THE EFFECTS OF A LION (*PANTHERA LEO*) RE-INTRODUCTION ON A RESIDENT CHEETAH (*ACINONYX JUBATUS*) POPULATION IN MOUNTAIN ZEBRA NATIONAL PARK, EASTERN CAPE, SOUTH AFRICA

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ABSTRACT

The global decline of large (> 10 kg) carnivores has resulted in a variety of conservation measures being put into practice to prevent extinctions. The establishment of predator-proof fences around protected areas has been a successful tool for reducing human-predator conflict. Furthermore, the re-introduction of large carnivores into small (< 1 000 km^2), enclosed reserves has aided in the conservation of many species. Cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*) have benefitted from such re-introductions. The re-introduction of cheetahs before lions into the Mountain Zebra National Park (MZNP) in the Eastern Cape Province of South Africa provided a unique opportunity to study the effects of lions on an already established cheetah population. Spatial data were downloaded remotely from GPS collared individuals (n=4) and cheetah kill data were collected using the GPS cluster method before (2012-2013) and after (2013-2014) the lion (n=3) re-introduction. The same methods were used for lion kill data collection once they had been re-introduced. In general, cheetah home range size did not change after the lion re-introduction. Cheetahs selected areas with a combination of open and closed vegetation covers, while lions selected either open or closed areas of vegetation covers. In addition, as vegetation cover became thicker, the presence of cheetahs decreased. The cheetahs preyed upon seven species before and 11 species after the lion re-introduction. Medium sized prey comprised the bulk of the cheetah diet with kudu (*Tragelaphus strepsiceros*) and springbok (*Antidorcas marsupialis*) being the preferred species both before and after the lion re-introduction. The lion diets consisted of medium to large sized prey, with the male lions selecting eland (*Tragelaphus oryx*) and buffalo (*Syncerus caffer*) and the lioness selecting red hartebeest (*Alcelaphus buselaphus*). The cheetahs had no significant dietary overlap with the lions and there was only one record of kleptoparasitism. The results of my study indicate that cheetahs are able to co-exist with lions when lions are at low densities in an enclosed reserve. The cheetahs did not experience landscape-level displacement because they made fine-scale adjustments to avoid lions within their environment. This adaptability may have important management implications for future re-introductions of cheetahs into enclosed game reserves.

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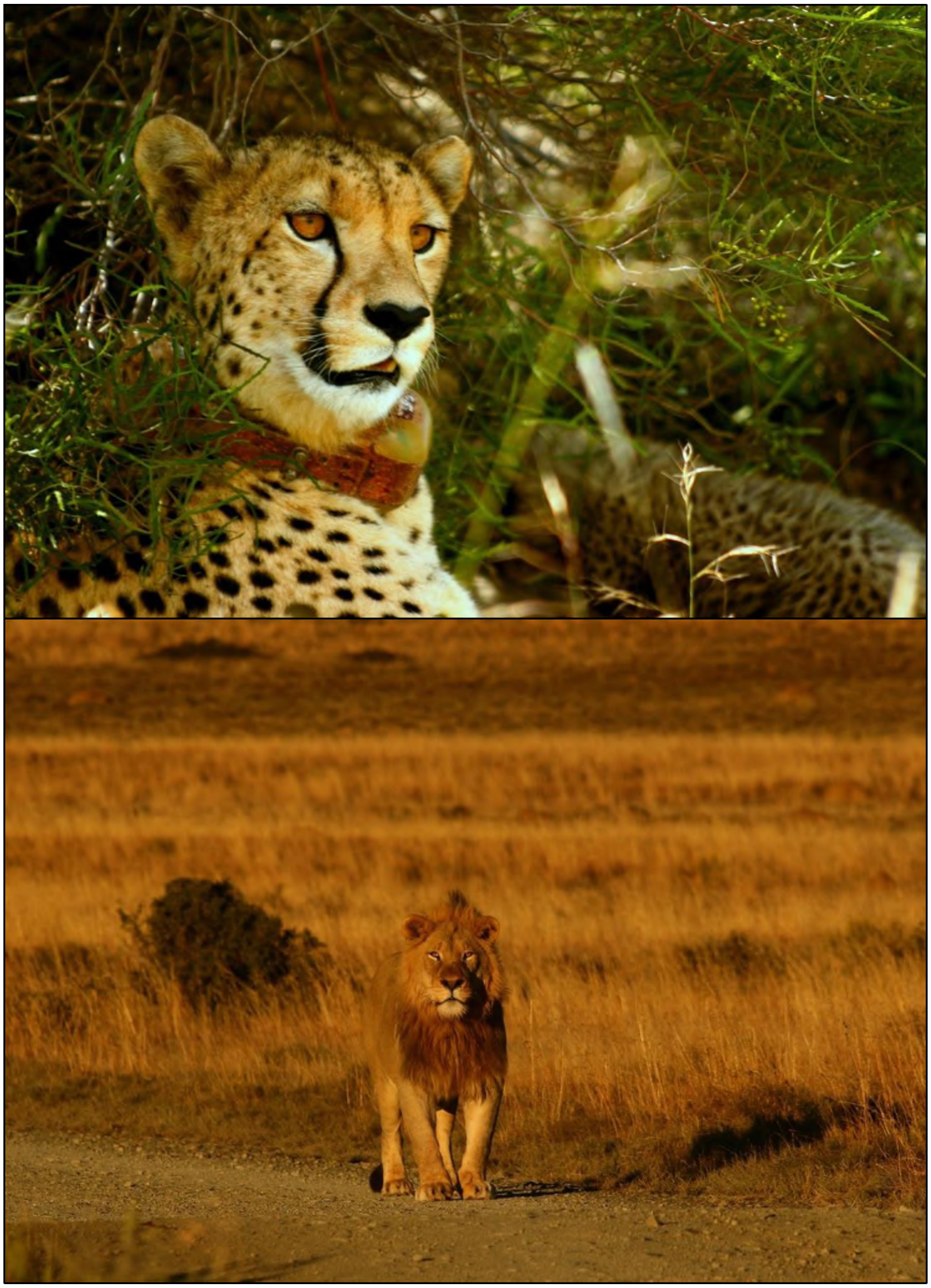
CHAPTER 1

GENERAL INTRODUCTION



“You know you are truly alive when you’re living amongst lions” – Karen Blixon

Images courtesy of C. Bissett.

The conservation of large (> 10 kg) carnivores across the globe is a high profile management issue (Ripple *et al.* 2014, Welch *et al.* 2015). Populations of large carnivores are declining globally, however, trends vary in accordance with their locations and geography, and severity and proximity to human threats (Bauer *et al.* 2015). In addition, the conservation of these large carnivores is further challenged by their low densities and wide ranging behaviour (Welch *et al.* 2015).

The order Carnivora consists of 245 extant terrestrial species inhabiting nearly every major habitat type on Earth (Ripple *et al.* 2014). In the vast majority of these habitats, large carnivores occupy the top position on the food web and have the ability to alter and influence the entire ecosystem via predation and interference competition (Ripple *et al.* 2014, Mills 2015). Smaller carnivores (< 10 kg) also have the capacity to influence ecosystem processes (see Waser 1980). However, it is the conservation of the large carnivores that has received a disproportionate share of attention from wildlife scientists (Mills 1991). This is due to large carnivores constituting the most influential and vulnerable elements of biodiversity and often being considered 'umbrella' species for overall biodiversity conservation (see Balme *et al.* 2014).

Globally, many carnivores have experienced significant decreases in population sizes, have been exposed to range contractions and have had their habitats fragmented by the growth in the human population (Riggio *et al.* 2013, Ripple *et al.* 2014, Bauer *et al.* 2015). In particular, it is the large carnivores that are most at risk to localized extinctions (Bauer *et al.* 2015, Pooley *et al.* 2016). This is due to large carnivores having slow growth/recruitment rates, large range requirements, occurring at low densities and often being subject to direct persecution as they are perceived to be the greatest threat to human lives and livelihoods (Nowell and Jackson 1996, Bissett 2007, Balme *et al.* 2014, Ripple *et al.* 2014). Consequently, the continued survival of large carnivores presents a challenge to conservationists and requires a dynamic set of conservation ideas to prevent total extinctions (Nelson *et al.* 2016, Pooley *et al.* 2016). Furthermore, Balme *et al.* (2014) called for innovative ideas that can positively influence conservation outcomes that can be implemented by wildlife managers. However, Pooley *et al.* (2016) found that the ideas for innovative mitigation to reduce the effects of human-wildlife conflict were still only at the conceptual stage and that interdisciplinary approaches must become increasingly more important.

The direct and indirect pressures of human growth to large carnivore existence has resulted in a reduction of 70% of their historical ranges across Africa, Australia, Europe and southeast Asia (Massey *et al.* 2014). However, the need for the conservation of biodiversity is felt most strongly in Africa because of the exponential growth in the human population, coupled with a constant tug-of-war between resource use and preservation (Massey *et al.* 2014, Bauer *et al.* 2015). Moreover, only 12% of the land in Africa is designated as protected areas (Riggio *et al.* 2013). Thus, the establishment of protected areas is argued to be one of the primary mechanisms for long term carnivore conservation. However, many protected areas are small (< 1 000 km²), not properly enclosed by predator-proof fences, isolated in space, and have limited budgets which reduces their overall capacity to conserve large carnivores (Massey *et al.* 2014, Bauer *et al.* 2015, Pooley *et al.* 2016).

In South Africa, large carnivore population declines occurred as a result of agricultural and economic developments in the early 20th century, extirpating many species from their native ranges (Hayward *et al.* 2007a). However, the recent development of ecotourism (from the early 1990s) in the country has led to the re-assessment of historical land use practices by the government and the private sectors (Langholz and Kerley 2006, Hayward *et al.* 2007a, Pooley *et al.* 2016). Over the past two decades there has been a conversion of land use from livestock farming to small (< 400 km²) enclosed private game reserves and national parks (Hayward *et al.* 2007b). In the Eastern Cape Province of South Africa, the rapid establishment of private game reserves and national parks has led to the re-introduction of many previously extirpated wildlife species (Hayward *et al.* 2007a). In the vast majority of these private game reserves in the Eastern Cape Province and some national parks, extirpated carnivore species such as lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*), spotted hyaenas (*Crocuta crocuta*) and brown hyaenas (*Hyaena brunnea*) have been re-introduced (Hayward *et al.* 2007b). However, the reasons for these large carnivore re-introductions are not only for restoring biodiversity but arguably more about satisfying the viewing preferences of photo-tourists (Lindsey *et al.* 2007).

Ecotourism is the fastest growing component of the tourism industry across South Africa, and Africa as a whole holds great potential for the continued conservation of many species in their respective protected areas (Lindsey *et al.* 2007, Massey *et al.* 2014). However, the narrow viewing preferences of many tourists revolve around the importance and availability of the “big five”, which are apparently needed for reserves and parks to be successful (Langholz and Kerley 2006). The species that constitute the “big five” (elephants (*Loxodonta africana*), white (*Ceratotherium simum*) and black (*Diceros bicornis*) rhinoceros, buffalo (*Syncerus caffer*), lions and leopards) are now very popular species amongst tourists, having originally been designated the “big five” by trophy hunters due to the difficulty in hunting these species (Lindsey *et al.* 2007). Ironically, these species are the most expensive to conserve and the expenses that can occur as a result of their re-introduction can also limit the number of individuals which are re-introduced into a reserve (Lindsey *et al.* 2007, Lindsey *et al.* 2011, Miller *et al.* 2013a). For example, O’Brien (2012) found that it cost $235 270.00 (exchange rate ZAR13.41 = $1, November 2016, NASDAQ) a year to sustain a large carnivore guild in just one enclosed reserve in South Africa.

Further challenges arise from the lack of post-release monitoring of these large carnivores (Hayward *et al.* 2007b, Lindsey *et al.* 2007). Considering the sensitivity of large carnivores to anthropogenic pressures, and their ability to influence and alter their environments, the importance of post-release studies becomes imperative for any re-introductions to be successful (Hayward *et al.* 2007b).

The process of large carnivore re-introductions in the Eastern Cape Province began in 2000 with Shamwari Private Game Reserve re-introducing lions and cheetahs (Hayward *et al.* 2007b). The first national park in the Eastern Cape Province to re-introduce large carnivores was Addo Elephant National Park in 2003 (Hayward *et al.* 2007b). The increase in the number of game reserves led to a large number of carnivores being re-introduced and this included the Mountain Zebra National Park, which re-introduced cheetahs in 2007 and lions in 2013 (Miller and Funston 2014).

The cheetah is one of the 36 species belonging to the Family Felidae and *Acinonyx jubatus jubatus* of five subspecies in southern Africa (Sunquist and Sunquist 2002, Krausman and Morales 2005, Durant *et al.* 2015). The cheetah is listed as Vulnerable by the World Conservation Union (IUCN) (Durant *et al.* 2015, van der Merwe *et al.* 2016). The subspecies that occurs throughout southern Africa is *Acinonyx jubatus jubatus* (Schreber 1775) and is also classified as Vulnerable by the IUCN (van der Merwe *et al.* 2016). Historically, cheetahs occurred across most of the non-forested areas of Africa, the Middle East and into southern Asia (Sunquist and Sunquist 2002). However, today cheetahs have disappeared from vast tracts of their historical range (Durant *et al.* 2015).

Cheetahs in Africa are thought to persist in only 10% of their former range, while populations in Asia are restricted to the central deserts of Iran (Farhadinia and Hemami 2010, Figure 1.1). In southern Africa, cheetah only occur in 22% (1 223 388 km^2) of their former historical range (Durant *et al.* 2015). The vast majority of these cheetahs survive in a single transboundary population stretching across Namibia, Botswana, south-western Angola, northern South Africa, south-western Mozambique and into southern Zambia (Durant *et al.* 2015, Figure 1.2). In South Africa, the cheetah population can be divided into three different groups based on land use and the level of management being implemented to sustain these populations (van der Merwe *et al.* 2016, Figure 1.2). These include; free-roaming cheetahs, cheetahs in large protected areas and managed metapopulations (see van der Merwe *et al.* 2016). In 1900, an estimated 100 000 cheetahs lived in 44 countries throughout Africa and Asia (Sunquist and Sunquist 2002). Today, an estimated 6 700 adult cheetahs survive in 29 subpopulations distributed across 21 countries (Durant *et al.* 2015). These demographics can be further broken down into regions; with southern Africa consisting of 4 190 adults, 1 960 adults in east Africa, 440 adults in west, central and north Africa and 80 adults in Iran (Durant *et al.* 2015). However, only 1 409 – 1 742 adult cheetahs are estimated to survive in South Africa (van der Merwe *et al.* 2016).

Interestingly, the factors affecting cheetah survival vary between regions and even populations (see Durant *et al.* 2015). However, the universal themes of habitat loss and fragmentation due to a growing human population are key drivers affecting cheetah success (Marnewick *et al.* 2007). In southern Africa, one of the most significant factors affecting cheetah survival is conflict with livestock owners and competition with other large carnivores within enclosed reserves (Marnewick *et al.* 2007, Bissett and Bernard 2007, Welch *et al.* 2015). In South Africa, poorly regulated captive trade, conflict-related persecutions, veterinary complications during immobilization and habitat fragmentation have all contributed to decreases in the cheetah population (van der Merwe *et al.* 2016). However, the establishment of enclosed reserves, those surrounded by a predator-proof fence, may present one of the greatest tools for the continued survival of cheetahs (Welch *et al.* 2015). Fences reduce the number of human-cheetah conflicts and routine large carnivore management and regulation by reserve managers do not normally allow carrying capacities to be exceeded (Marnewick and Somers 2015, Welch *et al.* 2015).

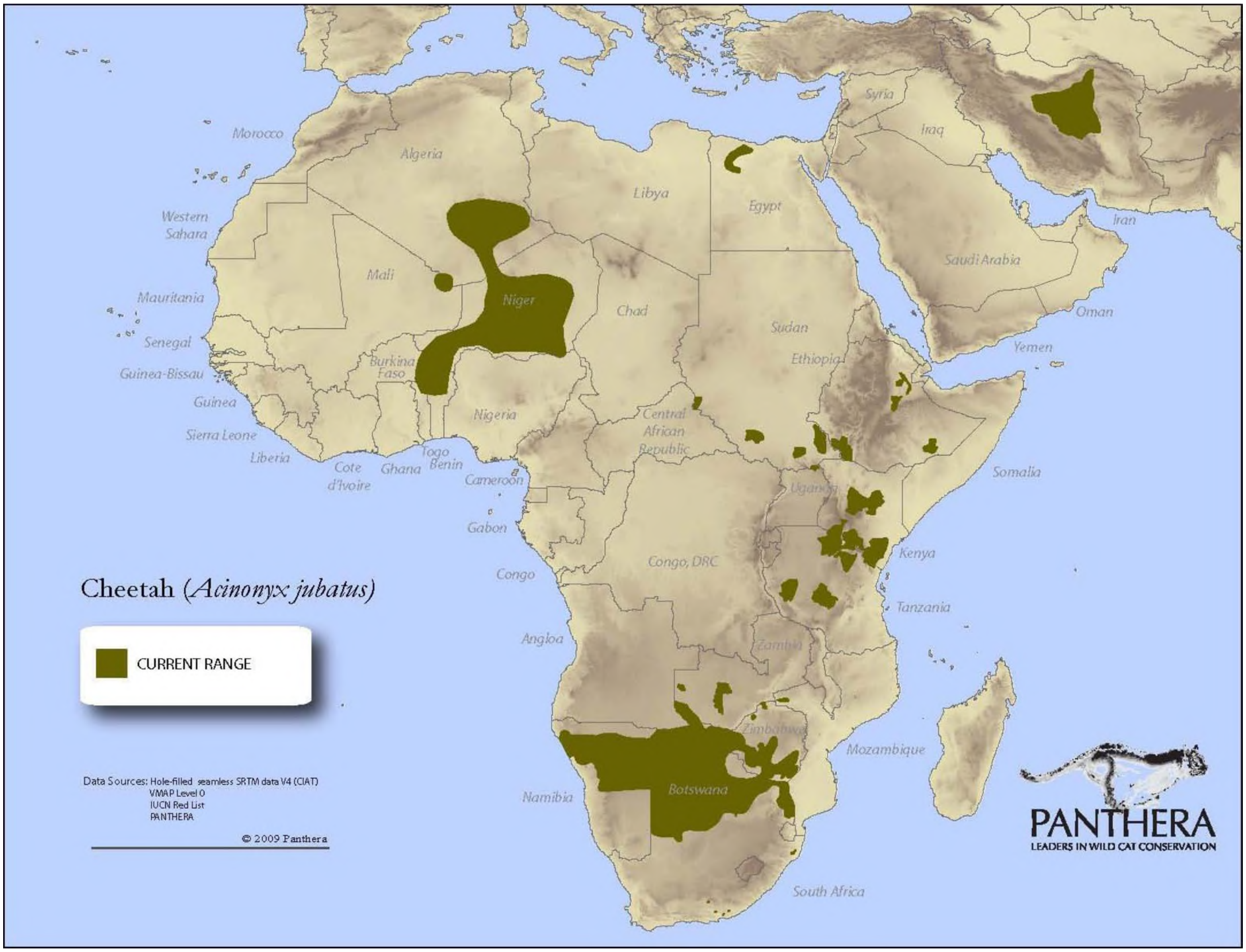


Figure 1.1: The global distribution of free roaming cheetahs in Africa and Asia (Taken from Panthera 2009).

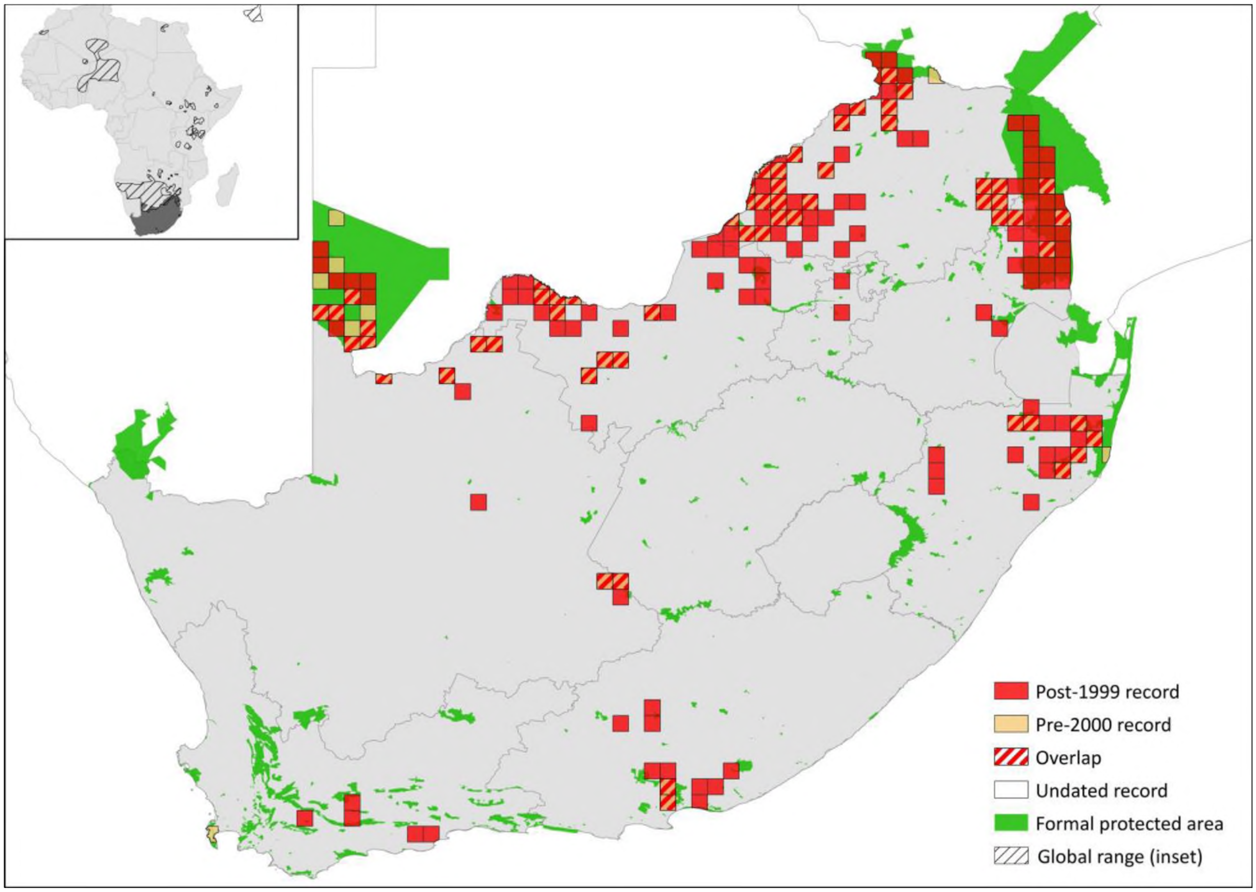


Figure 1.2. The distribution of free roaming cheetahs in South Africa. Insert refers to global distribution of cheetahs (Taken from van der Merwe *et al.* 2016).

Lions are one of 36 global felid species and have been divided into two subspecies; the Asian populations occurring in the Gir Forest of India (*Panthera leo persica*) and the African populations (*Panthera leo leo*). However, the current extent of the number of subspecies occurring within Africa is under review (see Bauer *et al.* 2016). The lion is currently listed as Vulnerable on the IUCN but the lion's status could change to Endangered if the overall population was to decline by at least 50% over three generations (Bauer *et al.* 2015, Miller *et al.* 2016). The lion population in southern Africa has increased by 12% and is classified as Least Concern by the IUCN (see Bauer *et al.* 2015, Miller *et al.* 2016, Figure 1.3). Nevertheless, despite the fluctuations of subpopulations, the total lion population in Africa has decreased by 43% over the past 21 years (Bauer *et al.* 2016, Figure 1.4). Historically, lions ranged over most of Africa, through southwest Asia, into Europe and east into India (Riggio *et al.* 2013). Today, lions are found in most sub-Saharan countries in Africa but only occupy 17% of their historical range (Riggio *et al.* 2013, Bauer *et al.* 2016). In

South Africa, lions only occur on 40 000 km^2 compared to 1.2 million km^2 of their former range and are almost exclusively found in fenced reserves (Miller *et al.* 2016). Bauer *et al.* (2015) estimated that 20 000 lions remained in 67 lion areas in Africa, compromising an area of 3.4 million km^2, which only covers 25% of Africa's savannas. The lion population in South Africa is estimated at 1 775 mature individuals and has not declined over the past 20 years (Miller *et al.* 2016).

The African lion exemplifies all the challenges associated with large carnivore conservation (Creel *et al.* 2013). Lions are the most well-studied of the large felids and it is not surprising that the various influences affecting their survival have been well documented (Creel *et al.* 2013). The factors affecting lion populations across their range are due to widespread habitat losses, a fragmented prey base, fragmented and isolated populations, resulting in inbreeding, direct persecution from humans as a result of human-wildlife conflict, over-exploitation from hunting and demands from traditional African and Chinese markets (see Loveridge *et al.* 2007, Everatt *et al.* 2014, Miller and Funston 2014, Bauer *et al.* 2016, Nelson *et al.* 2016). Despite these threats, lions in South Africa are not exposed to any major threats because most are limited to fenced reserves (Miller *et al.* 2016). However, isolated incidents of human-wildlife conflicts and associated persecutions have been reported (see Miller *et al.* 2016). Creel *et al.* (2013) stated the highest priority for lion conservation is to maintain viable populations in the face of the direct persecution. In addition, Packer *et al.* (2013) suggested that the building of fences around protected areas is likely the best way to conserve and ensure the long term survival of lions.

