

Elmhagen, B. & Rushton, S.P. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters*, **10:** 197-206.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, **37:** 194-206.

Gertenbach, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe*, **23:** 35-43.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe,* **26:** 9-121.

Gittleman, J.L. 1985. Carnivore body size: Ecological and taxonomic correlates. *Oecologia,* **67:** 540-554.

Harihar, A., Pandav, B. & Goyal, S.P. 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *Journal of Applied Ecology,* **48:** 806-814.

Hayward, M.W., O'Brien, J. & Kerley, G.I.H. 2007. Carrying capacity of large African predators: Predictions and tests. *Biological Conservation,* **139:** 219-229.

Hayward, M.W. & Slotow, R. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research,* **39:** 109-125.

Holdo, M.H., Sinclair, A.R.E., Dobson, A.P., Metzger, K.L. Bolker, B.M., Ritchie, M.E. & Holt, R.D. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for Ecosystem C. *PloS Biology,* **7:** 1000210.

Hooper, D., Coughlan, J., & Mullen, M.R. 2008. Structural equation modelling: Guidelines for determining model fit. *The Electronic Journal of Business Research Methods,* **6:** 53-60.

Jaksić, F.M., Greene, H.W. & Yáñez, J.L. 1981. The guild structure of a community of predatory vertebrates in central Chile. *Oecologia,* **49:** 21-28.

Johnson, C.N., Isaac, J.L. & Fisher, D.O. 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society,* **274:** 341-346.

Jolly, G.M. 1969. Sampling methods for aerial censuses of wildlife populations. *East African Agriculture Forestry Journal,* **34:**46-49.

Joubert, S.C.J. 1986. The Kruger National Park – An Introduction. *Koedoe,* **29:** 1-11.

Krebs, C.J. 1989. *Ecological methodology*. Harper-Collins Publishers, New York, USA.

Keet, D.F., Kriek, N.P.J., Penrith, M.-L., Michel, A. & Huchzermeyer, H. 1996. Tuberculosis in buffaloes (*Syncerus caffer*) in the Kruger National Park. Spread of the disease to other species. *Onderstepoort Journal of Veterinary Research,* **63:** 239-244.

Kissui, B.M. & Packer, C. 2004. Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society B,* **24:** 200-210.

Levy, O., Dayan, T., Kronfeld-Schor, N., & Porter, W.P. 2012. Biophysical modelling of the temporal niche: From first principles to the evolution of activity patterns. *The American Naturalist,* **179:** 794-804.

Maputla, N.W., Chimimba, C.T., & Ferreira, S.M. 2013. Calibrating a camera trap-based biased mark-recapture sampling design to survey the leopard population in the N'wanetsi concession, Kruger National Park, South Africa. *African Journal of Ecology,* **51:** 422-430.

Meiri, S., Dayan, T., & Simberloff, D. 2005. Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology,* **86:** 1432-1440.

Michel, A.L., Bengis, R.G., Keet, D.F., Hofmeyr, M., de Klerk, L.M., Cross, P.C., Jolles, A.E., Cooper, D., Whyte, I.J., Buss, P. & Godfroid, J. 2006. Wildlife tuberculosis in South African conservation areas: implications and challenges. *Veterinary Microbiology,* **112:** 91-100.

Mills, M.G.L., Juritz, J.M. & Zucchini, W. 2001. Estimating the size of spotted hyaena (*Crocuta crocuta*) populations through playback recordings allowing for non-response. *Animal Conservation,* **4:** 335-343.

Mills, M.G.L. & Funston , P.J. 2003. Large carnivores and savannah heterogeneity. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds: J.T. du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington, DC, USA.

Osborne, J.W. 2010. Improving your data transformations: Applying the Box-Cox transformation. *Practical Assessment, Research & Evaluation*. **15:** Available online http://pareonline.net/pdf/v15n12.pdf

Owen-Smith, N. & Mills, M.G.L. 2008a. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*. **89:** 1120-1133.

Owen-Smith, N. & Mills, M.G.L. 2008b. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology,* **77:** 173-183.

Palomares, F. & Caro, T.M. 1999. Interspecific killing among mammalian carnivores. *The American Naturalist,* **153:** 492-508.

Pianka, E.R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences USA,* **71:** 2141-2145.

Pickett, S.T.A., Cadenasso, M.L. & Benning, T.L. 2003. Biotic and abiotic determinants of savanna heterogeneity at a multiple spatiotemporal scales. In: *The Kruger experience: Ecology and management of a savanna heterogeneity.* Eds J.T. Du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington DC, USA.

Pulliam, H.R, Dunning, J.B. & Liu, J. 1992. Population dynamics in complex landscapes: a case study. *Ecological Application,* **2:** 165-177.

Ritchie, E.G. & Johnson, C.N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters,* **12:** 982-998.

Robinson, J.G., & Redford, K.H. 1986. Body size, diet, and population density of neotropical forest mammals. *The American Naturalist,* **128:** 665-680.

Romero-Muñoz, A., Maffei, L., Cuéllar, E. & Noss, A.J. 2010. Temporal separation between jaguar and puma in the dry forests of southern Bolivia. *Journal of Tropical Ecology,* **26:** 303-311.

Rosenzweig, M.L. 1966. Community structure in sympatric Canivora. *Journal of Mammalogy,* **47:** 602-612.

Roughgarden, J. 1975. Resource partitioning among competing species-a coevolutionary approach. *Theoretical Population Biology,* **9:** 388-424.

Roughgarden, J. 1983. Competition and theory in community ecology. *The American Naturalist,* **122:** 583-601.

Russell, J.C., Lecomte, V., Dumont, Y. & Le Corre, M. 2009. Intraguild predation and mesopredator release effect on long-lived prey. *Ecological Modelling.* **220:** 1098-1104.

Sinclair, A.R.E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical Transactions of the Royal Society of London* **B**, **358:** 1729-1740.

Sinclair, A.R.E., Mduma, S., & Brashares J.S. 2003. Patterns of predation in a diverse predator-prey system. *Nature*, **245:** 288-290.

Smit, I.P.J. 2011. Resources driving landscape-scale distribution patterns of grazers in an African Savanna. *Ecography,* **34:** 67-74.

Tanner, J.E., Hughes, T.P., & Connell, J.H. 1994. Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology,* **75:** 2204-2219.

Tanner, J.E., Hughes, T.P., & Connell, J.H. 1996. The role of history in community dynamics: a modelling approach. *Ecology,* **77:** 108-117.

Trewby, I.D., Wilson, G.J., Delahay, R.J., Walker, N., Young, R., Davison, J., Cheeseman, C., Robertson, P.A., Gorman, M.L. & McDonald, R.A. 2008. Experimental evidence of competitive release in sympatric carnivores. *Biology Letters,* **4:** 170-172.

Van Helden, P. & Uys, P. 2009. Modelling predator-predator population dynamics in the context of BTB. *Disease Risk Assessment Workshop Report: African Lion (Panthera leo) Bovine Tuberculosis.* Eds. Keet, D.F., Davies-Mostert,H., Bengis, R.G., Funston, P., Buss, P., Hofmeyr, M., Ferreira, S., Lane, E., Miller, P. & Daly, B.G. Conservation Breeding

Venter, F.J. & Gertenbach, W.P.D. 1986. A cursory review of the climate and vegetation of the Kruger National Park. *Koedoe,* **29:** 139-148.

Zar, J.H. 1999. *Biostatistical Analysis.* Englewood Cliffs, NJ: Prentice Hall.

Chapter 5. Spatio-temporal separation between lions and leopards in the Kruger National Park and the Timbavati Private Nature Reserve, South Africa

This chapter is formatted for submission to *Global Ecology and Conservation*

*Nakedi W. Maputla[a,b], Nkabeng T. Maruping[c], Christian T. Chimimba[b], Sam M. Ferreira[d]

*Corresponding author

a) *African Wildlife Foundation (AWF), AWF Conservation Centre, Ngong Road, Karen,*

P.O. Box 310, 00502, Nairobi, Kenya

Email: nwmaputla@zoology.up.ac.za

b) *Mammal Research Institute (MRI) and DST-NRF Centre of Excellence for Invasion Biology (CIB), Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa*

Email: ctchimimba@zoology.up.ac.za

c) *Department of Nature Conservation, Tshwane University of Technology, Private Bag X680, Pretoria West, 0001 South Africa*
Email: marupingntt@tut.ac.za

d) *Scientific Services, South African National Parks (SANPARKS), Skukuza, 1350 South Africa*

Email: sam.ferreira@sanparks.org

Running title: Spatial and temporal association between leopards and lions

Abstract

Understanding of the underlying processes that drive coexistence among apex predators is of great importance to landscape managers overseeing their persistence. Two pressing questions stand out. These questions relate to whether space use by subordinate carnivores is a function of resource distribution and shifts in resource availability or fine scale movement associations with sympatric top predators that dominate them. We hypothesised that leopard movements were primarily resource-driven and secondarily, competition driven. Using data from leopards and lions collared in the Kruger National Park (Kruger) and the neighbouring Timbavati Private Nature Reserve (Timbavati), we investigated the associations between leopard GPS fixes and resource distribution. We built landscapes of movement activities of lions to investigate the relationships with leopard movements. Results suggested that leopard movements were strongly resource-driven. Lion influence did not come out strongly on the male leopard collared in the Kruger, but associated with visitation rates by the female leopard. In the Timbavati however, lion movements appeared to strongly influence the male leopard movements. We concluded that resources were the main driver of leopard movement behaviour and that differences in observed behaviours between Kruger and Timbavati were as a result of different management regimes practised in the two reserves.

Keywords: coexistence; resources; competition; leopard; lion; Kruger National Park

Introduction

Mechanisms that drive processes underlying the co-existence of large mammalian carnivores highlight the importance or a lack thereof of apex predators in suppressing population abundances of smaller predators (Richie & Johnson 2009); altering space use by smaller predators (Harihar *et al.* 2011; Broekhuis *et al.* 2013; du Preez *et al.* 2015); and altering feeding ecology of smaller predators through interference competition (Elmhagen *et al.* 2010; Cozzi *et al.* 2012; du Preez *et al.* 2015). On the other hand, co-evolution of large carnivores that live sympatric may have resulted in the extant level of interaction among large carnivores (Owen-Smith & Mills 2008b).

In African carnivore assemblages, resource acquisition by leopards (*Panthera pardus*), cheetah (*Acynonyx jubatus*) and wild dogs (*Lycaon pictus*) was inherent to intraguild competition avoidance of lions (*P. leo)* (Vanak *et al.* 2013; du Preez *et al.* 2015). In addition to avoid immediate risk, cheetahs positioned themselves far from proximity of lions or spotted hyaenas (*Crocuta crocuta*) (Broekhuis *et al.* 2013). This is however, not only confined to relationships between predators. At the ecosystem level, intraguild relationships are intertwined with interguild interactions; thus influencing ecosystem structure and functionality by changing population dynamics and foraging behaviour, i.e., cascading effects (Johnson *et al.* 1992; Packer *et al.* 2005). For example, in Yellowstone National Park, U.S.A., the elk changed their movement behaviour in response to wolf presence, thus altering trophic cascades that led to reduction in the use of certain aspen patches (Fortin *et al.* 2012). Similarly, in South Africa, zebra (*Equus quagga*) in Kruger National Park were reported to alter their step lengths immediately after contacting or sensing lions and the step length shortened with increasing distance between the zebra and the lions (van Langevelde *et al.* 2013). In Hwange National Park, Zimbabwe, use of water sources by buffalo

(*Syncerus caffer*) was during the day when it was warm and lions were not active (Valeix *et al.* 2009).

Besides demonstrating predator-prey and predator-predator relationships, these examples emphasize the importance of predation in regulating top-down processes in an ecosystem. In small reserves, which lack heterogeneity (Vanak *et al.* 2013), interactions between apex predators and smaller predators may be accentuated (Creel & Creel 1996; Cristescu *et al.* 2013). In large reserves characterised by heterogeneous landscapes (Johnson *et al.* 1992); species-rich habitats with varying abundances of prey species (Gittleman 1985); and varying climatic conditions along a spatio-temporal scale gradient (Owen-Smith & Mills 2008a; Chapter 4) may buffer and mask these intra-guild interactions. In addition, anthropogenic activities - such as the introduction of an invasive species - coupled with stochastic events, for example, the emergence of extrinsic disease, may affect interactions between species concerned resulting in altered processes in an ecosystem (Clout & Russell 2007).

In Kruger, lions and leopards coexist throughout the park. At population level, it is unknown whether competition for space or resources influences coexistence (Owen-Smith & Mills 2008b). Even so, the meso-predator release hypothesis predicts that lions as apex predators, should influence land use by leopards (Trewby *et al.* 2012).

The emergence of an extrinsic disease, caused by the pathogen *Mycobacterium bovis* that causes bovine tuberculosis (bTB), is a major concern for conservationists (see Ferreira & Funston 2010). Introduced into the Kruger by human activities in the 1960s (Bengis *et al.* 2003), the disease has as a reservoir host, the Cape buffalo (*Syncerus caffer*). It spilled over into other species including greater kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*) (Caron *et al.* 2003; Keet *et al.* 1996). These affected species are important prey species for lions thus placing lions in direct contact with the disease where it is prevalent. Consequently, lions may be affected by the disease although population level effects are not detectable (Ferreira & Funston 2010). In addition, the disease may spread readily through the lion populations facilitated by intra-specific behavioural patterns in lions (Maruping 2014). Bovine tuberculosis may not affect the leopard population. Leopards are solitary, reducing intra-specific transmission mechanisms; and their diet is not dominated by reservoir hosts (Keet *et al.* 1996; Hayward *et al.* 2006; Owen-Smith & Mills 2008b; Renwick *et al.* 2007). Consequently, Van Helden & Uys (2009) predicted that bTB in lions could potentially lead to declines in lions; thus triggering meso-predator release in leopards. This prediction was however, weakened by the findings through numerical comparisons that meso-predator release may not materialize in the Kruger's leopard population (Chapter 4). Numerical comparisons did not, however, answer questions relating to space use by leopards.

Smit (2011) noted that the distribution of ruminants associated with areas of high quality forage. In a separate study, Wessels *et al.* (2006) found a modest relationship between herbaceous biomass and the Normalized Difference Vegetation Index (NDVI). Notionally, predators that feed on those ruminants, should forage in areas highly visited by those ruminants. By extension, we hypothesised that leopard movement patterns should associate with highly productive sites since resource distribution is an important variable in the use of landscape by leopards (Bailey 1993). We expected that thick herbaceous layer should provide enough cover for a hunting leopard, which relies on ambush to catch prey (Bailey 1993; Hayward *et al.* 2006). During the dry season, we expect water availability to be confined to a few permanent water points along the major rivers and smaller rivers in the study area; by extension, we expect to observe heightened leopard activity around those water points. In the rainy season however, we expect several temporary water points to be distributed patchily on the landscape as a result of the rain; thus water dependent herbivores would not be pressured to visit permanent water points, but use the water points that are in their close proximity.

Accordingly, we predicted that leopard space use should be primarily driven by resources that directly and indirectly affect food acquisition and secondarily, lion spatial use. Equally, lion abundances and space use are generally resource-driven (Owen-Smith & Mills 2008a). That means in areas of territorial overlap, conflicts between leopards and lions should be expected. Leopards being smaller predators, should therefore use the landscape as a function of lion space use. Consequently, these observations lead to the prediction that in addition to resource distribution, leopard movements may be influenced by lion space use.

Using spatial data from leopards and lions in the Kruger and the neighbouring Timbavati, we hypothesised that a set of variables including habitat productivity as predicted by Enhanced Vegetation Index models (EVI), water availability, proximity to roads, proximity to streams, and the presence of lions influenced leopard movement behaviour. Specifically we predicted that space use by leopards was primarily resource-driven and secondarily driven by lion space use. Conservation implications of this study may guide management decisions surrounding large carnivore management in large reserves.

