Cape Peninsula
University of Technology

SPATIAL AND TEMPORAL VARIATION IN LION (*PANTHERA LEO*) DIET WITHIN THE KALAHARI GEMSBOK NATIONAL PARK

by

Maya Beukes

Thesis submitted in partial fulfilment of the requirements for the degree

Master of Technology: Nature Conservation

in the Faculty of Applied Sciences

at the Cape Peninsula University of Technology

Supervisor: Dr Frans G. T. Radloff
Co-supervisor: Dr Sam M. Ferreira

Cape Town
May 2016

DECLARATION

I, Maya Beukes, declare that the contents of this thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

Beukes.

15 /08/2016

Signed **Date**

ABSTRACT

A survey in 2010 suggested that the lion (*Panthera leo*) population of the Kalahari Gemsbok National Park (KGNP) was exhibiting a skewed sex ratio in favour of males, which can ultimately lead to a decline in lion population numbers. In the KGNP artificial water provision has influenced the abundance of resident prey and potentially, lion diet and body condition. Changes in mammalian diet, and consequently body condition, have been found to influence the sex ratio of offspring. In response to a concern that diet may be influencing lion sex ratios in the KGNP, aspects of the spatial and temporal variation in lion diet were investigated between May 2013 and June 2015. The lion diet profile in the KGNP was described using evidence of prey remains identified through GPS cluster analysis (*n* = 278) from seven collared lionesses, lion scat analysis (*n* = 189) and opportunistic observations of lion feeding events (*n* = 52). Spatial variation in diet was investigated between three regional landscape types (north, south and west), based on the different vegetation types represented within each area, and two habitat types (riverbeds and dunes). Seasonal variations were assessed according to the hot-wet season (November to April), and the cold-dry season (May to October). Findings were also used to assess whether lion diet in KGNP has changed over the last 45 years through evaluating results from historical lion diet studies.

Accurately identifying lion diet can be challenging, as each technique available has some degree of bias. In order to obtain an accurate depiction of lion diet in an arid environment, it was necessary to determine the most accurate and suitable sampling approach, by identifying the sampling effort required, and the feasibility of different sampling methods. Results identified that a minimum sample size of 65 lion feeding events obtained through GPS cluster analysis, and 55 lion scats are needed to provide an reliable representation of overall lion diet in the KGNP. Opportunistic observations yielded too low a sample size for any meaningful deductions. Scat analysis provided the highest diversity of prey species (*n* = 11), as well as the highest representation of small prey (< 50 kg, 32%), but required extensive survey efforts (approximately 260 km driven per scat collected) in order to obtain an adequate sample size. The GPS cluster analysis technique yielded the highest number of feeding events over the shortest time frame, providing evidence of kills at 37% of investigated GPS cluster points (*n* = 823). GPS cluster analysis was found to underrepresent small prey items (3%), although it provided detailed information about the large prey species (> 50 kg) consumed. To identify the lion diet profile in an arid area, it is recommended that a combination of GPS cluster analysis and scat analysis be used.

Lions in the KGNP showed significant preference for large herbivores within the weight range of 150 – 650 kg including gemsbok, blue wildebeest, eland and kudu, and avoided prey the size of springbok and smaller. The largest prey species, giraffe, was also avoided. Large prey accounted for 68 to 97% of the lion diet profile. Gemsbok was identified as the primary prey species of lions in the KGNP across all landscape types, habitat types and seasons (range 42 – 79%). Of all the small prey species consumed by lion, porcupine was found to be the primary contributor to overall lion diet (range 7 – 18%). In terms of biomass contributions, small mammals contributed less than 5% to the lion diet profile.

The most notable spatial differences in the diet profiles of lion in the KGNP were between the dune and riverbed habitats (18% difference). Wildebeest made a significant contribution to lion diet in the riverbeds (36%), but not in the dunes (2%). Gemsbok were consumed at notably higher proportions in the dunes (79%), than in the riverbeds (52%). Even though differences were identified in the proportional prey availability between the wet and dry season (8% difference), there was no significant difference in the lion diet profiles between seasons. Gemsbok were proportionally the most abundant species across all seasons, landscape types, as well as in the dune habitats (range 28 – 57%). Prey abundance in the KGNP has changed in the past 45 years. In particular there has been an 8% decrease in springbok abundance in the Auob riverbed and 25% decrease in the Nossob riverbed. Gemsbok abundance has increased by 13% in the Nossob riverbed. Even though changes in lion diet over time were difficult to detect, due to differences in the techniques used between different studies, the changes in prey availability seemed to be reflected in the lion diet profile. Both scat analysis and GPS cluster analysis indicated a higher percentage use of gemsbok (51 and 73% respectively), in comparison with what was recorded historically through spoor tracking (26%) or opportunistic observations (32%). Small prey species were identified to be consumed proportionally less in the present study, using scat analysis (32%), than what was indicated in the historical study using spoor tracking (55%). Changes in sex ratios in the KGNP lion population were found to be occurring post parturition. Therefore, changes in prey availability and consequently lion diet are unlikely to be causing the sex skew in the KGNP lion population pre-parturition.

Results indicate that lion diet profiles vary to differing degrees, across the KGNP between all survey techniques, landscape types and habitat types, as well as over time. Large prey, particularly gemsbok, were found to be the primary contributors to lion biomass intake (≥ 95%) in the KGNP. Large herbivore dynamics are likely to be a key driver of lion population dynamics in the KGNP. In consequence, accurately identifying changes in lion diet as well as herbivore dynamics may help identify ecosystem changes that may impact lion survival in the KGNP.

ACKNOWLEDGEMENTS

- I would like to thank my supervisor, Dr Frans Radloff for his boundless guidance, patience and dedication to this project. His efforts far surpassed what could be expected.
- I would also like to thank my co-supervisor, Dr Sam Ferreira for sharing his knowledge and for his support throughout the project.
- I am forever grateful to the primary sponsors of the project, for their significant financial contributions or material support. The primary sponsors include (in alphabetical order):
    - The Cape Peninsula University of Technology, Post Graduate Bursary, for financial contributions.
    - The Cape Peninsula University of Technology, Mauerburger Postgraduate Bursary, for financial contributions.
    - The Fehlmann family, Switzerland for their endless love and support and all those who made such generous financial contributions in response to the ‘Fehlmann Brief’.
    - Land Rover and Jaguar, South Africa, in association with the SATIB Conservation Trust, for the sponsorship of a Land Rover Defender for use in project data collection and logistics. Particular gratitude goes to Mr Brian Courtney for his incredible contributions and support of the project.
    - The National Research Fund, South Africa, for financial support.
    - Peace Parks Foundation, for the donation of five GPS/VHF collars and travel expenses. Particular thanks to Mr Paul Bewsher, Mr Craig Beach and Ms Heloise de Villiers.
    - The University Research Fund, for financial contributions towards travel expenses.
- I would like to thank the Cape Peninsula University of Technology for their support. In particular I would like to thank, Ms Lillian Bingo, Dr Joseph Kioko and Ms Michelle Slabber for their unending support of the research as well as Dr Corrie Uys for her statistical advice and assistance.
- I would like to thank South African National Parks (SANParks) for allowing this research to be conducted in the Kalahari Gemsbok National Park (KGNP) and to all those who contributed to the success of this research. Several individuals within SANParks require a special word of gratitude including:
    - Managerial staff in the Kalahari Gemsbok National Park including, Mr Lucius Moolman (Regional Manager) and Mr Steven Smith (Park Manager). Many thanks to the KGNP Section Rangers including, Mr Micho Ferreira, Mr Kennet Makondo and Mr Brent Whittington, and their respective teams. Mr Johan Kruger (Technical Manager) and his team for providing assistance with the many vehicle problems. Mr Ben van Eeden (Tourism Manager), and Johan and Corri Pretorius (Shop Managers) who always positively supported the project.
    - From SANParks Scientific Services, I would like to thank Dr Charlene Bissett, Mr Ernest Daemane, Mr Lourens de Lange, Mr Greame Ellis, Ms Khosi Mathebula and Mr Pauli Viljoen who contributed significantly in their support of the project.
    - From SANParks Veterinary Wildlife Services, my gratitude goes to, Dr Markus Hoffmeyr and Dr Dave Zimmerman, for coordinating and implementing the collaring and de-collaring of lions in the KGNP during the study.
- I would like to thank the Republic of Botswana, Ministry of Environment, Wildlife and Tourism for allowing the research to be conducted in the Gemsbok National Park. In particular, I would like to thank Mr L. Boutshese, Dr M.V. Flyman and Mr B.S. Mokara for their support of the research.
- Thank you to all of the corporate sponsors who supported the research though the supply of equipment and services including (in alphabetical order):

    - Axiom Systems Africa, in particular Mr Mark Auer, for the supply of photographic and computer equipment.
    - AEW Auto in association with the 4x4 Hilux Forum and Repcom, in particular Mr Allan Venter, for mechanical services and two way radios.
    - Bantam Custom Trailers, in particular Mr Johann Botha, for the use of a 4x4 trailer.
    - Bundutec, in particular Mr Abri Hoffman and Mr Martin Rautenbach for the supply of a BunduTop vehicle roof top tent and BunduAwn vehicle awning.
    - Camp Master and Mass Mart, in particular, Mr Grant Eeckhoven and Mr Craige Pershouse for the sponsorship of outdoor camping equipment.
    - Columbia, in particular Jackie Badenhorst, for the supply of outdoor clothing and sleeping bags.
    - Due South, for winter apparel.
    - Escape Gear, in particular Mr Murray Thomas for 4x4 seat covers.
    - First Alignment Centre, in particular Mr Johann Viljoen for the supply of off-road tyres.
    - Gomad 4x4 in association with A-Z Branding, in particular Mr Ciske van Gijsen, for the supply of an aluminium canopy and modifications of a long range water tank.
    - Greensport, in particular Mr Wouter Hattingh, for sponsoring off-road equipment.
    - Ibenstein and Kuwuki, in particular Rene and Loni Kraft, for logistical support.
    - Idea Wild, in particular Ms Ann Marie Gage, for photographic equipment.
    - Prime Labels, in particular Tanya Lotz, for vehicle vinyl branding.
    - SATIB Conservation Trust, in particular Mr Brian Courtney, Gavin Courtney and Julian Friedmond for logistical support.
    - State Veterinary Services, Northern Cape, in particular, to Dr Bertus Nel for veterinary assistance.
    - Walkers Midas, Upington, for logistical support.
    - !Xaus Lodge, in particular Richard and Nola and all staff members for their support.
- Immense gratitude to Mrs Brenda Stauch for her editorial assistance and endless love and support.
- Mrs Adri Beukes-Harnett and Mr Tom Harnett are thanked for their logistical assistance and for their love and support.
- Ulla, Jody and Thandi Paulus (Belgium) provided generous logistic and financial support throughout the duration of the project.
- Numerous individuals and families supported the research in a significant ways and I would like to especially thank the following people:
    - Beukes, Mr R and Mrs A; South Africa
    - Brock, Ms J; South Africa
    - Cooper, Mr J and Mrs B; South Africa
    - Daly, Mr R; United Kingdom
    - Du Toit, Mr C and Mrs L; South Africa
    - Gastner family; South Africa
    - Gibbs family; South Africa
    - Haigh, Ms S; South Africa
    - Higson, Mr J and Mrs H; South Africa
    - Hinrichsen family; South Africa
    - Hinton, Mr D; United States of America

  - Kitching Mr D and Mrs A; South Africa
  - Kohne, Mr N; South Africa
  - Selby, Ms D; United Kingdom
  - Stauch, Mr B and Mrs C; South Africa
  - Stauch, Mr T and Mrs F; South Africa
  - Streicher, Mr J and Mrs G; South Africa
  - Webster, Ms R; United Kingdom
  - Wessels, Mrs C; South Africa
  - Whittington, Mrs M; South Africa
  - Winterton, Ms D; South Africa
  - Zeiher family; Germany
- I would also like to express my gratitude to all those who made financial contributions, or supported the project in other ways, that are not listed above.
- None of this would have been possible without God's grace and provision.

The financial assistance of the National Research Foundation towards this research is acknowledged. Opinions expressed in this thesis and the conclusions arrived at, are those of the author, and are not necessarily to be attributed to the National Research Foundation.

DEDICATION

To my husband, Otto Beukes, who shared this incredible experience with me, words cannot express, and to our daughter Leia who is due in September.

For my beloved Otto

TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION

CHAPTER 2: STUDY AREA

CHAPTER 3: EFFECTIVE ESTIMATION OF LARGE CARNIVORE DIET: LIONS (PATHERA LEO) IN THE KALAHARI GEMSBOK NATIONAL PARK

CHAPTER 4: SPATIAL AND SEASONAL VARIATION OF LION (*PATHERA LEO*) DIET IN THE KALAHRI GEMSBOK NATIONAL PARK

CHAPTER 5: VARIATION IN LION (*PANTHERA LEO*) DIET IN THE KALAHARI GEMSBOK NATIONAL PARK FROM 1970 TO 2015

LIST OF FIGURES

LIST OF TABLES

GLOSSARY

ANOVA	Analysis of variance
BM	Biomass
DNA	Deoxyribonucleic acid
FO	Frequency of Occurrence
GIS	Geographic Information System
GNP	Gemsbok National Park
GPS	Global Positioning System
IUCN	World Conservation Union
KGNP	Kalahari Gemsbok National Park
KTP	Kgalagadi Transfrontier Park
QGIS	Quantum GIS
RAI	Relative Abundance Index
RPD	Relative Percent Difference
SANParks	South African National Parks
VHF	Very High Frequency (30-300 MHz; 10-1m)
WMA	Wildlife Management Areas

CHAPTER 1

GENERAL INTRODUCTION

1.1 Rationale

In the Kgalagadi Transfrontier Park (KTP) lions (*Panthera* leo) are the apex predators and play a crucial role in maintaining ecological processes (Mills et al., 1978). In 2009, there were reported incidences of lions dying from an outbreak of distemper in the Kalahari Gemsbok National Park (KGNP), which makes up the South African portion of KTP, and this prompted a census in 2010 to detect changes in the KGNP lion population size and demographics (Ferreira et al., 2012). Results from the 2010 census indicated that the lion population numbers in the KGNP appeared to be stable, although the sex ratio of the population seemed to be favouring males (Ferreira et al., 2012). The present study was initiated against a background that changes in lion diet over time could cause the sex ratio of the KTP lion population to bias towards a higher proportion of males than could be expected (Ferreira et al., 2012). Evidence from previous studies has found a correlation between maternal body condition and sex ratios at birth, where females in good body condition are more likely to produce male offspring (Trivers & Willard, 1973; Meikle & Drickamer, 1986; Sheldon & West, 2004). As body condition is directly related to diet and prey abundance (Carbone et al., 1999; Hayward & Kerley, 2005; Hopcraft et al., 2010; Pereira et al., 2014), the present study set out to better understand lion diet within the KGNP and assess whether diet might have changed over time.

1.2 Ecological importance and conservation status of lions

As apex predators, lions play a critical role in ecosystem functioning (Beschta & Ripple, 2009; Loveridge & Canney, 2009; Pitman et al., 2012; Mills, 2015). A decline in their population can have numerous deleterious knock-on effects to other species (Loveridge et al., 2007). Complex relationships exist between large predators and their associated prey whose population numbers are regulated by either predation-related (top-down) or resource-related (bottom-up) factors (Owen-Smith & Mills, 2008; Beschta & Ripple, 2009; Anderson et al., 2010; Hopcraft et al., 2012; Sinclair & Arcese, 2013). Changes in herbivore dynamics impact lion demographics as well as pride dynamics (Valeix et al., 2009). Lions alter prey abundance and behaviour (Owen-Smith & Mills, 2008) and can have spatio-temporal influences on prey species (Valeix et al., 2009). This, in turn, has an effect on area specific habitat alteration, utilization and condition (Gittleman & Harvey, 1982). According to changes in prey availability lions may alter their selection of prey which can lead to either instability, through enhanced predation pressure, or stability, through reduced predation pressure, within herbivore populations (Ogutu & Owen-Smith, 2005; Owen-Smith & Mills, 2008). The susceptibility of herbivores to predation varies seasonally and spatially (Pereira et al., 2014). Lions alter their movements seasonally in relation to prey movements and hunt more frequently in areas where prey are easier to catch (Hopcraft et al., 2005). Herbivores may utilize areas that have higher predation risk zones when food is limited in other areas (Sinclair & Arcese, 2013).

Apex predators influence the abundance and behaviour of meso-predators which has implications for all trophic levels and ecosystem functioning (Miller et al., 2001; Hayward & Somers, 2009). Declines in the abundance of apex predators can lead to population eruptions in the meso-predator guild which can in turn trigger declines in prey populations (Prugh et al., 2009). Predators of a larger body size can negatively impact smaller predators due to increased conflict and competition through kleptoparasitism (Creel, 2010), although large carnivores rarely misappropriate carcasses captured by other predators in the KTP (Mills, 2015). Lions often kill other carnivores but usually do not consume the carcasses (Eloff, 1984). Smaller carnivores may benefit from larger carnivores through scavenging their prey remains (Pereira et al., 2014; Mills, 2015).

In addition to their importance in ecosystem functioning, lions also acts as a flagship species in biodiversity conservation (Loveridge & Canney, 2009). Lions heighten tourist experiences (Kerley et al., 2003) and have an economic incentive as a tourist attraction (Herrmann, 2004) which is based on the demand of people wanting to view lions in their natural habitat (Vorhies & Vorhies, 1993). Due to their iconic stature, lions have indirectly encouraged the protection of large areas of habitat from which numerous, less charismatic species have benefited (Loveridge & Canney, 2009).

Lions are listed as Vulnerable according to the World Conservation Union (IUCN) Red List of Threatened Species (IUCN, 2015) and are listed on Appendix II according to the Convention on International Trade in Endangered Species (CITES). Their numbers have continued to decline over the past two decades and the reasons for this are poorly understood and may not be reversible (IUCN, 2015). Fossil evidence suggests that lions were once the most widespread terrestrial mammal occurring in Africa and most of Eurasia and North America (Barnett et al. 2006). Today the range of wild, free-roaming lions is restricted to sub-Saharan Africa (Figure 1.1), except for a population (< 300 individuals) in the Gir Forest, north-western India (Skinner & Chimimba, 2005; Loveridge & Canney, 2009; Banerjee et al., 2013). Sub-Saharan Africa is now estimated to have between 23 000 and 39 373 lions remaining in 36 sub-populations, half of which are found in southern Africa (Chardonnet, 2002; Bauer & Van

Der Merwe, 2004). Habitat transformation together with human persecution and exploitation are likely to be the principal causes of the decline in lion numbers (Nowell & Jackson, 1996; Chardonnet et al., 2010; Banerjee et al., 2013). Other possible detrimental influences include trophy hunting (Whitman et al., 2004; Packer et al., 2011), compromised genetic diversity (Barnett et al., 2006; Hunter et al., 2013) and diseases (Alexander et al., 2010). Mortality due to disease is uncommon in wild lion populations even though they host a number of viral, bacterial and parasitic pathogens, including canine distemper virus, feline herpes virus, feline calicivirus, feline parvovirus and coronavirus (Packer et al., 1999; Alexander et al., 2010; Ferreira & Funston, 2010). However, periodic disease outbreaks have caused dramatic declines in localized populations (Roelke-Parker et al., 1996).

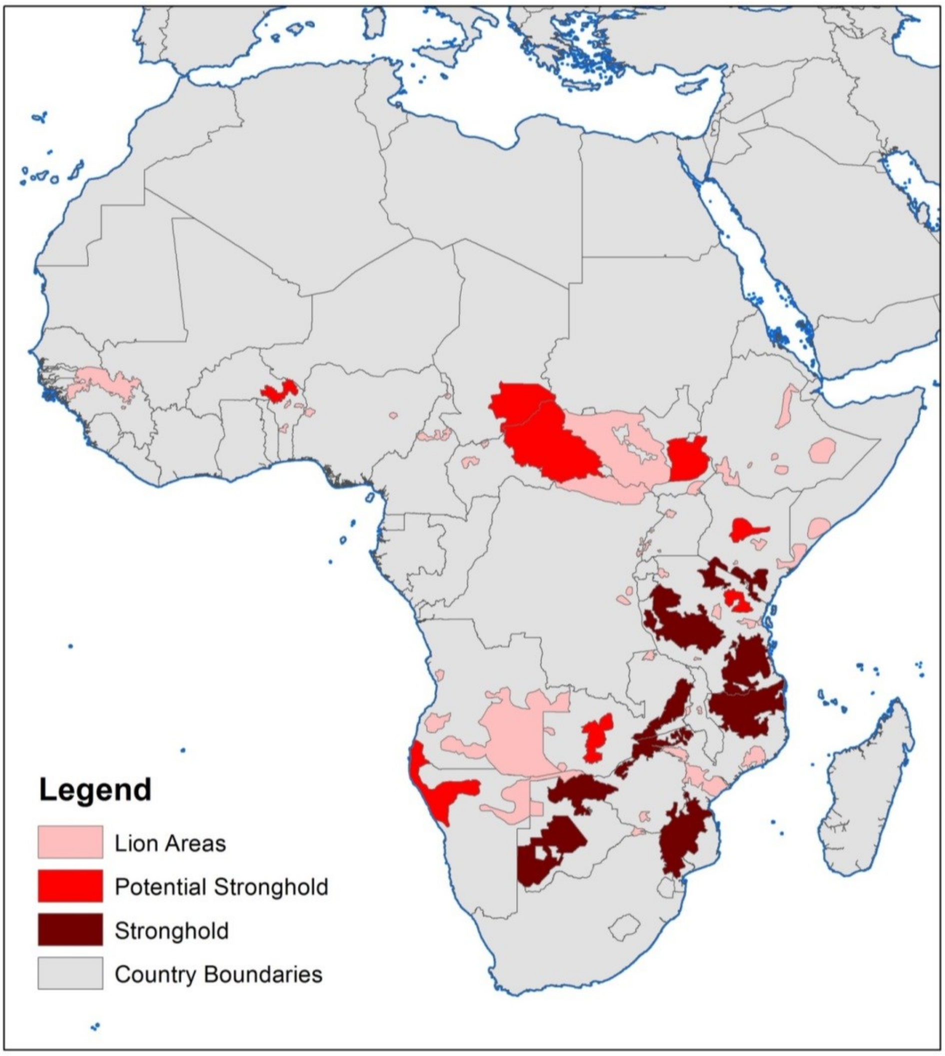


Figure 1.1 Map of Africa illustrating the location of lion populations within and outside of protected areas (Bauer et al., 2015).

In light of the precarious situation lions find themselves in globally, the persistence and sustainability of the lion in the KTP is particularly important as it is one of only ten locations in sub-Saharan Africa and one of only four locations in Southern Africa that is thought to have a viable lion population that is either stable or increasing (Riggio et al., 2013; Bauer et al., 2015).

1.3 Lion characteristics

Lions are the largest African carnivores with an average weight of 190 kg for males and 126 kg for females (Skinner & Chimimba, 2005). Living in prides of between 2 and 18 females and 1 and 9 males, lions are the only truly social felid (Schaller, 1972). The foundation members of a pride are usually related females and their offspring (Scheel & Packer, 1991). Pride members, made up of related and unrelated individuals contribute to rearing cubs (Packer et al., 2001), defending territories (Heinsohn, 1997) and hunting (Stander, 1992a). Hunting success increases with pride size but prides may form “fission-fusion” units depending on food availability (Schaller, 1972; Scheel & Packer, 1991; Heinsohn & Packer, 1995). Pride dynamics and behaviour can differ within an ecosystem according to localized variation in habitat and prey availability (Patterson, 2007). Lions have large home ranges due to their high metabolic requirements (Gittleman & Harvey, 1982). Home range sizes vary considerably in extent across habitats according to landscape features and resource distribution (Skinner & Chimimba, 2005). Roaring, scent-marking and patrolling are used to define territories and where possible avoid unsolicited encounters with lions from other prides (Schaller, 1972). Lions are mainly nocturnal, foraging at night and resting under shelter during the heat of the day (Schaller, 1972; Eloff, 1984; Stander, 1992b; Mills et al., 1995).

1.4 Lion foraging behaviour and diet

Food intake of lions varies according to prey size, prey selection, capture success (Green et al., 1984; Hayward et al., 2007) and seasonality (Stander, 1992b). Large carnivores expend a lot of energy hunting prey (Carbone et al., 1999). Energy obtained from prey consumed should equal or exceed energy expended during the hunt, therefore large carnivores will usually target larger prey species (Carbone et al., 1999; Radloff & du Toit, 2004) and first consume prey parts that render the highest energy (Ruhe et al., 2008). Lions regularly pursue individuals which are energetically disadvantaged i.e. injured, young, old, pregnant, or males preoccupied with breeding or alone (Sinclair & Arcese, 2013; Pereira et al., 2014). Prey species targeted by lions and the hunting techniques used to capture prey are also a function of pride size and dynamics as well as underlying terrain and vegetation type

(Stander, 1992b; Davies el al., 2016). Prey selection by lions changes in accordance with annual seasonal and environmental fluctuations which influence herbivore assemblages (Carlsson, 2005; Ruhe et al., 2008; Davidson et al., 2013).

There are numerous factors that influence a hunt and can be categorized according to prey-, lion- and environmental-related factors (Stander & Albon, 1993). The efficiency of capturing prey in open habitats increases when lions hunt cooperatively (Stander, 1992a). When hunting as a pride of two or more individuals, lions can display coordinated cooperation (Stander, 1992b). Hunting in a group increases their probability of success (Schaller, 1972; Scheel & Packer, 1991; Stander, 1992a), especially during hunts of large prey such as buffalo, *Syncerus caffer* (Schaller, 1972; Scheel & Packer, 1991). To capture prey, lions use a combination of stalking and ambushing prey from concealed locations i.e. tall grass or high bush density (Schaller, 1972; Scheel & Packer, 1991; Stander, 1992a). Prey are generally immobilized by lion grasping the neck or throat region and then killed by suffocation (Schaller, 1972). It has been surmised that lions in the Kalahari have a unique approach to capturing gemsbok, *Oryx gazella,* as it had been observed that they use the force from their jaws to dislocate a victim's vertebral column at the lumbo-sacral joint, which is an inherently weak area (Eloff, 1964). Kalahari lions potentially use the same method to subdue other large herbivores (Eloff, 1964).

Large carnivores generally target prey whose mean body mass is 45% or more than that of the predator's mass (Carbone et al., 1999; Radloff & du Toit, 2004). Lions exhibit preferences for certain prey species (Hayward & Kerley, 2005; Rapson & Bernard, 2007; Owen-Smith & Mills, 2008; Davidson et al., 2013) and tend to prey on species within a weight range of 190 - 550kg (Hayward & Kerley, 2005) or within the weight range of 32 - 632kg (Clements et al., 2014). Prey preference can be determined by identifying the numbers of prey species consumed in relation to their availability (Hayward & Kerley, 2005; Rapson & Bernard, 2007; Davidson et al., 2013). Species that are not preferred, but fall within the favoured weight range avoid predation pressure through morphological adaptations such as horns, occurring at low densities or by demonstrating behaviours that increase vigilance such as increased herd size (Hayward & Kerley, 2005). Males hunting alone or in coalitions show preference for larger prey such as buffalo and giraffe, *Giraffa camelopardalis,* whereas females will target medium-sized herbivores such as blue wildebeest, *Connochaetes taurinus,* and zebra, *Equus burchelli,* and tend to have a larger prey range (Funston et al., 1998; Radloff & du Toit, 2004). It is unsure if prey preference is a result of conscious choice or related to a prey species ease of capture (Hayward et al., 2011). A review of 32 lion dietary studies across 42 ranges indicated that lions show significant preference for gemsbok, buffalo, wildebeest, giraffe and zebra (Hayward et al., 2007).

Lions display the least dietary overlap with other carnivores and select the broadest variety of prey (Hayward & Kerley, 2005). Where dietary niches do overlap, such as between lion and spotted hyaena, prey abundance facilitates coexistence (Périquet et al., 2014). Prey is less abundant in the arid KTP, driving a higher degree of resource partitioning between carnivores, specialized hunting techniques, as well as diet flexibility (Mills, 2015).

1.5 Regional variation in lion diet

Lions occurring in the open tree savanna of the Kruger National Park, using GPS cluster analysis, were found to feed predominantly on zebra (25%), wildebeest (19%) and impala, *Aepyceros melampus,* (15%) although giraffe and buffalo contributed to almost 40% of their biomass intake (Tambling et al., 2012). In Hwange National Park Zimbabwe, a semi-arid savanna, using direct observations and scat analysis, buffalo was the most frequently consumed prey species for female lions (33%), followed by kudu, *Tragelaphus strepsiceros* (19%) and sable, *Hippotragus niger*, together with wildebeest (13%) (Davidson et al., 2013). From a biomass intake perspective buffalo contributed 39% of lion biomass intake, followed by elephant, *Loxodonta africana,* which accounted for only 8% of kills but comprised 20% of biomass intake (Davidson et al., 2013). The Serengeti ecosystem in East Africa is composed of open grassland and savannah. Direct observations indicate that lions in this environment consume predominately wildebeest and zebra (38%) followed by giraffe (15%) which make up 63% and 15% respectively of their biomass intake. Interestingly, small prey within a 2 - 45 kg weight range contributed 14% to the biomass intake (Sinclair et al., 2003). In a study conducted in Etosha National Park, northern Namibia, which incorporates the biotas of the southern savanna woodland, south-west arid and the Namib Desert, lions were recorded using continuous follows to hunt 16 prey species, although five species namely, springbok, *Antidorcas marsupialis,* zebra, wildebeest, gemsbok and springhare, *Pedetes capensis,* accounted for 95% of all observed hunts (Stander & Albon, 1993). Prey use of lions obtained using opportunistic observations and scat analysis in Tswalu Kalahari Reserve, in the south-eastern Kalahari region of South Africa, indicated that gemsbok and wildebeest were the most utilized prey at 24% and 18% respectively (Roxburgh, 2008). In relation to prey availability lions showed significant preference for warthog, *Phacochoerus africanus*, steenbok, *Raphicerus campestris,* and kudu, while zebra were avoided in Tswalu Kalahari Reserve (Roxburgh, 2008). Another Kalahari based study on a Namibian game farm, Kalahari Game Lodge, that borders the KGNP, found that lions consumed mainly eland, *Tragelaphus oryx,* (39%) and gemsbok (26%) (Stander, 2003). However, it was shown that lions on this game farm also consumed a relatively high proportion of smaller herbivore species (24%) including springbok, common duiker, *Sylvicapra grimmia*, and steenbok (Stander, 2003).

In the KGNP specifically, two previous studies have been conducted on lion diet over 30 years ago (Eloff, 1984; Mills, 1984). Subsequently there have been no further detailed studies in this area. Between 1970 and 1983 spoor follows of lions in the KGNP using Bushman trackers were conducted (Eloff, 1984). During this 13 year time period, lion tracks were followed over 195 occasions, for distances that covered approximately 24 hours of lion activity, and resulted in evidence of 92 lion feeding events (Eloff, 1984). The sparsely vegetated habitat and sandy soils of the KTP facilitate the efficacy of tracking spoor (Eloff, 1973; Bothma & Le Riche, 1984; Funston et al., 2010). The results of this study indicated that of the 17 species consumed by lion, porcupine, *Hystrix africaeaustralis,* were taken the most frequently (32%), followed by gemsbok (25%). The predisposition of lions to consume a large number of porcupine is unique to the KTP (Eloff, 1984) and has been suggested to be an adaptation to deal with the difficulty of food acquisition in an arid environment (Mills, 2015). The large proportion of small mammals as well as the low numbers of wildebeest in this sample could be a result of this study being conducted mainly in the dunes, in the northern section of the KGNP, and following individual lions which may show specific prey preferences.

Between 1974 and 1982 another study used direct opportunistic observations of lions feeding, as well as records of feeding events obtained from field ranger reports and diaries in order to accumulate data on 370 lion feeding events in the KGNP (Mills & Retief, 1984). Of these approximately 60% were observed in the riverbed areas and 40% in the dunes. Wildebeest were taken predominantly within the riverbeds (95%) and comprised 37% of the total records, whereas gemsbok made up 32% of all recorded kills and were found to be most frequently consumed in the dunes (74.2%). In proportion to their availability, springbok were consumed infrequently and comprised only 13% of recorded kills, although this could be a misrepresentation as lions can quickly consume a springbok carcass. This is likely to be the case for the underrepresentation of all other small prey items in this study as well (Mills, 1984).

It is clear that differences in lion diet exist across and within different biogeographical regions across Africa. How lion diet varies over extended time periods at specific locations is largely unknown, but diet will inevitably vary according to shifting prey dynamics in response to environmental fluctuations or anthropogenic interferences (Owen-Smith & Mills, 2008; Davidson et al., 2013; Bauer et al., 2014).

1.6 Herbivore dynamics in the Kgalagadi Transfrontier Park

Ecosystems fluctuate between states of equilibrium and non-equilibrium and are subject to change over time, resulting in a shift in ecosystem conditions that differs from the previous state (Briske et al., 2003; Schmitz et al., 2003; Barnosky et al., 2012). Ecosystems change in response to gradual changes in climate, nutrient availability, habitat degradation or exploitation of natural resources (Scheffer et al., 2001). State shifts normally occur slowly due to changing environmental conditions, however they can be amplified through anthropogenic activities (Suding et al., 2004), known as a “sledgehammer” effect (Barnosky et al., 2012).

Extensive rangelands, such as the KTP, are complex systems influenced by a multitude of factors and thus exist in alternate ecosystem states (Noy-Meir, 1975; Suding et al., 2004; Briske et al., 2005). Gradual changes in ecosystem states may be driven through factors such as enhanced grazing pressures over time (Van der Wal, 2006), whereas more sudden changes may occur through episodic ecological disruptions such as drought, fire and flood (Rapport & Whitford, 1999; Bond, 2005). Rainfall is regarded as the key ecological driver in savanna ecosystems (Coe et al., 1976; Mills et al., 1995; Owen-Smith & Mills, 2008). Herbivore and carnivore biomass are higher in areas with increased soil nutrients and annual rainfall (Loveridge & Canney, 2009; Celesia et al., 2010). Manmade barriers such as fences alter the natural distribution of animals and could result in a shift in population community structure and ecology (Williamson & Williamson, 1984; Cozzi et al., 2012).

Large scale migrations of herbivores across the broader Kalahari landscape, specifically by wildebeest and eland, are progressively being prevented by the increasing range and influence of human settlements and livestock farming activities (Williamson & Williamson, 1984; Verlinden, 1998). In the KTP game fences were erected between neighbouring farmlands along the south western boundary between South Africa and Namibia and in the south eastern section of Botswana and have inhibited the natural game migratory movements (Anonymous, 2008). Irregular events of large-scale movements of blue wildebeest, springbok, eland and red hartebeest, *Alcelaphus buselaphus,* were historically recorded in and out of the KTP during dry periods (Eloff, 1962; Verlinden, 1998). The range of these species has now instead become increasingly restricted to the KTP and they largely limit their movements within the boundaries of the KTP (Mills, 2015). Large scale seasonal migrations by herbivores are thought to be a response to periods of drought, where animals attempted to access permanent water sources, such as the Orange, Limpopo or Okavango Rivers and better grazing grounds, but these migration routes have been closed off with the erection of fences (Williamson & Williamson, 1988; Verlinden, 1998). Inhibiting these movement patterns may have consequences to the persistence of wild herbivores if mitigation measures, such as the provision of artificial water sources, are not implemented (Williamson & Williamson, 1984).

The provision of artificial water points, although often obligatory, also has an impact on an area's ecology (Smit et al., 2006; Shannon et al., 2009). In the KGNP the provision of artificial water points has altered herbivore assemblages (Van Rooyen et al., 2008; Funston, 2011) by increasing the abundance and distribution of water dependant species (Knight, 1995a; Owen-Smith, 1996). Of the ungulates represented in the KGNP, blue wildebeest are the most water dependent species and endure the highest mortality rates during periods of drought (Knight, 1995a). Being strictly grazers, wildebeest would have travelled large distances in this arid area to find sufficient, good-quality graze and water, especially during periods of drought (Williamson & Williamson, 1988). The provision of artificial waterholes in the KGNP, of which there are 41 in total, 17 situated in the Auob and 24 in the Nossob riverbeds (Mills & Retief, 1984; Knight, 1995a) could have resulted in grazers occuring at higher densities and become more sedentary, making them more vulnerable during periods of low annual rainfall (Knight, 1995a). Many of these waterholes were established in the KGNP in the 1930's (Knight, 1995a). Prior to their establishment, ungulates were reliant on obtaining water from ephemeral rain-filled pools (Williamson & Williamson, 1988) or from Tsamma melons, *Citrullus lanatus*, which provide an important water source for animals during the dry season and in the absence of waterholes (Knight, 1995b)

The KGNP lion population's pride composition and dispersal pattern are related to resident prey availability (Funston, 2011). An increased abundance and distribution of water dependant prey species (Knight, 1995a; Owen-Smith, 1996) may have led to lion prides, in close proximity to the artificial water sources, being exposed to a more reliable and predictable food source than in the past (Funston, 2011), which potentially led to better body condition and the consequent changes in the lions population's sex ratio (Ferreira et al., 2012).

1.7 Lion dynamics in the Kgalagadi Transfrontier Park

Lions in KTP have very large home ranges (1462 ± 388 km^2) and are able to move freely between the Kalahari Gemsbok National Park (KGNP) in South Africa and the bordering Gemsbok National Park and Wildlife Management Areas in Botswana (Funston, 2011). The average pride size in KTP, determined by the average number of adult females (Van Orsdol et al., 1985), is estimated to be 4.2 females per pride (Funston, 2001; van Vuuren et al., 2005). Lion population density is relatively stable and has been estimated to be between 0.7-1.2 lions per 100 km^2 (Mills et al., 1978; Funston, 2011). Interestingly, the proportions of males specifically in the sub-adult age classes, has gradually increased from 42% in 1976 to 75% in 2010 (van Vuuren et al., 2005; Ferreira et al., 2012).

Sex skews can be related to a number of factors such as changes in resource availability (Trivers & Willard, 1973; Celesia et al., 2010; Ferreira & Funston, 2010), social factors (Pusey & Packer, 1987; Ferreira et al., 2012a), life history (Holand et al., 2006), changes in hormone levels as a result of parasitic infection in relation to time of conception (James, 2004) and anthropogenic interferences (van Vuuren et al., 2005; Funston, 2011; Ferreira et al., 2012b). The factors that have triggered the sex skew specifically in the KGNP lion population are poorly understood and require further investigation (Ferreira et al., 2012a). One plausible cause of the skew was thought to be a change in lion diet (Ferreira et al., 2012b). Diet has an effect on body condition, which in turn has been found to influence reproductive sex ratios (Trivers & Willard, 1973; Meikle & Drickamer, 1986). In a review of 37 studies conducted on sex ratios in ungulates evidence was found correlating maternal condition and sex ratio (Sheldon & West, 2004), although no studies could be found relating sex ratios to maternal body condition for carnivores.

The skew towards males is a concern, as a sex-biased population in lions can lead to greater competition between males due to rivalry for breeding rights with females (Pusey & Packer, 1987). This increased competition could result in reduced reproductive success of males as well as increased incidences of infanticide from incoming male coalitions (Becker et al., 2013). Heightened male-male competition can also lead to male-biased dispersal (Pusey & Packer, 1987). Lion population growth rate is dependent on the number of breeding females (van Vuuren et al., 2005) and would decrease under a male biased population (Pusey & Packer, 1987).

The KGNP lion population is particularly vulnerable to the effects of environmental fluctuations and anthropogenic influences (Herrmann, 2004; Bauer & Iongh, 2005). This is due to their low population size, relative isolation and the arid and resource poor environment in which they occur (Mills et al., 1978; Castley et al., 2002; Loveridge & Canney, 2009). Land use and management practices in and around the KTP, such as livestock farming (Herrmann, 2004) and the provision of artificial water sources, influence natural population dynamics and may have an impact on the lion population (Van Rooyen et al., 1990; Funston, 2001; Ferreira et al., 2013). Lions that transgress the confines of the park into neighbouring farmlands have been found to predate on livestock (Mills et al., 1978; Herrmann, 2004), leading to lions being actively sought out and killed (Schiess-Meier et al., 2007; Funston, 2011). Accounts have indicated that at least one lion is killed per annum from each of the five prides that live adjacent to the KGNP park boundary (van Vuuren et al., 2005), placing additional pressures on the population (Herrmann, 2004).

There is the possibility that lion diet in the KGNP has changed over time in response to fluctuating environmental conditions and anthropogenic interferences. Temporal changes in lion diet may thus be indicative of broader environmental shifts (Davidson et al., 2013), which may in turn have potential consequences on the lion population (Bauer et al., 2014). A better understanding of lion diet in the KGNP and an assessment on whether it has changed over time might thus provide more clarity on whether lion diet could have been a driver of the observed changes in the sex ratios of the lion population. However, challenges exist in determining lion diet as each independent technique used provides a certain degree of bias in the results (Tambling et al., 2012).

1.8 Methods of investigating lion diet

A number of techniques have been used in assessing lion diet such as stomach content analysis (Smuts, 1979), faecal analysis (Mukherjee et al., 1994; Breuer, 2005; Banerjee et al., 2013; Davidson et al., 2013), tracking spoor (Eloff, 1984), continuous follows (Schaller, 1972; Stander, 1992b) opportunistic observations (Mills, 1984; Radloff & du Toit, 2004; Rapson & Bernard, 2007; Owen-Smith & Mills, 2008) and more recently GPS cluster analysis (Pitman et al. 2012; Tambling et al. 2010). DNA analysis has been used for scat analysis and diet determination in other species (Reed, 2004; Shehzad, 2011).

Continuous direct observations are widely regarded as the most accurate method to determine lion foraging activities (Mills, 1992), as other techniques may bias dietary representation to either smaller or larger prey species (Mills et al., 1978; Tambling & Belton, 2009). Direct observations also provide insight into consumption rates, killing frequency, and prey selection (Mills, 1992). However, continuous observation is seldom feasible due to logistical and financial constraints and in certain areas may cause disturbances influencing the outcome of a hunt (Mills, 1992). Opportunistic observations bias findings towards large prey items as predators will spend less time feeding on small carcasses and leave few remains (Mills, 1984).

The use of spoor tracking is an effective, non-invasive method of determining carnivore diet, especially in areas that are difficult to access (Bothma & Le Riche, 1984; Mills, 1992; Stander et al., 1997; Liebenberg et al., 1998; Melville et al., 2004) and has been previously used to determine lion diet in the KGNP (Eloff, 1984). Spoor tracking allows for the chronological interpretation of a predators movements and feeding behaviour (Bothma & Le Riche, 1984; Eloff, 1984; Stander et al., 1997). The efficacy of spoor tracking is reliant on a individuals expertise and ability to correctly interpret the spoor, this ability is largely restricted to indigenous people, such as the San people (Stander et al., 1997). In the present-day much of the San peoples traditional ecological knowledge is being lost (Fabricius & de Wet, 2002) and managers and researchers are instead opting to use modern research technologies and techniques (Stander et al., 1997).

Scat (faecal) analysis makes use of hair samples and undigested materials such as hair, hoof, quill and bone samples, extracted from scats to identify the prey species consumed (Ruhe et al., 2008; Tambling et al., 2012). Unlike bones, hairs remain largely undamaged through the digestive process making them particularly useful in identifying the species consumed (Keogh, 1983). To identify which species was consumed, hairs are assessed macroscopically (for colour, width and length), and microscopically, using conventional light microscopy (for cuticular scale patterns and cross sections of the medullary structure), and are compared against a reference library to confirm identification (Keogh, 1983; Douglas, 1989; Mukherjee et al., 1994). Scats may be used to identify small or large prey items and can be used to predict the mass of the prey species consumed if the ingestion to scat relationships are known (Ruhe et al., 2008). Provided that sufficient sample sizes are obtained, the proportions of prey derived from scats can be used to provide an indication of the average diet and make spatial and temporal dietary comparisons (Trites & Joy, 2005).

The technique of scat analysis is limited in that it does not depict the age and the sex of the prey, nor does it indicate if the prey was hunted or scavenged (Breuer, 2005). A number of methods have been used to obtain a representation of biomass consumed including correction factors, linear regression models and numbers of prey detected (Klare et al., 2011). Scat analysis may over represent smaller prey items when incorrect conversion factors are used in converting the dry matter remains obtained from scats to approximations of the quantity of prey matter consumed (Floyd et al., 1978; Ruhe et al., 2008). For lions, biomass estimates derived from scat analysis have been ascribed using the proportion of edible meat of a prey species in relation to its total weight (Funston et al., 1998; Tambling et al., 2012; Périquet et al., 2014). In order to provide an accurate depiction of diet a sufficient sample size of scats needs to be obtained (Mills, 1992; Trites & Joy, 2005). Care must also be taken to avoid pseudoreplication when collecting multiple scats at dens and kill sites or where carnivores deposit multiple scats following a large meal (Marucco et al., 2008). During field collection, a predators scat is usually identified using the size and shape of the faeces, along with other field signs such as spoor, although misidentification of the predator responsible for the deposition of the faeces is still possible and may provide prejudice in results (Farrell et al., 2000).

Recent advances in Global Positioning System (GPS) technology has allowed for investigations into carnivore diet and predator-prey interactions (Anderson & Lindzey, 2003; Sand et al., 2005). GPS cluster analysis provides a cost efficient and accurate method to identify kill sites using clustered location data points from within a given radius (“GPS clusters”) downloaded from predators fitted with GPS collars (Merrill et al., 2010; Tambling et al., 2010). GPS clusters are visited by an observer and investigated to confirm the presence or absence of prey remains (Anderson & Lindzey, 2003). Characteristics of prey remains, such as bones, jaws, horns and hairs may be used to identify species, sex, age and condition of the prey (Sinclair & Duncan, 1972; Tambling et al., 2012; Blecha & Alldredge, 2015). The use of GPS cluster analysis provides information on the time, location and frequency of feeding events (Sand et al., 2005) and is particularly useful in rugged terrains where other methods of determining predator diet, such as direct observations and scat collection, are difficult (Martins et al., 2011; Fröhlich et al., 2012). Furthermore, GPS spatial data can also be used to provide insights into the influence of landscape on predator hunting habits, predator-prey interactions and identify habitat risk zones for livestock (Merrill et al., 2010; Pitman et al., 2012; Cristescu et al., 2015; Latham et al., 2015; Davies et al., 2016).

The GPS cluster technique is limited in that it is biased towards large prey, as small prey are usually consumed too quickly to be detected through GPS cluster analysis (Bacon et al., 2011; Tambling et al., 2012). Additional challenges in the application of the GPS cluster analysis method include, the obstruction of signal from GPS collars in certain habitats which provides errors in the accuracy of GPS localities received, GPS device malfunctions, limited duration of the battery life of the GPS device and difficulties associated with the capture of animals to put on or remove collars (Boitani & Fuller, 2000; Frair et al., 2010; Hebblewhite & Haydon, 2010). Technological advances are rapidly addressing issues that have previously limited biological studies and are creating new opportunities to provide further insights into animal ecology that were not previously possible (Tomkiewicz et al., 2010; Kays et al., 2015; Pimm et al., 2015).

Numerous methods exist to evaluate the diet of predators, with each method having its own logistical and financial challenges and inherent biases. This study defines the present patterns of lion diet in the KGNP through the use of direct observations and indirect methods including lion scat analysis and Global Positioning Systems (GPS) cluster analyses. A comparison of the various techniques used to identify diet is made to determine which method is most effective at defining lion diet in an arid environment. The lion diet profile is then broken-down to assess spatial and seasonal variation in diet.

1.9 Objectives

The main objectives of this study were to:

i. define the present patterns of KGNP lion diet through direct observations and indirect methods using scat and GPS cluster analyses.
ii. parameterise the effectiveness of the respective techniques used in identifying lion diet and determine the amount of effort required to estimate lion diet in the KGNP.
iii. establish if there is any spatial variation in lion diet across the various habitat and regional landscape types represented within the KGNP.
iv. determine if there is any seasonal variation in lion diet in the KGNP.
v. evaluate whether lion diet in KGNP has changed over the last 45 years.

1.10 Structure of the thesis

This thesis is composed of five chapters of which Chapters 3 and 4 have been compiled as stand-alone manuscripts to facilitate publication, with limited alteration, in peer-reviewed journals.

Chapter 2 provides an extended description of the locality and ecology of the KTP, focusing on the study area which falls primarily within the boundaries of the KGNP.

Chapter 3 deals with the present pattern of KGNP lion diet. A combination of direct observations, scat analysis and GPS cluster analysis was used to determine the diet of lion in the KGNP. The respective methods are then compared to assess which method is the most effective in determining lion diet in an arid environment. Data on prey availability, derived from road transect game counts, is then used to identify lion prey preferences.

In Chapter 4, spatial and seasonal variability in lion diet are addressed. Lion diet is related spatially to the different habitat and landscape types. Within the KGNP two broad habitat types (rivers and dunes) were identified and three regional landscape types (north, south and west) were recognized according to the dominant vegetation types represented within each area. A comparison is made between lion diet profiles identified across two ecological seasons (hot-wet and cold-dry). Finally, lion diet is related to seasonal and spatial fluctuations in native prey availability.

In conclusion, Chapter 5 uses the results of Chapters 3 and 4 to assess whether lion diet in KGNP has changed over the last 45 years through critically evaluating the results of past and current studies.

1.11 References

Alexander, K.A., McNutt, J.W., Briggs, M.B., Standers, P.E., Funston, P., Hemson, G., Keet, D. & van Vuuren, M. 2010. Multi-host pathogens and carnivore management in southern Africa. *Comparative Immunology, Microbiology and Infectious Diseases*, 33(3): 249–265.

Anderson, C.R. & Lindzey, F.G. 2003. Estimating cougar predation rates from GPS location clusters. *The Journal of Wildlife Management*, 67(2): 307–316.

Anderson, T.M., Hopcraft, J.G.C., Stephanie, E., Ritchie, M., Grace, J.B. & Olff, H. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology*, 91(5): 1519–1529.

Anonymous. 2008. *Kalahari Gemsbok National Park management plan*. South African National Parks. Pretoria, South Africa.

Bacon, M.M., Becic, G.M., Epp, M.T. & Boyce, M.S. 2011. Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. *Wildlife Society Bulletin*, 35(4): 409–415.

Banerjee, K., Jhala, Y. V., Chauhan, K.S. & Dave, C. V. 2013. Living with Lions: The Economics of Coexistence in the Gir Forests, India. *PLoS ONE*, 8(1): e49457.

Barnett, R., Yamaguchi, N., Barnes, I. & Cooper, A. 2006. The origin, current diversity and future conservation of the modern lion (Panthera leo). *Proceedings of the Royal Society B: Biological Sciences*, 273: 2119–2125.

Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, M.W., Harte, J., Hastings, A., Marquet, P.A., Martinez, N.D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindel, D.P., Revilla, E. & Smith, A.. 2012. Approaching a state shift in Earth's biosphere. *Nature*, 486: 52–58.

Bauer, H. & Iongh, H.H. 2005. Lion (Panthera leo) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*, 43(3): 208–214.

Bauer, H. & Van Der Merwe, S. 2004. Inventory of free-ranging lions Panthera leo in Africa. *Oryx*, 38(01): 26–31.

Bauer, D., Schiess-Meier, M., Mills, D.R. & Gusset, M. 2014. Using spoor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density. *Canadian Journal of Zoology*, 92(2): 97–104.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B., Macdonald, D.W. & Packer, C. 2015. Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, 112(48): 14894–14899

Becker, M.S., Watson, F.G.R., Droge, E., Leigh, K., Carlson, R.S. & Carlson, A. a. 2013. Estimating past and future male loss in three Zambian lion populations. *Journal of Wildlife Management*, 77(1): 128–142.

Beschta, R.L. & Ripple, W.J. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, 142(11): 2401–2414.

Blecha, K.A. & Alldredge, M.W. 2015. Improvements on GPS location cluster analysis for the prediction of large carnivore feeding activities: Ground-truth detection probability and inclusion of activity sensor measures. *PLoS ONE*, 10(9): e0138915.

Boitani, L. & Fuller, T.K. 2000. *Research techniques in animal ecology*. New York: Columbia University Press.

Bond, W.J. 2005. Large parts of the world are brown or black : A different view on the ' Green World ' hypothesis. *Journal of Vegetation Science*, 16(3): 261–266.

Bothma, J.D.P. & Le Riche, E. a. N. 1984. Aspects of the ecology and the behavior of the leopard in the Kalahari desert. *Koedoe*, 27(2): 259–279.

Breuer, T. 2005. Diet choice of large carnivores in northern Cameroon. *African Journal of Ecology*, 43(3): 181–190.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. 2005. State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management*, 58(1): 1–10.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. 2003. Vegetation dynamics on rangelands: A critique of the current paradigms. *Journal of Applied Ecology*, 40(4): 601–614.

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature*, 402(6759): 286–288.

Carlsson, K. 2005. *Mammal communities in the southern Kalahari : differences between land use types and seasons differences between land use types and seasons*. Minor Field Study 112, Uppsala University, Sweden.