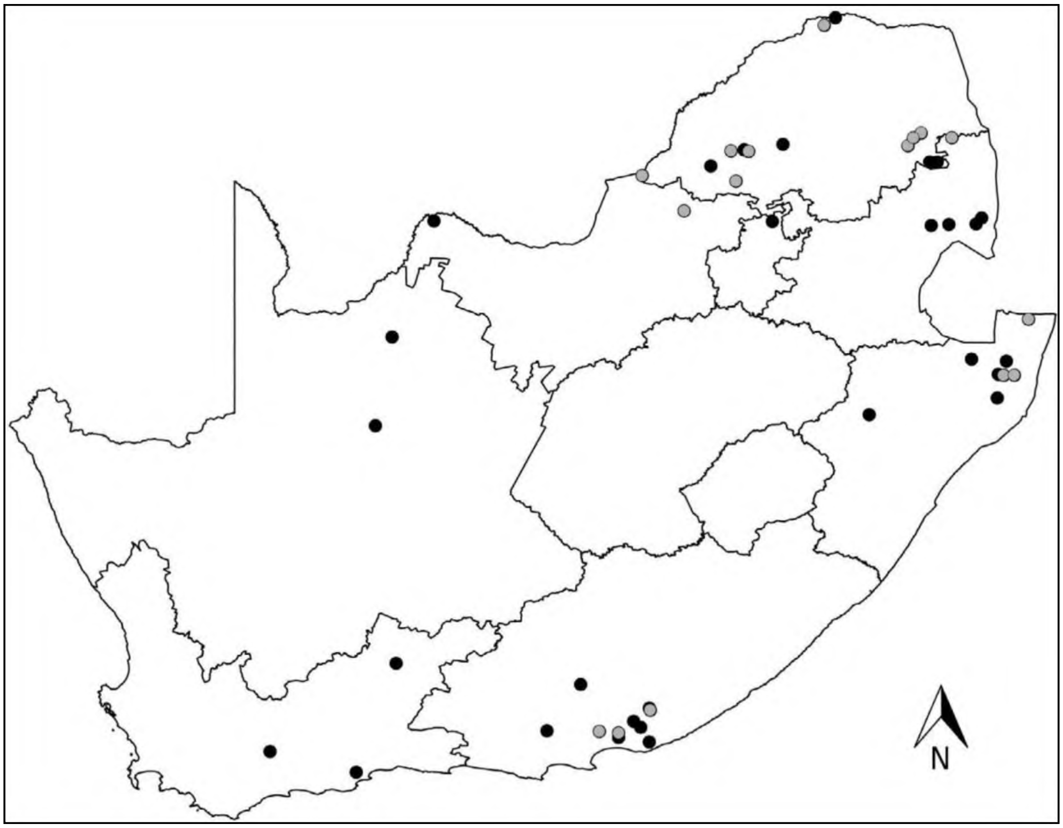


Figure 1.3. The distributions of enclosed reserves which have re-introduced lion populations in South Africa (Taken from Miller and Funston 2014).

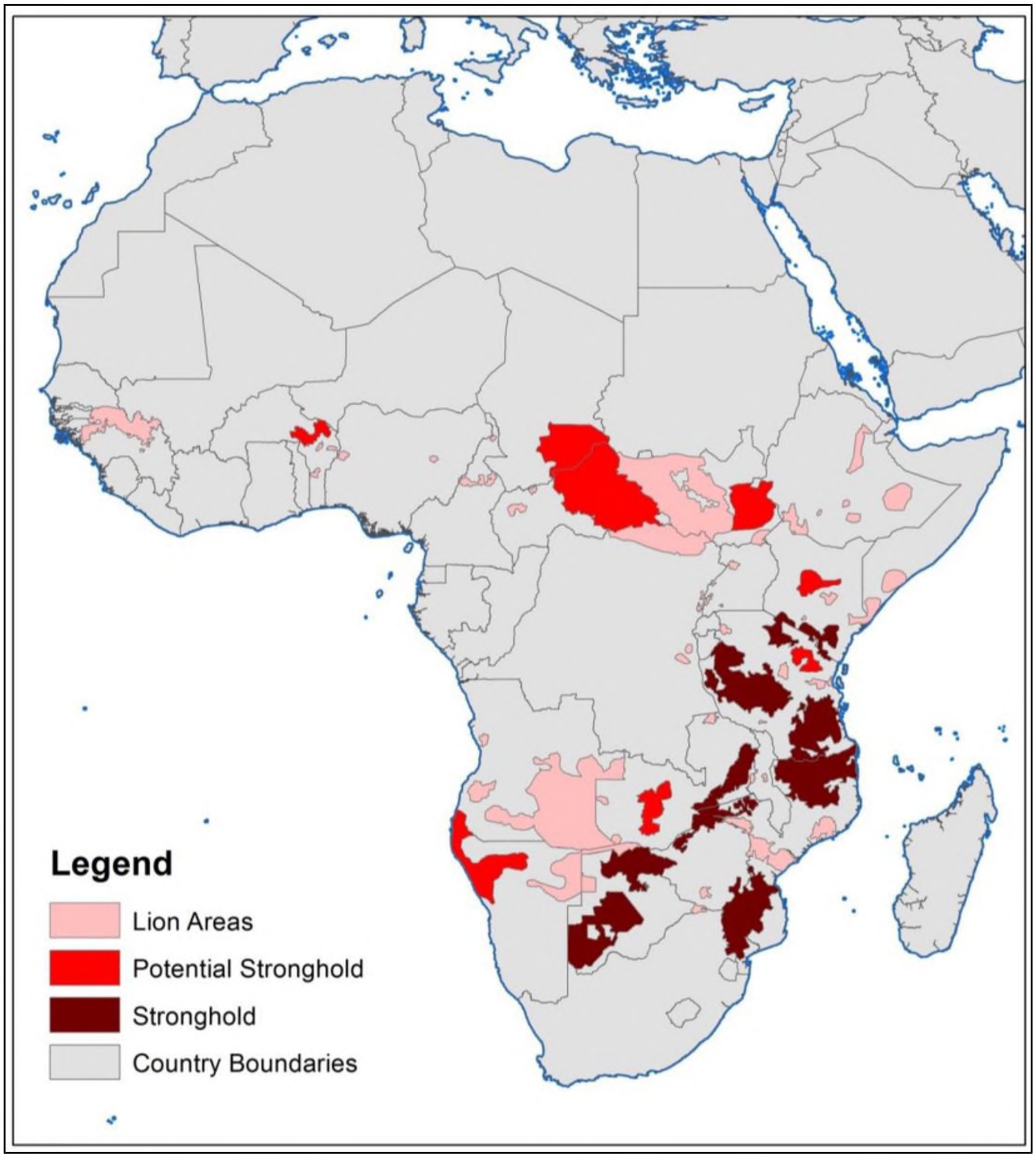


Figure 1.4. The distribution and locations of the lion populations within and outside protected areas across Africa (Taken from Bauer *et al*. 2016).

It is clear that for the continued existence of both cheetahs and lions, they need to be protected by fences in southern Africa and beyond (Durant *et al*. 2015, Bauer *et al*. 2016). While the confinement of large carnivores to fenced-off protected areas may remove the immediate problem of predator-human conflict, it poses a number of other ecological challenges (Bissett 2007). As apex predators, lions play a vital role in ecosystem functioning (Bauer *et al*. 2015, Bauer *et al*. 2016). Large, dominant carnivores such as lions, have the ability to influence the location, distribution and behaviour of smaller carnivores such as cheetahs, and within enclosed reserves, these effects can be exaggerated to the point of localized extinctions (Bissett and Bernard 2007, Lindsey *et al.* 2011). Furthermore, enclosed reserves require careful management of their carnivore populations because certain natural processes such as emigration, immigration and outbreeding cannot occur naturally (Welch *et al.* 2015).

The re-introductions of large carnivores into new environments, such as the cheetahs and lions into the Mountain Zebra National Park, South Africa have created opportunities to address fundamental questions in large carnivore biology (Bissett and Bernard 2007). Importantly, large carnivores were extirpated from the Eastern Cape Province long before any carnivore research had even started in Africa (Skead 2007). Consequently, the process of first re-introducing cheetahs followed by lions into Mountain Zebra National Park has created an opportunity to study the factors affecting the space use and diet of both these large carnivores. Not only is it imperative to understand how these large carnivores utilize different habitats but also how smaller carnivores may react to the changes in the structure of the large carnivore guild (see Bissett *et al.* 2015). Such studies add to our understanding of both cheetah and lion ecology and are vital for the overall conservation of these species in Africa. Thus, the central aim of my study was to determine the influence of a lion re-introduction on an already resident cheetah population within a small (0 - < 400 km^2), fenced game reserve.

CHAPTER 2

STUDY SITE

The dynamic landscape of Mountain Zebra National Park. Image used with permission from J. Vosloo.

Study area

Mountain Zebra National Park (hereafter referred to as MZNP; -32° 18’ S and 25° 24’ E) is a South African National Park (SANParks) situated in the Eastern Cape Province of South Africa (Figure 2.1). It is approximately 24 km west of the town of Cradock and falls within a transition zone of the Nama-Karoo, Grassland and Thicket Biomes (Spies 2016). MZNP is situated in a north-south orientation between the arid Nama-Karoo bushveld in the west and the drier but ‘sweeter’ grasslands of the east (Pond *et al*. 2002). It was proclaimed in 1937 for the sole purpose of conserving a remnant population of Cape mountain zebra (*Equus zebra zebra*). Subsequently, the park has expanded from the original 1 712 ha to 21 412 ha by buying adjacent farmland (Spies 2016). However, MZNP is no longer classified as a ‘species park’ and has aligned its objectives to restoring the biodiversity that once occurred in the area (Spies 2016).

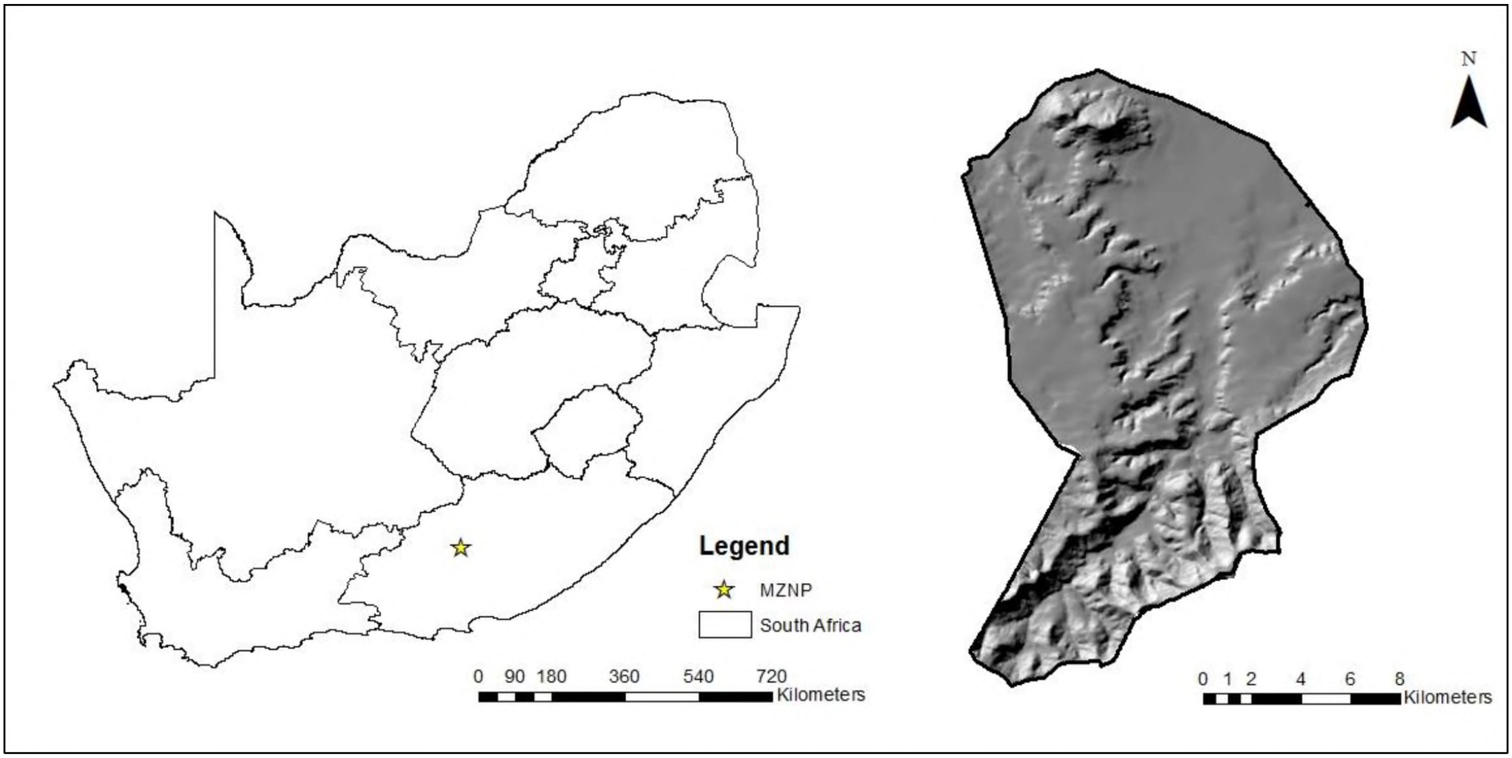


Figure 2.1. The geographic location and an enlarged map of Mountain Zebra National Park in South Africa (ArcGIS 10.2; map units: decimal degrees; not projected).

Topography and geology

The mountainous terrain of MZNP forms part of the Karoo Mountain Veld Complex, which is also part of the Great Escarpment (Gebeyehu and Samways 2002, Figure 2.2A). MZNP is located on the northern slopes of the Bankberg Mountain Range and is described as having a cool but arid climate (Spies 2016). The southern parts of MZNP are characterized by steep sided mountains (Pond *et al*. 2002). The main river, the Wilgerboom, traverses the park from the southern section through the central area before exiting in the north. However, it only flows seasonally and animals are supplied with artificial water throughout the year (Spies 2016, Figures 2.2B and 2.3A). The northern parts of the park are characterized by undulating slopes and seasonally dry river beds coming off the Rooiplaat plateau and a prominent mesa called Salpeterkop (Pond *et al*. 2002).

The landscape is composed of mudstone, sandstone and shale of the Beaufort Group which is part of the Karoo Supergroup (Pond *et al*. 2002). These mudstones and shales are relatively unstable and when subjected to mechanical and chemical weathering, erode and release rich clay and salts (Pond *et al*. 2002). These Beaufort Group rocks were penetrated by large scale Post-Karoo dolerite intrusions, which formed large sheets and an extensive network of dykes (Pond *et al*. 2002). The southern part of the park is characterized by these dolerite events, forming large, erosion resistant outcrops and giving rise to the Bankberg Mountain Range, which includes the highest point in MZNP, Bakenkop at 1 957 meters above sea level (Pond *et al*. 2002). The soils derived from dolerite rocks are more resistant to erosion compared to those derived from the shales and mudstones (Pond *et al*. 2002). Thus, soil coverage throughout the park is generally shallow, with vast parts of the park being very rocky with little to no top soil (Spies 2016, Figure 2.3B).

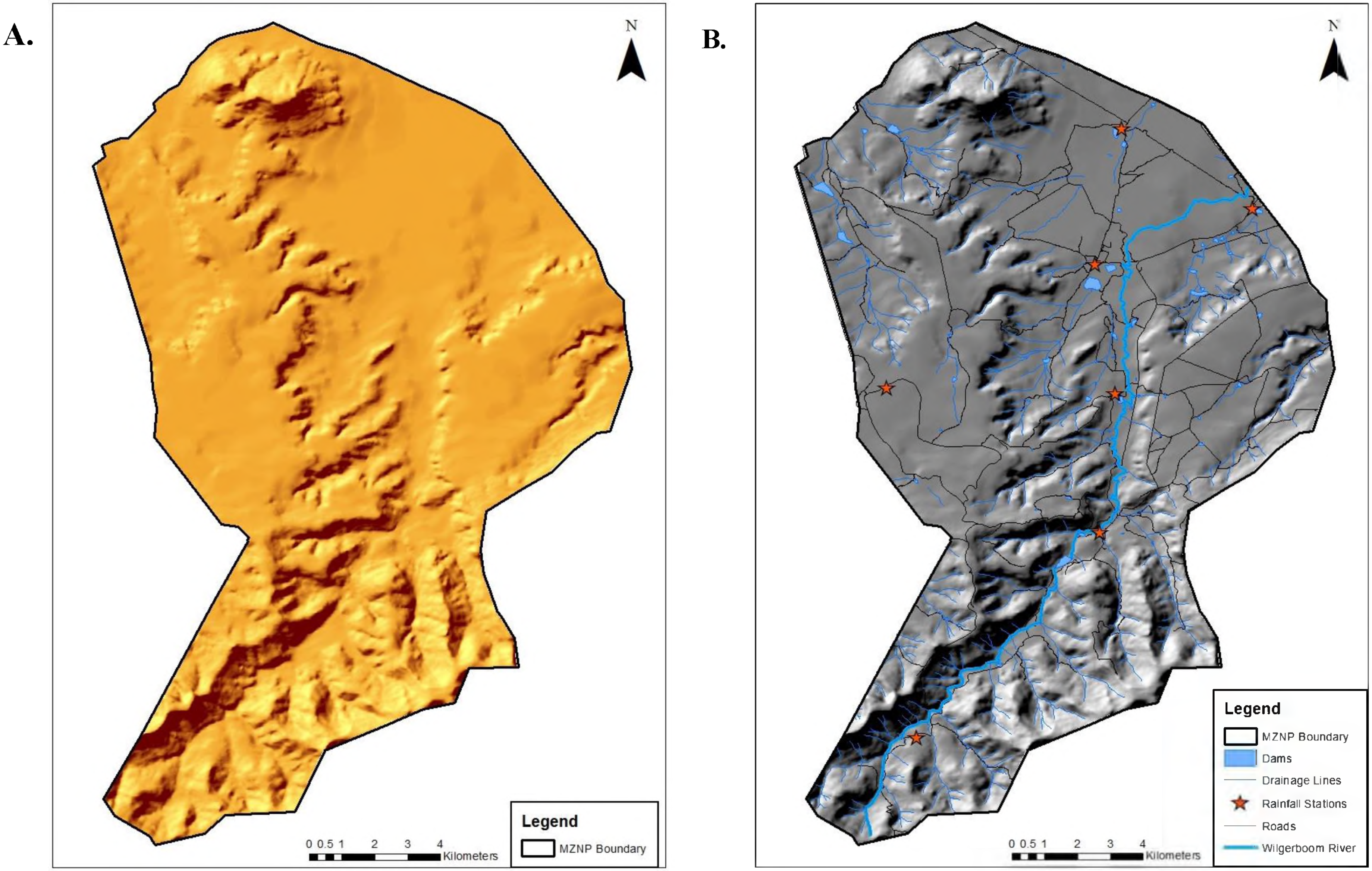


Figure 2.2. The varied topography of MZNP, note the steep southern section (A), and (B) the topographical layout.

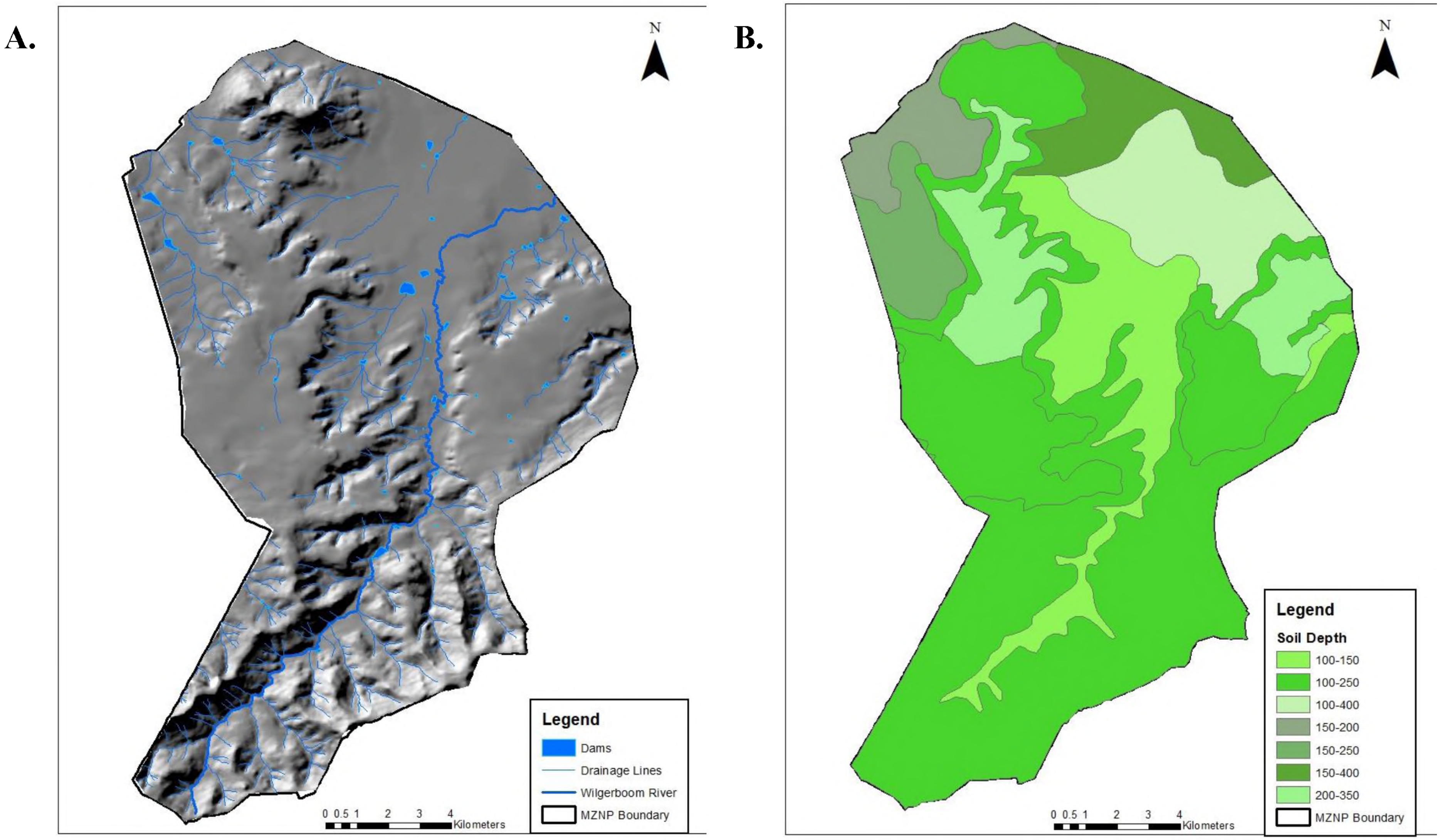


Figure 2.3. The positions of (A) water sources and (B) the soil map highlighting the shallow soil depths (mm) in MZNP.

Climate

The mean annual rainfall in MZNP is 405 mm, ranging between 153 - 651 mm (1962-2016, Figure 2.4A) with most of the rain falling in the late summer and early autumn (October to February, Pond *et al.* 2002, Spies 2016, Figure 2.4B). Mean monthly maximum and minimum temperatures in summer (September – March) vary from 6 °C to 28 °C and from -1 °C to 20 °C in the winter (April – August, Spies 2016, Figure 2.4C). MZNP is a landscape that can experience extreme temperatures that range from -12 °C in winter to 46 °C in summer (Figure 2.4C). Light snow falls are frequently experienced during the winter months and frost is common in the early mornings between May and October (Pond *et al.* 2002). The mountainous terrain of the southern part of the park is often exposed to increased cloud cover and extreme temperature variations, creating a number of microhabitats (Pond *et al.* 2002). However, the Bankberg Mountain Range that traverses the southern sections of MZNP forms a barrier to cold fronts in the winter (Pond *et al.* 2002).

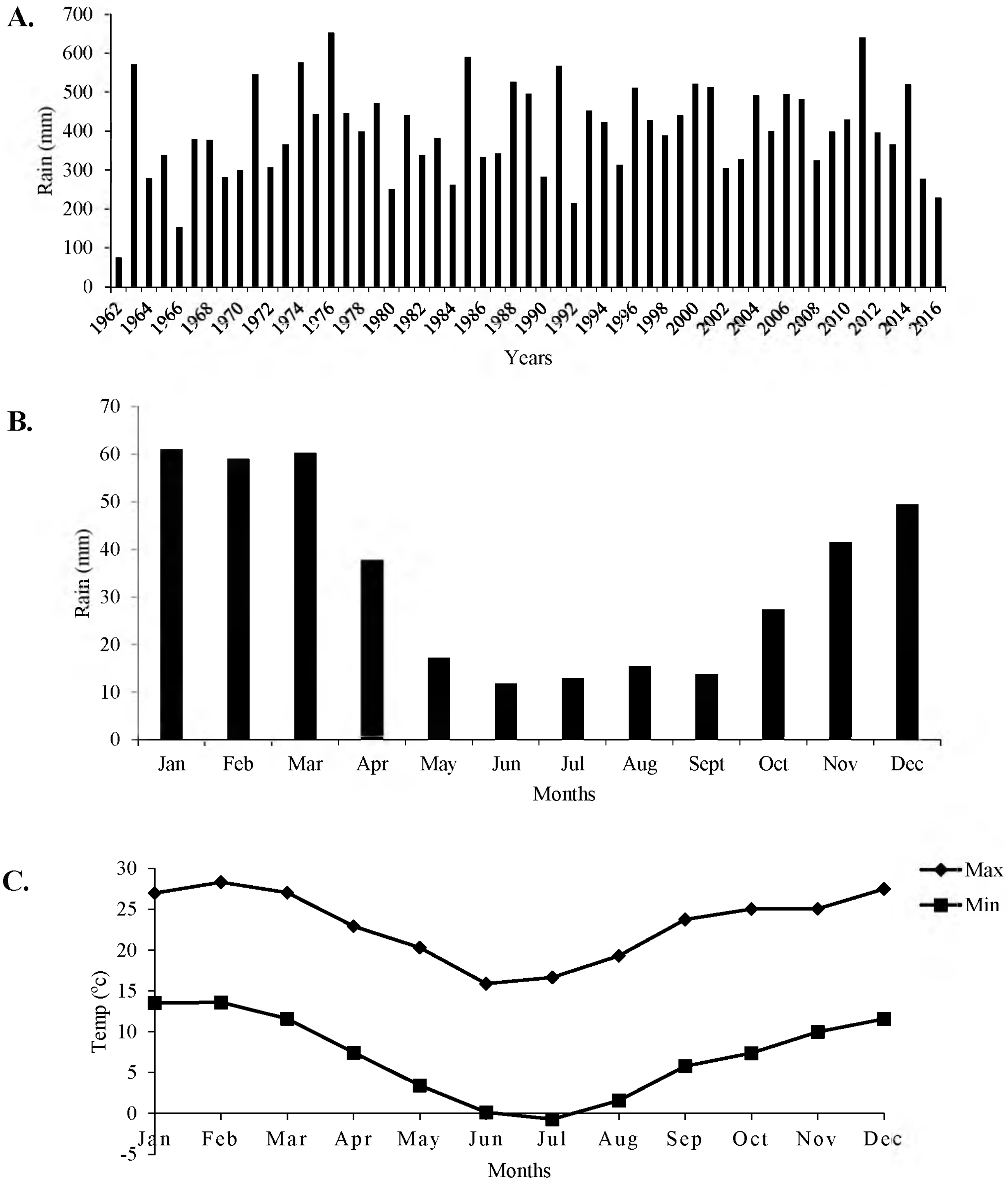


Figure 2.4. A – The annual rainfall (1962-2016), B- The mean monthly rainfall (1962- 2016), and C- Mean monthly maximum and minimum temperatures (1983-2016) recorded in MZNP.