Materials and methods

Study site

The Kruger is located at the north-east corner of South Africa between 22°25' - 25°32' S and 30°50' - 32°02' E. It covers an area ≈ 19495 km^2. In length, the park is ≈ 400 km while on average it is ≈ 65 km wide. The park borders Zimbabwe in the north and the entire length of the eastern boundary is shared with the Mozambican border. The topography of the park is variable and is reflected in the 35 landscapes that the park comprises. The landscapes also reflect an increasing north to south rainfall gradient (Joubert 1983) and two major soil types (the basalt soils in the east and the granite soils in the west) that characterise the park (Venter 1983). Two perennial rivers namely the Sabie River in the south and the Olifants River in the centre, dissect the park into northern, central and southern regions.

For this study, we focused on the central and southern regions south of the Olifants River (Fig. 1). The two regions have variable terrain characterised by extremely irregular incised areas immediately south of the Olifants River; moderately undulating and southern basalt plains in the east; and low mountains and hills represented by the Lebombo Mountains in the far east on the border with Moçambique and Malelane Mountains on the south west corner of Kruger (Gertenbach 1983; Venter *et al.* 2003). Notable large mammals that inhabit the area include buffalo, elephants, zebra, kudu, large numbers of impala and five large carnivore species including lions, spotted hyaenas, leopards, cheetahs, and wild dogs.

The Timbavati is situated between 24° 24'S and 31°21'E, covers an area ≈ 550 km^2 and is located on the central west border of the Kruger (Fig. 5.1). The reserve comprises *Combretum apiculatum*, *A. nigrescens*, and *Colophospermum mopani* as the dominant vegetation types with mostly granite or basalt as the principal soil types (Hall-Martin *et al.* 1975). The reserve is dominated by large numbers of impala (*Aepyceros melampus*), elephants (*Loxodonta africana*), and warthog, which are believed to have altered field conditions of the reserve (Pietersen 1992). Large carnivore species in the reserve include lions, spotted hyaenas, leopards, cheetahs and wild dogs.

Species	Individual	Sex	J	F	M	A	M	J	J	A	S	O	N	D	Year	Fixes
Leopards	CrocBridge	F	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	2012-13	1009
	Skukuza_m	M	▨	▨	▨	▨	▨	▨	▨	▨	▨			▨	2011-12	962
	Skukuza_f	F			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	2012	687
	Nwanedzi_f	F								▨	▨	▨			2012	125
	Nwanedzi_m1	M											▨	▨	2008	201
	Nwanedzi_m2	M	▨	▨	▨										2009	170
	Satara_f	F	▨	▨	▨	▨	▨	▨			▨	▨	▨	▨	2012-13	731
	Timbavati_m	M						▨	▨	▨	▨	▨	▨	▨	2011	380
Lions	Skukuza_Pride	F	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	2011-12	4841
	Timbavati_Pride	F	▨	▨	▨	▨	▨	▨	▨			▨	▨	▨	2011-12	1809
	Timbavati_Nomad	M	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	2011-14	5303

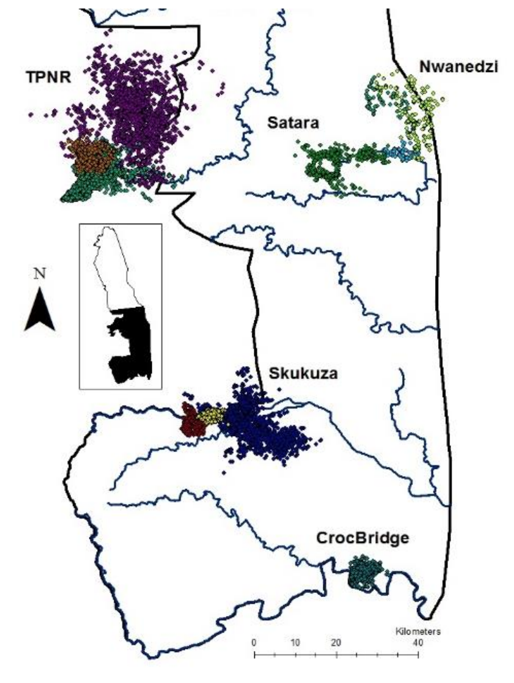


Figure 5.1. A map showing southern Kruger National Park (Kruger) and the Timbavati Private Nature Reserve (Timbavati), South Africa, where the study was undertaken. Lion data are from the Skukuza in Kruger and Timbavati study sites. Leopard data are from all the study sites. Shaded area represents the months that each collar was active.

Data collection

Study animals

All animal immobilisations followed strictest animal handling ethics approved by the South African National Parks Board and the Mpumalanga Tourism and Parks Agency. Three male and four female leopards were fitted with satellite (n = 5), and global system for mobile communications (GSM; n = 2) collars with global positioning system (GPS) capabilities between 2008 and 2013 in Kruger. One male leopard was fitted with a GSM collar in the Timbavati between June 2011 and December 2011 (African Wildlife Tracking; www.awt.co.za). Collars recorded between four and six GPS fixes per day from 16:00 when leopards became active, until 11:00 in the morning when leopard activities became minimal (Bailey 1993). All leopards in Kruger were captured using baited steel cages. The cages where placed on tree branches to discourage capture of non-target species. Consequently, captured leopards were immobilised and collared following guidelines described in Bailey (1993). The male leopard (Timbavati male) from Timbavati was free-darted at a bait station by a qualified veterinarian overseen by an experienced official from Mpumalanga Tourism and Parks Agency.

Standard procedure for lion captures were used (Smuts *et al.* 1977) and darting was performed by a qualified veterinary practitioner. A female lion was collared in the Skukuza area in the southern section of Kruger in 2011 (Maruping 2014). Two lions, a female within a pride and a nomadic male were collared in Timbavati between in October 2011. The collars were programmed to yield four GPS fixes daily when the lions were active.

Landscape features

For the Kruger study area, we obtained landscape and landform data as well as landscape features from the SANParks data repository and viewed these in ArcMap for ArcGIS 10.1 (Environmental Systems Research Institute [ESRI], Redlands, California, 1969). These included woody cover percentage and water distribution raster datasets as well as roads and drainage lines. Land features and rasters were clipped according to the minimum convex polygon for each individual leopard using the Clipping Tool in Data Management Tools for ArcGIS 10.1 to avoid including landscape features that were outside the leopards' home ranges in the analyses. Wessels *et al.* (2006) noted that vegetation productivity can be associated with interpolated Normalised Difference Vegetation Index (NDVI) tree cover images captured by Moderate Resolution Imaging Spectroradiometer (MODIS) satellite and processed by the Council for Scientific and Industrial Research's (CSIR), Meraka Institute, Pretoria, South Africa. For this study, we used the Enhanced Vegetation Index (EVI), an enhanced version of the NDVI. Similarly, Smit (2011) noted that ruminants in Kruger associated with the areas of high productivity. Accordingly, using the Spatial Analyst Tool in ArcTools for ArcGIS 10.1 (ESRI, Redlands, California 1969), we created mosaic raster datasets so that we had average EVI values throughout the park (CSIR Meraka). The mosaic raster datasets were arranged according to the duration that the collar was active during the dry and growing seasons. These were also clipped to the extent of the minimum convex polygon for each leopard collared.

Data extraction

We used the Near Tool within Proximity Tools (Analysis Tools; ArcTools) to measure the distance between GPS fixes and the nearest stream or road for each leopard from the Kruger study area. Data on landscape features for the Timbavati were not readily available, therefore the study area was excluded. Values from raster datasets including EVI, woody cover, and water distribution were extracted for each GPS fix using the Extraction Tool in Data Management Tools (ArcTools; Spatial Analyst Tools).

Visitation rates and duration of visit

We used T-Locoh (Lyons *et al.* 2013) a program that takes time into account when local hulls are constructed within Statistical Program R 3.1.0 (R Development Core Team). We calculated visitation rates (NSV) and duration of visit (MNLV) for every 15 nearest-neighbour points to create hulls that were time sensitive based on the dates and times of the geographical fixes. These were used to investigate how leopards associated with indices of resource distribution and lion landscape use. Preliminary data inspection revealed that movement patterns were not consistent between the males and females and between dry and wet seasons for the collared leopards. Dry season ran from April to the end of September while the wet season ran from October to March. Consequently, we analysed data by subdividing them according to sex and season. For the Kruger study area, most of the males were collared in the wet season with only the Skukuza male's collar functioning during both seasons. As a result, for the male leopards in the Kruger study area (n = 3), we only assessed the wet season.

Landscapes of activity for lions

Using Kriging, an interpolation method in ArcTools (ESRI, 1969), we constructed landscapes of activity from visitation rates and duration of stay for lions. To aid visual inspection of the association between animals, we ran HotSpots, a geoprocessing tool designed to identify statistically significant hotspots in ArcTools, from visitation rates and duration of stay; thus areas of high lion visitation rates had high pixel values when the activity landscapes were constructed for visitation rates and similarly, areas that the lions spent long durations of time had high pixel values when landscapes for the duration of stay were constructed for lions. We used the extraction tool in ArcTools (ESRI, 1969) to extract values from the lion activity landscapes to leopard GPS fixes. The values extracted were then used to determine the association between leopard GPS fixes and the lion activity landscapes for the visitation rates and for the duration of stay.

Data analysis

Statistical analyses were performed using statistical software R 3.1.0 (R Development Core Team 2012) and program Excel 2013 (Windows Office 2013). We plotted visitation rates against duration of stay for all the leopards in the study to evaluate their relationship (Lyons *et al.* 2013). All the data from the variables were continuous. Associations were not outright linear. Data were therefore analysed using Generalized Additive Models (GAMs), which uses non-parametric smoothers, which complement linear models, to indicate the relationships between variables (Crawley 2007). GAMs were run in the package “mgcv” in statistical software R (Wood 2014; R Development Core Team 2012). GAMs were used because there were multiple continuous explanatory variables and that we did not want to prejudge the relationships between the response variables (visitation rates and duration of stay by leopards) and predictor variables, namely: lion visitation rates, lion duration of stay, enhanced vegetation indices for growing and dry seasons, woody cover percentage, distances to roads and streams, and water distribution. Models were ranked according to the generalized cross validation and an unbiased risk estimator, which in essence, is a rescaled Akaike Information Criterion (Crawley 2007). Associations were considered significant when the *P*-value was less than 0.01.

Results

Duration of visit and visitation rates

On average, leopard collars yielded 533 (n = 8) geographical fixes per leopard that ranged from 125 to 1009 fixes (Fig. 5.1). There was a young female of approximately two years old. This individual was not used in the analysis as it was not a fully grown adult leopard. Lion geographical fixes on the other hand yielded 3984 (n = 3) points ranging from 1809 and 5303 fixes (Fig. 1). Basic statistics for the leopards collared in the Kruger revealed that on average leopards (n = 6) spent 5.35 (range: 2-15 days) days per hull. Leopard movements were characterised by areas that were visited frequently, but for short durations, usually less than five days; and a few areas that were less frequently visited, but with long durations of stay (Fig. 5.2). This pattern was observed in Skukuza (*n* = 2) and Crocodile Bridge (*n* = 1) where the collars were active for seven or more months. Leopards in the Nwanedzi study site (*n* = 3) showed a similar pattern albeit less pronounced because the collars there remained active for three or less months each (Fig. 5.1). The Timbavati male leopard used the landscape differently to the leopards collared in Kruger. Basic statistics revealed that the leopard stayed on average for 2.33 (range: 1.6-3.8 days) days per hull during the six months that the collar was active.

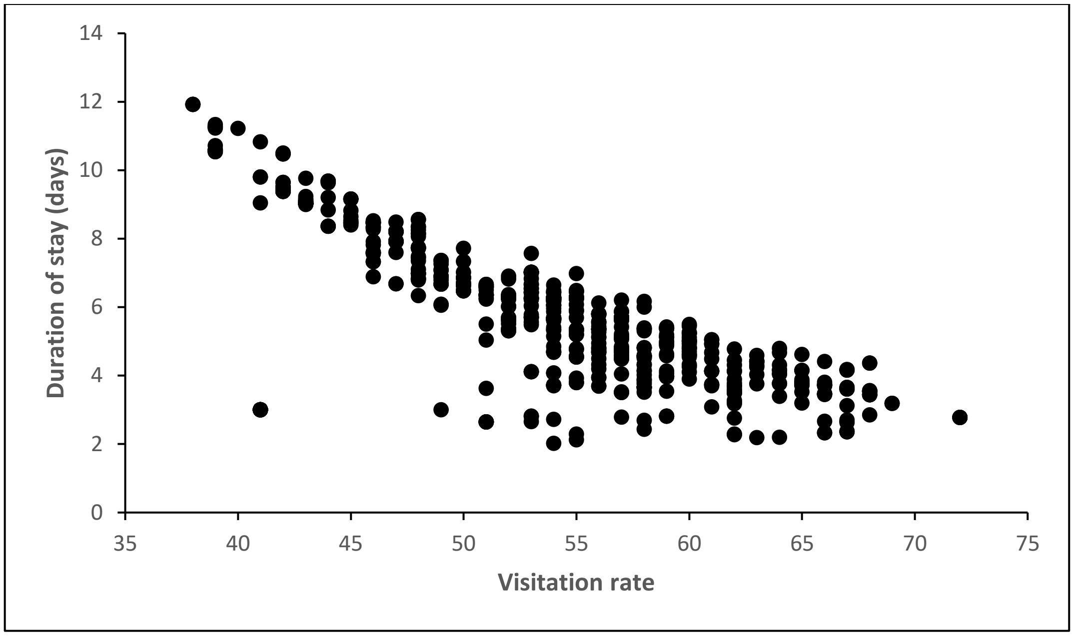


Figure 5.2. Scatter plot depicting the relationship between visitation rate and duration of visits to different hulls for the female leopard from Skukuza, Kruger National Park in South Africa.

Resources and visitations

Females – In the dry season, duration of stay by female leopards marginally associated with water distribution ($F_{1;\ 1230} = 6$; $P = 0.01$) and strongly associated with the enhanced vegetation index model ($F_{6.8;\ 1230} = 14$; $P < 0.01$), and with proximity to streams ($F_{2.2;\ 1230} = 4.93$; $P < 0.01$) (Fig. 5.3). Visitation rates by female leopards on the other hand significantly associated with all the variables including woody cover ($F_{5.1;\ 1230} = 7$; $P < 0.01$), water distribution ($F_{8.7;\ 1230} = 21.93$; $P < 0.01$), enhanced vegetation index model ($F_{8.4;\ 1230} = 150.77$; $P < 0.01$), proximity to streams ($F_{3.5;\ 1230} = 11.81$; $P < 0.01$) and finally proximity to roads ($F_{6.2;\ 1230} = 43.21$; $P < 0.01$) (Fig. 5.4).