Castley, J.G., Knight, M.H., Mills, M.G.L. & Thouless, C. 2002. Estimation of the lion (Panthera leo) population in the southwestern Kgalagadi Transfrontier Park using a capture-recapture survey. *African Zoology*, 37: 27–34.

Celesia, G.G., Townsend Peterson, a., Kerbis Peterhans, J.C. & Gnoske, T.P. 2010. Climate and landscape correlates of African lion (Panthera leo) demography. *African Journal of Ecology*, 48(1): 58–71.

Chardonnet, P. 2002. *Conservation of the African lion: Contribution to a status survey*. International Foundation for the Conservation of Wildlife, France and Conservation Force, USA.

Chardonnet, P., Soto, B., Fritz, H., Crosmary, W., Drouet-Hoguet, N., Mesochina, P., Pellerin, M., Mallon, D., Bakker, L., Boulet, H. & Lamarque, F. 2010. Managing the conflicts between people and lion. Review and insights from the literature and field experience. *Wildlife Management Working Paper (FAO)*.

Coe, M.J., Cumming, D.H. & Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22: 341–354.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turbull, L.A., Macdonald, D.W. & Scmid, B. 2012. Fear of the dark or dinner by moonlight ? Reduced temporal partitioning among Africa' s large carnivores. *Ecology*, 93(1): 2590–2599.

Creel, S. 2010. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15(1): 271–274.

Cristescu, B., Stenhouse, G.B. & Boyce, M.S. 2015. Predicting multiple behaviors from GPS radiocollar cluster data. *Behavioral Ecology*, 26(2): 452–464.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. 2013. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid Savanna. *PLoS ONE*, 8(2). e55182.

Davies, A.B., Tambling, C.J., Kerley, G.I.H. & Asner, G.P. 2016. Effects of vegetation structure on the location of lion kill sites in African thicket. *Plos One*, 11(2): e0149098.

Douglas, R.M. 1989. A new method of cross-sectioning hair of larger mammals. *South African Journal of Wildlife Research*, 19(2): 73–74.

Eloff, P. 1962. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park. part IV. *Koedoe*, 5(1): 128–136.

Eloff, F.C. 1964. On the predatory habits of lions and hyaenas. *Koedoe*, 7(1): 105–112.

Eloff, F.C. 1973. Water use by Kalahari lion Panthera leo vernayi. *Koedoe*, 16: 149–154.

Eloff, F.C. 1984. Food ecology of the Kalahari lion. *Koedoe*, 27(2): 249–258.

Fabricius, C. & de Wet, C.J. 2002. The influence of forced removals and land restitutions on conservation in South Africa. *Conservation and mobile indigenous people: Displacement, forced settlement, and sustainable development*, 10: 149–164.

Farrell, L.E., Roman, J. & Sunquist, M.E. 2000. Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology*, 9: 1583–1590.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Ferreira, S.M., Govender, D., Herbst, M. & Ellis, G. 2012. *Lion demographic, spatial and behavioural profiles as drivers of human wildlife interaction in the Kgalagadi*. Internal report submitted to South African National Parks Board, South Africa.

Floyd, T.J., Mech, L.D. & Jordan, P.A. 1978. Relating wolf scat content to prey consumed. *Journal of Wildlife Management*, 42(3): 528–532.

Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J. & Pedrotti, L. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1550): 2187–200.

Fröhlich, M., Berger, A., Kramer-Schadt, S., Heckmann, I. & Martins, Q. 2012. Complementing GPS cluster analysis with activity data for studies of leopard (Panthera pardus) diet. *South African Journal of Wildlife Research*, 42(2): 104–110.

Funston, P., Mills, M., Biggs, H. & Richardson, P. 1998. Hunting by male lions: ecological influences and socioecological implications. *Animal behaviour*, 56(6): 1333–1345.

Funston, P.J. 2001. *Kalahari Transfrontier lion project: final report*. Endangered Wildlife Trust, Johannesburg, South Africa.

Funston, P.J. 2011. Population characteristics of lions (Panthera leo) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 41: 1–10.

Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, a., Macdonald, D.M., Durant, S., Packer, C., Mosser, a. & Ferreira, S.M. 2010. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281(1): 56–65.

Gittleman, J.L. & Harvey, P.H. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10(1): 57–63.

Green, B., Anderson, J. & Whateley, T. 1984. Water and sodium turnover and estimated food consumption in free-living lions (Panthera leo) and spotted hyaenas (Crocuta crocuta). *Jounal of Mammalogy*, 65(4): 593–599.

Hayward, M.W. & Kerley, G.I.H. 2005. Prey preferences of the lion (Panthera leo). *Journal of Zoology*, 267: 309–322.

Hayward, M.W. & Somers, M.J. eds. 2009. *Reintroduction of top-order predators*. Wiley-Blackwell, London.

Hayward, M.W., Brien, J.O., Hofmeyr, M. & Kerley, G.I.H. 2007. Testing predictions of the prey of lion derived from modeled prey preferences. *The Journal of Wildlife Management*, 71(5): 1567–1575.

Hayward, M.W., Hayward, G.J., Tambling, C.J. & Kerley, G.I.H. 2011. Do lions Panthera leo actively select prey or do prey preferences simply reflect chance responses via evolutionary adaptations to optimal foraging? *PLoS ONE*, 6(9): e23607.

Hebblewhite, M. & Haydon, D.T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 365: 2303–2312.

Heinsohn, R. 1997. Group territoriality in two populations of African lions. *Animal Behaviour*, 53: 1143–1147.

Heinsohn, R. & Packer, C. 1995. Complex cooperative strategies in group-territorial African lions. *Science*, 269: 1260–1262.

Herrmann, E. 2004. *Modelling the effect of human-caused mortality on a lion sub-population using spreadsheets*. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

Holand, Ø., Mysterud, A., Røed, K.H., Coulson, T., Gjøstein, H., Weladji, R.B. & Nieminen, M. 2006. Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. *Proceedings of the Royal Society B: Biological Sciences*, 273: 293–299.

Hopcraft, J.G.C., Anderson, T.M., Perez-Vila, S., Mayemba, E. & Olff, H. 2012. Body size and the division of niche space : food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, 81: 201–213.

Hopcraft, J.G.C., Olff, H. & Sinclair, A.R.E. 2010. Herbivores , resources and risks : alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, 25(2): 119–128.

Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. 2005. Planning for success : Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74: 559–566.

Hunter, L.T.B.B., White, P., Henschel, P., Frank, L., Burton, C., Loveridge, A., Balme, G., Hunter, L.T.B.B., White, P., Henschel, P., Frank, L., Burton, C., Loveridge, A., Balme, G., Breitenmoser, C. & Breitenmoser, U. 2013. Walking with lions: why there is no role for captive-origin lions Panthera leo in species restoration. *Oryx*, 47(1): 19–24.

IUCN. 2015. *IUCN Red List of Threatened Species*. Version 2015-3. www.iucnredlist.org. Downloaded on 07 October 2015.

James, W.H. 2004. Further evidence that mammalian sex ratios at birth are partially controlled by parental hormone levels around the time of conception. *Human Reproduction*, 19(6): 1250–1256.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. 2015. Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240): aaa2478.

Keogh, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research*, 13(4): 91–131.

Kerley, G.I.H., Pressey, R.L., Cowling, R.M., Boshoff, A.F. & Sims-Castley, R. 2003. Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot , South Africa. *Biological Conservation*, 112: 169–190.

Klare, U., Kamler, J.F. & MacDonald, D.W. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review*, 41(4): 294–312.

Knight, M.H. 1995a. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33: 377–394.

Knight, M.H. 1995b. Tsama melons, *Citruffus fanatus*, a supplementary water supply for wildlife in the southern Kalahari. *African Journal of Ecology*, 33: 71–80.

Latham, A.D.M., Latham, M.C., Anderson, D.P., Cruz, J., Herries, D. & Hebblewhite, M. 2015. The GPS craze: Six questions to address before deciding to deploy GPS technology on wildlife. *New Zealand Journal of Ecology*, 39(1): 143–152.

Liebenberg, L., Blake, E., Steventon, L., Benadie, K. & Minye, J. 1998. Integrating traditional knowledge with computer science for the conservation of biodiversity. In *8th International Conference on Hunting and Gathering Societies Foraging and Post-Foraging Societies: History, Politics, and Future*. 26–30.

Loveridge, A.J. & Canney, S. 2009. *African Lion Distribution Modelling Project. Final Report*. Born Free Foundation, Horsham, UK.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134: 548–558.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology*, 283(2): 81–87.

Marucco, F., Pletscher, D.H. & Boitani, L. 2008. Accuracy of scat sampling for carnivore diet analysis: Wolves in the Alps as a case study. *Journal of Mammalogy*, 89(3): 665–673.

Meikle, D.B. & Drickamer, L.C. 1986. Food availability and secondary sex ratio in wild and laboratory house mice (Mus musculus). *Journal of Reproduction and Fertility*, 78: 587–591.

Melville, H.I.A.S., Bothma, J.D.P. & Mills, M.G.L. 2004. Prey selection by caracal in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 34(1): 67.

Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P. & Frair, J.L. 2010. Building a mechanistic understanding of predation with GPS-based movement data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550): 2279–2288.

Miller, B., Dugelby, B., Foreman, D., del Rio, C.M., Noss, R., Phillips, M., Reading, R., Soule, M.E., Terborgh, J. & Willcox, L. 2001. The importance of large carnivores to healthy ecosystems. *Endangered Species Update*, 18(5): 202–210.

Mills, M.G.L. 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. *Koedoe*, 27(2): 281–294.

Mills, M.G.L. 1992. *A comparison of methods used to study food habits of large African carnivores*. In Wildlife 2001: populations: 1112–1123. McCulloch; C. & Barret; R.H. (Eds). London: Elsevier.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 45(2): 127–137.

Mills, M.G.L. & Retief, P.F. 1984. The response of ungulates to rainfall along the riverbeds of the Southern Kalahari 1972-1982. *Koedoe*, 27(2): 129–141.

Mills, M.G.L., Biggs, H.C. & Whyte, I.J. 1995. The relationship between rainfall, lion predation and population trends in African herbivores. *Wildlife Research*, 22: 75–81.

Mills, M.G.L., Wolff, P., Le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion in Kalahari Gemsbok National Park. *Koedoe*, 2: 163–171.

Mukherjee, S., Goyal, S.P. & Chellam, R. 1994. Refined techniques for the analysis of Asiatic lion Panthera leo persica scats. *Acta Theriologica*, 39(4): 425–430.

Nowell, K. & Jackson, P. 1996. *Wild Cats*. Gland, Switzerland: IUCN/SSC Cat Specialist Group.

Noy-Meir, I. 1975. Stability of grazing systems: An application of predator-prey graphs. *The Journal of Ecology*, 63(2): 459–481.

Ogutu, J.O. & Owen-Smith, N. 2005. Oscillations in large mammal populations : are they related to predation or rainfall ? *African Journal of Ecology*, 43: 332–339.

Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organization (Panthers, leo). *Journal of Zoology*, 206(1): 97–112.

Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, 26(4): 107–112.

Owen-Smith, N. & Mills, M.G.L. 2008. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*, 89(4): 1120–1133.

Packer, C., Altizer, S., Appel, M., Brown, E., Martenson, J., O'Brien, S.J., Hofmann-Lehmann, R., Lutz, H. & Lutz, H. 1999. Viruses of the Serengeti : patterns of infection and mortality in African lions. *Journal of Animal Ecology*, 68: 1161–1178.

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(1): 142–153.

Packer, C., Pusey, A.E. & Eberly, L.E. 2001. Egalitarianism in Female African Lions. *Science*, 293: 690–693.

Patterson, B.D. 2007. On the nature and significance of variability in lions (Panthera leo). *Evolutionary Biology*, 34: 55–60.

Pereira, L.M., Owen-Smith, N. & Moleon, M. 2014. Facultative predation and scavenging by mammalian carnivores : seasonal, regional and intra-guild comparisons. *Mammal Review*, 44: 44–55.

Périquet, S., Fritz, H. & Revilla, E. 2014. The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biological Reviews*, 90(4): 1197–1214.

Pimm, S.L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z., Joppa, L., Kays, R. & Loarie, S. 2015. Emerging technologies to conserve biodiversity. *Trends in Ecology & Evolution*, 30(11): 685–696.

Pitman, R.T., Swanepoel, L.H. & Ramsay, P.M. 2012. Predictive modelling of leopard predation using contextual Global Positioning System cluster analysis. *Journal of Zoology*, 288: 222–230.

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(9): 779–791.

Pusey, A.E. & Packer, C. 1987. The evolution of sex-biased dispersal in lions. *Behaviour*, 101(4): 275–310.

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.

Rapport, D.J. & Whitford, W.G. 1999. How ecosystems respond to stress. *BioScience*, 49(3): 193–203.

Rapson, J.A. & Bernard, R.T.F. 2007. Interpreting the diet of lions (Panthera leo); a comparison of various methods of analysis. *South African Journal of Wildlife Research*, 37(2): 179–187.

Reed, J.E. 2004. *Diets of free-ranging Mexican Gray Wolves in Arizona and New Mexico*. M.Sc.Thesis, Texas Technical University, Texas.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L. & Pimm, S. 2013. The size of savannah Africa: A lion's (Panthera leo) view. *Biodiversity and Conservation*, 22(1): 17–35.

Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M.A., O'Brien, S.J., Pospischil, A., Hofmann-Lehmann, R., Lutz, H., Mwamangele, G.L.M., Mgasa, M.N., Machange, G.A., Summers, B.A. & Appel, M.J.G. 1996. A canine distemper virus epidemic in Serengeti lions (Panthera leo). *Nature*, 379: 441–445.

Roxburgh, D.J. 2008. *Prey and range use of lions on Tswalu Kalahari Reserve*. M.Sc. Thesis, University of Pretoria, Pretoria.

Ruhe, F., Ksinsik, M. & Kiffner, C. 2008. Conversion factors in carnivore scat analysis : sources of bias. *Wildlife Biology*, 14(4): 500–506.

Sand, H., Zimmermann, B., Wabakken, P., Andren, H. & Pedersen, H.C. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, 33(3): 914–925.

Schaller, G.B. 1972. *The Serengeti Lion: A study of predator–prey relations*. Chicago: The University of Chicago Press.

Scheel, D. & Packer, C. 1991. Group hunting behaviour of lions: a search for cooperation. *Animal Behaviour*, 41: 697–709.

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

Schiess-Meier, M., Ramsauer, S., Gabanapelo, T. & Konig, B. 2007. Livestock Predation-Insights From Problem Animal Control Registers in Botswana. *The Journal of Wildlife Management*, 71(4): 1267–1274.

Schmitz, O.J., Post, E., Burns, C.E. & Johnston, K.M. 2003. Ecosystem Responses to Global Climate Change : Moving Beyond Color Mapping. *BioScience*, 53(12): 1199–1205.

Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E. & Smith, R.J. 2009. The affects of artificial water availability on large herbivore ranging patterns in savanna habitats : a new approach based on modelling elephant path distributions. *Diversity and Distributions*, 15: 776–783.

Shehzad, W. 2011. *DNA-based diet analyses in carnivores*. P.Hd. Thesis, University of Grenoble, France.

Sheldon, B.C. & West, S.A. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *The American Naturalist*, 163(1). 40-54

Sinclair, A.R.E. & Arcese, P. 2013. Population consequences of predation-sensitive foraging : The Serengeti wildebeest. *Ecology*, 76(3): 882–891.

Sinclair, A.R.E. & Duncan, P. 1972. Indices of condition in tropical ruminants. *East African Wildlife Journal*, 10: 143–149.

Sinclair, A.R.E., Mduma, S. & Brashares, J.S. 2003. Patterns of predation in a diverse predator – prey system. *Nature*, 425: 288–290.

Skinner, J.D. & Chimimba, C.T. 2005. *The mammals of the Southern African Subregion*. Cape Town: Cambridge University Press, Cape Town.

Smit, I.P.J., Grant, C.C. & Devereux, B.J. 2006. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136: 85–99.

Smuts, G.L. 1979. Diet of lions and spotted hyaenas assessed from stomach contents. *South African Journal of Wildlife Research*, 9(1-2): 19–25.

Stander, P.E. 1992a. Cooperative hunting in lions : the role of the individual. *Behavioral Ecology and Sociobiology*, 29(6): 445–454.

Stander, P.E. 1992b. Foraging dynamics of lion in a semi-arid environment. *Canadian Journal of Zoology*, 70: 8–21.

Stander, P.E. 2003. *The ecology of lions and cheetahs re-introduced to the Kalahari Game Lodge, Namibia*. Unpublished report to the Kalahari Game Lodge, Namibia.

Stander, P.E. & Albon, S.D. 1993. Hunting success of lions in a semi-arid environment. *Symposium Zoological Society London*, (65): 127–143.

Stander, P.E., Ghau, I.I., Tsisaba, D., Oma, I.I. & Ui, I.I. 1997. Tracking and the interpretation of spoor: a scientifically sound method in ecology. *Journal of Zoology*, 242(2): 329–341.

Suding, K.N., Gross, K.L. & Houseman, G.R. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, 19(1): 46–53.

Tambling, C.J. & Belton, L.E. 2009. Feasibility of using proximity tags to locate female lion Panthera leo kills. *Wildlife Biology*, 15: 435–441.

Tambling, C.J., Laurence, S.D., Bellan, S.E., Cameron, E.Z., Toit, J.T. & Getz, W.M. 2012. Estimating carnivoran diets using a combination of carcass observations and scats from GPS clusters. *Journal of Zoology*, 286(2): 102–109.

Tomkiewicz, S.M., Fuller, M.R., Kie, J.G. & Bates, K.K. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365: 2163–2176.

Trites, A.W. & Joy, R. 2005. Dietary analysis from fecal samples: How many scats are enough? *Journal of Mammalogy*, 86(4): 704–712.

Trivers, R.L. & Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068): 90–92.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90(1): 23–30.

Van der Wal, R. 2006. Do herbivores cause habitat degradation or vegetation state transition ? Evidence from the tundra. *Oikos*, 114(1): 177–186.

Van Rooyen, M.W., Van Rooyen, N., Bothma, J.D.P. & Van den Berg, H.M. 2008. Landscapes in the Kalahari Gemsbok National Park, South Africa. *Koedoe*, 50(1): 99–112.

Van Rooyen, N., Bezuidenhout, D., Theron, G.K. & Bothma, J.D.P. 1990. Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe*, 33(1): 63–88.

Van Vuuren, J.H., Herrmann, E. & Funston, P.J. 2005. Lions in the Kgalagadi Transfrontier Park: Modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171.

Verlinden, A. 1998. Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, 36(117): 128.

Vorhies, D. & Vorhies, F. 1993. *Introducing lion into Pilanesberg: An economic assessment*. Eco Plus (Pty) Ltd. Unpublished report to Bophuthatswana National Parks & Wildlife Management Board, Johannesburg.

Whitman, K., Starfield, A.M., Quadling, H.S. & Packer, C. 2004. Sustainable trophy hunting of African lions. *Nature*, 428: 175–178.

Williamson, D. & Williamson, J. 1984. Botswana’s fences and the depletion of Kalahari wildlife. *Oryx*, 18(04): 218–222.

Williamson, D. & Williamson, J. 1988. Wildebeest migration in the Kalahari. *African Journal of Ecology*, 26(4): 269–280.

CHAPTER 2

STUDY AREA

2.1 Introduction

The Kalahari Gemsbok National Park (KGNP, 9 591 km^2) is situated in the north-western region of South Africa and is bordered by Namibia to the west and Botswana in the east. Together with Botswana's Gemsbok National Park (GNP, 27 672 km^2) the two protected areas constitute the Kgalagadi Transfrontier Park (KTP, 37 263 km^2) (Figure 2.1). The KGNP was proclaimed as a national park in 1931. Following on, in 1938 the British Government proclaimed a game reserve to the east of KGNP, in Botswana, which was further extended in 1971 to include the Mabuasehube Game Reserve and became known as the GNP. On the 12 May 2000 the presidents of South Africa and Botswana signed a treaty that declared the KTP as the first Transfrontier Conservation Area in Africa (Anonymous, 2008). Including Botswana's Wildlife Management Areas (WMA) to the east of the KTP (Figure 2.2), the area covers approximately 80 000 km^2, rendering it one of the largest conservation areas in the world (Herholdt & Anderson, 2006).

The expanse and absence of fences separating the KGNP and the GNP makes it possible for wildlife to migrate across the KTP (Shroyer et al., 2001). Furthermore, through the use of the corridors provided by the WMA's in Botswana, wildlife are able to migrate as far as the Central Kalahari Game Reserve (Williamson & Williamson, 1988; Verlinden, 1998) (Figure 2.2).

The present study was conducted primarily in the KGNP, although operations extended into a narrow section of the GNP adjacent to the KGNP (Figure 2.3). To investigate the spatial variation in lion diet, the study area was zoned according to the dominant habitat types and regional landscape types represented within the study area.

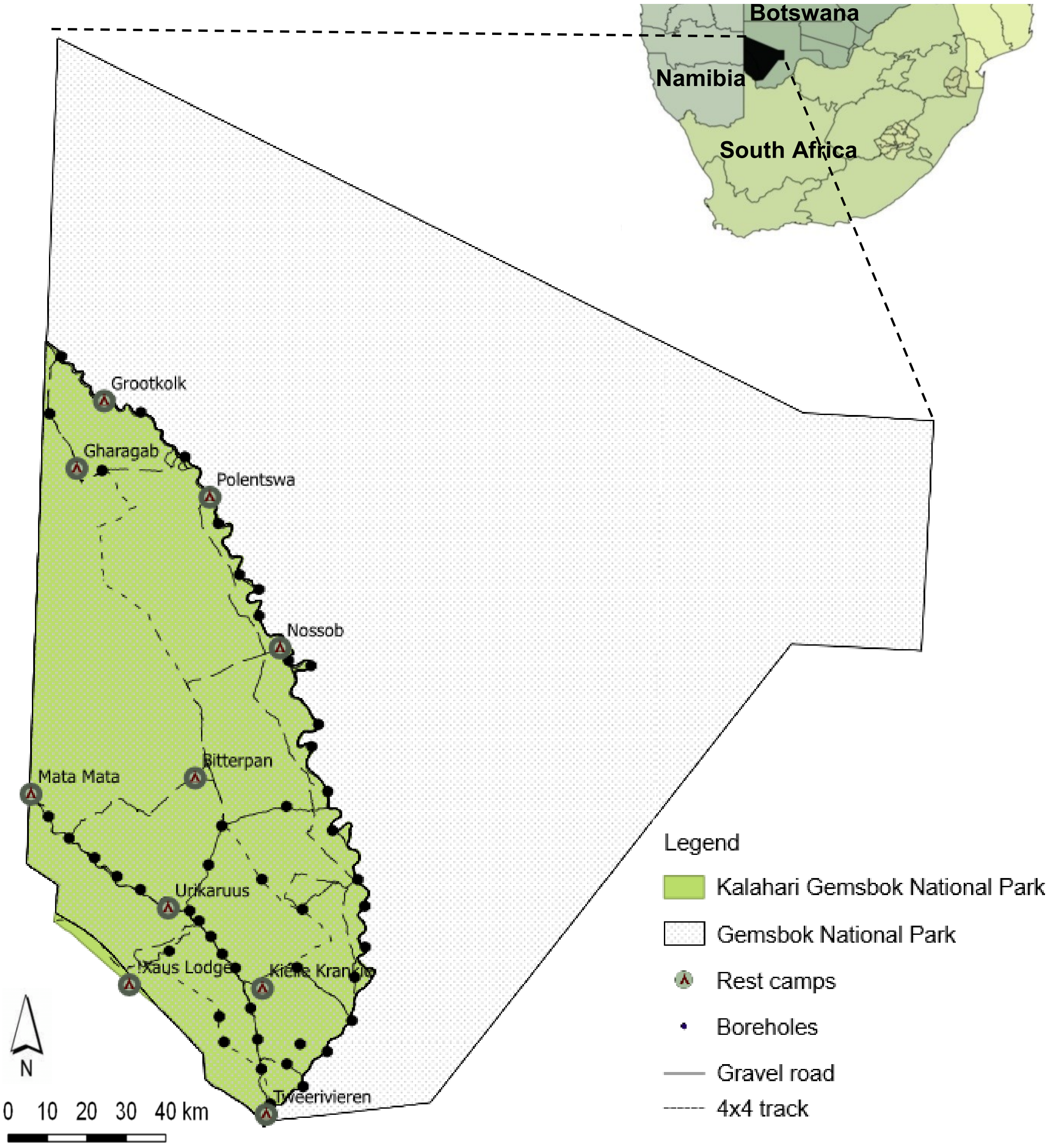


Figure 2.1 The Kalahari Gemsbok National Park in South Africa together with the Gemsbok National Park in Botswana make up the Kgalagadi Transfrontier Park. Map was created using QGIS software (Quantum GIS Development Team, 2016).

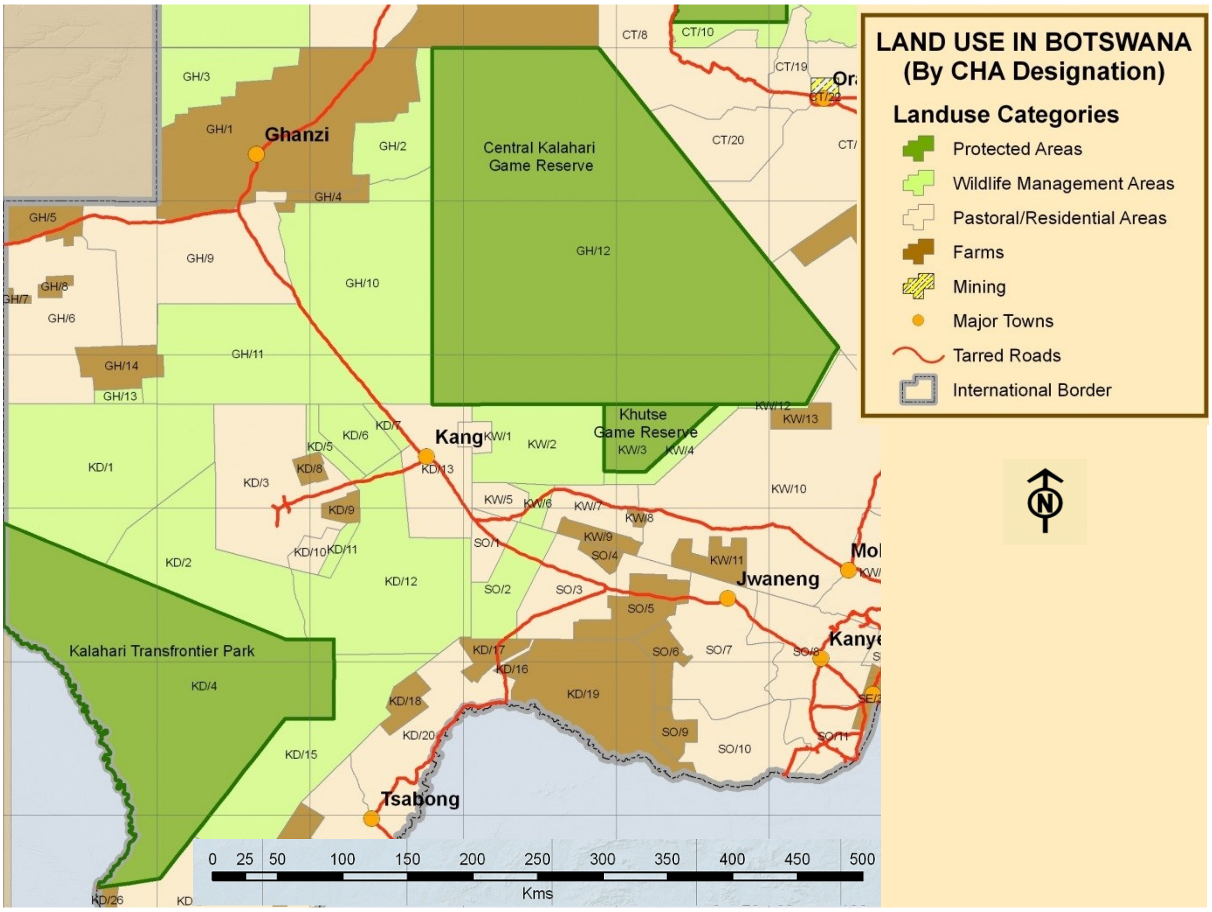


Figure 2.2 Land use in Botswana indicating the extent to which the Wildlife Management Areas link the KTP and Central Kalahari Game Reserve (Ngami Data Services, 2012).

2.2 Locality

The KTP forms part of the Kalahari Desert that is considered the largest sand filled basin in the world (Eloff, 1984). The Kalahari Desert stretches from the Orange Riverbed in the Northern Cape Province of South Africa to northern Botswana and eastern Namibia (Thomas & Shaw, 1991). It is underlain by the Kalahari Group of sedimentary rocks which cover over 2.5 million km², encompassing most of Botswana, Namibia, South Africa, Angola, Zambia and Zimbabwe (Haddon & McCarthy, 2005).

This study was primarily aimed at investigating lion diet within the KGNP and thus the greater part of the study was focused in this area between 24° 15’ S and 26° 30’ S, and 20° 00’ E and 20° 45’ E. The study area was extended to include a 25 km band east of the Nossob riverbed into the GNP, in accordance with `the movements and home ranges obtained from seven lions that were fitted with GPS tracking collars (Figure 2.3). Therefore, the total study area encompassed approximately 15 397 km^2.

Figure 2.3 The study area in which the lion data were collected was primarily in South Africa's KGNP, although operations extended a 25 km band east of the Nossob riverbed into Botswana's GNP.

2.3 Climate

The term Kalahari is derived from the Setswana word “Kgalagadi” and means “the great thirst” (Eloff, 1984; Haddon, 2005). The Kalahari system has been described as a desert (Leistner, 1967; Wergner, 1986; Eriksson et al., 1989), semi-desert (Keith & Renew, 1975; Bothma & Le Riche, 1984; Mills & Retief, 1984a) as well as a semi-arid area (Van Rooyen et al., 1994; Knight, 1995). The Kalahari is often referred to as the “Kalahari Desert” which is likely to be a more accurate classification as its characteristics are representative of a desert system with irregular summer rainfall (< 250 mm) and dry winters (Mills, 2015). Deserts are characterized by areas with, high summer temperatures, evaporation which exceeds precipitation, high rainfall variability, prominent winds, clear skies over 70% of the time and low (< 30%) humidity (Laity, 2008).

Rainfall in the KGNP is highly erratic (Bergstrom & Skarpe, 1999), falling predominantly in summer between January to April. The mean annual rainfall varies between 185 mm to 230 mm (Van Rooyen et al., 2008) with occasional drought years (Knight, 1995). Annual rainfall varies longitudinally across the KGNP from 150 mm in the southwest to 250 mm in the north (Grist et al., 1997; Anonymous, 2008). Rain often falls in short bouts of high intensity, isolated thunderstorm events (Anonymous, 2008) and because of this, annual rainfall can be highly inconsistent varying between < 100 mm to > 700 mm at any given location (Van Rooyen et al., 2008). Evapotranspiration rates are high (> 3 000 mm per annum) and natural surface water occurs only for short periods after heavy rain (Mucina & Rutherford, 2006). During the study period the mean annual rainfall in the KGNP amounted to approximately 220 mm (range 129 – 266) between 2013 and 2015 (Figure 2.4).

Temperatures are extreme and can fluctuate greatly on a daily as well as seasonal basis (Mills & Retief, 1984b). June and July are the coldest months and temperatures can reach a winter minimum of - 10.3°C, whereas in summer January is commonly the hottest month with a maximum temperature of 45.4°C (Leistner, 1967; Van Rooyen et al., 1990). The two ecological seasons identified in this study include the hot-wet season, November to April, and the cold-dry season, May to October (Bergstrom & Skarpe, 1999; Van Rooyen et al., 2008)

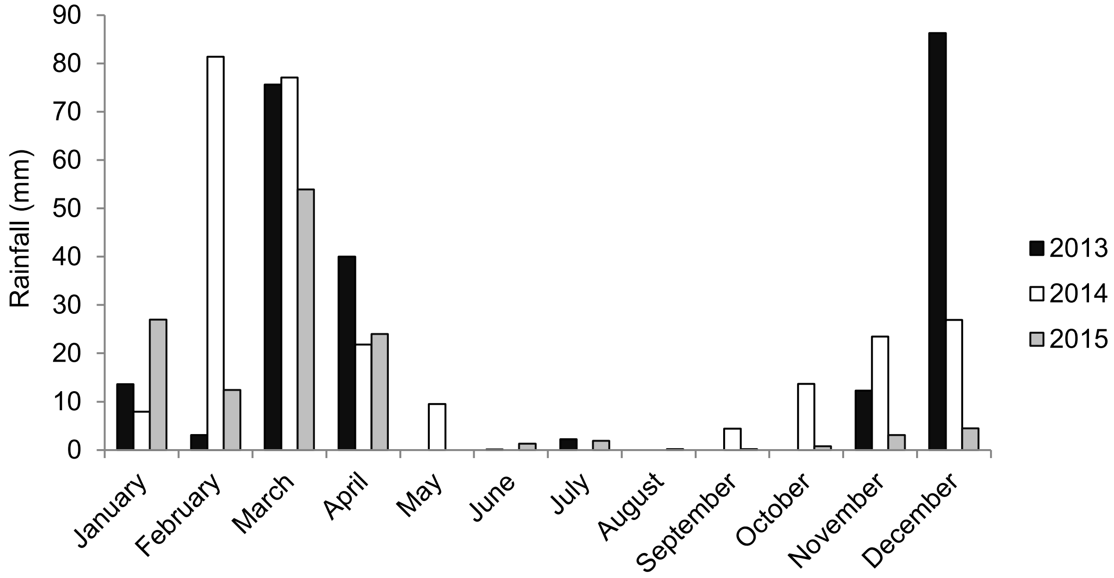


Figure 2.4 Monthly rainfall figures for 2013, 2014 and 2015 obtained from the weather station at Twee Rivieren.

2.4 Topography and geology

All basal material in the KGNP is from the Kalahari Group which is underlain by the Karoo Sequence (Malherbe, 1984). The Kalahari Group can be classified into gravels belonging to the Wessels Formation, red clay from the Budin Formation, sandstones from the Eden Formation, calcretes from the Mokalanen Formation, clayey limestone from the Lonely Formation, brown to white fine grained sands from the Goeboe Goeboe Formation and the most dominant and widespread sands of the Gordonia Formation (Malherbe, 1984).

Tectonic uplift in the Pliocene era exposed the sedimentary rocks to erosion. Over time through continued aeolian processes this formed sand which was transported and deposited to form the extensive dune fields that are present today (Haddon & McCarthy, 2005). The white, pink or red Kalahari sands are generally deep, poorly structured and devoid of most of the major and micro nutrients, although grazing and bush encroachment somewhat increase soil nutrients (Dougill & Thomas, 2004). The altitude in the KGNP ranges from 870 to 1 080 meters above sea level (Stapelberg et al., 2001).

2.5 Habitats

For the purposes of this study the KGNP was divided into two dominant habitat types, namely the dune habitats and riverbed habitats (hereafter referred to as dunes and riverbeds). The KGNP comprises of vast expanses of homogenous sandy areas or dune fields which are bisected by two dry riverbeds. The dune and riverbed areas vary significantly according to topography and vegetation composition (Leistner, 1967). Dunes made up 85% of the study area and the riverbeds, for which we incorporated a 2.5 km buffer area, covered the remaining 15% (Figure 2.5).

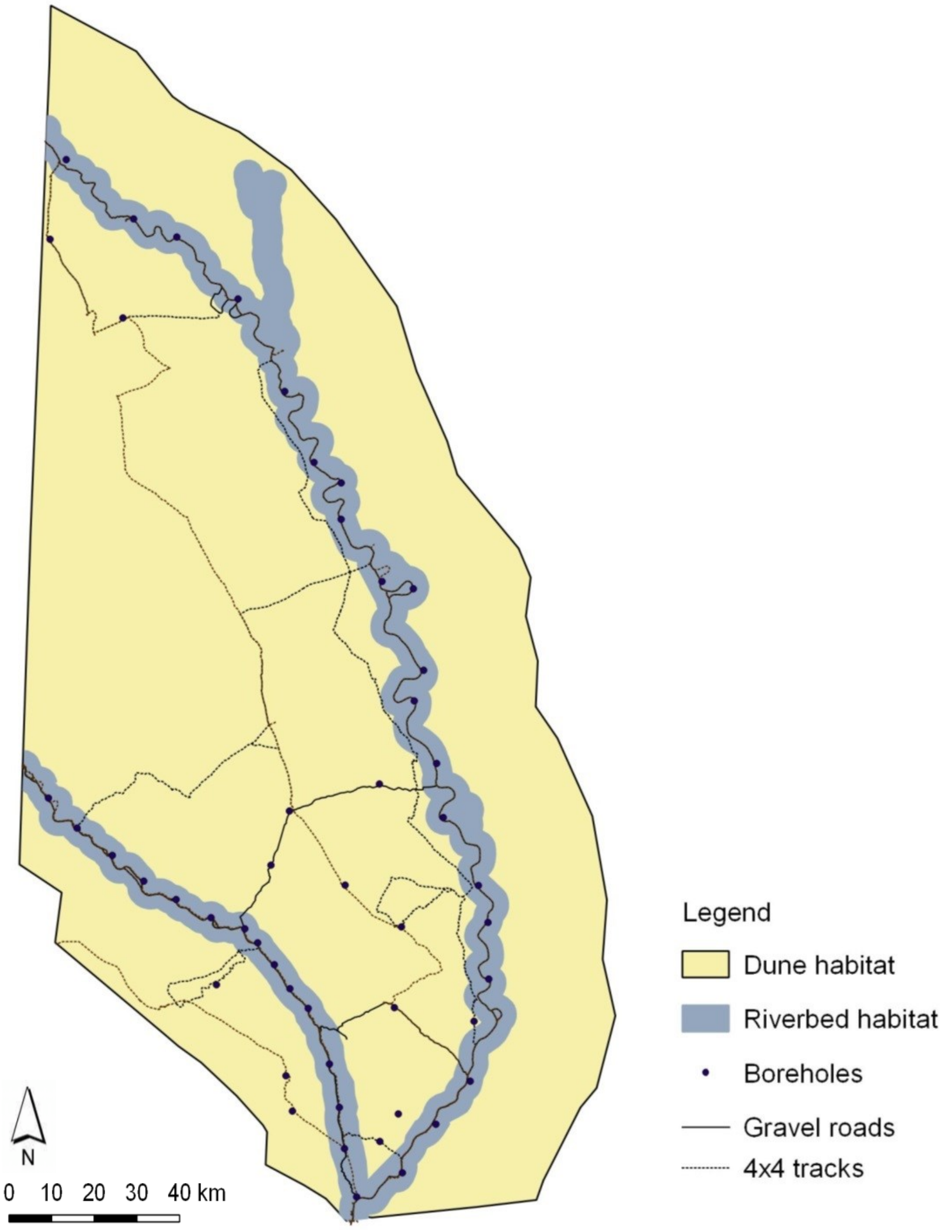


Figure 2.5 The areas occupied by the dune and riverbed habitat types in the KGNP.

2.5.1 Dunes

Most of the KGNP consists of undulating dunes (Van Rooyen et al., 2008) and are covered with moderately dense vegetation which restricts the mobility of sediments (Wiggs et al., 1995). Fluvial and aeolian processes during glacial periods were primarily accountable for dune formation (Heine, 1989). Long parallel dunes are characteristic of the south-western section of the KTP (Leistner, 1967) (Figure 2.6). These linear dunes form continuous dune fields as opposed to discrete dunes (Bullard et al., 1995). High dunes of up to 20 m are found in the south of the KGNP and along riverbeds and decrease in height northwards where they typically reach between six and nine meters high (Van Rooyen et al., 2008). Thirteen artificial waterholes are provided in the dune habitat (Figure 2.5).

Dune orientation in the north of the park is caused by northwest and northerly winds, whereas in the south, westerly winds dictate dune formation. The central area of the park is a transitional zone between the prevailing winds (Heine, 1989). Bare dunes, which are formed as a result of fire, drought or grazing, are subject to three times more soil movement from wind than vegetated dunes which remain relatively stable (Wiggs et al., 1994) (Figure 2.7). Sand grain size is coarser on the dune crests and finer in the inter-dune valleys where they are sheltered from movement by wind (Lancaster, 1986). Sand depth is relatively shallow in the dune valleys particularly in the north and western sections of the KTP (Leistner, 1967).

The dune landscapes can be classified into areas sparsely vegetated with trees and shrubs, bare dunes, flat grasslands and tree savannahs (Bothma & De Graaff, 1973). The dominant vegetation includes grasses (*Schmidtia kalahariensis, Stipagrostis amabilis, S. uniplumis, S. ciliata*, *Eragrostis lehmanniana, Centrapodia glauca*), scattered trees (*Vachellia erioloba, V. haematoxylon* and *Boscia albitrunca*) and shrubs (*Rhigozum trichotomum* and *Senegalia mellifera*). Within the dune fields there are areas of highly irregularly structured dunes (Van Rooyen et al., 2008).

Figure 2.6 Parallel dune fields covered with moderately dense vegetation are typical of the southern western section of the KGNP.

Figure 2.7 Bare dunes are formed as a result of fire, drought or grazing.

2.5.2 Riverbeds

The dune fields are bisected by two fossil riverbeds, namely the Auob and the Nossob riverbeds as well as scattered pans (Van Rooyen & Van Rooyen, 1998; Herholdt & Anderson, 2006). There is no permanent natural source of water in the riverbeds, although surface water is available for short periods after heavy rainfall (Knight, 1995). Both riverbeds seldom flow, with the last floods recorded in 1988 for the Nossob and in 2000 for the Auob (Mills & Mills, 2013). The sources of both the Auob and Nossob riverbeds are in the Anas Mountains, Namibia. Seventeen artificial waterholes (boreholes) are provided in the Auob and 24 in the Nossob riverbeds (Mills & Retief, 1984b; Knight, 1995) (Figure 2.5).

Calcretes and sandstones form outcrops and terraces along the riverbeds (Haddon, 2005). The Nossob varies in width (100 – 1000 m) forming a narrow channel through the calcretes ridges in the south (Figure 2.8) and becoming broader and more shallow in the north (Bothma & De Graaff, 1973; Mills & Retief, 1984b) (Figure 2.9). In contrast the Auob riverbed has steep-sided limestone banks (30 – 40 m deep) and forms a narrow channel (100 – 500 m wide) along its course in the KGNP (Leistner, 1967; Mills & Retief, 1984b) (Figure 2.10). Sands in the riverbeds have a higher lime content and form a shallow layer over the underlying calcretes (Leistner, 1967). The riverbeds form a confluence in the south of the KGNP at Saamevloeing (Heine, 1989) (Figure 2.3).

Figure 2.8 The Nossob riverbed forms a narrow channel through the calcretes ridges in the south of the KGNP.

Figure 2.9 The Nossob riverbed is broader and shallower in the northern KGNP than it is in the southern section.

Figure 2.10 The Auob riverbed has steep-sided limestone banks and forms a narrow channel along its course in the KGNP.

2.6 Vegetation

The KGNP is situated in the Kalahari Duneveld and Eastern Kalahari Bushveld Bioregions of the Savannah Biome (Mucina & Rutherford, 2006). The vegetation of the south-western Kalahari is relatively homogenous (Van Rooyen et al., 2008) owing to the uniform parent material (Scholes, 1990). Changes in the dominance and structuring of plant species are related to terrain morphology and soil characteristics (Van Rooyen et al., 2008). Species richness is lower on the dune crests and slopes than in the inter-dune valleys (Leistner, 1967).

The vegetation of the South Western Kalahari has formed the basis of many studies and has been described numerous times over several decades (Pole-Evans, 1936; Acocks, 1953; Brynard, 1958; Leistner, 1959a; Leistner, 1959b; Giess, 1971; Bothma & De Graaff, 1973; Leistner & Werger, 1973; Coetzee & Werger, 1975; Wergner, 1986; Van Rooyen et al., 1988; Van Rooyen & Van Rooyen, 1998; Mucina & Rutherford, 2006). The most recent review was conducted in conjunction with the refined mapping of the vegetation of South Africa and identifies seven vegetation types within the KGNP (Mucina & Rutherford, 2006). These include the Nossob Bushveld, Gordonia Kameeldoring Bushveld, Gordonia Duneveld, Auob Duneveld, Gordonia Plains Shrubland, Southern Kalahari Mekgacha and Southern Kalahari Salt Pans (Mucina & Rutherford, 2006) (Figure 2.11). No detailed map exists for the vegetation types of Botswana’s GNP, although it was noted that vegetation types immediately west of the Nossob riverbed were largely mirrored in the buffer zone to the east of the Nossob riverbed, based on visual observations (Figure 2.11). A brief description of each of the vegetation types presented in the study area is provided.

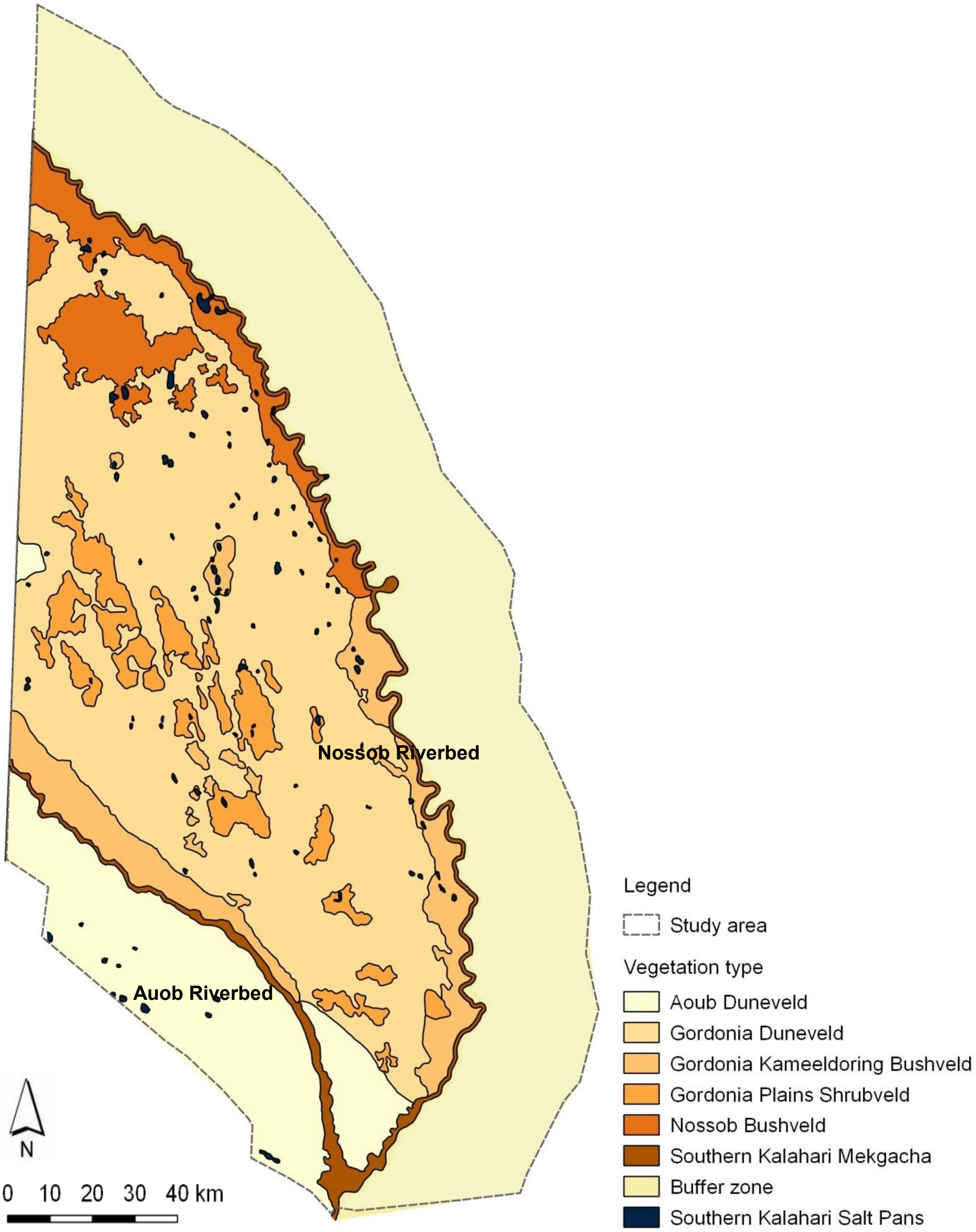


Figure 2.11 The vegetation types of the Kalahari Gemsbok National Park. Vegetation types immediately west of the Nossob riverbed were largely mirrored in the buffer zone to the east of the Nossob riverbed (pers. obs., 2013).

2.6.1 Nossob Bushveld

In the KGNP the Northern Bushveld is distributed along the border of the Nossob riverbed, extending from approximately Marie se Draai to Unions End. Areas of Nossob Bushveld can also be found further from the riverbeds in areas such as Dankbaar and Ou Gharagab (Mucina & Rutherford, 2006) (Figure 2.11).

The Northern Bushveld vegetation type is characterised by open bushveld with grassy plains and a conspicuous tree component (Figure 2.12). Common species include, Grasses: S*chmidtia kalahariensis, Stipagrostis uniplumis, Centropodia glauca* and *Eragrostis biflora.* Shrubs: *Grewia flava* and *Rhus tenuinervis*; Trees*: Acacia erioloba, A. luederitzii and Boscia albitrunca* (Mucina & Rutherford, 2006).

Figure 2.12 The Nossob Bushveld vegetation type between Union's End and Ou Gharagab, characterised by open bushveld with grassy plains and a conspicuous tree component.

2.6.2 Gordonia Plains Shrubland

In the KGNP the Gordonia Plains Shrubveld vegetation type is distributed in patches between the Nossob and Auob riverbeds, occurring at a higher density in the northern areas (Mucina & Rutherford, 2006) (Figure 2.11).

The Gordonia Plains Shrubveld vegetation is characterised by open grasslands with few dunes and scattered shrubs (Figure 2.13). Common species include, Grasses: *Aristida meridionalis, Centropodia glauca, Eragrostis lehmanniana, Schmidtia kalahariensis, Brachiaria glomerata* and *Stipagrostis uniplumis*; Shrubs: *Rhigozum trichotomum, Grewia flava, Nolletia arenosa* and *A. haematoxylon*; Trees: *Acacia erioloba, Indigofera poliotes* and *A. mellifera subsp. detinens* (Mucina & Rutherford, 2006).

Figure 2.13 Gordonia Plains Shrubland comprising of the characteristic open grasslands with few scattered shrubs.

2.6.3 Gordonia Duneveld

Gordonia Duneveld is the most widely distributed and abundant vegetation type in the northern and south eastern sections of the KGNP (Mucina & Rutherford, 2006) (Figure 2.11).

The Gordonia Duneveld is characterised by vegetated parallel dunes and dune valleys. Grasses grow predominantly on the dune crests, particularly *Stipagrostis amabilis*, whereas shrubs occur more frequently in the dune valleys (Figure 2.14). Common species include, Grasses: *Stipagrostis amabilis, S. ciliata, S. obtusa, S. uniplumis, Schmidtia kalahariensis, Brachiaria glomerata, Centropodia glauca* and *Eragrostis lehmanniana*; Shrubs: *Rhigozum trichotomum, Acacia haematoxylon, Grewia flava, Aptosimum albomarginatum* and *Monechma incanum*; Trees: *Acacia mellifera* (Mucina & Rutherford, 2006).

Figure 2.14 Gordonia Duneveld in the southern KGNP with the characteristic grass, *Stipagrostis amabilis,* growing on the dune crest and shrubs occupying the dune slopes and streets.

2.6.4 Gordonia Kameeldoring Bushveld

In the KGNP the Gordonia Kameeldoring Bushveld vegetation type is distributed along a strip to the east of the Auob Riverbed between Mata Mata and Gemsbokplien and on the western side of the Nossob Riverbed between Marie se Draai and Rooiputs. A few isolated patches are also found further from the riverbeds (Mucina & Rutherford, 2006) (Figure 2.11).

Gordonia Kameeldoring Bushveld vegetation type is characterised by dunes and dune valleys with a less pronounced grassy layer, and strewn trees and shrubs that occupy the dune valleys (Figure 2.15). Common species include, Grasses: *Aristida meridionalis, Centropodia glauca, Eragrostis lehmanniana, Schmidtia kalahariensis, Brachiaria glomerata, Stipagrostis ciliata, S. obtusa* and *S. uniplumis*; Shrubs: *A. haematoxylon, A. mellifera, Rhigozum trichotomum, Ehretia rigida, Grewia flava, Rhus tenuinervis* and *Aptosimum albomarginatum;* Trees: *Acacia erioloba* and *Boscia albitrunca* (Mucina & Rutherford, 2006).

Figure 2.15 Gordonia Kameeldoring Bushveld between Dikbaardskolk and Eland waterhole characterised by dunes and dune valleys with a less pronounced grassy layer and trees and shrubs occupying the dune valleys.

2.6.5 Auob Duneveld

In the KGNP the Auob Duneveld vegetation type is found largely to the west of the Auob Riverbed, as well as between the southern sections of the Nossob and Auob Riverbeds near to their confluence (Mucina & Rutherford, 2006) (Figure 2.11).