Vegetation

The classification of the vegetation at the park level shows that MZNP has three, broad vegetation types, the Eastern Upper Karoo (37%), the Karoo Escarpment Grassland (53%) and the Eastern Cape Thicket (10%, Mucina and Rutherford 2006). The Eastern Upper Karoo is characterized by either flat or gently sloping plains interspersed with rocky areas and the dominant flora are dwarf microphyllous shrubs, such as the Karoo bitter bos (*Pentzia globosa*) and Karoo anchor bos (*Pentzia incana*, Spies 2016, Figure 2.5). The Eastern Upper Karoo is a combination of grasses and shrubs but are subjected to changes as a result of variable rainfall (Mucina and Rutherford 2006). Common grasses recorded in the Eastern Upper Karoo are the three awn (*Aristida* spp.), love grass (*Eragrostis* spp.) and the red grass (*Themeda triandra*). The Karoo Escarpment Grassland is characterized by low mountains and hills and is dominated by grasses, such as mountain wire grass (*Merxmuellera disticha*) and shrubs, such as *Euryops annuus* (Mucina and Rutherford 2006, Figure 2.5). Fires are fairly common in the Karoo Escarpment Grassland (Pond *et al*. 2002). The Eastern Cape Thicket is prevalent on the steep sides of the escarpment and mountain with the dominant flora being Karee (*Searsia lancea*) and olive (*Olea europa africana*) trees (Mucina and Rutherford 2006).

The vegetation of MZNP is further classified into 12 different, fine-scale units (Figures 2.5 to 2.17; Van der Walt 1980, Pond *et al*. 2002, Brown and Bezuidenhout 2006). It was these 12 vegetation units which were used for determining the habitat preferences of the cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*) re-introduced into MZNP (Figure 2.5). The different vegetation units are classified as follows:

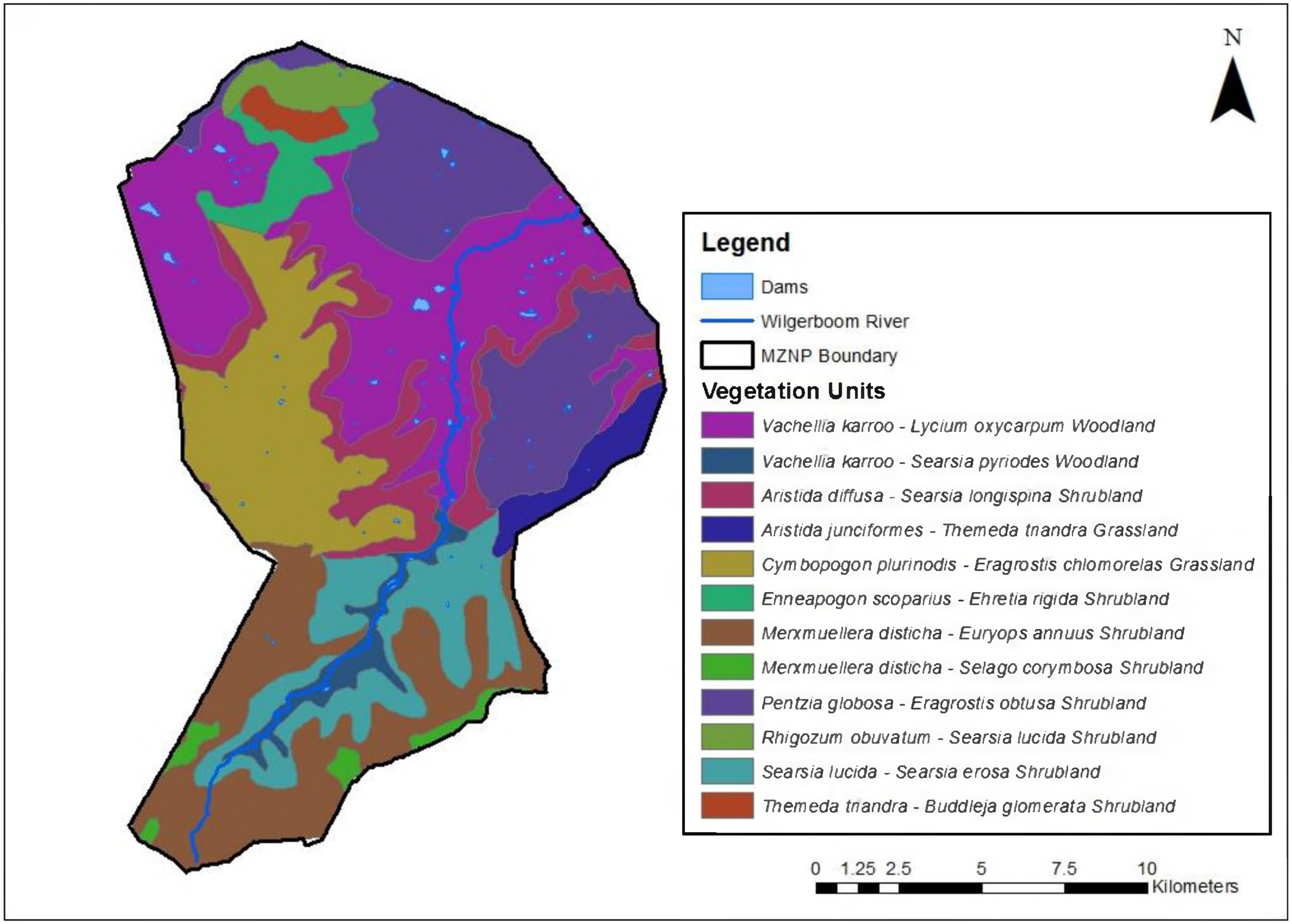


Figure 2.5. The distribution of the 12 vegetation units described by Brown and Bezuidenhout (2006).

1. *Vachellia karroo – Lycium oxycarpum* Woodland.

This vegetation unit occurs along the embankments of the Wilgerboom River and the northern plains of MZNP (Van der Walt 1980). *Vachellia karroo* trees form the tallest layer of cover and covers an area of 10-25%. *Lycium oxycarpum* forms the main shrub layer and covers an area of 15-35%, while grass species, such as *Chloris vergata* and *Panicum maximum* cover an area of 30-60% (Brown and Bezuidenhout 2006, Figure 2.6, Figure 2.5). This vegetation unit is also found along the many drainage lines of MZNP and because of the high numbers of palatable *Vachellia karroo* trees and palatable *Panicum maximum* grasses, it is favoured by browsing and grazing animals (Van der Walt 1980).

Figure 2.6. The male lions walking through the *Vachellia karroo – Lycium oxycarpum* Woodland.

2. *Vachellia karroo – Searsia pyroides* Woodland.

This vegetation unit consists of three layers, with the tallest layer comprised of *Searsia pyriodes* bushes which are 5 m in height (Brown and Bezuidenhout 2006, Figure 2.7, Figure 2.5). The mid-layer is mainly smaller *Vachellia karroo* trees of 1 to 2 m in height and the herbaceous layer approximately 0.4 m in height (Figure 2.7). A greater diversity of plant species occur in this vegetation unit compared to the *Vachellia karroo- Lycium oxycarpum* Woodland (Pond *et al.* 2002).

Figure 2.7. A herd of buffalo (*Syncerus caffer*) moving through the *Vachellia karroo – Searsia pyroides* vegetation unit.

3. *Aristida diffusa – Searsia longispina* Shrubland.

This vegetation unit occurs on the warm, dry footslopes and plateau areas of MZNP (Figure 2.8, Figure 2.5). Small to medium-sized rocks cover 15-60% of the area (Brown and Bezuidenhout 2006). Tree heights range from 2.5 to 3 m covering 15% of the area. Shrub size and height covers between 5-10% of the area and is between 1.5 m to 3.5 m and is characterized by *Searsia longispina*. Grass covers more than half of the area and is characterized by unpalatable *Aristida diffusa* (Figure 2.8). However, these areas are relatively steep and generally not utilized by ungulate species (Brown and Bezuidenhout 2005).

Figure 2.8. Cheetah male (CM39) walking in *Aristida diffusa – Searsia longispina* Shrubland.

4. *Aristida junciformes – Themeda triandra* Grassland.

This grassland is primarily located along the eastern boundary of MZNP (Brown and Bezuidenhout 2006, Figure 2.9, Figure 2.5). A large portion of this vegetation unit is covered by rocks (30-50%), with a small woody (2-10% and a large herbaceous layer (40-60%), approximately 1.2 m and 0.3 m in height respectively (Brown and Bezuidenhout 2006, Figure 2.9). *Vachellia karroo* trees are locally dominant in the drainage lines. However, most of the area is dominated by *Aristida junciformes* and *Themeda triandra* grasses, which was in relatively good condition with minimal effects from grazing animals at the time of the study (Brown and Bezuidenhout 2005, 2006, Figure 2.9).

Figure 2.9. CF6 resting after catching a kudu (*Tragelaphus strepsiceros*) calf in the *Aristida junciformes* – *Themeda triandra* vegetation unit.

5. *Cymbopogon plurinodis* – *Eragrostis chlomorelas* Grassland.

This predominately grassland vegetation unit is associated with a number of medium-sized rocks. These rocks provide a unique climate for species to grow, in an otherwise exposed area (Brown and Bezuidenhout 2006, Figure 2.5). This grassland occurs on the rocky plateau on the western side of MZNP and has most of the topsoil still intact (Van der Walt 1980, Figure 2.10). However, the effects of grazing on the *Cymbopogon plurinodis* and *Eragrostis chlomorelas* grasses can be severe outside of the areas protected by the rocks (Pond *et al*. 2002).

Figure 2.10. Typical *Cymbopogon plurinodis – Eragrostis chlomorelas* grassland found in MZNP.

6. *Ennaepogon scoparius – Ehretia rigida* Shrubland.

This vegetation unit is common on the southern slopes of Salpeterkop with varying gradients of 10° to 20° (Brown and Bezuidenhout 2006, Figure 2.5). A small woody layer is present and is dominated by *Vachellia karroo* trees, covering 10-20% of the area (Pond *et al*. 2002, Figure 2.11). The dwarf shrub, *Ehretia rigida*, intersperses the more dominant but unpalatable *Ennaepogon scoparius* grasses (Figure 2.11). However, *Ennaepogon scoparius* grasses can play an important role of anchoring and stabilizing the soil in overgrazed areas. Brown and Bezuidenhout (2006) observed that there was localized disturbances in certain areas of this vegetation unit because of overgrazing when the area was still used as farmland.

Figure 2.11. CF6 and her cubs lying on a midslope in the *Ennaepogon scoparius – Ehretia rigida* vegetation unit.

7. *Merxmuellera disticha – Euryops annuus* Shrubland.

This vegetation unit is only found in the high lying areas of MZNP and is strongly associated with cool sandstone midslopes (Brown and Bezuidenhout 2006, Figure 2.5). It consists of a shrub layer of *Euryops annuus* that is between 1 – 2 m in height and a grass layer of extremely unpalatable *Merxmuellera disticha* (Brown and Bezuidenhout 2006, Figure 2.12). Due to the high altitude and unpalatable species, it is generally avoided by most of the ungulate species (Van der Walt 1980).

Figure 2.12. An example of *Merxmuellera disticha – Euryops annuus* shrub-land transitioning into *Cymbopogon plurinodis – Eragrostis chlomorelas* grassland.

8. *Merxmuellera disticha – Selago crymbosa* Shrubland.

This vegetation unit occurs at some of the highest altitudes in MZNP, often 300 m above *Merxmuellera disticha – Euryops annuus* Shrubland (Van der Walt 1980, Brown and Bezuidenhout 2006, Figure 2.13, Figure 2.5). Thus, it is mainly found on the high, steep slopes of the Bankberg plateau where the climate is cool and moist (Van der Walt 1980, Figure 2.13). This is a complex layer of vegetation consisting of dense *Merxmuellera disticha* tussocks of ~0.3 m in height, with scattered shrub compositions of varying heights (0.3 – 1.3 m) and cover (Brown and Bezuidenhout 2006).

Figure 2.13. A small buffalo herd grazing in *Merxmuellera disticha – Selago corymbosa* Shrubland.

9. *Pentzia globosa – Eragrostis obtusa* Shrubland.

This vegetation unit is classified as a degraded shrubland with grasses and an intermittent tree layer being present (Brown and Bezuidenhout 2006, Figure 2.14, Figure 2.5). It is commonly found on the midslopes, lower footslopes and flat areas of MZNP, with shallow soils and small rocks covering an area between 0-30% (Brown and Bezuidenhout 2006). *Pentzia globosa* shrubs only reach a height of 0.3 m and cover 30% of the area. *Eragrostis obtusa* grasses dominate the area covering 25 – 60% and reach heights of 0.1 – 0.3 m (Brown and Bezuidenhout 2006).

Figure 2.14. A secretarybird (*Sagittarius serpentarius*) walking through the *Pentzia globosa – Eragrostis obtusa* Shrubland.

10. *Rhigozum obuvatum – Searsia lucida* Shrubland.

This vegetation unit is found on the northern footslopes, midslopes and steep slopes of Salpeterkop in MZNP (Brown and Bezuidenhout 2006, Figure 2.15, Figure 2.5). Large and small-sized rocks cover more than half of the area (50-60%), with a small percentage (<2%) of woody plants, a slightly larger covering of shrubs (15-30%) and a herbaceous layer covering 50-60% of the vegetation unit (Brown and Bezuidenhout 2006). The steep slopes are inaccessible to most game species but the lower slopes are readily overgrazed (Figure 2.15). If this vegetation unit is incorrectly managed it could convert into a dense thicket (Brown and Bezuidenhout 2006).

Figure 2.15. *Rhigozum obuvatum* – *Searsia lucida* Shrubland transitioning into *Themeda triandra* – *Buddleja glomerata* Shrubland on the slopes and crest of Salpeterkop.

11. *Searsia lucida* – *Searsia erosa* Shrubland.

This vegetation unit primarily occurs along the lower doleretic slopes of the Wilgerboom catchment area in the southern section of MZNP (Brown and Bezuidenhout 2006, Figure 2.16, Figure 2.5). Soils are rich in minerals and large, often over 5 m high *Searsia lucida* trees and smaller *Searsia erosa* shrubs dominate the warmer but lower southern slopes and valleys (Van der Walt 1980).

Figure 2.16. A transition zone of *Searsia lucida – Searsia erosa* shrubland into *Merxmuellera disticha – Euryops annuus* shrubland on the Bankberg Mountain Range in MZNP.

12. *Themeda triandra – Buddleja glomerata* Shrubland.

This vegetation unit is dominated by the woody shrub *Buddleja glomerata* that grows on steep slopes and on the crest of Salpeterkop with gradients of 50° to 58° and covers 20 -65% of the area (Brown and Bezuidenhout 2006, Figure 2.17, Figure 2.5). *Themeda triandra* is the dominate grass species and covers 10% to 60% of this vegetation unit. Dense stands of the succulent invader, *Opuntia ficus-indica*, are dispersed by baboons (*Papio ursinus*) across Salpeterkop (Brown and Bezuidenhout 2006).

Figure 2.17. *Themeda triandra* grasses interspersed with *Buddleja glomerata* shrubs on the slopes of Salpeterkop. Image courtesy of T. Kuiper.

Mammalian fauna

Prior to the proclamation and establishment of MZNP in 1937, the park was a series of privately owned, sheep (*Ovis aries*) and Boer goat (*Capra aegargus hircus*) farms (Van der Walt 1980). The vast majority of the indigenous large mammalian fauna had been extirpated by the early farmers but a number of small to medium-sized antelope species were present when MZNP was established (Van der Walt 1980). The species that were already present were kudu, mountain reedbuck (*Redunca fulvorufula*), grey rhebok (*Pelea capreolus*), grey duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*) and klipspringer (*Oreotragus oreatagus*, Van der Walt 1980). However, following the establishment of MZNP, 16 large mammal species were re-introduced in accordance with the SANParks policy of restoring the biodiversity that once occurred in the park (see appendix 1 for a full mammal list, Spies 2016). Blesbok (*Damaliscus pygargus phillipsi*), black wildebeest (*Connochaetes gnou*), eland (*Tragelaphus oryx*) and Ostrich (*Struthio camelus*) were all re-introduced in the 1950s and 1960s (Van der Walt 1980). Buffalo (*Syncerus caffer*) were re-introduced in 1998, followed by black rhinoceros (*Diceros bicornis bicornis*) and gemsbok (*Oryx gazella*) in 2002 (Spies 2016).

Caracal (*Caracal caracal*) were the dominant predators in MZNP until 2007, when four cheetahs (*Acinonyx jubatus*) were re-introduced from Samara Private Game Reserve and De Wildt Cheetah and Wildlife Centre. Three brown hyaenas (*Hyaena brunnea*) were re-introduced in 2008 from Mafunyane Game Reserve in the North-West Province, South Africa (Spies 2016). Three lions (*Panthera leo*), consisting of two males from Welgevoden Game Reserve in the Limpopo Province and a single female from the Nyathi section of Addo Elephant National Park were re-introduced into MZNP in April 2013 (Craig Williams, Senior Section Ranger of MZNP, pers. comm.). However, in April 2014, a park management decision was made to relocate the lioness to the Karoo National Park outside Beaufort West (Megan Taplin, Park Manager of MZNP, pers. comm.). The decision to relocate the lioness was due to her posing a safety risk to visitors, as she often chased small cars, jumping on them or biting tyres and mirrors. The continued growth of the herbivore populations has allowed the restoration of the carnivore guild back into MZNP (Gaylard *et al.* 2008, Spies 2016). Despite the re-introduction of the carnivores, herbivore populations still require regular offtakes to prevent overexploitation of resources (Table 2.1, Spies 2016). Annual aerial censuses are conducted by helicopter using standard SANParks game count techniques (Table 2.1, see Bissett 2007, Spies 2016).

Table 2.1: The total number of mammalian species and Ostriches recorded during the annual censuses conducted in Mountain Zebra National Park from 2002 to 2016 (no data for 2007 and 2014). Informal data from Van der Walt (1980) added for comparison.

		Totals												
Species	**1979***	**2002**	**2003**	**2004**	**2005**	**2006**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2015**	**2016**
black-backed jackal		9	10	9	5	16	16	26	28	14	32	39	31	33
black wildebeest	75	303	301	368	336	416	599	642	674	590	922	968	840	976
blesbok	135	276	226	259	149	219	139	102	168	148	156	215	301	205
buffalo		43	78	83	86	126	118	118	104	111	77	162	109	78
cheetah							4	12	32	26	8	7	5	10
eland	100-120	199	192	209	242	221	205	200	157	217	260	381	387	333
gemsbok	29		15	57	68	73	166	147	161	140	212	228	240	170
grey duiker	30-40	5	5	10	12	11	4	13	8	2	1	5	4	3
grey rhebok	10	81	57	127	109	108	139	52	102	67	58	28	123	137
klipspringer	20-30	14	13	25	9	14	2	3	14	8	3	6	21	19
kudu	11	169	145	191	373	165	292	250	254	249	299	193	221	173
lion												3	2	7
mountain reedbuck	600-700	445	272	699	502	271	592	510	317	164	120	89	81	54
mountain zebra	178	351	297	300	328	354	469	596	621	672	745	769	1191	1011
plains zebra		56	58	28	34	42	34	46	57	60	82	124	0	0
Ostrich	30	104	96	120	119	125	177	113	101	103	105	116	105	91
red hartebeest	42	235	249	282	326	251	355	326	430	341	427	614	546	492
springbok	150-160	881	818	1172	1119	1147	1446	1350	1226	998	1003	887	697	745
steenbok	20-30	18	22	8	11	11	5	3	2	1	3	2	5	1

*Informal census data taken from Van der Walt (1980).

Study animals

Between May and June of 2007, a coalition of two male and two female cheetahs were re-introduced into MZNP. Each animal was assigned a unique alpha-numeric number which followed the form of species/sex/number. For example, CM1, refered to cheetah male one (Bissett 2007). The numbering system is sequential so that each individual could be identified by a unique number and if an individual died or was relocated as part of the National Cheetah Metapopulation that number was not used again (Bissett 2007, Spies 2016, van der Merwe 2016). Even the cubs born on MZNP were numbered sequentially according to this system. In April 2013, three lions, two males and one female were re-introduced into MZNP. The lions were also assigned a unique alpha-numeric number using the same system as for the cheetahs. Throughout this thesis I will refer to the cheetahs and lions according to the alpha-numeric identification system.

Since the initial re-introduction of four cheetahs in 2007, the population quickly rose to over 30 individuals in 2010-2011 (C. Bissett, Senior Researcher, pers. obs.). This number exceeded the carrying capacity of 10 – 15 individual cheetahs proposed for the park (see Lindsey *et al.* 2011) and MZNP management successfully relocated the majority of the individuals to reserves in the Limpopo Province, South Africa during 2010 and 2011 (Welch *et al.* 2015).

At the beginning of my study, the composition of the cheetah groups had changed significantly from the original four individuals. My study was conducted between February 2013 and April 2014 when six individual cheetahs (four adult females and two adult males) remained in MZNP. This period also coincided with the re-introduction of the three lions into MZNP (Appendix 2).

However, not all six cheetahs were the focus of the study, as not all the individuals were present before and after the lion re-introduction. In an attempt to accurately determine the effects of the lion re-introduction on the space use and dietary requirements of the resident cheetahs, only the cheetahs which were present both before and after the lion re-introduction were used as my study animals. Consequently, only the four female cheetahs (CF3, CF4, CF6 and CF35) were included (Appendix 2).

Prior to the lion re-introduction, all four females were immobilized by SANParks veterinarians (using standard techniques, see Swan 2013) as part of routine park management and were fitted with African Wildlife Tracking VHF/GSM collars (Africa Wildlife tracking, Rietondale, South Africa). In addition, all the female cheetahs were chemically contracepted with Deslorelin (Suprelorin®, Peptech Animal Health, Sydney) by a SANParks veterinarian and remained on this contraceptive until 2014 (Welch *et al.* 2015). These same four cheetahs were re-collared at the beginning of 2013 with African Wildlife Tracking VHF/GPS collars. All three lions were also fitted with African Wildlife Tracking VHF/GPS collars at the time of their release in April 2013. All of the large carnivore collars were programmed to download four GPS fixes a day and download times were set to 06:00, 12:00, 18:00 and 00:00. These times were set to determine where the cheetahs and lions were located at the exact same time and to prolong the lifespan of the collars (Megan Taplin, Park Manager of MZNP, pers. comm.).

The data for this study for all four female cheetahs and the three lions were collected from April 2013 to April 2014. This was due to the relocation of the lioness (LF1) to Karoo National Park at the end of April 2014. The data collected by myself and Dr Bissett after the lion re-introduction for the cheetahs is referred to as ‘after’ in the analyses. The initial cheetah research, which was started by Dr Bissett in January 2010 after registering a project with SANParks (Project ID number: BISC864), collected the cheetah data from 2011 to 2013 and this was referred to as ‘before’ the lion re-introduction in the analyses. However, only data from January 2012 to January of 2013 was used to compare the ‘before’ and ‘after’ effects of the lion re-introduction on the four female cheetahs. These data were used because they were more robust than the previous years (2010-2011), having been collected from satellite collars as opposed to VHF collars. Furthermore, this approach allowed for the data sets from the cheetahs and lions to be more comparable.

CHAPTER 3

CHEETAH AND LION SPATIAL ECOLOGY

From left: CF6 watching a passing herd of springbok and LM1 looking at LM2. Images courtesy of C. Bissett.

INTRODUCTION

Habitat selection is central to understanding animal ecology, and as a selective process that may facilitate the co-existence of large carnivores (Pettorelli *et al.* 2008). The influence of interference and exploitation competition are important drivers in the shaping of predator-predator and predator-prey relationships (Hayward and Kerley 2008). Thus, the distribution of large carnivores within a landscape and their social organizations can provide insights to key resource requirements and what the limiting factors are that may restrict population growth (Loveridge *et al.* 2009).

Home range, as described by Burt (1943), is an area traversed by an individual during its normal activities of food gathering, mating and caring for young. However, Packer *et al.* (2013) argued that this definition excluded exploratory movements and is not a true reflection of the area covered within a lifetime. In addition, an animal's spatial utilization often reflects its relationship with resources (accessibility and abundance), water, human interference and mating opportunities (Packer *et al.* 2013). The effects pertaining to each of these factors can provide important information on the ecological requirements of a particular species (Mosser *et al.* 2009).

Marker *et al.* (2008) expressed concern that protected areas needed careful assessment in determining carnivore requirements and whether managers were providing the adequate resources for these species. Loveridge *et al.* (2009) added that the quality, quantity and distribution of resources in African ecosystems show extensive variations in time and space but are heavily influenced by rainfall. Rainfall, in turn, influences herbivore biomass and community structures, carnivore numbers and their respective home range sizes (Loveridge *et al.* 2009). Macdonald (1983) called this phenomenon 'resource dispersion' and argued that the distribution of food was the main factor in determining home range sizes and the locations of animals within the environment. Boyce *et al.* (2003) added that food was not the only influencing factor determining carnivore spatial organization but was a manifestation of separate selection pressures as a result of different social organizations and requirements.

Terrestrial mammals have been found to frequently exhibit distinct intersexual differences in ranging behaviour (Pettorelli *et al.* 2008). Amongst the felids, the distribution of females is dictated by food supply, high-quality habitats to raise young successfully, cover for hunting, water and access to mates (Durant 2000a, Sunquist and Sunquist 2002, Bissett and Bernard 2007). Female reproductive success is tied to their ability to exploit these resources (Boyce *et al.* 2003), whereas male home range requirements are influenced by their ability to access and successfully mate with a number of females without interference from neighbouring males (Boyce *et al.* 2003, Bissett and Bernard 2007).