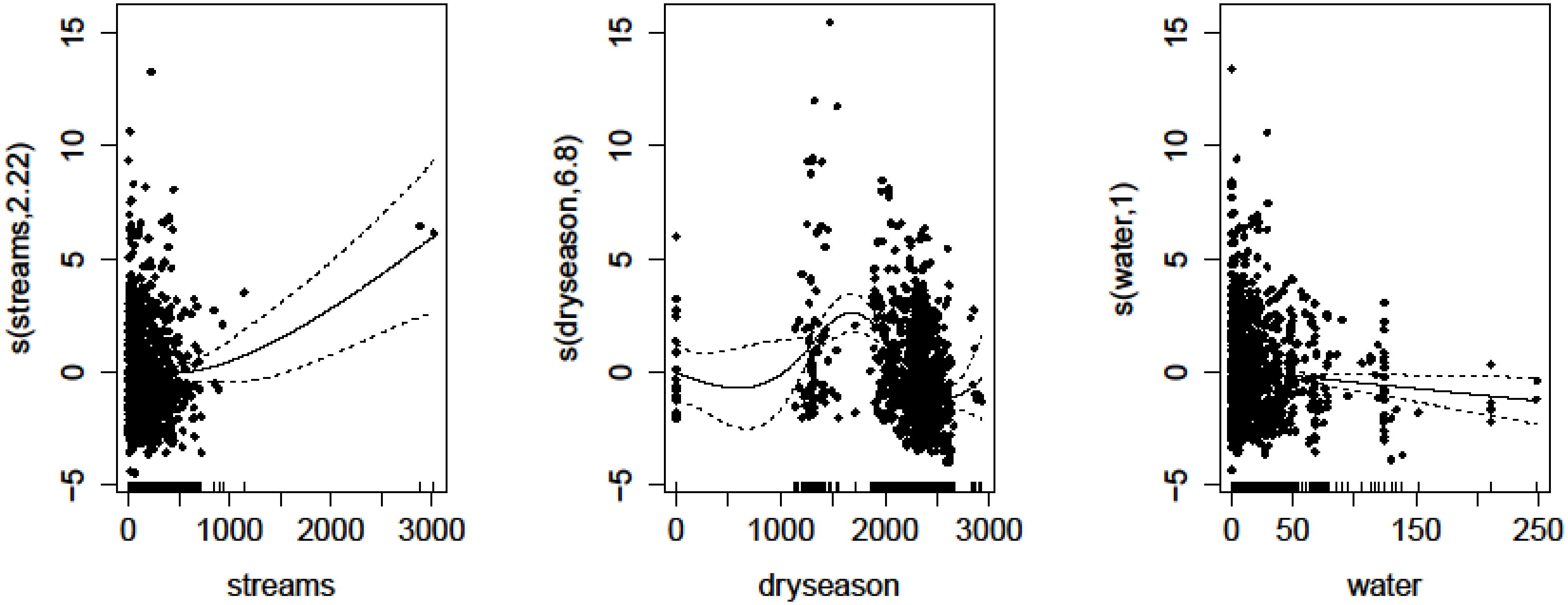


Figure 5.3. Associations between the duration of stay by female leopards and three predictor variables including proximity to streams (streams) – in metres –, enhanced vegetation index (dryseason) – in pixels –, and water distribution (water) – in pixels – in the Kruger National Park (KNP), South Africa. The etchings on the x-axis are the positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

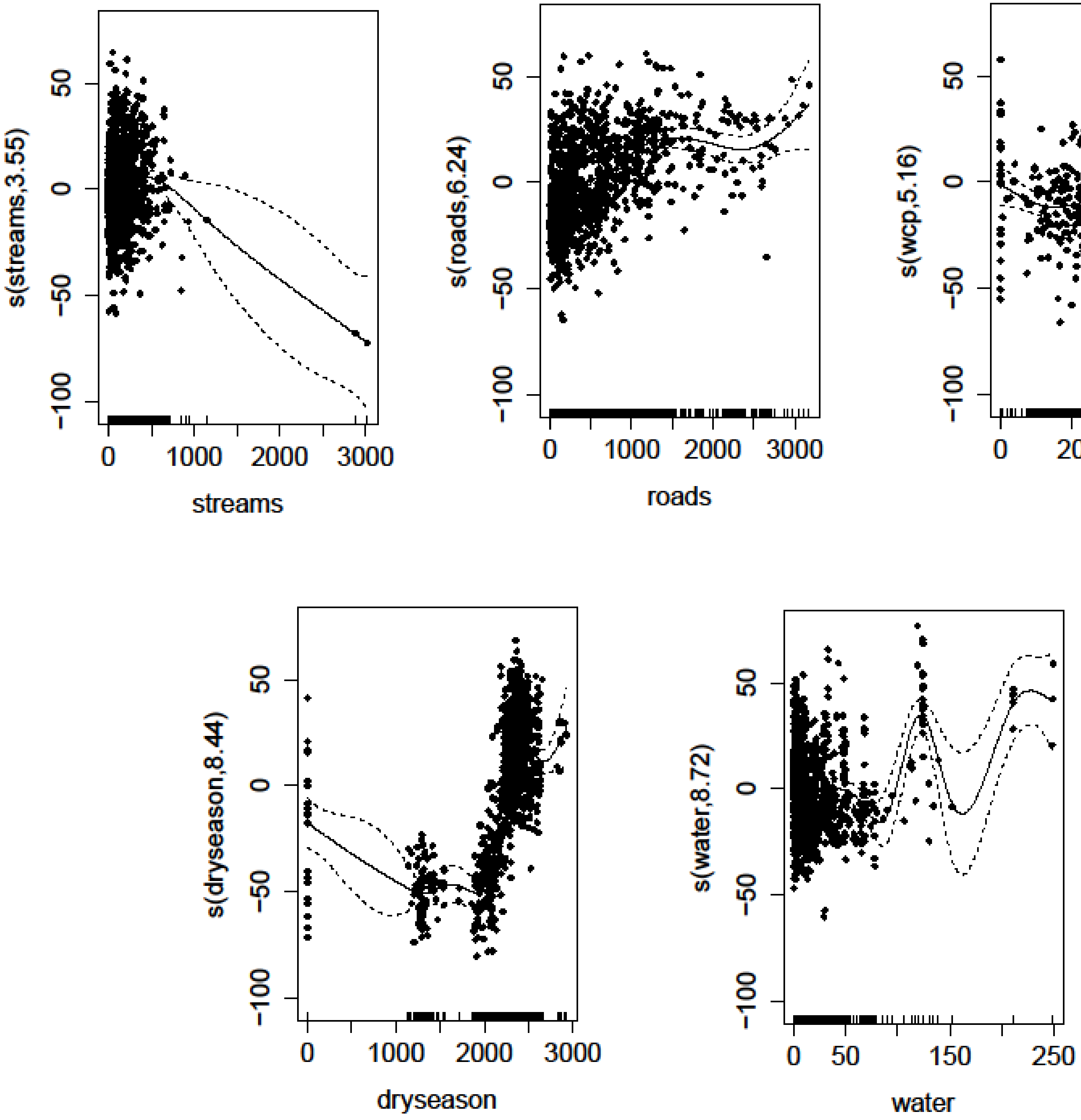

s(streams,3.55)
50
0
−50
−100
0
1000
2000
3000
streams
s(roads,6.24)
50
0
−50
−100
0
1000
2000
3000
roads
s(wcp,5.16)
50
0
−50
−100
0
20
40
60
wcp
s(dryseason,8.44)
50
0
−50
−100
0
1000
2000
3000
dryseason
s(water,8.72)
50
0
−50
−100
0
50
150
250
water

Figure 5.4. Association between visitation rates by female leopards and different variables in the dry season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in metres –, proximity to roads (roads) – in metres –, the woody cover percentage (wcp), enhanced vegetation index model (dryseason) – in pixels – in the dry season, and water distribution – in pixels. The etchings on the x-axis are the positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

Association between visitation rates by female leopards in the dry season revealed significant associations with the following interactions between variables: woody cover and enhanced vegetation index model, woody cover and proximity to roads, water distribution and enhanced vegetation index model, enhanced vegetation index model and proximity to streams, enhanced vegetation index model and proximity to roads, and proximity to streams and proximity to roads (Table 5.1). Association between the duration of stay by females poorly associated with interactions between variables except for the interaction between enhanced vegetation cover and proximity to roads (Table 5.1).

Table 5.1. Parameters used in the models that were selected from Generalized Additive Models for the dry season association between female leopard visitation rates/duration of stay and smoothed (using non-parametric smoothers) values for variables including woody cover percentage (wcp), water distribution (water), enhanced vegetation index (evi), proximity to streams (streams), and proximity to roads (roads) as well as their interactions; from the Kruger National Park, South Africa. Significant associations are in bold.

Visitation rates in the dry season

Variables	Estimated degrees of freedom	Reference degrees of freedom	F-statistic	p-value
s(wcp)	4.42	5.48	1.87	0.09
s(water)	**8.42**	**8.86**	**9.87**	**<0.01**
s(evi)	2.99	3.53	0.29	0.87
s(streams)	1.00	1.00	0.07	0.79
s(roads)	1.44	1.61	0.82	0.40
s(wcp,water)	0.00	27.00	0.00	0.59
s(wcp,evi)	**24.20**	**27.00**	**2.77**	**<0.01**
s(wcp,streams)	0.00	27.00	0.00	0.36
s(wcp,roads)	**9.57**	**27.00**	**0.68**	**<0.01**
s(water,evi)	**19.47**	**27.00**	**4.86**	**<0.01**
s(water,streams)	5.22	27.00	0.26	0.03
s(water,roads)	1.56	27.00	0.07	0.02
s(evi,streams)	**16.14**	**27.00**	**1.43**	**<0.01**
s(evi,roads)	**26.65**	**27.00**	**3.63**	**<0.01**
s(streams,roads)	**7.85**	**27.00**	**1.19**	**<0.01**

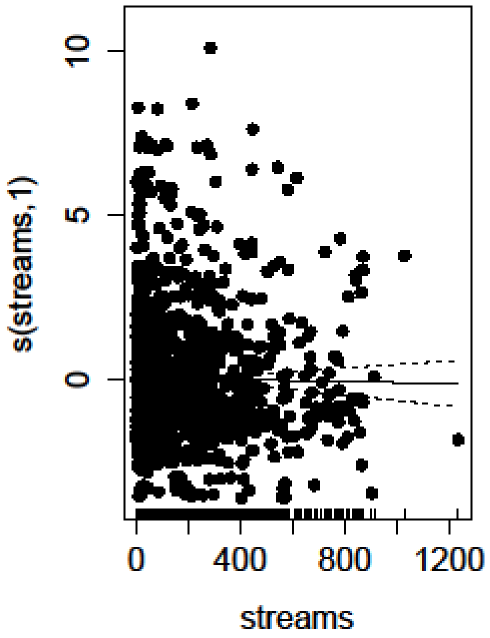
Parametric coefficients: Intercept = 62.31; Std. err = 0.44; t-value = 140.5; P <0.01
Adjusted R^2 = 0.79; Deviance explained = 81.2%

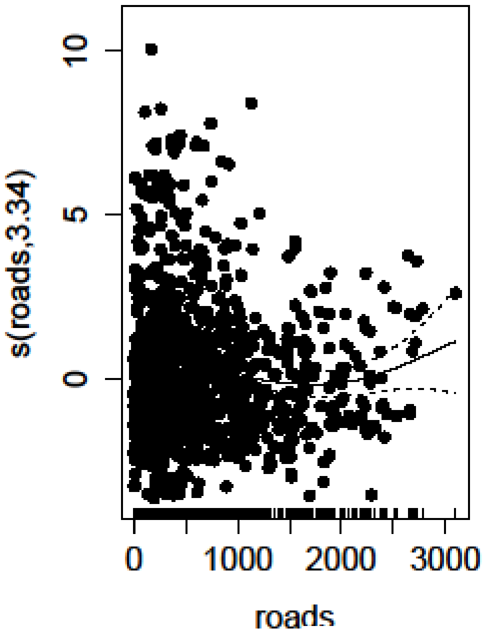
Duration of stay in the dry season

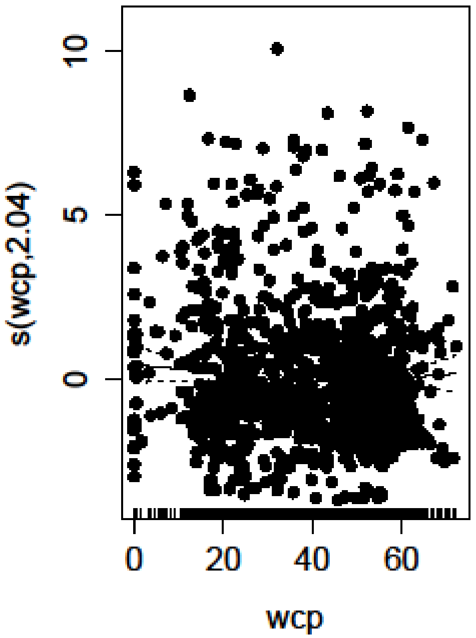
Variables	Estimated degrees of freedom	Reference degrees of freedom	F-statistic	p-value
s(water)	1.00	1.00	3.84	0.05
s(streams)	1.82	2.10	4.54	0.01
s(wcp,evi)	10.31	13.21	1.58	0.08
s(water,roads)	11.36	15.10	0.34	0.99
s(evi,roads)	**8.58**	**27.00**	**0.60**	**<0.01**
s(streams,roads)	2.22	27.00	0.10	0.11

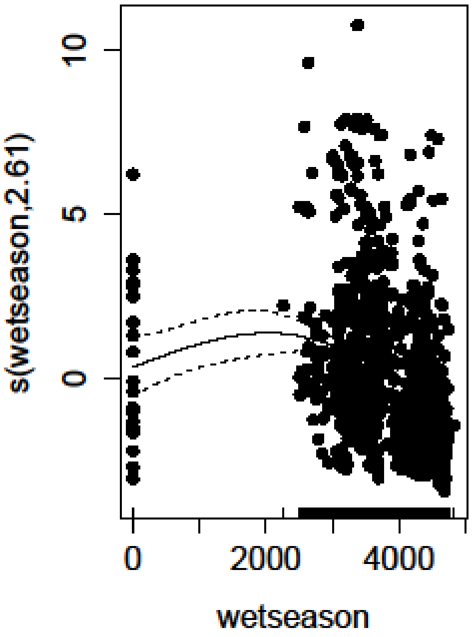
Parametric coefficients: Intercept = 5.8; Std. err = 0.06; t-value = 95.48; P <0.01
Adjusted R^2 = 0.142; Deviance explained = 16.6%

Females-wet season – Visitation rates in the wet season by female leopards significantly associated with the variables including woody cover ($F_{5.3;\ 1150} = 6.09$; $P < 0.01$), water availability ($F_{8.7;\ 1150} = 26.06$; $P < 0.01$), enhanced vegetation index model ($F_{8.1;\ 1150} = 444.65$; $P < 0.01$), and proximity to roads ($F_{6.6;\ 1150} = 6.35$; $P < 0.01$) (Fig. 5.5). The association between visitation rates by leopards and interacting variables were significant for the following interactions: woody cover and water availability, water availability and enhanced vegetation index model, water availability and proximity to roads, enhanced vegetation model index and proximity to roads, and lastly, proximity to streams and proximity to roads (Table 5.2).


s(streams,1)
10
5
0
0
400
800
1200
streams


s(roads,3.34)
10
5
0
0
1000
2000
3000
roads


s(wcp,2.04)
10
5
0
0
20
40
60
wcp


s(wetseason,2.61)
10
5
0
0
2000
4000
wetseason

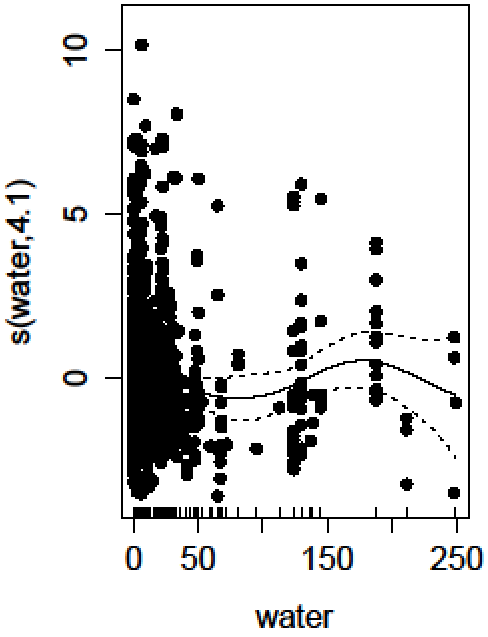

s(water,4.1)
10
5
0
0
50
150
250
water

Figure 5.5. Association between visitation rates by female leopards and different variables in the wet season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in metres –, proximity to roads – in metres –, the woody cover percentage (wcp), enhanced vegetation index model (wetseason) – in pixels – in the wet season, and water distribution (water) – in pixels. The etchings on the x-axis are the positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

Table 5.2. Parameters used in the models that were selected from Generalized Additive Models for the wet season association between female leopard visitation rates/duration of stay and smoothed (using non-parametric smoothers) values for variables including woody cover percentage (wcp), water distribution (water), enhanced vegetation index (evi), proximity to streams (streams), and proximity to roads(roads) as well as their interactions. Significant associations are in bold. The study was conducted in the Kruger National Park, South Africa.