The Auob Duneveld vegetation type is characterised by open dune fields with scattered grasses and low shrubs (Figure 2.16). Common species include, Grasses: *Schmidtia kalahariensis, Stipagrostis ciliata, S. amabilis S. uniplumis, Brachiaria glomerata, Centropodia glauca* and *Eragrostis trichophora*; Shrubs: *Acacia haematoxylon, A. mellifera, Rhigozum trichotomum* and *Grewia flava*; Trees: *Acacia erioloba* and *Boscia albitrunca* (Mucina & Rutherford, 2006).

Figure 2.16 The Auob Duneveld vegetation type between Tsama Pan and !Xaus Lodge, characterised by open dune fields with scattered grasses and low shrubs.

2.6.6 Southern Kalahari Mekgacha

The Southern Kalahari Mekgacha is the term used to describe the riverbed component of the KGNP and includes the Auob and Nossob riverbeds (Mucina & Rutherford, 2006) (Figure 2.11).

The vegetation composition varies somewhat between the different sections of the Nossob and Auob Rivers. Typically the riverbeds include a grass layer, scatter trees, predominantly *Acacia erioloba* and *Acacia haematoxylon* (in the Auob riverbed) and are rich in forbs such ad *Tribulus zeyheri* (Figure 2.17). Common species include, Grasses: *Chloris virgata, Panicum coloratum, Schmidtia kalahariensis Eragrostis porosa, E. bicolor, E. porosa, E. rotifer* and *Enneapogon desvauxii*; Trees: *Acacia erioloba A. haematoxylon*; Shrubs: *Lebeckia linearifolia* and *Rhigozum trichotomum* (Mucina & Rutherford, 2006).

Figure 2.17 The Southern Kalahari Mekgacha includes the riverbed component of the KGNP which is characterised by a grass layer, scatter trees, and is rich in forbs.

2.6.7 Southern Kalahari Salt Pans

The Southern Kalahari Salt Pans is the collective term used to describe the vegetated and bare pans found in the KGNP. One hundred and twenty six of the larger pans have been identified and mapped in the KGNP (Mucina & Rutherford, 2006) (Figure 2.11), although there are estimated to be over 1000 pans scattered across the KTP (Mills & Mills, 2013).

Pans are generally between 200 and 2000 m in diameter and are shallow, rounded depressions with a bare silt and clay base that is able to hold water periodically after rain (Bergstrom & Skarpe, 1999). The pans cover an area of approximately 0.28% of the KGNP (Van Rooyen et al., 2008) and increase in abundance from the centre of the park towards the north and east into Botswana (Stapelberg, 2007). Two types of pans are recognised, pans that are sparsely vegetated with grass (Figure 2.18), and pans devoid of vegetation which are often referred to as salt pans (Leistner, 1967; Van Rooyen & Van Rooyen, 1998; Mucina & Rutherford, 2006) (Figure 2.19). The pans high alkaline and mineral rich soils attract game which use them as “salt licks” (Carlsson, 2005). Vegetated pans have a lower mineral content then bare pans (Van Rooyen et al., 2008).

Southern Kalahari Salt Pans are characterised by white, calcareous, alkaline soils that are either bare or sparsely vegetated with grasses and dwarf shrubs. Common species include, Grasses: *Sporobolus rangei, Stipagrostis ciliata, S. obtusa Eragrostis echinochloidea, E. truncata, E. porosa* and *Enneapogon desvauxii*; Shrubs: *Rhigozum trichotomum, Monechma incanum, Zygophyllum tenue, Salsola etoshensis, S. namaqualandica, Eriocephalus aspalathoides* and *Lycium cinereum* (Van Rooyen et al., 2008).

.

Figure 2.18 Southern Kalahari Salt Pans can be sparsely vegetated with grass and dwarf shrubs.

Figure 2.19 Southern Kalahari Salt Pans that are devoid of vegetation are often referred to as salt pans.

2.7 Herbivore and carnivore assemblages

2.7.1 Herbivores

The stringent environmental conditions of the Kalahari limit ungulate diversity and abundance (Mills, 2015). The most abundant ungulate species found in KTP are adapted to arid conditions (Stapelberg et al., 2001) and include gemsbok*, Oryx gazella,* springbok, *Antidorcas marsupialis,* red hartebeest, *Alcelaphus buselaphus,* eland, *Tragelaphus oryx,* blue wildebeest, *Connochaetes taurinus* steenbok, *Raphicerus campestris,* and common duiker, *Sylvicapra grimmia* (Mills & Retief, 1984b). Other common resident species include ostrich, *Struthio camelus,* porcupine, *Hystrix africaaustralis,* springhare, *Pedetes capensis,* and hares, *Lepus spp.* (Mills, 1984).

Pans and riverbeds are the most intensively utilized habitats as they support a higher edible biomass of more nutritious short growing vegetation, which attracts increased densities of springbok, gemsbok, blue wildebeest and red hartebeest (Bergstrom & Skarpe, 1999). Another attraction of herbivores to the riverbeds and pans are areas of compressed clay soils which are used as natural licks by herbivores to supplement their diet (Stapelberg et al., 2001). This is further accentuated by the provision of artificial waterholes (Mills & Retief, 1984b; Knight, 1995). Overall herbivore numbers in the KGNP increase during the wet season with the animals congregating particularly within the riverbeds (Mills & Retief, 1984b) and dispersing again during the dry season (Mills & Retief, 1984b; Bergstrom & Skarpe, 1999).

The most recent estimates from aerial census data of large herbivores numbers in the KGNP indicate that gemsbok are the most abundant species in the KGNP with an estimated population of just over 8000 individuals (Ellis & Herbst, 2013). Gemsbok are sedentary in the KTP (Mills, 2015) and are the most widely and evenly distributed of the large herbivores across all landscape types, habitat types and seasons in the KTP (Leistner, 1959a; Eloff, 1962; Van Der Walt et al., 1984). Gemsbok are well adapted to arid environments and can survive long periods without access to water (Skinner & Chimimba, 2005) and therefore their distribution and movements in the KGNP are independent of the artificial water points provided (Mills & Retief, 1984a; Van Der Walt et al., 1984). Gemsbok numbers concentrate in the riverbeds and pans following grass growth in response to rainfall and disperse again in dry conditions once the grass subsides (Mills & Retief, 1984b; Bergstrom & Skarpe, 1999). Gemsbok alter their diet seasonally according to food availability, primarily grazing during the wet season but include a higher percentage of browse in their diets during the dry season (Leistner, 1959a; Lehmann et al., 2013). The physiological and behavioural adaptations of gemsbok to arid environments make them particularly resilient to die offs during periods of drought (Knight, 1995; Verlinden, 1998).

Springbok are the second most abundant herbivore species in the KGNP with an estimated population of just under 3000 individuals (Ellis & Herbst, 2013). Morphological and behavioural adaptations such as selective feeding, high birth rates, feeding time and seeking shade make springbok well-adjusted to surviving in arid areas (Skinner et al., 1984; Mills & Haagner, 1989; Nagy & Knight, 1994; Stapelberg et al., 2001). Springbok in the Kalahari region have been classified as a sub-species namely, *Antidorcas marsupialis hofmeyri,* according to their larger body size (males 42 kg, females 35 kg) and subtle differences in pelage colouration (Skinner & Chimimba, 2005). Mass migrations of springbok through the KTP were reported historically (Eloff, 1961). Due to manmade barriers mass migrations of springbok no longer occur, although migrations of a smaller scale are still known to take place (Child & Le Richie, 1969; Verlinden, 1998). In the KGNP springbok are largely restricted to the open riverbeds and pans, which is primarily thought to be due to diet preferences and an anti-predatory strategy (Mills & Retief, 1984b; Verlinden, 1998; Stapelberg et al., 2001).

Blue wildebeest population numbers in the KGNP are estimated around 1440 individuals (Ellis & Herbst, 2013). Of all the herbivores represented in the KGNP, blue wildebeest are the most water dependant species (Knight, 1995) and historically used to migrate out of the KTP during dry periods to find sufficient, good-quality graze and water (Williamson & Williamson, 1988). Large scale migrations of wildebeest into and out of the KTP have been severely inhibited by fences, which has had a negative influence on the overall wildebeest population across the Kalahari (Spinage, 1992). Due to the provision of artificial waterholes blue wildebeest have now instead established resident herds in the KGNP and occur mostly within the riverbed areas (Eloff, 1966; Knight, 1995), close to waterholes (Mills & Retief, 1984b). Blue wildebeest occurring in the riverbeds are sedentary but those occupying the dune areas are more nomadic (Eloff, 1966; Mills, 2015). Their water dependence coupled with being strictly grazers make wildebeest particularly vulnerable to die-off during droughts (Williamson & Williamson, 1988; Spinage, 1992; Knight, 1995).

Just over 1 100 red hartebeest were counted in the KGNP during 2013 (Ellis & Herbst, 2013) and are found predominantly within the dune habitats (Van Der Walt et al., 1984). Red hartebeest migrate seasonally across the KTP and their numbers in the KGNP reach a peak in the Nossob riverbed between February and March (Mills & Retief, 1984b). Hartebeest occur at notably lower densities in the Auob riverbed than in the Nossob riverbed (Mills & Retief, 1984b; Knight, 1995). Hartebeest are strictly grazers and are drawn to areas with new grass growth that is stimulated by rainfall or in areas that have been recently burnt (Van Der Walt et al., 1984; Skinner & Chimimba, 2005).

Eland have a relatively low occurrence in the KGNP and about 1 100 individuals were counted in 2013 (Ellis & Herbst, 2013), although these numbers are known to fluctuate widely as eland migrate into the KGNP during dry season and migrate back into Botswana during the wet season (Eloff, 1962; Bothma, 1972; Van Der Walt et al., 1984; Knight, 1995). As many as over 13 000 eland have been recorded in the KGNP at a time (Mills & Haagner, 1989). The majority of the eland that migrate into the KTP come from as far as the Central Kalahari Game Reserve in Botswana (Verlinden, 1998), largely avoiding areas occupied by human settlements (Verlinden, 1997). When in the KGNP, eland are seldom found in the riverbeds but rather display nomadic movements throughout the dune fields (Mills & Haagner, 1989) where they alter their diet between browse and graze according to what is available and most energetically profitable (Skinner & Chimimba, 2005). Eland in the KGNP are particularly susceptible to high numbers of die-off during periods of drought, which may be due to physiological stress caused by poor quality drinking water provided by artificial waterholes (Knight, 1995).

Kudu, *Tragelaphus oryx*, and giraffe, *Giraffa camelopardalis,* are the least abundant of the large herbivores in the KGNP. Kudu are seldom encountered during aerial count census (Ellis & Herbst, 2013) or road transect game counts (Carlsson, 2005). Kudu are primarily browsers and prefer areas with a higher shrub and tree density, which is limited in the KGNP (Leistner, 1959a), but increases in the north-eastern section of the KTP where kudu abundance is higher (Mills & Haagner, 1989). Eight giraffe were first introduced into the northern Auob riverbed of the KGNP in September 1990, and since then their numbers have grown to an estimated population of around 40 individuals (Bezuidenhout et al., 2010; Ellis & Herbst, 2013). Giraffe in the KGNP remain mostly in the vicinity of the northern Auob riverbed but have been noted to venture as far south as Auchterlonie (pers. obs., 2015). It is uncertain whether historically giraffe ever occurred naturally in the KGNP (Hall-Martin & De Graaff, 1978). Giraffe and browsers and feed predominantly in the canopies of trees (Skinner & Chimimba, 2005) and their browsing pressure may have a negative impact on the trees of the KGNP (Hall-Martin & De Graaff, 1978; Viljoen, 2013).

Physiological and behavioural adaptations make ostrich well suited to survive in arid areas (Williams et al., 1993) and particularly resilient during periods of drought (Knight, 1995). Ostriches are widespread across the KTP and are able to utilize a broad variety of habitats throughout all seasons (Van Der Walt et al., 1984), although they indicate a preference for pans and riverbeds, especially during the wet season (Bergstrom & Skarpe, 1999). In the KGNP ostrich are sedentary (Mills, 2015) and their population numbers are estimated to be around 1550 individuals (Ellis & Herbst, 2013).

The smaller antelopes found in the KTP, including steenbok and common duiker, are also sedentary (Eloff, 1962) and their occurrence is mostly restricted to the dune habitats where the vegetation provides more cover (Eloff, 1962; Leistner, 1959a; Mills & Haagner, 1989). Both steenbok and duiker are browsers and are well adapted to areas independent of water

(Skinner & Chimimba, 2005). In the KTP steenbok are more abundant then duiker (Eloff, 1962; Mills & Haagner, 1989). A small population of warthog, *Phacochoerus africanus*, is resident to the KGNP, although they are infrequently sighted (Mills & Haagner, 1989; Ellis & Herbst, 2013).

2.7.2 Carnivores

African ecosystems are characterised by the presence and influences of large (> 20 kg) carnivores (Mills, 2015). In the KTP these are represented by lion, spotted hyaena, *Crocuta crocuta*, cheetah, *Acinonyx jubatus*, leopard, *Panthera pardus* and brown hyaena, *Hyaena brunnea* (Mills, 1984). The community assemblage of large carnivores in the KTP is more evenly distributed than that of more mesic areas, and differ further, with the inclusion of brown hyaena and exclusion of African wild dog, *Lycaon pictus* (Mills, 2015).

The brown hyaena is regarded to be the most abundant of the large carnivores in the KTP (Mills, 1990) with the last population estimates being just under 180 individuals occupying the KGNP (Mills, 1984). Their ability to thrive in an arid environment is likely due to their catholic diet including insects, rodents and fruits, although they are primarily scavengers (Mills & Mills, 1978). Brown hyaenas are able to occur at higher densities due to the low numbers of spotted hyaenas in the KTP (Mills, 1990). Spotted hyaenas occur at higher densities in mesic areas and their numbers decline in more arid areas (Mills, 2015). In the KGNP the spotted hyaena are estimated to have a low population size, with the last estimates indicating a population of under 90 individuals (Mills, 1984). Spotted hyaenas obtain their food predominantly from hunting as opposed to scavenging and consume mainly large to medium sized herbivores (Eloff, 1964; Mills, 1990). Spotted hyaenas have a high degree of dietary overlap with lions and where they co-exist in high densities there is a lot of competition between the two species (Périquet et al., 2014). In the KTP there is less competition between spotted hyaenas and lions due to their occurrences at low densities (Mills, 2015).

Two other large cat species are found in the KTP, namely cheetah and leopard (Bothma & Le Riche, 1984; Mills & Haagner, 1989). Cheetahs occur at low densities across the entire KTP and have an estimated population size of 204 individuals in the KTP (Funston, 2001). Cheetah diet varies between habitat types in the KGNP, with springbok constituting the majority of cheetah diet in the riverbed habitats, whereas steenbok are consumed predominantly in the dune habitats (Mills & Mills, 2013). The leopard density in the KTP is the lowest of all the large cats with an estimated population of 151 individuals (Funston, 2001). Leopards in the KGNP are opportunistic hunters and consume a wide variety of prey ranging from rodents to large herbivores, although medium sized prey constitute the majority of their diet (Bothma & Le Riche, 1984). The large home range size of cheetah (241 – 849 km^2: Houser et al., 2009) and leopard (300 – 1000 km^2: Bothma & Le Riche, 1984; Mills & Mills, 2013) in addition to the narrow dietary overlap with lion, limits competition between these carnivores in the KTP (Mills, 1984; Mills, 2015).

Some of the smaller carnivore species found in the KTP include black backed jackal, *Canis mesomelas*, Cape Fox, *Vulpes chama,* bat eared fox, *Octocyon megalotis,* African wild cat, *Felis lybica*, caracal, *caracal caracal,* and honey badger, *Mellivora capensis* (Kruuk & Mills, 1983; Melville et al., 2004; Herbst & Mills, 2006; Blaum et al., 2008). Apex carnivores such as lion play an important role in regulating populations of meso-predators (Prugh et al., 2009).

2.8 References

Acocks, J.P.H. 1953. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa*, 57: 1–146.

Anonymous. 2008. *Kalahari Gemsbok National Park management plan*. South African National Parks. Pretoria, South Africa.

Bergstrom, R. & Skarpe, C. 1999. The abundance of large wild herbivores in a semi-arid savanna inrelation to seasons, pan and livestock. *African Journal of Ecology*, 37: 26–37.

Bezuidenhout, H., Ferreira, S. & Herbst, M. 2010. *An assessment of the proposed giraffe translocation from the Mata Mata section to Unions End in the Kalahari Gemsbok National Park*. Unpublished report. SANParks, Scientific Services. Kimberley.

Blaum, N., Engeman, R.M., Wasiolka, B. & Rossmanith, E. 2008. Indexing small mammalian carnivores in the southern Kalahari, South Africa. *Wildlife Research*, 35(1): 72–79.

Bothma, J.D.P. 1972. Short-term response in ungulate numbers to rainfall in the Nossob river of the Kalahari Gemsbok National Park. *Koedoe*, 15: 127–133.

Bothma, J.D.P. & De Graaff, G. 1973. A habitat map of the Kalahari Gemsbok National Park. *Koedoe*, 16(1): 181–188.

Bothma, J.D.P. & Le Riche, E. a. N. 1984. Aspects of the ecology and the behavior of the leopard in the Kalahari desert. *Koedoe*, 27(2): 259–279.

Brynard, A.M. 1958. Verslag insake voorlopige ondersoek rakende toestande in die Nasionale Kalahari-Gemsbokpark. *Koedoe*, 1: 162–183.

Bullard, J.E., Thomas, D.S.G., Livingstone, I. & S., Wiggs, G.F. 1995. Analysis of linear sand dune morphological variability; southwestern Kalahari Desert. *Geomorphology*, 11(3): 189–203.

Carlsson, K. 2005. *Mammal communities in the southern Kalahari : differences between land use types and seasons differences between land use types and seasons*. Minor Field Study 112, Uppsala University, Sweden.

Child, G. & Le Richie, E.A.N. 1969. Recent springbok treks (mass movements) in south-western Botswana. *Mammalia*, 33(3): 499–504.

Coetzee, B.J. & Werger, M.J. a. 1975. A west-east vegetation transect through Africa south of the Tropic of Capricorn. *Bothalia*, 11(4): 539–560.

Dougill, a. J. & Thomas, a. D. 2004. Kalahari sand soils: Spatial heterogeneity, biological soil crusts and land degradation. *Land Degradation and Development*, 15(3): 233–242.

Ellis, G. & Herbst, M. 2013. *Kalahari Gemsbok National Park aerial census report*. Unpublished report to South African National Parks. Pretoria. South Africa.

Eloff, F.C. 1961. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park, Part III. *Koedoe*, 4(1): 18–30.

Eloff, F.C. 1962. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park. part IV. *Koedoe*, 5(1): 128–136.

Eloff, F.C. 1964. On the predatory habits of lions and hyaenas. *Koedoe*, 7(1): 105–112.

Eloff, F.C. 1966. Range extension of the blue wildebeest. *Koedoe*, 9: 34–36.

Eloff, F.C. 1984. The Kalahari ecosystem. *Koedoe*, 27(2): 11–20.

Eriksson, P.G., Nixon, N., Snyman, C.P. & Bothma, J. du P. 1989. Ellipsoidal parabolic dune patches in the southern Kalahari Desert. *Journal of Arid Environments*, 16(1): 111–124.

Funston, P.J. 2001. *Kalahari Transfrontier lion project: final report*. Endangered Wildlife Trust, Johannesburg, South Africa.

Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria*, 4: 5–114.

Grist, J., Nicholson, S.E. & Mpolokang, A. 1997. On the use of NDVI for estimating rainfall fields in the Kalahari of Botswana. *Journal of Arid Environments,*, 35(2): 195–214.

Haddon, I.G. 2005. *The geology and tectonic evolution of the Kalahari Basin, Southern Africa*. Doctoral dissertation, University of the Witwatersrand, Johannesburg, South Africa.

Haddon, I.J. & McCarthy, T.S. 2005. Mesozoic–Cenozoic interior sag basins of Central Africa: The Late-Cretaceous–Cenozoic Kalahari and Okavango basins. *Journal of African Earth Sciences*, 43(1): 316–333.

Hall-Martin, A.J. & De Graaff, G. 1978. A note on the feasibility of ontroducing giraffe to the Kalahari Gemsbok National Park. *Koedoe*, 21(1): 191–193.

Heine, K. 1989. Some observations concerning the age of the dunes in the western Kalahari and palaeoclimatic implications. *Palaeoecology of Africa and the Surrounding Islands*, 21: 161–178.

Herbst, M. & Mills, M.G.L. 2006. Techniques used in the study of African wildcat, Felis silvestris cafra, in the Kgalagadi Transfrontier Park (South Africa/Botswana). *Koedoe*, 52(1): 1–6.

Herholdt, J.J. & Anderson, M. d. 2006. Observations on the population and breeding status of the African White- backed Vulture , the Black-chested Snake Eagle , and the Secretarybird in the Kgalagadi Transfrontier Park. *Ostrich*, 77(3&4): 127–135.

Houser, A., Somers, M.J. & Boast, L.K. 2009. Home range use of free-ranging cheetah on farm and conservation land in Botswana. *South African Journal of Wildlife Research*, 39(1): 11–22.

Keith, M.E. & Renew, A. 1975. Notes on some edible wild plants found in the Kalahari. *Koedoe*, 18: 1–12.

Knight, M.H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33: 377–394.

Kruuk, H. & Mills, M.G.L. 1983. Notes on food and foraging behaviour of the honey badger Mellivora capensis in the Kalahari Gemsbok National Park. *Koedoe*, 26: 153–157.

Laity, J.J. 2008. *Deserts and desert environments (Vol. 3)*. Wiley-Blackwell Publishes House, UK.

Lancaster, N. 1986. Grain-size characteristics of linear dunes in the southwestern Kalahari. *Journal of Sedimentary Research*, 56(3): 395–400.

Lehmann, D., Mfune, J.K.E., Gewers, E., Cloete, J., Brain, C. & Voigt, C.C. 2013. Dietary plasticity of generalist and specialist ungulates in the Namibian desert: a stable isotopes approach. *PLoS ONE*, 8(8): e72190.

Leistner, O.A. 1959a. Notes on the vegetation of the Kalahari Gemsbok National Park with special reference to its influence on the distribution of antelopes. *Koedoe*, 2: 128– 151.

Leistner, O.A. 1959b. Preliminary list of plants found in the Kalahari Gemsbok National Park. *Koedoe*, 2: 152–172.

Leistner, O.A. 1967. The plant ecology of the southern Kalahari. *Memoirs of the Botanical Survey of South Africaoirs of the Botanical Survey of South Africa*, 38: 1–172.

Leistner, O.A. & Werger, M.J.A. 1973. Southern Kalahari phytosociology. *Vegetation*, 28: 353–399.

Malherbe. 1984. The Geology of the Kalahari Gemsbok National Park. *Koedoe*: 33–44.

Melville, H.I.A.S., Bothma, J.D.P. & Mills, M.G.L. 2004. Prey selection by caracal in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 34(1): 67.

Mills. 1984. The comparative behavioural ecology of the brown hyaena Hyaena brunnea and the spotted hyaena Crocuta crocuta in the southern Kalahari. *Koedoe*, 27: 237–247.

Mills, M.G.L. 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. *Koedoe*, 27(2): 281–294.

Mills, M.G.L. 1990. *Kalahari hyaenas. The comparative behavioural ecology of two species*. Unwin Hyman, London.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 45(2): 127–137.

Mills, M.G.L. & Haagner, C. 1989. *Guide to the Kalahari Gemsbok National Park*. Southern Book Publishers, Johannesburg.

Mills, M.G.L. & Mills, M.E. 1978. The diet of the brown hyaena Hyaena brunnea in the southern Kalahari. *Koedoe*, 2(1): 125–149.

Mills, M.G.L. & Mills, M. 2013. *A natural history guide to the arid Kalahari*. Black Eagle Media. Cape Town.

Mills, M.G.L. & Retief, P.F. 1984a. The effects of windmill closure on the movement patterns of ungulates along the Auob riverbed. *Koedoe*, 27(2): 107–118.

Mills, M.G.L. & Retief, P.F. 1984b. The response of ungulates to rainfall along the riverbeds of the Southern Kalahari 1972-1982. *Koedoe*, 27(2): 129–141.

Mucina, L. & Rutherford, M.C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute. Pretoria.

Nagy, K.A. & Knight, M.H. 1994. Energy, water, and food use by springbok antelope (Antidorcas marsupialis) in the Kalahari Desert. *Journal of Mammalogy*, 75(4): 860–872.

Ngami Data Services. 2012. Land use in Botswana. Map viewed 06 April 2016. URL http://www.nds–printingbotswana.com/maps–gis–pro.

Périquet, S., Fritz, H. & Revilla, E. 2014. The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biological Reviews*, 90(4): 1197–1214.

Pole-Evans, I.B. 1936. A vegetation map of South Africa. *Memoirs of the Botanical Survey of South Africa*: 1–23.

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(9): 779–791.

Quantum GIS Development Team. 2016. QGIS Geographic Information System. Open Source Geospatial Foundation. URL http://qgus.osgeo.org.

Scholes, R.J. 1990. The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography*, 17: 415–419.

Shroyer, M., Engelbecht, M. & Kaketso, O. 2001. Wilderness Management in the Kgalagadi Transfrontier Park. *International Journal of Wilderness*, 7(2): 11–15.

Skinner, J.D., Aarde, R.J. Van & van Jaarsveld, A.S. 1984. Adaptations in three species of large marmnals (Antidorcas marsupialis, Hystrix africaeaustralis, Hyaena brunnea) to arid environments. *South African Journal of Zoology*, 19: 82–86.

Skinner, J.D. & Chimimba, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press, Cape Town.

Spinage, C.A. 1992. The decline of the Kalahari wildebeest. *Oryx*, 26(3): 147–150.

Stapelberg, F.H. 2007. *Feeding ecology of the Kalahari springbok Antidorcas marsupialis in the Kgalagadi Transfrontier Park, South Africa*. Magister Scientiae, University of Pretoria, South Africa.

Stapelberg, H., Van Rooyen, M., Bothma, J.D.P., Van der Linde, M.J. & Groeneveld, H.T. 2001. Springbok behaviour as affected by environmental conditions in the Kalahari. *Koedoe*, 50(1): 145–153.

Thomas, D.S.G. & Shaw, P.A. 1991. *The Kalahari Environment*. Cambridge University Press, Johannesburg.

Van Rooyen, N. & Van Rooyen, M.. 1998. Vegetation of the southwestern arid Kalahari: an overview. *Transactions of the Royal Society of South Africa*, 52(2): 113–140.

Van Rooyen, N., Bezuidenhout, D., Theron, G.K. & Bothma, J.D.P. 1990. Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe*, 33(1): 63–88.

Van Rooyen, N., Bredenkamp, G.J., Theron, G.K., Bothma, J.D.P. & Le Richie, E.A.N. 1994. Vegetational gradients around artificial watering points in the Kalahari Gemsbok National Park. *Journal of Arid Environments*, 26: 349–361.

Van Rooyen, N., Van Rensburg, D.J., Theron, G.K. & Bothma, J.D.P. 1988. A check list of flowering plants of the Kalahari Gemsbok National Park. *Koedoe*, 31: 115–135.

Van Rooyen, M.W., Van Rooyen, N., Bothma, J.D.P. & Van den Berg, H.M. 2008. Landscapes in the Kalahari Gemsbok National Park, South Africa. *Koedoe*, 50(1): 99–112.

Verlinden, A. 1997. Human settlements and wildlife distribution in the southern Kalahari of Botswana. *Biological Conservation*, 82(2): 129–136.

Verlinden, A. 1998. Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, 36(117): 128.

Viljoen, S. 2013. *Habitat use and diet preference of extralimital giraffes in the Kgalagadi Transfrontier Park*. Doctoral dissertation, University of Cape Town, South Africa.

Van Der Walt, P.T., Retief, P.F., Le Richie, E.A.N., Mills, M.G.L. & De Graaff, G. 1984. Features of habitat selection by larger herbivorous mammals and ostrich in the southern Kalahari conservation areas. *Koedoe*, 27(2): 119–128.

Wergner, M.J.. 1986. The Karoo and southern Kalahari. In: Evenari, M., Noy-Meir, I. & Goodall, D.W. (eds.). Hot desert and arid shrublands. *Amsterdam: Elsevier*: 283–359.

Wiggs, G.F., Thomas, D.S., Bullard, J.E. & Livingstone, I. 1995. Dune mobility and vegetation cover in the southwest Kalahari Desert. *Earth Surface Processes and Landforms*, 20(6): 515–529.

Wiggs, G.F.S., Livingstone, I., E, Thomas, D.S.G. & Bullard, J. 1994. Effect of vegetation removal on airflow patterns and dune dynamics in the southwest Kalahari Desert. *Land Degradation & Development*, 5(1): 13–24.

Williams, J.B., Siegfried, W.R., Milton, S.J., Adams, N.J., Dean, W.R.J., du Plessis, M.A. & Jackson, S. 1993. Field metabolism, water requirements, and foraging behavior of wild ostriches in the Namib. *Ecology*, 74: 390–404.

Williamson, D. & Williamson, J. 1988. Wildebeest migration in the Kalahari. *African Journal of Ecology*, 26(4): 269–280.

CHAPTER 3

EFFECTIVE ESTIMATION OF LARGE CARNIVORE DIET: LIONS (*PATHERA LEO*) IN THE KALAHARI GEMSBOK NATIONAL PARK

3.1 Introduction

Understanding lion (*Panthera leo*) diet provides important insights into their behavioural ecology as well as the influence they have on prey populations (Mills 1992; Owen-Smith & Mills 2008a). In predator-prey systems herbivore populations are regulated by both food and predation (Sinclair & Arcese, 2013). Lions have the effect of altering prey abundance and behaviour (Owen-Smith & Mills, 2008b) and so can have spatio-temporal influences on prey species (Valeix et al., 2009), which ultimately influences habitat selection, utilization and condition (Gittleman & Harvey, 1982). Dietary studies can also be used to determine the effects of predation on prey populations by investigating predator density in relation to kill rates and prey density (Owen-Smith & Mills, 2008a; Merrill et al., 2010). Understanding the potential impacts of prey selection of large carnivores provides valuable information that support conservation management practices (Hayward et al., 2006; Ferreira et al., 2012).

As apex predators, lions play a critical role in ecosystem functioning (Mills et al., 1978). Prey selection by lions can have a regulatory effect on herbivore populations (Fryxell et al., 2007) and predation pressure can lead to instability within preferred prey populations (Owen-Smith & Mills, 2008b). In turn, prey availability influences lion population density and survival rates (Ferreira & Funston 2010). Diet selection by lions not only has an effect on prey populations, but can also impact lion population demographics (Becker et al., 2013). This is because diet has an influence on body condition, which has been found to influence the sex ratios of offspring pre-parturition (Trivers & Willard, 1973). Various studies have indicated that a female in good body condition is more likely to produce a male (Trivers & Willard, 1973; Meikle & Drickamer, 1986; Sheldon & West, 2004), although no studies could be found relating sex ratios to maternal body condition for carnivores. Census data from a study conducted in 2010 on the lion population in the Kalahari Gemsbok National Park (KGNP) indicated a skew in the sex ratio in favour of male lions (Ferreira et al. 2012). A sex ratio in favour of males lions may lead to increased competition between males for breeding rights with females, resulting in reduced reproductive success and ultimately causing a population decline (Becker et al., 2013). A decline in a lion population can have numerous deleterious knock-on effects to other species (Loveridge et al., 2007). To establish whether lion body condition, and consequently diet could have played a role in creating the observe sex skew, a better understanding of lion diet in the KGNP is needed.

Accurately identifying diet can be challenging as each techniques that has been used in determining carnivore diet has inherent benefits and limitations, and provides some degree of bias in the results (Mills, 1992). The most commonly applied methods used in identifying carnivore diet include stomach content analysis (Smuts, 1979), faecal analysis (Mukherjee et al., 1994; Breuer, 2005; Davidson et al., 2013), tracking spoor (Eloff, 1984a), continuous follows (Schaller, 1972; Stander, 1992a), and opportunistic observations (Mills, 1984; Radloff & du Toit, 2004; Owen-Smith & Mills, 2008b). More recently developed methods of dietary investigations include, GPS cluster analysis (Sand et al., 2005; ; Tambling et al., 2010; Pitman et al., 2012), isotopic analysis (Hilderbrand et al., 1996; Zhao & Schell, 2004; Newsome et al., 2009) and DNA analysis (Reed, 2004; Shehzad, 2011).

The emerging techniques of using stable carbon and nitrogen isotope analysis acquired from animal tissues (Hilderbrand et al., 1996; Zhao & Schell, 2004; Newsome et al., 2009), and the identification of unique DNA sequences obtained from carnivore scat (Reed, 2004; Haag et al., 2009; Shehzad, 2011), to identify predator diet are, for the most part in developmental stages and are costly to impliment (Piggott & Taylor, 2003; Codron et al., 2007; Haag et al., 2009). Stomach content analysis is an invasive method, requiring a sample to be obtained from the predators gut either through immobilization or euthanasia (Smuts, 1979). Scat (faecal) analysis is a widely applied, non-invasive method of determining diet through identifying undigested remains that have passed through an animal’s digestive system (Klare et al., 2011; Ciucci et al., 2014). In lion dietary studies it may be used to identify small prey items and can be used to provide an estimate of biomass consumed (Ruhe et al., 2008; Tambling et al., 2012). Scat analysis is limited in that it generally over-represents smaller prey items (Floyd et al., 1978), does not depict the age and the sex of the prey, nor does it indicate if the prey was hunted or scavenged (Breuer, 2005). In order to provide an accurate depiction of diet through scat analysis, a sufficient sample size of scats needs to be obtained (Mills, 1992; Trites & Joy, 2005). A study conducted in the northern Cameroon recommends a minimum sample size of 70 lion scats (Breuer, 2005). However, what constitutes a sufficient sample size of scats in order to determine lion diet has not been clearly defined. Only one published study could be found that specifically addressed the issue of sample size requirements and that was conducted on a marine mammal (Steller sea lions, *Eumetopias jubatus*), recommends that a minimum sample size of 59 scats is required to identify a dietary profile (Trites & Joy, 2005).

Continuous opportunistic observations have been widely regarded as the most accurate method in determining lion foraging activities (Hayward & Kerley, 2005; Tambling & Belton, 2009), as other techniques may prejudice dietary representation towards either small or large prey species (Mills et al., 1978; Mills, 1992; Tambling et al., 2012). However, continuous observation is seldom feasible due to logistical and financial constraints, and may influence behaviour, of both the subject and their prey (Mills, 1992). Tracking spoor, like continuous follows, has a high accuracy in determining diet but can only be used in certain habitats and requires extensive efforts and specialized ground-tracking skills (Eloff, 1984a; Mills, 1992). Using opportunistic observations of lion kills as a method of determining lion diet skews data towards large prey species, as small prey are quickly consumed and often go undetected (Mills 1984; Radloff & du Toit 2004).

GPS cluster analysis is a technique used to identify a predator's kill sites by means of clustered locality data points downloaded from animals fitted with GPS collars (Tambling et al., 2010). Data from GPS collars can also be used to identify the potential influence of predators on their preferred prey by identifying prey preference and rates of predation (Anderson & Lindzey, 2003). Further insights into foraging behaviour that can be obtained through GPS cluster analyses include the time spent on a kill, duration between kills, landscape utilization and age and sex of prey (Merrill et al., 2010). However, GPS cluster analysis often provides an overestimation of large prey items (Bacon et al., 2011; Tambling et al., 2012).

Even though numerous methods on determining carnivore diet exist, there is a lack of information pertaining to the optimal sampling effort, sample size and sampling techniques required in order to accurately determine lion diet. Therefore, in order to obtain a true depiction of lion diet in KGNP, it was necessary to not only to identify diet using a variety of techniques, but to also identify the most suitable sampling approach by identifying the sampling effort required and feasibility of the sampling method. It was also necessary to determine the minimum sample size required per method applied, to be able to evaluate the reliability of the respective techniques to determine lion diet in an arid environment.

This chapter not only aims to provide a better understanding of lion diet, but also critically evaluates the effectiveness of various techniques used to portray lion diet in an arid environment. To determine the lion diet profile in the KGNP, a combination of techniques was used including recording lion kills from areas of clustered GPS locality points (GPS cluster analysis), determining prey species consumed through the analyses of lion scats (scat analysis) and recording feeding events from lions that were opportunistically observed to be feeding on a carcass (opportunistic observations). Lastly, the data on prey availability, derived from game counts, was compared to the estimated lion diet to determine if lions in the KGNP actively select prey and show preference for certain prey species. Findings from this study can be used to help direct future research by defining suitable sampling approaches required to determine the lion diet profile in an arid environment.

3.2 Material and methods

3.2.1 Study area

The study was conducted in the Kalahari Gemsbok National Park (9 591 km^2: between 24° 15’ S and 26° 30’ S, and 20° 00’ E and 20° 45’ E) which comprises the South African section of the Kgalagadi Transfrontier Park (KTP) (Anonymous, 2008). The study area included a 25 km band east of the Nossob River into the Gemsbok National Park (27 672 km^2), the Botswana constitute of KTP (Figure 3.1).

The Kalahari Gemsbok National Park has predominantly summer rainfall between January to April, with the annual mean varying between 185 mm to 230 mm (Van Rooyen et al., 2008). Evapotranspiration rates are high and natural surface water occurs only for short periods after heavy rain (Knight, 1995). Temperatures fluctuate greatly on a daily, as well as seasonal basis (Mills & Retief, 1984), reaching a winter minimum of -10.3°C and a summer maximum of 45.4°C (Van Rooyen et al., 1990).

KGNP is situated in the Kalahari Duneveld and Eastern Kalahari Bushveld Bioregions of the Savannah Biome (Rutherford et al., 2006). The KGNP has two dominant habitat types, namely the dunes and the riverbeds. The dune habitats cover approximately 85% of the study area and can be classified into areas sparsely vegetated with trees and shrubs, bare dunes, flat grasslands and tree savannahs (Bothma & De Graaff, 1973). The dune fields are bisected by two ephemeral riverbeds and scattered pans (van Rooyen 1984).

In this study the riverbed habitats were defined as the two riverbeds (Auob and Nossob), as well as a 2500 m buffer area around them, and cover approximately 15% of the study area. The riverbeds support higher densities of game than the dunes (Bergstrom & Skarpe, 1999) and are the most intensively utilized habitats by varying numbers of springbok, *Antidorcas marsupialis*, blue wildebeest, *Connochaetes taurinus,* gemsbok, *Oryx gazella* and red hartebeest, *Alcelaphus buselaphus* (Mills & Retief, 1984). Blue wildebeest and springbok occur mainly within the riverbed areas (Mills, 2015). In the KTP gemsbok, blue wildebeest, ostrich, *Struthio camelus,* steenbok, *Raphicerus campestris,* and common duiker, *Sylvicapra grimmia* are sedentary (Eloff, 1962; Mills, 2015), whereas springbok, eland, *Tragelaphus oryx,* and red hartebeest are nomadic across the KTP (Mills, 2015). A more detailed account of the biotic and abiotic features of the KTP and study area has been described in Chapter 2. All maps were created using QGIS software (Quantum GIS Development Team, 2016).

3.2.2 Data collection

Three different techniques were used to determine lion diet in the KGNP, including GPS cluster analysis, scat analysis and opportunistic observations.

3.2.2.1 GPS cluster analysis

In an attempt to obtain an overall idea of lion diet within the KGNP seven adult female lions, holding territories across the park, were fitted with GPS/ VHF and satellite transmitter collars (African Wildlife Tracking^{cc}, Pretoria, South Africa). This allowed for known individuals and their associated prides to be observed on a regular basis (Tambling et al., 2010). Lions were captured for collaring, using the standard techniques employed by the South African National Parks wildlife veterinary services (Smuts et al., 1977; Anonymous, 2008).

Collars were programed to record lion localities at hourly intervals, creating a movement pattern of collared lions over time (Sand et al., 2005; Tambling, 2010). Four or more consecutive fixes, occurring within a 100m radius (Tambling et al., 2012; Davidson et al., 2013) and between two hours before sunset to two hours after sunrise, provided the best indications of potential feeding event sites and therefore defined a GPS cluster location. GPS cluster locations (hereafter referred to as GPS clusters) occurring outside of these parameters were largely excluded from investigations except for a few randomly selected samples to verify the selection protocol.

The x:y coordinates of the first downloaded point of an identified GPS cluster were uploaded onto a hand held GPS unit (Garmin E-Trex, Garmin International, Olathe, KS, USA). The location was tracked to by vehicle and a 100 m radius around the point was searched for evidence of prey remains (Tambling et al., 2012; Sand et al., 2005). If no evidence of a feeding event was found, the coordinates of the last location of the GPS cluster were located and a new 100 m radius search area was initiated.

A feeding event site was confirmed if material evidence of a predation event were found, such as irregular soil disturbance and trampled vegetation as a result of a struggle or feeding frenzy, along with remains such as rumen content, hair, bone, jaw, horn, blood or a carcass (Pitman et al. 2012; Davidson et al. 2013). Remains were used to classify prey according to species and where possible age and sex (Tambling et al. 2012).

3.2.2.2 Opportunistic observations

Opportunistic observations of lions were conducted when lions where encountered by chance across the study area (Mills, 1984; Eloff, 1984a). Opportunistic observation periods were short term, of less than 24 hours (Funston et al., 1998). Lions were observed from a vehicle at a distance of 20 – 100 m (Stander & Albon, 1993). Where lions were found feeding on a carcass the time, date, GPS location, numbers of lions, including notes on their age, sex, stomach index and body condition, species consumed and where possible the age and sex of the prey were recorded. Carcasses that were opportunistically encountered were considered as kills made by lions, if there was evidence of lion spoor around the carcass and if there was no evidence of other large predators in close proximity to the carcass.

3.2.2.3 Lion scat analysis

Lion scats (faeces) were collected throughout the study period when opportunistically encountered across the study area, as well as from GPS cluster locations. Lion scats collected at GPS cluster points that contained remains of the prey species found at that cluster, or at a preceding cluster not older than 24 hours, were excluded from analysis (Tambling et al., 2012).

Monthly transects driven during road transect game counts, as well as the extensive distances travelled whilst investigating GPS cluster points, helped to distribute sampling effort across the study area. Lion scat was identified according to shape, diameter, colour, ingested hair and evidence of spoor (Reed, 2004; Breuer, 2005). When encountered, scat was photographed together with a reference number and placed in a labelled brown paper bag and allowed to air dry. The reference number, date, GPS reading and a description of location were recorded.

Dried scat was soaked in water overnight to separate the organic components and then washed under running water using a 2 mm sieve to collect undigested material such as hair, hoof, quill and bone samples (Ruhe et al., 2008; Tambling et al., 2012). A randomly selected subsample (approximately ¼ of the undigested material) was cleaned in a 16.5% sodium chloride sterilizing fluid (Procter & Gamble Co.) and then allowed to dry naturally. The subsample was then evenly distributed over an 8 x 8 cm gridded sectioning board, with each row and column containing a demarcated block. Four hairs were randomly selected from each demarcated block (≥ 32 strands) and soaked in alcohol to clean.

Hair samples extracted from scats were assessed macroscopically for colour, width and length and microscopically, using conventional light microscopy, for cuticular scale patterns and cross sections of the medullary structure (Mukherjee et al., 1994; Douglas, 1989; Keogh, 1983). Cuticle scale pattern imprints were made by laying hairs on clear nail varnish. When dry, the hairs were pulled off and the imprint was left behind (Douglas, 1989; Ott et al., 2007; Martins et al., 2011). Cross sections were obtained through setting hairs in paraffin wax inside plastic tubes. Once set, a scalpel was used to thinly slice the cross sections (Douglas, 1989; Tambling, 2010). A reference library of prey hair samples was made, using hairs collected from carcasses encountered in the field, and was used to assist with the identification of hair samples obtained from lion scat (Mukherjee et al., 1994).

3.2.2.4 Prey abundances

Prey distribution and availability were identified from game counts conducted along road transects, as well as from an aerial game count that was performed by SANParks in September 2013 (Ellis & Herbst, 2013). The road transects were sampled throughout the study period on a monthly basis and comprised of two transects driven in both the dune and riverbed habitats. Transects were driven between sunrise and sunset at a speed of 35 km per hour (Figure 3.1). Fifteen road transect game counts were conducted in the dune habitats (330 km) and 15 game counts were conducted in the riverbed habitats (446 km).

Two observers counted all species, over five kilograms, that were encountered along the road transect. A Trimble Juno 3B handheld computer with integrated GPS (Trimble Navigation Limited, Sunnyvale, California, USA) and CyberTracker software (version 3.295, http:// www.cybertracker.co.za) were used to record the species, herd size and where possible, age and sex. Herbivores were subjectively placed into three age categories namely calves, sub-adults and adults, according to their physical attributes (Knight, 1995).

The aerial game count made use of two observers to count all species (over five kilograms) encountered from a fixed-wing Cessna 206 aircraft, flying over 23 transects, that were evenly spaced across the KGNP (Castley, 2005; Ellis & Herbst, 2013). Aerial game count provided abundance estimates for gemsbok, red hartebeest, ostrich, springbok, steenbok, blue wildebeest, eland and Kori bustard, *Ardeotis kori*, in the KGNP.

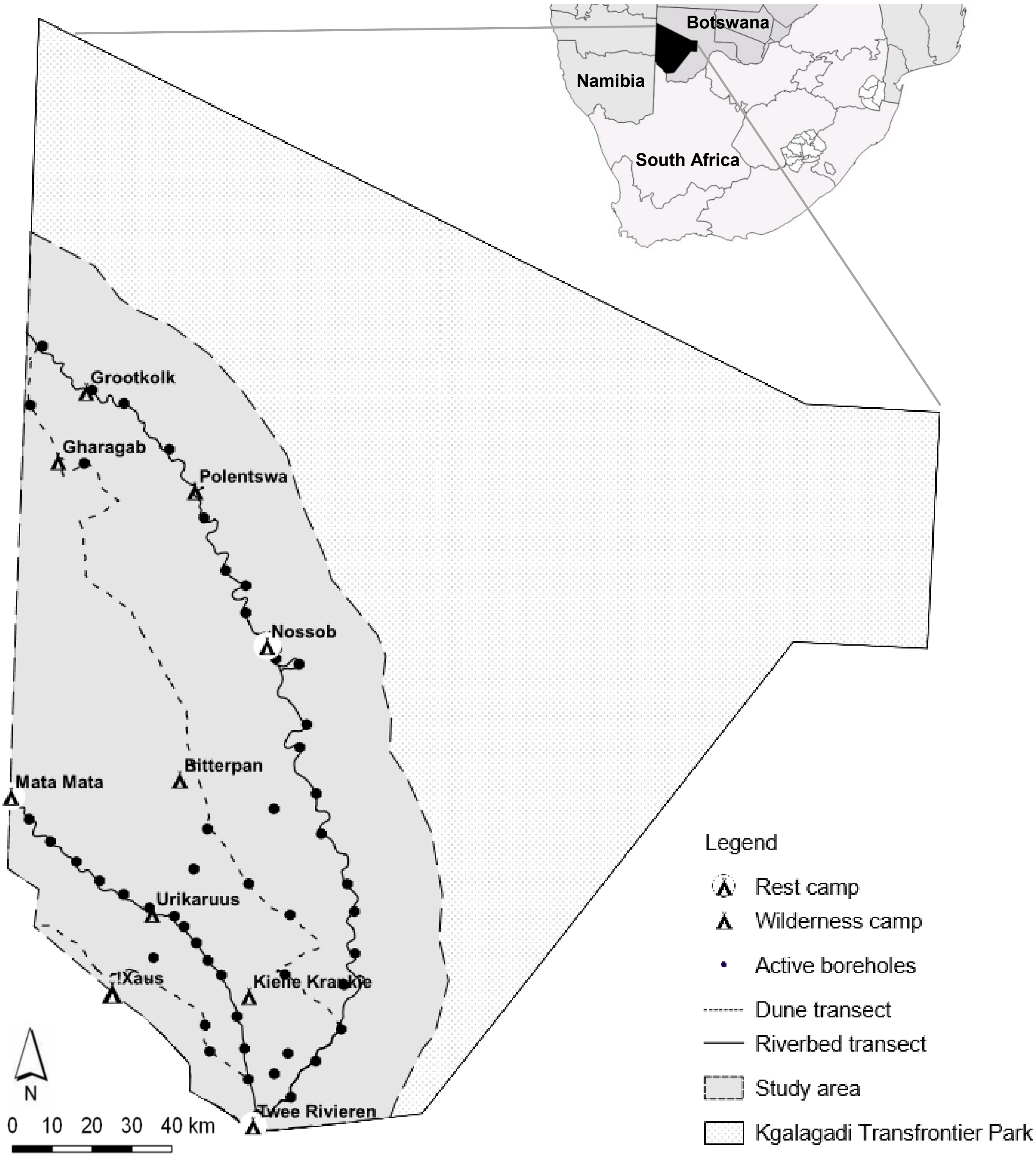


Figure 3.1 The study area in the Kgalagadi Transfrontier Park, showing road transect game count routes conducted in the dune and riverbed habitats.

3.2.3 Data analyses

3.2.3.1 Defining lion diet

The proportional representation of prey in lion diet, as well as the biomass contributions of prey in different size classes, were calculated for each method that was used to determine lion diet in the KGNP. Lion diet was quantified by the relative proportions of the different prey species represented in GPS cluster analysis, scat analysis and opportunistic observations respectively (*i.e.* the number of occurrences of each prey item divided by the total sample size for each respective method).

The frequency of prey occurrence in lion diet was converted into relative biomass indices (RBI) (Balme et al., 2010). The body mass for adult male and female mammalian prey species were taken from Skinner & Chimimba (2005). Sub-adult and juvenile RBI were calculated by multiplying the adult female mass by 0.7 and 0.3 respectively (Radloff & du Toit 2004). Where the age and sex was unknown, RBI was subjectively assigned using the female RBI multiplied by 0.75, which would account for juveniles and males (Radloff & du Toit 2004; Tambling et al. 2012). Unit mass was ascribed in the same manner for prey that were not ungulates as well as avifauna (Owen-Smith, 1988; Radloff & du Toit, 2004).

Prey was also ascribed into two categories according to mass, namely large prey (≥ 50 kg), such as eland*,* gemsbok, blue wildebeest, red hartebeest and ostrich etc. and small prey (≤ 50 kg), such as springbok, steenbok, porcupine, *Hystrix africaeaustralis,* Kori bustard and springhare, *Pedetes capensis,* etc. Information on the age and sex structure of prey was obtained from prey remains found at GPS clusters and opportunistic observations.

3.2.3.2 Defining optimal sampling

The proportional representation of all prey species detected in lion diet for GPS cluster points, scats analysis and opportunistic observations, as calculated from the total amount of samples obtained for each method, was used as reference against which dietary profiles from smaller sample sizes were compared for accuracy. The extent to which the proportional representations of prey species, at various sample sizes, varied from the reference sample were identified using the Bray-Curtis distance (or index of dissimilarity) and Euclidian distance sampling (Bray & Curtis, 1957; Danielsson, 1980). Distance sampling metrics test the deviation of a sample from the mean and can be used to compare several traits concurrently (Darimont et al., 2007). Bray-Curtis and Euclidian distance sampling were used to provide a numeric “ecological distance” measure that represented the difference between species compositions, at various sample sizes, from the reference sample. The closer the ecological distance was to 0.5 for the Bray-Curtis distance, and to zero for the Euclidean distance, the more similar the species composition was to the reference sample. The further the ecological distance was numerically from the reference sample value, the greater the variance was between the samples and the more they differed (Bray & Curtis, 1957; Danielsson, 1980).

To identify how sample size influenced the reliability of lion dietary profile estimates, 1000 Monte Carlo simulations (Rollett & Manohar, 2004) were run by sub-sampling, with replacement, at various sample sizes from the total number of samples collected. The variability of ecological distances calculated from these simulations, at different sample sizes, provided an indication of reliability (Leblois et al., 2003). Both Bray-Curtis and Euclidian distance sampling were applied as the Bray-Curtis distance is more sensitive to the presence or absence of a species within a sample, whereas the Euclidian distance is more sensitive to species abundance within a sample (Kindt & Coe, 2005).

The Hartley's F-max test for homogeneity of variance (Hartley, 1950) was then used to establish the minimum number of samples required to provide an accurate representation of lion diet. A sufficient sample size was identified when there was no significant difference in the variance between the plausible Bray-Curtis and Euclidean distances at grouped sample sizes, compared at ascending increments of tens. Homogeneity of variance was obtained when the F-max value reached the point where it was less than, and remained less than the tabulated F-max value (1.67) (Hartley, 1950) for both the Bray-Curtis and Euclidean distances.

3.2.3.3 Sample effort

Sample effort was defined by dividing the number of samples obtained using each method, by the number of sample days it took to collect the samples using each method. For GPS clusters, the number of samples obtained included only the GPS cluster points that contained identifiable prey remains. Sample days for GPS clusters were represented by the number of days for which the GPS collars submitted locality data. For scat analysis and opportunistic observations, sample days were represented as the number of days spent conducting field operations.