In most felid species, females often rear their offspring in the absence of males and reproductive success is greatly influenced by accessibility to food (Durant 2000a). Thus, female ranging behaviour is generally configured around the distribution and density of suitable prey and how the prey is distributed in time and space (Durant 2000a, Sunquist and Sunquist 2002). By contrast, male felid spacing patterns are thought to be largely influenced by the distribution of females (Boyce *et al.* 2003), and to a lesser extent by accessibility and distribution to food, refuges and suitable hunting areas (Caro 1994, Loveridge *et al.* 2009). However, different felid species utilize different resources at different times and at different spatial scales (Boyce *et al.* 2003, Packer *et al.* 2013). For example, Funston and Mills (2006) found that lions (*Panthera leo*) in the Kruger National Park decreased their range size and predation on semi-migratory zebra (*Equus quagga*) in drier periods and preyed more heavily on buffalo (*Syncerus caffer*). In addition, Loveridge *et al.* (2009) found that lions in Hwange National Park, Zimbabwe had smaller home ranges as a result of increased availability of resources. However, when resource availability varied, larger home ranges may be needed to facilitate the spatial (patches of high quality habitats) and temporal (grass regeneration and peak calving intervals) variabilities of these resources (Loveridge *et al.* 2009).

It is widely accepted that the home range sizes of different carnivores vary depending on the size of the traversing area, age and specific metabolic needs (see Nilsen *et al.* 2005). In some terrestrial carnivores, males have been found to have large home ranges that can overlap several female home ranges (Pettorelli *et al.* 2008). For example, male pumas (*Puma concolor*) and American black bears (*Ursus americanus*) have significantly larger home ranges than females (Koehler and Pierce 2003, Mills *et al.* 2006). Similarly, Houser *et al.* (2008) found that home ranges of male cheetahs (*Acinonyx jubatus*) encompassed those of several females in Botswana. Pettorelli *et al.* (2008) stated that younger leopards (*Panthera pardus*) had smaller home ranges than older individuals. Nevertheless, carnivores can increase or decrease their home range size while using the same habitat in the exact same way (Owen 2012). For example, Caro (1994) found that cheetahs in the

Serengeti had home ranges which ranged from 37 km^2 to 833 km^2 but this was in order to track the migration of their preferred prey Thomson's gazelle (*Eudorcas thomsonii*).

Several studies have reported extensive variation in cheetah home range sizes in different parts of their geographic range (see Broomhall *et al.* 2003, Mills *et al.* 2004, Bissett and Bernard 2007). For example, cheetahs in Namibia had home ranges as large as 1651 km^2 (Maker *et al.* 2008), while denning females in Kwandwe Private Game Reserve had a home range of just 11 km^2 (Bissett and Bernard 2007). However, there appears to be a relationship between home range size and the amount of suitable space, as compared to total available space (Broomhall *et al.* 2003). Studies that have been conducted where suitable space is restricted have reported smaller home ranges (Purchase and du Toit 2000, Bissett and Bernard 2007). This is further complicated by cheetahs having a variable social system (see Caro 1994). This variation in social organization for different cheetah groups can vary in size, sex, age and number of individuals resulting in different spatial requirements (Broomhall *et al.* 2003, Bissett and Bernard 2007). Furthermore, female cheetahs tend to select thicker habitats for cub rearing, however, age and reproductive status have also been found to influence habitat use (Durant 2000a, Pettorelli *et al.* 2008). For example, Pettorelli *et al.* (2008) explained that young female cheetahs (4 years old and less) were not as confident as older cheetahs and were therefore less likely to extend their home ranges into new habitats. The importance of thicker vegetation is not only limited to cub rearing and also provides a refuge from large carnivores such as lions (Durant 2000a, Durant 2000b).

Variations in lion home range sizes have been reported across their range in Africa, with size variations ranging from < 20 km^2 to > 2000 km^2 (van Orsdol *et al.* 1985, Stander 1991, Power 2002, Funston and Mills 2005, Loveridge *et al.* 2009). Lions are the most social of the family Felidae and live in fusion-fission groups called prides (Schaller 1972, Sunquist and Sunquist 2002). Lion pride sizes have been found to vary considerably from two to 35 individuals (see van Orsdol *et al.* 1985) and the factors explaining such a range are thought to be driven by maintaining access to desirable habitats and cub defense against intruding male lions (Funston *et al.* 2003, Loveridge *et al.* 2009). Prides of lionesses (which are often related) defend a permanent home range and can persist for a number of generations, while males defend access to these females (Schaller 1972). Lion home ranges vary in response to the location conditions and are influenced by food, water and den site availability (Loveridge *et al.* 2009, Mosser *et al.* 2009). Packer and

Pusey (1997) stated that when lion prides cannot defend their home ranges, they cannot move elsewhere and often perish.

The continued effects of habitat fragmentation has restricted many large carnivores to protected conservation areas across Africa (Packer *et al.* 2013). In South Africa, large carnivores have been re-introduced into a number of national and private reserves, which are enclosed by predator-proof fences (Hayward *et al.* 2007b, Packer *et al.* 2013). The restriction of large carnivores within enclosed reserves can influence how these carnivores interact and utilize the available space and resources (Packer *et al.* 2013). Carnivores competing within an enclosed guild are often competing for similar prey species and the same number of resources (Packer *et al.* 2013). Thus, interference competition amongst these carnivores can result in the avoidance or exclusion of smaller competitors from areas with higher densities of larger competitors (Darnell *et al.* 2014).

Cheetahs are known to be negatively affected by interactions with larger competitors, such as lions, through kleptoparasitism of kills or direct mortalities (Durant 2000a, Bissett and Bernard 2007). In an attempt to minimize encounters with larger carnivores, cheetahs have been found to shift their home ranges away from potential high risk areas (see Caro 1994, Durant 2000a). Darnell *et al.* (2014) found that the effects of inter-guild carnivore competition can restrict spatial distributions, habitat use and access to prey resulting in an increase of smaller guild member mortalities. Due to the confinement of large carnivores, coupled with their abilities to cover vast distances, they may be forced to interact more frequently, increasing the effects of interference competition (Packer *et al.* 2013, Darnell *et al.* 2014).

An understanding of how carnivores respond to spatial and temporal variations because of higher rates of interference competition is thus vital for their long term conservation, particularly within enclosed reserves (Boyce *et al.* 2003, Packer *et al.* 2013). The aim of this chapter was to determine and compare the habitat selection and space use of resident cheetahs in Mountain Zebra National Park, before and after a lion re-introduction. In addition, I hypothesized that the re-introduction of lions would decrease the overall home range sizes of the resident cheetahs. I further hypothesized that the cheetahs would be restricted or excluded to resource poor habitats within MZNP after the lion re-introduction.

METHODS

Data collection

All the lions and cheetahs re-introduced to Mountain Zebra National Park (MZNP) were followed via satellite tracking (see Chapter 2) by accessing the African Wildlife Tracking (AWT, Rietondale, Pretoria, South Africa) website and downloading the data remotely (Welch *et al.* 2015). However, when field work was conducted, individual animals were also located daily from February 2013 to April 2014 via radio-telemetry using a Telonics RA-23 receiver and Telonics RA-2A directional antenna (Telonics, Mesa, Arizona, United States of America) and their positions were recorded using a handheld global positioning system (GPS; Garmin GPSMap 62s). The monitoring of individual study animals outside of the programmed GPS download times increased the resolution of the spatial data (i.e. more GPS locations). Multiple GPS locations (hereafter referred to as fixes) per day present autocorrelation problems and one location per day per animal is deemed sufficient for statistical independence of observations (Gehrt and Fritzell 1998, Mizutani and Jewell 1998, Broomhall *et al.* 2003, Tambling *et al.* 2009). However, all GPS fixes were used in this study to determine home range sizes of the collared large carnivores within the park. Hebblewhite and Haydon (2010) stated that in order to better understand how animals utilize and move within their environment, particularly at fine-scale levels, an increase in the number of GPS fixes is needed.

Home range estimates

White and Garrott (1990) explained that an animal's home range and core area, which is utilized more intensively, can be determined by using an accumulation of 95% and 50% of their GPS fixes respectively. The extent of the core areas are not only important as indicators of areas of intense usage, but also for identifying critical habitats and habitat requirements within the environment for the species (Samuel *et al.* 1985).

The fixed kernel utilization distribution (UD) method uses probability density estimations and calculates home ranges by using the relative amount of time that an animal spends within the different areas of its range (Worton 1989). The 50% and 95% UD probabilities were selected for my study because they are considered to be the most robust estimators for determining an animal's home range and exclude unutilized outlying areas (Mizutani and Jewell 1998, Jhala *et al.* 2009b, Rodgers and Kie 2011, Darnell *et al.* 2014).

The home ranges and core areas of the cheetahs and lions re-introduced to MZNP were determined using a bivariate normal fixed-kernel estimator in Geospatial Modeling Environment (v1.5; H.L. Beyer, Spatial Ecology, LLC), with smoothing factors calculated using a diagonal plug-in in R language (v3.0.1, R Development Core Team, 2014, Darnell *et al.* 2014). The kernel density layers were obtained by running the Geospatial Modeling Environment to obtain isopleth polygons of 95% for the home ranges and 50% for the core areas (Darnell *et al.* 2014). The UD method, explained by Seaman and Powell (1996), assigns a probability density (kernel) to each GPS location which is placed into a rectangular grid. A density estimate is produced for each grid intersection for all overlapping kernels. By using the density estimates from each intersection, a kernel density estimator is calculated across the entire grid (Seaman and Powell 1996). The density estimates will be higher in areas with higher concentrations of fixes and lower in areas with a lower number of fixes. The accumulations of kernels at the grid intersections allow for the creation of contour lines or isopleths, which in turn allow for home range estimates to be made (Seaman and Powell 1996, Darnell *et al.* 2014). Where necessary, the UDs were clipped to exclude regions that fell outside the park boundaries and the respective areas were recalculated (Bissett and Bernard 2007, Welch *et al.* 2015). The 50% UD and 95% UD were calculated for the female cheetahs (n = 4) before the lions were re-introduced; and for the same female cheetahs (n = 4) after the lion re-introduction. The same UD's were also calculated for the male lions and the lioness.

Home range overlap

Home range overlap was determined between each pair-wise combination of all individual cheetahs. Furthermore, home range overlap was determined for the 50% UD between cheetahs and the lions.

A percentage overlap for two individuals (A and B) was calculated, using the equation from Poole (1995):

% overlap =100 x 2AB / (A+B)

Where A and B signify home range areas and AB represents the area common to both animals (Poole 1995, Welch *et al.* 2015).

Habitat use

The vegetation map of MZNP (Chapter 2) was used to determine habitat availability, defined as the proportion of each home range covered by each vegetation unit (Creel & Creel 2002). Using ArcMap 10.2 (ESRI, Redlands, California, USA), observed habitat use was calculated as the proportion of GPS fixes for each cheetah that fell into each vegetation unit within a particular cheetah's home range. Expected habitat use, assuming habitat use is random, was calculated by multiplying the total number of fixes by the percentage of each vegetation unit occurring in the 95% UD for each individual cheetah and lion. To test if cheetahs and lions used certain habitats in proportion to its availibilty or not, observed habitat use was compared to expected habitat use using chi-square goodness-of-fit tests in R language (version 3.0.1, R Development Core Team, 2014).

Shrub cover

The usage of shrub cover by the cheetahs and lions in MZNP was determined by using a functional vegetative shrub cover map created by Welch *et al.* (2015). Aerial photographs and existing botanical maps were used to classify the vegetation into a categorical scale of 1-6, which represented increasing densities of vegetation within MZNP (Welch *et al.* 2015). Welch *et al.* (2015), defined the categories as follows:

Category 1 represented an area covering only 1.6% and was characterized by bare ground with minimal vegetation cover. Category 2 covered the largest area of MZNP (49.9%) and was characterized by old agricultural lands and short grassland. Category 3 covered an area of 16.3% and was characterized by tall grasses, shrubs and bush clumps. Category 4 has the second largest covering of the park (20.8%) and is characterized by individual bush clumps. Category 5 covers 8.9% of the park and is characterized by dense bush clumps with open areas in between. Category 6 only covers 2.2% of the park and is characterized by dense riverine bush with very few open areas (for further examples of shrub covers see Welch *et al.* 2015).

Proximities

The distances (m) from the lions of each GPS fix for the cheetahs in the 95% and 50% UDs were calculated in ArcMap 10.2 using the near feature (Welch *et al.* 2015). These fixes were used to calculate the mean distance (m) for each cheetah fix from the lion positions.

RESULTS

Home range and core area estimates

The adult females CF3 and CF35 had the largest 95% UD (183km^2 and 182km^2 respectively) before the lions were re-introduced. These home ranges covered more than 85% of the park. CF6 had the smallest 95% UD (142km^2) before the lion re-introduction (Table 3.1).

Following the lion re-introduction, CF3 and CF35 still had the largest 95% UD (182km^2 and 167km^2) of the resident cheetahs and utilized more than two-thirds of the park (Table 3.1). CF4 and CF6 had the smallest 95% UD's (139km^2 and 141km^2) after the lions were re-introduced. Interestingly, CF4 experienced the largest 95% UD reduction of all the cheetahs and her home range contracted by 18% after the lions were re-introduced (Table 3.1).

Table 3.1: Home range and core area sizes of cheetahs before and after the lion re-introduction to MZNP. The percentage of the reserve used by individual animals before and after the re-introduction is also shown. Sample size refers to the number of GPS fixes used to calculate the home ranges.

			Area (km^2)				**% of MZNP**			
	Sample size		**95%**		**50%**		**95%**		**50%**	
Animal ID	**Before**	**After**	**Before**	**After**	**Before**	**After**	**Before**	**After**	**Before**	**After**
CF3	1774	734	183	182	54	53	87	87	26	25
CF4	1963	1486	176	139	53	45	84	66	25	21
CF6	1513	1461	142	141	40	36	68	67	19	17
CF35	797	1413	182	167	67	46	87	80	32	22
LM1 and LM2		1423		105		36		50		17
LF1		1552		156		50		74		24

Home range overlap

The home range overlap for the 95% and 50% UD's of the female cheetahs was high before the lion re-introduction (Tables 3.2 and 3.3).

Table 3.2: The 95% UD overlap of the cheetah females prior to the lion re-introduction in MZNP.

	CF3	**CF4**	**CF6**	**CF35**
CF3	-	85.4	76.1	86.9
CF4		-	74.9	85.2
CF6			-	75.9
CF35				-

The mean cheetah overlap amongst individuals at the 95% UD was just under two-thirds of their ranges (Table 3.2). The home ranges of the four female cheetahs spanned the vast majority of MZNP (Figure 3.1A). The overlap at the 95% UD revealed that CF3 and CF4 overlapped more extensively than with CF6. However, CF6 was the daughter of CF3 and avoidance should be expected (Table 3.2, Figure 3.1A).

Table 3.3: The 50% UD overlap of the cheetah females prior to the lion re-introduction in MZNP.

	CF3	**CF4**	**CF6**	**CF35**
CF3	-	25.4	21.8	28.4
CF4		-	21.7	28.2
CF6			-	23.8
CF35				-

The mean overlap amongst individual cheetahs at the 50% UD was a fifth of their respective ranges. Despite this reduction in overlap size, the female cheetahs still shared roughly 25% of their UD's (Table 3.3, Figure 3.1B). CF35 had the greatest 50% UD overlap with CF3 and CF4 (Figure 3.2B). While CF6 had the lowest overlapping 50% UD with the other three females (Table 3.3, Figure 3.1B). Interestingly, despite the variations in 50% UD, the female cheetahs' core areas were situated in the northern, central and eastern sections of MZNP (Figure 3.1B).

Table 3.4: The 95% UD overlap of the cheetah females and lions after the lion re-introduction in MZNP.

	CF3	**CF4**	**CF6**	**CF35**	**LM1 and LM2**	**LF1**
CF3	-	75.04	75.7	82.9	63.4	80
CF4		-	66.6	72.2	56.9	70
CF6			-	72.8	57.3	70.5
CF35				-	61.4	76.8
LM1 and LM2					-	59.7
LF1						-

Following the re-introduction of the lions, the 95% UD's of the four female cheetahs overlapped across the center of the park (Table 3.4, Figure 3.3A). CF35 (Figure 3.6) still had the greatest overlap with CF3 (Figure 3.3) and CF4 (Figure 3.4), while CF6 (Figure 3.5) had the lowest overlapping 95% UD with the other female cheetahs (Figure 3.2A). Despite the decrease in home range overlap compared to before the lion re-introduction, all the female cheetahs overlapped by more than two-thirds of the park (Table 3.4). Interestingly, all the female cheetahs had a greater overlap with LF1 than with LM1 and LM2. However, LM1and LM2 and LF1 overlapped by nearly 60% in their home ranges (Figure 3.2B).

Table 3.5: The 50% UD overlap of the cheetah females and lions after the lion re-introduction in MZNP.

	CF3	**CF4**	**CF6**	**CF35**	**LM1 and LM2**	**LF1**
CF3	-	23.1	20	23.4	20.4	24.4
CF4		-	19	21.7	19.1	22.5
CF6			-	19.2	17.1	19.9
CF35				-	19.2	22.8
LM1 and LM2					-	19.9
LF1						-

After the re-introduction of lions, the female cheetahs overlapped by roughly 20% of their 50% UD's (Table 3.5, Figure 3.2B). CF35 (Figure 3.6) and CF6 (Figure 3.5) still had the highest and lowest overlap amongst the cheetahs respectively. All the female cheetahs had a higher overlap with LF1 than with the male lions at the core area level (Figures 3.3B, 3.7). However, all the female cheetahs and lions 50% UD's were centered in the middle of MZNP (Figure 3.2B).

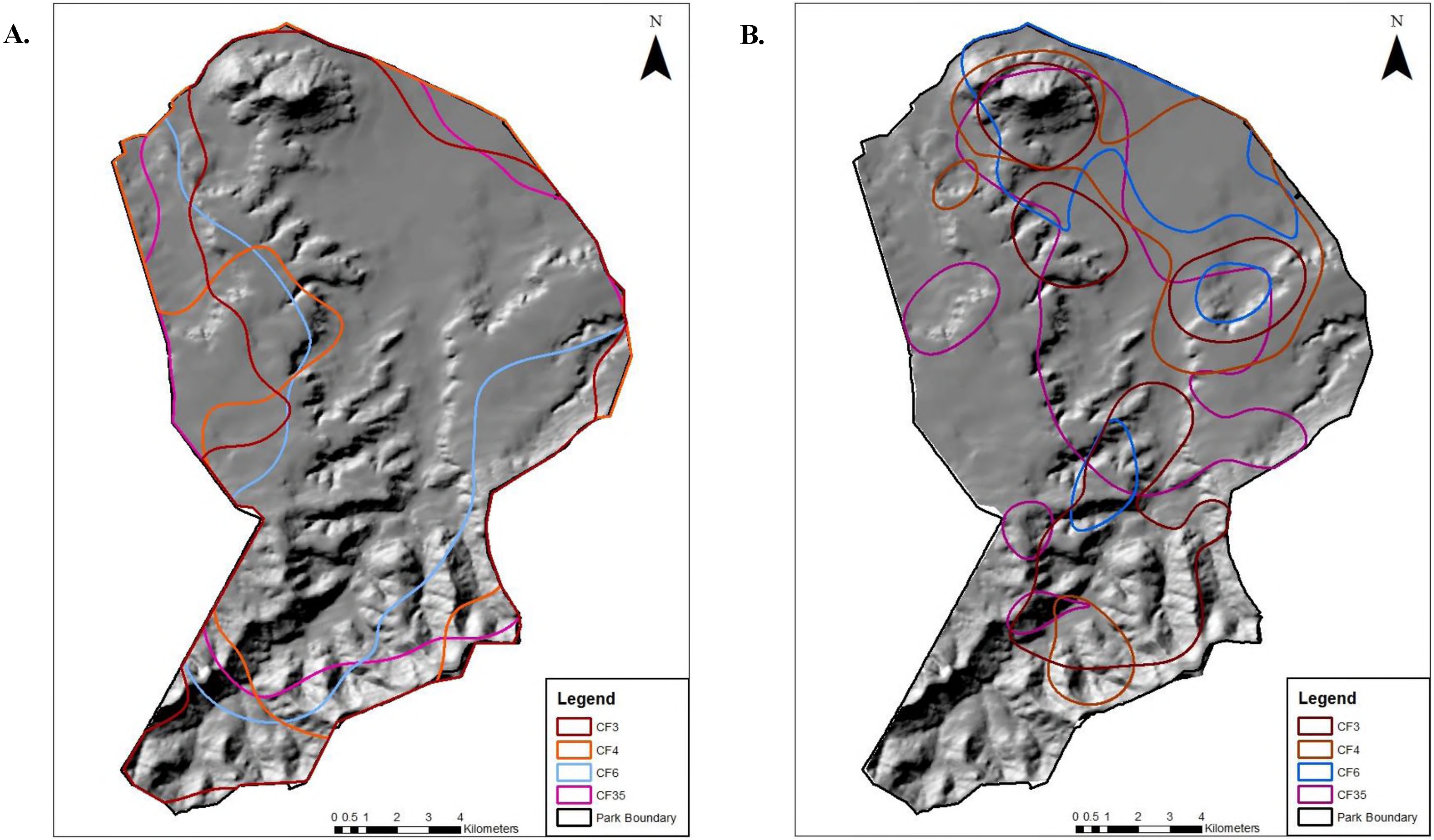


Figure 3.1. The home ranges and core areas of the four female cheetahs before the re-introduction of lions into MZNP. Map A is the 95% UD or home range and Map B is the 50% UD or core area (ArcGIS 10.2; map units: decimal degrees; not projected).

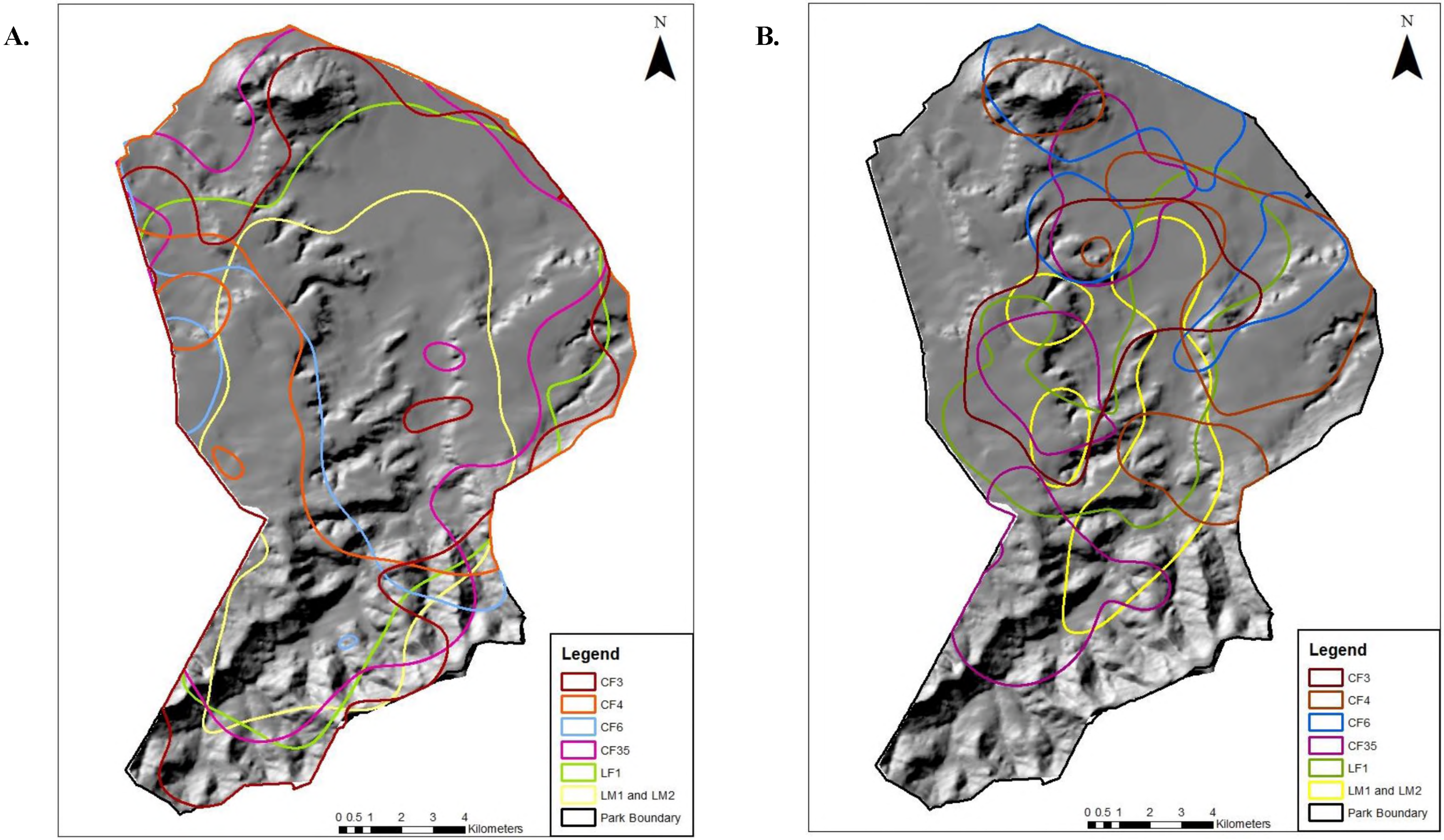


Figure 3.2. The home ranges of the four cheetahs and the three lions, after the re-introduction of lions into MZNP. Map A is the 95% UD or home range and Map B is the 50% UD or core area (ArcGIS 10.2; map units: decimal degrees; not projected).