Visitation rates in the wet season

Variables	Estimated degrees of freedom	Reference degrees of freedom	F-statistic	p-value
s(wcp)	**6.18**	**7.59**	**2.78**	**0.01**
s(water)	**9.00**	**9.00**	**5.97**	**<0.01**
s(wcp,water)	**23.48**	**27.00**	**2.76**	**<0.01**
s(wcp,evi)	12.90	15.23	0.12	1.00
s(wcp,streams)	2.53	3.22	0.27	0.86
s(wcp,roads)	13.13	15.58	0.14	1.00
s(water,evi)	**19.88**	**27.00**	**2.71**	**<0.01**
s(water,streams)	4.85	27.00	0.21	0.03
s(water,roads)	**13.50**	**27.00**	**0.58**	**<0.01**
s(evi,roads)	**21.70**	**27.00**	**3.72**	**<0.01**
s(streams,roads)	**5.93**	**27.00**	**0.95**	**<0.01**

Parametric coefficients: Intercept = 56.33; Std. err = 0.3; t-value = 186.5; P <0.01
Adjusted $R^2 = 0.93$; Deviance explained = 93.3%

Duration of stay in the wet season

Variables	Estimated degrees of freedom	Reference degrees of freedom	F-statistic	p-value
s(evi)	1.00	1.00	0.08	0.78
s(wcp,water)	9.45	12.81	1.43	0.14
s(wcp,evi)	0.00	27.00	0.00	0.10
s(wcp,streams)	8.31	10.99	0.31	0.98
s(wcp,roads)	1.00	1.00	1.28	0.26
s(water,evi)	**20.30**	**27.00**	**2.51**	**<0.01**
s(water,streams)	**15.31**	**27.00**	**0.73**	**<0.01**
s(water,roads)	7.50	27.00	0.37	0.01
s(evi,streams)	**2.60**	**27.00**	**0.28**	**<0.01**
s(evi,roads)	**17.09**	**27.00**	**1.78**	**<0.01**
s(streams,roads)	4.21	27.00	0.32	0.01

Parametric coefficients: Intercept = 5.92; Std. err = 0.06; t-value = 102.9; P <0.01
Adjusted $R^2 = 0.28$; Deviance explained = 32.9%

There was poor support for the association of the duration of stay by female leopards and the majority of the variables selected for the study in the wet season. However, duration of stay by females significantly associated with enhanced vegetation index model ($F_{2.6; 1150} = 26.48$; $P < 0.01$) (Fig. 5.6).

Association with variable interactions revealed significant association for the following interactions: water availability and enhanced vegetation index model, water availability and proximity to streams, enhanced vegetation index model and proximity to streams, and finally, enhanced vegetation index model and proximity to roads (Table 5.2).

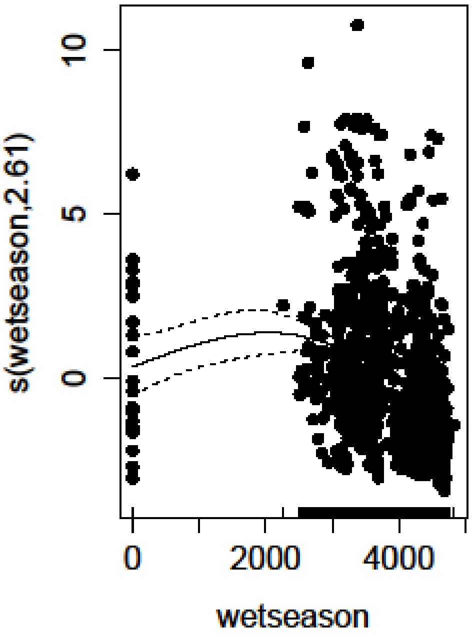
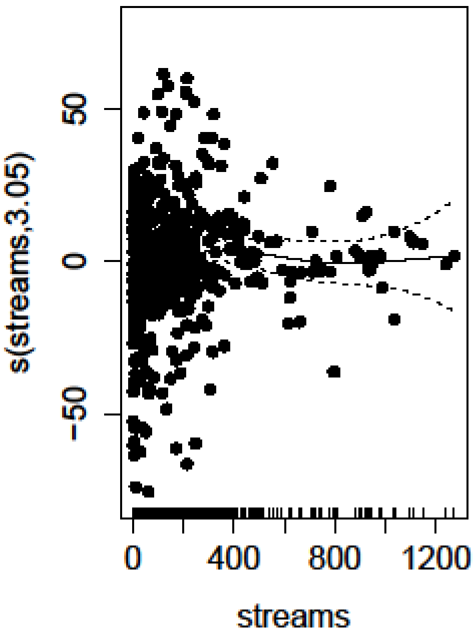
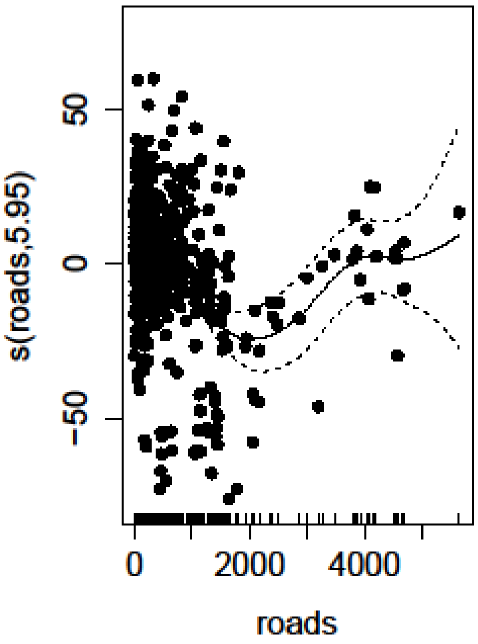
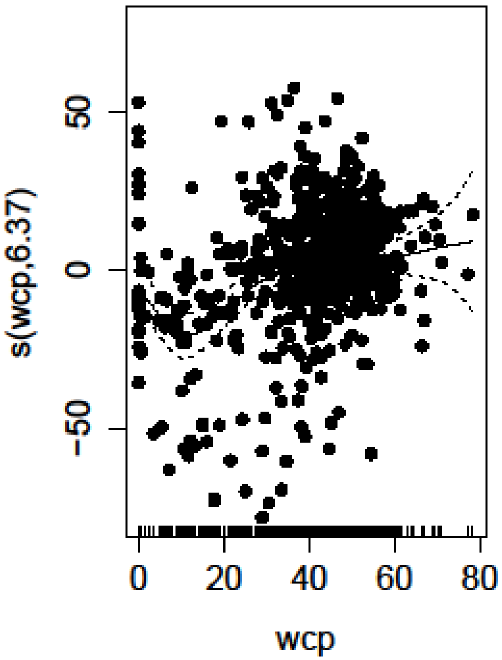


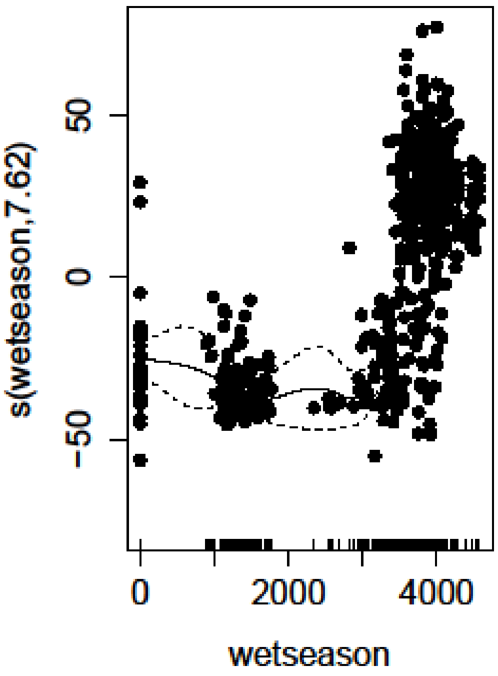
Figure 5.6. Association between duration of stay by female leopards and the enhanced vegetation index (wetseason) – in pixels – in the dry season in the Kruger National Park, South Africa. The etchings on the x-axis are the positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the enhanced vegetation index values. The number following the predictor variable on the y-axis is the estimated degrees of freedom.

Males - All but one male leopard had data for the wet season only. The wet season visitation rates by males significantly associated with woody cover ($F_{6.4;\ 695} = 5.52$; $P < 0.01$), water availability ($F_{7.7;\ 695} = 13$; $P < 0.01$), enhanced vegetation index model ($F_{7.6;\ 695} = 78.52$; $P < 0.01$), and proximity to roads ($F_{5.9;\ 695} = 8.66$; $P < 0.01$) (Fig. 7). There was poor support for the visitation rates and proximity to streams ($F_{3.1;\ 695} = 2.14$; $P = 0.08$).


s(streams,3.05)
50
0
-50
0
400
800
1200
streams


s(roads,5.95)
50
0
-50
0
2000
4000
roads


s(wcp,6.37)
50
0
-50
0
20
40
60
80
wcp


s(wetseason,7.62)
50
0
-50
0
2000
4000
wetseason

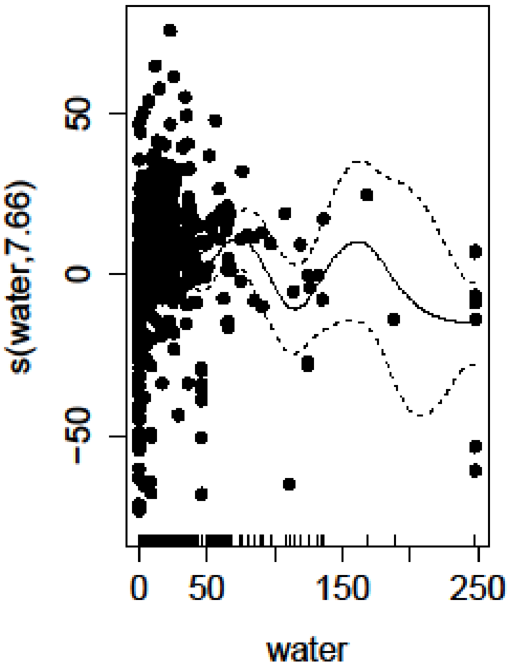
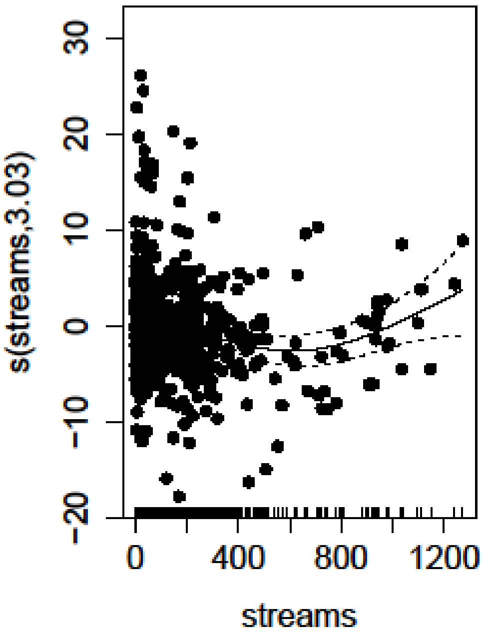
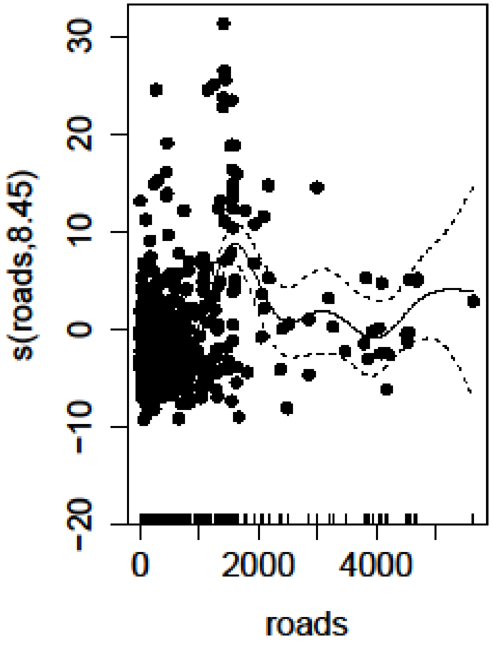

s(water,7.66)
50
0
-50
0
50
150
250
water

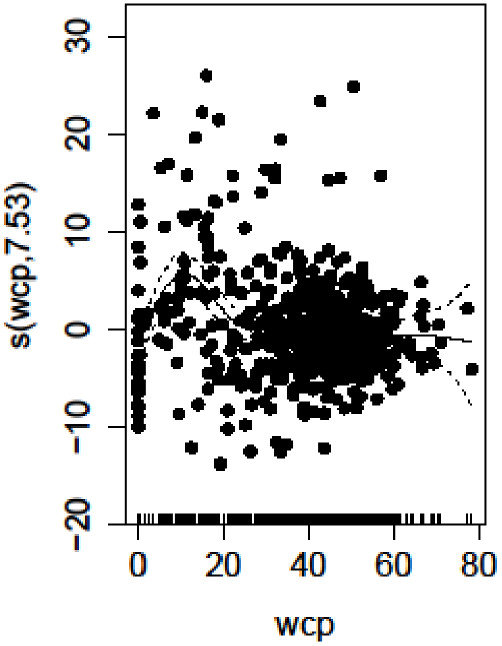
Figure 5.7. Association between visitation rates by male leopards and different variables in the wet season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in metres –, proximity to roads (roads) – in metres – , the woody cover percentage (wcp), enhanced vegetation index model in the wet season (wetseason) – in pixels-, and water distribution (water) – in pixels. The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

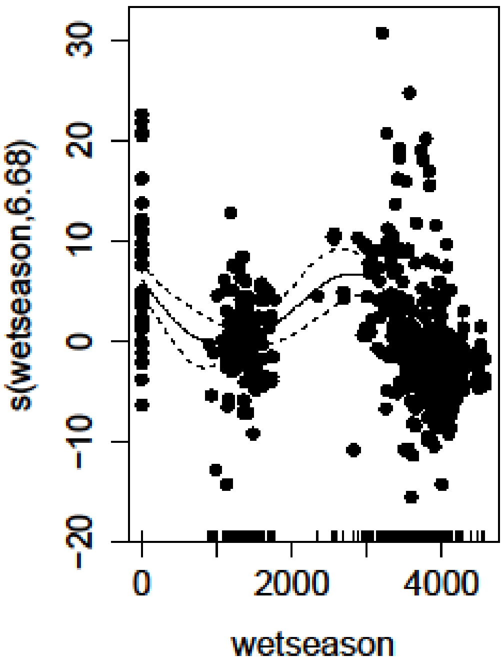
Duration of stay by males strongly associated with all the variables including woody cover ($F_{7.5; 695} = 4.19$; $P < 0.01$), water availability ($F_{6.8; 695} = 5.87$; $P < 0.01$), enhanced vegetation index model ($F_{6.7; 695} = 16.86$; $P < 0.01$), proximity to streams ($F_{3; 695} = 4.78$; $P < 0.01$), and proximity to roads ($F_{8.4; 695} = 10.46$; $P < 0.01$) (Fig. 5.8).