Method-based species accumulation curves were developed using the number of prey species represented in the diet at ascending sample sizes (Kindt & Coe, 2005). An asymptote on species accumulation was identified when the total number of prey species identified in lion diet were represented within each method (Breuer, 2005).

3.2.3.4 Relative prey abundance

Two methods of obtaining relative abundance indices (RAI) for herbivores have been used in the KGNP and include road transect game counts and aerial census game counts. Due to the methodological differences, road transect game counts and aerial game counts are likely to provide abundance estimates that differ (Jachmann, 2002). Therefore, the RAI of herbivores in the KGNP was derived from both road transect game counts, performed throughout the study period, as well as an aerial game count that was conducted by SANParks in September 2013 (Ellis & Herbst, 2013).

Prey RAI, using encounter rates of individuals as a proxy for abundance, were assigned by using the data obtained from 15 dune and 15 riverbed road transect game counts. To account for the fact that the dunes occupy 85% of the study area, whilst the riverbeds only occupy approximately 15% of the study area, the road transect game count data (RAI) was weighted in accordance to the proportion area occupied by the dunes and riverbeds (Caro, 1999). To obtain a total weighted RAI for each prey species, across the entire study area, the average percent RAI, derived from the game counts in each habitat type (dune counts, n = 15; river counts, n = 15), were multiplied by the proportional area occupied by each habitat type (dune = 85%, riverbed area = 15%) and then added together, in the equation:

$RAIs = (RAI_d \times D) + (RAI_r \times R)$

where $RAIs$ is the weighted percent RAI for a particular species across the entire study area, RAI_d is the average RAI of that species in the dunes and RAI_r is the average RAI for that species in the riverbed. D and R are the proportions of study area occupied by the dune and riverbed habitats respectively. The 15 weighted game counts per habitat type were used to derive the mean and 95% confidence intervals for the RAI for each species within each habitat type.

The RAI of prey for aerial game counts was derived from the only aerial game count that was conducted during the study period in September 2013 (Ellis & Herbst, 2013). The RAI from road transect game counts and aerial game counts are presented together to illustrate the similarity in RAI results between the two methods.

3.2.3.5 Comparison of methods used

Two category comparisons were made using the Pearson’s Chi-square test (Pearson, 1900) to test if prey apportionment in lion diet varied significantly across methods. Due to low sample sizes, for large prey species, kudu, *Tragelaphus strepsiceros,* and ostrich were grouped in a category called “other large prey” and all small prey (< 50 kg) were grouped in a category called “small prey” to allow for comparison (see Kindt & Coe 2005 for bias in Chi-square values).

3.2.3.6 Prey preference

The Jacobs’ index was used to measure prey preference (*D*) (Jacobs, 1974; Hayward & Kerley, 2005; Rapson & Bernard, 2007; Davidson et al., 2013):

$$D = \frac{r - \mathrm{p}}{r + p - 2rp}$$

where *r* is the proportional contribution of a species in the dietary sample and *p* is the proportional availability of that species. Lion feeding events obtained from GPS cluster, scat analysis and opportunistic observations data provided *r* and *p* was derived from the weighted road transect game counts, as well as from the aerial game count (Ellis & Herbst, 2013). The Jacobs’ index was tested independently for GPS cluster analysis (D_{gps}), scat analysis (D_{sca}) and opportunistic observations (D_{obs}) (*r*), for both the weighted game counts and the aerial game count (*p*). The Jacobs’ index scores a value between -1 (indicating species that are highly avoided) and 1 (indicating species that are highly preferred) (Jacobs, 1974). A value between -0.2 and 0.2 indicated that the species was consumed proportionally to what could be expected (Hayward et al., 2011). A one-way analysis of variance (ANOVA) was used to compare the differences between the Jacobs’ indices of scat analysis, GPS cluster analysis and opportunistic observations, for both game counts and aerial census.

3.3 Results

3.3.1 Lion diet

GPS collar locality point downloads revealed 823 potential lion feeding event sites, which were identified from clustered locality points (GPS clusters) (Table 3.1). GPS clusters were investigated on average 33 days after occurrence. Evidence of identifiable prey remains were found at 36.5% (*n* = 278) of GPS cluster sites (Table 3.1 and Figure 3.2). Prey remains at GPS cluster points that could not be identified to a species level were removed from analysis (*n* = 23). Collectively, gemsbok, wildebeest, hartebeest and eland contributed to 92% of the species consumed (Table 3.2) and 98% of the biomass intake derived from GPS cluster data (Figure 3.3). Lionesses fitted with GPS collars were found to associate with males on average 31% of the time (range 0 – 50%), therefore lion diet derived from GPS collar data is likely to be skewed towards female diet and may not adequately represent male diet.

Table 3.1 The number of GPS cluster points investigated, number kill remains found at GPS clusters and the number of prey species identified within each landscape area (North, South and West) where lionesses were fitted with GPS tracking collars.

	North	**South**	**West**	**Total**
Clusters investigated	338	184	301	823
Kill remains found	104	66	108	278
No. of prey species	7	4	7	9

Table 3.2 The percentage contributions of prey species to lion diet derived from GPS clusters, scat analysis and opportunistic observations. Sample sizes are provided in brackets.

		Cluster (278)		**Scat (189)**		**Observations (52)**	
Large prey	Gemsbok	73	(203)	50.8	(96)	44.3	(23)
	Blue Wildebeest	10	(28)	8.5	(16)	25	(13)
	Eland	4.3	(12)	3.7	(7)	17.3	(9)
	Red Hartebeest	4.7	(13)	3.7	(7)	1.9	(1)
	Ostrich	3.6	(10)	0.5	(1)	1.9	(1)
	Kudu	1.1	(3)	0.5	(1)	0	(0)
	Cattle	0	(0)	0 (0)	(0)	1.9	(1)
Subtotal		96.7	(269)	67.7	(128)	92.3	(48)
Small prey	Porcupine	0	(0)	12.7	(24)	1.9	(1)
	Steenbok	2.5	(7)	7.4	(14)	1.9	(1)
	Springbok	0.4	(1)	9.5	(18)	0	(0)
	Kori Bustard	0.4	(1)	0	(0)	3.9	(2)
	Springhare	0	(0)	2.2	(4)	0	(0)
	Jackal	0	(0)	0.5	(1)	0	(0)
Subtotal		3.3	(9)	32.3	(61)	7.7	(4)

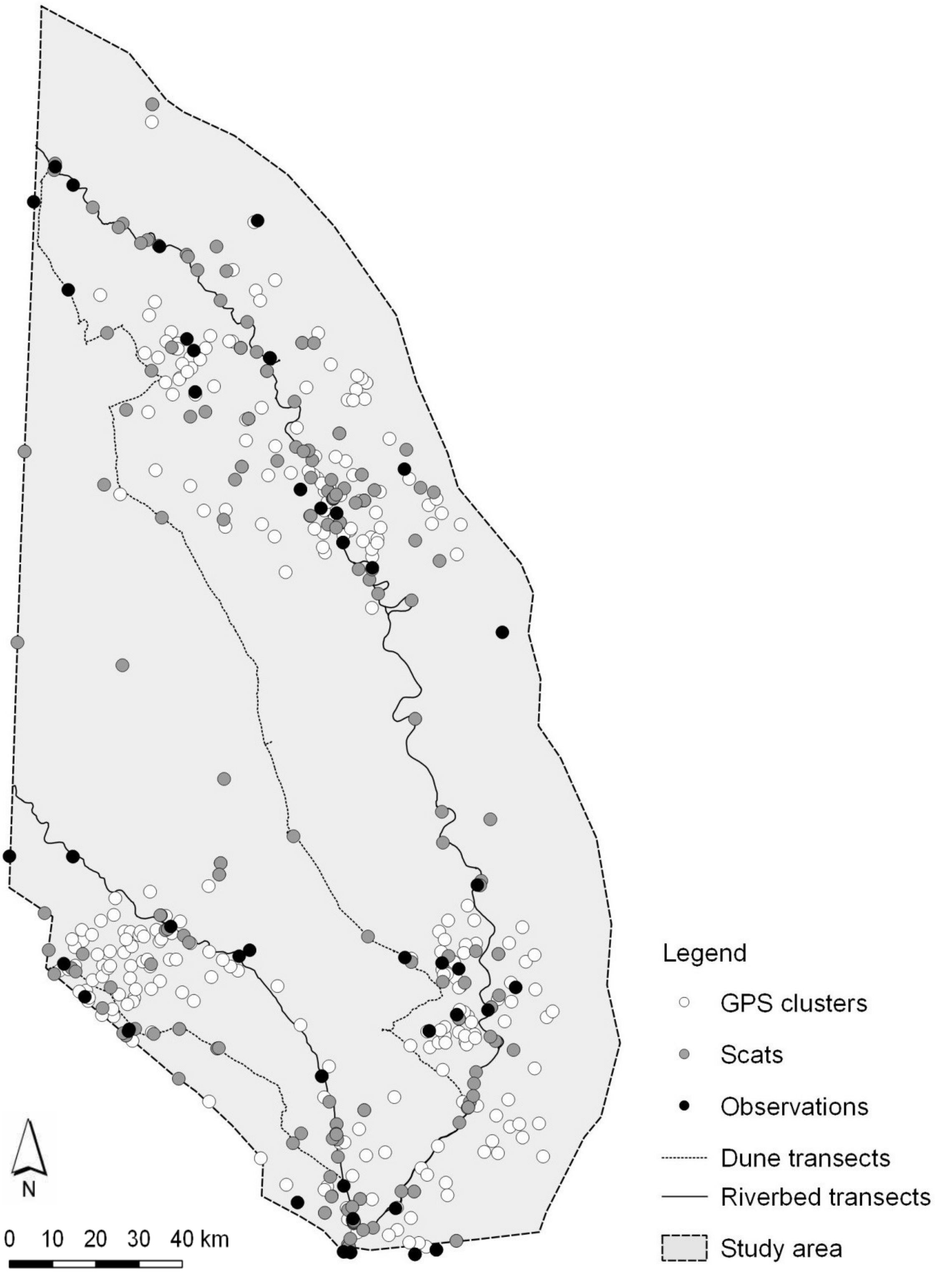


Figure 3.2 The study area in the Kgalagadi Transfrontier Park, with circular markers indicating the independent locations of opportunistic observations of lion kills (n = 52), lion scats collected (n = 189) and lion prey remains located at GPS cluster points (n = 278).

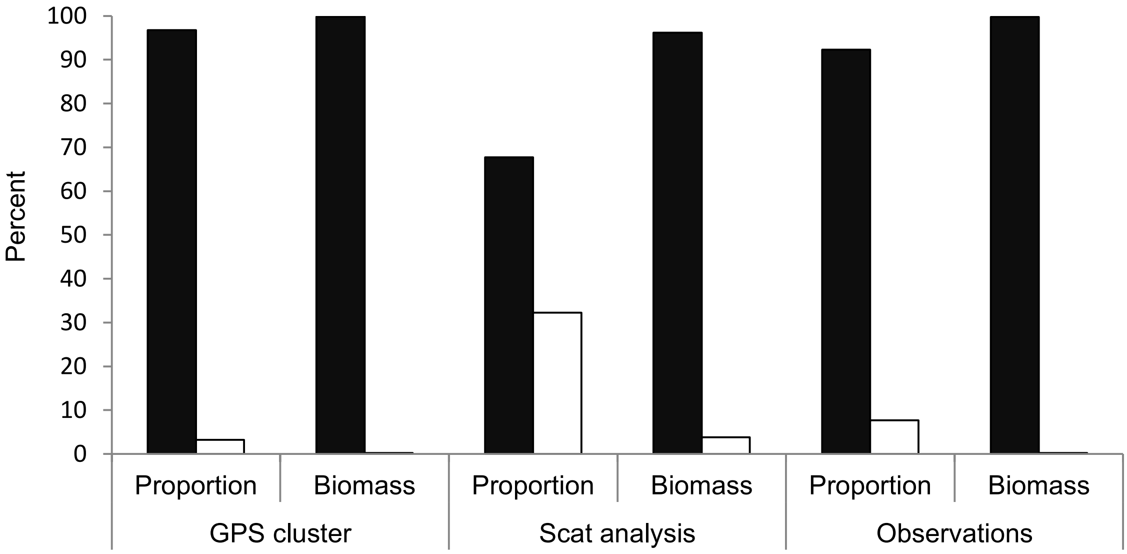


Figure 3.3 Proportional lion diet composition and biomass contributions of large prey (≥ 50 kg; black bars) and small prey (≤ 50 kg; white bars).

A total of 221 lion scats were collected (Figure 3.2), of which 79 (39%) were collected at GPS clusters. After the exclusion of scats that represented the same prey species as found at GPS clusters, a total of 189 (86%) scats could be used in analysis. The dominant prey items identified from scat analyses were gemsbok, porcupine, springbok and blue wildebeest, which constituted 82% of lion diet from scat analysis (Table 3.2). Even though small prey accounted for 32% of the prey intake recorded from scat analysis, they comprised less than 4% of the biomass intake, whereas large prey contribute to 96% of the lion biomass intake derived from scat analysis data (Figure 3.3). Only 17% of all encounters with lions (*n* = 299) were when they were feeding on a carcass (*n* = 52) (Figure 3.2). Of the observed lion feeding events, 92% constituted large prey species (≥ 50 kg) (Figure 3.3). Of the large prey identified through opportunistic observations, gemsbok, wildebeest and eland contributed to 86% of lion diet (Table 3.2). Small prey comprised 8% of opportunistic observations of lion feeding events but contributed less than 0.5% to the biomass intake (Figure 3.3).

The age and sex of prey species could be determined for 46% (*n* = 128) of all identifiable GPS cluster lion feeding records. A further 66 records (70% of GPS cluster feeding event records) could be identified as adults but the sex was unknown. These GPS cluster records revealed that 79.2% of all kills were adults, 15.1% were juveniles and 5.7% were calves (Table 3.3). Of the adults where sex could be identified 61.4% were males (*n* = 54) and 38.6% were females (*n* = 34). Adult males were taken predominantly with respect to ostrich (85.7%), blue wildebeest (60%) and gemsbok (65.6%). Females were taken most frequently with respect to eland (100%) and red hartebeest (80%), although the sample sizes are probably too small for robust deductions.

Table 3.3 The sex and age structure of large prey species, derived from carcass remains that were located at GPS cluster points.

	Sex		**Age**		
	Female	**Male**	**Adult**	**Juvenile**	**Calf**
Gemsbok	22	42	110	27	9
Blue Wildebeest	2	3	16	0	0
Eland	5	0	10	1	0
Red Hartebeest	4	1	7	1	2
Ostrich	1	6	7	0	0
Kudu	0	2	2	0	0
Total	34	54	152	29	11

3.3.2 Optimal sample size

The difference in Monte Carlo simulation calculations of lion diet composition at different sample intensities, as reflected by Bray-Curtis and Euclidean distance estimations, showed that, as expected, the ecological distances were greater within smaller sample sizes, and decreased as the sample size increased (Figure 3.4). The mean ecological distance for GPS clusters, derived from a 1000 simulations out of the reference sample across all sampling intensities, was minimal for both Bray-Curtis (0.49, range 0.4 – 0.5) and Euclidean distances (0.05, range 0 – 0.05). For scat analysis, the mean value for both Bray-Curtis (0.46, range 0.3 – 0.5) and for Euclidean distances (0.06, range 0 – 0.40) also showed little variability from the reference sample. However, the mean ecological distance for opportunistic observations was higher than it was for GPS cluster analysis and scat analysis for both Bray-Curtis (0.39, range 0.0 – 0.5) and Euclidean distances (0.15, range 0.0 – 1.3) (Figure 3.4).

The minimum sample size required to give an accurate representation of lion diet was identified when homogeneity of variance was achieved (*F-max* ≤ tabulated *f-value*) for both the Bray-Curtis ($F\text{-}max_{bc}$) and Euclidean distances ($F\text{-}max_{eu}$). For GPS cluster analysis, even though homogeneity of variance (*F-max* ≤ 1.67) was reached on occasion before 65 samples, it was not consistent throughout, for instance at 60 samples homogeneity of variance was not achieved. Therefore, homogeneity had not yet been achieved for GPS clusters before 65 samples (Table 3.4). For GPS cluster analysis, homogeneity of variance was reached again at 65 samples ($F\text{-}max_{bc} = 1.12$; $F\text{-}max_{eu} = 1.02$) and was then maintained at sample sizes greater than 65 (Table 3.4). For scat analysis, homogeneity of variance ($F\text{-}max \leq 1.67$) was achieved at 55 samples ($F\text{-}max_{bc} = 0.96$; $F\text{-}max_{eu} = 1.14$) and was maintained at sample sizes greater than 55 (Table 3.4). The mean ecological distance between the diet profile obtained from the total sample size of 268 GPS clusters and that obtained from 65 samples was nominal for both the Bray-Curtis (0.49) and Euclidean distances (0.05). The minimum of 55 samples identified for scat analysis also showed nominal mean distances from the reference sample (Bray-Curtis 0.45 and Euclidean 0.09), confirming that a sufficient sample size had been achieved. Homogeneity of variance was not obtained for opportunistic observations as the *F-max* value remained greater than the tabulated value (1.67) at 45 to 50 samples for the Euclidean distance ($F\text{-}max_{eu}= 1.71$; $F\text{-}max_{bc} = 0.17$). Therefore, the sample size of 52 samples obtained for opportunistic observations was identified as insufficient to provide an accurate representation of lion diet in the KGNP.

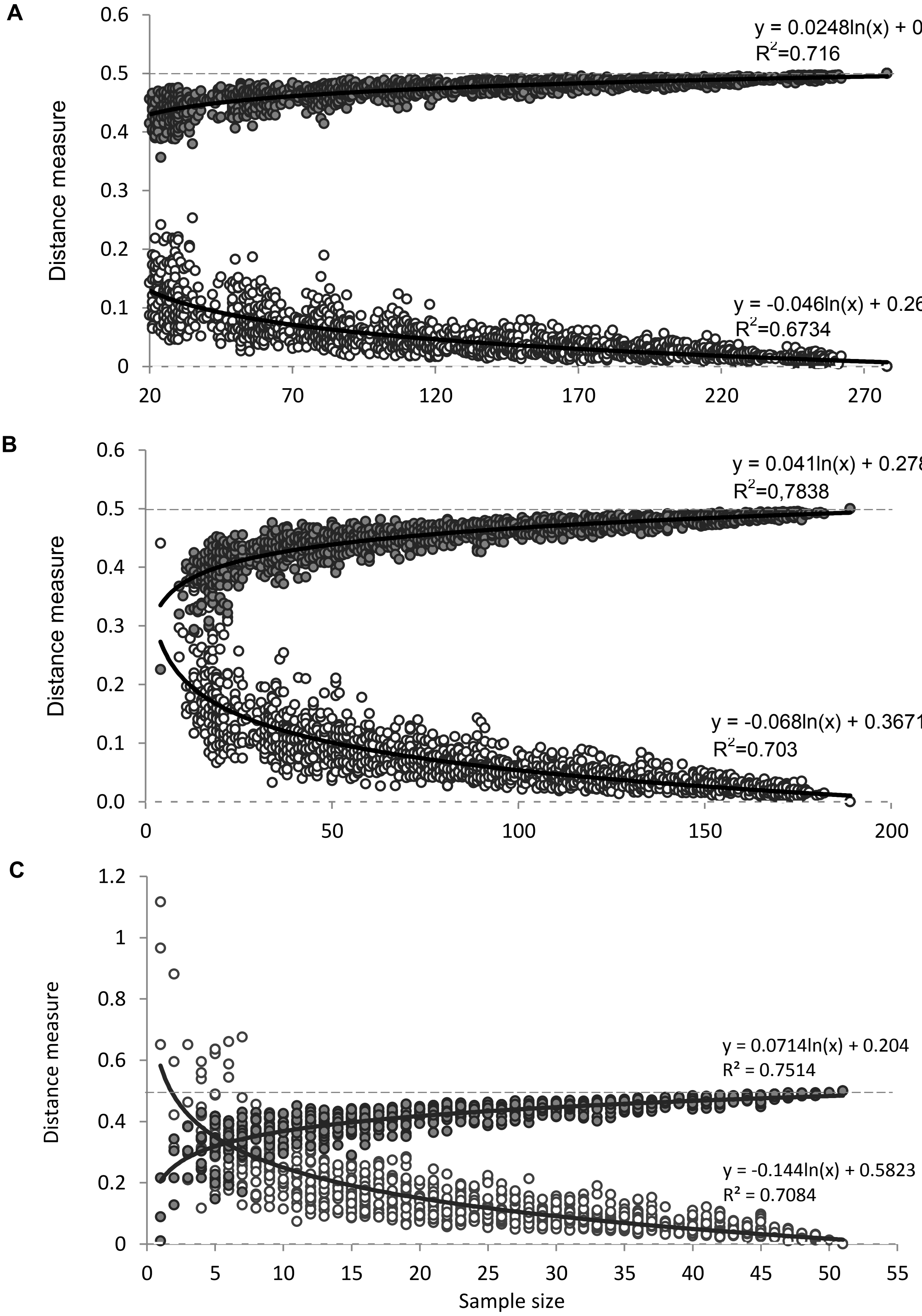


Figure 3.4 The difference in 1000 Monte Carlo simulation calculations of lion diet composition at different sample intensities, as reflected by Bray-Curtis (grey symbols) and Euclidean (white symbols) distance estimations for GPS cluster analysis (A), scat analysis (B) and opportunistic observations (C). The reference samples are represented at “0.5” for the Bray-Curtis distance and at “0” the Euclidean distance. Logarithmic trendlines (black lines) represent the fitted relationship between ecological distances and the rate of change in data by indicating the general course or tendency. The ecological distances were greater for smaller sample sizes, and decreased as the sample size increased.

Table 3.4 A summary of variance between the Euclidean and Bray-Curtis distances at ascending increments of sample size (*df* = 1) for scat analysis and GPS cluster analysis. Homogeneity of variance was achieved when the F-max value was identified to be less and remained less, across all larger sample sizes, than the F-max tabulated value of 1.67 for both the Bray-Curtis and Euclidean distances. The point at which homogeneity of variance was obtained for both scat analysis and GPS cluster analysis is presented in italics. Opportunistic observations did not reach homogeneity and are thus not presented.

No. Samples	**Scat**		**GPS cluster**	
	***F-max* Value: Euclidean Distance**	***F-max* Value: Bray-Curtis Distance**	***F-max* Value: Euclidean Distance**	***F-max* Value: Bray-Curtis Distance**
40 – 44	1.059	1.187	1.613	1.250
45 – 49	1.168	1.036	1.134	1.030
50 – 54	1.833	1.681	1.270	1.304
55 – 59	*1.138*	*0.960*	1.353	1.097
60 – 64	1.324	1.295	2.390	2.417
65 – 69	0.823	0.917	*1.019*	*1.119*
70 – 74	1.559	0.580	0.503	0.523
75 – 79	1.559	1.051	0.517	0.584
80 – 84	1.101	1.051	0.527	0.479

3.3.3 Sample effort

A total of 49 784 km were driven in search of lions and signs of their activities across the KGNP. The average number of kilometres driven per sample collected was substantially higher for opportunistic observations of lion kills (957 km per sample) than for lion scat collection (263 km per sample) (Table 3.5). Throughout the KGNP, 4 200 km were travelled in search of prey remains at GPS cluster points (Table 3.5). The average distance travelled between GPS clusters investigated (*n* = 823) was 5 km and an average of 15 km were driven between clusters where identifiable evidence of lion kills were found (*n* = 278).

GPS collars fitted to seven adult female lions across the study period amounted to a total of 2 028 collar days. There were on average seven days between identifiable feeding event records from the GPS cluster points that were investigated. The minimum sample size of 65 samples required to obtain an accurate representation of lion diet from GPS cluster analysis, was obtained within approximately 90 sample days, using five active GPS collars and investigating 97 cluster points. Approximately 263 km were driven per lion scat collected (Table 3.5), obtaining a minimum sample size of 55 lion scats, required 93 sample days, in which 14 487 km were driven. Only 52 opportunistic observations of lions feeding on a carcass were recorded over 317 field days and travelling 49 784 km, which amounts to approximately 957 km per opportunistic feeding sighting (Table 3.5).

Table 3.5 An indication of sample effort derived from the number of kilometres driven and sample days per sample technique and per sample collected for lion scat analysis, GPS cluster analysis and opportunistic observations.

	Scat	**GPS cluster**	**Observations**
Kilometres driven	49784	4200	49784
Kilometres per sample	263	166	957
Sample days	317	370	317
Days per sample	1.7	1.2	6.1

Scat analyses revealed the highest number of prey items (*n* = 11) while GPS clusters and opportunistic observations showed less diversity with a total of 9 species identified through both methods. All species that were observed to be consumed by lion using GPS cluster analysis were identified after the investigation of 250 GPS clusters points which included ± 350 collar days, using five active GPS collars, and travelling 3 500 km. All species that were observed to be consumed by lion using scat analysis were identified after the collection of 160 lion scat samples, which took ± 270 sample days and traveling 42 145 km across the dune and riverbed habitats. After 50 opportunistic observations of lions feeding on a carcass, all species that were observed to be consumed by lion using opportunistic observations were identified, which took ± 310 sample days and travelling 47 869 km across the dune and riverbed habitats.

3.3.4 Comparison of methods used to identify lion diet

Chi-square tests revealed a significant difference between the results of all methods used in identifying lion (Table 3.6). Scat analysis differed significantly from GPS cluster analysis ($\chi2$ = 77.22, *df* = 5, *p* = <0.01) specifically between gemsbok ($\chi2$ = 38.29, *df* = 1, *p* = <0.01) and in the "other large prey" category comprising ostrich and kudu ($\chi2$ = 8.07, *df* = 1, *p* = <0.01), with a higher detection and proportional representation of gemsbok, kudu and ostrich in GPS cluster analysis than in scat analysis (Table 3.2). Scat analysis also differed significantly from GPS cluster analysis with small prey ($\chi2$ = 38.63, *df* = 1, *p* = <0.01), as all small prey species had a higher detection probability in scat analysis, than in GPS cluster analysis. Scat analysis differed significantly from opportunistic observations ($\chi2$ = 29.27, *df* = 5, *p* = <0.01), with gemsbok ($\chi2$ = 44.78, *df* = 1, *p* = <0.01), red hartebeest ($\chi2$ = 4.5, *df* = 1, *p* = 0.04) and small prey ($\chi2$ = 47.51, *df* = 1, *p* = <0.01) being detected more frequently in lion diet using scat analysis than in opportunistic observations. GPS cluster analysis and opportunistic observations differed significantly ($\chi2$ = 30.54, *df* = 5, *p* = <0.01) with blue wildebeest ($\chi2$ = 5.49, *df* = 1, *p* = 0.02) being detected more frequently and contributing more to the lion diet profile obtained through opportunistic observations than from GPS cluster analysis. Gemsbok ($\chi 2$ = 143.4, *df* = 1, *p* = <0.01), red hartebeest ($\chi 2$ = 10.29, *df* = 1, *p* = <0.01) and other large prey (ostrich and kudu, $\chi 2$ = 10.29, *df* = 1, *p* = <0.01) were detected significantly more in the lion diet profile obtained through GPS cluster analysis than from opportunistic observations (Table 3.6).

Table 3.6 Comparison of the scat analysis (Scat), GPS cluster (Cluster) methods used to identify lion diet in the KGNP indicating the Degrees of Freedom (*df*) and depicting results for left tailed Chi-square test (χ 2) and P-value (*p*).

	Scat vs Cluster			**Scat vs Observed**			**Cluster vs Observed**		
	χ 2	***df***	***p***	**χ 2**	***df***	***p***	**χ 2**	***df***	***P***
Gemsbok	38.29	1	<0.01	44.78	1	<0.01	143.4	1	<0.01
Blue wildebeest	3.27	1	0.07	0.31	1	0.58	5.49	1	0.02
Eland	1.32	1	0.25	0.25	1	0.62	0.43	1	0.51
Red hartebeest	1.8	1	0.18	4.5	1	0.04	10.29	1	<0.01
Other large prey	8.07	1	<0.01	0.33	1	0.56	10.29	1	<0.01
Small prey	38.63	1	<0.01	47.51	1	<0.01	1.14	1	0.29
Total	77.22	5	<0.01	29.27	5	<0.01	30.54	5	<0.01

3.3.5 Prey relative abundance

The relative prey abundances indices (RAI) varied between the dune and riverbed habitat types, most notably for springbok which had a 3% RAI in the dunes (95% *CI* = 0.3 – 6.4) and a 57% RAI in the riverbeds (95% *CI* = 50.8 – 62.2) (Figure 3.5). Wildebeest RAI was higher in the riverbeds at 19%, (95% *CI* = 15.5 – 21.7), than in the dunes where they only contributed 1.4%, (95% *CI* = 0.0 – 2.9) to the total availability of prey. The RAI of gemsbok was substantially higher in the dunes at 45%, (95% *CI* = 40.0 – 50.9), than the riverbeds at 14.6%, (95% *CI* = 9.4 – 19.8) (Figure 3.5). Due to the conspicuous differences in the RAI of prey between the dune and riverbed habitat types the road transect game counts conducted in the dunes and riverbeds were weighted to provide a more accurate representation of the overall prey availability across the KGNP.

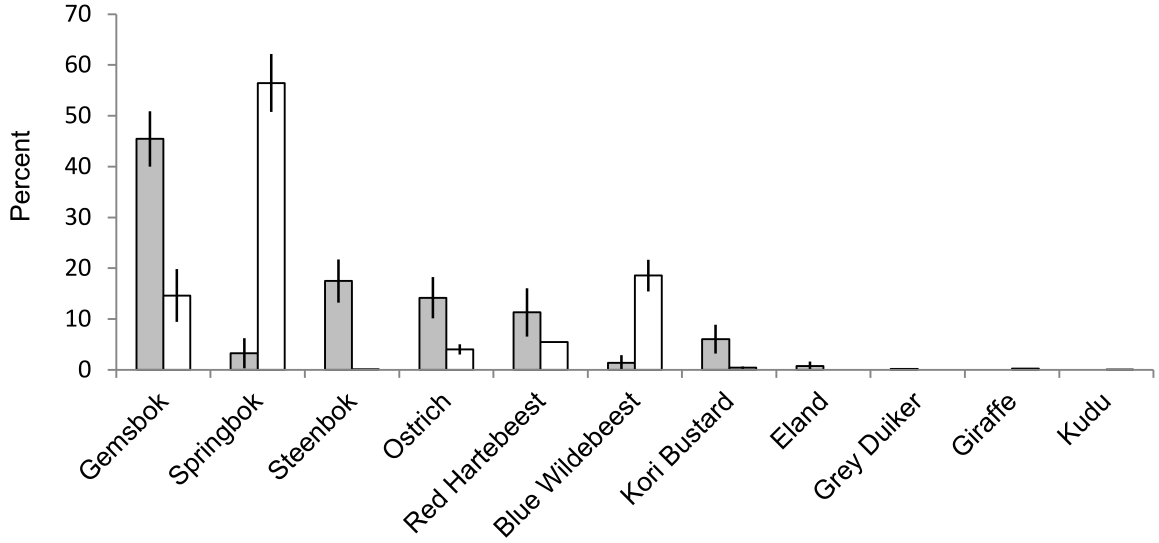


Figure 3.5 The relative abundance indices of prey in the KGNP derived from road transect game counts conducted in the dunes (grey bars) and riverbeds (white bars). Error bars represent the 95% confidence intervals derived from 15 game counts conducted in the dunes and 15 game counts conducted in the riverbeds.

Weighted road transect game counts are presented together with the aerial game count conducted across the KGNP in 2013 (Figure 3.6). Gemsbok was the most abundant species in both weighted road transect game counts at 41% (95% *CI* = 36.3 – 45.3) and the aerial game count at 45% (95% *CI* = 41 – 48). The second most abundant species for weighted road transect game counts was steenbok at 15% (95% *CI* = 11.2 – 18.5), whereas for the aerial game counts it was springbok at 15% (95% *CI* = 0.0 – 32.7) (Figure 3.6). Blue wildebeest had a higher representation in the aerial game count at 8% (95% *CI* = 3.2 – 12.6) than in weighted road transect game counts at 4% (95% *CI* = 2.5 – 5.4). Springbok accounted for 11% (95% *CI* = 95% 8.4 – 14.1) of the proportional prey availability for weighted road transect game counts. In both weighted road transect game counts and the aerial census game count, eland occurred the infrequently with 1%, (95% *CI* = 0.0 – 1.4) and 6% (95% *CI* = 2.5 – 9.4) respectively. Giraffe, grey duiker and kudu were not included in the overall abundance estimates for the aerial game count data (Ellis & Herbst, 2013) and had a very low RAI for weighted road transect game counts (Figure 3.6).

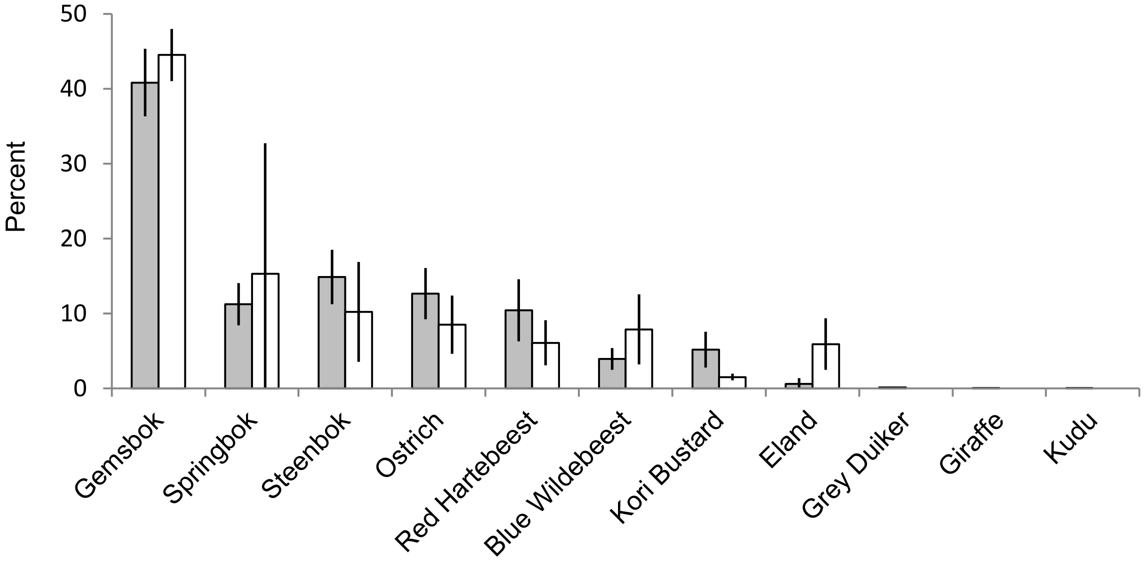


Figure 3.6 The relative abundance indices of prey in the KGNP derived from weighted road transect game counts (grey bars) and an aerial game count conducted in September 2013 (white bars) (Ellis & Herbst, 2013). Error bars represent the 95% confidence intervals derived from 15 weighted game counts and the aerial census data provided by SANParks (Ellis & Herbst, 2013).

3.3.6 Prey preferences

Jacobs' indices for GPS cluster analysis, scat analysis and opportunistic observations revealed that lions showed preference for large prey (> 50 kg) (Figure 3.7). Overall, eland seemed to be the most preferred prey species when tested against prey availabilities, derived from both weighted road transect game count data (D_{gps} = 0.76, D_{sca} = 0.72, D_{obs} = 0.94) and aerial game count data (D_{gps} = 0.19, D_{sca} = 0.11 , D_{obs} = 0.74). All methods indicated that wildebeest was preferred when tested against weighted road transect game count data (D_{gps} = 0.46, D_{sca} = 0.38, D_{obs} = 0.78) and aerial game count data (D_{gps} = 0.20, D_{sca} = 0.10, D_{obs} = 0.63). All methods indicated that springbok (road transect game counts D_{gps} = -0.94, D_{sca} = -0.07, D_{obs} = -1.0; aerial game counts D_{gps} = -0.98, D_{sca} = -0.48, D_{obs} = -1.0), ostrich (road transect game counts D_{gps} = -0.59, D_{sca} = -0.93, D_{obs} = -0.75; aerial game counts D_{gps} = -0.34, D_{sca} = -0.87, D_{obs} = -0.57) and hartebeest (road transect game counts D_{gps} = -0.41, D_{sca} = -0.50, D_{obs} = -0.70; aerial game counts D_{gps} = -0.28, D_{sca} = -0.39, D_{obs} = -0.62) were avoided (Figure 3.7).

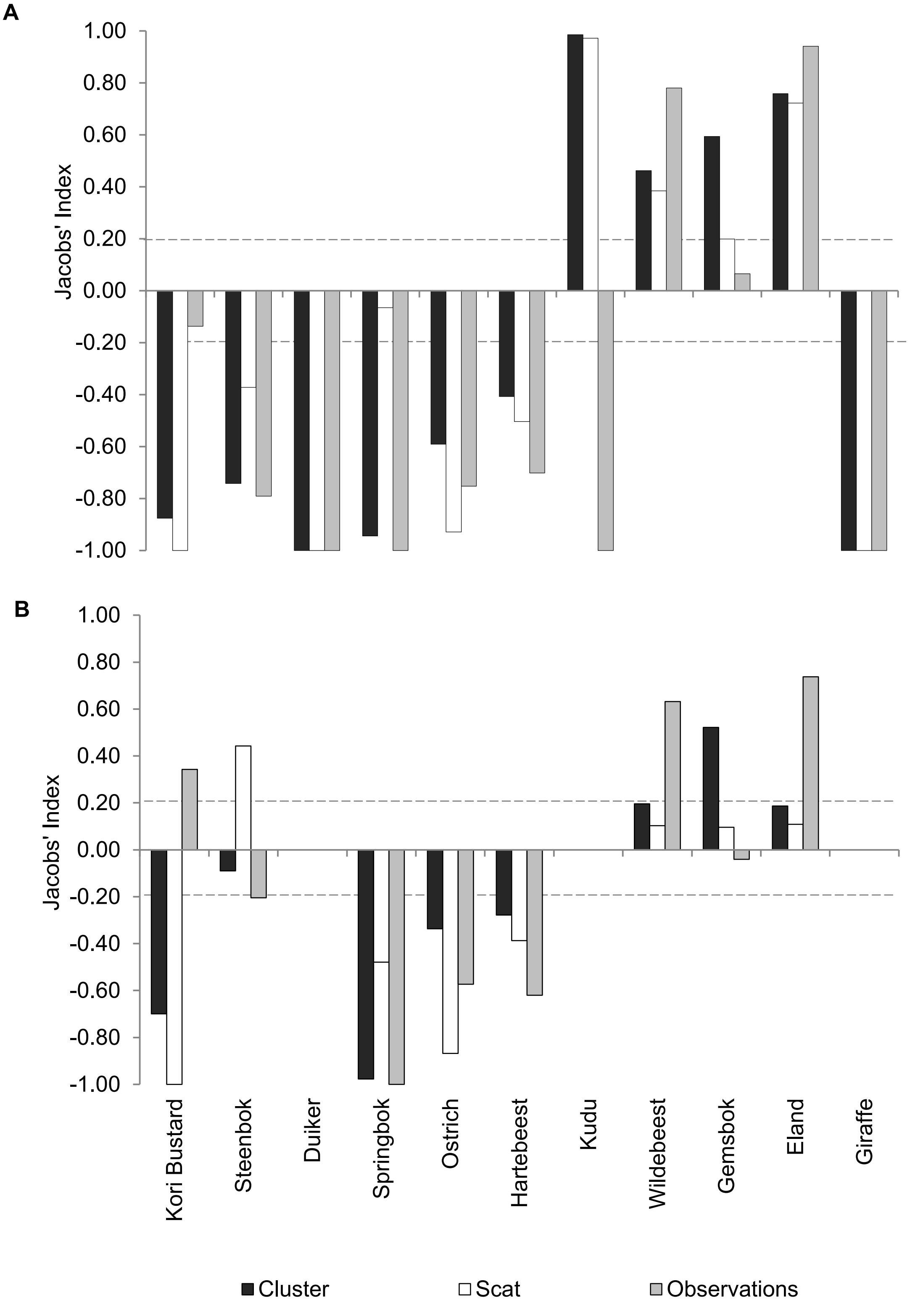


Figure 3.7 Results from Jacobs' index test, which provides an indication of prey preference by comparing the proportion of prey consumed to the proportional prey availability. Figure A compares lion diet to the proportional prey availability derived from weighted road transect game counts in the KGNP, whereas Figure B compares lion diet to proportional prey availability derived from aerial game counts in the KGNP. Data on the proportional prey availability was not available for duiker, kudu and giraffe for the aerial game count and therefore these species are not included in Figure B. Values of greater than 0.2 signifies preference and less than -0.2 signifies avoidance (dashed lines). Values between indicated that the species was consumed proportionally to what was available.

For weighted road transect game count data lions also showed preference for gemsbok (D_{gps} = 0.59, D_{sca} = 0.2) and kudu (D_{gps} = 0.99, D_{sca} = 0.97) and in all methods showed avoidance for Kori bustard (D_{gps} = -0.88, D_{sca} = -1.0, D_{obs} = -0.14), steenbok (D_{gps} = -0.74, D_{sca} = -0.37, D_{obs} = -0.79) and duiker (D_{gps} = -1.0, D_{sca} = -1.0, D_{obs} = -1.0). For aerial game count data, lions also showed preference for gemsbok (D_{gps} = 0.52) and avoidance was indicated for steenbok (D_{obs} = -0.28) and Kori bustard (D_{gps} = -1.0, D_{sca} = -1.0). A marginal preference was indicated for steenbok (D_{sca} = 0.44) and for Kori bustard (D_{obs} = 0.34) using aerial game count data (Figure 3.7). No aerial game count data was available for the RAI of duiker, kudu and giraffe and therefore, these species were not included in the prey preference analysis for the aerial census game count. There was no significant difference found, using ANOVA, in the prey preferences between the weighted road transect game counts and aerial game counts derived from GPS cluster analysis (f = 0.01, df = 1, p = 0.91), scat analysis (f = 0.34, df = 1, p = 0.86) or opportunistic observations (f = 0.10, df = 1, p = 0.76).

3.4 Discussion

Due to the arid environment of the Kalahari, natural resources are limited, resulting in low densities of lions as well as their associated prey (Eloff, 1984b; Mills, 2015). The low population density of lions and the limitations associated with various survey techniques can provide challenges in accurately determining the diet profile of lion in the KGNP. Extensive survey efforts were required in order to acquire a sufficient sample size that would accurately depict lion diet in an arid environment. To obtain the diet profile of lion in the KGNP three techniques that are widely used in discerning predator diet were used, including GPS cluster analysis (Tambling et al., 2010; Pitman et al., 2012), scat analysis (Floyd et al., 1978; Mukherjee et al., 1994) and opportunistic observations (Mills, 1984; Radloff & du Toit, 2004; Rapson & Bernard, 2007; Owen-Smith & Mills, 2008a). A combination of methods was used because each method, when applied independently, provides inherent bias in the results (Mills et al., 1978; Tambling et al., 2012).

Scat analysis provided the most holistic representation of lion diet as it identified the highest diversity of prey items including both small and large prey species. If a sufficient sample size can be obtained, scat analyses can provide a representative account of lion diet (Mills, 1992). However, scat analysis may over-represent the contribution of small prey species (Floyd et al., 1978; Ruhe et al., 2008). Out of all the methods applied in this study, scat analysis yielded the highest proportional representation of small prey (32%) as well as the highest diversity of prey species (n = 11). Other lion dietary studies that made use of the scat analysis technique also show that a wider variety of prey, including small prey, is able to be detected using scat analysis (Breuer, 2005; Banerjee et al., 2013; Davidson et al., 2013).

It was identified that a minimum sample size of 55 lion scats were needed to obtain a representative interpretation of lion diet. This is in standing with the recommended methods and sample size (59 scats) required for dietary interpretation using the scat analysis technique, in a study conducted on Steller sea lions (Trites & Joy, 2005) but lower than the sugested sample size of 70 scats for lions (Breuer, 2005). The main factor limiting the efficacy of the scat analysis technique in the KGNP are the extensive efforts required (approximately 260 km per scat collected and aided to some extent by GPS collars), in order to collect an adequate sample size. Sample acquisition of lion scats was slower in the summer months (November to April) than in winter (May-October), owing to the rapid removal and deterioration of scat by coprophagous insects and rain during the wet season (Tambling et al., 2012; Davidson et al., 2013). It was identified that a minimum sample size of 65 records of lion feeding events from GPS cluster points were needed to obtain a representative interpretation of lion diet. The effort required to obtain 65 feeding event records from GPS clusters included approximately 90 sample days, using five active GPS collars and investigating 97 cluster points. Clusters were investigated on average 33 days after occurrence. A study conducted on the use of GPS clusters to detect lion kills in the Kruger National Park found no difference in the likelihood of detecting prey remains between four and fourteen weeks after the cluster occurred (Tambling et al., 2010).

Of all the methods applied in this study, opportunistic observations of lion kills was the least effective and least feasible method of determining lion diet in the KGNP. This is due to the extensive time periods required for data collection and minimal return on data acquisition for opportunistic observations in comparison to the GPS cluster and scat analysis methods. Lion feeding event data obtained from opportunistic observations was skewed towards findings obtained in the riverbed habitat. Lion kills were opportunistically encountered more frequently in the riverbeds (79%) and less frequently in the dunes (21%). The riverbed habitat has a road network that provides a more extensive and representative coverage of the riverbed habitat, than that of the road network coverage of the dune habitat. The dune habitat is vast and has a limited road network in proportion to the total area that the dunes cover. Opportunistic observations provided a much higher proportional representation of blue wildebeest, which is a species that is found almost exclusively within the riverbed habitat, than the other methods. Previous lion dietary studies conducted in the KGNP also identified that feeding event records from opportunistic observations could skew data towards prey species that frequent the riverbeds (Mills, 1984). However, ad-hoc opportunistic observations of lion feeding events collected by park staff, over extended time periods, can provide useful insights into lion dietary trends, provided that sufficient sample sizes can be obtained (Mills, 1984; Radloff & du Toit, 2004). Notwithstanding, a sufficient sample size for the use of opportunistic observations to define lion diet has not been identified for the KGNP. A study conducted historically on carnivore diet in the KGNP, made use of 221 opportunistic observations of lion feeding events, to derive a description of lion diet (Mills, 1984). Lion dietary data from this study was collected over an eight year period, which rendered similar return rates of data collection (± 27 records per annum) and provided similar bias as identified in the present study when using opportunistic observations in the KGNP.

In this study, opportunistic observations and GPS cluster analysis techniques revealed less diversity of prey in lion diet than the scat analysis technique, as a result of under-representing the smaller prey species in lion diet. Other studies have also indicated that small mammals are under-represented in lion diet using the opportunistic observation (Mills, 1984; Rapson & Bernard, 2007; Owen-Smith & Mills, 2008b) and GPS cluster analysis techniques (Bacon et al., 2011; Tambling et al., 2012). It has been found that if GPS cluster analysis were to be supplemented with scat analysis, such as using lion scat found at GPS cluster points, it could provide a relatively accurate chronological interpretation of lion diet, as well as reduce the bias towards large prey species (Tambling et al., 2012). In this study the GPS cluster analysis technique yielded the highest number of kills over the shortest time frame. GPS cluster analysis has the added advantage of providing GPS locality data which can be used to further investigate predator-prey dynamics as well as lion foraging dynamics and demographics (Anderson & Lindzey, 2003; Sand et al., 2005; Merrill et al., 2010; Tambling et al., 2010; Pitman et al., 2012). Even though GPS cluster analysis may under-represent small prey items, it still provides valuable information into the lion diet profile of large prey species, which remain the major contributors (~ 98%) to lion biomass intake. The GPS cluster analysis technique is however limited by the relatively high costs and logistical challenges, associated with the capture of animals, to put on and remove GPS collars from study subjects (Boitani & Fuller, 2000; Frair et al., 2010; Hebblewhite & Haydon, 2010).

Even though continuous follows are widely regarded as the most effective method of determining lion diet (Mills, 1992), in the current study it was found that this method is not suitable in the KGNP. During the study, four adult female lions were followed for continuous periods of between two to four days, to observe foraging behaviour. Only one feeding event (of a porcupine) was observed during 21 days of continuous follows. Following lions at night across the dune landscapes, which can be difficult to navigate by vehicle, was observed to cause a disturbance to prey and seemed to hinder the lions ability to hunt, especially when conducted at night. Lions rely on ambushing prey (Schaller, 1972; Scheel & Packer, 1991; Stander, 1992a) and the presence and noise from a vehicle may alarm prey and prompt them to move off, before lions are presented with an opportunity to hunt. It was therefore decided to cease continuous follows. Considering the perceived disturbance caused to lions’ hunting abilities by continuous follows, it is recommend that continuous follows of lions through the night should not be conducted in the KGNP

The affinity for lions to target large prey is well documented across their range (Stander & Albon, 1993; Radloff & du Toit, 2004; Hayward & Kerley, 2005; Davidson et al., 2013), although lions are known to have a catholic diet taking a wide range of prey including small prey species such as steenbok, porcupine and springhare (Eloff, 1984a; Stander & Albon, 1993; Sinclair et al., 2003; Stander, 2003; Roxburgh, 2008). In this study large herbivores dominated the lion diet profile obtained from GPS cluster analysis (96.8%) and opportunistic observations (92.3%). This is largely because small prey species are consumed quickly, and often entirely, and were thus seldom detected using these methods (Mills, 1992; Tambling et al., 2012). Lions are inefficient at catching smaller prey species, from which the energetic profitability is low, but will attempt a hunt when an opportunity presents itself (Sinclair et al., 2003). Scat analysis revealed that small prey contributed more significantly (32%) to the overall lion diet profile. Scat analysis therefore provided a lion dietary profile for both small prey and large prey. Even though it is a useful method to determine lion diet, the scat analysis technique is restricted in that it does not depict the age and sex profile of prey consumed (Breuer, 2005) and misidentification of scat collected may provide prejudice in results (Farrell et al., 2000).

Of all the lion feeding events recorded through GPS cluster analysis, where age could be determined, 79% were adults. In GPS cluster analysis the juveniles and calves of herbivores contributed to 21% of lion feeding event records. A larger sample size for the age and sex profile of gemsbok was obtained than for other prey species and revealed a somewhat larger contribution of prey in the juvenile and calf age category (25%). Due to the small body size of juveniles and calves, it is likely that they are consumed quickly with fewer remains being left behind. Therefore, juveniles and calves may have been underrepresented in the lion diet profile obtained from GPS cluster analysis. However, estimates from two previous studies conducted in the KGNP, suggest that juveniles and calves contribute on average 22% (Eloff, 1984a) and 25% (Mills, 1984) to lion diet, which are similar proportions to what was found in the current study. In the adult age category, where sex could be identified, lions showed a predisposition towards male gemsbok (66%), which is in standing with a previous study that found a ratio of one male taken for every 0.6 females in the KGNP (Mills, 1984).

In all methods used, gemsbok was identified as the primary prey species of lions, and consequently, may be influential in determining lion population density and survival rates in the KGNP. Gemsbok are the most widespread and abundant species in the KGNP occupying the dunes and riverbed areas alike (Van Der Walt et al., 1984). Gemsbok's sedentary nature (Mills, 2015) and specialized adaptations to arid environments (Knight, 1995) make them a reliable food source for lion in the KGNP throughout the year.

Interestingly however, lions did not show a high degree of preference for gemsbok, meaning that gemsbok were neither preferred nor avoided but rather consumed in relation to their availability.

Out of all the prey species observed to be consumed by lion in KGNP, lions showed the highest rates of preference for eland. Eland were also the largest (♀ = ± 460 kg, ♂ = ± 650 kg, Skinner & Chimimba, 2005) of the prey species predated on by lions in the KGNP. Eland contributed 17% to lion diet observed through opportunistic observations but contributed 35% to the lion biomass intake observed through opportunistic observations. Eland are nomadic across the KTP and may seasonally occur in large herds (Eloff, 1962; Verlinden, 1998). Large herd size increases vigilance and makes eland more difficult to hunt (Hayward & Kerley, 2005). Because eland form herds and are nomadic, they are less widely distributed and are infrequently encountered in the KGNP. Based on their low encounter rates in the KGNP, eland are hunted by lion more frequently than would be expected.

Springbok and blue wildebeest are seldom encountered in the dunes and are found almost exclusively in the riverbeds and pans (Eloff, 1962) which cover only approximately 15% of the KGNP (Van Rooyen et al., 2008). Thus, lions are only likely to come into contact with, and have the opportunity to hunt springbok and wildebeest in the riverbed habitat. To capture prey, lions make use of stalking and ambushing prey from concealed locations (Schaller, 1972; Scheel & Packer, 1991; Stander, 1992b). The riverbeds and pans are mostly covered with intensively grazed, low vegetation (Van Rooyen et al., 1994) providing limited cover from which lions would be able to ambush prey. This, in conjunction with their low biomass yield, could contribute to why springbok are infrequently predated on by lion (Stander & Albon, 1993). And why wildebeest, for which lions show preference, only contribute ~ 10% to lion diet.