Individual home ranges

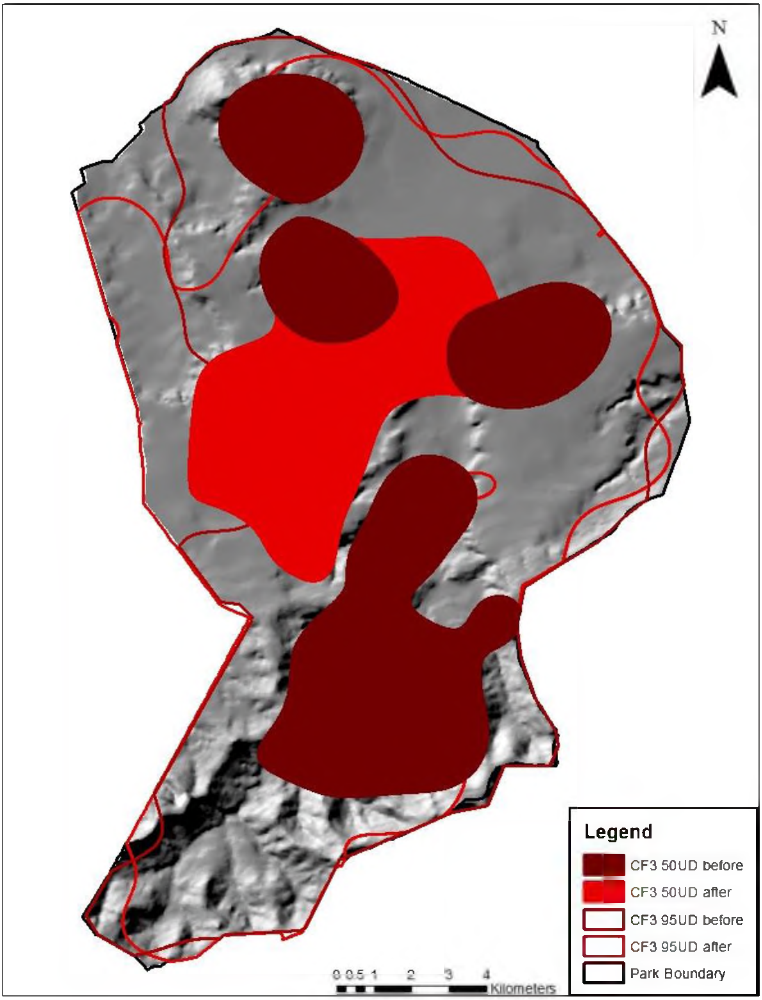


Figure 3.3. The home ranges and core areas of CF3 before and after the re-introduction of lions into MZNP.

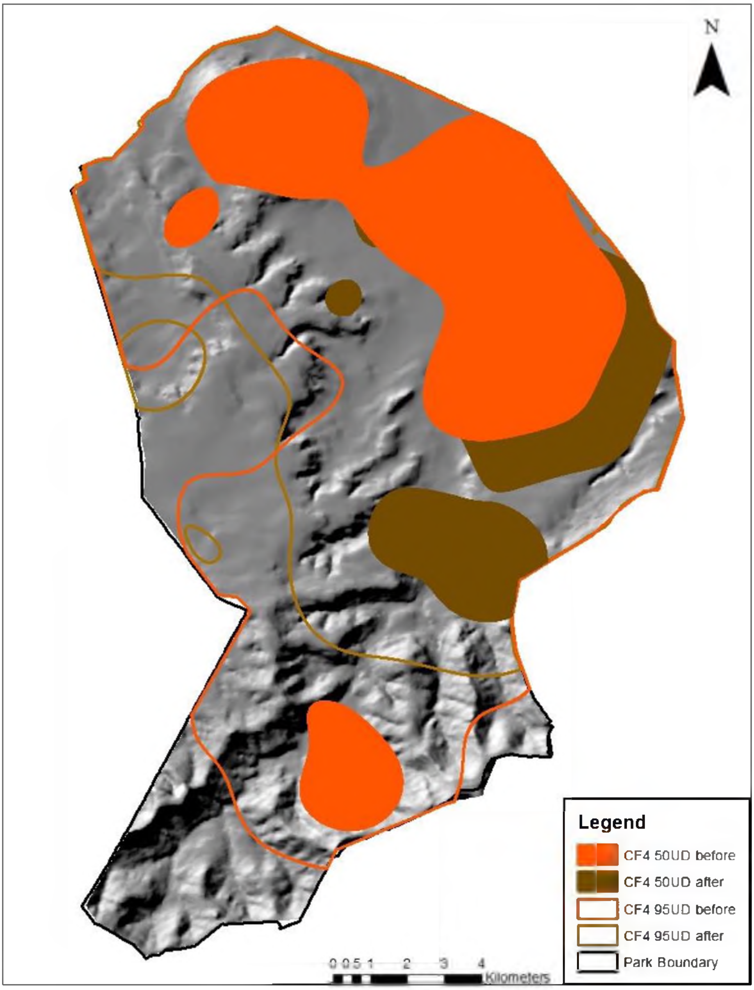


Figure 3.4. The home ranges and core areas of CF4 before and after the lion re-introduction into MZNP.

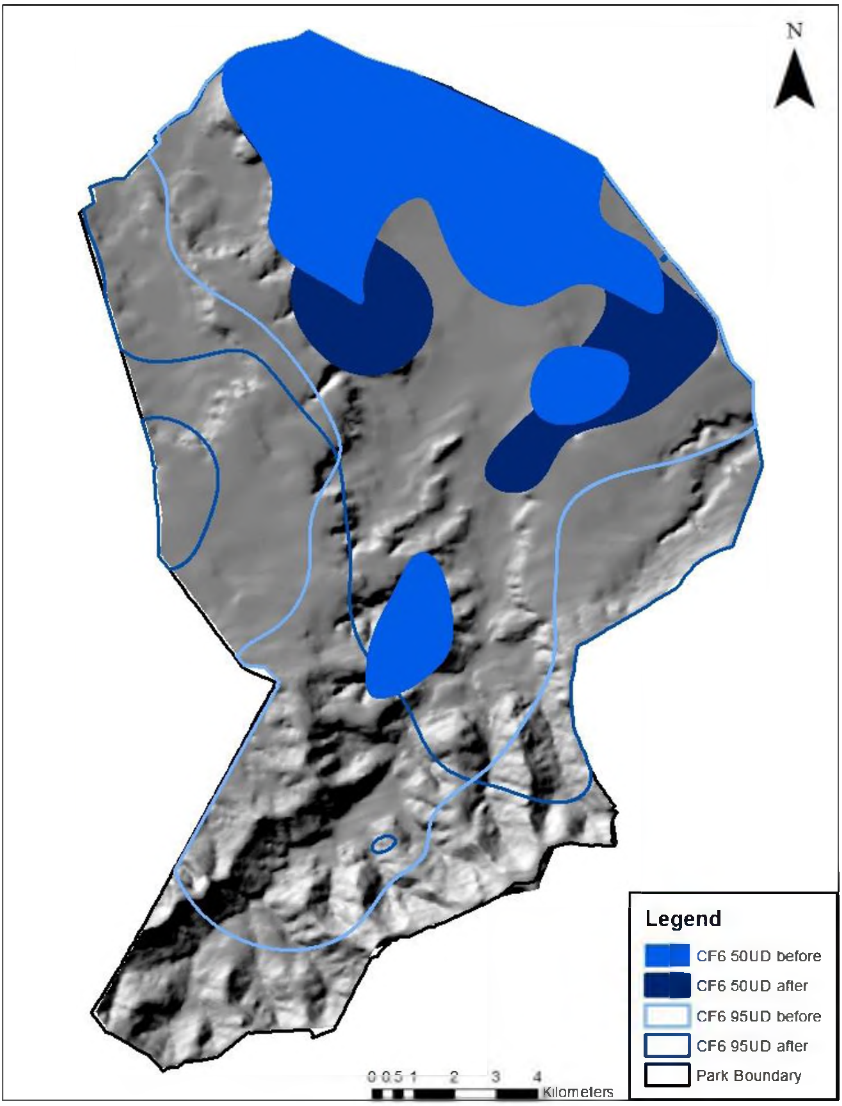


Figure 3.5. The home ranges and core areas of CF6 before and after the re-introduction of lions into MZNP.

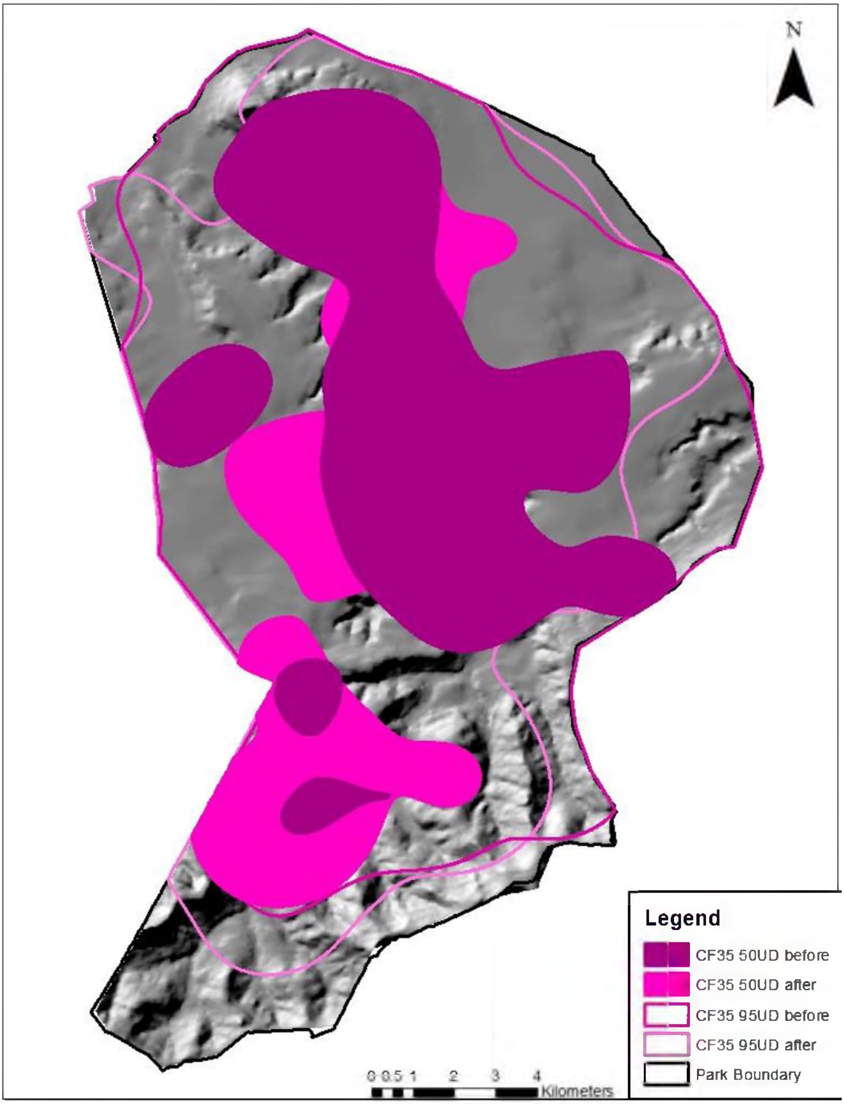


Figure 3.6. The home ranges and core areas of CF35 before and after the re-introduction of lions into MZNP.

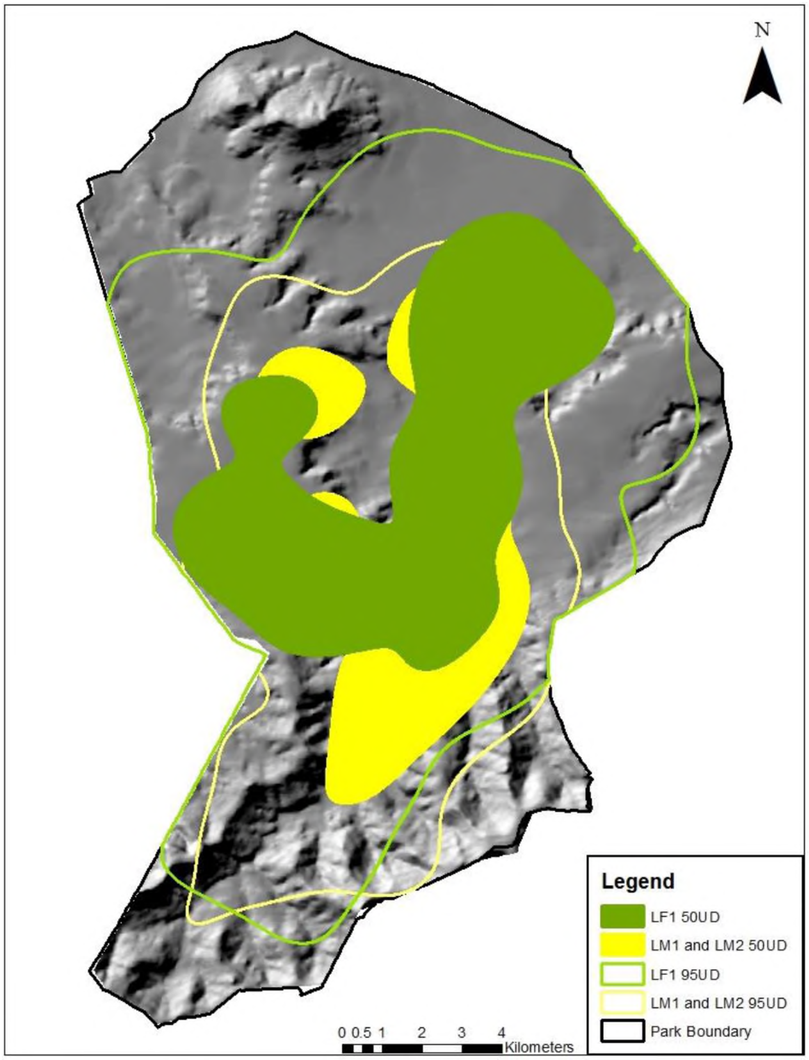


Figure 3.7. The home ranges and core areas of the male lions (LM1 and LM2) and the lioness (LF1) following their re-introduction into MZNP.

Habitat use

95% UD before the lion re-introduction

CF3's home range was characterized by four main vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Aristida diffusa - Searsia longispina* shrubland, *Merxmuellera disticha - Euryops annuus* shrubland, *Searsia lucida - Searsia erosa* shrubland) which made up 68.1% of her home range (Table 3.6). Within this home range, CF3 did not use all available vegetation units relative to their availability (χ^2=132.16, df=11, p<0.05) but showed a selection for *Merxmuellera disticha - Euryops annuus* shrubland and *Themeda triandra - Buddleja glomerata* shrubland (Table 3.7) and under utilized *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland.

CF4's home range was characterized by five main vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Pentzia globosa - Eragrostis obtusa* shrubland, *Aristida diffusa - Searsia longispina* shrubland, *Merxmuellera disticha - Euryops annuus* shrubland, *Searsia lucida - Searsia erosa* shrubland) which made up 79.4% of her home range (Table 3.6). Within this home range, CF4 did not use all the vegetation units relative to their availability (χ^2=95.20, df=10, p<0.05) but utilized *Merxmuellera disticha - Euryops annuus* shrubland and *Searsia lucida - Searsia erosa* shrubland and avoided *Aristida junciformes - Themeda triandra* grassland (Table 3.7).

The home range of CF6 was characterized by four vegetation units (*Pentzia globosa - Eragrostis obtusa* shrubland, *Aristida diffusa - Searsia longispina* shrubland, *Vachellia karroo - Lycium oxycarpum* woodland and *Rhigozum obuvatum - Searsia lucida* shrubland) and this made up 75.7% of the home range used (Table 3.6). CF6 showed a preference for *Pentzia globosa - Eragrostis obtusa* shrubland and *Searsia lucida - Searsia erosa* shrubland and under utilized *Aristida junciformes - Themeda triandra* grassland (χ^2=66.78, df=11, p<0.05; Table 3.7).

The home range of CF35 was characterized by three vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Aristida diffusa - Searsia longispina* shrubland and *Pentzia globosa - Eragrostis obtusa* shrubland) which comprised 62.7% (Table 3.6). CF35, like the other females, did not use the vegetation units relative to their availability but selected *Vachellia karroo - Lycium oxycarpum* woodland and *Aristida diffusa - Searsia longispina* shrubland (χ^2=142.68, df=10, p<0.05) and under utilized *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland and *Merxmuellera disticha - Euryops annuus* shrubland relative to its availability (Table 3.7).

Table 3.6: Home range (95% UD) characteristics for the individual cheetahs before the lion re-introduction.

	Cheetahs			
	CF3	**CF4**	**CF6**	**CF35**
Characteristics				
HR size (km²)	183	176	142	182
Vegetation units (%)				
Vc-Lo	13.1	29.6	18.6	26.3
Vc-Sp	4.5	1.4	1.5	1.5
Ad-Sl	24.3	12.4	18.3	22.9
Aj-Tt	2.3	3	0.2	4.7
Cp-Ec	4.2	3.2	0.6	7.3
Es-Er	2.1	4.4	6.7	5.3
Md-Ea	17.3	8.5	5.6	8.2
Md-Sc	1	0	0.1	0.1
Pg-Eo	6.8	22.2	27.2	13.5
Ro-Sl	1	3.7	11.7	3.5
Sl-Se	13.3	6.7	6.3	5.3
Tt-Bg	10.1	4.7	3.3	1.3

The vegetation units are described in Chapter 2: Vk-Lo = *Vachellia karroo - Lycium oxycarpum*; Vk-Sp = *Vachellia karroo - Searsia pyriodes*; Ab-Sl = *Aristida diffusa - Searsia longispina*; Aj-Tt = *Aristida junciformes - Themeda triandra*; Cp-Ec = *Cymbopogon plurinodis - Eragrostis chlomorelas*; Es-Er = *Enneapogon scoparius - Ehretia rigida*; Md-Ea = *Merxmuellera disticha - Euryops annuus*; Md-Sc = *Merxmuellera disticha - Selago corymbosa*; Pg-Eo = *Pentzia globosa - Eragrostis obtusa* shrubland; Ro-Sl = *Rhigozum obuvatum - Searsia lucida*; Sl-Se = *Searsia lucida - Searsia erosa*; Tt-Bg = *Themeda triandra - Buddleja glomerata*.

Table 3.7: The vegetation units used by the cheetahs before the re-introduction of lions at 95% UD. The observed figure is the actual number of locations per vegetation unit and the expected figure was calculated by multiplying the total number of locations by the percentage of each vegetation unit occurring in the 95% UD.

Animal ID	**Vk-Lo**	**Vk-Sp**	**Ad-Sl**	**Aj-Tt**	**Cp-Ec**	**Es-Er**	**Md-Ea**	**Md-Sc**	**Pg-Eo**	**Ro-Sl**	**Sl-Se**	**Tt-Bg**	**χ^2 Results**
CF3													
Observed	227	78	423	40	73	37	301	17	119	17	231	175	$\chi2=132.16, df=11, p<0.05$
Expected	256	67	421	32	209	30	263	12	115	13	192	127	
CF4													
Observed	574	28	240	58	63	86	166		432	72	131	92	$\chi2=95.20, df=10, p<0.05$
Expected	526	20	326	91	60	80	103		473	64	101	98	
CF6													
Observed	274	22	269	3	9	98	82	1	400	172	92	49	$\chi2=66.78, df=11, p<0.05$
Expected	297	13	273	32	10	90	54	1	379	205	66	52	
CF35													
Observed	208	12	181	37	58	42	65		107	28	42	10	$\chi2=142.67, df=10, p<0.05$
Expected	159	14	134	16	107	31	129		97	21	78	5	

The areas left blank are when the particular vegetation unit did not occur within a particular animals 95% UD.

The vegetation unit are described in Chapter 2: Vk-Lo = *Vachellia karroo - Lycium oxycarpum*; Vk-Sp = *Vachellia karroo - Searsia pyriodes*; Ad-Sl = *Aristida diffusa - Searsia longispina*; Aj-Tt = *Aristida junciformes - Themeda triandra*; Cp-Ec = *Cymbopogon plurinodis - Eragrostis chlomorelas*; Es-Er = *Enneapogon scoparius - Ehretia rigida*; Md-Ea = *Merxmuellera disticha - Euryops annuus*; Md-Sc = *Merxmuellera disticha - Selago corymbosa*; Pg-Eo = *Pentzia globosa - Eragrostis obtusa* shrubland; Ro-Sl = *Rhigozum obuvatum - Searsia lucida*; Sl-Se = *Searsia lucida - Searsia erosa*; Tt-Bg = *Themeda triandra - Buddleja glomerata*

95% UD after the lion re-introduction

CF3's home range was characterized by three vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Aristida diffusa - Searsia longispina* shrubland and *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland) and this made up 73.6% of her home range (Table 3.8). CF3 did not use the vegetation units relative to their availabilty but selected *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland and *Vachellia karroo - Lycium oxycarpum* woodland (χ^2= 317.97,df=11,p<0.05) and under utilized *Themeda triandra - Buddleja glomerata* shrubland relative to its availability (Table 3.9).

The vegetation units characterizing the home range of CF4 was dominated by *Pentzia globosa - Eragrostis obtusa* shrubland, *Vachellia karroo - Lycium oxycarpum* woodland, *Aristida diffusa - Searsia longispina* shrubland and *Aristida junciformes - Themeda triandra* grassland and this made up 80.5% of the home range (Table 3.8). CF4 utilized *Aristida diffusa - Searsia longispina* shrubland and *Aristida junciformes - Themeda triandra* grassland (Table 3.9) and under utilized *Merxmuellera disticha - Euryops annuus* shrubland relative to their availabilities (χ^2= 126.66,df=10,p<0.05).

The home range of CF6 was characterized by four main vegetation units (*Pentzia globosa - Eragrostis obtusa* shrubland, *Vachellia karroo - Lycium oxycarpum* woodland, *Aristida diffusa - Searsia longispina* shrubland and *Rhigozum obuvatum - Searsia lucida* shrubland) which made up 81.4% of the home range (Table 3.8). CF6 did not use the vegetation units relative to their availability but preferred *Rhigozum obuvatum - Searsia lucida* shrubland, and under utilized *Merxmuellera disticha - Euryops annuus* shrubland and *Searsia lucida - Searsia erosa* shrubland relative to its availability within MZNP (χ^2= 79.91,df=10,p<0.05; Table 3.9).

CF35's home range was characterized by five vegetation units (*Merxmuellera disticha - Euryops annuus* shrubland, *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland, *Vachellia karroo - Lycium oxycarpum* woodland, *Aristida diffusa - Searsia longispina* shrubland and *Searsia lucida - Searsia erosa* shrubland), which made up 81.1% of the home range (Table 3.8). CF35 did not utilize the vegetation units relative to their availability but utilized more *Merxmuellera disticha - Euryops annuus* shrubland and *Searsia lucida - Searsia erosa* shrubland (Table 3.9) and under utilized *Aristida junciformes - Themeda triandra* grassland reltative to their availabilities (χ^2= 94.99,df=10,p<0.05).

The home range of LM1 and LM2 was characterized by four vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland, *Vachellia karroo - Searsia pyriodes* woodland and *Themeda triandra - Buddleja glomerata* shrubland) which made up 79.2% of the home range (Table 3.8). The male lions did not use the vegetation units relative to their availabilities but utilized more *Vachellia karroo - Searsia pyriodes* woodland (Table 3.9) and under utilized *Aristida diffusa - Searsia longispina* shrubland and *Pentzia globosa - Eragrostis obtusa* shrubland (χ^2= 145.70,df=10,p<0.05).

LF1's home range was characterized by four vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland, *Pentzia globosa - Eragrostis obtusa* shrubland and *Aristida diffusa - Searsia longispina* shrubland) which made up 80.6% of the home range (Table 3.8). LF1, like all the other cheetahs and male lions, did not use the vegetation units relative to their availabilities but utilized more *Aristida diffusa - Searsia longispina* shrubland and *Pentzia globosa - Eragrostis obtusa* shrubland (χ^2= 490.78,df=9,p<0.05) and under utilized *Themeda triandra - Buddleja glomerata* shrubland relative to their availabilities (Table 3.9).

Table 3.8: Home range (95% UD) characteristics for the individual cheetahs and lions after the lion re-introduction to MZNP.

	Animals					
	CF3	**CF4**	**CF6**	**CF35**	**LM1 and LM2**	**LF1**
Characteristics						
HR size (km²)	182	139	141	176	105	156
Vegetation units (%)						
Vc-Lo	18.7	23.8	22	15.9	31.5	34.5
Vc-Sp	2.4	0.5	0.2	1.9	15.7	7.1
Ad-Sl	24	22.7	18.8	13	5.4	10.1
Aj-Tt	0.7	7	4.6	0.3	0.5	1.8
Cp-Ec	30.9	2.9	0.8	17.7	25.2	24.6
Es-Er	0.8	3.7	5.4	3	2.8	0.2
Md-Ea	9.8	1	1.3	21.6	3.4	5.8
Md-Sc	0	0	0	0	0.1	0.1
Pg-Eo	6.1	27.1	24	11.4	4.3	12
Ro-Sl	0.3	2.8	16.6	2	0	0
Sl-Se	5.5	3.1	2.4	12.8	4.3	3.7
Tt-Bg	0.7	5.5	3.9	0.3	6.8	0
Distance (m)						
LM1 and LM2	342.7±330.5	552.4±419.6	874.6±753.5	390.3±315.7	-	219.5±281.1
LF1	304.1±307.9	459.8±422.1	860.6±768.9	382.9±335.4	261.6±241.7	-

Vegetation key see Table 3.6.

Table 3.9: The vegetation units used by the cheetahs and lions after the re-introduction of lions at the 95% UD level. The observed figure is the actual number of locations per vegetation unit and the expected figure was calculated by multiplying the total number of locations by the percentage of each vegetation unit occurring in the 95% UD.