Visitation rates by male leopards had significant associations with interactions between variables including woody cover and water availability, woody cover and enhanced vegetation index model, woody cover and proximity to roads, water and enhanced vegetation index model, enhanced vegetation index and proximity to roads, and the interaction between proximity to roads and proximity to streams (Table 5.3). Duration of stay associated significantly with interactions between several variables, but which included water availability, woody cover, and proximity to roads (Table 5.3).


s(streams,3.03)
30
20
10
0
−10
−20
0
400
800
1200
streams


s(roads,8.45)
30
20
10
0
−10
−20
0
2000
4000
roads


s(wcp,7.53)
30
20
10
0
−10
−20
0
20
40
60
80
wcp


s(wetseason,6.68)
30
20
10
0
−10
−20
0
2000
4000
wetseason

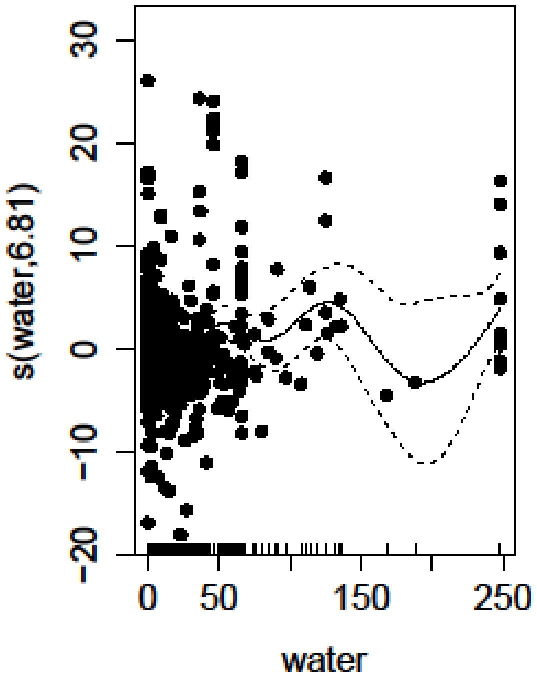

s(water,6.81)
30
20
10
0
−10
−20
0
50
150
250
water

Figure 5.8. Association between duration of stay by male leopards and different variables in the wet season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in metres-, proximity to roads (roads) – in metres – , the woody cover percentage (wcp), enhanced vegetation index model in the wet season (wetseason) – in pixels-, and water distribution (water) – in pixels. The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

Table 5.3. Parameters used in the models that were selected from Generalized Additive Models for the wet season association between male leopard visitation rates/duration of stay and smoothed (using non-parametric smoothers) values for variables including woody cover percentage (wcp), water distribution (water), enhanced vegetation index (evi), proximity to streams (streams), and proximity to roads(roads) as well as their interactions. Significant associations are in bold. The study was conducted in the Kruger National Park, South Africa.

Visitation rates

Variables	Estimated degrees of freedom	Reference degrees of freedom	F-statistic	p-value
s(wcp)	6.3	7.6	1.13	0.34
s(water)	4.5	5.7	0.89	0.50
s(evi)	1.0	1.0	0.13	0.72
s(streams)	1.0	1.0	4.71	0.03
s(roads)	1.0	1.0	0.07	0.79
s(wcp,water)	**27.0**	**27.0**	**3.44**	**<0.01**
s(wcp,evi)	**19.9**	**27.0**	**1.31**	**<0.01**
s(wcp,streams)	0.0	27.0	0.00	0.44
s(wcp,roads)	**12.8**	**27.0**	**0.69**	**<0.01**
s(water,evi)	**4.6**	**27.0**	**0.46**	**<0.01**
s(water,streams)	0.0	27.0	0.00	0.34
s(water,roads)	0.0	27.0	0.00	0.03
s(evi,streams)	0.0	27.0	0.00	0.44
s(evi,roads)	**14.9**	**27.0**	**1.61**	**<0.01**
s(streams,roads)	**16.2**	**27.0**	**1.13**	**<0.01**

Parametric coefficients: intercept = 45.69; Std-err = 0.58; t-value = 78.72; P <0.01
Adjusted R^2 = 0.87; Deviance explained = 88.7%

Duration of stay

Variables	Estimated degrees of freedom	Reference degrees of freedom	F-statistic	p-value
s(wcp)	**8.5**	**8.9**	**6.74**	**<0.01**
s(wcp,water)	**26.6**	**27.4**	**4.27**	**<0.01**
s(wcp,streams)	**21.5**	**23.3**	**2.06**	**<0.01**
s(wcp,roads)	**26.2**	**26.6**	**2.93**	**<0.01**
s(water,evi)	**25.5**	**26.6**	**2.58**	**<0.01**
s(water,streams)	**27.0**	**27.0**	**2.12**	**<0.01**
s(water,roads)	**21.8**	**27.0**	**2.52**	**<0.01**
s(evi,roads)	**23.3**	**27.0**	**3.24**	**<0.01**
s(streams,roads)	**26.1**	**27.0**	**2.62**	**<0.01**

Parametric coefficients: intercept =10.34; Std-err =0.13; t-value =78.64; P <0.01
Adjusted R^2 = 0.87; Deviance explained = 85.7%

Site specific associations: Resources and lion landscapes of activity.

Female – In the Skukuza area, there were differences and similarities in the response of visitation rates and durations of stay by the female and the male leopards given different variables. Visitation rates by the female leopard strongly associated with the landscapes based on visitation rates by lions ($F_{3.8;\ 440} = 3.25$; $P < 0.01$) and the duration of stay by lions ($F_{7.6;\ 440} = 2.91$; $P < 0.01$) (Fig. 5.9). Visitation rates also associated, albeit not significantly, with woody cover ($F_{4.8;\ 440} = 2.27$; $P = 0.04$) (Fig. 5.9).

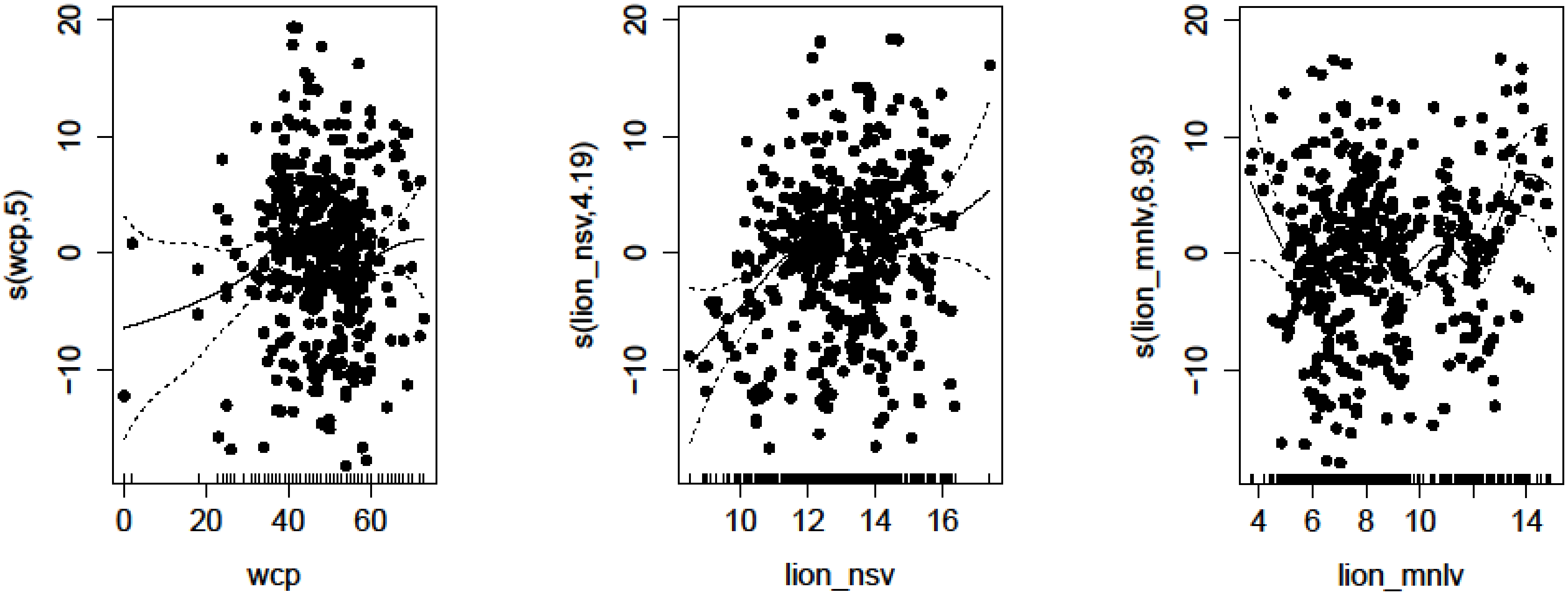
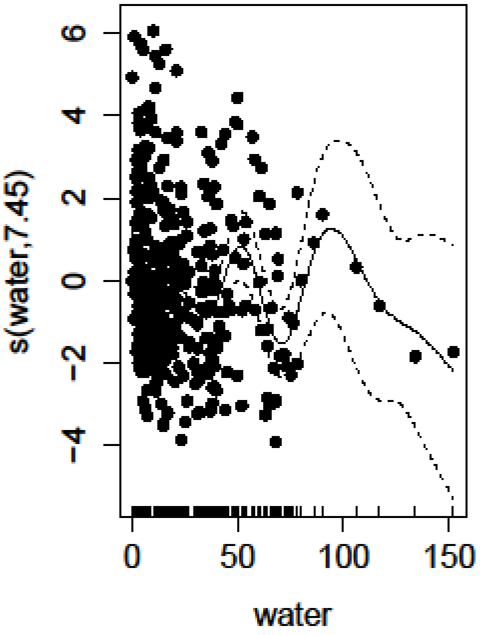


Figure 5.9. Association between visitation rates by the Skukuza female leopard and (i) the woody cover percentage (wcp); (ii) lion visitation rates (lion_nsv) – in pixels-, and lion duration of stay (lion_mnlv) – in pixels. The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

There was poor support for the duration of stay by the female with lion landscapes of activity. However, there was support for the association between durations of stay by the female leopard and water availability ($F_{7.4;\ 440} = 4.71$; $P < 0.01$); and slight evidence with poor support for the association with woody cover ($F_{3.8;\ 440} = 2.54$; $P = 0.03$) (Fig. 5.10).



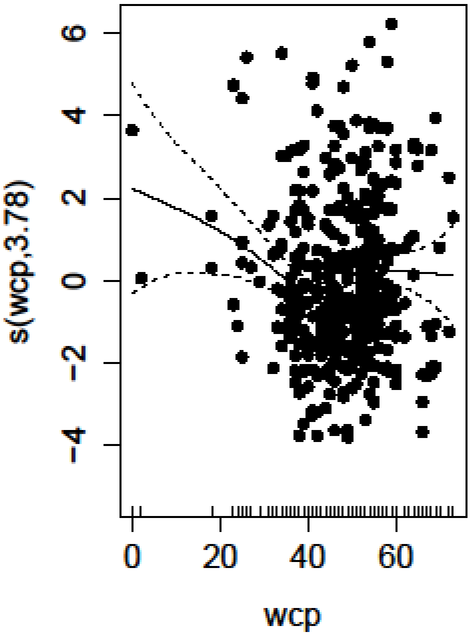


Figure 5.10. Association between the duration of stay by the Skukuza female leopard and water distribution (water) – in pixels – and the woody cover percentage (wcp). The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

Male – Visitation rates by the male leopard from Skukuza strongly associated with enhanced vegetation index ($F_{1;\ 335} = 22.59$; $P < 0.01$) and also with visitation rates by the lion pride from the Skukuza area ($F_{2.7;\ 335} = 4.63$; $P < 0.01$) (Fig. 5.11). There was poor support for the association between visitation rates by the male leopard and other variables including woody cover, water availability, distances to streams distances to roads and land use by lions based on their duration of stay in the area. With regards to the duration of stay by the male leopard, there was poor support for the association between the duration of stay by the leopard and any of the selected variables.

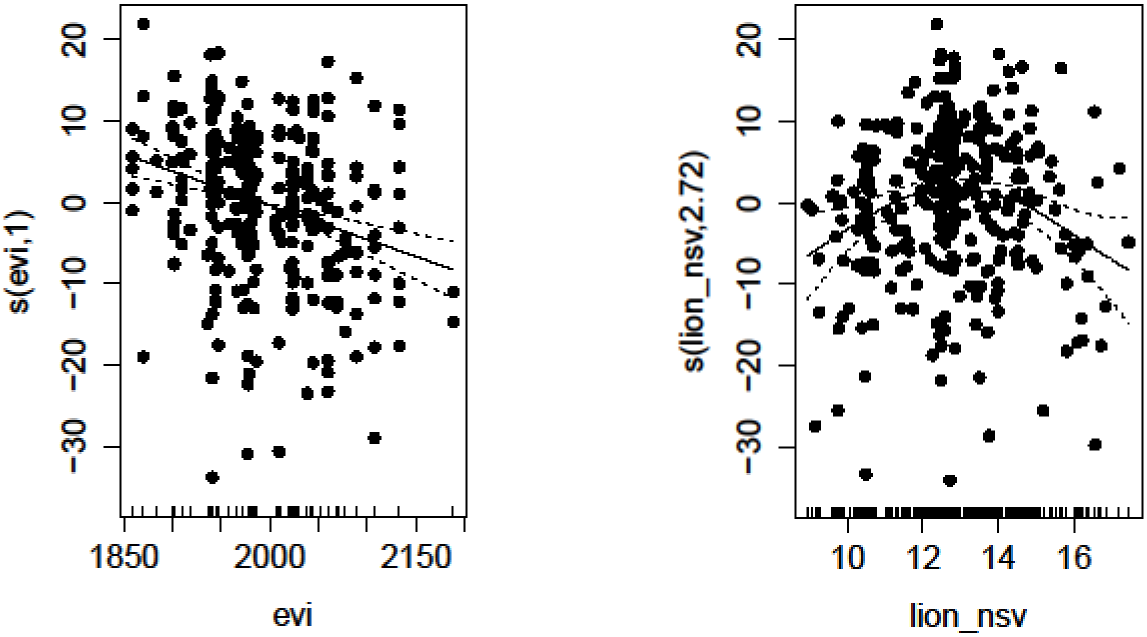


Figure 5.11. Association between visitation rates by the Skukuza male leopard and the enhanced vegetation index model – in pixels – and lion visitation rates (lion_nsv) – in pixels. The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

Visitation rates by the Timbavati leopard significantly associated with enhanced vegetation index ($F_{8.4;\ 340} = 3.42$; $P < 0.01$), visitation rates by the lion pride ($F_{6.2;\ 340} = 5.45$; $P < 0.01$), duration of stay by the pride ($F_{5.5;\ 340} = 12.89$; $P < 0.01$), and visitation rate by the nomadic male lion ($F_{7.9;\ 340} = 4.75$; $P < 0.01$) (Fig. 5.12). There was slight evidence of significant association between the leopard and the duration of stay by the nomadic male lion ($F_{4.6;\ 340} = 2.76$; $P = 0.01$) (Fig. 5.12). The interaction between variables that yielded strong positive associations with the visitation rates by the leopard mostly involved enhanced vegetation index and also landscape of visitation rates by lions (Table 5.4).