Across the dunes steenbok and ostrich are widespread and thus have a relatively high proportional availability, although they are avoided by lions in the KGNP. Avoidance for steenbok and ostrich has also been observed in other areas (Hayward & Kerley, 2005) and is likely to be as a result of their relatively low energetic profitability (Radloff & du Toit, 2004; Hayward et al., 2011).

Resource limitations in arid areas drive carnivores to develop specialized hunting techniques that focus on specific prey species (Mills, 2015). Lions significantly prefer large prey within the weight range of 150 - 650 kg including kudu, wildebeest, gemsbok and eland, and avoided prey in the size categories of small (< 50 kg) and megaherbivores (≥ 1 000 kg) (Owen-Smith, 1988), such as springbok and giraffe. It may be of little relevance that small prey were underrepresented in the lion diet profile, using the opportunistic observations and GPS cluster analysis techniques, as they contributed to less than 4% of the total biomass intake of lion in all methods. Instead, smaller prey species are likely to serve as opportunistic “top-ups” to lion diet between large kills (Eloff, 1984a). This could be particularly pertinent to lions hunting alone, as hunting success generally increases with increased pride size (Scheel & Packer, 1991; Packer & Pusey, 1997). Small prey items may also be of particular importance during periods of drought, when large herbivores experience high mortality rates (Knight, 1995) and certain species are prone to migration out of the KGNP (Verlinden, 1998). If large herbivore populations where to dwindle, it is possible that small prey species would contribute more significantly to lion diet, although they are unlikely to meet the daily biomass requirements of lions (Stander, 1992b).

Large herbivore dynamics of prey species within the preferred weight range (150 - 650 kg) are likely to be key drivers of the lion population in the KGNP (Ferreira & Funston 2010). Changes in the dynamics of these herbivores are likely to influence lion density, demography as well as pride dynamics (Valeix et al., 2009). In consequence, identifying changes in lion diet as well as herbivore dynamics may help identify ecosystem changes that may impact lion survival in the KGNP.

To identify the lion diet profile in an arid area it is recommend to use a combination of GPS cluster analysis and scat analysis. Combining these methods will augment the information obtained from these methods when applied independently. Supplementing GPS cluster analysis with lion scat analysis will help overcome the bias of over or underrepresenting certain prey species within lion diet (Tambling et al., 2012). This technique could be further modified to profile lions and identify prey through the use of DNA analysis. Even though it is costly and is still largely in developmental stages, DNA analysis can be used to determine the prey species consumed using prey remains found in scat, as well as identify the predator from mucosal cells transferred from the predator’s gut onto the faeces (Reed et al., 1997; Piggott & Taylor, 2003; Casper et al., 2007; Marnewick et al., 2007). The identification of a predator can be refined to recognise individuals within a population, which can be used to provide an indication of population size (Mills et al., 2000; Kindberg et al., 2001). Combining GPS cluster analysis, scat analysis and DNA analysis may thus provide a non-invasive, reliable representation of lion diet, whilst also be applied to provide information on lion demographics.

The data presented in this chapter will be used in the final synthesis chapter to critically evaluate whether lion diet in the KGNP has changed over time considering the techniques used, as well as the sample sizes obtained from previous studies.

3.5 Ethics statement

Research was conducted with clearance of the Cape Peninsula University of Technology Ethics Committee (Ref. 09/2013). All necessary permits were obtained from the South African National Parks, Skakuza, South Africa; Ministry of Environment, Wildlife and Tourism, Gaborone, Botswana; and the Department of Environment and Nature Conservation, Northern Cape, South Africa.

3.6 References

Anderson, C.R. & Lindzey, F.G. 2003. Estimating cougar predation rates from GPS location clusters. *The Journal of Wildlife Management*, 67(2): 307–316.

Anonymous. 2008. *Kalahari Gemsbok National Park management plan*. South African National Parks. Pretoria, South Africa.

Bacon, M.M., Becic, G.M., Epp, M.T. & Boyce, M.S. 2011. Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. *Wildlife Society Bulletin*, 35(4): 409–415.

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(3): 315–323.

Banerjee, K., Jhala, Y. V., Chauhan, K.S. & Dave, C. V. 2013. Living with Lions: The Economics of Coexistence in the Gir Forests, India. *PLoS ONE*, 8(1): e49457.

Becker, M.S., Watson, F.G.R., Droge, E., Leigh, K., Carlson, R.S. & Carlson, A. a. 2013. Estimating past and future male loss in three Zambian lion populations. *Journal of Wildlife Management*, 77(1): 128–142.

Bergstrom, R. & Skarpe, C. 1999. The abundance of large wild herbivores in a semi-arid savanna inrelation to seasons, pan and livestock. *African Journal of Ecology*, 37: 26–37.

Boitani, L. & Fuller, T.K. 2000. *Research techniques in animal ecology*. Columbia University Press, New York.

Bothma, J.D.P. & De Graaff, G. 1973. A habitat map of the Kalahari Gemsbok National Park. *Koedoe*, 16(1): 181–188.

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27(4): 325–349.

Breuer, T. 2005. Diet choice of large carnivores in northern Cameroon. *African Journal of Ecology*, 43(3): 181–190.

Caro, T.M. 1999. Conservation monitoring: Estimating mammal densities in woodland habitats. *Animal Conservation*, 2(4): 305–315.

Casper, R.M., Jarman, S., Deagle, B.E., Gales, N. & Hindell, M.A. 2007. Detecting prey from DNA in predator scats: A comparison with morphological analysis, using Arctocephalus seals fed a known diet. *Journal of Experimental Marine Biology and Ecology*, 347: 144–154.

Castley, J.G. 2005. *Standard operating procedures for conducting aerial surveys in South African National Parks – Southern Parks.* SANParks unpublished report, SANParks, Pretoria.

Ciucci, P., Tosoni, E., Di Domenico, G., Quattrociocchi, F. & Boitani, L. 2014. Seasonal and annual variation in the food habits of Apennine brown bears, central Italy. *Journal of Mammalogy*, 95(3): 572–586.

Codron, D., Codron, J., Lee-Thorp, J. a., Sponheimer, M., De Ruiter, D., Sealy, J., Grant, R. & Fourie, N. 2007. Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, 273(1): 21–29.

Danielsson, P.E. 1980. Euclidean distance mapping. *Computer graphics and image processing*, 14(3): 227–248.

Darimont, C.T., Paquet, P.C. & Reimchen, T.E. 2007. Stable isotopic niche predicts fitness of prey in a wolf-deer system. *Biological Journal of the Linnean Society*, 90(1): 125–137.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. 2013. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid Savanna. *PLoS ONE*, 8(2). e55182.

Douglas, R.M. 1989. A new method of cross-sectioning hair of larger mammals. *South African Journal of Wildlife Research*, 19(2): 73–74.

Ellis, G. & Herbst, M. 2013. *Kalahari Gemsbok National Park aerial census report*. Unpublished report to South African National Parks. Pretoria. South Africa.

Eloff, F.C. 1962. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park. part IV. *Koedoe*, 5(1): 128–136.

Eloff, F.C. 1984a. Food ecology of the Kalahari lion. *Koedoe*, 27(2): 249–258.

Eloff, F.C. 1984b. The Kalahari ecosystem. *Koedoe*, 27(2): 11–20.

Farrell, L.E., Roman, J. & Sunquist, M.E. 2000. Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology*, 9: 1583–1590.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Ferreira, S.M., Govender, D., Herbst, M. & Ellis, G. 2012. *Lion demographic, spatial and behavioural profiles as drivers of human wildlife interaction in the Kgalagadi*. Internal report submitted to South African National Parks Board, South Africa.

Floyd, T.J., Mech, L.D. & Jordan, P.A. 1978. Relating wolf scat content to prey consumed. *Journal of Wildlife Management*, 42(3): 528–532.

Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J. & Pedrotti, L. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1550): 2187–200.

Fryxell, J.M., Mosser, A., Sinclair, A.R.E. & Packer, C. 2007. Group formation stabilizes predator-prey dynamics. *Nature*, 449(7165): 1041–1043.

Funston, P., Mills, M., Biggs, H. & Richardson, P. 1998. Hunting by male lions: ecological influences and socioecological implications. *Animal behaviour*, 56(6): 1333–1345.

Gittleman, J.L. & Harvey, P.H. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10(1): 57–63.

Haag, T., Santos, A.S., De Angelo, C., Srbek-Araujo, A.C., Sana, D. a., Morato, R.G., Salzano, F.M. & Eizirik, E. 2009. Development and testing of an optimized method for DNA-based identification of jaguar (Panthera onca) and puma (Puma concolor) faecal samples for use in ecological and genetic studies. *Genetica*, 136(3): 505–512.

Hartley, H.O. 1950. The maximum F-ratio as a short-cut test for heterogeneity of variance. *Biometrica*: 308–312.

Hayward, M.W., Hayward, G.J., Tambling, C.J. & Kerley, G.I.H. 2011. Do lions Panthera leo actively select prey or do prey preferences simply reflect chance responses via evolutionary adaptations to optimal foraging? *PLoS ONE*, 6(9): e23607.

Hayward, M.W., Hofmeyr, M., Brien, J.O. & Kerley, G.I.H. 2006. Prey preferences of the cheetah (Acinonyx jubatus) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *Journal of Zoology*, 270: 615–627.

Hayward, M.W. & Kerley, G.I.H. 2005. Prey preferences of the lion (Panthera leo). *Journal of Zoology*, 267: 309–322.

Hebblewhite, M. & Haydon, D.T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 365: 2303–2312.

Hilderbrand, G. V, Farley, S.D., Robbins, C.T., Hanley, T.A., Titus, K. & Servheen, C. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology*, 74: 2080–2088.

Jachmann, H. 2002. Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology*, 39: 841–852.

Jacobs, J. 1974. Quantitative measurement of food selection. *Oecologia*, 14(4): 413–417.

Keogh, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research*, 13(4): 91–131.

Kindberg, J., Swenson, J.E., Ericsson, G., Bellemain, E., Miquel, C. & Taberlet, P. 2001. Estimating population size and trends of the Swedish brown bear Ursus arctos population. *Wildlife Biology*, 17(2): 114–123.

Kindt, R. & Coe, R. 2005. *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF), Nairobi.

Klare, U., Kamler, J.F. & MacDonald, D.W. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review*, 41(4): 294–312.

Knight, M.H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33: 377–394.

Leblois, R., Estoup, A. & Rousset, F. 2003. Influence of mutational and sampling factors on the estimation of demographic parameters in a 'continuous' population under isolation by distance. *Molecular Biology and Evolution*, 20(4): 491–502.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134: 548–558.

Marnewick, K., Beckhelling, A., Cilliers, D., Lane, E., Mills, G., Herring, K., Caldwell, P., Hall, R. & Meintjes, S. 2007. The status of the cheetah in South Africa. *CAT News*, 3: 22–31.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology*, 283(2): 81–87.

Meikle, D.B. & Drickamer, L.C. 1986. Food availability and secondary sex ratio in wild and laboratory house mice (Mus musculus). *Journal of Reproduction and Fertility*, 78: 587–591.

Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P. & Frair, J.L. 2010. Building a mechanistic understanding of predation with GPS-based movement data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550): 2279–2288.

Mills, M.G.L. 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. *Koedoe*, 27(2): 281–294.

Mills, M.G.L. 1992. *A comparison of methods used to study food habits of large African carnivores*. In Wildlife 2001: populations: 1112–1123. McCulloch; C. & Barret; R.H. (eds). London: Elsevier.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 45(2): 127–137.

Mills, M.G.L. & Retief, P.F. 1984. The response of ungulates to rainfall along the riverbeds of the Southern Kalahari 1972-1982. *Koedoe*, 27(2): 129–141.

Mills, M.G.L., Wolff, P., Le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion in Kalahari Gemsbok National Park. *Koedoe*, 2: 163–171.

Mills, L.S., Citta, J.J., Lair, K.P., Schwartz, M.K. & Tallmon, D. a. 2000. Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. *Ecological Applications*, 10(1): 283–294.

Mukherjee, S., Goyal, S.P. & Chellam, R. 1994. Refined techniques for the analysis of Asiatic lion Panthera leo persica scats. *Acta Theriologica*, 39(4): 425–430.

Newsome, S.D., Tinker, M.T., Monson, D.H., Oftedal, O.T., Ralls, K., Staedler, M.M., Fogel, M.L. & Estes, J.A. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (Enhydra lutris nereis). *Ecology*, 90(4): 961–974.

Ott, T., Kerley, G.I.H. & Boshoff, A.R. 2007. 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(1): 31–37.

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

Owen-Smith, N. & Mills, M.G.L. 2008b. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*, 89(4): 1120–1133.

Owen-Smith, R.N. 1988. *Megaherbivores: The influence of very large body size on ecology*. Cambridge: Cambridge University Press, Cambridge.

Packer, B.C. & Pusey, A.E. 1997. Divided we fall: cooperation among lions. *Scientific American*, 265(5): 52–59.

Pearson, K. 1900. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. *Philosophical Magazine Series*, 5(50): 157–175.

Piggott, M.P. & Taylor, A.C. 2003. Remote collection of animal DNA and its applications in conservation management and understanding the population biology of rare and cryptic species. *Wildlife Research*, 30(1): 1–13.

Pitman, R.T., Swanepoel, L.H. & Ramsay, P.M. 2012. Predictive modelling of leopard predation using contextual Global Positioning System cluster analysis. *Journal of Zoology*, 288: 222–230.

Quantum GIS Development Team. 2016. QGIS Geographic Information System. Open Source Geospatial Foundation. URL http://qgus.osgeo.org.

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.

Rapson, J.A. & Bernard, R.T.F. 2007. Interpreting the diet of lions (Panthera leo); a comparison of various methods of analysis. *South African Journal of Wildlife Research*, 37(2): 179–187.

Reed, J.E. 2004. *Diets of free-ranging Mexican Gray Wolves in Arizona and New Mexico*. M.Sc.Thesis, Texas Technical University, Texas.

Reed, J.Z., Tollit, D.J., Thompson, P.M. & Amos, W. 1997. Molecular scatology: the use of molecular genetic analysis to assign species, sex and individual identity to seal faeces. *Molecular ecology*, 6(3): 225–234.

Rollett, A.D. & Manohar, P. 2004. Chapter 4 of the Monte Carlo method. Continuum scale simulation of engineering materials. In *Fundamentals-Microstructures-Process Applications*. Wiley-VCH Verlag, NY.

Roxburgh, D.J. 2008. *Prey and range use of lions on Tswalu Kalahari Reserve*. M.Sc. Thesis, University of Pretoria, Pretoria.

Ruhe, F., Ksinsik, M. & Kiffner, C. 2008. Conversion factors in carnivore scat analysis : sources of bias. *Wildlife Biology*, 14(4): 500–506.

Rutherford, M.C., Mucina, L. & Leslie, W. 2006. Biomes and Bioregions of Southern Africa. In L. Mucina & M. C. Rutherford, eds. *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria: Strelitzia 19: 31–51.

Sand, H., Zimmermann, B., Wabakken, P., Andren, H. & Pedersen, H.C. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, 33(3): 914–925.

Schaller, G.B. 1972. *The Serengeti Lion: A study of predator–prey relations*. The University of Chicago Press, Chicago.

Scheel, D. & Packer, C. 1991. Group hunting behaviour of lions: a search for cooperation. *Animal Behaviour*, 41: 697–709.

Shehzad, W. 2011. *DNA-based diet analyses in carnivores*. Doctoral dissertation, University of Grenoble, France.

Sheldon, B.C. & West, S.A. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *The American Naturalist*, 163(1). 40-54.

Sinclair, A.R.E. & Arcese, P. 2013. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology*, 76(3): 882–891.

Sinclair, A.R.E., Mduma, S. & Brashares, J.S. 2003. Patterns of predation in a diverse predator – prey system. *Nature*, 425: 288–290.

Skinner, J.D. & Chimimba, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press, Cape Town.

Smuts, G.L. 1979. Diet of lions and spotted hyaenas assessed from stomach contents. *South African Journal of Wildlife Research*, 9(1-2): 19–25.

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

Stander, P.E. 1992a. Cooperative hunting in lions : the role of the individual. *Behavioral Ecology and Sociobiology*, 29(6): 445–454.

Stander, P.E. 1992b. Foraging dynamics of lion in a semi-arid environment. *Canadian Journal of Zoology*, 70: 8–21.

Stander, P.E. 2003. *The ecology of lions and cheetahs re-introduced to the Kalahari Game Lodge, Namibia*. Unpublished report to the Kalahari Game Lodge, Namibia.

Stander, P.E. & Albon, S.D. 1993. Hunting success of lions in a semi-arid environment. *Symposium Zoological Society London*, (65): 127–143.

Tambling, C.J. 2010. *Movement analysis for monitoring predation by large carnivores: lions in Kruger National Park*. Doctoral dissertation, University of Pretoria, South Africa.

Tambling, C.J. & Belton, L.E. 2009. Feasibility of using proximity tags to locate female lion Panthera leo kills. *Wildlife Biology*, 15: 435–441.

Tambling, C.J., Cameron, E.Z., du Toit, J.T. & Getz, W.M. 2010. Methods for locating african lion kills using global positioning system movement data. *Journal of Wildlife*

Management, 74(3): 549–556.

Tambling, C.J., Laurence, S.D., Bellan, S.E., Cameron, E.Z., Toit, J.T. & Getz, W.M. 2012. Estimating carnivoran diets using a combination of carcass observations and scats from GPS clusters. *Journal of Zoology*, 286(2): 102–109.

Trites, A.W. & Joy, R. 2005. Dietary analysis from fecal samples: How many scats are enough? *Journal of Mammalogy*, 86(4): 704–712.

Trivers, R.L. & Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068): 90–92.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90(1): 23–30.

Van Der Walt, P.T., Retief, P.F., Le Richie, E.A.N., Mills, M.G.L. & De Graaff, G. 1984. Features of habitat selection by larger herbivorous mammals and ostrich in the southern Kalahari conservation areas. *Koedoe*, 27(2): 119–128.

Van Rooyen, M.W., Van Rooyen, N., Bothma, J.D.P. & Van den Berg, H.M. 2008. Landscapes in the Kalahari Gemsbok National Park, South Africa. *Koedoe*, 50(1): 99–112.

Van Rooyen, N., Bezuidenhout, D., Theron, G.K. & Bothma, J.D.P. 1990. Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe*, 33(1): 63–88.

Van Rooyen, N., Bredenkamp, G.J., Theron, G.K., Bothma, J.D.P. & Le Richie, E.A.N. 1994. Vegetational gradients around artificial watering points in the Kalahari Gemsbok National Park. *Journal of Arid Environments*, 26: 349–361.

Verlinden, A. 1998. Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, 36(117): 128.

Zhao, L. & Schell, D.M. 2004. Stable isotope ratios in harbor seal Phoca vitulina vibrissae : effects of growth patterns on ecological records. *Marine Ecology Progress Series*, 281: 267–273.

CHAPTER 4

SPATIAL AND SEASONAL VARIATION OF LION (*PATHERA LEO*) DIET IN THE KALAHRI GEMSBOK NATIONAL PARK

4.1 Introduction

Investigating lion (*Panthera leo*) diet is essential for understanding their role in terrestrial ecosystems (Mills et al., 1978; Fryxell et al., 2007; Owen-Smith & Mills, 2008a). In the Kgalagadi Transfrontier Park (KTP) lions are the apex predator and play a crucial role in maintaining ecological processes (Mills et al., 1978; Eloff, 1984a). Understanding the diet of high-level predators can provide valuable insights into spatial and temporal ecosystem dynamics (Lake et al., 2003). Through prey selection lions may have spatio-temporal influences on herbivores (Valeix et al., 2009), which in turn can have an effect on habitat alteration, utilization and condition (Gittleman & Harvey, 1982). Herbivores alter their movements across a landscape seasonally according to environmental constraints (Mills et al., 1995; Valeix et al., 2009). In accordance, lions alter their movements in relation to prey movements, hunting more frequently in areas where prey are easier to catch (Hopcraft et al., 2005). The susceptibility of herbivores to predation varies according to their behavioural responses to seasonal fluctuations and landscape characteristics (Pereira et al., 2014). Herbivores may utilize areas where there is a higher risk of predation when food is limited in other areas (Sinclair & Arcese, 2013).

Herbivore numbers and distribution patterns are primarily determined by seasonal fluctuations in temperature and rainfall (Oksanen & Oksanen, 2000; Fritz et al., 2011; Mills, 2015), although predation might also play a key role in specific circumstances (Hopcraft et al., 2010; Sinclair & Arcese, 2013). In extreme habitats such as the Kalahari, rainfall and soil nutrients are limited, resulting in low plant biomass especially during the hot-dry season (Van Rooyen et al., 2008; Mills, 2015). Overgrazing by herbivores in resource constrained environments such as the Kalahari, can lead to bush encroachment and desertification (Reed & Dougill, 2003; Thomas & Twyman, 2004). Predation pressures exerted through high carnivore densities in relation to prey density may help curtail overgrazing (Oksanen & Oksanen, 2000). Predation may have a regulatory influence on a landscape's ecology and a marked increase or decline in lion numbers could result in numerous deleterious knock-on effects (Loveridge et al., 2007). Data on carnivore feeding behaviour may thus be used to assess the impact that predation could have on resident herbivore population dynamics

(Sidorovich et al., 2008), providing insights into ecosystem changes over time (Pace et al., 1999).

In order to meet the metabolic requirements of their large body size, lions require a sizeable home range as well as a relatively high prey density (Gittleman & Harvey, 1982; LaBarbera, 1989; Carbone et al., 1999; Patterson, 2007). Even though individual lions within the population may have similar access to prey, their diet and caloric intake may differ according to their movement patterns, age, sex and reproductive status (Thiemann et al., 2011). In the KTP, the average lion pride composition (5.18 individuals, 4.18 ♀: 1.45 ♂) and dispersal patterns are related to resident prey availability (Funston, 2011). Climatic factors including temperature and rainfall, which regulate prey availability, are also key drivers of lion social and behavioural ecology (Celesia et al., 2010; Patterson, 2007). Due to the resource limitations in the KTP, lions have large home ranges (2 823 ± 498 km^2) (Funston, 2011) and occur at low densities of approximately 0.7 - 1.2 lion per 100 km^2 (Mills et al., 1978; Castley et al., 2002; Funston, 2011; Ferreira et al., 2013).

Lion prey diversity and abundance in the KTP is limited to species with specialized adaptions to arid environments such as gemsbok, *Oryx gazella,* red hartebeest, *Alcelaphus buselaphus,* springbok, *Antidorcas marsupialis* and eland, *Tragelaphus oryx* (Eloff, 1984b; Stapelberg et al., 2001; Mills, 2015). Of the ungulates represented in the area, blue wildebeest, *Connochaetes taurinus* is the most water dependent species (Mills & Retief, 1984a; Knight, 1995). Historically wildebeest used to migrate out of the Kalahari Gemsbok National Park (KGNP), which makes up the South African portion of the more expansive KTP, during the dry season, but have become sedentary since the provision of artificial waterholes in the 1930's (Eloff, 1966). Seasonal migrations have also been recorded for springbok, eland and red hartebeest (Eloff, 1962; Verlinden, 1998) while gemsbok, ostrich, *Struthio camelus,* and small antelopes such as steenbok, *Raphicerus campestris,* are sedentary (Eloff, 1962; Mills, 2015). The riverbed habitats in the KTP support higher densities of game than the dune habitats (Bergstrom & Skarpe, 1999) and are the most intensively utilized habitats by varying numbers of springbok, blue wildebeest, gemsbok and red hartebeest (Mills & Retief, 1984b). Higher game densities in the riverbeds are supported by the provision of water through artificial water points, of which there are 17 situated in the Auob and 24 in the Nossob riverbeds (Mills & Retief, 1984b; Knight, 1995). Blue wildebeest occur mainly within the riverbed areas (Mills, 2015). During the wet season herbivore numbers increase in the KGNP, and decrease again during the dry season when herbivores disperse (Mills & Retief, 1984b; Bergstrom & Skarpe, 1999)

Anthropogenic activities that alter environments lead to shifts in the natural distribution of animals, population community structures and ecology (Bauer & Iongh, 2005; Cardillo et al., 2006). In and around the KTP human land use and management practices include livestock farming (Herrmann, 2004), the provision of artificial water sources (Van Rooyen et al., 1990; Funston, 2001; Ferreira et al., 2013) and the construction of manmade barriers, such as fences (Williamson & Williamson, 1984; Cozzi et al., 2012). The provision of artificial water points has altered herbivore assemblages in the KGNP, resulting in an increase in the abundance and distribution of water dependant species such as blue wildebeest (Eloff, 1966; Mills & Retief, 1984a; Van Rooyen et al., 1994; Knight, 1995). Lion prides in close proximity to artificial water sources may thus be exposed to a more reliable food source than in the past (Funston, 2011), this in turn may influence diet selection which impacts lion body condition, population density and survival rates (Ferreira & Funston 2010).

The KTP is regarded as a relatively homogenous landscape with regards to the substrate and vegetation diversity at a bioregion scale (Mucina & Rutherford, 2006; Van Rooyen et al., 2008). At a finer scale a number of localized differences occur across the area in terms of vegetation composition and topography, resulting in the classification of several landscape (Van Rooyen et al., 2008), habitat (Bothma & De Graaff, 1973) and vegetation types (Mucina & Rutherford, 2006). Even though it has not been well studied, it has been documented that herbivore populations in the KTP differ in how they utilize these various landscape, habitat and vegetation types, spatially as well as seasonally (Mills & Retief, 1984b; Eloff, 1962; Knight, 1995; Stapelberg et al., 2001). These variations could potentially drive seasonal and spatial variation in lion diet across the KGNP.

This chapter investigated the spatial and temporal variability of lion diet in the KGNP over the study period between May 2013 and June 2015. The lion diet profile is evaluated in relation to seasonal and spatial fluctuations in native prey availability. Spatial variation in lion diet and associated factors across the KGNP was investigated across two main categories namely regional landscape types and habitat types. The regional landscape divisions were made according to the dominant vegetation types represented within the north, south and west. The habitat type divisions were based on the difference between the dunes and the riverbeds (Mills & Retief, 1984b; Van Der Walt et al., 1984). Temporal variation in lion diet is investigated across two ecological seasons, namely the hot-wet and cold-dry (Bergstrom & Skarpe, 1999; Van Rooyen et al., 2008)

4.2 Materials and methods

4.2.1 Study area

The study area encompassed an area of approximately 15 396 km^2 between 24° 15’ S and 26° 30’ S, and 20° 00’ E and 20° 45’ E. The study area was primarily situated in the Kalahari

Gemsbok National Park (KGNP) which comprises the South African section of the Kgalagadi Transfrontier Park (KTP). The KGNP is situated in the Kalahari Duneveld and Eastern Kalahari Bushveld Bioregions of the Savannah Biome (Mucina & Rutherford, 2006). The KTP has predominantly summer rainfall between January and April, with the annual mean varying between 185 mm to 230 mm (Van Rooyen et al., 2008). Temperatures fluctuate greatly on a daily as well as seasonal basis (Mills & Retief, 1984b) reaching a winter minimum of -10.3°C and a summer maximum of 45.4°C (Van Rooyen et al., 1990). Based on the annual variation in rainfall and temperature two ecological seasons can be identified namely the hot-wet (November to April), and the cold-dry (May to October) seasons (Mills & Retief, 1984b; Bergstrom & Skarpe, 1999; Van Rooyen et al., 2008). To investigate the spatial variation in lion diet across the study area it was zoned according to terrain, as well as the dominant vegetation types present.

4.2.1.1 Habitat categorisation

The two dominant habitat types identified in the study area were the dune and riverbed habitats. The dunes cover approximately 85% of the study area and are characterized by areas that are sparsely vegetated with trees and shrubs, bare dunes, flat grasslands and tree savannahs (Bothma & De Graaff, 1973). The dune fields are bisected by two ephemeral riverbeds and scattered pans (Van Der Walt et al., 1984). The riverbed habitats are defined by the two riverbeds (Auob and Nossob), as well as a 2 500 m buffer area on both sides of the riverbeds, and cover approximately 15% of the study area. Water is only available in the riverbeds for short periods after heavy rainfall (Knight, 1995). The vegetation of the riverbeds is generally characterised by grasses and scattered trees (Van Rooyen et al., 2008). For a detailed discussion of the different habitat types refer to Chapter 2.

4.2.1.2 Regional landscape categorisation

The three regional landscape types (hereafter referred to as landscape types) were categorised according to the composition of the dominant vegetation types (Mucina & Rutherford 2006) represented in the north, south and west (Figure 4.1). The north (622 888 Ha, 41% of study area) comprised 85% dune and 15% riverbed habitat and was represented by the dominant vegetation types of Nossob Bushveld, Gordonia Plains Shrubveld and Gordonia Duneveld. The south (667 055 Ha, 43% of the study area) incorporated 88% dune and 12% riverbed habitat and included the vegetation types of Gordonia Plains Shrubveld, Gordonia Duneveld and Gordonia Kameeldoring Bushveld. The west (249 703 Ha, 16% of the study area) of which 77% comprise dune and 23% riverbed habitat, contain the vegetation types of Auob Duneveld and Southern Kalahari Mekgacha (Mucina & Rutherford, 2006) (Figure 4.1). The biotic characteristics of these vegetation types are described in more detail in Chapter 2.

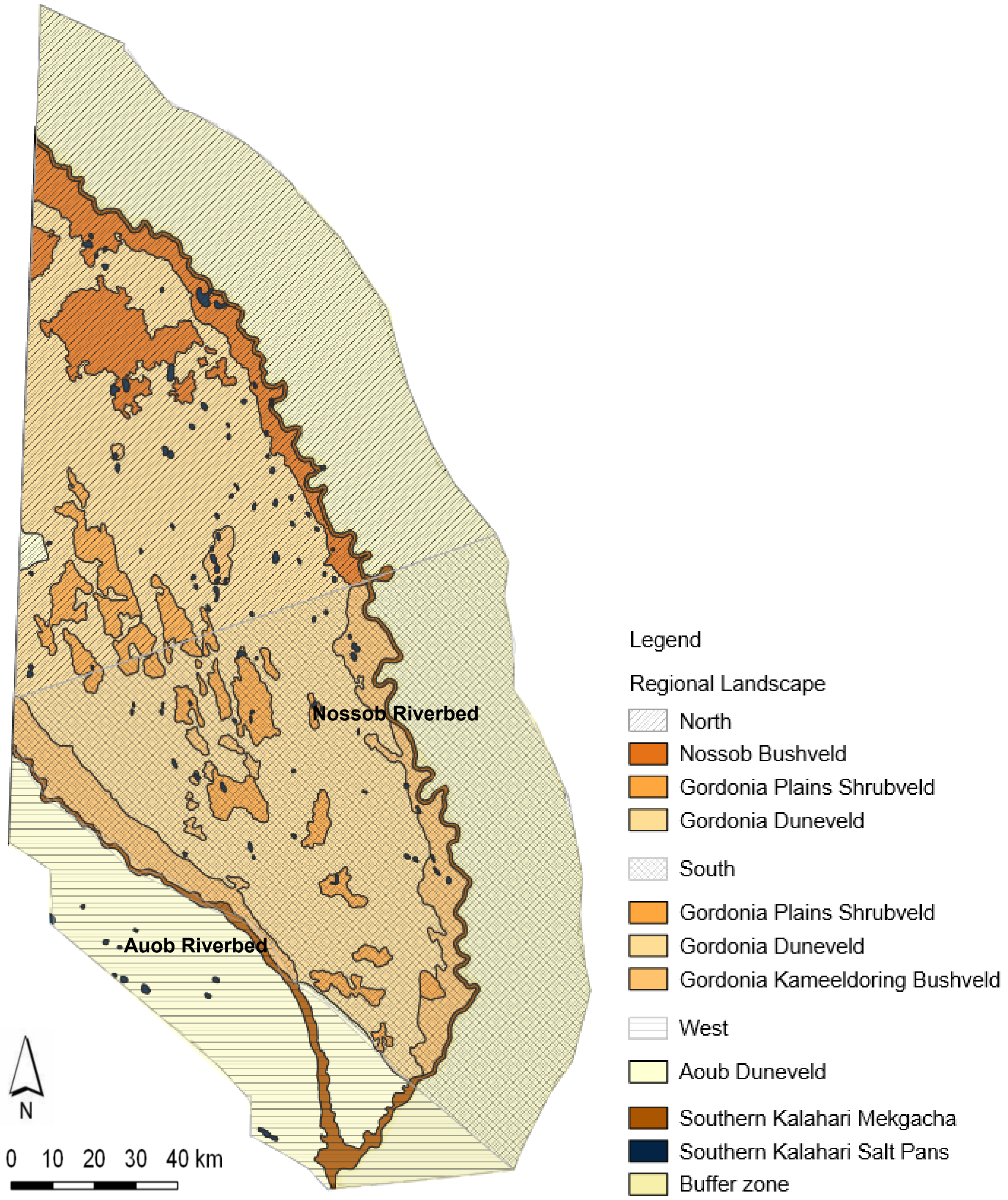


Figure 4.1 The area covered by the regional landscapes types of the north, south and west, which were classified according to the dominant vegetation types represented within each area in the KGNP. Vegetation types immediately west of the Nossob riverbed were largely mirrored in the buffer zone to the east of the Nossob riverbed (pers. obs., 2013).

4.2.2 Data collection

4.2.2.1 Lion diet data collection

To determine the diet profile of lion across landscape types, habitat types and seasons both GPS cluster analysis and scat analysis were used. The GPS cluster analysis technique made use of clustered GPS locality points to identify and locate lion prey remains (Tambling & Belton, 2009; Davidson et al., 2013). GPS data was obtained from seven lionesses fitted with GPS/VHF collars holding territories across the study area for the duration of the study (African Wildlife Tracking^{cc}, Pretoria, South Africa). Two collared lionesses in north together provided GPS data for 17 months collectively. Two collared lions in the south together provided data for a total of 18 months and three collared lions in the west provided data for 19 months collectively.

Lion scat was collected when opportunistically encountered across the park, as well as from GPS clusters. Lion scats that were collected at GPS cluster points and contained remains of the prey species found at that cluster, or at preceding clusters that were made within 24 hours of the other, were excluded from analysis (Tambling et al., 2012). Determining the prey species consumed was achieved through the macroscopic and microscopic analyses of hair samples extracted from the lion scats (Mukherjee et al., 1994; Ogara et al., 2010; Tambling et al., 2012). Hairs obtained from scats were assessed against a reference library of prey hair samples, to assist with the identification (Mukherjee et al., 1994). See Chapter 3 for a detailed description of the scat analysis methodology.

To analyse lion diet data across the two spatial scales and across seasons an attempt was made to distribute survey effort evenly across the three landscape types and two habitat types, as well as across the two ecological seasons (hot-wet and cold-dry). GIS software was used to identify the location of GPS cluster points and where lion scats were retrieved, in order to categorise them into the three landscape types. GIS software (Quantum GIS Development Team, 2016) was also used to classify GPS cluster points according to habitat type. Lion feeding events observed from GPS cluster analysis within the riverbeds, and within 2.5 km of the riverbed, were considered as feeding events within the riverbed habitat and the rest of the feeding events were attributed to the dune habitats. Dietary data obtained from scats could not be used to interrogate lion dietary differences on the basis of the habitat types, as there was no way of confirming the locality where the kill was made, from where the scat was deposited. Classifying lion scat according to landscape type was possible as the three landscape areas were vast and lion (unless occurring directly on the border) where unlikely to move between the dominant landscape types directly after a feeding event. GPS cluster points and lion scats were also classified according to the season in which they were collected.

4.2.2.2 Prey abundance data collection

Six road transects were surveyed across the study, including three in the dune habitats (one transect in the north, south and west respectively), and three in the river habitats (one transect in the northern, southern and western landscape respectively). Fifteen game counts were conducted in the dune landscapes, which comprise 85% of the study area, and 15 game counts were conducted in the riverbed landscapes, which included a 2 500 m buffer zone and cover approximately 15% of the study area (Table 4.1). Eight game counts were conducted in the wet season and seven game counts were conducted in the dry season During road transect game counts, the species, herd size and, where possible, age and sex were recorded. Herbivores were subjectively placed into three age categories, namely calves, sub-adults and adults, according to their physical attributes (Knight, 1995). A more detailed account on how prey abundance data was collected is presented in Chapter 3.

Table 4.1 The area size (ha), area coverage (%) and transect lengths (km) driven to obtain animal abundance data for the different habitat types (riverbed and dune) and landscape types (north, south and west).

	North			**South**			**West**			**Total**		
	Ha	**Area (%)**	**Km**	**Ha**	**Area (%)**	**Km**	**Ha**	**Area (%)**	**Km**	**Ha**	**Area (%)**	**Km**
River	94669	0.15	139	79538	0.12	182	58223	0.23	125	232430	0.15	595
Dune	528218	0.85	134	587517	0.88	121	191480	0.77	78	1307215	0.85	332
Total	622887	40	272	667055	43	303	249703	16	202	1539645	100	927

4.2.3 Data analyses

4.2.3.1 Spatial and seasonal lion diet

The frequency of prey occurrence in lion diet (FO) was quantified separately for GPS clusters and scat analyses. The relative proportions of the different prey species represented in the lion feeding event records were further separated by landscape type (north, south, west), habitat type (dune and river) and season (wet and dry). The FO was converted into approximate biomass contribution of prey (BM) to lion diet for each factor. The relative biomass index of prey was ascribed using the body mass for adult male and female mammalian prey species taken from Skinner & Chimimba (2005). Sub-adult and juvenile BM were calculated by multiplying the adult female mass by 0.7 and 0.3 respectively (Radloff & du Toit 2004). Where the age and sex was unknown, BM was subjectively assigned using the female BM multiplied by 0.75, which would account for juveniles and males (Radloff & du Toit 2004; Tambling et al. 2012). Unit mass was ascribed in the same manner for prey that were not ungulates as well as avifauna (Owen-Smith, 1988; Radloff & du Toit, 2004).

4.2.3.2 Prey abundance

Relative prey abundance indices (RAI) were derived from the number of road transect game counts conducted per landscape type, habitat type and season (Owen-Smith & Mills, 2008b). Count data, derived from the various road transect game counts, were weighted in accordance with the percentage area (of the entire study area) occupied by the respective landscape types and habitat types represented in each area.

a) Prey abundance per habitat type

Prey RAI, using encounter rates of individuals as a proxy for abundance, according to habitat types, were assigned by using the data obtained from road transect game counts conducted in the dune and riverbed habitats respectively. To derive prey RAI for the dune habitat, 15 road transect game counts were conducted in the dunes, and 15 road transect game counts were conducted in the riverbeds to derive RAI for the riverbed habitat. The 15 road transect game counts conducted per habitat type were used to derive the mean RAI and 95% confidence intervals.

b) Prey abundance per landscape type

The RAI for prey according to landscape type was estimated from data obtained from 15 road transect game counts conducted in the dune habitats of the north, south and western landscape types and 15 road transect game counts conducted in the riverbed habitats of the north south and western landscape types. To account for the fact that the dune and riverbed habitat types occupy different area proportions within each landscape type, data from road transect game counts were weighted in accordance with the proportion area occupied by the respective habitat types represented within each landscape type (Caro, 1999) (Table 4.1), in the equation:

$$RAI_L = (RAI_{dl} \times D) + (RAI_{rl} \times R)$$

where RAI_L is the weighted percent RAI for a particular species within a particular landscape type (north, south or west), RAI_{dl} is the average RAI of that species in the dunes of the same landscape type (north, south or west) and RAI_{rl} is the average RAI for that species in the riverbed of the same landscape type (north, south or west landscape). D and R are the total proportions of the study area occupied by the dune and riverbed habitats in the north, south or west landscape type respectively. The 15 weighted game counts per landscape type were used to derive the means and 95% confidence intervals for the RAI for each species within each landscape type.

c) Prey abundance per season

The overall RAI for prey in the KGNP, according to season, was assigned from data obtained from 15 road transect game counts (according to habitat type) that were conducted in the hot-wet season (n = 8) and cold-dry season (n = 7). To account for the fact that the dune habitat occupies 85% of the study area, whilst the riverbed habitat only occupies approximately 15% of the study area, the road transect game count data was weighted in accordance to the proportion area occupied by the dunes and riverbeds (Caro, 1999). To obtain a total weighted RAI for each prey species within each season, the average percent RAI, derived from the game counts in each habitat type (dune counts, n = 15; river counts, n = 15), were multiplied by the proportional area occupied by each habitat type (dune = 85%, riverbed area = 15%) and then added together, in the equation:

$$RAIs_E = (RAI_{ds} \times D) + (RAI_{rs} \times R)$$

where $RAIs_E$ is the weighted percent RAI for a particular species per season (hot-wet or cold-dry), RAI_{ds} is the average RAI of that species in the dunes in a particular season and RAI_{rs} is the average RAI for that species in the riverbed in that same season. D and R are the proportions of study area occupied by the dune and riverbed habitats respectively. The eight weighted game counts for the hot-wet season, and the seven weighted game counts for the cold-dry season, were used to derive the means and 95% confidence intervals for the RAI for each species within each season.

4.2.3.3 Prey preference

The Jacobs' Index (D) was used to measure prey preference of lion within the KGNP (Hayward & Kerley, 2005; Rapson & Bernard, 2007; Davidson et al., 2013). The Jacobs' index scores a value between -1 (prey highly avoided) and 1 (prey highly preferred) (Jacobs, 1974). A value of greater than 0.2 signifies preference and less than -0.2 signifies avoidance (Hayward et al., 2011). Values between -0.2 and 0.2 indicated that the species was consumed proportionally to what was available (Hayward et al., 2011). Prey preference (D) was investigated for the FO of prey in lion diet from GPS cluster data across the whole park, as well as per landscape type, habitat type and season. For scat data, prey preference was only determined per landscape type and season.

4.2.3.4 Spatial and temporal variation in lion diet

The statistical techniques used to investigate the potential differences in lion diet between landscape type, habitat and season included relative percent difference (Lepš et al., 2006; Sluiter et al., 2005), two-way analysis of variance and three-way analysis of variance (Sokal & Rohlf, 1981). The relative percent difference (RPD) was calculated to determine the degree to which lion diet composition varies between landscape type, habitat type and season (Sluiter et al., 2005). Relative percent difference was used to compare the frequency of occurrence of prey in lion diet and the biomass contributions of prey for both GPS cluster analysis and scat analysis, as well as the relative prey abundance. The degree of overlap between two dietary profiles was expressed on a scale between 0 (no similarity) and 100 (maximum similarity) (Lepš et al., 2006; Sluiter et al., 2005).

Three-factor analysis of variance without replication (three-way ANOVA) was used to analyse the GPS cluster data for the frequency of occurrence of prey in lion diet (FO) and biomass contributions of prey to lion diet (BM), as well as relative prey abundance indices (RAI). The three factor levels were landscape type, season and habitat. Nine separate analyses were conducted for each of the nine species represented in lion diet for GPS cluster analysis. Considering that the ANOVA Model I (with no replication) was used, it is assumed that the three-way interaction is 0 (MS error = 0). As a result, the ANOVA Model I could not be used to calculate F-values (since F = MS/MS_{error}), thus MS_{AxBxC} is used as the denominator for all other F-values and the F-value is not calculated for MS_{AxBxC} since it is assumed to be “0” and is therefore not significant (Sokal & Rohlf, 1981).

Two-factor analysis of variance without replication (two-way ANOVA) was used to analyse the scat analysis data for FO and BM in lion diet (Sokal & Rohlf, 1981). The two factor levels were landscape type and season. Eleven separate analyses were conducted for each of the separate species represented in lion diet from scat analysis.

4.3 Results

A total of 49 784 km were surveyed across the study area of which 11 665 km were driven to conduct road transect game counts in the riverbed and dune habitats. For the road transect game counts, efforts in terms of kilometres driven, where relatively evenly distributed across the landscape types of the north (35%), south (39%) and west (26%). In the habitat types, 57% of the survey efforts were in the riverbeds, and 43% were in the dunes.

The effort resulted in the retrieval of 189 lion scats across the park and identification of 278 lion prey remains at GPS cluster points which together account for 467 lion feeding events. A breakdown of the locations where prey remains were found at GPS cluster points, and where lion scats were collected in relation to landscape type and season, is presented in Table 4.2. According to landscape type, 37% of GPS clusters were recorded in the north, 33% in the south and 30% in the west. Of the lion scats analysed 48% were collected in the north, 18% in the south and 34% in the west. Only nine lion scats collected were within five kilometres of the landscape boundary lines. Substantially fewer scats were obtained in the hot-wet season (23%) than in the cold-dry season (77%). Similar sample sizes were collected for GPS cluster analysis in the hot-wet (54%) and the cold-dry (46%) season (Table 4.2). Lion feeding events that were recorded according to habitat type, using GPS cluster analysis, revealed more than nearly double the amount of feeding events were in the located dunes (*n* = 187) in comparison with the riverbeds (*n* = 91).

Table 4.2 Number of lion feeding events records from GPS cluster points and number of lion scats collected from each landscape type per season.

	North		**South**		**West**		**Total**	
	Cluster	**Scat**	**Cluster**	**Scat**	**Cluster**	**Scat**	**Cluster**	**Scat**
Wet	49	26	54	7	46	11	149	44
Dry	53	64	39	27	37	54	129	145
Total	102	90	93	34	83	65	278	189

4.3.1 Lion diet and prey availability according to landscape type

4.3.1.1 Lion diet profile across landscape types

GPS cluster analysis and scat analysis both reflected that lions consumed predominantly gemsbok in the landscapes of the north (GPS clusters 62%, scat analysis 47%), south (GPS clusters 78%, scat analysis 54%) and west (GPS clusters 68%, scat analysis 43%). Both methods also found that gemsbok contributed most to lion biomass intake in all landscape types (range = 65 - 82%) (Table 4.3). According to GPS cluster analysis, wildebeest was the second most frequently consumed of the large prey (>50 kg) species in the north (16%) and the west (10%). In the south, eland was consumed second most (9%) and was consumed more often than wildebeest (5%). Prey remains obtained from GPS cluster points indicate that large mammals contributed more than 92% to lion diet and more than 99% to the biomass consumed in all landscape types.

Table 4.3 The percentage frequency of occurrence and biomass contributions of various large (> 50 kg) and small (< 50 kg) prey species represented in lion diet through prey remains obtained from GPS cluster points and scat analysis in the landscape types of the north, south and west.

		Frequency occurrence						**Biomass**					
		GPS cluster			**Scat analysis**			**GPS cluster**			**Scat analysis**		
		North	**South**	**West**	**North**	**South**	**West**	**North**	**South**	**West**	**North**	**South**	**West**
Large	Gemsbok	61.5	78.4	68.0	46.5	53.7	42.5	68.6	81.8	75.0	70.6	74.3	64.3
	Wildebeest	15.5	4.6	10.4	11.1	4.9	8.2	16.3	3.8	9.4	14.4	3.5	11.1
	Eland	4.4	8.8	2.2	3.0	7.3	5.5	9.9	11.8	9.0	6.9	16.8	15.8
	Hartebeest	6.1	5.1	4.4	4.0	4.9	5.5	3.2	1.6	2.5	2.7	2.3	4.1
	Ostrich	4.4	3.1	6.4	2.0	0.0	0.0	1.6	1.0	1.5	0.5	0.0	0.0
	Kudu	0.0	0.0	5.3	2.0	0.0	0.0	0.0	0.0	2.5	1.2	0.0	0.0
Subtotal		92.0	100.0	96.7	68.7	70.7	61.6	99.6	100.0	99.9	96.3	96.9	95.3
Small	Porcupine	-	-	-	11.1	7.3	17.8	-	-	-	0.9	0.4	1.7
	Steenbok	4.4	0.0	3.3	6.1	12.2	8.2	0.2	0.0	0.1	0.4	0.8	0.6
	Springbok	1.8	0.0	0.0	10.1	9.8	9.6	0.2	0.0	0.0	2.3	1.9	2.4
	Kori bustard	1.8	0.0	0.0	-	-	-	0.0	0.0	0.0	-	-	-
	Springhare	-	-	-	4.0	0.0	2.7	-	-	-	0.1	0.0	0.0
Subtotal		8.0	0.0	3.3	31.3	29.3	38.4	0.4	0.0	0.1	3.7	3.1	4.7

Scat analysis indicated that small mammals (< 50 kg) contributed 31% of prey consumed in the north, 29% in the south and 38% in the west. In scat analysis for all landscape types the prey species that contributed the highest proportion of small mammals to lion diet were porcupine (north 11%; south 7%; west 18%), steenbok (north 6%; south 12%; west 8%) and springbok (north 10%; south 10%; west 10%). In terms of biomass contribution derived from scat analysis in all landscape types, small mammals contributed < 5% to lion diet, whereas large mammals made up > 95% of the biomass intake. For both GPS cluster analysis and scat analysis in all landscape types, gemsbok, wildebeest and eland together were the main contributors to lion biomass intake (range = 91 – 97%). The highest diversity of prey species found in lion diet through scat analysis was in the north (*n* = 10), followed by the west (*n* = 8) and the lowest diversity of prey was in the south (*n* = 7).

A pairwise comparison of lion diet composition between the different landscape types, using an index of relative percent difference (RPD) for GPS cluster analysis, revealed a RPD lower than 5% across all landscape type comparisons (Table 4.4). Biomass comparisons using the GPS cluster data revealed even lower differences (range 1.5 – 4.1%) between landscapes. For scat analysis the RPD, for the frequency occurrence of prey in lion diet, was 4% between the north and south and around 1% between the north and west, as well as the south and west. Differences in biomass contribution for scat analysis were close to 3% across all landscape comparisons (Table 4.4).

Table 4.4 The relative percent difference (RPD) scores comparing variation in the frequency of occurrence of prey in lion diet (FO) and the biomass contribution of prey to lion diet (BM) between the landscape types represented in the north, south and west for GPS cluster analysis and scat analysis.

	Frequency of Occurrence			**Biomass contribution**		
	North *vs.* South	**North *vs.* West**	**South *vs.* West**	**North *vs.* South**	**North *vs.* West**	**South *vs.* West**
GPS cluster	4.8	3.7	4.1	4.1	1.5	2.5
Scat analysis	4.1	1.4	0.9	3.3	2.5	2.9

Three-way ANOVA analysis of GPS cluster analysis results revealed that the only significant differences in lion diet across landscape types were related the consumption of wildebeest (*f* = 97.6, *df* = 2, *p* = 0.01) (Table 4.5). Wildebeest's contribution to lion diet was only 4.6 % in the south, increased to over 10% in the west and was nearly 16% in the north (Table 4.3). The biomass contribution of wildebeest was significantly higher in the north (16%) than in the south (4%) or west (9%) (*f* = 102, *df* = 2, *p* = 0.01). The biomass contribution of eland found in GPS analysis was also significantly different across landscapes (*f* = 24.18, *df* = 2, *p* = 0.04) (Table 4.5), with eland contributing more to the biomass intake of lion diet in the south (12%), than in the north (10%) or west (9%) (Table 4.3). The proportion of all other species in lion diet and their biomass contributions did not differ significantly across landscape type.

Table 4.5 Three-way and Two-way ANOVA analysis of prey frequency of occurrence in lion diet (FO), biomass contribution of prey to lion diet (BM) and relative abundance index of prey in the study area (RAI) between landscape type, habitat type and season for GPS cluster analysis and scat analysis.