Animal ID	**Vk-Lo**	**Vk- Sp**	**Ab-Sl**	**Aj-Tt**	**Cp-Ec**	**Es-Er**	**Md-Ea**	**Md-Sc**	**Pg-Eo**	**Ro-Sl**	**Sl-Se**	**Tt-Bg**	**χ^2 Results**
CF3													
Observed	135	17	173	5	223	6	71		44	2	40	5	χ2=317.979,df=11,p<0.05
Expected	106	28	175	13	87	13	109	5	48	6	79	53	
CF4													
Observed	347	7	332	102	42	54	14		396	41	46	80	χ2=126.662,df=10,p<0.05
Expected	395	15	246	69	45	60	77		355	49	76	74	
CF6													
Observed	268	2	229	56	10	66	16		292	202	29	47	χ2=79.917,df=10,p<0.05
Expected	245	11	225	27	9	74	44		313	169	55	43	
CF35													
Observed	188	23	154	3	210	36	256		135	24	152	3	χ2=94.993,df=10,p<0.05
Expected	237	21	201	24	161	47	192		145	31	116	8	
LM1 and LM2													
Observed	467	233	80	7	374	42	51	1	63		63	101	χ2=145.70,df=10,p<0.05
Expected	490	168	115	17	369	22	69	1	121		59	50	
LF1													
Observed	526	108	154	27	375	3	89	2	183		56		χ2=490.781,df=9,p<0.05
Expected	503	173	119	17	380	23	71	2	125		60	51	

The areas left blank are when the particular vegetation unit did not occur in a particular animals 95% UD.
Vegetation key see Table 3.6.

50% UD before the lion re-introduction

The core area of CF3 was characterized by four vegetation units (*Aristida diffusa - Searsia longispina* shrubland, *Merxmuellera disticha - Euryops annuus* shrubland, *Searsia lucida - Searsia erosa* shrubland and *Themeda triandra - Buddleja glomerata* shrubland) which made up 76.8% of the core area (Table 3.10). CF3 did not use the vegetation units relative to their availabilties but utilized *Merxmuellera disticha - Euryops annuus* shrubland and *Themeda triandra - Buddleja glomerata* shrubland (Table 3.11) and under utilized *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland (χ^2=192.03,df=10,p<0.05).

CF4's core area was characterized by five vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Pentzia globosa - Eragrostis obtusa* shrubland, *Themeda triandra - Buddleja glomerata* shrubland, *Enneapogon scoparius - Ehretia rigida* shrubland and *Rhigozum obuvatum - Searsia lucida* shrubland) which made up 80.2% (Table 3.10). CF4 did not use the vegetation relative to their availability but utilized *Vachellia karroo - Lycium oxycarpum* woodland (χ^2= 83.54,df=8,p<0.05) and under utilized *Aristida diffusa - Searsia longispina* shrubland (Table 3.11).

The core area utilized by CF6 was characterized by three vegetation units (*Pentzia globosa - Eragrostis obtusa* shrubland, *Rhigozum obuvatum - Searsia lucida* shrubland and *Vachellia karroo - Lycium oxycarpum* woodland) which made up 74.6% (Table 3.10). The vegetation units were not used relative to their availabilty and *Pentzia globosa - Eragrostis obtusa* shrubland was utilized more (χ^2=47.13,df=7,p<0.05) and *Aristida diffusa - Searsia longispina* shrubland was under utilized (Table 3.11).

The core area used by CF35 was characterized by four vegetation units (*Aristida diffusa - Searsia longispina* shrubland, *Vachellia karroo - Lycium oxycarpum* woodland, *Pentzia globosa - Eragrostis obtusa* shrubland and *Enneapogon scoparius - Ehretia rigida* shrubland) which made up 87.7% (Table 3.10). CF35 utilized *Aristida diffusa - Searsia longispina* shrubland and *Vachellia karroo - Lycium oxycarpum* woodland (χ^2=279.69,df=8,p<0.05; Table 3.11) and under utilized *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland, *Merxmuellera disticha - Euryops annuus* shrubland and *Searsia lucida - Searsia erosa* shrubland relative to their availabilities.

Table 3.10: Home range (50% UD) characteristics for the individual cheetahs before the lion re-introduction.

	Cheetahs			
	CF3	**CF4**	**CF6**	**CF35**
Characteristics				
HR size (km²)	54	53	40	46
Vegetation units (%)				
Vc-Lo	9.7	32	15.4	31.3
Vc-Sp	6.4	1.6	0	0
Ad-Sl	29.5	9.6	9.8	31.9
Aj-Tt	1.1	0	0	4.3
Cp-Ec	1.6	0	0.2	2.9
Es-Er	2.5	7.1	8.9	8.3
Md-Ea	16.4	5.1	0	4.6
Md-Sc	0	0	0	0
Pg-Eo	1.1	28.8	40.4	12.2
Ro-Sl	0.8	4.3	18.8	0.4
Sl-Se	15.8	3.4	1.1	2.1
Tt-Bg	15.2	8	5.4	2.1

Vegetation key see Table 3.6.

Table 3.11: The vegetation units used by the cheetahs before the re-introduction of lions at 50% UD. The observed figure is the actual number of locations per vegetation unit and the expected figure was calculated by multiplying the total number of locations by the percentage of each vegetation unit occurring in the 50% UD.

Animal ID	Vk-Lo	Vk-Sp	Ab-Sl	Aj-Tt	Cp-Ec	Es-Er	Md-Ea	Md-Sc	Pg-Eo	Ro-Sl	Sl-Se	Tt-Bg	χ^2 Results
CF3													
Observed	111	73	337	12	18	28	187		13	9	180	173	$\chi2=192.03,df=10,p<0.05$
Expected	153	54	338	9	151	21	137		14	7	132	127	
CF4													
Observed	369	19	111		0	82	59		332	50	39	92	$\chi2=83.54,df=8,p<0.05$
Expected	296	12	197		4	61	36		345	36	36	95	
CF6													
Observed	140		89		2	81			368	171	10	49	$\chi2=47.13,df=7,p<0.05$
Expected	139		140		2	71			297	203	5	52	
CF35													
Observed	151		154	21	14	40	22		59	2	10	10	$\chi2=279.69,df=8,p<0.05$
Expected	87		80	8	56	28	101		54	1	57	4	

The areas left blank are when the particular vegetation unit did not occur in a particular animals 50% UD.
Vegetation key see Table 3.6.

50% UD after the lion re-introduction

The core area utilized by CF3 was characterized by three vegetation units (*Cymbopogon plurinodis - Eragrostis chlomorelas* grassland, *Aristida diffusa - Searsia longispina* shrubland and *Vachellia karroo - Lycium oxycarpum* woodland) which made up 98.5% of the total area (Table 3.12). CF3 did not use the vegetation units relative to their availabilities but utilized *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland (χ^2=129.77,df=3,p<0.05) and under utilized *Merxmuellera disticha - Euryops annuus* shrubland, *Searsia lucida - Searsia erosa* shrubland and *Themeda triandra - Buddleja glomerata* shrubland (Table 3.13). Interestingly, CF3 under utilized all the vegetation units she was utilizing prior to the re-introduction of the lions (Tables 3.9 and 3.10).

CF4's core area was characterized by three vegetation units (*Pentzia globosa - Eragrostis obtusa* shrubland, *Aristida diffusa - Searsia longispina* shrubland and *Vachellia karroo - Lycium oxycarpum* woodland) which made up 75.6% of the total area (Table 3.12). CF4 did not utilize all the vegetation units relative to their availability but utilized *Aristida diffusa - Searsia longispina* shrubland (χ^2=155.1,df=10,p<0.05) and under utilized *Merxmuellera disticha - Euryops annuus* shrubland, *Enneapogon scoparius - Ehretia rigida* shrubland and *Vachellia karroo - Lycium oxycarpum* woodland (Table 3.13). CF4 did not utilize the same vegetation units in her core area following the re-introduction of lions.

The core area utilized by CF6 was characterized by four vegetation units (*Rhigozum obuvatum - Searsia lucida* shrubland, *Pentzia globosa - Eragrostis obtusa* shrubland, *Aristida diffusa - Searsia longispina* shrubland and *Vachellia karroo - Lycium oxycarpum* woodland) which made up 87% of the total area (Table 3.12). The vegetation units were not used relative to their availability and CF6 utilized more *Rhigozum obuvatum - Searsia lucida* shrubland and *Aristida diffusa - Searsia longispina* shrubland (χ^2=50.21,df=6,p<0.05) and under utilized *Searsia lucida - Searsia erosa* shrubland (Table 3.13) relative to their availabilities. There was minimal variation in the vegetation units used by CF6 before and after the lion re-introduction.

CF35's core area was characterized by three vegetation units (*Merxmuellera disticha - Euryops annuus* shrubland, *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland and *Searsia lucida - Searsia erosa* shrubland) which made up 67.5% of the total area (Table 3.12). CF35 did not utilize the vegetation units relative to their availabilities but utilized *Searsia lucida - Searsia erosa* shrubland and *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland (χ^2=

169.15,df=7,p<0.05) and under utilized *Aristida diffusa - Searsia longispina* shrubland and *Vachellia karroo - Lycium oxycarpum* woodland relative to their availabilities (Table 3.13). Interestingly, the vegetation units under utilized by CF35 before the lion re-introduction, were the same units she utilized more after the lions were re-introduced (Tables 3.11 and 3.13).

The core area of LM1 and LM2 was characterized by three vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Vachellia karroo - Searsia pyriodes* woodland and *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland) which made up 89.4% of the total area (Table 3.12). The vegetation units were not used relative to availability and *Vachellia karroo - Searsia pyriodes* woodland was utilized more (χ^2=130.59,df=6,p<0.05) while *Pentzia globosa - Eragrostis obtusa* shrubland was under utilized relative to availability (Table 3.13).

The core area of LF1 was characterized by three vegetation units (*Vachellia karroo - Lycium oxycarpum* woodland, *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland and *Pentzia globosa - Eragrostis obtusa* shrubland) which made up 87.1% of the area (Table 3.12). The vegetation units were not used relative to availability and LF1 utilized *Cymbopogon plurinodis - Eragrostis chlomorelas* grassland and *Pentzia globosa - Eragrostis obtusa* shrubland (χ^2=123.67,df=6,p<0.05), while *Vachellia karroo - Searsia pyriodes* woodland and *Searsia lucida - Searsia erosa* shrubland were under utilized (Table 3.13).

The vegetation units characterizing the core areas of the lions revealed that LF1 was avoiding the areas utilized by LM1 and LM2 (Table 3.13). Interestingly, the female cheetahs also avoided the vegetation units they utilized prior to the lion re-introduction and utilized the habitat units the lions avoided (Tables 3.12 and 3.13).

Table 3.12: Home range (50% UD) characteristics for the individual cheetahs after the lion re-introduction.

	Animals					
	CF3	**CF4**	**CF6**	**CF35**	**LM1 and LM2**	**LF1**
Characteristics						
HR size (km²)	53	45	36	46	36	50
Vegetation units (%)						
Vc-Lo	23.5	17.9	15.2	9.0	41.4	42.9
Vc-SP	0.0	0.2	0.0	2.4	25.9	3.0
Ad-Sl	29.8	26.4	22.1	6.4	5.2	9.1
Aj-Tt	0.0	6.5	0.0	0.0	0.0	0.0
Cp-Ec	45.3	0.9	0.1	17.3	22.1	38.0
Es-Er	0.0	3.1	6.6	4.3	0.0	0.0
Md-Ea	0.0	0.8	0.0	32.0	0.1	0.2
Md-Sc	0.0	0.0	0.0	0.0	0.0	0.0
Pg-Eo	1.5	31.3	23.3	10.4	0.3	6.2
Ro-Sl	0.0	1.6	26.5	0.0	0.0	0.0
Sl-Se	0.0	2.8	0.0	18.2	5.0	0.6
Tt-Bg	0.0	8.5	6.2	0.0	0.0	0.0
Distance (m)						
LM1 and LM2	560.7±431.8	2303.3±1540.0	3957.9±2004.9	1299.4±912.8	-	560.7±431.8
LF1	525.6±525.5	1385.4±1404.8	3016.0±1833.4	2169.4±1500.6	1534.4±1239.3	-

Vegetation key see Table 3.6

Table 3.13: The vegetation units used by the cheetahs and lions after the re-introduction of lions at the 50% UD level. The observed figure is the actual number of locations per vegetation unit and the expected figure was calculated by multiplying the total number of locations by the percentage of each vegetation unit occurring in the 50% UD.

Animal ID	Vk-Lo	Vk-Sp	Ab-Sl	Aj-Tt	Cp-Ec	Es-Er	Md-Ea	Md-Sc	Pg-Eo	Ro-Sl	Sl-Se	Tt-Bg	χ^2 Results
CF3													
Observed	97	0	123	0	187	0	0		6	0	0	0	$\chi2=129.77, df=3, p<0.05$
Expected	55	19	122	3	54	7	50		5	2	48	46	
CF4													
Observed	167	2	246	61	8	29	7		292	15	26	79	$\chi2=155.1, df=10, p<0.05$
Expected	240	9	160	27	4	50	30		279	29	29	76	
CF6													
Observed	115		168		1	50			177	201	0	47	$\chi2=50.21, df=6, p<0.05$
Expected	116		117		1	60			248	169	5	44	
CF35													
Observed	65	17	46		125	31	231		75	0	131	0	$\chi2=169.15, df=7, p<0.05$
Expected	129	10	120		83	43	152		80	1	84	6	
LM1 and LM2													
Observed	317	198	40		169		1		2		38		$\chi2=130.59, df=6, p<0.05$
Expected	323	108	55		231		1		25		21		
LF1													
Observed	345	24	73		306		2		50		5		$\chi2=123.67, df=6, p<0.05$
Expected	339	114	58		244		2		27		22		

The areas left blank are when the particular vegetation unit did not in a particular animals 50% UD.
Vegetation key see Table 3.6.

Shrub cover

95% UD before and after the lion re-introduction

There were no significant differences between the shrub usage of the female cheetahs before and after the lion re-introduction at the 95% UD (χ^2 =31.48,df=23,p>0.05). However, the differences in shrub cover usage could be attributed to the shift in cheetah home range positions following the lion re-introduction. The main cover types utilized by the female cheetahs before the lions were categories 2, 3 and 4, while bare ground and very thick vegetation was generally avoided or not utilized (Table. 3.14). Following the lion re-introduction, there was a slight increase in the use of categories 3 and 4, and the use of category 2 decreased (Table 3.14). The lions utilized category 2 extensively, the male lions utilized category 6 more than the other carnivores (Table 3.14). Both large carnivores generally avoided the bare areas in the park and as the vegetation became thicker, the presence of cheetah decreased in their 95% UDs (Table 3.14).

Table 3.14: The shrub cover used by the female cheetahs and the lions in their 95% UD before and after the lion re-introduction.

	Animals									
	CF3		**CF4**		**CF6**		**CF35**		**LM1 and LM2**	**LF1**
Shrub cover	**Before**	**After**	**Before**	**After**	**Before**	**After**	**Before**	**After**	**After**	**After**
1	1.2	0.2	1.4	0.3	1	0.5	0.3	0.4	3	3.4
2	28.4	28.9	42.3	40.4	31.5	28.8	31.5	33.2	40.1	42.5
3	22.7	25.5	20.3	22.5	19	25.4	21.8	16.1	12.5	11.2
4	34.3	37.6	28.8	29	37.2	37.5	35.5	43.3	16.3	17
5	10.4	7.3	6.7	6.7	10.2	7.2	9	6.2	12.9	17.2
6	2.9	0.6	0.6	1.2	1	0.6	2	0.7	15.2	8.6

Shrub cover explanations – see methods.

50% UD before and after the lion re-introduction

There were significant differences (χ^2=63.71,df=21,$p < 0.05$) in the shrub cover usage of the four cheetah females in the 50 % UD before and after the lion re-introduction (Table 3.15). Categories 2, 3 and 4 were the main cover types in the 50% UD's of the female cheetahs. CF6 and CF35 showed an increase in the usage of categories 2 and 4 after the lion re-introduction (Table 3.15). CF3 increased her usage of category 2 and decreased category 3 before and after the lion re-introduction (Table 3.15). Category 1 was not an important cover type for either of the large carnivore species at the 50% UD level. However, the lions utilized this cover category more than the cheetahs (Table 3.15). Category 2 was by far the most utilized cover type by the cheetahs and lions but it is not surprising considering it covers the largest area of the park. The lions utilized the other cover categories more evenly than the cheetahs and the presence of cheetah decreased as the vegetation cover became thicker (Table 3.15). The near absence of cheetahs from the thickest areas of the park could be a result of the lions utilizing these areas more frequently.

Table 3.15: The shrub cover used by the cheetahs and the lions in their 50% UD before and after the lion re-introduction.

	Animals									
	CF3		CF4		CF6		CF35		LM1 and LM2	LF1
Shrub cover	**Before**	**After**	**Before**	**After**	**Before**	**After**	**Before**	**After**	**After**	**After**
1	1	0	0.6	0.1	1	0.1	0.2	0.5	4.6	5
2	20.8	46.5	44.2	42.3	30.2	25	23.8	29.1	38.6	43.9
3	26.3	15.5	21.7	23.3	23	29.1	24.2	14.6	11	10.5
4	36.4	27.6	28.5	28.3	34.8	40	41.8	51.2	10.4	13.5
5	12.3	6.5	4	5.4	10	5.7	8.5	4.2	12.8	17.5
6	3.3	3.9	1	0.6	0.7	0	1.4	0.4	22.7	9.7

Shrub cover explanations - see methods.

Distance from the lions

There was extensive variations in the mean distances of the female cheetahs from the lions at the 95% UD level (Table 3.8). CF3 had the closest mean distance to LM1 and LM2 and LF1, while CF6 stayed the furthest away from the lions and was nearly always at least one kilometre away. Interestingly, the mean distances from the female cheetahs were further away from LM1 and LM2 than LF1 (Table 3.8). At the core area level (50% UD), CF3 was again, the closest to the lions, while the other female cheetahs varied between 1 200 m to just under 4 000 m away (Table 3.12). Similarly, the mean cheetah distances were further away from LM1 and LM2 than LF1 at the core area level (Table 3.12).

DISCUSSION

Lions can become locally overly abundant, following their re-introductions into enclosed reserves (Hayward *et al.* 2007a). This is due to their resilience to the effects of translocations, and their ability to exploit a wide range of prey through opportunistic predation facilitated by prey naivety (see Hayward and Kerley 2005) to newly introduced large carnivores (Hayward *et al.* 2007b). In addition, lions are competitively dominant carnivores and are more resilient to the re-introduction process than smaller, more threatened species such as cheetahs and African wild dogs (*Lycaon pictus*) (Hayward *et al.* 2007b). Furthermore, the re-introductions of cheetahs have apparently been less successful when dominate carnivores, such as lions, are already present (Hayward *et al.* 2007b). However, the spatial ecology of the female cheetahs in MZNP did not appear to be affected by the lion re-introduction at the park level, even though they did demonstrate some individual variation.

Cheetah home ranges at MZNP varied from 142 km² to 183 km² before the lion re-introduction and from 141 km² to 182 km² after the lion re-introduction. Nevertheless, despite the similarity in cheetah home range sizes, the positions of the individual cheetah's home range sizes shifted in the park following the lion re-introduction. These home range shifts were evident by the utilization of different areas and vegetation units by the individual female cheetahs after the lion re-introduction. For example, CF4 demonstrated a range contraction of 18% following the lion re-introduction. However, the cheetahs' home ranges (95% UD) still overlapped by more than 70%. Bissett (2007) explained that the distribution of suitable habitat for hunting and the hard boundaries of enclosed reserves could result in female cheetah home ranges overlapping. Furthermore, the large home ranges of cheetahs in MZNP could be due to cheetahs moving between 'patches' of preferred cover (Broomhall *et al.* 2003, Marnewick and Somers 2015). All the female cheetahs in MZNP favoured category 4 shrub cover, which only covered 20% of MZNP, and the cheetahs could have been moving greater distances to incorporate this form of cover into their home ranges.

Cheetah home ranges vary in size from 29 km² in Matusadona National Park, Zimbabwe (Purchase and du Toit 2000) to > 1 600 km² in the rangelands of Namibia (Marker *et al.* 2008). The drivers facilitating the variations in cheetah home range sizes are different habitat structures, prey availability, sex differences, availability of useable space and the presence of large, competing carnivores (Durant 2000a, Purchase and du Toit 2000, Broomhall *et al.* 2003, Bissett and Bernard

2007, Pettorelli *et al.* 2008, Lindsey *et al.* 2011). Similarly, lion habitat requirements have also been linked to a range of factors (Celesia *et al.* 2010, Bissett *et al.* 2012). Habitat selection of lions is determined by the distribution and availability of prey, accessibility and distance to water, the availability of cover for stalking and resting, and the spacing of den sites (Schaller 1972, Spong 2002, Loveridge *et al.* 2009, Celesia *et al.* 2010, Davies *et al.* 2016). Celesia *et al.* (2010) further added that lion density was related to herbivore biomass, rainfall, soil nutrients and variations in temperatures. Moreover, the densities of lions and the sizes of their home ranges are inversely related. For example, in the arid regions of the Kalahari, home ranges in excess of 1 400 km^2 have been recorded, while in the Serengeti, lion home range sizes are usually smaller than 300 km^2 (Celesia *et al.* 2010, Cozzi *et al.* 2013).

Interestingly, at the core area level (50% UD), the female cheetahs overlapped with each other by more than 20% both before and after the lion re-introduction. In contrast, Bissett (2007) found female cheetahs had little to no overlap in their core areas. Durant *et al.* (2004) explained that reproductive female cheetahs were influenced by the availability of suitable den sites and thus tried to avoid intraspecific encounters by limiting core area overlap. However, all the female cheetahs at MZNP were chemically contracepted during the study period, and this could explain the lack of core area avoidance and extensive overlap amongst individuals (Welch *et al.* 2015). Bissett (2007) found that habitat selection by denning cheetahs had no core area overlap with any other cheetah groups and that dens were positioned as far away as possible from lion home ranges. This suggests that the threats of detection were greatest to cheetah mothers and their immobile cubs (Bissett 2007). Given that all of the female cheetahs in MZNP were contracepted during my study, there may not have been a need to avoid each other and this could explain the higher levels of core area overlap.

The home ranges of the lions were smaller in MZNP compared to lion home ranges in larger systems, where prey are migratory or semi-migratory (Schaller 1972, Stander 1991, Celesia *et al.* 2010). However, the lion home ranges in MZNP were similar to home ranges in Manyara National Park (20 - 200 km^2, Schaller 1972), Kruger National Park (21-132km^2, Funston *et al.* 2003), Kwandwe Private Game Reserve (89 - 120 km^2, Bissett 2007), Karongwe Game Reserve (50 – 70 km^2, Lehmann *et al.* 2008a) and Tswalu Kalahari Reserve (56 - 111km^2, Roxburgh 2008). The home range sizes of lions vary across habitats and have been found to be inversely related to dry/lean seasonal prey biomass (Loveridge *et al.* 2009). However, the smaller home range sizes of the lions at MZNP could be attributed to a combination of factors, including, the extremely low lion density (3 individuals in 21 412 ha), the enclosed boundaries and the presence of lions in an enclosed breeding facility on a neighbouring property (Bissett 2007, Lehmann *et al.* 2008a, Packer *et al.* 2013). Packer *et al.* (1990) found male lions have the ability to 'count' and this was achieved by exposing territorial males to a series of recorded playbacks from other roaring lions. The number of territorial males determined how close they would respond to the 'intruding' males. For example, a coalition of two male lions did not respond to the playbacks of five or more lions (Packer *et al.* 1990). Considering that the lions in MZNP heard lions roaring from the breeding facility on the neighbouring property north of the park, they may have perceived that they were outnumbered, due to an unnaturally high number of male lions, and avoided the northern sections in order to minimize their risks of encountering another (larger) lion pride. In addition, Funston *et al.* (2003) found that young male lions stayed close to their natal range after leaving their natal pride, as opposed to becoming nomadic, and found that access to preferred prey and dense bush for concealment could delay dispersal. Funston *et al.* (2003) further found that the acquisition of suitable territories was an important driver for lion pride sizes and success. Given that MZNP only re-introduced three lions; their small pride size, young age (males were two years of age at the time of their release) and possibility of encountering other lions (which they may have perceived to be within the park) could all have resulted in small home range sizes. However, the fact that the lions had just been released into MZNP could have also attributed to their small home range sizes. Hunter (1998) stated that the period immediately after release was crucial for the establishment of large carnivores into new reserves. Large carnivores have to orientate themselves and assess local conditions which may be important for their survival (Hunter 1998). For example, the presence of conspecifics, location of water sources, availability and distribution of prey and location of boundaries can all influence a lions' decision to slowly and cautiously explore their new environment (Hunter 1998).

Following the lion re-introduction, the female cheetahs in MZNP had a greater overlap with the lioness than the male lions at both the home range (95% UD) and core area (50% UD) levels. Durant (2000a) found that the immediate risk of cheetahs encountering a pride of lions was an important factor influencing their spatial distributions. Thus, the threat of more than one lion suggests that cheetahs may have the ability to perceive the level of danger, assess the risk and adjust their behaviour according to the number of lions in a group (Durant 2000a). The female cheetahs in MZNP may have perceived the male lions as a greater threat than the lone lioness and attempted to minimize their encounter with the males. Considering the findings of Packer *et al.* (1990) who found that male lions are able to 'count' and avoid confrontation with other lions when they were outnumbered, it may be possible that the female cheetahs were employing a similar strategy in MZNP. However, this needs to be more comprehensively tested.

Lindsey *et al.* (2011) concluded that large areas (±703 km^2) are needed for the re-introduction of cheetahs to be successful in the presence of larger, competing carnivores, such as lions. Even though this may be true across a number of reserves with varying topography and prey densities, this was not the case in MZNP. The female cheetahs appeared to have the ability to make temporal and spatial adjustments in response to the perceived threat of larger carnivores in order to co-exist with them (Durant 2000a, Bissett and Bernard 2007, Swanson *et al.* 2014).

The ability of cheetahs to utilize different habitats other than grassland plains has received particular attention recently (see Purchase and du Toit 2000, Broomhall *et al.* 2003, Bissett and Bernard 2007, Tambling *et al.* 2014). Not only are cheetahs highly adaptable in utilizing varied habitats, but they have also been found to co-exist with larger predators by making fine-scale adjustments within their home ranges (see Swanson *et al.* 2014). It has been well documented that lions steal prey from cheetahs and kill adults and cubs (Durant 2000a, Bissett and Bernard 2007, Lindsey *et al.* 2011, Mills and Mills 2013, Scantlebury *et al.* 2014). Thus, the utilization of different vegetation units by cheetahs could be an attempt to minimize their encounters with lions.