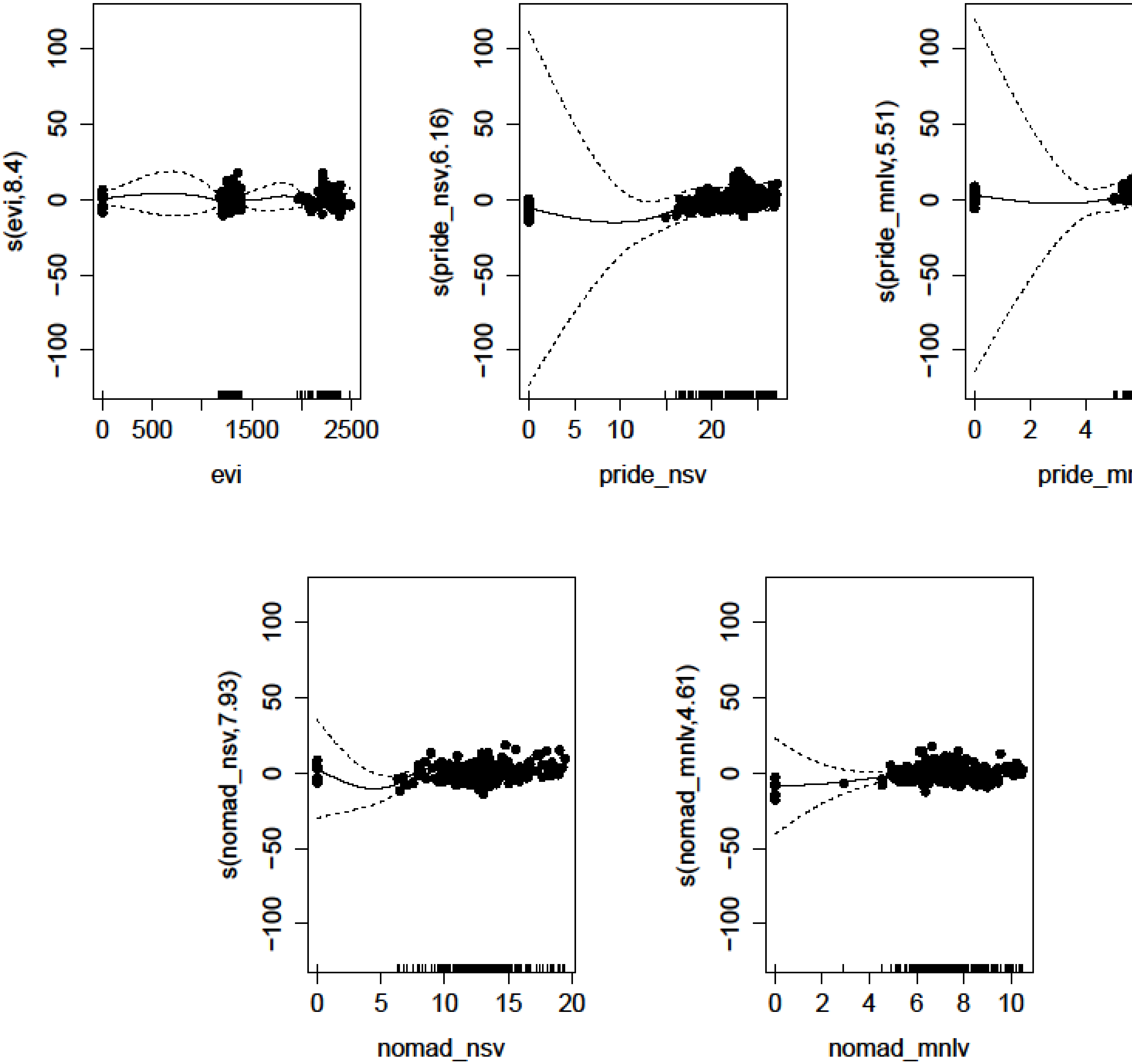
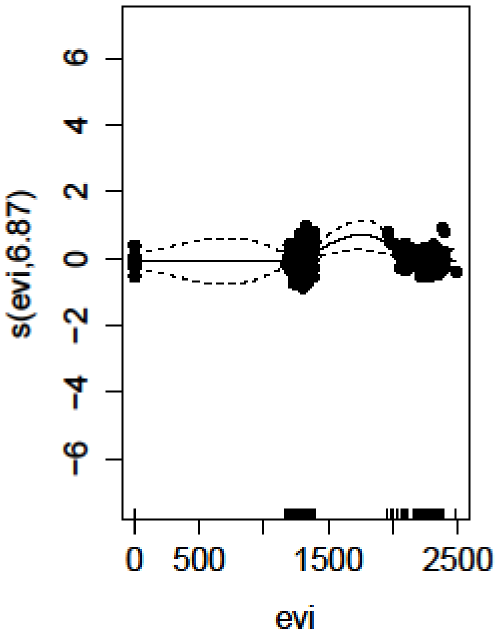
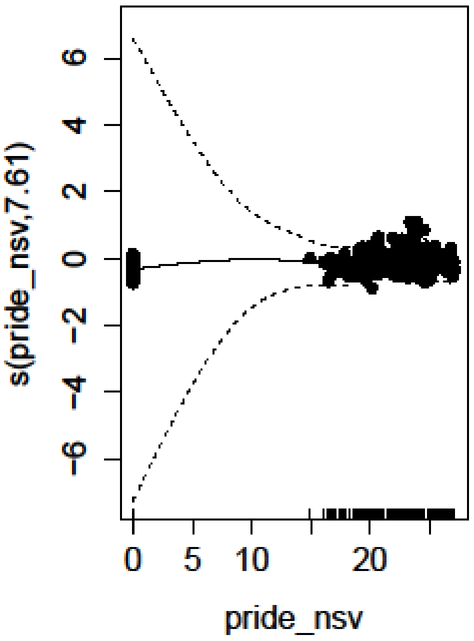
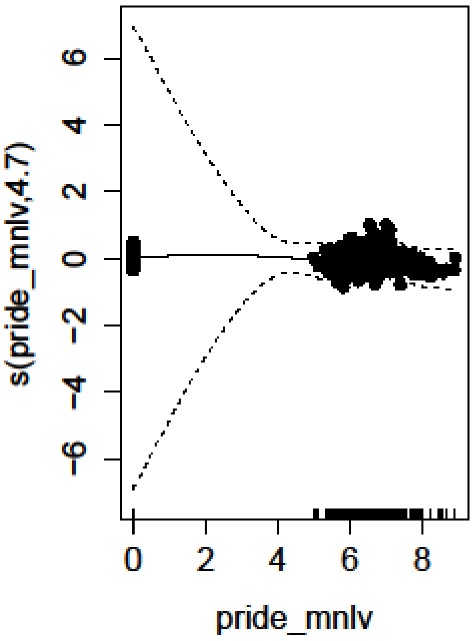

s(evi,8.4)
100
50
0
−50
−100
0
500
1500
2500
evi
s(pride_nsv,6.16)
0
5
10
20
pride_nsv
s(pride_mnlv,5.51)
0
2
4
6
8
pride_mnlv
s(nomad_nsv,7.93)
0
5
10
15
20
nomad_nsv
s(nomad_mnlv,4.61)
0
2
4
6
8
10
nomad_mnlv

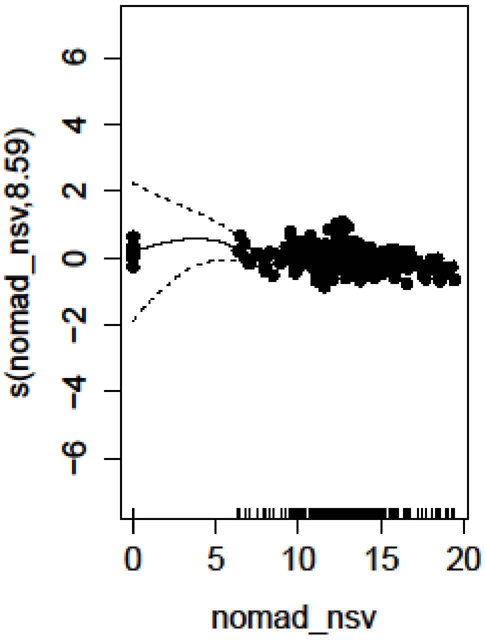
Figure 5.12. Association between visitation rates by the Timbavati male leopard and (i) the enhanced vegetation index model (evi); (ii) lion pride visitation rates (pride_nsv) – in pixels – ; (iii) and lion pride duration of stay (pride_mnlv) – in pixels –; (iv) visitation rates of nomadic male lion (nomad_nsv) – in pixels –; and (v) nomadic male lion's duration of stay (nomad_mnlv) – in pixels –. The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

Duration of stay by the Timbavati male leopard strongly associated with enhanced vegetation index model ($F_{6.9; 340} = 2.25$; $P < 0.01$), visitation rates by the lion pride ($F_{7.6; 340} = 4.13$; $P < 0.01$), duration of stay by the pride ($F_{4.7; 340} = 5.5$; $P < 0.01$), visitation rate by the nomadic male lion ($F_{8.6; 340} = 6.41$; $P < 0.01$), and duration of stay by the nomadic male lion ($F_{4.5; 340} = 6.35$; $P < 0.01$) (Fig. 5.13). Significant associations were observed mostly with the enhanced vegetation index model and with the landscape of visitation rates by the pride (Table 5.4).


s(evi,6.87)
6
4
2
0
−2
−4
−6
0
500
1500
2500
evi


s(pride_nsv,7.61)
6
4
2
0
−2
−4
−6
0
5
10
20
pride_nsv


s(pride_mnlv,4.7)
6
4
2
0
−2
−4
−6
0
2
4
6
8
pride_mnlv


s(nomad_nsv,8.59)
6
4
2
0
−2
−4
−6
0
5
10
15
20
nomad_nsv

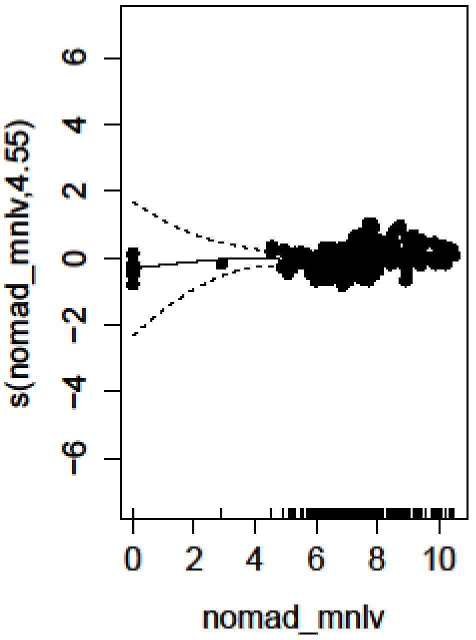

s(nomad_mnlv,4.55)
6
4
2
0
−2
−4
−6
0
2
4
6
8
10
nomad_mnlv

Figure 5.13. Association between the duration of stay by the Timbavati male leopard and (i) the enhanced vegetation index model (evi); (ii) lion pride visitation rates (pride_nsv) – in pixels – ; (iii) and lion pride duration of stay (pride_mnlv) – in pixels –; (iv) visitation rates by the nomadic male lion (nomad_nsv) – in pixels –; and (v) nomadic male lion's duration of stay (nomad_mnlv) – in pixels –. The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the estimated degrees of freedom.

Table 5.4. Parameters used in the models that were selected from Generalized Additive Models for the wet season association between male leopard visitation rates/duration of stay and smoothed (using non-parametric smoothers) values for variables including woody cover percentage (wcp), water distribution (water), enhanced vegetation index (evi), proximity to streams (streams), and proximity to roads(roads) as well as their interactions. Significant associations are in bold. The study was conducted in the Kruger National Park, South Africa.

Visitation rates

Variables	**Estimated degrees of freedom**	**Reference degrees of freedom**	**F-statistic**	**p-value**
s(evi)	1.00	1.00	0.08	0.78
s(pride_nsv)	5.72	5.94	0.11	0.99
s(pride_mnlv)	1.76	2.02	0.08	0.92
s(nomad_nsv)	1.00	1.00	0.76	0.38
s(nomad_mnlv)	1.00	1.00	0.04	0.84
s(evi,pride_nsv)	0.00	27.00	0.00	0.31
s(evi,pride_mnlv)	**9.41**	**27.00**	**0.32**	**<0.01**
s(evi,nomad_nsv)	**8.29**	**26.00**	**0.23**	**<0.01**
s(evi,nomad_mnlv)	**0.03**	**25.00**	**0.00**	**<0.01**
s(pride_nsv,pride_mnlv)	**14.68**	**27.00**	**1.45**	**<0.01**
s(pride_nsv,nomad_nsv)	**3.09**	**27.00**	**0.20**	**0.01**
s(pride_nsv,nomad_mnlv)	**13.14**	**27.00**	**0.81**	**<0.01**
s(nomad_nsv,nomad_mnlv)	**2.31**	**27.00**	**0.14**	**<0.01**

Parametric coefficients: intercept = 28; Std-err = 0.23; t-value = 120; P <0.01
Adjusted R^2 = 0.62; Deviance explained = 68.5%

Duration of stay

Variables	**Estimated degrees of freedom**	**Reference degrees of freedom**	**F-statistic**	**p-value**
s(evi)	1.00	1.00	5.39	0.02
s(pride_nsv)	1.32	1.34	0.10	0.83
s(pride_mnlv)	1.00	1.00	3.23	0.07
s(nomad_nsv)	1.00	1.00	0.08	0.78
s(nomad_mnlv)	1.00	1.00	0.00	0.95
s(evi,pride_nsv)	**16.46**	**27.00**	**0.58**	**<0.01**
s(evi,pride_mnlv)	**0.00**	**27.00**	**0.00**	**0.01**
s(evi,nomad_nsv)	**4.53**	**26.00**	**0.12**	**<0.01**
s(evi,nomad_mnlv)	0.00	25.00	0.00	0.02
s(pride_nsv,pride_mnlv)	**17.79**	**27.00**	**2.50**	**<0.01**
s(pride_nsv,nomad_nsv)	**8.14**	**27.00**	**0.49**	**0.01**
s(pride_nsv,nomad_mnlv)	**8.72**	**27.00**	**0.54**	**<0.01**
s(nomad_nsv,nomad_mnlv)	**15.67**	**27.00**	**1.13**	**<0.01**

Parametric coefficients: intercept = 2.33; Std-err = 0.13; t-value = 179.8; P <0.01
Adjusted R^2 = 0.66; Deviance explained = 73.6%

Discussion

The use of T-Locoh (Lyons *et al.* 2013) has enabled us to account for time in our analysis and to show strong territorial behaviour predicted for leopards. The study also revealed a shift in these associations depending on the season. Leopard visits and durations of stay positively associated with resources and in particular areas with high EVI values, close to drainage lines, high woody cover percentage and close to permanent water points; more so during the dry season than the wet season. In the Skukuza study site in Kruger, lion visitation rates and durations of stay did not seem to play a significant role in how leopards used the landscape, except that there were subtle indications of positive association with the female leopard and with the male leopard. However, in the Timbavati study area, lions seemed to play a significant role on the movement behaviour of the male leopard collared there. We note that there were no nomadic male lions collared in the Skukuza study site and thus their role on leopard visitation rates and durations of stay cannot be substantiated. Equally, the role of spotted hyaenas cannot be substantiated for all study sites at this stage. Despite that, the present data revealed that lions may be responsible for the land use behaviour by the male leopard from the Timbavati. Thus this study revealed site specific differences in large carnivore assemblages between Kruger and Timbavati. Overall, the results indicate strong territorial behaviour in leopards.

Strong positive relationship between leopards and resources are in agreement with the prediction that leopard movements in Kruger were mostly resource driven. As expected, leopard visitation rates associated significantly with their proximity to roads. Roads play an important role as leopards use them to traverse and possibly for patrolling their territories (Bailey 1993). Woody cover and proximity to streams appeared to be important variables on visitation rates for the female and male leopards that were collared in Kruger; more so for females in the dry season. This is indicative of the foraging behaviour described for leopards in southern Africa (see Bailey 1993; Hayward *et al.* 2006). There was a shift in the association between visitation rates by females and proximity to streams associated with the dry and the wet seasons. In the dry season visitation rates significantly associated with proximity to streams, but in the wet season there was not enough evidence to suggest a positive association. Similarly, visitation rates did not associate significantly with proximity to streams in the wet season. This observation agrees with our prediction that prey animals were likely to concentrate around permanent water points in the dry season and move away from these during the wet season; thus explaining the shift observed in the female leopards. The Kruger is very heterogeneous since animal behaviour is a function of a host of variables as a result of a patchy distribution of resources (du Toit 2003). Interestingly, leopard visitation rates significantly associated with the dense herbaceous layer, which we used as a proxy for food resources for leopard prey and by extension, for the leopards. Duration of stay by female leopards associated significantly with water distribution, herbaceous layer and proximity to streams. However, in the wet season there was poor association between female leopards and all the variables except for the herbaceous layer; thus highlighting the importance of water resources for leopards in Kruger. In contrast to the patterns observed for the duration of stay by female leopards, duration of stay by males significantly associated with all the variables used during the analysis; highlighting differences between males and females on landscape use. The differences between male and females may be as a result of dissimilarities in home range sizes and ranging behaviour. For example, Bailey (1993) noted that males spend a considerable amount of time patrolling their territories and females may happen to be rearing the young (Steyn & Funston 2011). These observations make a strong case for the prediction that leopard foraging behaviour was likely to associate with the herbaceous layer; following the extrapolations that high scores obtained for vegetation cover from satellite imagery associated with high herbaceous layer biomass (Wessels *et al.* 2006) and that ruminants tended to associate with highly productive patches in the landscape as suggested by Smit (2011).