	Gemsbok			**Wildebeest**			**Eland**			**Porcupine**			**Steenbok**			**Hartebeest**			**Springbok**			**Ostrich**			**Kori bustard**			**Springhare**			**Kudu**		
	df	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***
GPS Cluster Analysis: Three-way Anova FO																																	
Landscape	2	1.14	0.47	2	97.60	_0.01*_	2	0.63	0.61	-	-	-	2	0.52	0.66	2	0.35	0.74	2	1.00	0.50	2	7.62	0.12	2	1.00	0.50	-	-	-	2	2.43	0.29
Habitat	1	9.89	0.09	1	563.2	_0.00*_	1	1.29	0.37	-	-	-	1	4.74	0.16	1	2.68	0.24	1	1.00	0.42	1	9.46	0.09	1	1.00	0.42	-	-	-	1	0.05	0.85
Season	1	0.07	0.82	1	57.86	0.20	1	0.01	0.93	-	-	-	1	0.38	0.60	1	0.00	0.96	1	1.00	0.42	1	4.21	0.18	1	1.00	0.42	-	-	-	1	0.60	0.52
Habitat × Landscape	2	0.14	0.88	2	58.77	_0.02*_	2	0.14	0.88	-	-	-	2	0.52	0.66	2	0.52	0.66	2	1.00	0.50	2	2.41	0.29	2	1.00	0.50	-	-	-	2	0.05	0.95
Season × Landscape	2	0.05	0.95	2	3.88	0.20	2	0.23	0.81	-	-	-	2	1.00	0.50	2	2.78	0.26	2	1.00	0.50	2	12.38	0.07	2	1.00	0.50	-	-	-	2	0.60	0.62
Habitat × Season	1	1.49	0.35	1	98.59	0.00*	1	0.65	0.50	-	-	-	1	0.38	0.60	1	0.02	0.90	1	1.00	0.42	1	3.44	0.20	1	1.00	0.42	-	-	-	1	1.00	0.42
Scat Analysis: Two-way Anova FO																																	
Landscape	2	8.54	0.24	2	2.42	0.41	2	0.03	0.97	2	5.71	0.28	2	2.17	0.43	2	0.65	0.66	2	0.16	0.87	2	0.02	0.98	-	-	-	2	0.15	0.88	2	0.02	0.98
Season	1	4.35	0.28	1	0.02	0.92	1	1.00	0.50	1	0.03	0.90	1	0.63	0.57	1	0.08	0.83	1	1.79	0.41	1	0.02	0.91	-	-	-	1	0.37	0.65	1	0.02	0.91
Season × Landscape	2	1.12	0.56	2	0.21	0.84	2	0.70	0.65	2	1.18	0.54	2	1.02	0.57	2	0.81	0.62	2	0.48	0.71	2	0.02	0.98	-	-	-	2	0.15	0.88	2	0.02	0.98
GPS Cluster Analysis: Three-way Anova BM																																	
Landscape	2	0.62	0.62	2	102.0	_0.01*_	2	24.18	_0.04*_	-	-	-	2	0.00	1.00	2	0.18	0.85	2	0.02	0.98	2	1.60	0.38	2	0.00	1.00	-	-	-	2	4.17	0.19
Habitat	1	13.30	0.07	1	571.7	_0.00*_	1	0.26	0.66	-	-	-	1	0.02	0.91	1	2.27	0.27	1	0.02	0.90	1	1.80	0.31	1	0.00	0.97	-	-	-	1	0.28	0.65
Season	1	0.01	0.94	1	36.58	_0.03*_	1	13.37	0.07	-	-	-	1	0.00	0.97	1	0.01	0.93	1	0.02	0.90	1	1.23	0.38	1	0.00	0.97	-	-	-	1	1.49	0.35
Habitat × Landscape	2	0.01	0.99	2	61.77	_0.02*_	2	14.17	0.07	-	-	-	2	0.00	1.00	2	0.11	0.90	2	0.02	0.98	2	0.32	0.76	2	0.00	1.00	-	-	-	2	0.28	0.78
Season × Landscape	2	0.60	0.63	2	4.15	0.19	2	15.59	0.06	-	-	-	2	0.00	1.00	2	0.74	0.58	2	0.02	0.98	2	2.11	0.32	2	0.00	1.00	-	-	-	2	1.49	0.40
Habitat × Season	1	0.97	0.43	1	58.82	_0.02*_	1	3.18	0.22	-	-	-	1	0.00	0.97	1	0.13	0.76	1	0.02	0.90	1	0.16	0.73	1	0.00	0.97	-	-	-	1	1.83	0.31
Scat Analysis: Two-way Anova BM																																	
Landscape	2	0.73	0.64	2	0.53	0.70	2	0.01	0.99	2	0.01	0.99	2	0.00	1.00	2	0.06	0.95	2	0.00	1.00	2	0.00	1.00	-	-	-	2	0.00	1.00	2	0.00	1.00
Season	1	1.28	0.46	1	0.00	0.96	1	1.00	0.50	1	0.00	1.00	1	0.00	0.99	1	0.00	0.96	1	0.01	0.93	1	0.00	0.98	-	-	-	1	0.00	1.00	1	0.00	0.97
Season × Landscape	2	0.60	0.67	2	0.03	0.97	2	0.69	0.65	2	0.00	1.00	2	0.00	1.00	2	0.06	0.94	2	0.00	1.00	2	0.00	1.00	-	-	-	2	0.00	1.00	2	0.00	1.00
Three-way Anova RAI																																	
Landscape	2	1.64	0.38	2	17.7	_0.05*_	2	0.09	0.91	-	-	-	2	1.87	0.35	2	19.98	_0.05*_	2	418.5	_0.00*_	2	1.34	0.43	2	7.89	0.11	-	-	-	2	0.00	1.00
Habitat	1	18.85	0.05*	1	131.8	_0.01*_	1	0.09	0.79	-	-	-	1	78.72	_0.01*_	1	8.01	0.11	1	18791.5	_0.00*_	1	137.9	_0.01*_	1	178.5	_0.01*_	-	-	-	1	0.00	0.96
Season	1	0.12	0.76	1	0.87	0.45	1	0.01	0.93	-	-	-	1	3.60	0.20	1	6.04	0.13	1	0.85	0.34	1	0.00	1.00	1	7.48	0.11	-	-	-	1	0.00	0.98
Habitat × Landscape	2	1.21	0.45	2	16.01	0.06	2	0.09	0.91	-	-	-	2	1.78	0.36	2	0.20	0.83	2	825.2	_0.00*_	2	8.42	0.11	2	8.99	0.10	-	-	-	2	0.00	1.00
Season × Landscape	2	0.09	0.92	2	1.17	0.46	2	0.01	0.99	-	-	-	2	0.27	0.79	2	1.24	0.45	2	24.59	_0.04*_	2	7.57	0.12	2	3.67	0.21	-	-	-	2	0.00	1.00
Habitat × Season	1	1.40	0.36	1	8.19	0.10	1	0.01	0.93	-	-	-	1	3.72	0.19	1	0.23	0.68	1	31.71	_0.03*_	1	0.21	0.69	1	4.45	0.17	-	-	-	1	0.00	0.98

*Significant variables $p < 0.05$ at a 95% confidence level.

Two-way ANOVA of scat analysis did not find any significant differences between the frequency of occurrence of prey species represented in lion diet or the biomass contributions of prey to lion diet between landscapes (Table 4.5).

4.3.1.2 Prey availability across landscape types

There was some variation in prey availability across the park between landscape types (Figure 4.2). In terms of the weighted relative prey abundance index (RAI), gemsbok was the most abundant and widespread of the large prey species, making up 28% of the large prey population in the north, 51% in the south and 46% in the west. Eland was the least abundant of the prey species with <1.5% RAI in all areas. Hartebeest were more abundant in the north (16%) than in the south (8%) and west (3%) (*f* = 20, *df* = 2, *p* = 0.05). Wildebeest had a relatively low RAI of 6%, 3% and 3% in the north, south and west respectively (*f* = 18, *df* = 2, *p* = 0.05). Ostrich had a relatively high RAI in all landscape type categories (12%, 12% and 15%) in the north, south and west respectively. Of the small herbivores steenbok had the highest RAI in the north (17%), south (15%) and west (9.2%). Springbok also maintained a relatively high RAI across the landscape types of the north (14%), south (7%) and west (17%) (*f* = 418, *df* = 2, *p* = 0.00) (Figure 4.2).

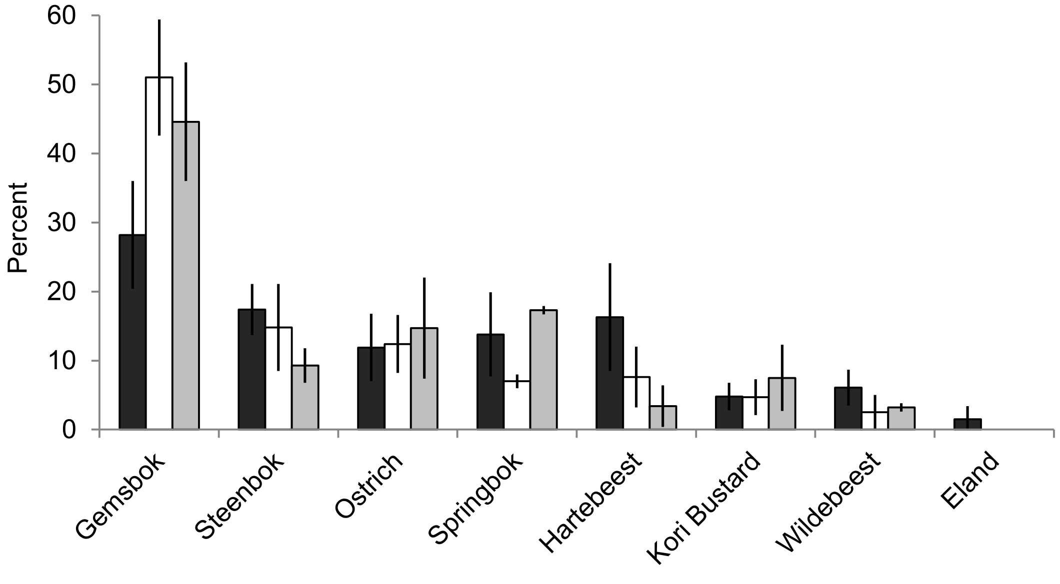


Figure 4.2 The relative abundance indices of prey represented in the landscape types of the north (black bars), south (white bars) and west (grey bars). Error bars depict 95% confidence intervals.

In terms of the number of animals per kilometre, as a relative abundance estimate, the riverbed habitats had the highest number of prey in the north 10.1 km^{-1}, south 8.2 km^{-1} and west 9.5 km^{-1}. The number of animals per kilometre was lower in the dunes (north 0.9 km^{-1}, south 0.5 km^{-1}, south; 0.8 km^{-1} and west 1.1 km^{-1}) than the riverbeds. Springbok in the riverbeds had the highest numbers overall in the west (7.2 km^{-1}), followed by the south (4.4 km^{-1}) and north (1.5 km^{-1}). Wildebeest were the second most abundant species in the riverbed of the north (2.6 km^{-1}) and west (1.2 km^{-1}). Gemsbok had the highest occurrence per kilometre in the dunes of the north (0.3 km^{-1}), south (0.3 km^{-1}), and west (0.5 km^{-1}). Steenbok was the second most abundant species in the dunes of the north (0.2 km^{-1}), south (0.1 km^{-1}) and west (0.1 km^{-1}), followed by red hartebeest in the north (0.1 km^{-1}) and south (0.1 km^{-1}). In all landscape types eland, steenbok and Kori bustard were more abundant in the dunes than the riverbeds and all other species had a higher representation per kilometre in the riverbeds than the dunes (Figure 4.3).

Prey proportional abundance between the landscape types showed that the greatest relative percent difference (RPD) was between the north and the west (13%). The south and the west had a 7.3% RPD and the north and south had the lowest RPD of 6.7%. Three-way ANOVA analysis indicate that the RAI of wildebeest differed significantly between landscape types ($F = 17.7$, $df = 2$, $p = 0.05$), owing to a higher relative abundance of wildebeest in the north (Figure 4.2). Springbok RAI also differed significantly across landscape types ($F = 418.5$, $df = 2$, $p = 0.00$), with a higher RAI in the west and north and lower in the south (Figure 4.2). Hartebeest RAI also varied significantly across landscape types ($F = 19.98$, $df = 2$, $p = 0.05$), owing to a higher RAI in the north (Figure 4.2). The RAI of all other prey species did not vary significantly between landscape types (Table 4.5).

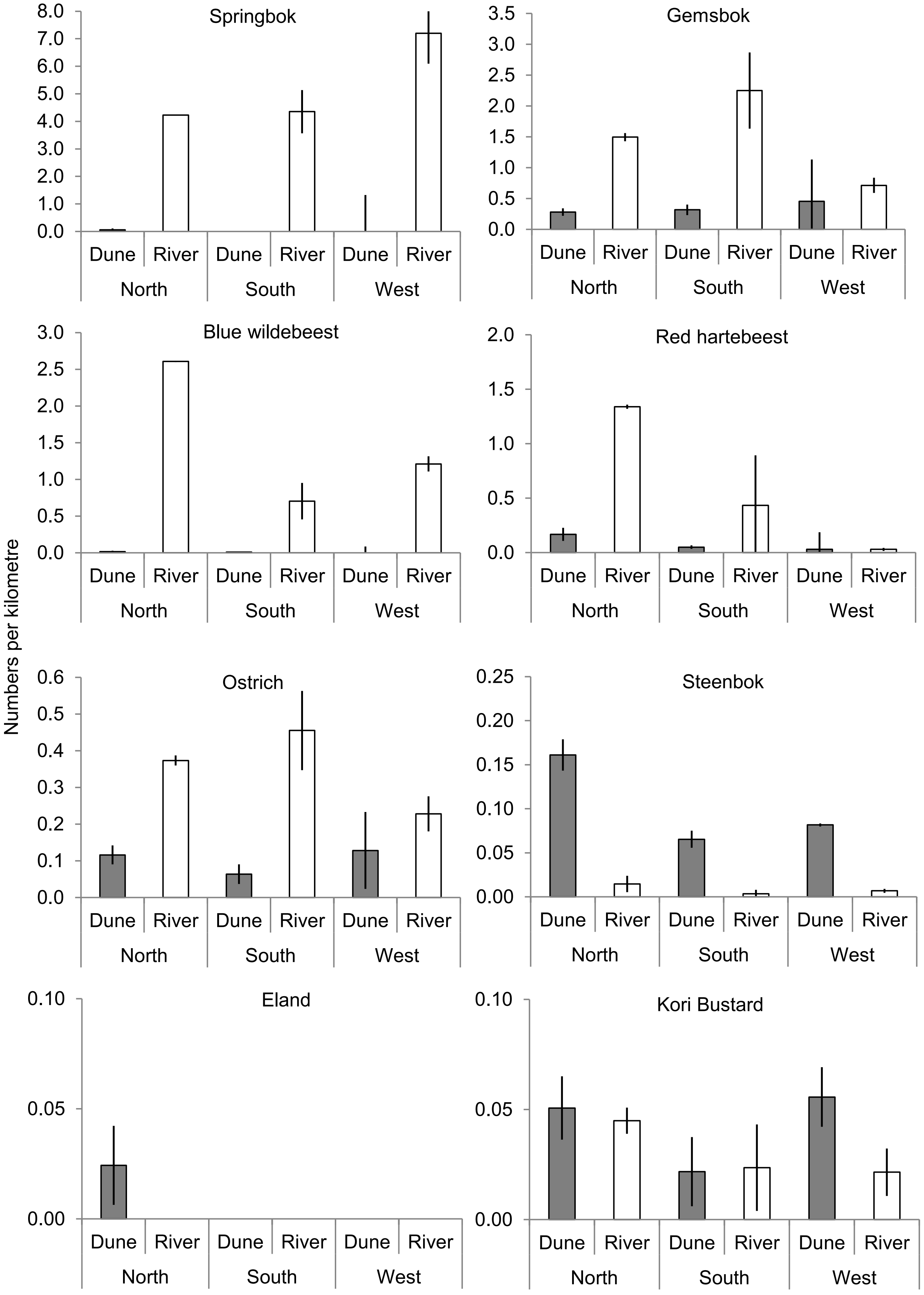


Figure 4.3 The number of animals per kilometre in the dune habitats (grey bars) and riverbed habitats (white bars) within the landscape type categories represented in the north, south and west. Error lines depict 95% confidence intervals.

4.3.1.3 Prey preference across landscape types

Using the Jacobs' Index (*D*) to determine prey preference for FO of prey in lion diet using GPS cluster analysis (D_{gps}) and scat analysis (D_{sca}), found that lions in the north showed a preference for gemsbok (D_{gps} = 0.6, D_{sca} = 0.4), wildebeest (D_{gps} = 0.5, D_{sca} = 0.3) and eland (D_{gps} = 0.3, D_{sca} = 0.2) (Figure 4.4). Kudu was preferred in the west (D_{gps} = 1.0) and north (D_{sca} = 1.0). In the north avoidance was indicated for all other species recorded in the diet for which the prey RAI was available. In the south lion showed significant preference for eland (D_{gps} = 1.0, D_{sca} = 1.0), less so for gemsbok (D_{gps} = 0.5, D_{sca} = -0.1) and wildebeest (D_{gps} = 0.4, D_{sca} = 0.3) and avoidance was indicated for all other prey species. In the west preference was shown for eland (D_{gps} = 1.0, D_{sca} = 1.0), wildebeest (D_{gps} = 0.4, D_{sca} = 0.5), and kudu (D_{gps} = 1.0), whereas gemsbok (D_{gps} = 0.4, D_{sca} = -0.1) and hartebeest (D_{gps} = 0.2, D_{sca} = 0.2) were taken in accordance to their proportional availability, and all other species were avoided (Figure 4.4).

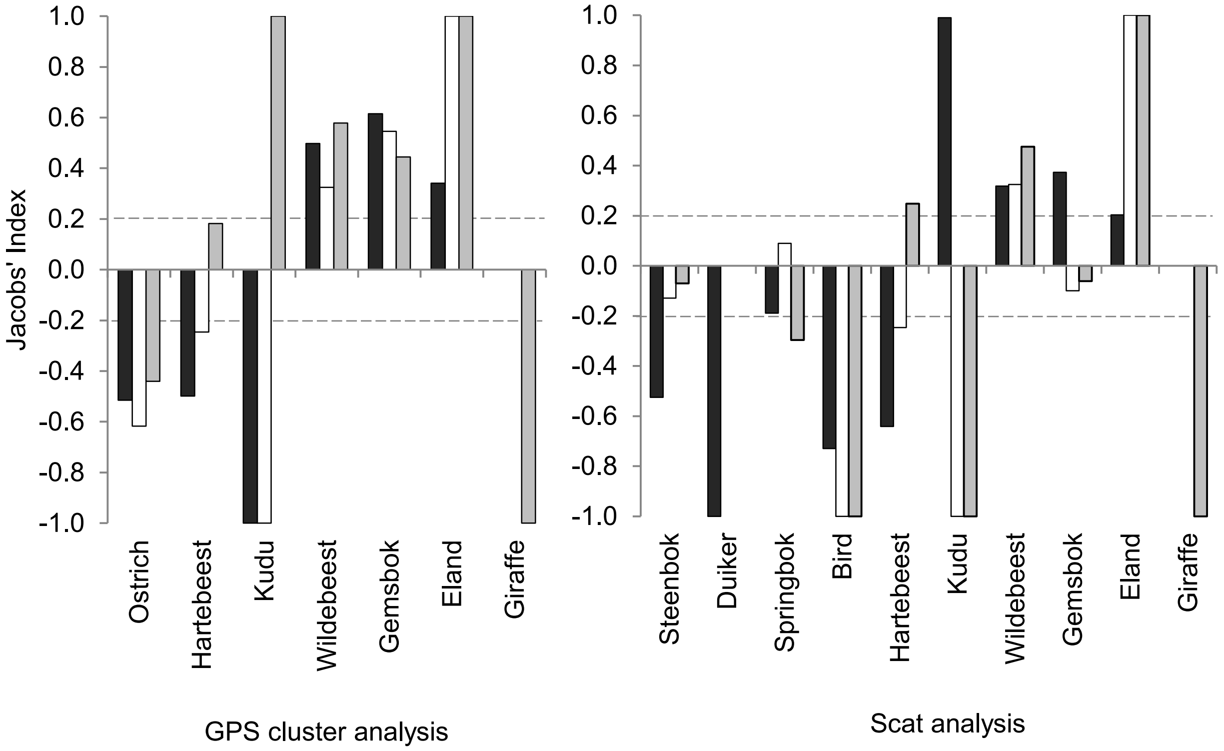


Figure 4.4 Prey preference of lion in the landscape types of the north (black bars), south (white bars) and west (grey bars) derived from the Jacobs' Index for GPS cluster analysis and scat analysis. Values of greater than 0.2 signifies preference and less than -0.2 signifies avoidance (dashed lines). Values between -0.2 and 0.2 indicated that the species was consumed proportionally to what was available .

4.3.2 Variations in lion diet and prey availability according to habitat types

4.3.2.1 Lion diet profile across habitat types

Based on the GPS cluster data, in both the dune and riverbed habitat types, gemsbok was the most frequently consumed species at 79.4% in the dunes and 51.6% in the riverbeds (Figure 4.5). A higher proportion of wildebeest was consumed in the riverbeds (35.9%) than in the dunes (2.3%) (F = 563, df = 1, p = 0.00). Springbok were exclusively consumed in the riverbeds (1.6%). In the dunes, ostrich (4.2%) and hartebeest (5.1%) were consumed more than in the riverbeds (1.6% and 3.1% respectively). Steenbok (3.3%) and Kori bustard (0.5%) were consumed exclusively in the dune habitat. Eland were consumed relatively equally in the dunes (4.2%) and in the riverbeds (4.7%) (Figure 4.5).

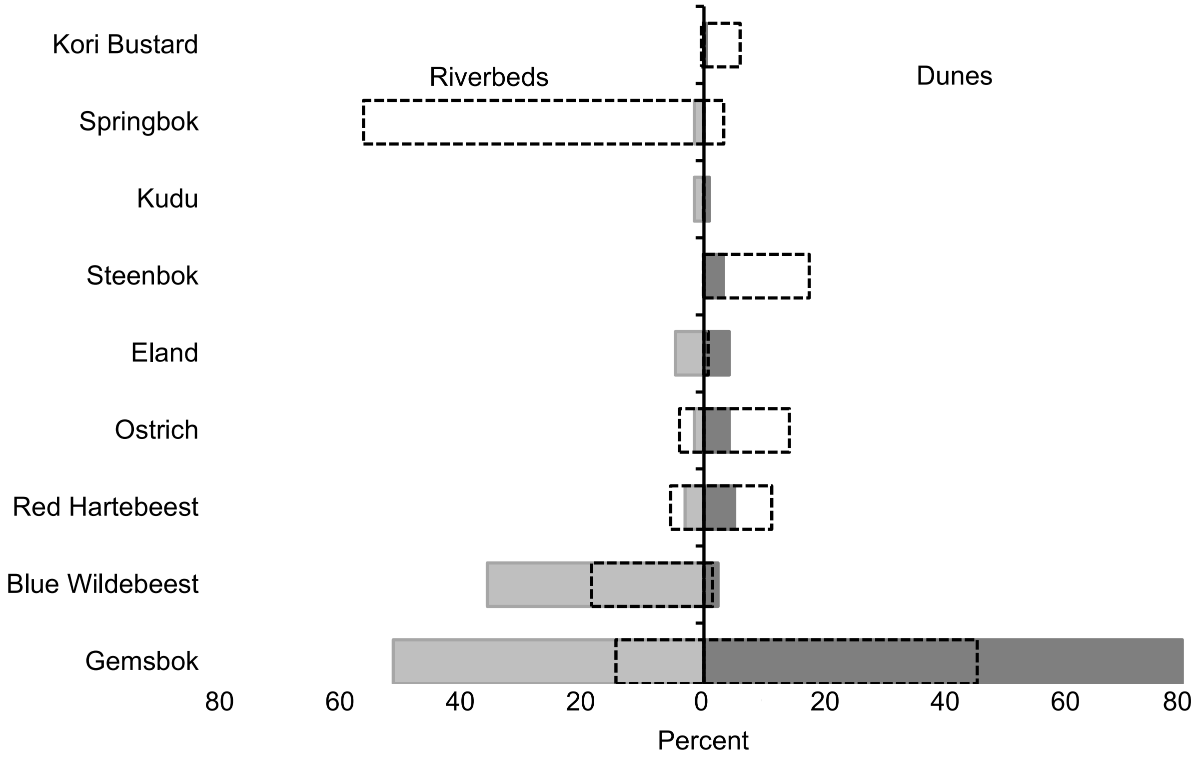


Figure 4.5 Frequency of occurrence of prey in lion diet (solid bars) and prey availability (dashed lines) in the riverbeds (light grey bars) and dunes (dark grey bars) for GPS cluster analysis.

Gemsbok contributed the most to lion biomass consumed in the dunes (82.6%) and riverbeds (52.4%) (Figure 4.6). Wildebeest contributed 33.6% to the biomass intake of lion in the riverbeds and only 2.2% in the dunes (*F* = 571.7, *df* = 1, *p* = 0.00). The biomass contribution of eland was similar in the dunes (9.6%) and in the riverbeds (10.4%). The remaining species together contributed 5.5% of the biomass in the dunes and 3.5% in the riverbeds (Figure 4.6).

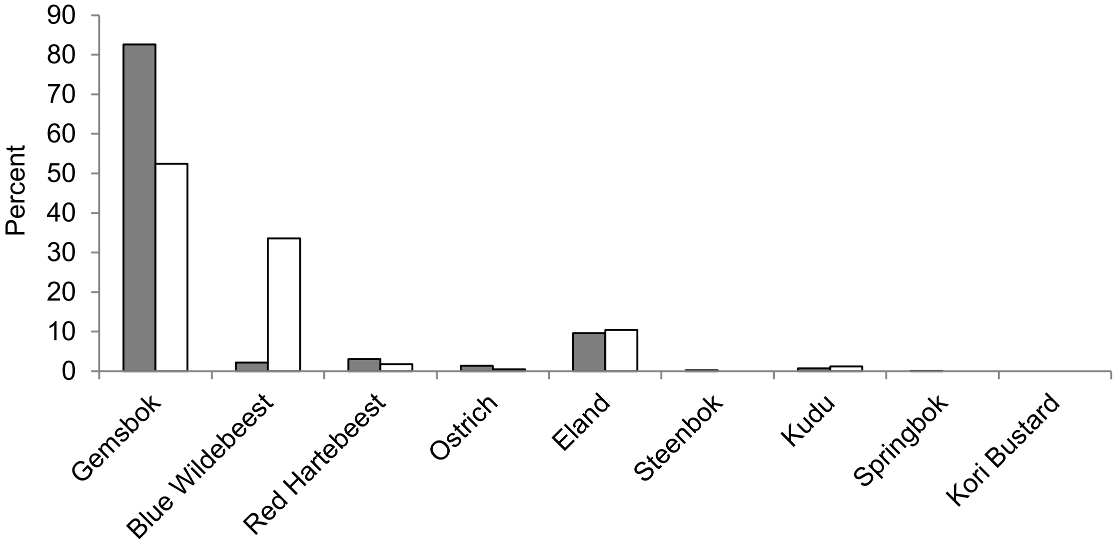


Figure 4.6 The proportional biomass contribution of prey to lion diet as determined from GPS cluster analysis in the dune habitat (grey bars) and riverbed habitat (white bars).

The proportional lion diet composition between the dunes and riverbeds had a relative percent difference of 18%. The overall biomass contributions of prey to lion diet according to habitat had a 16% relative percent difference. The relative difference in diet composition can be attributed mostly to wildebeest which were consumed significantly more (*F* = 563.2, *df* = 1, *p* = < 0.01) and contributed considerably more to the biomass intake (*F* = 571.1, *df* = 1, *p* = < 0.01) of lion in the riverbeds (Table 4.5 and Figures 4.5 & 4.6). The proportional and biomass contribution of all other species to lion diet did not vary significantly between habitat types (Table 4.5).

4.3.2.2 Prey availability across habitat types

According to prey relative abundance indices, gemsbok had the highest proportional RAI in the dune habitat (45%, *F* = 18.9, *df* = 1, *p* = 0.05) and springbok in the riverbed habitat (57%, *F* = 18791, *df* = 1, *p* = 0.00) (Figure 4.5). Wildebeest had a higher proportional representation in the riverbeds (19%,) than in the dunes (1%,) (*F* = 131.8, *df* = 1, *p* = 0.01). In the dunes steenbok (18%, *F* = 78.7, *df* = 1, *p* = 0.01), ostrich (14%, *F* = 137.9, *df* = 1, *p* = 0.01) and hartebeest (11%,) had a higher proportional representation than in the riverbeds at 0.1%, 4% and 6% respectively.

The number of animals per kilometre was higher in the riverbed habitat (9.2 km^{-1}, 95% *CI* = 6.7 – 11.4), than the dune habitat (0.5 km^{-1}, 95% *CI* = 0.4 - 0.7). Springbok were the most abundant species in the riverbed (5.1 km^{-1}, 95% *CI* = 4.6 – 5.6), followed by gemsbok (1.6 km^{-1}, 95% *CI* = 0.7 – 2.5) and wildebeest (1.4 km^{-1}, 95% *CI* = 1.3 – 1.6). Gemsbok were the most abundant species in the dune (0.25 km^{-1}, 95% *CI* = 0.19 – 0.3) followed by steenbok (0.08 km^{-1}, 95% *CI* = 0.07 – 0.09). Eland, steenbok and Kori bustard were more abundant in the dunes than the riverbeds. All other species had a higher representation per kilometre in the riverbeds (Figure 4.7).

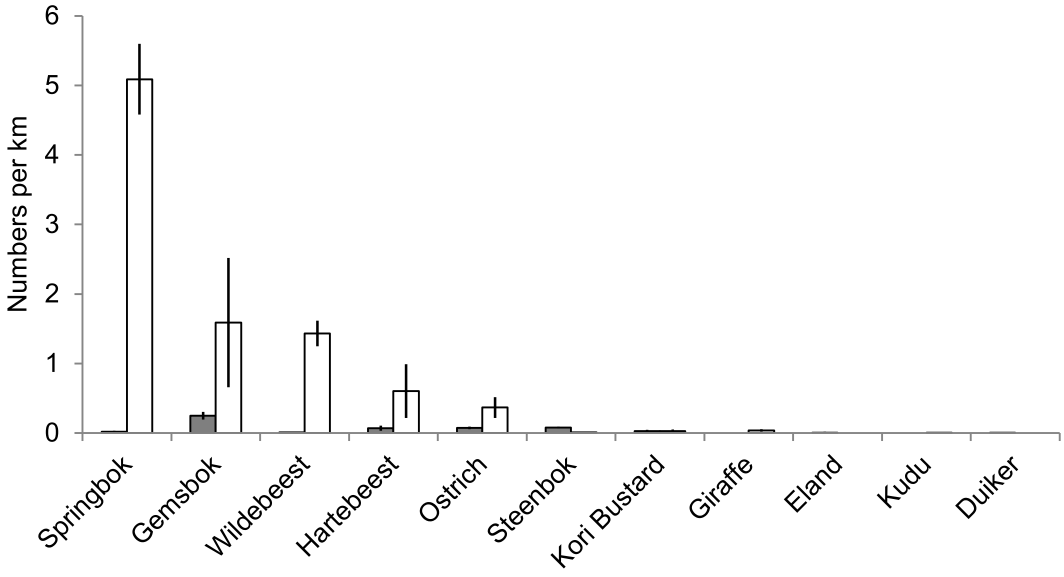


Figure 4.7 The number of prey available per kilometre in the dune habitats (grey bars) and riverbed habitats (white bars). Error bars depict 95% confidence intervals.

The relative percent difference in the proportional prey abundance was 40% between the habitat types. Springbok were significantly (*F* = 18791.5, *df* = 1, *p* = < 0.01) more abundant in the riverbed habitats, whereas steenbok (*F* = 78.7, *df* = 1, *p* = 0.01), ostrich (*F* = 137.9, *df* = 1, *p* = 0.01) and Kori bustard (*F* = 178.5, *df* = 1, *p* = 0.01) were significantly more abundant in the dunes (Figure 4.5 and Table 4.5). The relative abundance of the remainder of the species did not vary significantly between the two habitat types (Table 4.5).

4.3.2.3 Prey preference across habitat types

Results of the Jacobs Index between habitat types indicated that in both the dune (D_{dun}) and riverbed (D_{riv}) habitats lion showed preference for eland (D_{dun} = 1.0, D_{riv} = 1.0), gemsbok (D_{dun} = 0.6, D_{riv} = 0.7), wildebeest (D_{dun} = 0.2, D_{riv} = 0.4) and kudu (D_{dun} = 1.0, D_{riv} = 1.0) (Figure 4.8). Avoidance was indicated for ostrich (D_{dun} = -0.6, D_{riv} = -0.3) and hartebeest ($D_{dun}{}^{n}$ = -0.4, D_{riv} = -0.3) (Figure 4.8).

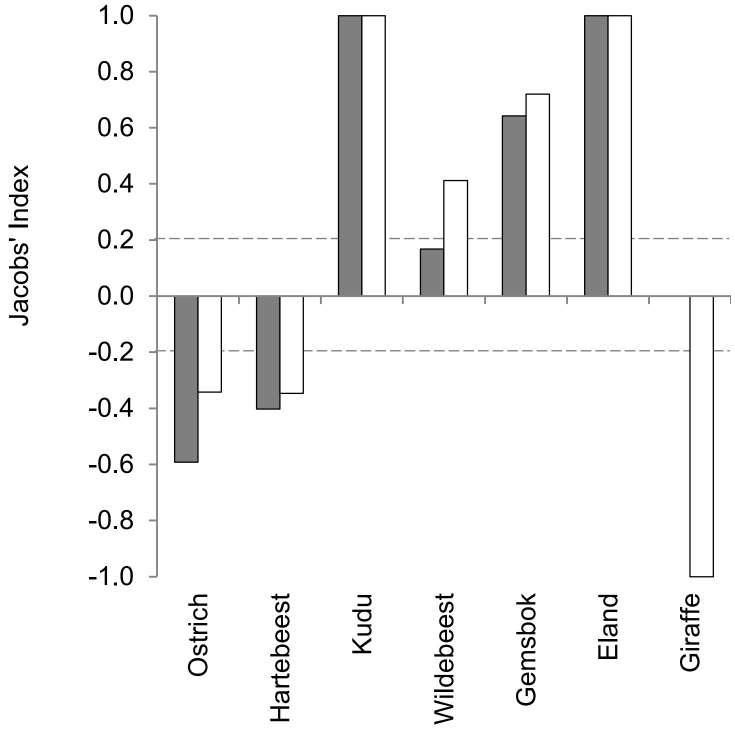


Figure 4.8 Prey preference of lion in the dune habitats (grey bars) and riverbed habitats (white bars) derived from the Jacobs Index scores for GPS cluster analysis. Values over 0.2 indicate preference and below -0.2 indicate avoidance (dashed lines). Values between 0.2 and -0.2 indicated that the species was consumed proportionally to what was available.

4.3.3 Seasonal variations in lion diet and prey availability

4.3.3.1 Lion diet profile across seasons

Lion diet composition showed almost no variation between the wet and the dry season for GPS cluster analysis, or scat analysis (Table 4.6). The greatest variation found in scat analysis was between gemsbok, constituting 55% of lion diet in the wet season and 50% in the dry season. Eland were found to be taken more frequently in the dry season than in the wet season for both GPS cluster analysis (wet 6% vs. dry 3%) and scat analysis (wet 2% vs. dry 4%). Steenbok were also consumed more frequently in the dry season for both GPS cluster analysis (wet 2%; dry 3%) and scat analysis (wet 5%; dry 8%). In terms of prey biomass contributions to lion diet between seasons, eland contributed 5% (GPS cluster) and 6% (scat analysis) more to lion diet in the dry season than in the wet season (Table 4.6) Gemsbok contributed 6% more to lion biomass in the wet season than in the dry season for both GPS cluster and scat analysis. The biomass contributions of all other prey species varied marginally (< 2%) between the wet and dry season, for both GPS cluster and scat analysis data (Table 4.6).

Table 4.6 The percentage frequency of occurrence and biomass contributions of various large (> 50 kg) and small (< 50 kg) prey species represented in lion diet through GPS cluster analysis and scat analysis in the wet and dry season.

		Frequency occurrence				**Biomass**			
		GPS cluster		**Scat analysis**		**GPS cluster**		**Scat analysis**	
		Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
Large	Gemsbok	74.7	71.1	54.5	50	77.5	71.6	75.3	69
	Wildebeest	10	10.2	9.1	8.3	9.3	11.1	11.6	10.6
	Eland	3.3	5.5	2.3	4.2	7.3	12.3	6.9	12.6
	Hartebeest	4.7	4.7	2.4	4.2	2.8	3.1	1.7	3.2
	Ostrich	3.3	3.8	0	0.7	1.2	1.7	0	0.3
	Kudu	1.3	0.8	0	0.7	1.7	0	0	0.7
Subtotal		97.3	96.1	68.3	68.1	99.8	99.8	95.5	96.4
Small	Porcupine	-	-	13.6	12.5	-	-	1.1	1
	Steenbok	2	3.1	4.5	8.3	0.1	0.2	0.3	0.6
	Springbok	0.7	0	13.6	8.3	0.1	0	3.1	1.9
	Kori bustard	0	0.8	-	-	0	0	-	-
	Springhare	-	-	0	2.8	-	-	0	0.1
Subtotal		2.7	3.9	31.7	31.9	0.2	0.2	4.5	3.6

A comparison of lion diet composition, in the wet and the dry season, indicated 1.2% relative percent difference (RPD) for GPS cluster data and 1.9% RPD for scat analysis data. The RPD between the lion biomass intake across seasons was 2% for GPS cluster analysis and 1.9% for scat analysis. The three-way ANOVA indicated that the only significant difference in lion diet between seasons was in the biomass contribution of wildebeest to lion diet profile obtained from GPS cluster analysis (F = 36.58, df = 1, p = 0.03). Wildebeest contributed a higher proportion to lion biomass intake in the dry season (11%) than in the wet season (9%). The results of the two-way ANOVA and three-way ANOVA tests for all other prey species indicated that there was no significant difference in the proportional or biomass contribution of the species to lion diet across seasons for both GPS cluster analysis and scat analysis (Table 4.5).

4.3.3.2 Prey availability across seasons

In terms of the overall relative prey abundance in the dunes, gemsbok was the most abundant prey species in both seasons. There was a higher abundance of gemsbok in the dry season (48%), than in the wet season (35%) (Figure 4.9). The proportional availability of hartebeest and steenbok was lower in the dry season (8% and 13% respectively) than in the wet season (13% and 18%). Wildebeest proportional availability increased from 3% in the dry season to 5% in the wet season. The proportional abundance of ostrich, springbok, eland and kudu recorded remained relatively constant between the wet and dry season (Figure 4.9).

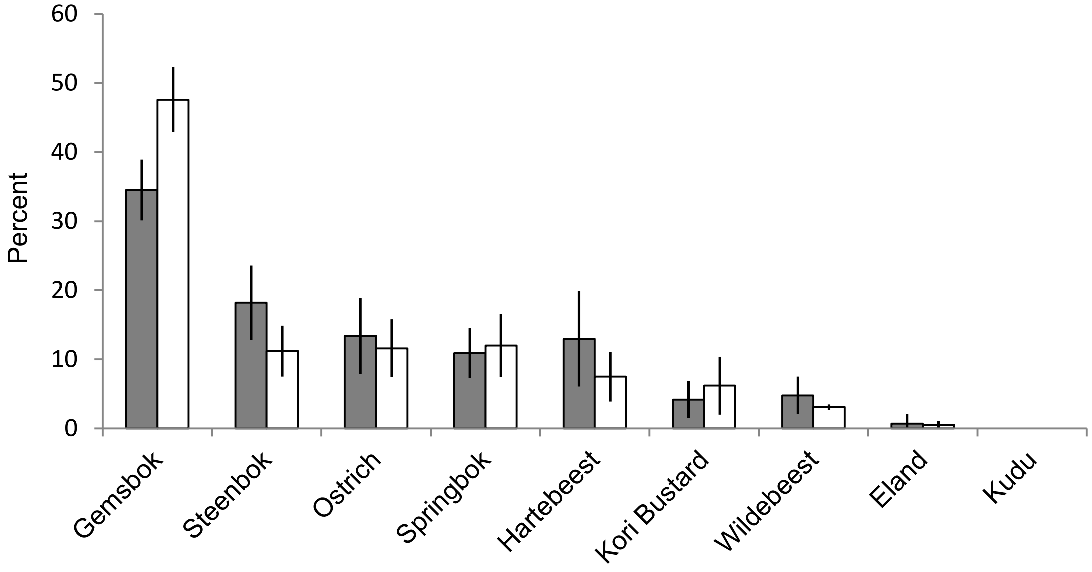


Figure 4.9 The relative abundance indices of prey in the wet season (grey bars) and dry season (white bars). Error bars represent 95% confidence intervals.

According to the number of animals recorded per kilometre between seasons, in the riverbed habitat, springbok was the most abundant species and their proportional abundance remained relatively constant across the wet season (56%) and dry season (57%). In the riverbeds the proportional abundance of gemsbok and hartebeest increased in the riverbeds from 13% and 4%, respectively in the dry season to 17% and 7% respectively in the wet season. Wildebeest proportional abundance in the riverbed decreased from the dry season (21%) to the wet season (17%).

Gemsbok numbers in the dunes increased from the wet season (0.3 km^{-1}) to the dry season (0.4 km^{-1}) (Figure 4.10). Wildebeest numbers also increased in the dunes from the dry season (where they were not recorded in the dunes) to the wet season (0.02 km^{-1}). Red hartebeest numbers in the dunes decreased from the wet season (0.1 km^{-1}) to the dry season (0.06 km^{-1}). The numbers of all other prey species per kilometre in the dunes remained relatively constant between the wet and the dry season (Figure 4.10). In the riverbeds gemsbok numbers increased from the dry season (0.9 km^{-1}) to the wet season (2 km^{-1}). Springbok and hartebeest numbers also increased in the riverbeds from the dry season (4.9 km^{-1} and 0.3 km^{-1} respectively) to the wet season (5.5 km^{-1}and 0.9 km^{-1}respectively). The numbers of all other prey species per kilometre in the riverbeds remained relatively constant between the wet and the dry season (Figure 4.10). The relative abundance of prey varied marginally between seasons with a relative percent difference of 4%. The three-way ANOVA indicated that there was no significant difference found between the relative abundance of prey in the wet seasons versus the dry season (Table 4.5).

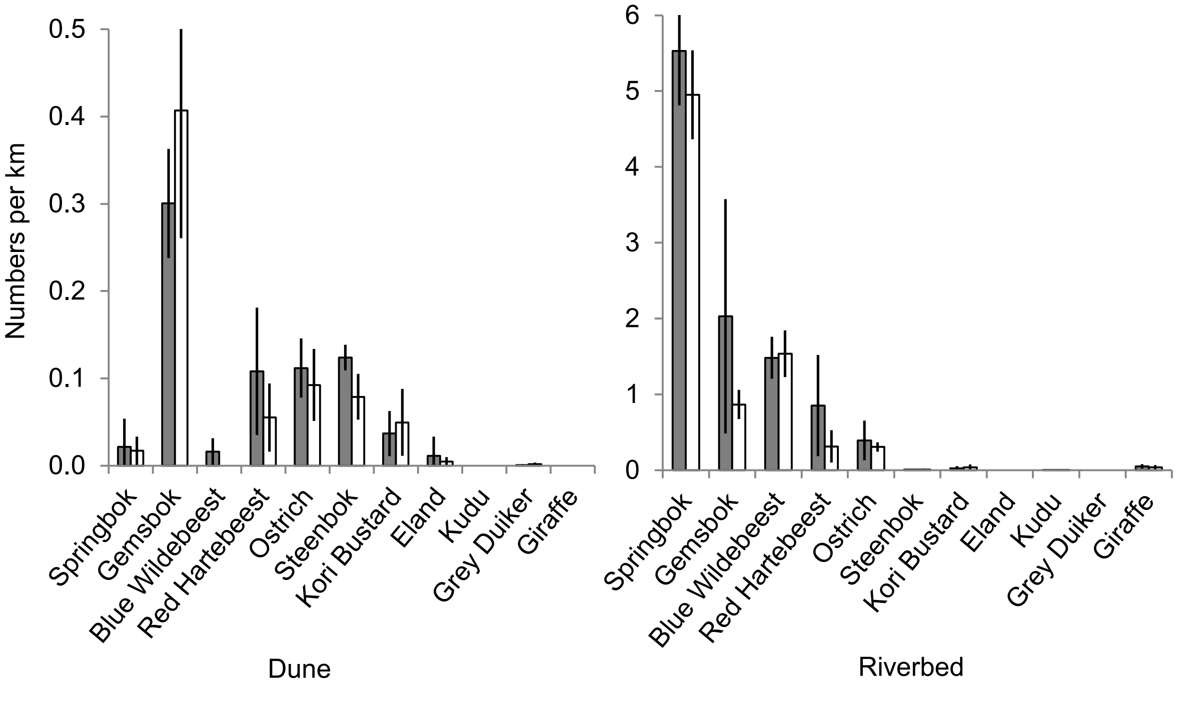


Figure 4.10 The number of animals per kilometre in the dune and riverbed habitats in the wet season (grey bars) and dry season (white bars). Error lines depict 95% confidence intervals.

4.3.3.3. Prey preference across seasons

There was little variation in prey preference between the wet (D_{wet}) and the dry (D_{dry}) season for GPS cluster analysis. In both the wet and the dry season, lion preferred eland (D_{wet} = 0.5; D_{dry} = 0.7), gemsbok (D_{wet} = 0.7; D_{dry} = 0.5), wildebeest (D_{wet} = 0.4; D_{dry} = 0.6) and kudu (D_{wet} = 1.0; D_{dry} = 1.0). Lions avoided all other species (Figure 4.11). Lion prey preference using scat analysis varied slightly in that springbok were taken in proportion to their availability in the wet season (D_{wet} = 0.1) and were avoided in the dry season (D_{dry} = -0.2). Using scat analysis as the diet estimate, lions showed preference for kudu (D_{wet} = 1; D_{dry} = 0.9), eland (D_{wet} = 0.4; D_{dry} = 0.6) and wildebeest (D_{wet} = 0.3; D_{dry} = 0.3). Using scat analysis, gemsbok where preferred in the wet season (D_{wet} = 0.4), although gemsbok were taken in proportion to their availability in the dry season (D_{dry} = 0.03) (Figure 4.11).

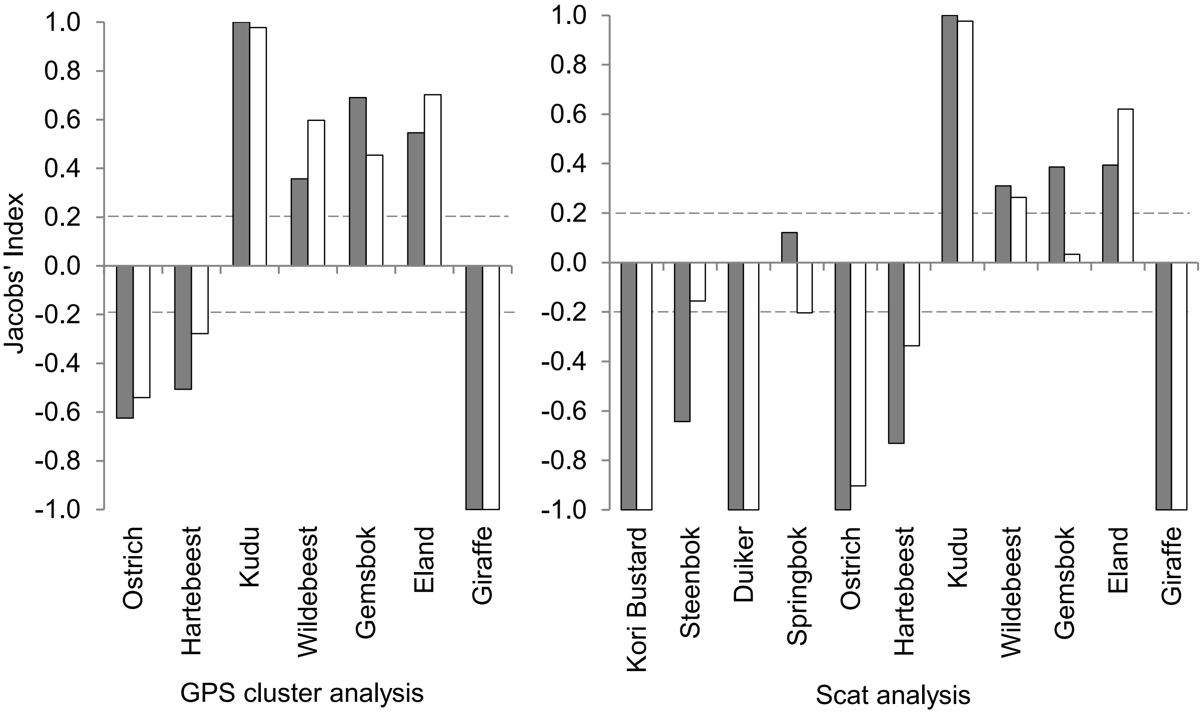


Figure 4.11 Prey preference of lion according to the wet season (black bars) and dry season (white bars) derived from the Jacobs' Index scores from GPS cluster analysis. Values over 0.2 indicate preference and below -0.2 indicate avoidance (dashed lines). Values between 0.2 and -0.2 indicated that the species was consumed proportionally to what was available.

4.3.4 Interrelationship between landscape types, habitat types and seasons

4.3.4.1 Interrelationship of the lion diet profile between landscape types, habitat types and seasons

A significant interaction was found for GPS cluster analysis in the proportion and biomass contributions of wildebeest in lion diet between habitat and season (*F* = 98.6, *df* = 1, *p* < 0.01), as well as between habitat and landscape (*F* = 58.7, *df* = 2, *p* = 0.02). The interaction of all other prey species compared across these factors for GPS cluster analysis showed no significant variation (Table 4.5). No significant interaction was found for scat analysis for any of the prey species between habitat and season or between habitat and landscape.

The proportion and biomass contributions of wildebeest between habitat and season (*F* = 98.6, *df* = 1, *p* < 0.01), as well as between habitat and landscape (*F* = 58.7, *df* = 2, *p* = 0.02) varied significantly for GPS cluster analysis. The interaction of all other prey species compared across these factors for GPS cluster analysis showed no significant variation (Table 4.5). No significant interaction was found for scat analysis for any of the prey species between habitat and season or between habitat and landscape.

4.3.4.2 Interrelationship of prey availability between landscape types, habitat types and seasons

The interaction between the relative prey abundance of springbok varied significantly between habitat and season (*F* = 31.7, *df* = 1, *p* = 0.03), habitat and landscape (*F* = 825.2, *df* = 2, *p* = < 0.01), and between landscape and season (*F* = 24.6, *df* = 2, *p* = 0.04). None of the interactions for any of the other prey species abundances varied significantly between these factors (Table 4.5).

4.4 Discussion

4.4.1 Sampling method

Each of the sampling methods used in this study to determine lion diet has inherent bias. GPS cluster analysis is known to over represent large prey in lion diet (Tambling et al., 2012, Chapter 3) and contradictorily scat analysis generally over represents small prey items (Floyd et al., 1978; Ruhe et al., 2008). The use of both GPS cluster analysis and scat analysis helps reduce this bias, by sampling large and small prey species, and provides a more accurate representation of lion diet (Tambling et al., 2012; Davidson et al., 2013). In Chapter 3 it was identified that a minimum sample size of 65 GPS cluster feeding events, and 55 lion scats is recommended to provide an accurate account of lion diet in the KGNP. Therefore, to assess lion diet accurately across landscape types, habitat types and season, this minimal sample size should be collected within each of these landscape types, habitat types or seasons. If the minimum recommended sample size is not obtained then the results would need to be reviewed with caution. In this study, sufficient sample sizes were obtained for determining lion diet according to landscape type, habitat and season, using GPS cluster analysis. Even so, the GPS cluster data could still be biased as a result of individual lion diet specialization, as the prey data for each landscape type was obtained from only two lionesses that were fitted with GPS collars in the north and south and three collared lionesses in the west. Thus, when the results of two or three females are extrapolated to represent the diet of all lions in a particular landscape, the results may be biased towards females which have individual dietary specializations (Boitani & Fuller, 2000). The results may also be skewed towards female lion diet and might not accurately represent the diet of males which may differ (Funston et al., 1998). For scat analysis, substantially fewer lion scats were collected in the wet season than in the dry season. The number of scats collected in the wet season (n = 44) was below the minimum recommended sample size of 55 samples. This small sample size was mostly as a result of the rapid removal and deterioration of scat by coprophagous insects and rain during the wet season, and has also been noted in other lion dietary studies (Tambling et al., 2012; Davidson et al., 2013). An insufficient sample size for lion scat analysis was also obtained in the landscape type of the south (n = 34). The small scat sample collected in the south was not due to a lack of effort, as the southern section had the highest sampling effort and so the reason for this is unknown. Low sample sizes collected for scat analysis in the wet season and in the southern landscape type, could thus have created a bias in the results within these parameters.

A small sample size could have limited the efficacy in testing for the potential influence of landscape type and season on lion diet represented by lion scat. It can be argued that the small sample size may still be representative of broader changes in lion diet, particularly for the dominant prey species, as collecting a low sample size reduces the ability to detect prey species that are consumed less frequently (Trites & Joy, 2005). Therefore, low sample sizes mostly hinder the ability for fine scale dietary interpretations. Results presented for lion diet obtained from scat analysis for the southern landscape type and season should thus be interpreted with caution.

4.4.2 Primary prey

Across all landscape types, habitat types and seasons in both GPS analysis and scat analysis, gemsbok was found to be the most frequently consumed prey species (range 42 –

79%). Gemsbok also contributed the highest proportion to lion biomass intake across all landscape types, habitats and seasons (range 55 – 82%). Therefore, gemsbok are the primary prey species for lion in the KGNP. Gemsbok have also been identified as a primary prey species in other lion dietary studies conducted in the broader Kalahari ecosystem (Eloff, 1984a; Mills, 1984; Stander, 2003; Roxburgh, 2008), Etosha National Park, Namibia (Stander, 1992) and Shamwari Private Game Reserve, South Africa (Rapson & Bernard, 2007). An additional study, which reviewed lion diet across 48 geographical locations, identified that gemsbok are a preferred prey species of lion, as they are generally consumed at higher proportions in relation to their availability (Hayward & Kerley, 2005).