The vegetation units utilized by the cheetahs at MZNP before the lion re-introduction were under under utilized relative to their availabilities following the lion re-introduction. Generally, all the female cheetahs used a combination of open woodland, shrubland and grassland habitats, while the lions selected thicker woodland and grassland habitats. However, the usage of the *Lycium* woodland was an important vegetation unit for both the lions and the cheetahs in MZNP. The usage of shrub cover by the cheetahs at the home range level (95% UD) did not change following the lion re-introduction. However, significant differences were recorded for the cheetahs at the core area (50% UD) level following the lion re-introduction. The cheetahs preferred to use the shrub cover categories 2, 3 and 4 which were characterized by a combination of bush clumps with open spaces but the presence of cheetahs was found to decrease as the availability of cover became thicker following the lion re-introduction. Yet, both the cheetahs and the lions used category 2, which was not surprising considering it covers more than half of MZNP. My findings in MZNP are similar to the findings of Muntifering *et al.* (2005) in Namibia, Pettorelli *et al.* (2008) in the Serengeti and Broekhuis *et al.* (2013) in the Okavango Delta in northern Botswana.

Pettorelli *et al.* (2008) found that cheetahs first selected for vegetation cover, not only for providing safe denning sites but also for stalking prey and for concealment from other large carnivores. Cheetah hunting behaviour in the Serengeti showed that they used the edges of dense habitat patches and configured their home ranges to include a mix of habitat types (Muntifering *et al.* 2005). Muntifering *et al.* (2005) also found that high-use cheetah areas were characterized by adequate grass cover and good visibility and that they did not select sparsely bushed areas. Broekhuis *et al.* (2013) further added that the response of cheetahs to the risks posed by lions is predator-specific, habitat-specific and dependent on the severity of the threat. Moreover, cheetahs did not consistently avoid certain habitats with a high likelihood of encountering lions but adjusted their behaviour according to the short term or immediate presence of lions (Broekhuis *et al.* 2013).

Despite the behavioural adjustments of cheetahs in response to lions, the perceived risk of predation was likely too great in the thickest habitats at MZNP (Pettorelli *et al.* 2008) because the female cheetahs always under utilized the thickest habitats which were utilized more by the lions. However, female cheetahs inhabiting woodland habitats have been shown to be able to avoid detection by lions and maintain closer proximities than cheetahs in more open savannas (Mills *et al.* 2004). Broekhuis *et al.* (2013) also found that cheetahs can be closer than expected to lions in mixed woodland. Since it is unlikely that cheetahs will actively move towards lions (see Bissett 2007, Lindsey *et al.* 2011), cheetahs in thicker habitats are either not able to detect lions or they rely on crypsis to remain undetected (Broekhuis *et al.* 2013). Thus, mixed habitats may provide safer refuges than the thicker habitats for cheetahs because of the lower likelihood of detection by lions (Muntifering *et al.* 2005, Broekhuis *et al.* 2013), and remain habitats which result in successful prey capture (Mills *et al.* 2004).

Broekhuis *et al.* (2013) suggested that cheetahs respond to the presence of lions by being reactive as opposed to predictive. Less competitive species, such as cheetahs, can reduce or minimize negative encounters by selecting areas or habitats that have fewer competitors (Durant 2000a, Broekhuis *et al.* 2013). Durant *et al.* (2004) added that cheetahs are known to avoid other large carnivores in the ecosystem they are inhabiting and concentrate their hunting in areas where carnivore densities are low. Durant *et al.* (2004) concluded that cheetahs in the Serengeti were negatively affected by the presence of lions because high levels of competition lowered the recruitment rates of cheetahs and ultimately restricted cheetahs to areas of low prey and carnivore densities. Bissett (2007) stated that even though food availability influenced predator space use, it may be expected to have less of an effect when prey is readily accessible as is the case of most enclosed reserves in South Africa. The individual home range variations shown by the cheetahs at MZNP may be a response to the small lion population. However, the lion population in MZNP has grown since the completion of this study (D. van de Vyver pers. obs.). Thus, future research may show a complete change in cheetah's use of space in response to a growing lion population in MZNP (Bissett 2007).

Durant *et al.* (2004) proposed that increased mobility was key to the cheetah's co-existence with lions. By constantly moving cheetahs may allow for increased spatial avoidance from lions (Durant *et al.* 2004). Swanson *et al.* (2014), however, challenged the idea of mobility influencing cheetah co-existence by stating they were only 110 m away from lions at any one time in the Serengeti. At MZNP, the female cheetahs maintained a mean distance of 540 m away from the male lions and 501 m away from the lioness. Swanson *et al.* (2014) further stated that cheetahs are able to co-exist with lions within enclosed reserves by making fine-scale adjustments because of their inability to move considerable distances away from lions. Swanson *et al.* (2014) found that cheetah population densities varied inversely with reserve size because of a relatively consistent number of animals being maintained by reserve management or because the smaller reserves were either established in richer habitats or restocked with prey on an annual basis. The overall findings by Swanson *et al.* (2014) showed that there was no large scale displacement of cheetahs by lions and that cheetahs employed fine-scale adjustments, such as divergent life histories to allow for co-existence. Broekhuis *et al.* (2013) found that cheetahs did not necessarily benefit from avoiding areas with a high chance of encountering lions. This could further explain why the cheetahs selected the *Lycium* woodland despite the lion's preference for this habitat in MZNP. The extensive overlap in home ranges and habitat usage between cheetahs and lions in MZNP is therefore likely to be driven by the relatively even distribution of resources (Broekhuis *et al.* 2013, Swanson *et al.* 2014).

It is widely accepted that the availability of food is an important factor in influencing space use of large carnivores (Gittleman and Harvey 1982). For example, Spong (2002) stated that vegetation cover is important for lion hunts to be successful, with the highest success rates occurring in dense scrub cover. In the Selous Game Reserve, lions had smaller home ranges than their counterparts on the Serengeti plains which were situated in riverine habitats, as these habitats created good ambush opportunities for stalking predators like lions (Spong 2002). Despite the preferences for riverine habitats, lion habitat preference also reflects prey abundance and 'prey catchability' within the different available habitats (Spong 2002, Hopcraft *et al.* 2005). Kittle *et al.* (2016) stated that lion predation events were influenced by habitat features, such as steep gullies and thick vegetation near rivers, which increased prey vulnerability. Funston *et al.* (2003) found that the preferred prey of male lions in the Kruger National Park was buffalo. These buffalo were found in higher densities in tree savanna habitats, affording the lion greater cover to successfully hunt them. The male lions at MZNP utilized a similar hunting strategy to catch their preferred prey (eland and buffalo) along the main river system (see Chapter 4). The selection of thicker habitats in MZNP could be further explained by the challenges of catching prey in more open habitats, which promote improved predator detection by prey and lower success rates of hunting lions (Kittle *et al.* 2016).

The before and after effects of the lion re-introduction at MZNP did not result in the immediate suppression of the cheetah population nor did it exclude the cheetahs from their preferred habitats. The cheetahs employed fine-scale adjustments to facilitate their co-existence with the lions, as found by Swanson *et al.* (2014).

Despite the small sample size of large carnivores in MZNP, the responses shown by the cheetahs to the re-introduction of lions opposed the widespread perception of lions suppressing cheetahs (Swanson *et al.* 2014). This study has provided a meaningful contribution to improving our understanding of how cheetahs respond to the presence of lions and how they utilize the high altitude terrain of MZNP. Jhala *et al.* (2009b) observed, that public perception of cheetahs and their habitats were influenced by wildlife films made in the Serengeti. These films depicted cheetahs and lions as inhabitants of open savanna, which is in stark contrast to the many studies that have furthered our understanding of large carnivore space use requirements outside the grassland habitats (Jhala *et al.* 2009b).

The fragmentation of habitats, coupled by continued re-introductions and/or removals from enclosed reserves requires a knowledge of the fundamental factors influencing large predator space use and habitat selection (Kittle *et al.* 2016). Bauer *et al.* (2015) stated that management budgets and the presence of predator-proof fences were the two most important requirements for short-term large carnivore conservation. For large carnivore conservation to be sustainable, increased intervention efforts are required to maintain viable and ecologically diverse populations (Bauer *et al.* 2015). However, fenced reserves in South Africa, such as MZNP, only have small carnivore populations which require extensive metapopulation management, resulting in limited contributions to overall species conservation (Bauer *et al.* 2015, van der Merwe *et al.* 2016). Irrespective of how small the scale of fenced reserve conservation may be to the greater large carnivore populations, it still plays a significant role in maintaining the existence of large carnivores. However, future research is needed on the space use and habitat selection of resident cheetahs in MZNP and elsewhere, over longer time frames, to fully explore the effects of the lion re-introduction, and these efforts should also include male cheetahs.

CHAPTER 4

CHEETAH AND LION FEEDING ECOLOGY

From top left: LF1 with a kudu bull kill, CF3 and cubs eating a springbok ram, LM1 and LM2 fighting over an aardvark in Mountain Zebra National Park. Top images courtesy of C. Bissett.

INTRODUCTION

The vast majority of our understanding of large carnivore diets in Africa is based on autecological studies (Bissett 2007). Examples of autecological studies are those conducted by Eaton (1970) in Nairobi National Park on cheetahs (*Acinonyx jubatus*), Schaller (1972) in the Serengeti on lions (*Panthera leo*), Kruuk (1972) in the Serengeti on spotted hyaenas (*Crocuta crocuta*), Eloff (1973) in the Kalahari on lions and Stander (1991) in Namibia on lions, Caro (1994) on cheetahs in the Serengeti and Bothma (1998) in the Kalahari on leopards (*Panthera pardus*). Indeed, carnivore predation is one of the key regulators in shaping prey communities (Cooper *et al.* 2007).

Predator-prey relationships are vital for influencing ecosystem functioning and stability (Davies *et al.* 2016). The imbalances that occur as a result of incorrect predator to prey ratios, or an absence of predators, has been found to cause major shifts in ecosystem functioning (Cooper *et al.* 2007, Davies *et al.* 2016). Additional challenges arise in the long term maintenance and/or attempted restoration of the carnivore guild within protected areas across southern and eastern Africa (Davies *et al.* 2016). Studies from restored (Hunter 1998, Bissett 2007, Hayward *et al.* 2007a) and intact (Durant 2000a, Mills *et al.* 2004, Radloff and du Toit 2004, Mills 2015) carnivore guilds, show that African ecosystems are dominated by large, competitive predators, such as lions and spotted hyaenas, with smaller, less competitive predators, such as cheetahs and African wild dogs (*Lycaon pictus*), occupying the lower trophic positions (Mills 2015).

The re-introduction of large carnivores into enclosed reserves (defined as areas of < 1 000 km^2, see Lindsey *et al.* 2011) has experienced significant growth in South Africa since the 1990s (Hayward *et al.* 2007b). From the early 1990s, large areas (0 - 400 km^2) of agricultural land have been transformed into private game reserves or incorporated into existing national parks (Hayward *et al.* 2007b). The expansion of protected land has allowed for the restoration of previously extirpated species (such as lions, hyaenas, leopards, cheetahs and wild dogs) into their historical ranges. These re-introductions were done in order to restore the overall biodiversity of South Africa (Hunter 1998, Hayward *et al.* 2007b). The conservation of endangered species and the economic benefits of ecotourism have been welcome spin-offs from these re-introductions (Mossaz *et al.* 2015). However, Hayward *et al.* (2007b) observed there was a lack of post-release, large carnivore monitoring following these re-introductions. Due to the lack of post-release monitoring, reserve managers did not know the specific requirements for large carnivore re-introductions to be successful, nor do they necessarily know the effects of large carnivore predation on prey within enclosed reserves (Hayward *et al.* 2007b). For example, lions re-introduced into Schotia Safaris Private Game Reserve had to be supplementary fed after they had significantly reduced the numbers of free roaming prey (Hayward *et al.* 2007b).

Moreover, there is little information on the re-introduction of smaller carnivores, such as cheetahs, preceding the re-introductions of larger carnivores into the same reserve (Hayward *et al.* 2006b, Lindsey *et al.* 2011).

Individual feeding ecologies are an important aspect of determining carnivore niches (Welch and Parker 2016), as behavioural, morphological and physiological adaptations enables carnivores to prey upon a variety of species (Farhadinia and Henami 2010). Knowledge of a carnivore's diet is imperative for assessing the role it plays in the environment, which includes the level of competition with other carnivores (Mbizah *et al.* 2012). Hayward *et al.* (2007a) stated that earlier research identified the relationships between predator and prey densities but more recent studies on prey preferences allowed for these investigations to be intensified. Lion densities were found to be influenced by the biomass of all available prey species and cheetah densities by the availability of prey weighing between 15-60 kg, coupled with a negative relationship with lion density (Hayward and Kerley 2005, Hayward and Kerley 2006b, Hayward *et al.* 2007a). However, when economically important or endangered species are concerned, an in depth knowledge of species specific dietary requirements are vital (Hayward *et al.* 2007a, Mbizah *et al.* 2012). Comprehensive dietary studies have allowed for the recognition of both interference and exploitation competition as an important mechanism in shaping carnivore guilds (Mbizah *et al.* 2012). In many of these situations, it is the smaller carnivore that is adversely affected by the larger carnivore (Hayward and Kerley 2006b).

Carnivores play a role in influencing prey numbers (Power 2002, Bissett 2007, Owen 2012). However, in enclosed reserves, carnivores can regulate prey to the point of localized extinctions because prey cannot migrate or move away from predator hotspots (Power 2002, Owen 2012, Jooste *et al.* 2013). Furthermore, the larger carnivores can play a crucial role in regulating smaller carnivores, in the form of mesopredator suppression (Hayward and Kerley 2006b, Lindsey *et al.* 2011, Swanson *et al.* 2014). Mesopredator suppression occurs when lower ranked carnivores are exposed to the top-down control of apex carnivores resulting in reduced population sizes and competitive exclusions from suitable habitat types (Brassine and Parker 2011). Gordon *et al.* (2015) further explained that mesopredators can be regulated by large carnivores via two mechanisms: consumptive (i.e lethal) and non-consumptive (i.e. non-lethal) effects. Consumptive effects occur through direct killing of a perceived competitor and non-consumptive effects occur when smaller carnivores adjust their habitat use to reduce risk exposure to larger carnivores (Gordon *et al.* 2015).

Swanson *et al.* (2014) found that mesopredator suppression is influenced by interference competition, which either involves direct interactions or behavioural avoidance by the smaller carnivore to minimize the risk of encountering the larger carnivore. Large carnivores have been found to account for > 50% of smaller carnivore mortalities (Swanson *et al.* 2014). The effects of mesopredator suppression are not restricted to African guilds but have been recorded from various studies in other countries. For example, dingoes (*Canus lupus dingo*) excluding red foxes (*Vulpes vulpes*) in Australia (Moseby *et al.* 2012) and coyotes (*Canis latrans*) excluding swift foxes (*Vulpes velox*) in North America (Kamler *et al.* 2003). However, the effects of mesopredator suppression are more complicated in Africa, due to a large diversity of predators being able to occupy a variety of ecological niches and trophic scales (Swanson *et al.* 2014, Welch and Parker 2016). Mesopredators have been found to adopt strategies such as spatio-temporal partitioning (Durant 2000a) and active avoidance to reduce the frequency of direct aggression and facilitate co-existence with larger carnivores within enclosed systems (Swanson *et al.* 2014).

The feeding biology of cheetahs has been extensively studied (Schaller 1968, Pienaar 1969, Eaton 1970, Caro 1994, Hunter 1998, Purchase and du Toit 2000, Mills *et al.* 2004, Radloff and du Toit 2004, Bissett and Bernard 2007, Hayward *et al.* 2006b, Marnewick *et al.* 2007, Farhadinia and Henami 2010, Tambling *et al.* 2014 and Mills 2015). In addition, lions are one of Africa's most studied large carnivores (see de Waal 2002, Funston and Mills 2005, Hayward and Kerley 2005, Loveridge *et al.* 2009, Tambling *et al.* 2010, Mills 2015). When large predators co-exist, sustaining balanced predator-predator and predator-prey interactions in these reserves requires an understanding of these carnivores and their environment (Davies *et al.* 2016). Improved understandings of hunting behaviour becomes vital because they can determine the impact predators have, not only on each other, but on prey distributions and abundance (Mills 1992, Davies *et al.* 2016). Prey availability and distributions can influence selection, hunting success and the spatial distributions of large carnivores (Breuer 2005). The presence of lions has been of particular interest in predator-prey studies because they have the ability to create regime shifts in the ecosystem through predation (Mills 1992, Power 2002, Hayward and Kerley 2005). For example, Davies *et al.* (2016) stated that when lions are present, they were responsible for the majority of mammalian herbivore and carnivore mortalities of prey species larger than 10 kg. Thus, lions can be important ecosystem regulators (Funston *et al.* 2001, Davies *et al.* 2016).

Cheetahs have shown preferences for the most abundant medium sized antelope (30-65 kg) occurring within a reserve (Hayward *et al.* 2006b). However, when cheetahs co-exist with lions, they have been found to feed upon smaller prey (see Mills *et al.* 2004). By contrast, lions preferentially prey upon species within a weight range of 190-550 kg, with the most preferred weight of prey being 350 kg (Hayward and Kerley 2005). Lions, unlike cheetahs, preferred prey within a particular weight range irrespective of their availability (Hayward and Kerley 2005).

The selective killing of prey (i.e. specific age, size and sex classes) by cheetahs and lions has been widely reported across Africa (see Fitzgibbon 1989, Bissett 2007, Clements *et al.* 2014). Cheetahs have been found to hunt larger prey when they are in coalitions, while solitary females select smaller prey than males (Bissett and Bernard 2007, Tambling *et al.* 2014). Cheetahs also show preferences for either adults or juveniles for their hunted prey (Eaton 1970, Hunter 1998, Mills *et al.* 2004, Bissett and Bernard 2007, Clements *et al.* 2014, Tambling *et al.* 2014). The variations in cheetah prey selection can be explained either by their unusual social system (see Caro 1994) or by trying to avoid detection from kleptoparasites (Mills *et al.* 2004). Cheetah societies are unique because males can be either solitary or in a coalition, whereas females are usually solitary unless they are accompanied by cubs (Caro 1994). Male cheetahs in a coalition require a greater biomass of food per unit time when compared to solitary cheetahs and these gains could be met by catching and killing larger sized prey or hunting adults more regularly (Caro 1994, Bissett and Bernard 2007, Clements *et al.* 2014, Tambling *et al.* 2014).

Lions have been found to be opportunistic predators (Hayward and Kerley 2005, Hopcraft *et al.* 2005). Variations in prey sizes and in the demographics of species killed has been found across Africa (Schaller 1972, van Orsdol 1984, Hunter 1998, Funston *et al.* 2001, Radloff and du Toit

2004, Tambling and Belton 2009, Valeix *et al.* 2009b, Bissett *et al.* 2012, Mills 2015, Davies *et al.* 2016).

The patterns of prey selection by large carnivores are complex (Clements *et al.* 2014) and a variety of factors have been described to explain these extensive variations in prey choices (Funston *et al.* 2001). Furthermore, lion prey selection not only varies in space between study sites (Hayward and Kerley 2005) but several of these studies have shown that lion diets follow seasonal changes in prey availability (Owen-Smith 2008. Loveridge *et al* 2009, Valeix *et al.* 2009b). However, these variations in lion prey selection re-iterate that they are not influenced by prey abundance but more by availability and 'catchability' within the landscape (Hayward and Kerley 2005, Hopcraft *et al.* 2005, Davies *et al.* 2016).

Hubel *et al.* (2016) stated that hunting predators needed to outperform their prey by using a combination of surprise, speed, stealth, agility and endurance. Cheetahs use high speeds, fast accelerations and maneuverability after stalking within range of unsuspecting prey (Hubel *et al.* 2016). Lions are considered to be ambush predators and have been found to rely heavily on concealment during hunting (Davies *et al.* 2016). The variation in vegetation structures and topographies, therefore, have been found to affect a large carnivore's decision to hunt (Hopcraft *et al.* 2005, Cooper *et al.* 2007), as it influences visibility, both in terms of predator concealment and limits prey detection, and the ability of prey to escape (Davies *et al.* 2016). Furthermore, the majority of cheetah research has been conducted in open grassland systems (Kruuk and Turner 1967, Eaton 1970, Caro and Collins 1987, Durant *et al.* 1988, Caro 1994, Kelly *et al.* 1998, Durant 2000a), however, more recent work has been conducted in woodland (Purchase and du Toit 2000, Mills *et al.* 2004, Radloff and du Toit 2004, Tambling *et al.* 2014) and thicket (Bissett and Bernard 2007) habitats.

The aim of this chapter was to determine and compare the dietary preferences of the resident cheetah population in MZNP before and after a lion re-introduction. I hypothesized that the cheetahs would kill larger prey, such as adult springbok (*Antidorcus marsupialis*), juvenile black wildebeest (*Connochaetes gnou*), red hartebeest (*Alcelaphus buselaphus*), blesbok (*Damaliscus pygargus phillipsi)* and kudu (*Tragelaphus strepsiceros*), in the absence of the lions. Following the lion re-introduction, I expected the cheetahs to switch to smaller prey, such as steenbok

(*Raphicerus campestris*), duiker (*Sylvicapra grimmia*) and juvenile springbok, in an attempt to reduce kleptoparasitism from the lions.

METHODS

Data collection

Prior to the re-introduction of the lions, the cheetahs in MZNP were fitted with VHF collars (African Wildlife Tracking, see Chapter 2). However, from 2012 onwards, all of the cheetahs and lions were fitted with satellite collars (African Wildlife Tracking), which also have a VHF component. Data on feeding ecology were collected by Dr Charlene Bissett and MZNP staff for the cheetahs prior to the lion re-introduction. Post lion re-introduction, data were collected by myself, Dr Charlene Bissett and MZNP staff. Lion and cheetah kill data were collected using the Global Positioning System (GPS) cluster method (Anderson and Lindzey 2003, Tambling *et al.* 2010) and through the opportunistic location of cheetah and lion kills when in the field. Scats from both predators were also collected opportunistically when checking for potential kill remains.

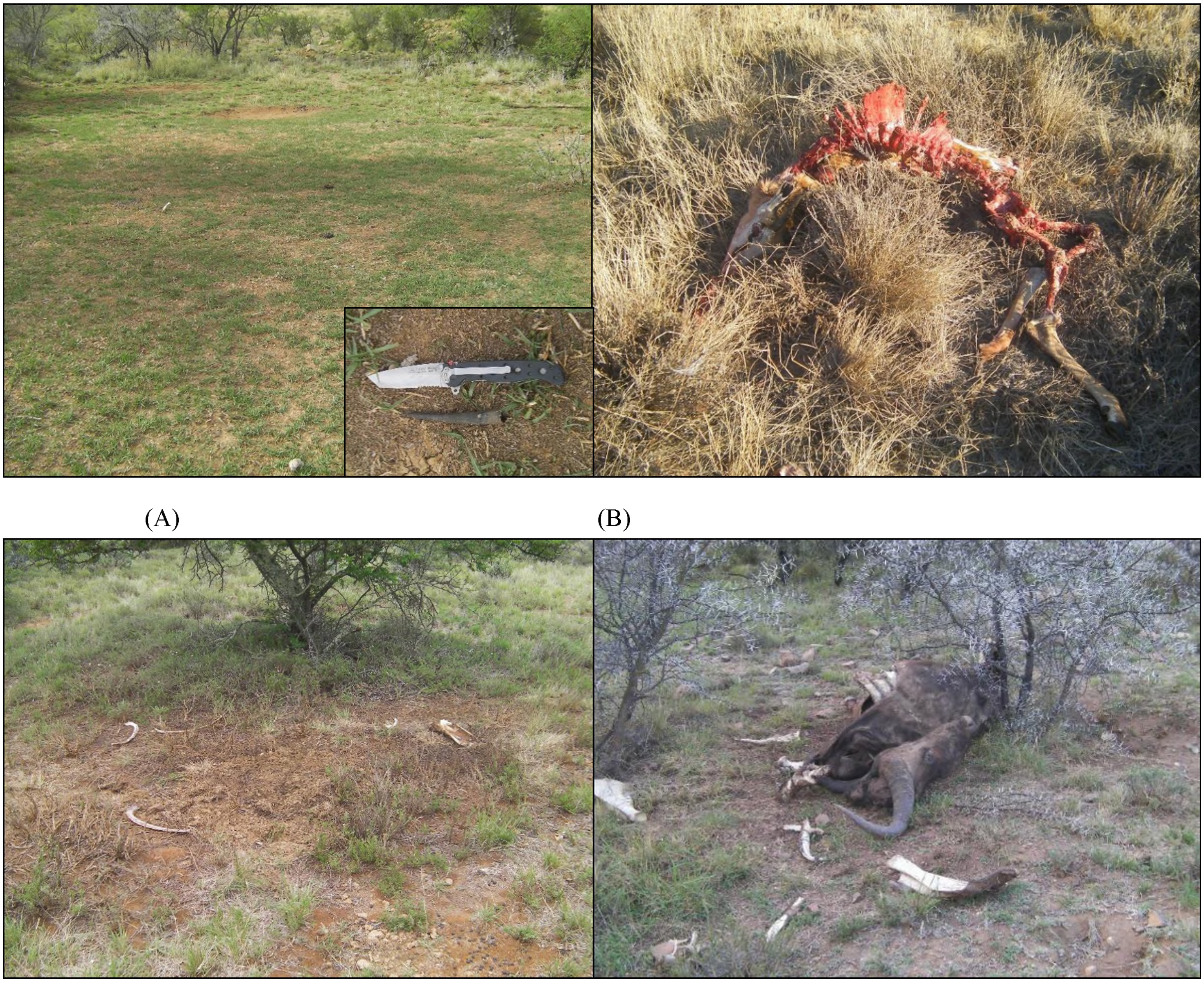
GPS cluster method and opportunistic observations

The use of GPS data fixes has provided valuable insights into the diet and prey selection of a number of predators; including pumas (*Puma concolor*; Anderson & Lindzey 2003), wolves (*Canis lupus*; Sand *et al.* 2005 and Demma *et al.* 2007), lynx (*Lynx lynx*; Mejlgaard *et al.* 2012), tigers (*Panthera tigris*; Athreya *et al.* 2014), snow leopard (*Panthera uncia*; Shehzad *et al.* 2012), lions (Valeix *et* al. 2009a, Tambling *et al.* 2010, Davidson *et al.* 2013), leopards (*Panthera pardus*; Martins *et al.* 2011, Miller *et al.* 2013b) and cheetahs (Hubel *et al.* 2016). A GPS cluster - was defined as > 2 consecutive recorded times with each pair of fixes < 100 m apart (Tambling *et al.* 2010). Location fixes were plotted in ArcGIS 10.2 (ESRI, Redlands, California, USA) and sequentially inspected to identify potential kill clusters. Once potential clusters were identified, cluster co-ordinates were uploaded onto a handheld GPS unit (see Chapter 3) and investigated on foot. GPS locations can be inaccurate (Webb *et al.* 2008) and kill remains can be scattered around actual positions. Thus, an area of approximately 20 m around the cluster was thoroughly investigated for prey remains (Tambling *et al.* 2010, Fröhlich *et al.* 2012). Tambling *et al.* (2010) suggested that all potential clusters in the vicinity of each other should be investigated for kill remains. Potential predation events at the GPS clusters were identified from the presence of prey stomach contents, teeth, hooves, hair or bones and used to determine/identify prey species (Tambling *et al.* 2010, Fröhlich *et al.* 2012, Figures 4.1A-D). Whenever possible, age (juvenile, sub-adult, adult) of the prey was recorded. Age categories were defined using the criteria proposed by Skinner and Chimimba (2005) and refined by Davidson *et al*. (2013):

a) juvenile was a small and dependent calf or lamb;

b) sub-adult was a young, independent animal not fully grown and not reproductively active;

c) adult was a full grown, reproductive animal.