It is interesting that there was significant association between the visitation rate by the female leopard and the lion landscapes of visitation rates and duration of stay. However there was insufficient evidence to suggest that the duration of stay by the female leopard was impacted by the landscapes of activity by lions. Similarly, the visitation rate by the male leopard significantly associated with the lion visitation rates, but not with the duration of stay by lions. This suggests that the leopard visitation rates were impacted by the same resources that drove landscape use by lions, but the leopards stayed for extended periods in areas where lion activity was minimal. Although lions were suggested as possible drivers of leopard movement behaviour, in the Kruger study area, they did not come out as strongly as the predictions suggested. Possible reasons for this are firstly that there were not enough data to draw outright conclusions for the observed patterns in leopard movements against the lion landscape of activity. Secondly, the overlap between the male leopard and the lion home range was not complete – only the female leopard home range fell within the lion pride home range (unpublished data). And thirdly, male lions were not collared during the Kruger study site, thus weakening the predictions around the influence of lions on leopard movement behaviour. However, the observation that leopards in Kruger could stay in an area for more than ten consecutive days suggest that lion space use did not have a significant impact on leopard space use. This may be because while there is some overlap, diet partitioning is quite profound for lions and leopards in Kruger as suggested by Owen-Smith & Mills (2008b).

The lion-specific prey may just be using the terrain differently to movement behaviour by leopard-specific prey species (see du Toit 2003). This does not negate the fact that given lion presence, leopards are likely to move away (du Preez *et al.* 2015). The results therefore concur with results published by Vanak *et al.* (2013), where leopard movements were minimally affected by lions whereas cheetah and wild dogs were more affected. Results from the Timbavati study area paints a different picture. The visitation rate and duration of stay by the leopard significantly associated with duration of stay and visitation rates by both the pride and the nomadic male. That means the likelihood of encounters were quite high in the Timbavati; thus allowing the leopard movements there to be strongly influenced by lions. This was shown by the leopard’s duration of visits, which were markedly shorter than those observed for leopards from the Kruger study site. This may be an example of risk avoidance behaviour, thus supporting the findings of Broekhuis *et al.* (2013) and du Preez *et al.* (2014) that suggested that cheetahs and leopards avoided immediate presence of lions respectively. Similarly, in India findings by Harihar *et al.* (2011) suggested that leopards moved to the periphery of the reserve after tigers were re-introduced. Whereas the Kruger study site did not have sufficient data to support the influence of lions on leopards, the reason for profound separation between observed trends in the Kruger leopards and the solitary Timbavati leopard may simply be that lion presence was much stronger in the Timbavati than at the Kruger study site. The second reason is that the two study areas are managed differently. Whereas there is no hunting in the Kruger, there is occasional legal hunting in the Timbavati including carnivore hunting and culling of impala. These two reasons and that fences dominate land demarcation in western section of the reserve, where the study was undertaken, suggest that movement behaviour of the leopard was subjected to different variables to the Kruger study area. These results therefore, are pre-emptive of the roles that different management regimes play in the persistence of species of concern depending on the objectives.

Conclusion

Results from this study agree with the predictions that leopards in the study area are primarily resource-driven and secondarily, lion driven although lion data were scanty. This is especially true in the Skukuza study site. Although the prediction did not come out as clearly in the Timbavati study site as in the Kruger, resources and lions are the likely drivers of the leopard movement and these results are attributed to differences in management regimes between the two reserves. Furthermore, our results strengthen conclusions that meso-predator release mechanisms are unlikely to be realised in the Kruger ecosystem based on heterogeneity and high abundance of prey species (Chapter 4). We attribute our observations to co-evolution between lions and leopards in the absence of constraints such as small reserves and strict management criteria. In conclusion, we suggest that in the management of leopards, adaptive management strategy, that encompasses resources, competitors and landscape heterogeneity be adopted in order for the species to persist.

Acknowledgements

Approval of the study was granted by The South African National Parks (SANParks) and Mpumalanga Tourism and Parks Authority. We are grateful for financial support from Charlotte Scholarship Fund, Karl Meyer Stiftung, Nancy-Carroll Draper Foundation, the KCI Pacific Foundation, Singita Lebombo and Sweni Lodges, Ajubatus, Peter and Charmian Corne, Paul Levy, SANParks' Veterinary Wildlife Services (in addition to logistics and animal handling), and the University of Pretoria. SATIB Trust provided the clothing.

References

Bailey, T.N. 1993. The African Leopard: ecology and behaviour of a solitary felid. Columbia University Press, New York, USA

Bengis, R.G., Grant, R. & de Vos, V. 2003. Wildlife diseases and veterinary controls: A savanna ecosystem perspective. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds: J.T. du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington, DC, USA.

Broekhuis, F., Cozzi, G., Valeix, M, McNutt, J.W. & Macdonald, D.W. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82:** 1098-1105.

Clout, M.N & Russell, J.C. 2007. The invasion ecology of mammals: a global perspective. *Wildlife Research*, **35:** 180-184.

Crawley, M.J. 2007. *The R Book.* John Wiley & Sons, Ltd. London, United Kingdom.

Cristescu, B., Bernard, R.T.F. & Krause, J. 2013. Partitioning of space, habitat, and timing of activity by large felids in an enclosed South African System. *Journal of Ethology*, **31:** 285-298.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W. & Schmidt, B. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, **93:** 2590-2599.

Du Preez, B., Hart, T., Loveridge, A.J., & Macdonald, D.W. 2015. Impact of risk on animal behaviour and habitat transition probabilities. *Animal Behaviour*, **100:** 22-27.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, **37:**

194-206.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86:** 1320-1330.

Gertenbach, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe-African Protected Area Conservation and Science*, **23:** 35-43.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe-African Protected Area Conservation and Science*, **26:** 9-121.

Hall-Martin, A.J., Skinner, J.D. & Van Dyk, J.M. 1975. Reproduction in the giraffe in relation to some environmental factors. *East African Wildlife Journal*, **13:** 237-248.

Harihar, A., Pandav, B. & Goyal, S.P. 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *Journal of Applied Ecology*, **48:** 806-814.

Hayward, M.W., Hayward, G.J., Druce, D.J. & Kerley, G.H.I. 2009. Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity Conservation*, **18:** 887-904.

Hayward, M.W., O'Brien, J. & Kerley, G.I.H. 2007. Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, **139:** 219-229.

Hayward, M.W. & Slotow, R. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research*, **39:** 109-125.

Johnson, A.R., Wiens, J.A., Milne, B.T. & Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology*, **7:** 63-75.

Joubert, S.C.J. 1986. The Kruger National Park – An Introduction. *Koedoe-African Protected Area Conservation and Science*, **29:** 1-11.

Lyons, A.J., Turner, W.C. & Getz, W.M. 2013. Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology*, **1:** 2.

Owen-Smith, N. & Mills, M.G.L. 2008a. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*, **89:** 1120-1133.

Owen-Smith, N. & Mills, M.G.L. 2008b. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, **77:** 173-183.

Packer, C., Hilbon, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, **307:** 390-393.

Pietersen, L.M. 1992. Quality of food and voluntary intake of male impala (*Aepyceros melampus*) in the Timbavati area. MSc. Thesis. University of Pretoria, Pretoria, RSA.

R Core team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Smit, I.P.J. 2011. Resources driving landscape-scale distribution patterns of grazers in an African Savanna. *Ecography*, **34:** 67-74.

Smuts, G.L., Whyte, I.J. & Dearlove, T.W. 1977. Amass capture technique for lions. *East African Wildlife Journal*, **15:** 81-87.

Trewby, I.D., Wilson, G.J., Delahay, R.J., Walker, N., Yung, R., Davison, J., Cheeseman, C., Robertson, P.A., Gorman, M.L., & McDonald, R. 2008. Experimental evidence of competitive release in sympatric carnivores. *Biology Letters*, **4:** 170-172.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Morindagomo, F. &

Macdonald, D.W. 2009. Behavioural adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90:** 23-30.

Valeix, M., Loveridge, A.J. & Macdonald, D.W. 2012. Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis. *Ecology*, **93:** 2490-2496.

Van Helden, P. & Uys, P. 2009. Modelling predator-predator population dynamics in the context of BTB. *Disease Risk Assessment Workshop Report: African Lion (Panthera leo) Bovine Tuberculosis.* Eds. Keet, D.F., Davies-Mostert, H., Bengis, R.G., Funston, P., Buss, P., Hofmeyr, M., Ferreira, S., Lane, E., Miller, P. & Daly, B.G. Conservation Breeding.

Van Langevelde, F., Van Woersem, A., De Boer, F., De Bie, S., Slotow, R., Burger, A., Swart, J., & Prins, H. 2013. Prey on the run: influence of predators on spatial distribution and movement of prey. 2013 Annual Savanna Science Network Meeting, Skukuza, Mpumalanga, South Africa.

Vanak, A.T., Fortin, D, Thaker, M., Ogden, M., Owen, C., Greatwood, S. & Slotow, R. 2013. Moving to stay in place: behavioural mechanisms for coexistence of African large carnivores. *Ecology*, **94:** 2619-2631.

Venter, F.J. & Gertenbach, W.P.D. 1986. A cursory review of the climate and vegetation of the Kruger National Park. *Koedoe-African Protected Area Conservation and Science*, **29:** 139-148.

Wessels, K.J., Prince, S.D., Zambatis, N., Macfadyen, S., Frost, P.E., & Van Zyl, D. 2006. Relationship between herbaceous biomass and 1-km^2 Advanced Very High Resolution Radiometer (AVHRR) NDVI in Kruger National Park, South Africa. *International Journal of Remote Sensing*, **27:** 951-973.

Chapter 6. Synthesis, recommendations and conclusions

Introduction

Population ecology, community ecology, and landscape ecology form the theoretical basis in the design and approach adopted by conservation biologists tasked with upholding the persistence of ecosystem processes (see Gaylard *et al*.2003; Rogers 2003). Population ecology is concerned with the interactions within members of a population and the environment. Community ecology looks at patterns in species composition, species abundances, and their interactions with each other and with the environment (Vellend 2010). Landscape Ecology on the other hand, looks at patterns in a spatio-temporal continuum, patch dynamics and environmental heterogeneity as important processes that describe the functionality of ecosystems and how species respond at a landscape level (Turner *et al.* 2001; Pickett *et al.*, Cadenasso & Benning 2003; Rogers 2003). This dynamic oscillation between pattern and process therefore is best explained by conjecturing of mechanisms that drive functionality and productivity of ecosystems. For example, the use of competition theory to elucidate underlying processes driving patterns in population dynamics and community structure in a given ecosystem (Simberloff 1982; Hopf, Valone & Brown 1993), has greatly improved our understanding of the mechanisms explaining co-existence by members of the same guild. In turn, results obtained from the testing of the applicability of these mechanisms in different ecosystems, inform conservation ecology. Conservation ecology links biodiversity conservation with policy by providing managers with tools to suggest possible solutions to conservation challenges (Macdonald & Service 2007); thus providing conservation practitioners with a platform to influence the outcomes of decision-making when environmental policies are drafted.

Currently however, it is recognised that theories are developed at a faster rate than empirical and applied ecology; a gap which needs to be filled timeously to support advances in ecology (Biggs & Rogers 2003; Agrawal *et al.* 2007, Colyvan *et al.* 2009). There are three noteworthy limitations that may delay advancement in ecology. The first constraint deals with the importance of linking mathematical models, deductive reasoning and empirical data to explain observed natural phenomena in ecology (Codling & Dumbrell 2012; Levin 2012). Second, is the question of scale in explaining patterns and processes (Levin 1992), to ensure that relevant questions are asked and to enable proper alignment of effort and resources in addressing pressing conservation challenges. The third constraint is concerned with the merging of different ecological levels of organisation into one ensemble, in order to conjecture realistic mechanisms as the underlying drivers of ecosystem performance (Wu & Hobbs 2002; Wu 2013). Addressing these constraints therefore enhances the efficacy with which management strategies are implemented.

Globally, the large carnivore guild is subjected to mechanisms underpinned by processes operating at the three levels of organisation including population, community, and landscape levels. As a key component of ecosystem functionality and productivity, predation drives top-down processes within an ecosystem (Kissui & Packer 2004). In certain instances, together with changing rainfall patterns and abundances of prey species relative to each other, predation influences herbivore dynamics (Owen-Smith *et al.* 2005; Owen-Smith & Mills 2006; Owen-Smith & Mills 2008). Despite the benefits predation provides to ecosystem performance, carnivores are exposed to a range of stressors that may threaten their persistence.

First, anthropogenic activities alter the landscape by causing habitat loss and fragmentation, thereby impacting life history patterns of a multitude of species. These changes, together with the retaliatory killing of carnivores by humans often put large carnivores under pressure by driving them to local extinctions or creating small disjointed populations with limited gene flow between them; thus rendering them unable to respond to stochastic environmental perturbations (Balme *et al*. 2009; Athreya *et al.* 2013; McManus *et al.* 2014).

Second, large carnivores are affected by variations in resource availability driven by different environmental spatio-temporal processes. For example, in areas where large carnivores exist: (i) leopard (*Panthera pardus*) abundances and space use are a function of resource distribution (Bailey 2003); (ii) lions (*Panthera leo*) respond to changing environmental disturbances by shifting prey choices according to prey abundance (Owen-Smith & Mills 2008); and (iii) carnivores may adapt to abrupt or gradual changes in the environment by altering ranging behaviour and pride dynamics in the case of lions (Packer *et al.* 2005). Resources therefore, are a key driver in carnivore persistence.

Third, within species interactions (Kissui *et al.* 2010) and intra-guild interactions including competitive exclusions, predation, and klepto-parasitism create disturbances that may favour certain species while placing other species at a disadvantage (Palomares & Caro 1999; Cozzi *et al.* 2012; Broekhuis *et al.* 2013; Marnewick *et al.* 2014; Vanak *et al.* 2014). This observation leans strongly on the availability and distribution of resources. It nonetheless highlights the importance of interactions in sympatric carnivores.

Fourth, mammalian carnivores are exposed to diseases, which often drive affected populations to relatively low abundances (Ormerod 2002; Bengis *et al.* 2003). A classic example is the impact that rabies had on the wild dog (*Lycaon pictus*) population of the Serengeti in

Tanzania and the Ethiopian wolf (*Canis simiensis*) population in Ethiopia (see Riordan *et al.* 2007 for the review). The effects of disease can as a result influence the direction that ecosystem processes take by causing disturbances that lead to altered community structure.