Gemsbok were the most widespread of the large prey species encountered across the study area, occupying the dune and riverbed habitats alike, and were the most abundant species across all three landscape types, as well as in the dune habitat specifically. The proportional abundance of gemsbok was lower in the riverbeds than in the dunes, although their availability per kilometre in the riverbeds was at least four times higher than that represented in the dunes. Gemsbok were also proportionally the most abundant of the large prey species throughout the year. The proportional abundance of gemsbok increased in the dry season by 13%, whereas the proportional abundance for most other species decreased. This is likely due to seasonal movements of other species such as eland and hartebeest out of the area during the dry season (Mills & Retief 1984b). Gemsbok numbers per kilometre also increased across the dune habitats during the dry season.

Gemsbok are adapted to live independently of surface water and are resilient during periods of drought (Knight, 1995; East, 1999). Being largely sedentary in the KGNP (Mills, 2015), gemsbok are a reliable prey base to lion throughout the year, as well as during periods of drought. Gemsbok are also within the preferred prey weight range of lion (Hayward & Kerley, 2005). Thus, it is likely that gemsbok population dynamics are crucial to lion persistence in the KGNP.

4.4.3 Spatial variations

Differences shown in lion diet between landscape and habitat types are likely to reflect variations in the environment and prey availability across the KGNP. The proportional contributions of prey to lion diet across landscapes and habitats, may also provide an indication of how lions influence localized ecosystem dynamics through predation pressures on preferred prey species (Gittleman & Harvey, 1982; Fryxell et al., 2007; Owen-Smith & Mills, 2008b). Spatial variations in landscape structure influence lion hunting techniques and success (Loarie et al., 2013). Even though the study area in the KGNP is relatively homogenous, fine-scale differences exist between the topography, vegetation and landscape structure found in the north, south and west, as well as between the dunes, riverbeds and pans (Bothma & De Graaff, 1973; Van Rooyen et al., 2008).

The influence of regional landscape types represented in the north, south and west of the study area, had little influence on the overall lion diet composition. Of all the prey species available to lion in the KGNP, gemsbok, wildebeest and eland were the main contributors to lion biomass intake across all landscape types. Through scat analysis, lions in the west of the study area were identified to prey on a higher proportion (36%) of small prey species (< 50 kg), including porcupine, steenbok and springbok, than in the north (27%) or south (29%). Porcupine, in particular was consumed more frequently in the west (18%) than in the north (11%) or south (7%). No fine scale data exists on the abundance of porcupine across the KGNP. Therefore it is uncertain whether this can be attributed to localized variations in the abundance of porcupine or due to individual specialization in lion foraging behaviour.

Hartebeest were more abundant in the north, although they were not observed to be consumed more frequently in the north and their biomass contribution to lion diet remained relatively low in all areas (range 2 – 4%). A higher proportion of eland consumed in the south (8%) could be attributed to a migration of eland back into the KGNP from bordering farmlands, noticed during the study period. These herds of eland were observed but were not detected along the designated game count transects and where therefore not reflected in the prey RAI results. The movement of these herds of eland was impeded by the fences around the South African border of the park, causing the herds to remain largely sedentary for a period of a couple of weeks. During this time these eland herds seemed to be targeted by the lioness fitted with a GPS tracking collar and her associated pride. The game fences as well as the provision of artificial waterholes have inhibited the natural migration movement of eland (and other migratory species) making them more susceptible to die-off during periods of drought (Knight, 1995), as well as more vulnerable to predation by lion, who show significant preference for eland. Preference for eland by lion in the Kalahari ecosystem has been identified in a number of studies (Stander, 2003; van Vuuren et al., 2005; Roxburgh, 2008), although in other areas, eland are typically consumed in relation to their availability (Hayward & Kerley, 2005).

The riverbed habitats vary considerably across the KGNP, being broader in the north (up to 1000 m in diameter) and forming a narrower channel (to a minimum of 100 m in diameter) through calcrete and limestone ridges in the south and west (Leistner, 1967; Mills & Retief, 1984b). These topographical changes influence herbivore densities, as well as how they utilize the riverbeds (Bergstrom & Skarpe, 1999). This is further accentuated by the provision of artificial waterholes in the riverbeds (Mills & Retief, 1984b; Knight, 1995). Even though springbok and wildebeest had a relatively high occurrence per kilometre across all landscape types, they were found almost exclusively within the riverbed habitats (Williamson & Williamson, 1988). Thus, only lion that frequent the riverbed habitat would have regular access to this prey base. Wildebeest were significantly more abundant in the riverbeds in the north and were consumed significantly more in the north than in the south and west. Springbok were the most abundant species in the riverbeds in all areas and maintained a relatively high proportional abundance across all landscape types, which is likely to be due to their occurrence in large herds (Stapelberg et al., 2001). It is likely that springbok may have been underrepresented in the GPS cluster data, as due to their small body size they would have been consumed quickly leaving very few remains. Wildebeest and springbok were almost exclusively consumed within the riverbed habitat as opposed to the dune habitats. Wildebeest in the riverbeds contributed a large proportion to lion diet. All methods indicated that springbok were largely avoided by lion and are likely to only have been preyed upon opportunistically as opposed to being actively sought out.

4.4.4 Seasonal variations

Movements of large herbivores at various temporal scales, triggering fluctuations in localized prey availability, influence lion diet selection and biomass intake in Serengeti National Park, Tanzania (Schaller, 1972), Etosha National Park, Namibia (Stander, 1992), Kruger National Park, South Africa (Owen-Smith & Mills, 2008a) and Hwange National Park, Zimbabwe (Loveridge et al., 2009; Davidson et al., 2013). In the KGNP no significant variance was identified in lion diet between seasons, although changes were identified in the proportional prey availability and prey abundance between the wet and dry season.

The main difference in seasonal lion diet was a higher prevalence of eland in lion diet during the dry season (5 – 12% wet *vs.* 3 – 4% dry) and a higher occurrence of springbok in lion diet during the wet season (1 – 14% wet *vs.* 0 – 8% dry). It is possible that the higher occurrence of eland in lion diet during the dry season could be related to seasonal migrations of eland through the KTP (Eloff, 1962; Verlinden, 1998). The higher occurrence of springbok in lion diet in the wet season could be accredited to the lambing season and lions opportunistically feeding on the more vulnerable lambs. All but one record of springbok in lion diet were obtained through scat analysis, thus the age of the prey could not be determined. But it is known from other studies that lions will opportunistically target more vulnerable prey such as lambs or calves (Mills, 1984; Hayward & Kerley, 2005; Davidson et al., 2013).

Although the results on proportional prey availability between seasons were not significant, overall it was noted that herbivore numbers increased during the wet season, congregating particularly within the riverbeds and dispersed again during the dry season, this trend was also noted in previous studies on game movements in the KGNP (Mills & Retief, 1984b; Bergstrom & Skarpe, 1999). Wildebeest numbers in the riverbed decreased slightly in the wet season. This could be attributed to wildebeest being a water dependant species and thus able to graze further from waterholes during the wet season due to the presence of temporary surface water in ephermal pans (Williamson & Williamson, 1988; Van Der Walt et al., 1984). Gemsbok and hartebeest numbers on the other hand, increased in the riverbeds during the wet season as they are likely to be attracted to the flush of new growth in the riverbeds. Exceptionally high numbers of gemsbok and hartebeest have been recorded in the riverbeds during periods of good rainfall (Mills & Retief, 1984b). Even though these seasonal variations exist in the numerical abundance of prey, it does not seem to have a large influence on the overall proportional availability of prey across the KGNP. Thus, changes in prey abundance are unlikely to affect lion diet selection seasonally in the KGNP, as the relative proportional prey availability remains similar across seasons.

4.4.5 Interactions between spatial and seasonal variations

The interactions between habitat types and landscape types, as well as between habitat types and seasons were found to be significant for both lion diet selection and relative prey abundance. Wildebeest were identified as the primary cause for these significant relationships. This is likely as a result of wildebeest being a water dependant species that are largely confined to, and therefore consumed within the riverbed habitats.

4.5 Conclusion

Of the small prey species found in lion diet through scat analysis, porcupine was the main contributor to lion diet across all landscape types and seasons (range 7 – 18%). Nonetheless, in terms of biomass contributions, small mammals (< 50 kg) contributed less than 5% to lion diet across all landscape types and seasons. Even though small mammals do not contribute significantly spatially or seasonally to lion diet, they may play an important role in providing additional energetic contributions to lions, between acquisitions of large prey (Eloff, 1984a; Mills, 1984). In the semi-arid environment of Etosha National Park, small mammals (< 50 kg), specifically springbok, were found to contribute to 73% of lion diet and 50% of lion biomass intake, although lions in this area still showed preference for large prey (Stander, 1992).

In all landscape types, habitat types and seasons in the KGNP, lion preferred eland and wildebeest. Even though gemsbok was the most frequently consumed prey species, they were also found to be consumed in accordance to their availability in the southern and western landscape type, and in the dry season. Prey over 120 kg were the most important contributors to lion diet and accounted for over 95% of lion biomass intake for all survey methods, in all areas and seasons. Lions largely avoided all prey species weighing less than 120 kg.

Overall prey availability in the KGNP fluctuated between landscape types, habitat types and seasons, although these fluctuations in prey availability were not significant for the majority of prey species and had minimal influence on the spatial and seasonal diet selection of lion. Nonetheless, it has been identified that long term fluctuations in prey availability is the primary driving force of carnivore persistence (Fuller & Sievert, 2001). To be able to identify trends and track changes in predator-prey dynamics, it is important to understand how lions utilize their environment on various spatial and temporal scales, and the implications this may have on the ecological functioning of an environment (Hopcraft et al., 2005; Owen-Smith & Mills, 2008b; Valeix et al., 2009; Davidson et al., 2013; Sinclair & Arcese, 2013; Pereira et al., 2014; Loveridge et al., 2009). In the KGNP dramatic changes in prey availability over time, in response to shifting ecological conditions, such as drought, can influence prey dynamics (Knight, 1995) and may have serious implications on lion survival when these conditions persist over extended periods (van Vuuren et al., 2005). In light of potential shifting ecological conditions, gemsbok, as the primary prey species are of particular importance to lion in the KGNP, as they are well adapted to arid conditions and are resilient during periods of harsh ecological conditions (Knight, 1995; East, 1999).

The influence of spatial and seasonal differences on lion diet in the KGNP has now been identified, although the impact of long term ecological fluctuations on lion diet in the KGNP remains unknown. In Chapter 5 changes in lion diet are investigated over the last 45 years to determine if there has been a shift in lion diet over time.

4.6 References

Bauer, H. & Iongh, H.H. 2005. Lion (Panthera leo) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*, 43(3): 208–214.

Bergstrom, R. & Skarpe, C. 1999. The abundance of large wild herbivores in a semi-arid savanna inrelation to seasons, pan and livestock. *African Journal of Ecology*, 37: 26–37.

Boitani, L. & Fuller, T.K. 2000. *Research techniques in animal ecology*. Columbia University Press, New York.

Bothma, J.D.P. & De Graaff, G. 1973. A habitat map of the Kalahari Gemsbok National Park. *Koedoe*, 16(1): 181–188.

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature*, 402(6759): 286–288.

Cardillo, M., Mace, G.M., Gittleman, J.L. & Purvis, A. 2006. Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 103(11): 4157–4161.

Caro, T.M. 1999. Conservation monitoring: Estimating mammal densities in woodland habitats. *Animal Conservation*, 2(4): 305–315.

Castley, J.G., Knight, M.H., Mills, M.G.L. & Thouless, C. 2002. Estimation of the lion (Panthera leo) population in the southwestern Kgalagadi Transfrontier Park using a capture-recapture survey. *African Zoology*, 37: 27–34.

Celesia, G.G., Townsend Peterson, a., Kerbis Peterhans, J.C. & Gnoske, T.P. 2010. Climate and landscape correlates of African lion (Panthera leo) demography. *African Journal of Ecology*, 48(1): 58–71.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turbull, L.A., Macdonald, D.W. & Scmid, B. 2012. Fear of the dark or dinner by moonlight ? Reduced temporal partitioning among Africa' s large carnivores. *Ecology*, 93(1): 2590–2599.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. 2013. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid Savanna. *PLoS ONE*, 8(2). e55182.

East, R. 1999. *African antelope database 1998 (Vol. 21)*. IUCN. Gland, Switzerland.

Eloff, F.C. 1962a. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park, Part IV. *Koedoe*, 5(1): 128–136.

Eloff, F.C. 1962b. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park. part IV. *Koedoe*, 5(1): 128–136.

Eloff, F.C. 1966. Range extension of the blue wildebeest. *Koedoe*, 9: 34–36.

Eloff, F.C. 1984a. Food ecology of the Kalahari lion. *Koedoe*, 27(2): 249–258.

Eloff, F.C. 1984b. The Kalahari ecosystem. *Koedoe*, 27(2): 11–20.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Floyd, T.J., Mech, L.D. & Jordan, P.A. 1978. Relating wolf scat content to prey consumed. *Journal of Wildlife Management*, 42(3): 528–532.

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M. & Clobert, J. 2011. A food web perspective on large herbivore community limitation. *Ecography*, 34(2): 196–202.

Fryxell, J.M., Mosser, A., Sinclair, A.R.E. & Packer, C. 2007. Group formation stabilizes predator-prey dynamics. *Nature*, 449(7165): 1041–1043.

Fuller, T. & Sievert, P. 2001. *Carnivore demography and the consequences of changes in prey availability*. In: Gittleman JL, Funk SM, Macdonald D, Wayne RK (eds) Carnivore conservation. Cambridge University Press, Cambridge.

Funston, P.J. 2001. *Kalahari Transfrontier lion project: final report*. Endangered Wildlife Trust, Johannesburg, South Africa.

Funston, P.J. 2011. Population characteristics of lions (Panthera leo) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 41: 1–10.

Gittleman, J.L. & Harvey, P.H. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10(1): 57–63.

Hayward, M.W. & Kerley, G.I.H. 2005. Prey preferences of the lion (Panthera leo). *Journal of Zoology*, 267: 309–322.

Hayward, M.W., Hayward, G.J., Tambling, C.J. & Kerley, G.I.H. 2011. Do lions Panthera leo actively select prey or do prey preferences simply reflect chance responses via evolutionary adaptations to optimal foraging? *PLoS ONE*, 6(9): e23607.

Herrmann, E. 2004. *Modelling the effect of human-caused mortality on a lion sub-population using spreadsheets*. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

Hopcraft, J.G.C., Olff, H. & Sinclair, A.R.E. 2010. Herbivores , resources and risks : alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, 25(2): 119–128.

Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. 2005. Planning for success : Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74: 559–566.

Jacobs, J. 1974. Quantitative measurement of food selection. *Oecologia*, 14(4): 413–417.

Knight, M.H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33: 377–394.

LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics*, 20: 97–117.

Lake, S., Burton, H. & Hoff, J. Van Den. 2003. Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Marine Ecology Progress Series*, 254: 293–305.

Leistner, O.A. 1967. The plant ecology of the southern Kalahari. *Memoirs of the Botanical Survey of South Africaoirs of the Botanical Survey of South Africa*, 38: 1–172.

Lepš, J., de Bello, F., Lavorel, S. & Berman, S. 2006. Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia*, 78(4): 481–501.

Loarie, S.R., Tambling, C.J. & Asner, G.P. 2013. Lion hunting behaviour and vegetation structure in an African savanna. *Animal Behaviour*, 85(5): 899–906.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134: 548–558.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography*, 32(6): 953–962.

Mills, M.G.L. 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. *Koedoe*, 27(2): 281–294.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 45(2): 127–137.

Mills, M.G.L. & Retief, P.F. 1984a. The effects of windmill closure on the movement patterns of ungulates along the Auob riverbed. *Koedoe*, 27(2): 107–118.

Mills, M.G.L. & Retief, P.F. 1984b. The response of ungulates to rainfall along the riverbeds of the Southern Kalahari 1972-1982. *Koedoe*, 27(2): 129–141.

Mills, M.G.L., Biggs, H.C. & Whyte, I.J. 1995. The relationship between rainfall, lion predation and population trends in African herbivores. *Wildlife Research*, 22: 75–81.

Mills, M.G.L., Wolff, P., Le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion in Kalahari Gemsbok National Park. *Koedoe*, 2: 163–171.

Mucina, L. & Rutherford, M.C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Mukherjee, S., Goyal, S.P. & Chellam, R. 1994. Refined techniques for the analysis of Asiatic lion Panthera leo persica scats. *Acta Theriologica*, 39(4): 425–430.

Ogara, W.O., Gitahi, N.J., Andanje, S. a, Oguge, N., Nduati, D.W. & Mainga, A.O. 2010. Determination of carnivores prey base by scat analysis in Samburu community group ranches in Kenya. *African Journal of Environmental Science and Technology*, 4: 540–546.

Oksanen, L. & Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *The American Naturalist*, 155(6): 703–723.

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

Owen-Smith, N. & Mills, M.G.L. 2008b. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*, 89(4): 1120–1133.

Owen-Smith, R.N. 1988. *Megaherbivores: The influence of very large body size on ecology*. Cambridge: Cambridge University Press, Cambridge.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, 14: 483–488.

Patterson, B.D. 2007. On the nature and significance of variability in lions (Panthera leo). *Evolutionary Biology*, 34: 55–60.

Pereira, L.M., Owen-Smith, N. & Moleon, M. 2014. Facultative predation and scavenging by mammalian carnivores : seasonal, regional and intra-guild comparisons. *Mammal Review*, 44: 44–55.

Quantum GIS Development Team. 2016. QGIS Geographic Information System. Open Source Geospatial Foundation. URL http://qgus.osgeo.org.

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.

Rapson, J.A. & Bernard, R.T.F. 2007. Interpreting the diet of lions (Panthera leo); a comparison of various methods of analysis. *South African Journal of Wildlife Research*, 37(2): 179–187.

Reed, M.S. & Dougill, A.J. 2003. Facilitating grass-roots sustainable development through sustainability sndicators: a Kalahari Case Study. *Proceedings of Frontiers*, 2: 1–19.

Roxburgh, D.J. 2008. *Prey and range use of lions on Tswalu Kalahari Reserve*. M.Sc. Thesis, University of Pretoria, Pretoria.

Ruhe, F., Ksinsik, M. & Kiffner, C. 2008. Conversion factors in carnivore scat analysis : sources of bias. *Wildlife Biology*, 14(4): 500–506.

Schaller, G.B. 1972. *The Serengeti Lion: A study of predator–prey relations*. The University of Chicago Press, Chicago.

Sidorovich, E., Solovej, I.A., Sidorovich, A.A. & Dyman, A.A. 2008. Seasonal and annual variation in the diet of the raccoon dog Nytereutes procyonoides in northern Belarus: The role of habitat type and family group. *Acta Theriologica*, 53(1): 27–38.

Sinclair, A.R.E. & Arcese, P. 2013. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology*, 76(3): 882–891.

Skinner, J.D. & Chimimba, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press, Cape Town.

Sluiter, A., Ruiz, R., Scarlata, C., Sluiter, J. & Templeton, D. 2005. *Determination of extractives in biomass*. National Renewable Energy Laboratory Golden, Battelle.

Sokal, R.R. & Rohlf, F.J. 1981. *The principles and practice of statistics in biological research*. W. H. Freeman, New York.

Stander, P.E. 1992. Foraging dynamics of lion in a semi-arid environment. *Canadian Journal of Zoology*, 70: 8–21.

Stander, P.E. 2003. *The ecology of lions and cheetahs re-introduced to the Kalahari Game Lodge, Namibia*. Unpublished report to the Kalahari Game Lodge, Namibia.

Stapelberg, H., Van Rooyen, M., Bothma, J.D.P., Van der Linde, M.J. & Groeneveld, H.T. 2001. Springbok behaviour as affected by environmental conditions in the Kalahari. *Koedoe*, 50(1): 145–153.

Tambling, C.J. & Belton, L.E. 2009. Feasibility of using proximity tags to locate female lion Panthera leo kills. *Wildlife Biology*, 15: 435–441.

Tambling, C.J., Laurence, S.D., Bellan, S.E., Cameron, E.Z., Toit, J.T. & Getz, W.M. 2012. Estimating carnivoran diets using a combination of carcass observations and scats from GPS clusters. *Journal of Zoology*, 286(2): 102–109.

Thiemann, G.W., Iverson, S.J., Stirling, I. & Obbard, M.E. 2011. Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. *Oikos,* 120(10): 1469-1478.

Thomas, D.S.G. & Twyman, C. 2004. Good or bad rangeland? Hybrid knowledge, science, and local understandings of vegetation dynamics in the Kalahari. *Land Degradation and Development*, 15: 215–231.

Trites, A.W. & Joy, R. 2005. Dietary analysis from fecal samples: How many scats are enough? *Journal of Mammalogy*, 86(4): 704–712.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90(1): 23–30.

Van Der Walt, P.T., Retief, P.F., Le Richie, E.A.N., Mills, M.G.L. & De Graaff, G. 1984. Features of habitat selection by larger herbivorous mammals and ostrich in the southern Kalahari conservation areas. *Koedoe*, 27(2): 119–128.

Van Rooyen, M.W., Van Rooyen, N., Bothma, J.D.P. & Van den Berg, H.M. 2008. Landscapes in the Kalahari Gemsbok National Park, South Africa. *Koedoe*, 50(1): 99–112.

Van Rooyen, N., Bezuidenhout, D., Theron, G.K. & Bothma, J.D.P. 1990. Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe*, 33(1): 63–88.

Van Rooyen, N., Bredenkamp, G.J., Theron, G.K., Bothma, J.D.P. & Le Richie, E.A.N. 1994. Vegetational gradients around artificial watering points in the Kalahari Gemsbok National Park. *Journal of Arid Environments*, 26: 349–361.

Van Vuuren, J.H., Herrmann, E. & Funston, P.J. 2005. Lions in the Kgalagadi Transfrontier Park: Modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171.

Verlinden, A. 1998. Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, 36(117): 128.

Williamson, D. & Williamson, J. 1984. Botswana’s fences and the depletion of Kalahari wildlife. *Oryx*, 18(04): 218–222.

Williamson, D. & Williamson, J. 1988. Wildebeest migration in the Kalahari. *African Journal of Ecology*, 26(4): 269–280.

CHAPTER 5

VARIATION IN LION (*PANTHERA LEO*) DIET IN THE KALAHARI GEMSBOK NATIONAL PARK FROM 1970 TO 2015

5.1 Introduction

Lion (*Panthera leo*) diet is known to change in response to shifting ecological conditions over time (Schaller, 1972; Stander, 1992; Owen-Smith & Mills, 2008b; Davidson et al., 2013). Biological systems exist in certain “states” that are controlled by both biotic and abiotic components (Schmitz et al., 2003). Ecosystems fluctuate between states of equilibrium and non-equilibrium which are subsequently subject to change over time, resulting in a shift in ecosystem conditions that differs from the previous state (Briske et al., 2003; Barnosky et al., 2012). Ecosystems change in response to gradual changes in climate, nutrient availability, habitat degradation or exploitation of natural resources (Scheffer et al., 2001), which in turn has an influence on lion diet and demography (Owen-Smith & Mills, 2008b; Celesia et al., 2010; Davidson et al., 2013). The rate at which ecological state shifts normally occur, can be amplified through anthropogenic activities (Suding et al., 2004; Barnosky et al., 2012). Ecological state shifts have an influence on herbivore dynamics which in turn, impact lion demographics (Valeix et al., 2009). It is plausible that progressive shifts in diet over time may provide an indicator of state shifts, most notably in accordance with ecological infliction points, such as drought (Boutin, 1995). Consequently, identifying temporal changes in lion diet could provide an indicator of environmental state shifts and may signal when management interventions might be required (Suding et al., 2004; Davidson et al., 2013).

Extensive rangelands, such as the Kgalagadi Transfrontier Park (KTP) are complex systems that are influenced by a multitude of factors (Noy-Meir, 1975; Suding et al., 2004; Briske et al., 2005). The key ecological driver in savanna ecosystems is rainfall (Coe et al., 1976; Mills et al., 1995; Owen-Smith & Mills, 2008b). However, annual rainfall in the KTP is limited (< 250 mm), resulting in low herbivore and carnivore biomass (Loveridge & Canney, 2009; Celesia et al., 2010; Mills, 2015). The resource poor environment, relative isolation and low population size of lions in the KTP (Mills et al., 1978; Castley et al., 2002; Loveridge & Canney, 2009), makes them particularly vulnerable to the effects of environmental fluctuations and anthropogenic influences (Herrmann, 2004; Bauer & Iongh, 2005). Due to the extreme climatic conditions, arid areas such as the Kalahari have been identified to have a relatively high “latent extinction risk” for mammalian species (Cardillo et al., 2006). Land use and management practices in and around the KTP, such as livestock farming

(Herrmann, 2004), the provision of artificial water sources (Van Rooyen et al., 1990; Funston, 2001; Ferreira et al., 2013), and the construction of manmade barriers such as fences, further influence natural population dynamics (Williamson & Williamson, 1984;). Anthropogenic interferences may impact a lion population, as changes in the natural distribution of animals can result in a shift in lion population community structure and ecology (Loveridge et al., 2009).

Herbivore dynamics are likely to have changed in the KTP over time due to the erection of game fences, causing animals which were once migratory over vast distances, such as springbok, *Antidorcas marsupialis,* eland, *Tragelaphus oryx,* and red hartebeest, *Alcelaphus buselaphus*, to instead restrict their movements to the KTP (Eloff, 1962; Mills & Haagner, 1989; Verlinden, 1998a). The provision of artificial water points since the 1930's in the Kalahari Gemsbok National Park (the South African section of the KTP), have also altered herbivore assemblages in the KTP (Eloff, 1966; Van Rooyen et al., 1994; Funston, 2011). Artificial waterholes Kalahari Gemsbok National Park (KGNP) have resulted in an increase in the abundance and distribution of the water dependent blue wildebeest*, Connochaetes taurinus,* which seem to have established resident herds that stopped migrating altogether, and it appears that some springbok herds have also become sedentary in the KGNP (Knight, 1995; Owen-Smith, 1996). Lion prides in close proximity to artificial water sources may thus be exposed to a more reliable food source than in the past (Funston, 2011), influencing diet selection which in turn may impact on lion body condition, population density and survival rates (Ferreira & Funston, 2010; Loveridge et al., 2009).

The KGNP lion population's pride composition and dispersal patterns are related to resident prey availability (Castley et al., 2002; Funston, 2011). Herbivore populations are regulated by both primary production and predation (Sinclair & Arcese, 2013), and an increase or decline in lion numbers could negatively impact herbivore population dynamics (Miller et al., 2001; Loveridge et al., 2007). Through prey selection, lions can have spatio-temporal influences on prey species (Valeix et al., 2009), which can have an effect on habitat alteration, utilization and condition (Gittleman & Harvey, 1982). The susceptibility of herbivores to predation varies seasonally and spatially (Sinclair & Arcese, 2013; Pereira et al., 2014). Changes in lion diet over time can potentially lead to a skew in the sex ratio of a population (Ferreira & Funston 2010), since diet has an effect on body condition, which in turn has been found to influence the sex ratio of offspring, where a female in good body condition is more likely to produce male progeny (Trivers & Willard, 1973; Meikle & Drickamer, 1986). Numerous studies conducted on sex ratios have provided evidence correlating maternal condition and sex ratio (Sheldon & West, 2004). Census data indicated a skew in the sex ratio in favour of male lions in the KGNP in 2010, that might be a consequence of female lions being in better body condition (Ferreira et al. 2012). Therefore, identifying whether there has been a change in lion diet might shed some light into the hypothesis that the sex skew in the KGNP may be related to a change in lion diet over time.

In this chapter the diet of the lions in the KGNP, as described in Chapters 3 and 4, is compared with published historical dietary records from the 1970's and early 1980's (Eloff, 1984; Mills, 1984), to investigate whether there has been a detectable shift over the last 45 years. Changes in lion diet are then compared to shifting prey dynamics over time and the potential drivers of lion diet in the KGNP are discussed.

5.2 Material and methods

5.2.1 Data collection

5.2.1.1 Lion diet

To address the changes in lion diet over the past 45 years, a database was created by collating data from historical and recent publications and reports related to lion diet and prey abundance in KGNP. Data sets from two studies conducted on lion diet in the KGNP, both of which occurred over 30 years ago (Eloff, 1984; Mills, 1984), were compared with the results of the present study to assess changes in lion diet over time. The first of these studies was conducted intermittently between 1970 and 1983 in the northern section of the KGNP. This study used Bushman trackers to survey the spoor of lion made within 24 hours, over 195 periods (Eloff, 1984). The second study was conducted within a similar time frame, between 1974 and 1982, but differed in that it used opportunistic observations of lion feeding events collated from ranger reports and diaries across the KGNP (Mills, 1984). The present study made use of lion feeding event data obtained from GPS cluster analysis as well as lion scat analysis. The methods used for data collection in the present study are discussed in detail in Chapters 3 and 4.

5.2.1.2 Prey abundance

Game count data was used to determine the relative abundance indices (RAI) of prey in the KGNP for both the current and historical study periods. Data on prey abundance was obtained from aerial game counts and road transect game counts. Aerial game count data for the dry seasons was obtained for the period between 1978 and 1984 (Knight, 1995), and during the study period in 2013 (SANParks unpublished data). Aerial game counts were conducted by SANParks using the standard operating procedures for conducting aerial surveys in South African National Park (Castley, 2005). Data from road transect game counts that were conducted in the Auob and Nossob riverbeds between 1972 and 1982 (Mills &

Retief, 1984) was obtained for comparison with riverbed game counts that were conducted throughout the current study period. Further details on how road transect game counts were conducted in the present study are presented in Chapter 4.

5.2.2 Data analysis

5.2.2.1 Lion diet

The proportions of each prey species represented in lion diet and their relative biomass contribution to lion diet are presented for the two methods used to determine lion diet in the present study, as well as the two methods used in the historical studies. Prey were categorized according to their mass as large prey (≥ 50 kg) *i.e.* ostrich, *Struthio camelus* and larger, or small prey (< 50 kg) *i.e.* springbok and smaller. The lion diet profiles of the historical and present studies were then broken down into two separate data sets. One data set dealt specifically with large prey species, and their proportional contribution to the total sample of large prey represented in lion diet, by the respective studies. The other data set dealt specifically with small prey species, and the proportional contribution of the different small prey species to the total sample of small prey represented in lion diet by the respective studies. This was done to reduce the potential bias of over- or underrepresenting small or large prey as a result of survey technique used when comparing various studies.

Two finer scaled comparisons were also made between the historical studies and the present study according to the survey methods used and method bias. A fine scaled comparison was made between the large and small prey data sets obtained from the historical study, which made use of bushman trackers in the north of the park (Eloff, 2002) and the lion diet profile of the present study, obtained from lion scat data collected in the northern section of the KGNP. The other fine scale comparison was made between the large prey dataset of the historical dietary study from opportunistic observations that were primarily conducted in the riverbed habitats (Mills, 1984) and the lion diet profile obtained from GPS cluster data from the riverbeds. The frequency of occurrence of prey in lion diet was converted into approximate biomass contribution of prey (BM) to lion diet for each data set. The relative biomass index of prey was ascribed according to the methods outlined in Chapter 4.

To test how significantly the lion diet compositions have varied over the past 45 years, two category comparisons of the large prey data set and small prey data set were made using the Pearson's Chi-square test (Pearson, 1900). The composition of large prey species, represented in the lion diet profile of the large prey data sets including gemsbok, *Oryx gazella*, blue wildebeest, red hartebeest, eland, *Tragelaphus oryx,* ostrich, *Struthio camelus,* and kudu, *Tragelaphus strepsiceros,* were tested for differences in overall lion diet composition between studies. The composition of small prey species, represented in the lion diet profile of the small prey data sets including springbok, porcupine, *Hystrix africaeaustralis,* steenbok, *Raphicerus campestris*, springhare, *Pedetes capensis*, aardvark, *Orycteropus afer*, bat-eared fox, *Otocyon megalotis*, Kori bustard, *Ardeotis kori* and common duiker, *Sylvicapra grimmia*, were tested for differences in overall lion diet composition between studies. The large prey data sets obtained from the historical studies were compared with the large prey data sets obtained from the present study for both GPS cluster data as well as with scat analysis data. The small prey data sets obtained from the historical studies were compared with the small prey data sets obtained from the present study for scat analysis data. GPS cluster data was not compared for the small prey data set, as there was an insufficient sample size of small prey to allow for comparison.

The extent to which lion diet composition varied over the past 45 years between the four survey methods used was calculated using the Pearson's Chi-square test (Pearson, 1900) and the relative percent difference index (Lepš et al., 2006; Sluiter et al., 2005). To prevent bias in Chi-square values large prey were grouped and small prey were grouped to allow for comparison (Kindt & Coe 2005). The relative percent difference index was used to compare the frequency of occurrence of prey in lion diet for GPS cluster and scat analysis. The degree of overlap between the ratios of prey in lion diet obtained from the historical studies and the ratios of prey in lion diet obtained from the present study were compared to assess similarity. Similarity was expressed on a scale between 0 (no similarity) and 100 (maximum similarity) (Lepš et al., 2006; Sluiter et al., 2005).

5.2.2.2 Prey abundance

Two different comparisons were made to determine changes in prey abundance over the past 45 years. Aerial game count data was used to determine changes in prey availability across the KGNP. Road transect game count data was used to determine finer scale differences within the riverbed habitats as an indication of game trends across the broader KGNP. Four sources of prey availability data for the KGNP were compared (two historical and two present) to detect changes in prey availability over time. Historical data on the relative abundance of the six dominant large herbivores, was obtained from aerial game count data for gemsbok, springbok, blue wildebeest, red hartebeest, eland and ostrich (Knight, 1995). From historical road transect game count data the relative abundance was available for four dominant herbivores, namely gemsbok, springbok, wildebeest and red hartebeest (Mills & Retief, 1984). Historical road transect game count data was only provided separately for the Auob and Nossob riverbeds (Mills & Retief, 1984). The historical road transect game count data was therefore compared with road transect data from the present study independently for the Auob riverbed and the Nossob riverbed. During the current study period herbivore numbers were obtained from an aerial game count conducted in September 2013 (Ellis & Herbst, 2013) and from 15 monthly road transect game counts conducted each in the Auob and Nossob riverbeds (Chapter 4).

To test how significantly the prey dynamics have varied over the past 45 years using aerial game counts and road transect game counts, two category comparisons were made using the Pearson's Chi-square test (Pearson, 1900). For road transect game counts, historical data was only available for the four most abundant large herbivores. For aerial game counts, historical and present data was available for six large herbivore species. The relative percent difference index used to compare the relative prey abundance between the historical and present studies. The degree of overlap between the prey abundance ratios obtained from the historical studies and the ratios obtained from the present studies were compared to assess similarity. Similarity was expressed on a scale between 0 (no similarity) and 100 (maximum similarity) (Lepš et al., 2006; Sluiter et al., 2005).

5.3 Results

5.3.1 Historical and present lion diet profile

The historical study that made use of tracking lion spoor, conducted between 1970 and 1983 (hereafter referred to as "spoor tracking"), provided evidence of 92 lion feeding events. The study using opportunistic observations of lions found feeding on carcasses (hereafter referred to as "opportunistic observations"), was conducted between 1974 and 1982, and recorded evidence of 370 lion feeding events (Table 5.1). The present study, conducted between 2013 and 2015, used investigations of GPS cluster points to record evidence of 278 feeding events, as well as lion scat analysis which recorded evidence of 189 lion feeding events. Overall sixteen species were noted to have been consumed by lion in the KGNP. Gemsbok was the most frequently consumed species in the present study using both GPS cluster analysis and scat analysis. In the historic study that made use of spoor tracking, porcupine was consumed most frequently (Eloff, 1984). In the historic study using opportunistic observations wildebeest was the most frequently preyed upon species (Mills, 1984) (Table 5.1).

Table 5.1 The percentage proportional contribution of different prey species represented in lion diet for the present study using GPS cluster analysis and scat analysis and historical studies using spoor tracking and opportunistic observations in the KGNP. Numbers displayed in brackets provide the actual sample size.

		Spoor tracking 1970 - 1983 (Eloff, 1984)		**Opportunistic observations 1974 - 1982 (Mills, 1984)**		**GPS cluster Analysis 2013 - 2015 (Present)**		**Scat analysis 2013 - 2015 (Present)**	
Large prey	Gemsbok	26.1	(24)	73	(203)	50.8	(96)	32.4	(120)
	Wildebeest	3.3	(3)	10.1	(28)	8.5	(16)	37	(137)
	Hartebeest	8.7	(8)	4.6	(13)	3.7	(7)	7	(26)
	Eland	1.1	(1)	4.3	(12)	3.7	(7)	4.3	(16)
	Ostrich	4.3	(4)	3.6	(10)	0.5	(1)	4.1	(15)
	Kudu	0	(0)	1.1	(3)	0.5	(1)	0	(0)
	Lion	1.1	(1)	0	(0)	0	(0)	0	(0)
Subtotal		44.6	(41)	96.7	(269)	67.7	(128)	84.8	(314)
Small prey	Springbok	10.9	(10)	0.4	(1)	9.5	(18)	13	(48)
	Porcupine	33.7	(31)	0	(0)	12.7	(24)	1.9	(7)
	Steenbok	1.1	(1)	2.5	(7)	7.4	(14)	0	(0)
	Springhare	1.1	(1)	0	(0)	2.2	(4)	0	(0)
	Aardvark	3.2	(3)	0	(0)	0	(0)	0.3	(1)
	Bat-eared fox	3.2	(3)	0	(0)	0	(0)	0	(0)
	Kori bustard	1.1	(1)	0.4	(1)	0	(0)	0	(0)
	Duiker	1.1	(1)	0	(0)	0	(0)	0	(0)
	Jackal	0	(0)	0	(0)	0.5	(1)	0	(0)
Subtotal		55.4	(51)	3.3	(9)	32.3	(61)	15.2	(56)
Total		100	(92)	100	(278)	100	(189)	100	(370)

A clear difference was found in the proportions of large and small prey consumed and their biomass contributions to lion diet across the studies (Figure 5.1). Large prey had the largest representation in the GPS cluster analysis (96.7%), scat analysis (67.7%) and opportunistic observations (84.8%) data. Whereas, in the spoor tracking data, small prey (55.4%) contributed the highest proportion to the data set (Figure 5.1). When the proportion of prey was converted to provide an index of biomass contribution to lion diet, large prey species in GPS cluster analysis (99.8%), opportunistic observations (97.3%) and scat analysis (99.8%) made up the most significant contribution to the overall lion diet profile (Figure 5.1). Even though spoor tracking resulted in a higher proportional representation of small prey, when converted to biomass contribution, large prey still contributed most notably to the total biomass estimation (82.3%). The biomass contributions of small mammals was higher for the historical studies using spoor tracking (17.6%) and opportunistic observations (2.7%) than in the present studies using GPS cluster analysis (0.2%) and scat analysis (0.2%) (Figure 5.1).

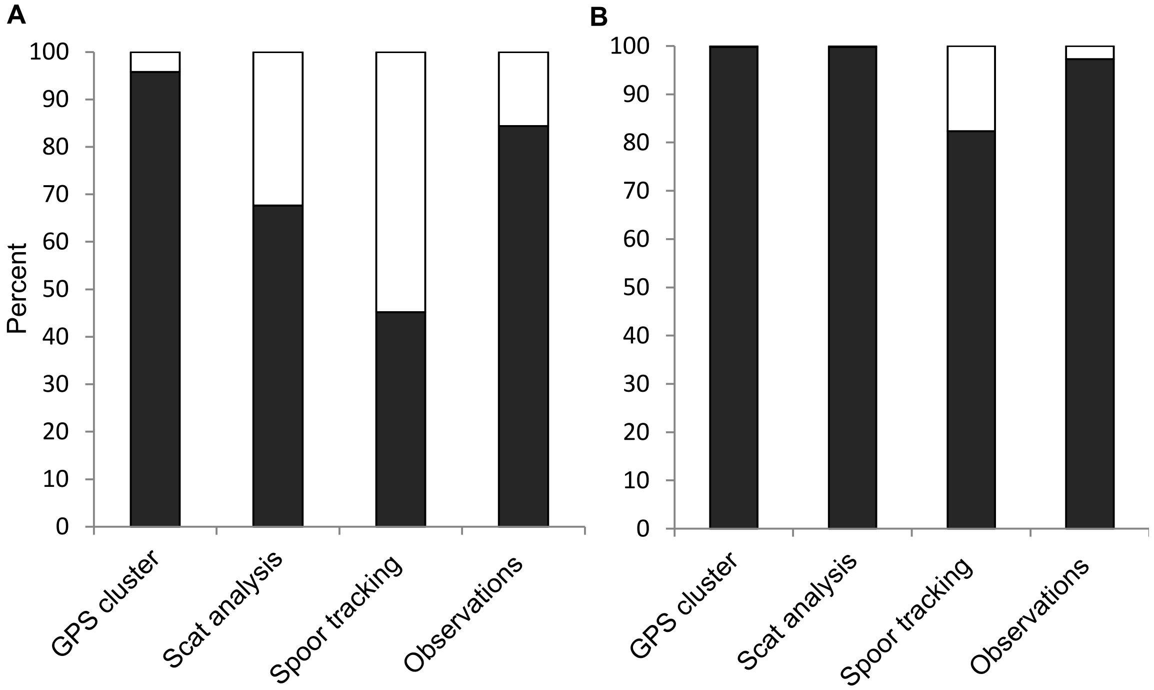


Figure 5.1 The proportion of large (black bars) and small (white bars) prey species represented in lion diet (A) and their relative biomass contributions (B) obtained from the four methods used to determine lion diet in the KGNP. See Table 5.1 for a list of the small and large species.

5.3.2 Lion diet composition in relation to large prey

When large prey data records were extracted from the total data sets and dealt with independently it becomes apparent that gemsbok was the main contributor to the data set obtained from GPS cluster analysis (75.5%), scat analysis (75.3%) and spoor tracking (60%), whereas wildebeest was the main contributor to the data set generated from opportunistic observations (43.6%) (Figure 5.2). In the GPS cluster analysis data set gemsbok contributed 32% more than was the case in the opportunistic observations data set. Wildebeest records were 33% more frequent in the opportunistic observations data set than in the GPS cluster analysis data set (Figure 5.2). The spoor tracking data set had the lowest representation of wildebeest (7.5%). Hartebeest (20%) and ostrich (10%) were found in higher proportions in the spoor tracking data set, than in all other methods. The relative proportional contribution of eland to the data set remained low in all studies, but was highest in the scat analysis data set (5.4%). Kudu only featured in the more recent GPS cluster analysis (1.1%) and scat analysis (0.8%) data sets (Figure 5.2).

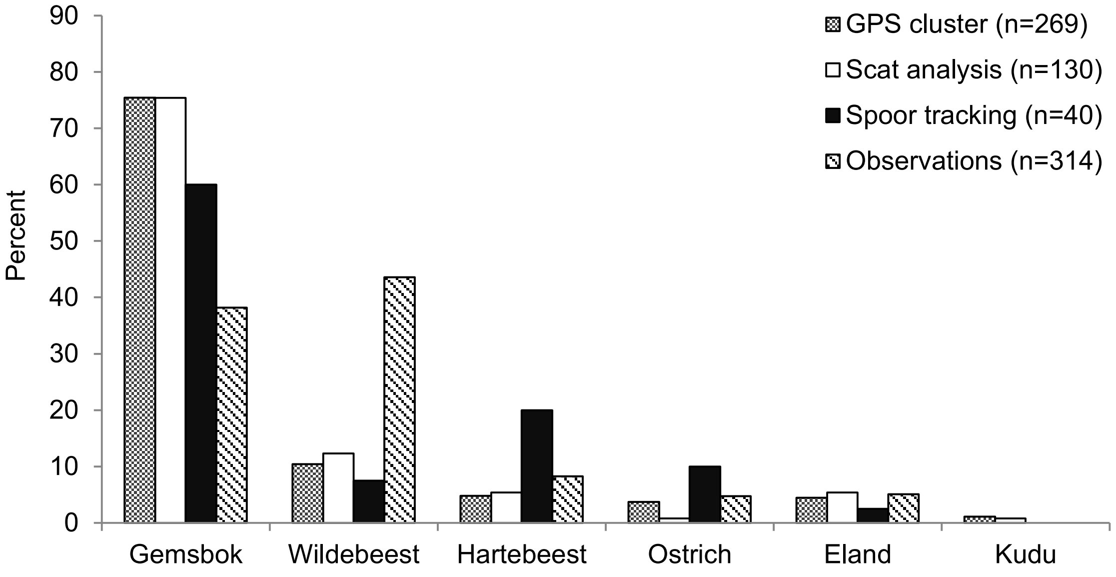


Figure 5.2 The proportional break down of large prey species, within the large prey species data sets of lion diet, obtained from the present study using GPS cluster and scat analysis and from historical studies, using spoor tracking and opportunistic observations. Sample sizes of large prey for each method are shown in brackets.

Within the large prey data set the proportions of all large prey differed significantly between the present study using GPS cluster analysis and the historical studies using spoor tracking ($\chi 2$ = 167.7, *df* = 1, *p* = <0.01) and opportunistic observations ($\chi 2$ = 3.47, *df* = 1, *p* = 0.05) (Table 5.2). The proportions of all large prey also differed significantly between the present study using scat analysis and the historical studies using spoor tracking ($\chi 2$ = 44.79, *df* = 1, *p* = <0.01) and opportunistic observations ($\chi 2$ = 78.27, *df* = 1, *p* = <0.01) (Table 5.2). Gemsbok contributed more to the large prey data set in the present study using GPS cluster analysis and scat analysis than in the historical studies using opportunistic observations and spoor tracking (Figure 5.2). Wildebeest contributed more to the large prey data set in the historical study using opportunistic observations than in the present study using GPS cluster analysis and scat analysis (Figure 5.2). Hartebeest had a higher representation in the large prey data set using spoor tracking than in GPS cluster analysis or scat analysis (Figure 5.2). The two historical studies differed significantly in the overall proportional contributions of large prey to the large prey data set ($\chi 2$ = 209.9, *df* = 1, *p* = <0.01). The proportional contribution of wildebeest to the large prey data set was higher in the historical study using opportunistic observations than in the historical study which made use of spoor tracking. The proportion of hartebeest to the large prey data set was higher in the historical study using spoor tracking than in the historical study which made use of opportunistic observations. The proportional contributions of all other large prey (ostrich, kudu and eland) in the large prey data set did not seem to vary notably between the present and historical studies or between the historical studies.

Table 5.2 A comparison of the large prey species data set of the lion diet profile, identified from the historical lion dietary study using spoor tracking (Eloff, 1984), and the large prey species data sets from the present study obtained from GPS cluster data, overall scat analysis data and the scat analysis data from the northern landscape of the study area (A). Secondly a comparison is made between the large prey species data set, identified from the historical lion dietary study using opportunistic observations (Mills, 1984) and the large prey species data sets identified from the present study obtained from overall GPS cluster data, overall scat analysis data and GPS cluster data from the riverbed habitats. Results are given for Chi-square test (*χ 2*) and P-value (*p*) and indicating the Degrees of Freedom (*df*).

	GPS cluster			**Scat analysis**			**Scat analysis north**			**GPS cluster riverbed**		
	χ 2	***df***	***p***	***χ 2***	***df***	***p***	***χ 2***	***df***	***P***	***χ 2***	***df***	***p***
A. Spoor	167.7	1	<0.01	44.79	1	<0.01	4.28	5	0.04	-	-	-
B. Observations	3.47	1	0.05	78.27	1	<0.01	-	-	-	167.1	1	<0.01

*Significant variables *p* ≤ 0.05 at a 95% confidence level.

5.3.3 Lion diet composition in relation to small prey

GPS cluster analysis in the present study was ineffective at detecting small prey. Small prey contributed only 3% (*n* = 9) of the overall lion diet profile obtained from the GPS cluster analysis data set (*n* = 278). Considering the underrepresentation of small prey, GPS cluster analysis was excluded from the comparisons of the small prey data sets between studies. In the small mammal data set obtained from scat analysis, 61 small prey items constituted 32% to the total data set (*n* = 189). Small prey constituted 55% (*n* = 51) of the total dietary records obtained from the historical study using spoor tracking (*n* = 92). Of the overall dietary records obtained from the historical study using opportunistic observations (*n* = 370), small prey contributed 15% (*n* = 56).

When the small prey items are extracted from the overall lion dietary data sets, and the proportional contributions of small species to these small prey data sets are analysed, it reveals that porcupine contributed the highest proportion to the small prey data sets obtained from the spoor tacking (62%) and scat analysis (40%) (Figure 5.3). Springbok contributed the highest proportion to the small prey data set obtained through opportunistic observations (85.7%). Porcupine was the second highest contributor to the small prey data set obtained through opportunistic observations (12.5%). Springbok was the second highest contributor the small prey data set represented in scat analysis (23.3%) and spoor tracking (20%). Steenbok were detected in higher proportions in the present study using scat analysis (23.3%) than in the historical studies using spoor tracking (2%) and opportunistic observations (0%). Aardvark was only detected in historical studies and was detected more frequently in spoor tracking (6%) than in opportunistic observations (1.8%). Springhare was only found in the present study scat analysis (6.7%) and historical study using spoor tracking (2%). Kori bustard was only detected in the historical study using spoor tracking (2%) (Figure 5.3).

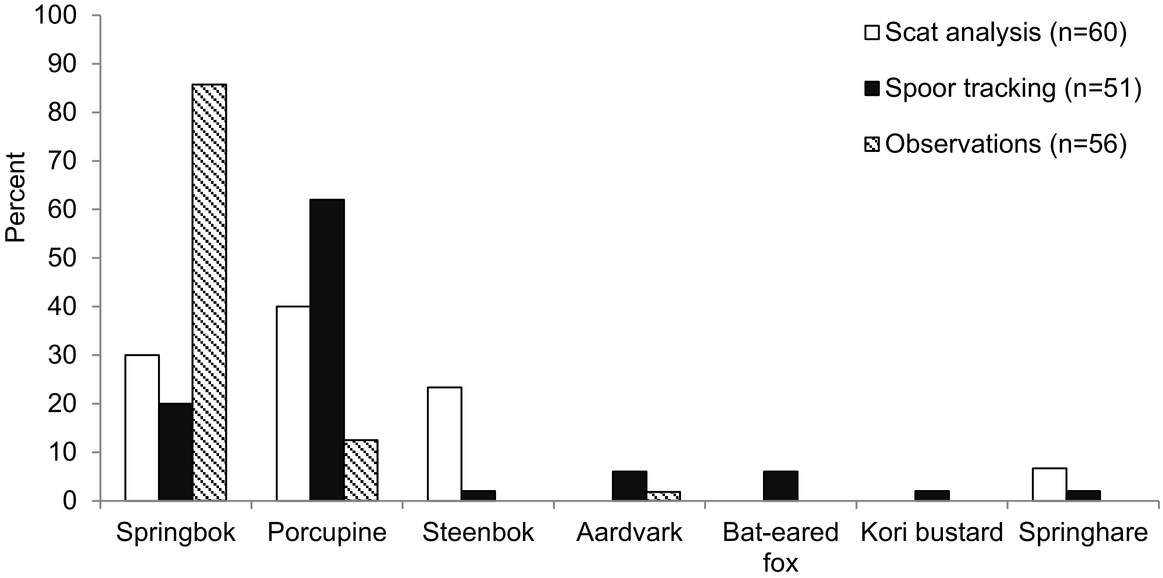


Figure 5.3 The proportional break down of small prey species, within the small prey species data set, obtained from the present study using scat analysis and from historical studies using spoor tracking and opportunistic observations (observations). Sample sizes of small prey for each method are shown in brackets.

Overall the small prey data sets differed significantly between the present study using scat analysis and the historical study using opportunistic observations ($\chi 2$ = 16.88, *df* = 1, *p* = <0.01) (Table 5.3). The small prey data set also differed significantly between the historical study using spoor tracking and the present study using scat analysis data collected in the north ($\chi 2$ = 6.87, *df* = 1, *p* = 0.01) (Table 5.3). However the overall small prey data sets did not differ significantly between the historical study using spoor tracking and the present study using scat analysis ($\chi 2$ = 0.91, *df* = 1, *p* = 0.34) (Table 5.3). In the historical study, using opportunistic observations, the proportion of springbok to the small prey data set was higher than it was in scat analysis (Figure 5.3). The proportional contribution of porcupine and other small prey species, including aardvark, bat-eared fox, duiker and Kori bustard, to the small prey species data set was higher in the spoor tracking data set than in the scat analysis data set (Figure 5.3). Steenbok had a higher representation in the small prey data set obtained from scat analysis than it did in the small prey data set for spoor tracking (Figure 5.3). The contribution of all small prey species, excluding springbok, to the small prey data set was higher in the historical study using spoor tracking, than the historical study using opportunistic observations (Figure 5.3).

Table 5.3 A comparison of the small prey species data set of the lion diet profile, identified from the historical lion dietary study using spoor tracking (Eloff, 1984), and the small prey species data sets from the present study obtained from GPS cluster data, overall scat analysis data and the scat analysis data from the northern landscape of the study area (A). Secondly a comparison is made between the small prey species data set, identified from the historical lion dietary study using opportunistic observations (Mills, 1984) and the small prey species data sets identified from the present study obtained from overall GPS cluster data, overall scat analysis data and GPS cluster data from the riverbed habitats. Results are given for Chi-square test (χ 2) and P-value (*p*) and indicating the Degrees of Freedom (*df*).

	Scat analysis			**Scat analysis north**		
	χ 2	***df***	***p***	**χ 2**	***df***	***P***
A. Spoor tracking	0.91	1	0.34	6.87	1	0.01
B. Observations	16.88	1	<0.01	-	-	-

*Significant variables $p \leq 0.05$ at a 95% confidence level.

5.3.4 The lion diet profile derived from spoor tracking compared with scat analysis data collected in the north of the study area

Making use of bushman trackers between 1973 and 1983, to follow lion spoor (spoor tracking) resulted in evidence of 92 lion feeding events, of which 45% (*n* = 41) constituted large prey and 55% (*n* = 51) constituted small prey species (Eloff, 1984). Scat analysis data collected from the north of the study area, in the present study, resulted in evidence of 89 feeding events, of which 70% (*n* = 62) constituted large prey and 30% (*n* = 27) constituted small prey species.

When the large prey items are extracted from the diet data sets and the large prey species are compared independently, results indicate that the proportional representation of large prey to the large prey data set obtained from the historical spoor tracking and present scat analysis data from the north of the study area did not vary significantly overall (Table 5.2). Gemsbok contributed the highest proportion to the large species data set obtained from the historical study using spoor tracking (58.5%) and the present study using scat analysis (72.6%) (Figure 5.4). Hartebeest was the second highest contributor to the large prey data set obtained from spoor tracking (19.5%), whereas wildebeest was the second highest contributor to the large prey data set obtained from scat analysis. Wildebeest contributed 7.3% to the large prey data set from the spoor tracking study. All other large prey species contributed less than 2.5% to the large prey data set in both spoor tracking and scat analysis.

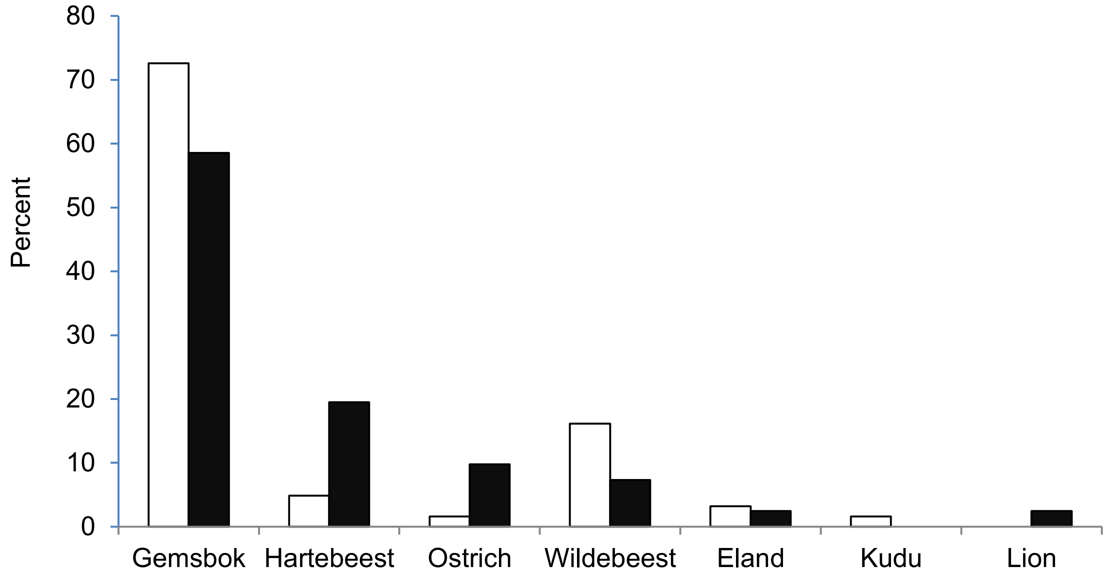


Figure 5.4 The proportional break down of large prey species, within the large prey species data sets of lion diet, obtained from the present study using scat analysis data from the north of the study area (white bars), in comparison with the lion dietary data obtained from the historical study using spoor tracking between 1973 and 1983 (black bars).

The proportional representation of small prey to the small prey data sets, obtained from the historical spoor tracking and present scat analysis data, did not vary significantly overall (Table 5.3). When the small prey items are extracted from the dietary data sets and the small prey species are compared independently, results indicate that porcupine contributed the highest proportion to the small prey data set obtained from the historical study using spoor tracking (62%) and the present study using scat analysis data (37%) (Figure 5.5). Springbok was the second highest contributor to the small prey data set obtained from spoor tracking (20%), and scat analysis data (33.3%). Steenbok and springhare had a higher proportional representation in the present study from scat analysis data (18.5% and 11.1% respectively), than from the historical study using spoor tracking (2%). Aardvark and bat-eared fox contributed 6% to the historical small prey data set using spoor tracking but were not detected in the small prey data set of the present study using scat analysis data (Figure 5.5).

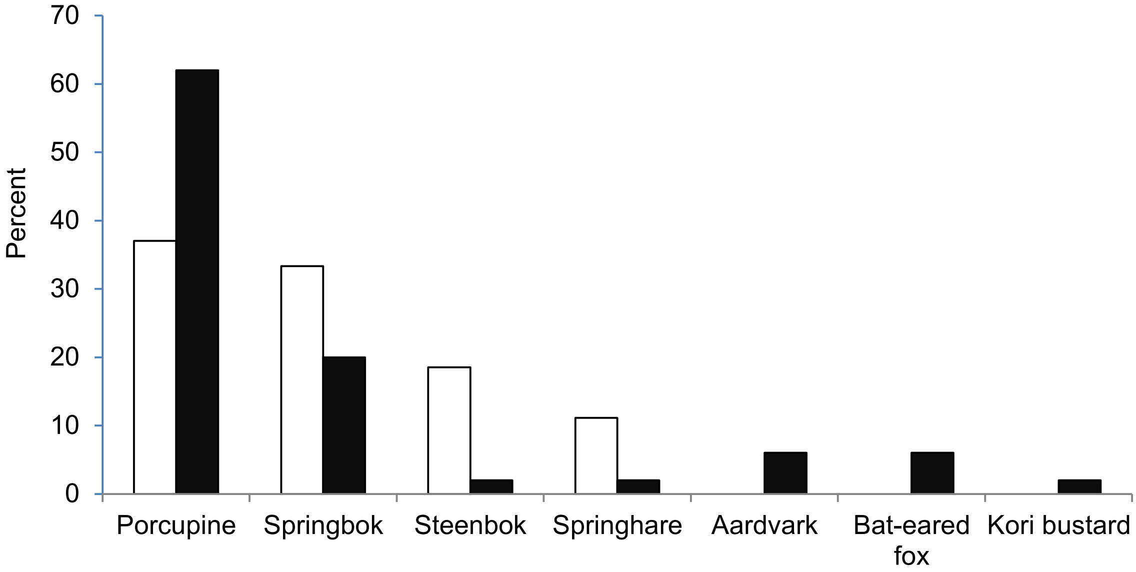


Figure 5.5 The proportional break down of small prey species, within the small prey species data sets of lion diet, obtained from the present study using scat analysis data from the north of the study area (white bars), in comparison with the lion dietary data obtained from the historical study using spoor tracking between 1973 and 1983 (black bars).

5.3.5 The lion diet profile derived from opportunistic observations compared with GPS cluster analysis data collected in the riverbeds

Opportunistic observations of lion feeding events, observed historically between 1974 and 1982 across the KGNP (opportunistic observations), resulted in 370 records of lion feeding events of which 85% constituted large prey species and 15% small prey species (Mills, 1984). GPS cluster records from the present study collected from the riverbed areas resulted in 64 lion feeding events of which 98% constituted large prey species and 2% small prey species. Due to the poor representation of small prey species obtained from GPS cluster analysis only the large prey data set was compared between the historical study using opportunistic observations and GPS cluster records from the present study collected (Figure 5.6).

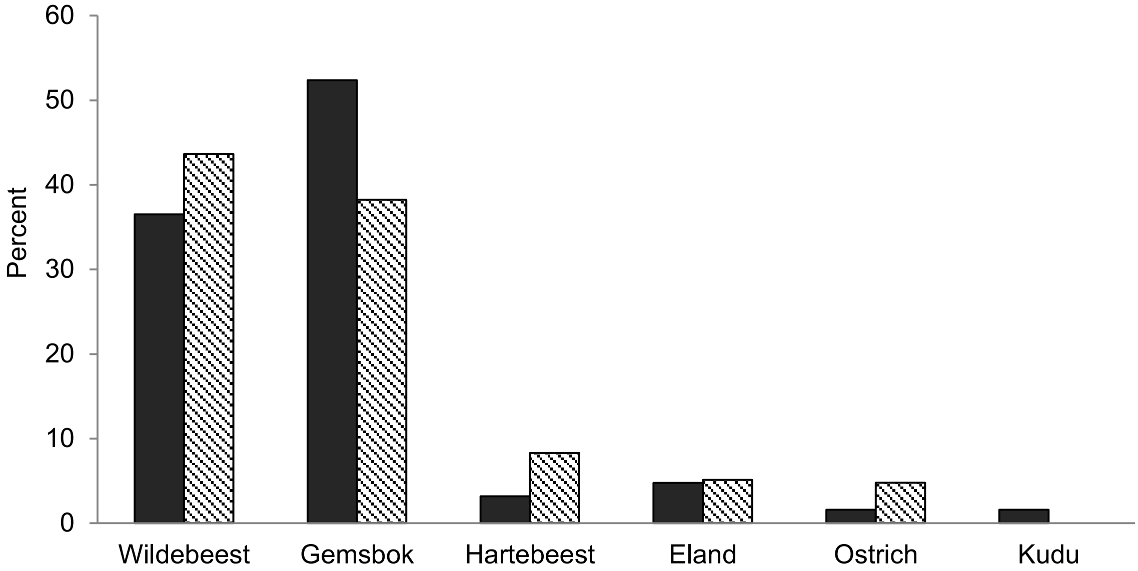


Figure 5.6 The proportional break down of large prey species, within the large prey species data sets of lion diet, obtained from GPS cluster data in the riverbed habitats (black bars), in comparison with the proportional representation of large prey species obtained from the historical study using opportunistic observations of lion feeding events between 1974 and 1982 (diagonal bars).

The proportional representation of large prey in the large prey data sets, obtained in the present study using GPS cluster analysis data, did not differ significantly overall from the historical study using opportunistic observations (Table 5.2). When the large prey items are extracted from the dietary data sets and the large prey species are compared independently, results indicate that wildebeest (43.6%) had the highest proportional representation in the large prey data set obtained from the historic opportunistic observation study. Of the large prey represented in the data set from GPS cluster data from the riverbed habitats, gemsbok (52.4%) had the highest proportional representation followed by wildebeest (36.5%). Gemsbok was the second highest contributor to the large prey data set represented by the historical opportunistic observations study (38.2%). Hartebeest, eland and ostrich had a higher representation in the historic study using opportunist observations (8.3%, 5.1% and 4.8% respectively), than in the present study using GPS cluster data (3.2%, 4.8% and 1.6 % respectively). Kudu was detected in the present study using GPS cluster data and contributed 1.6% to the large prey data set but was not detected in the historic study (Figure 5.6).

5.3.6 Lion diet composition in relation to survey method

The lion diet profile obtained from spoor tracking in the historical study had a 29% relative percent difference (RPD) from GPS cluster data in the present study and was the largest RPD observed between the overall diet profiles in all methods (Table 5.4). The RPD was the smallest (9.9%) between the overall diet profile from the historical study using opportunistic observations and the present study using GPS cluster data from the riverbed habitats. The overall proportion of prey consumed by lion in the historical study using opportunistic observations differed from the present study using GPS cluster data by 22% RPD. Scat analysis in the present study differed from spoor tracking and opportunistic observations in the historical studies with a 20% and 19% RPD respectively. When the lion diet profile obtained from the two historical studies, using spoor tracking and opportunistic observations, were compared they had a 23% RPD dissimilarity. The present study using scat analysis data from the north, and historical lion feeding event data collected from spoor tracking, had a 20% RPD. GPS cluster data from the riverbeds, in the present study, differed by 10% RPD from opportunistic observations in the historical study (Table 5.4).

Table 5.4 The relative percent difference (RPD) given for the overall proportions of prey in lion diet (A), as well as for the proportions of large prey to large prey data set (B) and small prey to the small prey data set (C), for the present study using GPS cluster analysis and scat analysis, in comparison with the historical studies conducted using spoor tracking and opportunistic observations.

		GPS cluster	**Scat analysis**	**Scat analysis north**	**GPS cluster riverbed**	**Spoor tracking**
A. Overall	Spoor tracking	29.1	19.5	19.5	-	-
	Observations	22	19.3	-	9.9	22.8
B. Large prey	Spoor tracking	10.7	12.3	12.6	-	-
	Observations	19.2	19	-	7.9	19.5
C. Small prey	Spoor tracking	42.4	18	19.5	-	-
	Observations	44.4	28.8	-	7.1	32.9

When the lion diet profile was broken down to assess large prey independently between methods, the large prey data sets from the two historical studies had the highest RPD (20%). The large prey data set from the GPS data collected from the riverbed habitats and the large prey data set from opportunistic observations had the lowest RDP (8%). When the lion diet profile was broken down to assess the proportional contributions of small prey independently between methods, the small prey data sets from the historic study using opportunistic observations had the lowest relative percent difference (7%) from the GPS cluster data collected from the riverbeds (Table 5.4).

The overall lion diet profiles obtained from each method, across all of the studies, differed significantly when compared (Table 5.5). The significant differences between the overall lion diet profiles obtained from the present study using GPS cluster analysis and the two historical studies seem to be attributed mainly to differences in the proportions of gemsbok, wildebeest, springbok, porcupine and small prey species identified to be consumed in each method (Table 5.1). The differences between the overall lion diet profiles obtained from the present study using scat analysis and the two historical studies, seem to be attributed to significant differences in the proportions of gemsbok, wildebeest, porcupine and small mammals in lion diet (Table 5.1). The difference between the two historical studies seems to be due to large variations in the proportions of wildebeest, porcupine and small mammals in lion diet (Table 5.1). The present study using scat analysis data from the north, and historical lion feeding event data collected from spoor tracking, seemed to vary according to proportional differences of porcupine, gemsbok and wildebeest in the overall lion diet profile (Table 5.1). GPS cluster data from the riverbeds, in the present study, and opportunistic observations in the historical study differed in the proportions of springbok and gemsbok represented in the diet (Table 5.1).

Table 5.5 Comparison of the lion diet profile identified from the historical spoor tracking study (A), with the lion diet profile from the present study obtained from GPS cluster data, overall scat analysis data and the scat analysis data from the northern landscape of the study area. A comparison of the lion diet profile identified from historical opportunistic observations (B) with the lion diet profile from the present study obtained from overall GPS cluster data, scat analysis data and GPS cluster data from the riverbed habitat. Results are given for Chi-square test (χ 2) and P-value (*p*) and indicating the Degrees of Freedom (*df*).

	GPS cluster			**Scat analysis**			**Scat analysis north**			**GPS cluster riverbed**		
	***χ* 2**	***df***	***p***	***χ* 2**	***df***	***P***	***χ* 2**	***df***	***p***	***χ* 2**	***df***	***P***
A. Spoor	136.5	1	<0.01	13.62	1	<0.01	11.13	1	<0.01	-	-	-
B. Observations	24.9	1	<0.01	21.31	1	<0.01	-	-	-	8.81	1	<0.01

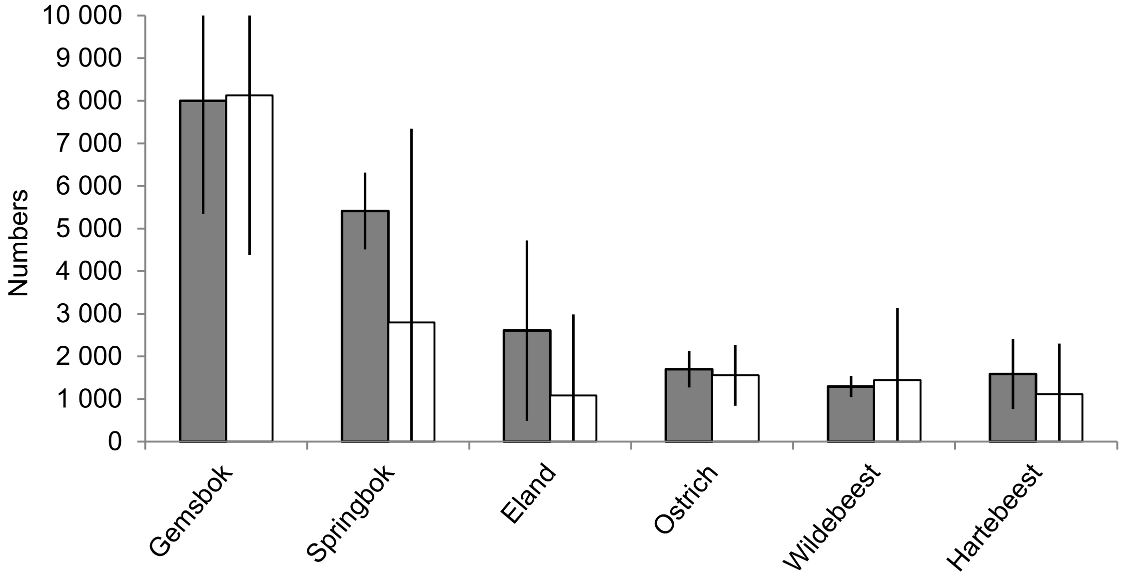
*Significant variables *p* ≤ 0.05 at a 95% confidence level.

When broken down to assess the proportions of large prey to the large prey data sets independently, significant differences were found between all methods, except for the comparison between spoor tracking and scat analysis data from the north of the study area (Table 5.2). The significant differences in the large prey data sets seem to be as a result of notable differences in the proportional contributions of gemsbok, wildebeest and hartebeest in the different methods to the large prey data sets (Figure 5.2). When broken down to assess the proportions of small prey to the small prey data sets obtained from each method independently, the only significant difference found was between the opportunistic observations and scat analysis methods (Table 5.3). In the small prey data set obtained from opportunistic observations, springbok were identified at higher proportions than any other of the small prey species (Figure 5.3). Opportunistic observations seemed to be an inefficient method of detecting small prey species other than springbok, in lion diet (Figure 5.3). Spoor tracking did not vary significantly from scat analysis according to the proportional representations of small prey to the small prey data sets (Table 5.3).

5.3.7 Prey availability

5.3.7.1 Prey availability derived from aerial game counts

A comparison of aerial game count data that was collected in the dry seasons, between 1978 and 1984 (Knight, 1995) and the aerial game count conducted in the dry season of 2013 revealed that, of the six prominent large herbivores in the KGNP, gemsbok was the most abundant species, followed by springbok (Figure 5.7). The proportional abundance of springbok declined by 12%, between the historical aerial game counts to the present aerial game counts. The proportional abundance and overall numbers of wildebeest and ostrich seemed to have remained relatively constant over time. The proportional availability of eland and hartebeest were lower in 2013 aerial game counts than historically (Figure 5.7). The proportional availability of herbivores indicated a relative percent difference of 7.8% between the historical aerial game counts and the present aerial game count.



.

Figure 5.7 Aerial game count data providing the average numbers of large herbivores in the KGNP in the dry seasons of 1978 to 1984 (grey bars) and 2013 (white bars). Error bars depict 95% confidence intervals.

5.3.7.2 Prey availability derived from riverbed road transect game counts

A comparison between the relative abundance of large herbivores derived from riverbed road transect game counts that were conducted historically between 1972 and 1982 (Mills & Retief, 1984), and riverbed road transect game counts that were conducted during the current study period between 2013 and 2015, revealed that the major difference was related to springbok numbers (Figure 5.8). Springbok numbers were the most numerous of the herbivores in both the Auob and Nossob riverbeds in both the historical and present road transect game counts. The mean numbers of springbok were found to have decreased by 8% in the Auob riverbed and 25% in the Nossob riverbed from the historical to the present road transect game counts. Gemsbok numbers seem to have increased in the Nossob riverbed by 13% but remained relatively consistent in the Auob riverbed. Wildebeest have increased by 4% in the Auob riverbed and 8% in the Nossob riverbed. Hartebeest numbers seem to have remained relatively constant in the two riverbeds between the two survey periods (Figure 5.8).

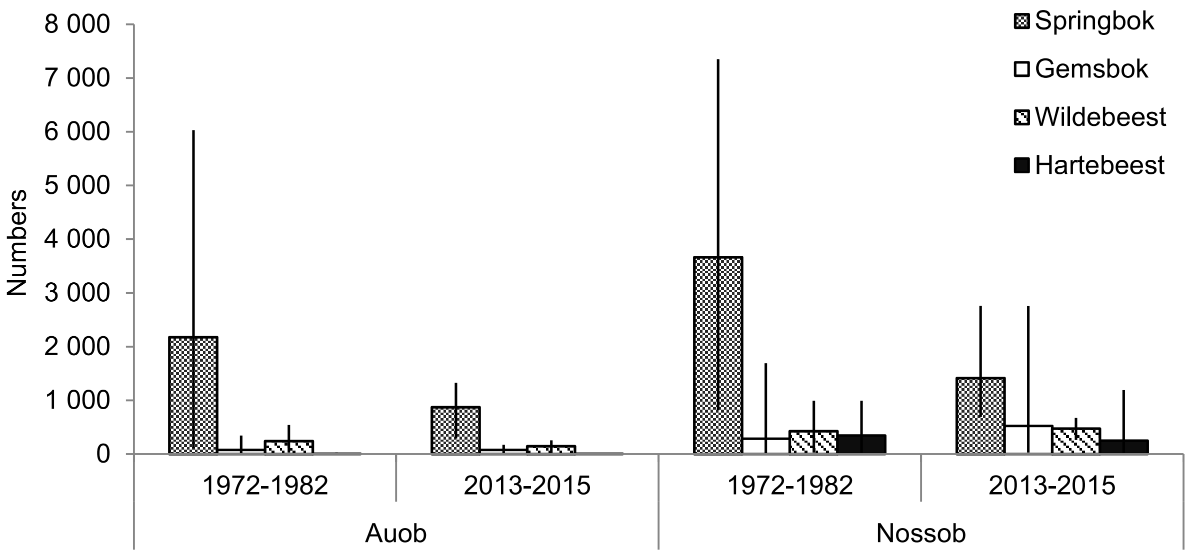


Figure 5.8 Comparison of the mean prey availability derived from riverbed counts conducted historically between 1972 and 1982 (Mills & Retief, 1984), and in the present study between 2013 and 2015. Error bars depict the maximum and minimum numbers of animals counted during each survey period.

The maximum numbers of animals recorded per species in the Auob riverbed has decreased for all four herbivore species in the present road transect game counts compared with the historical road transect game counts (Figure 5.8). The minimum number of animals recorded per species in the Auob riverbed was higher in present counts than it was in historical road transect game counts for springbok and gemsbok. The minimum numbers of wildebeest recorded in the Auob river were lower in the present than in the historical road transect game counts. In the Nossob riverbed the maximum numbers of springbok, wildebeest and hartebeest recorded were lower in the present study than in historic road transect game counts. The maximum gemsbok numbers recorded in the Nossob riverbed were higher presently than in historical road transect game counts. The minimum number of animals recorded in the Nossob riverbed historically was lower for gemsbok, wildebeest and hartebeest, and higher for springbok, than in the present road transect game counts (Figure 5.8).

The average number of animals encountered in the riverbed per kilometre, as a relative index of abundance, shows that in both historical and present road transect game counts, springbok were the most abundant species (Table 5.6). Springbok numbers per kilometre dropped by more than half in both the Auob and the Nossob riverbeds from the historical to the present road transect game counts, whereas gemsbok numbers increased slightly. Wildebeest numbers increased in the Nossob but decreased in the Auob riverbed from the historical to the present road transect game counts. Hartebeest numbers per kilometre seem to have remained relatively constant over time (Table 5.6).

Table 5.6 The average number of animals per kilometre in the Auob and Nossob riverbeds derived from road transect game counts conducted historically, between 1972 and 1982, and in the present study between 2013 and 2015.

	Auob		**Nossob**	
	1972 – 1982	**2013 - 2015**	**1972 - 1982**	**2013 – 2015**
Springbok	18.60	7.03	12.40	7.73
Gemsbok	0.60	0.62	1.00	2.86
Wildebeest	2.10	1.18	1.40	2.60
Hartebeest	0.03	0.03	1.20	1.35
Total	21.33	8.86	16.00	14.54

The overall mean, maximum and minimum herbivore numbers varied significantly between the road transect game counts that were conducted historically between 1972 to 1984 and road transect game counts that were conducted presently between 2013 to 2015, in the Nossob and Auob riverbeds (Table 5.7). The numbers of animals per kilometre also varied significantly between the historical and present road transect game counts in both the Auob and Nossob riverbeds (Table 5.7). The significant differences between the historical and present road transect game counts are likely to be primarily a result of a notable decrease in the overall springbok numbers, and an increase in gemsbok and wildebeest numbers in the Nossob riverbed (Figure 5.8). The maximum numbers of all four herbivore species in the Auob riverbed were significantly higher in the historical than the present road transect game counts (Table 5.7). In the Nossob riverbed, the maximum numbers of springbok and hartebeest where higher historically, whereas the maximum numbers of gemsbok were higher presently (Figure 5.8). The minimum numbers of animals recorded in the Auob riverbed differed significantly (Table 5.7), with a lower minimum number of wildebeest presently than as recorded in the historical road transect game counts. The minimum number of all four herbivores differed significantly in the Nossob riverbed (Table 5.7), with higher minimum numbers recorded for gemsbok and wildebeest, and lower minimum numbers recorded for springbok and hartebeest in the present than in the historical road transect game counts (Figure 5.8).

Table 5.7 Comparisons of the mean, maximum and minimum herbivore abundances, as well as numbers of animals per kilometre in the KGNP, identified from road transect game counts conducted in the Auob and Nossob riverbeds historically between 1972 to 1984 and presently between 2013 to 2015. Results are provided for Chi-square test (χ *2*) and P-value (*p*) and indicate the Degrees of Freedom (*df*).

	Mean			**Max**			**Min**			**No. per Km**		
	χ **2**	***df***	***p***	χ **2**	***df***	***P***	χ **2**	***df***	***p***	χ **2**	***df***	***P***
A. Auob	43.11	3	<0.01	167.1	3	<0.01	15.19	3	<0.01	39.9	3	<0.01
B. Nossob	558.2	3	<0.01	1759	3	<0.01	216.5	3	<0.01	228.4	3	<0.01

The mean numbers of animals recorded per kilometre were significantly different between the historical and present road transect game counts (Table 5.7), with presently higher numbers per kilometre for gemsbok in the Nossob riverbed and notably lower numbers for springbok in both the Auob and the Nossob riverbeds (Table 5.6). The mean numbers of wildebeest per kilometre where higher in the Auob riverbed and lower in the Nossob riverbed in historical road transect game counts than in present road transect game counts (Table 5.6).

5.4 Discussion

Despite the difficulties associated with detecting change in lion diet, due to differences in the techniques used, the results of this study have indicated changes in the diet profile of lion in the Kalahari Gemsbok National Park (KGNP) over the past 45 years (1970 - 2015). The lion diet profile in the present study was identified through the use of GPS cluster analysis and scat analysis between 2013 and 2015, while historical studies made use of tracking lion spoor between 1970 and 1983, and opportunistic observations of lion feeding events conducted between 1974 and 1982. The focal areas in which these various studies were conducted across the KGNP differed somewhat between studies. The discrepancies in sampling technique and focal areas between studies presented challenges when comparing the results. It is known that GPS cluster analysis and opportunistic observations bias results towards large prey species (Mills, 1992; Radloff & du Toit, 2004; Tambling et al., 2012), whereas spoor tracking and scat analysis detect higher proportions of small prey species (Floyd et al., 1978; Mills, 1992; Ruhe et al., 2008). This is clearly shown with only 3% and 15% of small prey detected in the lion diet profile using GPS and direct observations versus 55% and 32% using spoor tracking and scat analysis.

The present study had a relatively evenly distributed sampling effort for GPS cluster analysis and scat analysis across the various landscape and habitat types represented within the study area (Chapter 3). The results of the present study were used to identify that a minimum sample size of 65 kill records from GPS clusters and 55 lion scats are needed to obtain a representative interpretation of lion diet in the Kalahari (Chapter 3). These recommended sample sizes were well exceeded, to be able to adequately represent the lion diet profile in the KGNP, for both GPS cluster analysis (n = 278) and scat analysis (n = 189). The historic study which made use of spoor tracking, was focused primarily in the dune habitat of the northern landscape of the KGNP, and resulted in a relatively small sample size of 91 lion feeding events (Eloff, 1984; Eloff, 2002). The second historical study utilized opportunistic observations of lion feeding events, and resulted in 370 feeding records collected across the KGNP, although efforts were biased towards the riverbed habitats (60%) (Mills, 1984). The minimum sample sizes required to provide an accurate representation of lion diet are unknown for the spoor tracking and opportunistic observation methods when applied in an arid environment. When the overall lion diet profiles obtained from each survey method were compared, results indicated that the lion diet profile obtained from the historical spoor tracking study varied the most notably from the present study using GPS cluster analysis and scat analysis, as well as from the other historical study using opportunistic observations. The overall lion diet profiles, obtained from the historical study that made use of opportunistic observations, and the present study using GPS cluster analysis data collected in the riverbed habitats, varied the least.

Direct comparisons of the lion diet profiles obtained from the four survey methods used in the present and historical studies may not necessarily only depict variation in lion diet but may also highlight differences in the survey techniques (Mills, 1992). Comparisons between survey methods may have been further inhibited by demographic uncertainties of the lion population studied. No mention is made of the demographics of the lions observed in the historical studies using spoor tracking or opportunistic observations. In the present study GPS cluster data is likely to be biased towards female diet as males were only noticed to associate with the collard females 31% of the time (range 0 – 50%), whereas scat analysis would provide a representation of a combination of male and female diet. Discrepancies in survey techniques and focal areas could thus have exaggerated the variance detected in the lion diet profiles between present and historical lion diet profiles. To reduce this bias and present a more accurate investigation of changes in lion diet over time, prey species observed per method were separated into two data sets, namely a large prey data set (> 50 kg) and a small prey data set (< 50 kg). When investigating the contribution of large prey species to the large prey data set, gemsbok was the most frequently consumed species in the present studies using GPS cluster analysis (76%) and scat analysis (75%), as well as in the historical study using spoor tracking (60%). In the historical study using opportunistic observations, wildebeest (44%) was the most frequently consumed prey species followed by gemsbok (38%). All methods indicate that proportional contribution of gemsbok to the large prey data set of lions seems to have increased from the historical lion dietary studies to the present study.

The GPS cluster analysis method was inefficient at detecting small prey. Only 3% of all lion feeding events recorded from GPS cluster analysis in this study were of small prey species. Of the small prey species, porcupine contributed the most notably to the small prey data set in the historical spoor tracking study (62%) and in the present scat analysis study (40%). In the historical study using opportunistic observations, springbok (86%) was the most frequently detected small prey species in the small prey species data set. Opportunistic observations seemed to be ineffective at detecting all small prey species, other than springbok, as represented in the small prey dataset. Steenbok seemed to be detected more frequently in the present lion dietary studies than in historical studies. The historical study conducted using spoor tracking, detected a broader diversity of small prey species ($n = 8$) to the small prey data set, than all other methods ($n = \leq 5$).

Lion dietary profiles of large and small prey data sets, obtained from the present and historical lion dietary studies, were further broken down to compare data that was collected within the same landscape and habitat types in the KGNP. Survey techniques which were compared included GPS cluster analysis data from the riverbed habitats with opportunistic observations, and scat analysis data collected from the north of the study area with spoor tracking. The results of these more detailed comparisons, between similar landscape and habitat types, still indicated a significant difference in the lion diet profile between the present and historical studies. However, the degrees to which the studies varied were somewhat reduced. The most notable changes from these more fine scaled comparisons seem to indicate that a higher proportion of gemsbok, in the large prey data sets, and fewer porcupine and springbok in the small prey data sets, are being consumed by lions presently than what was recorded historically. These results seem to support the notion that there has been a subtle shift in lion diet in the KGNP over the past 45 years.

Even though the two historical studies (Eloff, 1984; Mills, 1984) were conducted during a similar time period, when directly compared, they provided significant differences in the lion diet profiles obtained from the large prey data sets and small prey data sets. This could be largely attributed to differences in survey techniques used, as well as the focal areas in which the studies were conducted. It may also be likely that because the spoor tracking study was conducted within a specific focal area, in the northern landscape type, that the same individual lions and their associated prides would have been followed on numerous occasions. Thus, the historical spoor tracking study would not account for potential individual lion diet specialization (Power & Compion, 2009), which may skew the results when extrapolated to depict the overall lion diet profile across the KGNP. Carnivores may develop diet specialization in areas where resources are limited, and in response to area specific habitat utilization, competition and anthropogenic influences (Balme et al., 2007; Newsome et al., 2009; Power & Compion, 2009; Yeakel et al., 2009). Therefore, the lion diet depicted in historical study using spoor tracking in the north (Eloff, 1984), may not be representative of the diet profile of lion across the KGNP but rather of the lion diet profile of the northern landscape type of the KGNP.

The depiction of lion diet over time from various studies conducted in the KGNP is also likely to be influenced by variations in the landscapes, habitats and seasons in which the studies were conducted. Therefore, the current diet profile of lion was investigated across various landscapes, habitats and seasons presented in the KGNP, to test for variability in the diet profile across these factors (Chapter 4). The results of these spatial comparisons indicated that there were variations in the lion diet profiles between the various habitat types and between landscape types. Results further suggested that seasons do not seem to significantly influence the overall lion diet profiles in the KGNP (Chapter 4). The main differences in lion diet between habitat types and landscape types seemed to be attributed to variations in prey availability, as a result of localized prey abundance. The most notable spatial differences, in the lion diet profiles, as well as prey availability in the KGNP, were between the dune and riverbed habitats (Chapter 4). Hence, the more fine scaled comparisons of lion diet between the historical opportunistic observations and the present GPS cluster analysis data from the riverbed habitats, as well as between the historical study using spoor tracking and the present study using scat analysis data from the north of the study area, were further merited. Variation in lion diet in response to fluctuations in prey dynamics have also been identified in the Serengeti National Park, (Schaller, 1972), Etosha National Park, Namibia (Stander, 1992), Kruger National Park, South Africa (Owen-Smith & Mills, 2008a) and Hwange National Park, Zimbabwe (Loveridge et al., 2009; Davidson et al., 2013).

In the KGNP there was considerable variation between how herbivores utilized the dune and riverbed habitats. Overall prey abundance was much higher in the riverbed habitats than in the dune habitats (Chapter 4). Wildebeest and springbok were largely restricted to the riverbed habitats. Hartebeest occurred in lower densities in the Auob than in the Nossob riverbed. Similar observations on how herbivores utilize the riverbeds differently in the KGNP have been noted in historical studies (Mills & Retief, 1984; Knight, 1995). Eland and hartebeest numbers were lower in 2013 than historically, but this could be as a result of fluctuations in seasonal migration patterns. Eland are known to migrate seasonally into the KGNP during dry seasons (Verlinden, 1998a). Between the early and mid-1970’s the KGNP experienced a period of high rainfall (Knight, 1995). This led to marked increases in the overall abundance of the four primary herbivores represented in riverbed game counts in the

KGNP, namely gemsbok, springbok, wildebeest and red hartebeest (Mills & Retief, 1984). Following on from 1978 to 1984 the KGNP experienced a period of below annual rainfall which in turn led to sharp declines in the population sizes of eland, wildebeest and to a lesser extent hartebeest (Knight, 1995). The numbers of gemsbok and springbok also declined in the riverbed terrains during the drought period (Mills & Retief, 1984), although relatively few mortalities of gemsbok and springbok were observed during the 1978 to 1984 dry period (Knight, 1995). Gemsbok and springbok were instead thought to disperse more widely during dry periods (Knight, 1995).

The cause for the much higher contribution of small mammals, particularly porcupine, to the lion diet profile represented by the historical dietary study conducted using spoor tracking, than what was recorded in the present study is unknown. It is possible that this was attributed to diet specialization of lions that were observed to occupy the dune habitats. Drought influences prey dynamics and can lead to marked reductions in the availability of large herbivores in the KGNP (Knight, 1995; Verlinden, 1998b). Decreased availability and accessibility of large prey to lion during a drought due to wider dispersal of prey across the dunes, is likely to result in extended time periods between kills of large prey items. This could lead to an increased necessity for small prey to be consumed opportunistically by lion to sustain their energetics between large kills (Carbone et al., 1999). Lion are known to have a catholic diet, consuming a wide diversity of prey. However, lions are dependent on large prey in order to meet their metabolic requirements (Sunquist & Sunquist, 1989; Radloff & du Toit, 2004; Hayward et al., 2011).

In the broader Kalahari area, man-made barriers such as fences have inhibited the seasonal natural migration routes of large herbivores, in particular wildebeest, to permanent water sources, such as in the Boteti region in Botswana, leading to a decline in their overall abundance (Williamson & Williamson, 1988; Verlinden, 1998b). Considering that overall wildebeest numbers across the KGNP have hardly changed over the past 45 years, it is believed that the provision of artificial water points, developed around 1948, facilitated the wildebeest population to become more sedentary, which in turn stabilized population numbers in the park, especially within the riverbeds (Eloff, 1966; Mills & Retief, 1984). Historically large herds of nomadic wildebeest would enter the KGNP during the wet season and disperse again in the dry season (Eloff, 1966). Wildebeest numbers observed across this study support the notion of wildebeest becoming more sedentary in the KGNP. Fewer nomadic wildebeest enter the KGNP seasonally, as reflected by little variability in population numbers derived from monthly road transect game counts in the present study. Wildebeest migration patterns and population size do not seem to have varied between the time periods in which the previous lion dietary studies took place and the present study (Mills & Retief, 1984; Knight, 1995). Thus, the accessibility and availability of wildebeest to lion in the KGNP can be expected to have remained similar between the historical study and present study periods. It is therefore not surprising that the contribution of wildebeest to lion diet, in relation to their availability, has not changed significantly over the past 45 years, when comparing GPS cluster data from the riverbeds and opportunistic observations conducted between 1974 and 1982 (Mills, 1984).

Riverbed road transect game count data from this study indicates that gemsbok is the only species whose relative abundance seems to have increased notably in the Nossob riverbed of the KGNP over time. The maximum numbers of gemsbok recorded in the Nossob riverbed were also considerably higher in the present study than in historical road transect game count data. Of the large herbivores available to lion in the KGNP, gemsbok is the most widely distributed and abundant species (Chapter 4). Considering this, and the high frequency and proportion in which it was noted to be consumed in all studies, make gemsbok the most important prey species to lion in the KGNP. Gemsbok has also been identified as the primary large prey species of lion in other studies conducted in the Kalahari (Eloff, 1984; Mills, 1984; Stander, 2003; Roxburgh, 2008) and have been identified further afield as a prey species for which lions show significant preference (Hayward & Kerley, 2005).

In conclusion, even though there were notable fluctuations in prey availability in the KGNP between vegetation types, terrains and seasons, this seemed to have minimal influence on lion diet selection. Over the past 45 years, more significant changes in the abundance of large herbivores have been recorded, mostly with regards to an overall marked decrease in springbok abundance and an increase in the abundance of gemsbok in the Nossob riverbed. These changes seem to also be reflected in the current lion diet profile, with notably fewer springbok being consumed, and may also potentially explain the higher proportions of gemsbok being consumed. In addition, results indicate that overall small prey species are being consumed proportionally less than that what was indicated in historical studies. These changes in the prey availability and lion diet profile, are potentiality indicative of ecological changes that have occurred in the KGNP over the past 45 years, such as the influence of drought represented in the historical studies between 1978 and 1984 (Knight, 1995).

Secondly, anthropogenic activities have altered prey dynamics in the KGNP over time. These include the erection of game fences, inhibiting migration routes (Williamson & Williamson, 1984), and the instillation of artificial waterholes, which have changed the seasonal movement patterns of large herbivores across the Kgalagadi Transfrontier Park (Eloff, 1966; Williamson & Williamson, 1984; Verlinden, 1998b). Even though the effects of anthropogenic influences have been noted to influence prey dynamics in the KGNP, the effect of this on lion diet remains unknown, as no data exists on lion diet prior to the erection of fences or instillation of artificial waterholes. Nonetheless, shifting prey dynamics are known to influence lion diet selection (Owen-Smith & Mills, 2008b; Davidson et al., 2013), and are thus likely to have led to changes in the KGNP lion diet profile over time (prior to the scope of the 45 years that this study investigated). One suggested change may be a higher proportion of wildebeest in lion diet presently than historically. Historically, prior to 1948, wildebeest would have only been available to lion during seasonal migrations (Eloff, 1966). Post 1948, due to the provision of artificial waterholes, wildebeest established resident herds within the KGNP (Eloff, 1966; Knight, 1995), making them a more reliable prey base to lion throughout the year, especially within the riverbeds, than in the past.

It was postulated that the trend towards a higher proportion of male lions, identified in the KGNP lion population, may have been as a result of changes in lion diet over time in response to shifting prey dynamics (Ferreira et al. 2012). Anthropogenic activities could have led to increased prey availability (Knight, 1995; Owen-Smith, 1996), a higher proportion of female lions in good body condition than in the past, and consequently changes in the sex ratios of the lion population, as females in good body condition are more likely to produce male offspring (Trivers & Willard, 1973; Meikle & Drickamer, 1986). It has now been identified that the changes in sex ratios in the KGNP lion population seem to be occurring post parturition (Beukes, 2016). Therefore, the theory that changes in prey availability and consequently lion diet may be influencing the pre-birth sex selection in the KGNP lion population, does not seem to hold true presently. However, lion diet influences survival rates and fecundity (van Vuuren et al., 2005; Ferreira & Funston, 2010; Becker et al., 2013) and is likely to influence the sex ratio and age structures of lion in the KGNP post-partum.

Results indicate that a degree of variance exists in lion diet profiles across the KGNP between all survey techniques, landscape types and habitat types, as well as over time. It has also been detected that these differences in the lion diet profiles are influenced to some extent by spatial and temporal variations in prey dynamics. Spatial and temporal variations in prey dynamics appear to influence the proportions of large and small prey represented in lion diet. Nonetheless, in all studies, when converted to relative biomass contributions of prey to lion diet, large prey contribute the majority (minimum 82%) to lion biomass intake, whereas the biomass contribution of small prey (maximum 18%) was markedly lower. This indicates the vital contribution of large prey, specifically gemsbok, to lion energetics in the KGNP. Therefore, continuing to monitor the lion diet profile, in relation to herbivore dynamics, will provide valuable information on lion ecology in the KGNP. A better understanding of the ecology of lion and their associated prey in the KGNP, will present an indication on when management interventions may be required to ensure lion persistence throughout the KTP.

5.5 References

Balme, G., Hunter, L. & Slotow, R. 2007. Feeding habitat selection by hunting leopards Panthera pardus in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, 74(3): 589–598.

Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, M.W., Harte, J., Hastings, A., Marquet, P.A., Martinez, N.D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindel, D.P., Revilla, E. & Smith, A.. 2012. Approaching a state shift in Earth's biosphere. *Nature*, 486: 52–58.

Bauer, H. & Iongh, H.H. 2005. Lion (Panthera leo) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*, 43(3): 208–214.

Becker, M.S., Watson, F.G.R., Droge, E., Leigh, K., Carlson, R.S. & Carlson, A. a. 2013. Estimating past and future male loss in three Zambian lion populations. *Journal of Wildlife Management*, 77(1): 128–142.

Beukes, B.O. 2016. *Demographic characteristics of lion (Panthera leo) in the Kalahari Gemsbok National Park*. Unpublished masters thesis. Cape Peninsula University of Technology. Cape Town. South Africa.

Boutin, S. 1995. Testing predator-prey theory by studying fluctuating populations of small mammals. *Wildlife Research*, 22(1): 89.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. 2005. State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management*, 58(1): 1–10.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. 2003. Vegetation dynamics on rangelands: A critique of the current paradigms. *Journal of Applied Ecology*, 40(4): 601–614.

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature*, 402(6759): 286–288.

Cardillo, M., Mace, G.M., Gittleman, J.L. & Purvis, A. 2006. Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 103(11): 4157–4161.

Castley, J.G. 2005. *Standard operating procedures for conducting aerial surveys in South African National Parks – Southern Parks.* SANParks unpublished report, SANParks, Pretoria.

Castley, J.G., Knight, M.H., Mills, M.G.L. & Thouless, C. 2002. Estimation of the lion (Panthera leo) population in the southwestern Kgalagadi Transfrontier Park using a capture-recapture survey. *African Zoology*, 37: 27–34.

Celesia, G.G., Townsend Peterson, A., Kerbis Peterhans, J.C. & Gnoske, T.P. 2010. Climate and landscape correlates of African lion (Panthera leo) demography. *African Journal of Ecology*, 48(1): 58–71.

Coe, M.J., Cumming, D.H. & Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22: 341–354.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turbull, L.A., Macdonald, D.W. & Scmid, B. 2012. Fear of the dark or dinner by moonlight ? Reduced temporal partitioning among Africa' s large carnivores. *Ecology*, 93(1): 2590–2599.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. 2013. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid Savanna. *PLoS ONE*, 8(2). e55182.

Eloff, F.C. 1962. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park. part IV. *Koedoe*, 5(1): 128–136.

Eloff, F.C. 1966. Range extension of the blue wildebeest. *Koedoe*, 9: 34–36.

Eloff, F.C. 1984. Food ecology of the Kalahari lion. *Koedoe*, 27(2): 249–258.

Eloff, F.C. 2002. *Hunters of the dunes: The story of the Kalahari lion*. Sunbird Publishers. Cape Town.

Ferreira, S.M. & Funston, P.J. 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, 37(3): 194–206.

Ferreira, S.M., Govender, D. & Herbst, M. 2013. Conservation implications of Kalahari lion population dynamics. *African Journal of Ecology*, 51(1): 176–179.

Floyd, T.J., Mech, L.D. & Jordan, P.A. 1978. Relating wolf scat content to prey consumed. *Journal of Wildlife Management*, 42(3): 528–532.

Funston, P.J. 2001. *Kalahari Transfrontier lion project: final report*. Endangered Wildlife Trust, Johannesburg, South Africa.

Funston, P.J. 2011. Population characteristics of lions (Panthera leo) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 41: 1–10.

Gittleman, J.L. & Harvey, P.H. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10(1): 57–63.

Hayward, M.W. & Kerley, G.I.H. 2005. Prey preferences of the lion (Panthera leo). *Journal of Zoology*, 267: 309–322.

Hayward, M.W., Hayward, G.J., Tambling, C.J. & Kerley, G.I.H. 2011. Do lions Panthera leo actively select prey or do prey preferences simply reflect chance responses via evolutionary adaptations to optimal foraging? *PLoS ONE*, 6(9): e23607.

Herrmann, E. 2004. *Modelling the effect of human-caused mortality on a lion sub-population using spreadsheets*. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

Knight, M.H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33: 377–394.

Lepš, J., de Bello, F., Lavorel, S. & Berman, S. 2006. Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia*, 78(4): 481–501.

Loveridge, A.J. & Canney, S. 2009. *African Lion Distribution Modelling Project. Final Report*. Born Free Foundation, Horsham, UK.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134: 548–558.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography*, 32(6): 953–962.

Meikle, D.B. & Drickamer, L.C. 1986. Food availability and secondary sex ratio in wild and laboratory house mice (Mus musculus). *Journal of Reproduction and Fertility*, 78: 587–591.

Miller, B., Dugelby, B., Foreman, D., del Rio, C.M., Noss, R., Phillips, M., Reading, R., Soule, M.E., Terborgh, J. & Willcox, L. 2001. The importance of large carnivores to healthy ecosystems. *Endangered Species Update*, 18(5): 202–210.

Mills, M.G.L. 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. *Koedoe*, 27(2): 281–294.

Mills, M.G.L. 1992. *A comparison of methods used to study food habits of large African carnivores*. In Wildlife 2001: populations: 1112–1123. McCulloch; C. & Barret; R.H. (eds). London: Elsevier.

Mills, M.G.L. 2015. Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research*, 45(2): 127–137.

Mills, M.G.L. & Haagner, C. 1989. *Guide to the Kalahari Gemsbok National Park*. Southern Book Publishers, Johannesburg.

Mills, M.G.L. & Retief, P.F. 1984. The response of ungulates to rainfall along the riverbeds of the Southern Kalahari 1972-1982. *Koedoe*, 27(2): 129–141.

Mills, M.G.L., Biggs, H.C. & Whyte, I.J. 1995. The relationship between rainfall, lion predation and population trends in African herbivores. *Wildlife Research*, 22: 75–81.

Mills, M.G.L., Wolff, P., Le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion in Kalahari Gemsbok National Park. *Koedoe*, 2: 163–171.

Newsome, S.D., Tinker, M.T., Monson, D.H., Oftedal, O.T., Ralls, K., Staedler, M.M., Fogel, M.L. & Estes, J.A. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (Enhydra lutris nereis). *Ecology*, 90(4): 961–974.

Noy-Meir, I. 1975. Stability of grazing systems: An application of predator-prey graphs. *The Journal of Ecology*, 63(2): 459–481.

Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, 26(4): 107–112.

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

Owen-Smith, N. & Mills, M.G.L. 2008b. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*, 89(4): 1120–1133.

Pearson, K. 1900. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. *Philosophical Magazine Series*, 5(50): 157–175.

Pereira, L.M., Owen-Smith, N. & Moleon, M. 2014. Facultative predation and scavenging by mammalian carnivores : seasonal, regional and intra-guild comparisons. *Mammal Review*, 44: 44–55.

Power, R.J. & Compion, R.X.S. 2009. Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *African Zoology*, 44(1): 36–44.

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.

Roxburgh, D.J. 2008. *Prey and range use of lions on Tswalu Kalahari Reserve*. M.Sc. Thesis, University of Pretoria, Pretoria.

Ruhe, F., Ksinsik, M. & Kiffner, C. 2008. Conversion factors in carnivore scat analysis : sources of bias. *Wildlife Biology*, 14(4): 500–506.

Schaller, G.B. 1972. *The Serengeti Lion: A study of predator–prey relations*. The University of Chicago Press, Chicago.

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

Schmitz, O.J., Post, E., Burns, C.E. & Johnston, K.M. 2003. Ecosystem responses to global climate change: Moving beyond color mapping. *BioScience*, 53(12): 1199–1205.

Sheldon, B.C. & West, S.A. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *The American Naturalist*, 163(1): 40-54.

Sinclair, A.R.E. & Arcese, P. 2013. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology*, 76(3): 882–891.

Sluiter, A., Ruiz, R., Scarlata, C., Sluiter, J. & Templeton, D. 2005. *Determination of extractives in biomass*. National Renewable Energy Laboratory Golden, Battelle.

Stander, P.E. 1992. Foraging dynamics of lion in a semi-arid environment. *Canadian Journal of Zoology*, 70: 8–21.

Stander, P.E. 2003. *The ecology of lions and cheetahs re-introduced to the Kalahari Game Lodge, Namibia*. Unpublished report to the Kalahari Game Lodge, Namibia.

Suding, K.N., Gross, K.L. & Houseman, G.R. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, 19(1): 46–53.

Sunquist, M.E. & Sunquist, F.C. 1989. Ecological constraints on predation by large felids. *Carnivore behavior, ecology, and evolution*: 283–301. Springer, USA.

Tambling, C.J. & Belton, L.E. 2009. Feasibility of using proximity tags to locate female lion Panthera leo kills. *Wildlife Biology*, 15: 435–441.

Trivers, R.L. & Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068): 90–92.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90(1): 23–30.

Van Rooyen, N., Bezuidenhout, D., Theron, G.K. & Bothma, J.D.P. 1990. Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe*, 33(1): 63–88.

Van Rooyen, N., Bredenkamp, G.J., Theron, G.K., Bothma, J.D.P. & Le Richie, E.A.N. 1994. Vegetational gradients around artificial watering points in the Kalahari Gemsbok National Park. *Journal of Arid Environments*, 26: 349–361.

Van Vuuren, J.H., Herrmann, E. & Funston, P.J. 2005. Lions in the Kgalagadi Transfrontier Park: Modelling the effect of human–caused mortality. *International Transactions in Operational Research*, 12(2): 145–171.

Verlinden, A. 1998a. Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, 36(117): 128.

Verlinden, A. 1998b. Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, 36: 117–128.

Williamson, D. & Williamson, J. 1984. Botswana’s fences and the depletion of Kalahari wildlife. *Oryx*, 18(04): 218–222.

Williamson, D. & Williamson, J. 1988. Wildebeest migration in the Kalahari. *African Journal of Ecology*, 26(4): 269–280.

Yeakel, J.D., Patterson, B.D., Fox-Dobbs, K., Okumura, M.M., Cerling, T.E., Moore, J.W., Koch, P.L. & Dominy, N.J. 2009. Cooperation and individuality among man-eating lions. *PNAS*, 106(45): 19040–19043.