In the KNP, the introduction of an extrinsic disease, bovine tuberculosis (bTB) that is casued by *Mycobacterium bovis*, is of great concern to biodiversity managers. The challenge is with the impact the disease may have on the lion population (Keet *et al.* 1996) although the disease effects cannot be fully substantiated presently (Ferreira & Funston 2010; Maruping 2014). For leopards, the density-dependent nature of the disease is not strongly supported by the leopard behaviour and ecology (Renwick *et al.* 2007). Notwithstanding, that did not stop conservation ecologists from proposing that should the disease cause a decline in the lion population abundance, it would trigger cascading effects in leopards such that their numbers would increase rapidly (van Helden & Uys 2009); a legitimate concern on the grounds that at the time, it was feared that the disease effects would cause a decline in the lion population abundances. Consequently, this would directly implicate the two mechanisms presently used to explain relationships between sympatric carnivores and stemming from the competition theory (Simberloff 1982): the meso-predator release (Johnson *et al.* 2007) and the niche packing (Pianka 1974) hypotheses.

Accordingly, this synthesis takes into account bTB as the likely trigger of the cascading effects in the KNP ecosystem; and in particular how these effects may indirectly affect the leopard population. Therefore three disciplines including population, community, and landscape ecology are invoked to explain mechanisms and processes driving the leopard population trends. The synthesis then discusses principles of theoretical biology to highlight cause and effect of observed patterns in the leopard population structure. Current observations include: (i) variations in leopard population abundances throughout the KNP; (ii) the association between leopard abundances and other large carnivore abundances in the KNP including lion, spotted hyaena (*Crocuta crocuta*) cheetah (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*); and (iii) the association between leopard movement behaviour and indices of resource distribution and lion space use. Lastly, the study assesses the landscape level mechanisms with emphasis on different management strategies adopted for KNP and the TPNR. Of particular interest, in as far as this study is concerned, is the persistence of leopards and how adaptive management strategy can incorporate them when decisions are made.

Population level considerations

This study revealed that at population level, leopard abundances in KNP are site-specific, depending on the physiognomy of the habitat or landscape they are found in. Leopard abundances were highest in the Pretoriuskop sweet veld, which receives the highest rainfall in the KNP and is characterised by thick vegetation (Chapter 4). The lowest abundance estimates were obtained in the Tshokwane study area where there were too few captures to estimate abundances with confidence. An inconsistency, which cannot be overlooked however, was that the capture yields from camera-traps were skewed towards males. A similar pattern was observed in a study conducted in the calibration phase of this study (Maputla *et al.* 2013) and in the Cederberg, South Africa (Martins & Harris 2013). These findings may be indicative of sexual separation in the movement behaviour of leopards. It also poses questions on the use of game paths by female leopards since camera-traps were generally placed on game paths. It is likely that females seldom use the game paths hence the poor representation of females in the captures. One way of addressing this challenge would be to investigate capture rates of females on game paths *versus* on dry river beds.

Another perplexing anomaly was with an excessively high leopard estimates for the Pretoriuskop study area. The present study did not address this finding. This raised several questions with regards to the leopard population in that area. Indeed Pretoriuskop is different from other study sites in that it receives the highest amount of rainfall in the KNP (Venter *et al.* 2003); and that the vegetation is dominated by very tall grasses. This suggests that leopard resource base at the Pretoriuskop study site is different from the rest of the study sites surveyed during this study. In addition, due to the tall grasses, medium-sized to small ungulates were likely to be under-represented during aerial surveys; suggesting that a different approach must be adopted in order to answer questions relating to leopards in the Pretoriuskop study site. Given that the estimates were so high, one would expect home ranges to be smaller than elsewhere in the KNP. Another expectation was that mechanisms driving intraspecific interactions would be more exaggerated there than in other study sites. Collaring of leopards in this study site would shed some light into the leopard ecology in this area.

Community and landscape considerations

At community level, the present study focused on the relationship between leopards and other large carnivores, in particular lions and spotted hyaenas. The cheetah and wild dog abundances were too small to be associated with leopards. Two theories, which in the case of KNP are contradicting each other, the meso-predator release and niche packing mechanisms underpinned the theoretical framework of these relationships. The first consideration, which had not been tested before was with regards to numerical comparisons. The rationale was that leopard abundances would reflect the presence of high or low lion and hyaena abundances throughout the KNP. Results revealed that leopard abundances were independent of lion or spotted hyaena abundances. In conclusion, niche packing hypothesis took precedence over meso-predator release as the most likely mechanism to explain these relationships. There was no discernible pattern when the relationship between leopards and prey biomass were assessed. This observation brings about questions relating to herbivore surveys. It appears as though smaller herbivores are under-represented in the mammal aerial surveys except for the impala (*Aepyceros malempus*). The reason for this is that most ruminants are generally attracted to highly productive herbaceous layer (Smit 2011) under a thick woody cover along riverine habitats. This obscures their visibility from the air. Using indices of resource availability as proxies to estimating leopard prey biomass instead of counts may help address this problem and shed light into the relationship between leopard abundances and prey biomass.

The second question had to do with movement behaviour by leopards. The theoretical framework of this question was underpinned by resource distribution, meso-predator and niche packing hypotheses. The rationale was that first and foremost leopards were likely to use space in response to resource distribution. The second rationale involved the meso-predator release and niche packing mechanisms as leopards are sympatric with lions. The results in this study confirmed the prediction that leopards were primarily resource-driven. The influence of lions was not observed in the KNP, but was observed in the TPNR. Notwithstanding, leopards appeared to respond to resources more so than lions. A gap in the analysis is with regards to edge effects, which were not accounted for in this study. Whereas this was not necessary in KNP, study animals in the

TPNR have a different set of challenges that include edge effects in response to how wildlife is managed there. At landscape level, the KNP is spatially variable and as a result the response to this variability by leopards was reflected in their density estimates according to landscape type. Leopards also showed site-specific differences in visitation rates against durations of visit throughout the KNP. This presents a clear indication that conservation managers have to take aspects of landscape variability into consideration when management decisions are made.

Conservation implications

The KNP has experienced many consequences of management strategies, the effects of which still haunt the park managers to date. Pertinent to this study and with regards to the large carnivore guild, is the apparent local extinction of the brown hyaena (*Parahyaena brunnea*) and the worryingly small population abundances of cheetah and wild dog. Both these problems are a consequence of past management practices coupled with stochastic environmental effects (Mills & Funston 2003; Marnewick *et al.* 2014). It is not clear how past management efforts affected leopard distribution in the KNP, therefore making it a challenge to suggest management strategies or to model past, present, and future population trends.

This is further exacerbated by the observation that leopard resources and in particular prey base, in as far as KNP is concerned, does not appear to have dipped below the required threshold to become a limiting factor for leopard persistence. Bailey (1993) noted that leopards often succumbed to starvation, but not because of reduced prey biomass. Following the rinderpest outbreak, and a period of unsustainable hunting preceding the outbreak, events which reduced the majority of mammalian species abundances (Bengis *et al.* 2003), it is not clear how these events may have affected leopard persistence in the KNP. Bailey (1993) by noting and even modelling leopard abundances in KNP from impala abundances and distribution provides an *a priori* conjecture in support for this observation. It is thus important that in merging mathematical modelling, theoretical deductions and field-based research about leopards to come up with viable management strategies, the situation in KNP should be taken into account. It would be difficult to model the response of the leopard population if their prey base were to fall below the required threshold using KNP as an example. Observations from elsewhere may provide answers to this question. Results from the TPNR, where there is occasional hunting of carnivores and yearly culling of impala, may provide answers to this question. For example, currently, it is not clear how these activities impact the large carnivore guild in the reserve. However, by carefully monitoring the number of animals removed from the population and their age, and by monitoring the response by members of the large carnivore guild, it may be possible to model the impact culling of prey species has on predators and in particular leopards.

Consequently, observations from this study have important connotations on leopard management in reserves. The following recommendations may be taken into account when leopard management strategies are drafted

(1) Pertinent to leopard persistence is the availability of resources. The study showed that leopard prey availability in KNP during the time of this study did not become a limiting factor in leopard abundances and space use, however, it may have been the case in the TPNR study site;

(2) If disease or any other agent were to cause a decline in lion abundances, there would not be an increase in leopard numbers as a response; and

(3) Assuming that (i) resource availability stays constant; and (ii) the reserve is as large as KNP, competition theory (Simberloff 1982; Hopf *et al.* 1993) can be counted upon for the leopard population to self-regulate rather than by other carnivores or culling.

References

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J.L., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J., Strauss, S., Turner, M.G. & Werner, E. (2007). Filling key gaps in population and community ecology. *Biological Science Faculty Publications*, Paper 242. http://scholarworks.umt.edu/biosci_pubs/242.

Athreya, V., Odden, M., Linnell, J.D., Krishnaswamy, J. & Karanth, U. 2013. Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PloS One*, **8:** e57872. **doi:** 10.1371/journal.pone.0057872.

Bailey, T.N. 1993. *The African Leopard: ecology and behaviour of a solitary felid.* Columbia University Press, New York, USA.

Balme, G.A., Slotow, R. & Hunter, L.T.B. 2009. Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation*, **142:** 2681-2690.

Bengis, R.G., Grant, R. & de Vos, V. 2003. Wildlife diseases and veterinary controls: A savanna ecosystem perspective. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds: J.T. du Toit, K.H. Rogers & H.C. Biggs. Island Press, Washington, DC, USA.

Biggs, H.C. & Rogers, K.H. 2003. An adaptive system to link science, monitoring and management in practice. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds. J.T. Du Toit, K.H. Rodgers & H.C. Biggs. Island Press. Washington, USA.

Broekhuis, F., Cozzi, G., Valeix, M, McNutt, J.W. & Macdonald, D.W. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*. **82:** 1098-1105.

Codling, E.A. & Dumbrell, A.J. 2012. Mathematical and theoretical ecology: linking models with ecological processes. *Interface Focus*, **2:** doi: 10.1098/rsfs.2012.008.

Colyvan, M., Linquist, S., Grey, W., Griffiths, P.E., Odenbaugh, J. & Posingham, H.P. 2009. Philosophical issues in ecology: recent trends and future directions. *Ecology and Society*, **14:** 22.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W. & Schmid, B. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*. **93:** 2590-2599.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildlife Research* **37:** 194-206.

Gaylard, A., Owen-Smith, N. & Redfern, J. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds. J.T. Du Toit, K.H. Rodgers & H.C. Biggs. Island Press. Washington, USA.

Hopf, F.A., Valone, T.J. & Brown, J.H. 1993. Competition theory and the structure of ecological communities. *Evolutionary Ecology*, **7:** 142-154.

Johnson, C.N., Isaac, J.L. & Fisher, D.O. 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society*. **274:** 341-346.

Keet, D.F., Kriek, N.P.J., Penrith, M.-L., Michel, A. & Huchzermeyer, H. 1996. Tuberculosis in buffaloes (*Syncerus caffer*) in the Kruger National Park. Spread of the disease to other species. *Onderstepoort Journal of Veterinary Research*, **63:** 239-244.

Kissui, B.M. & Packer, C. 2004. Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of The Royal Society London B,* **271:** 1867-1874.

Kissui, B.M., Mosser, A. & Packer, C. 2010. Persistence and local extinction of lion prides in the Ngorongoro Crater, Tanzania. *Population ecology*, **52:** 103-111.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology,* **7:** 1943-1967.

Levin, S.A. 2012. Towards the marriage of theory and data. *Interface Focus,* **2: doi:** 10.1098/rsfs.2012.006.

Macdonald, D.W & Service, K. 2007. Why bother? In: *Key Topics in Conservation Biology*. Eds. D. Macdonald and K. Service. Blackwell Publishing, UK.

Maputla, N.W., Chimimba, C.T., & Ferreira, S.M. 2013. Calibrating a camera trap-based biased mark-recapture sampling design to survey the leopard population in the N’wanetsi concession, Kruger National Park, South Africa. *African Journal of Ecology*, **51:** 422-430.

Marnewick, K., Ferreira S.M., Grange, S., Watermeyer, J., Maputla, N. &Davies-Mostert, H.T. 2014. Evaluating the status of African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist-based photographic surveys in the Kruger National Park. *PloS One*, **9:** e86265.

Martins, Q. & Harris, S. 2013. Movement activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *African Journal of Ecology*, **51:** 571-579.

Maruping, N.T. 2014. Drivers and consequences of bovine tuberculosis in lions of the Kruger National Park, South Africa. DTech Thesis, Tshwane University of Technology, R.S.A

McManus, J.S., Dickman, A.J., Gaynor, D., Smuts, B.H. & Macdonald, D.W. 2014. Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. *Oryx,* **doi:** 10.1017/S0030605313001610.

Mills, M.G.L. & Funston, P.J. 2003. Large carnivores and savanna heterogeneity. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity.* Eds. J.T. Du Toit, K.H. Rodgers & H.C. Biggs. Island Press. Washington, USA.

Ormerod, S.J. 2002. Applied issues with predators and predation: editor's introduction. *Journal of Applied Ecology*, **39:** 181-188.

Owen-Smith, N., Mason, D.R. & Ogutu, J.O. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. *Journal of Animal Ecology*, **74:** 774-788.

Owen-Smith, N. & Mills, M.G.L. 2006. Manifold interactive influences on the population dynamics of multispecies ungulate assemblage. *Ecological Monographs*, **76:** 73-92.

Owen-Smith, N. & Mills, M.G.L. 2008. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*, **89:** 1120-1133.

Packer, C., Hilbon, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science.* **307:** 390-393.

Palomares, F. & Caro, T.M. 1999. Interspecific killing among mammalian carnivores. *American Naturalist*, **153:** 492-508.

Pianka, E.R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Science USA*, **71:** 2141-2145.

Pickett, S.T.A., Cadenasso, M.L. & Benning, T.L. 2003. Biotic and abiotic variability as key determinants of savannah heterogeneity at multiple spatiotemporal scales. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds. J.T. Du Toit, K.H. Rodgers & H.C. Biggs. Island Press. Washington, USA.

Renwick, A.R., White, P.C.L. & Bengis, R.G. 2007. Bovine tuberculosis in southern African wildlife: a multi-species host-pathogen system. *Epidemiology and Infection*, **135:** 529-540.

Riordan, P., Hudson, P. & Albon, S. 2007. Do parasites matter? Infectious diseases and the conservation of host populations. In: *Key Topics in Conservation Biology*. Eds. D. Macdonald and K. Service. Blackwell Publishing, UK.

Rogers, K.H. 2003. Adopting a heterogeneity paradigm: implications for management of protected savannas. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds. J.T. Du Toit, K.H. Rodgers & H.C. Biggs. Island Press. Washington, USA.

Simberloff, D. 1982. The status of competition in ecology. *Annales Zoologici Fennici*, **19:** 241-253.

Smit, I.P.J. 2011. Resources driving landscape-scale distribution patterns of grazers in an African Savanna. *Ecography*, **34:** 67-74.

Turner, M.G., Gardner, R.H. & O'Neill, R.V. 2001. *Landscape Ecology in Theory and Practice.* Springer-Verlag, New York, USA.

van Helden, P. & Uys, P. 2009. Modelling predator-predator population dynamics in the context of BTB. *Disease Risk Assessment Workshop Report: African Lion (Panthera leo) Bovine Tuberculosis*. Eds. Keet, D.F., Davies-Mostert, H., Bengis, R.G., Funston, P., Buss, P., Hofmeyr, M., Ferreira, S., Lane, E., Miller, P. & Daly, B.G. Conservation Breeding.

Vanak, A.T., Fortin, D, Thaker, M., Ogden, M., Owen, C., Greatwood, S. & Slotow, R. 2013. Moving to stay in place: behavioural mechanisms for coexistence of African large carnivores. *Ecology*, **94:** 2619-2631.

Vellend, M. 2010. Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, **85:** 2.

Venter, F.J., Scholes, R.J. & Eckhardt, H.C. 2003. The abiotic template and its associated vegetation pattern. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Eds. J.T. Du Toit, K.H. Rodgers & H.C. Biggs. Island Press. Washington, USA.

Wu, J. & Hobbs, R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecology*, **17:** 355-365.

Wu, J. 2013. Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. *Landscape Ecology*, **28:** 1-11.