(A) (B)

(C) (D)

Figure 4.1: Examples of located cheetah (A-B) and lion (C-D) kills. Note, the range in difficulty in determining species from kill remains at the various kill sites. A – cheetah kill site for CF6 and

all that was found was a duiker ram's horn, see inset. B – a freshly killed springbok ewe made by CF3. C – adult eland (*Tragelaphus oryx*) killed by LF1, kill ID was determined through hair analysis and bone remains. D – adult buffalo (*Syncerus caffer*) cow killed by the male lions.

The vegetation unit in which the kill was made, the location and GPS fix(s) of the kill was recorded. When field data were being collected, all cheetahs were located daily to determine whether a kill had been made or to see if the cheetahs had fed recently. If an individual had made a kill, determined using stomach size (see Hunter 2008), fixes were backtracked in an attempt to locate the potential kill site. However, these direct observations and opportunistic kill locations can artificially increase the frequency of large kills in predator diets. Cheetahs are more likely to spend longer periods on larger kills and thus larger kills are more likely to be found than smaller kills (Caro 1994, Bissett and Bernard 2007). In an attempt to bridge any potential gaps in kills, scats were also collected opportunistically when in the field. Scat collection was done to help determine 'missed kills' and to further determine large carnivore diets especially for smaller prey items or prey caught in between GPS fixes (Wachter *et al.* 2006). The same methods were applied to the collection of the lion kill data.

Scat and hair analysis

Scats and hairs were collected opportunistically from kill sites where carcass remains proved insufficient at being able to identify the species killed. GPS fixes were recorded and allocated were applicable, for both the cheetahs and lions. Following collection, scats were washed, hairs were extracted, washed again, filtered and air-dried using standard techniques (Wachter *et al.* 2006, Tambling *et al.* 2010, Mbizah *et al.* 2012, Tambling *et al.* 2012). Lion scats were washed with running water through a metal sieve to remove indigestible items (such as bone shards, pieces of hooves and horns) before extracting hair (Tambling *et al.* 2012). Hairs were examined both macroscopically (length, colour and texture) and microscopically (cross-section and cuticle scale characteristics) to identify prey species (Tambling *et al.* 2012). Cuticle scale imprints were made from hair samples using the method proposed by Keogh (1983) and refined by Wachter *et al.* (2006). A teaspoon (5 ml) of gelatin (Royal) was added to 250 ml of hot water and this solution was thinly applied to glass slides and hairs were placed into position using a pair of fine forceps. Prepared slides were left to dry for approximately 24 - 48 hours before hairs were removed and analysed. Six randomly selected hairs were placed onto each slide and a total of four slides were made per collected scat (Foster *et al.* 2010). Cross sections of the hairs were also made using the methods outlined by Douglas (1989). Ten to twenty hairs were randomly selected and were placed into a disposable pipette and filled with molten wax (Paraplast Plus, Sherwood Medical Co. St Louis). Filled pipettes were cooled rapidly by being placed into a beaker filled with ice. Once cooled, pipettes were cut into section of ± 2 mm and six to eight sections were placed onto slides using the molten wax. Both cross-section and cuticle-scale imprints from collected hairs were examined under a light microscope (Zeiss Primostar HAL/LED microscope, fixed-Köhler, stage L, FOV 18) and compared to the Rhodes University hair reference collection and other published literature (Buys and Keogh 1984) to identify them to species level.

Data analysis

Observed kill data from both the lions and cheetahs were analysed in terms of species killed, their age, sex and size. In order to determine whether the cheetahs changed their diet after the re-introduction of the lions, their diets were compared before and after the lion re-introduction (Davidson *et al.* 2013). Lion kill data were analysed to determine any differences between the males and the female and to assess whether there was any dietary overlap between the lions and cheetahs. Species that were preyed upon were assigned to different size classes in accordance to the age of the prey caught. Due to the extensive variation of size classes in the literature, species were assigned to a size class according to categories used by Hunter (1998).

Prey preference for the lions and cheetahs was assessed using Jacobs' selection index (Jacobs 1974):

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

Where r is the proportion of the total number of kills of a particular species and p is the proportional availability (derived from annual census data) of the prey species killed (Spies 2016). Jacob's index has a range of -1, 0, and 1, where -1 is highly avoided, 0 where kills are in proportion to availability and 1 where a species is highly selected. The benefit of this index is that it minimizes the biases associated with small sample sizes (Davidson *et al.* 2013).

Dietary overlap between the cheetahs and lions was calculated using Pianka's index (Pianka 1973) but using the equation of Mbizah *et al.* (2012):

$$\mathrm{Oab} = \frac{(\Sigma n\ \mathrm{P}ia\ \mathrm{P}ib)}{(\Sigma n \mathrm{P}ia^2 \Sigma n \mathrm{P}ib^2)^{1/2}}$$

Where Oab is dietary overlap between species a and species b. Pia is the relative frequency of the prey item i found in the diet of species a. Pib is the relative frequency of i found in the diet of species b and n is the total number of prey species in the carnivore diet (Mbizah *et al.* 2012). The index ranges from 0 (indicating no overlap) to 1 (indicating complete overlap). Diet overlap increases as the Pianka index increases and overlap is generally considered to be biologically significant when the value exceeds 0.60 (see Navia *et al.* 2007).

Chi – square goodness-of-fit tests were used to determine whether the lion re-introduction affected the overall diet of cheetahs. Significance of chi-square tests was based on a probability level of $P < 0.05$ (Schermelleh-Engel and Moosbrugger 2003). All statistical analyses were conducted using R language (version 3.0.1, R Development Core Team, 2014).

RESULTS

Cheetah prey sizes

Prior to the lion re-introduction, the cheetah preyed primarily upon medium sized prey. Following the lion re-introduction, the cheetah continued to prey upon medium sized prey, but there was a small increase in the predation of smaller sized prey species (Table 4.1).

Table 4.1: The prey categories as used by Hunter (1998). Total is the number of recorded GPS cheetah kills before and after the lion re-introduction.

Kill Size	Weight Range	Typical examples	Total Before	 After
small	< 30 kg	grey duiker, steenbok , scrub hare, juvenile springbok, grey rhebok	14	22
medium	30 - 65 kg	springbok, mountain reedbuck, juvenile kudu, Ostrich, juvenile gemsbok, black wildebeest, red hartebeest and blesbok	63	62
large	> 65 kg	kudu, black wildebeest, red hartebeest, blesbok, mountain zebra and eland	5	6

Lion prey sizes

The male lions caught primarily large prey but they caught more small prey than the lioness. The lioness caught medium and large prey species (Table 4.2).

Table 4.2: The prey categories as used by Hunter (1998). Total is the number of recorded GPS kills for the male and female lions.

			Total	
Kill Size	**Weight**	**Typical Examples**	**LM1 & LM2**	**LF1**
small	<60 kg	grey rhebok, grey duiker, mountain reedbuck, springbok	23	9
medium	60-120 kg	blesbok, Ostrich, red hartebeest, bushpig	6	27
large	>120 kg	eland, gemsbok, buffalo, kudu, black wildebeest, mountain zebra	40	25

Before the lion re-introduction

A total of 82 cheetah kills with known GPS fixes, comprising seven species were recorded from April 2012 to April 2013 in MZNP (Table 4.3).

Table 4.3: The species preyed upon by the cheetahs (n = 4) before the re-introduction of lions.

	Before	
Prey Species	**No**	**%**
kudu	48	58.5
springbok	22	26.8
grey duiker	3	3.7
unknown	3	3.7
grey rhebok	2	2.4
mountain reedbuck	2	2.4
gemsbok	1	1.2
steenbok	1	1.2
Total	**82**	**100**

Three of the seven species preyed upon by the cheetahs made up 89% of their diet. However, kudu and springbok comprised 85.3% of all the animals killed in MZNP prior to the re-introduction of lions (Table 4.3).

After the lion re-introduction

A total of 90 cheetah kills, comprising 11 species were recorded after the lion re-introduction (April 2013 to April 2014). Only one record of kleptoparasitism was recorded when the lioness chased a female cheetah (CF6) off her springbok kill in September 2013 (Table 4.4).

Table 4.4: The species preyed upon by the cheetahs (n = 4) following the re-introduction of lions.

	After	
Prey Species	**No**	**%**
springbok	35	38.9
kudu	34	37.8
grey rhebok	6	6.7
black wildebeest	3	3.3
unknown	3	3.3
red hartebeest	2	2.2
steenbok	2	2.2
Crowned Lapwing	1	1.1
grey duiker	1	1.1
Grey-winged Francolin	1	1.1
Ostrich	1	1.1
Pied Crow	1	1.1
Total	**90**	**100**

Following the lion re-introduction, three of the 11 species (kudu, springbok and grey rhebok (*Pelea capreolus*)) preyed upon by the cheetahs comprised 83.4% of their diets. Despite the re-introduction of lions, kudu and springbok still made up the bulk of the species (76.7%) caught by the cheetahs.

In terms of prey sizes medium sized prey were caught the most, followed by small and then large sized prey (Table 4.1). A comparison of the sizes of prey caught by the cheetahs before and after the lion re-introduction, shows that there was a slight increase in the number of small sized prey, but large and medium sized prey remained constant (Table 4.1).

Lion kills

Male and female lion kill data were analysed collectively (i.e. at the park level) and independently (i.e. the individual level) because they hunted separately. The male lions made a total of 67 kills comprising 10 species from April 2013 to April 2014. The lioness made a total of 60 kills comprising 10 species from April 2013 to April 2014 (Table 4.5).

Table 4.5: The prey species caught by the male (n = 2) and female (n = 1) lions in MZNP.

	Male Lions		**Lioness**	
Species	**No**	**%**	**No**	**%**
eland	18	26.9	4	6.5
buffalo	16	23.9	1	1.6
mountain zebra	9	13.4	4	6.5
kudu	7	10.4	10	16.1
black wildebeest	3	4.5	10	16.1
gemsbok	3	4.5	4	6.5
porcupine	3	4.5	3	4.8
red hartebeest	3	4.5	21	33.9
bushpig	2	3.0	1	1.6
grey duiker	2	3.0	0	0.0
grey rhebok	0	0.0	2	3.2
springbok*	0	0.0	1	1.6
unknown	1	1.5	1	1.6
Total	**67**	**100**	**61**	**100**

*Kleptoparasitism record

Collectively, the lions made a total of 127 kills comprising 11 species. Six of these species (eland, buffalo, mountain zebra (*Equus zebra zebra*), black wildebeest (*Connochaetes gnou*), red hartebeest (*Alcelaphus buselaphus*) and kudu) comprised 84.2% of the diet. Four of the 10 species caught by the male lions (eland, buffalo, mountain zebra and kudu) comprised 74.6% of their diet. Eland and buffalo constituted just over half (50.8%) of all male lion kills. The diet of the lioness consisted of three main species, red hartebeest, kudu and black wildebeest which comprised 66.1% of all animals killed.

The lions preyed upon species in all three weight categories (Table 4.2). The male lions preyed more upon both the large and the small prey and the lioness preyed more upon the medium and large sized prey (Table 4.2).

Scat analysis

Cheetah scats

A total of 25 cheetah scats were analysed following the re-introduction of lions, all (100%) scats were from the collared females (n = 4). Six prey species were found in the cheetah scats and all scats contained hair from a single species. The species identified in the scats were the same as the species observed as cheetah kills (Table 4.4). A greater percentage of kudu (52%) and a lower percentage of springbok (32%) were found in the scats compared to the observed kills (Table 4.6). Two prey species (springbok and kudu) comprised 84% of all species analysed in the cheetah scats, which was greater than the two prey species observed as kills (76.7%).

Table 4.6: Composition of species found in cheetah scats. Species from observed kills are also shown.

	Observed Kills		**Scats**	
Prey Species	**No**	**%**	**No**	**%**
springbok	35	38.9	8	32.0
kudu	34	37.8	13	52.0
grey rhebok	6	6.7	1	4.0
black wildebeest	3	3.3	1	4.0
unknown	3	3.3	0	0.0
red hartebeest	2	2.2	1	4.0
steenbok	2	2.2	0	0.0
Crowned Lapwing	1	1.1	0	0.0
grey duiker	1	1.1	1	4.0
Grey-winged Francolin	1	1.1	0	0.0
Ostrich	1	1.1	0	0.0
Pied Crow	1	1.1	0	0.0
Total	**90**	**100**	**25**	**100**

Lion scats

A total of 69 lion scats were collected and analysed, of which 44 (63.8%) were from the male lions and 25 (36.2%) were from the lioness. Six prey species were found in all analysed lion scats, five for the male lions and five for the lioness (Table 4.7). Three species; buffalo (40.9%), eland (36.4%) and red hartebeest (9.1%) had a higher frequency of occurrence when compared to observed kills for the male lions. Two species; red hartebeest (44.0%) and black wildebeest

(28.0%) had a higher frequency of occurrence than observed kills for the lioness (Table 4.7). Overall, scat analysis showed the lion diet was dominated by two species (buffalo and eland for male lions and red hartebeest and black wildebeest for lioness), comprising 77.3% and 72% respectively.

Table 4.7: Composition of prey species identified from lion scats. Species from observed kills are added for comparison.

	Obs. Male Lion Kills		**Male lion Scats**		**Obs. Lioness Kills**		**Lioness Scats**	
Species	**No**	**%**	**No**	**%**	**No**	**%**	**No**	**%**
eland	18	26.9	16	36.4	4	6.5	3	12.0
buffalo	16	23.9	18	40.9	1	1.6	1	4.0
mountain zebra	9	13.4	0	0.0	4	6.5	0	0.0
kudu	7	10.4	3	6.8	10	16.1	1	4.0
black wildebeest	3	4.5	3	6.8	10	16.1	7	28.0
gemsbok	3	4.5	0	0.0	4	6.5	0	0.0
porcupine	3	4.5	0	0.0	3	4.8	0	0.0
red hartebeest	3	4.5	4	9.1	21	33.9	11	44.0
bushpig	2	3	0	0.0	1	1.6	2	8.0
grey duiker	2	3	0	0.0	0	0	0	0.0
grey rhebok	0	0	0	0.0	2	3.2	0	0.0
springbok*	0	0	0	0.0	1	1.6	0	0.0
unknown	1	1.5	0	0.0	1	1.6	0	0.0
Total	**67**	**100**	**44**	**100**	**61**	**100**	**25**	**100**

*Kleptoparasitism record

Cheetah prey preferences

Before the lion re-introduction

The Jacob's index calculations for prey preference for the cheetahs GPS kill data before the lion re-introduction generated values ranging from 0.94 for kudu to -0.67 for gemsbok (*Oryx gazella*) (Figure 4.2).

Index values for kudu, which was the most preyed upon species, had the highest preference value of all species caught by the cheetahs suggesting that they were hunted preferentially (Figure 4.2). Grey rhebok had a relatively low number of individuals caught but had a relatively high preference index. Springbok, an abundant prey species in the park, were hunted in accordance to their abundance. Interestingly, mountain reedbuck (*Redunca fulvorufula*), a species with a low abundance in the park, were caught relative to abundance. Gemsbok were avoided by cheetah prior to the lion introduction (Figure 4.2).

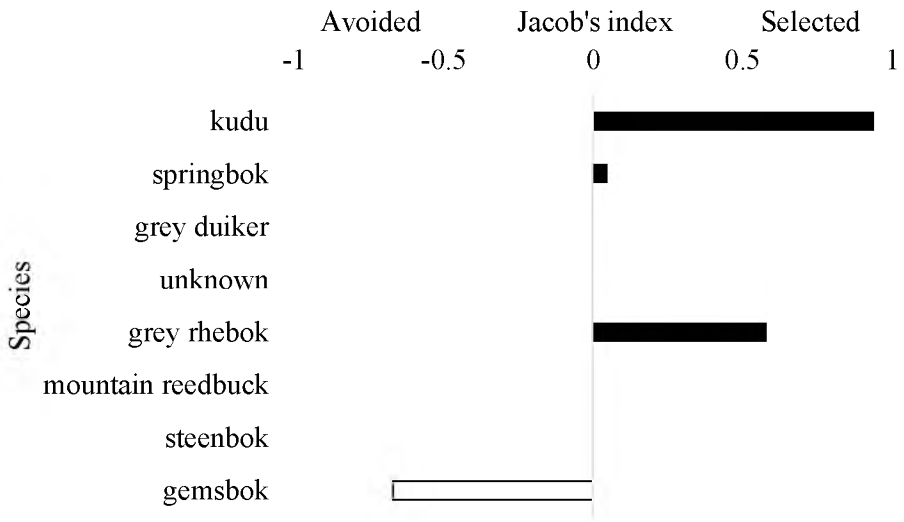


Figure 4.2: The Jacob's index values for species preyed upon by the cheetahs before the re-introduction of lions. Blank spaces are species not counted during the census, e.g. the birds and small antelope species. Note, mountain reedbuck had a preference index of 0.

After the lion re-introduction

Jacob's index calculations for the prey preference of the cheetahs GPS kill data after the lion re-introduction generated values ranging for 0.80 for kudu to -0.83 for black wildebeest (Figure 4.3).

Cheetah preference index values were the highest for kudu, which was the same as before the lion re-introduction, suggesting that kudu were again hunted preferentially. Interestingly, despite springbok being abundant in the park, there was an increase in their preference value after the lion re-introduction (Figures 4.2, 4.3). Grey rhebok experienced a slight decrease in preference. Cheetahs avoided Ostrich (*Struthio camelus*) and showed a strong avoidance for black wildebeest and red hartebeest (Figure 4.3).

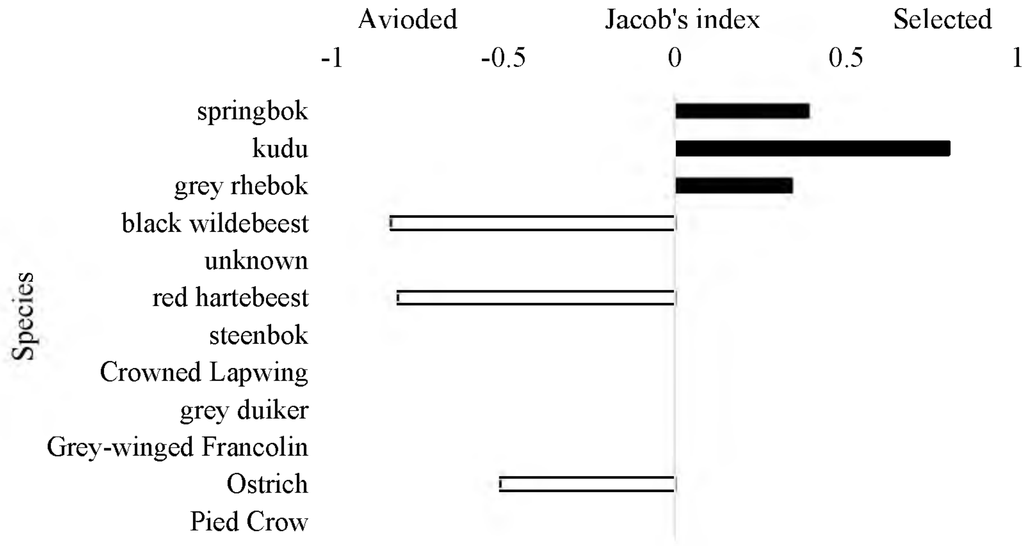


Figure 4.3: The Jacob's index values for species preyed upon by the cheetahs after the re-introduction of lions. Blank spaces are due to those particular species (birds) not being counted during the census.

Lion prey preferences

Preference values for GPS kill data ranged from 0.82 for buffalo to -0.71 for black wildebeest for the male lions. Values ranged from 1 for red hartebeest to -0.51 for buffalo for the lioness (Figure 4.4).

The male lions showed a strong selection for buffalo and eland, kudu were also selected and mountain zebra were caught relative to their abundance (Figure 4.4). Interestingly, black wildebeest and red hartebeest, which comprised almost a third of all individual prey animals in the park, were strongly avoided by the male lions.

By contrast, the lioness showed a strong preference for red hartebeest and grey rhebok (Figure 4.4). Kudu and gemsbok were also selected by the lioness, kudu was the only species preferred by both the cheetahs and lions (Figures 4.2, 4.3, 4.4). Eland and black wildebeest were caught relative to their abundance by the lioness. Mountain zebra and buffalo were strongly avoided by the lioness.

Analysis of Jacob's index preference values suggest that whatever the male lions were selecting, the lioness was either avoiding or catching relative to the species abundance in the park, with the exceptions of kudu (Figure 4.4).

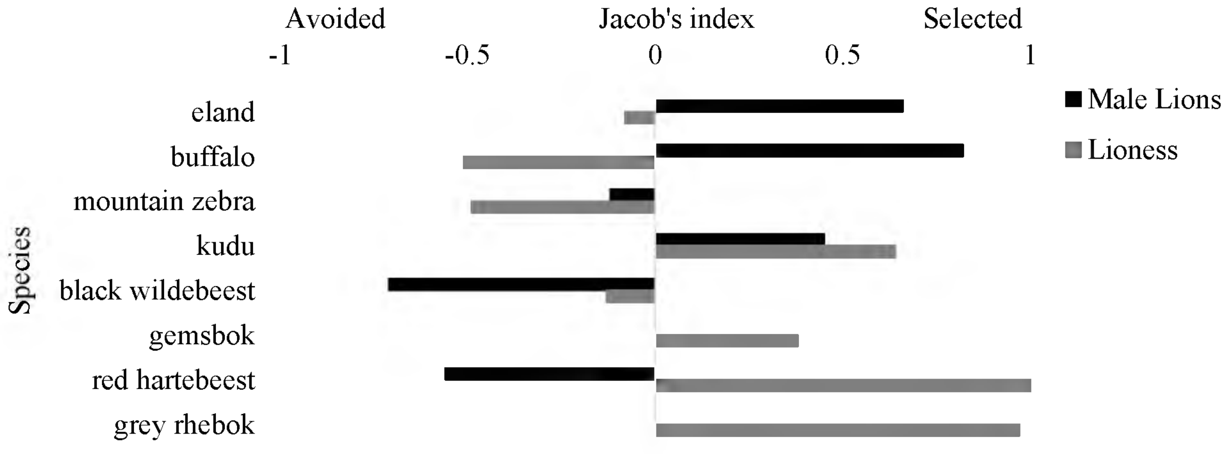


Figure 4.4: The Jacob's index values for the species preyed upon by the male lions, LM1 and LM2, and lioness, LF1.

Kill demographics

Age classes

Before the re-introduction of the lions, the cheetahs caught primarily adults and juveniles of the species they hunted. Following the lion re-introduction, the same pattern was evident. However, there was a significant increase in the number of 'unknowns' recorded (Figure 4.5A; χ^2=29.73; d.f.=3; $p<0.05$). Juveniles and 'unknowns' contributed 58.9% of the cheetah diet after the lions were re-introduced.

Sexes

Prior to the lion re-introduction, cheetahs killed more males than females, but a high percentage of kills remained unknown (Figure 4.5B). This was due to a large number of juveniles being caught by the cheetahs and it was difficult to determine the sexes of these juveniles (e.g. 53.6% of kudu caught were juveniles). Following the lion re-introduction, there was an increase in the number of females being caught, but the majority of recorded sexes remained unknown. There was no significant difference (χ^2=9.4; d.f.=2; $p>0.05$) in the number of male and female prey caught by the cheetahs before and after the lion re-introduction.

Sizes

The majority of the prey caught by the cheetahs before and after the lion re-introduction were in the medium sized category (Table 4.1; Figure 4.5C). Before the lions, 76.9% of all prey species caught were medium sized and after the lions 68.9% of all prey caught was medium sized. There were no significant differences ($\chi^2=2.16$;d.f.=2; $p>0.05$) in the numbers of the different sized prey killed by the cheetahs before and after the lion re-introduction.

Cheetahs vs lions

Age classes

The age composition of species caught by the cheetahs and lions revealed there to be significant differences ($\chi^2=122.62$;d.f.=3;$p<0.05$) across all the age groups (Figure 4.7A). The cheetahs killed more juveniles than the lions, while the lions killed more adults than the cheetahs (Figure 4.7A). A high percentage of juveniles and 'unknowns' were recorded for both the cheetahs and the lions.

Sexes

A comparison of the prey sexes caught by the cheetahs and lions showed that there was a significant difference ($\chi^2=60.26$;d.f.=2; $p<0.05$) between the two species (Figure 4.6). The lions caught significantly more male animals than the cheetahs. Interestingly, both the cheetahs and lions had a high number of unknowns in their diets.

Dietary overlap

Analyses of the diets before and after the re-introduction revealed a near complete overlap (O = 0.93) of cheetah diets (Figure 4.8). The diets of the cheetahs and lions did not have a significant overlap (O = 0.26). A comparison of the cheetah's dietary overlap with the male lions (LM1 and LM2) revealed there to be very little overlap (O = 0.15). The cheetahs had a greater overlap with the female lion (LF1; O = 0.42). However, there was no significant overlap (< 0.60) between the cheetahs and lions at the park level or individual level (Figure 4.8).

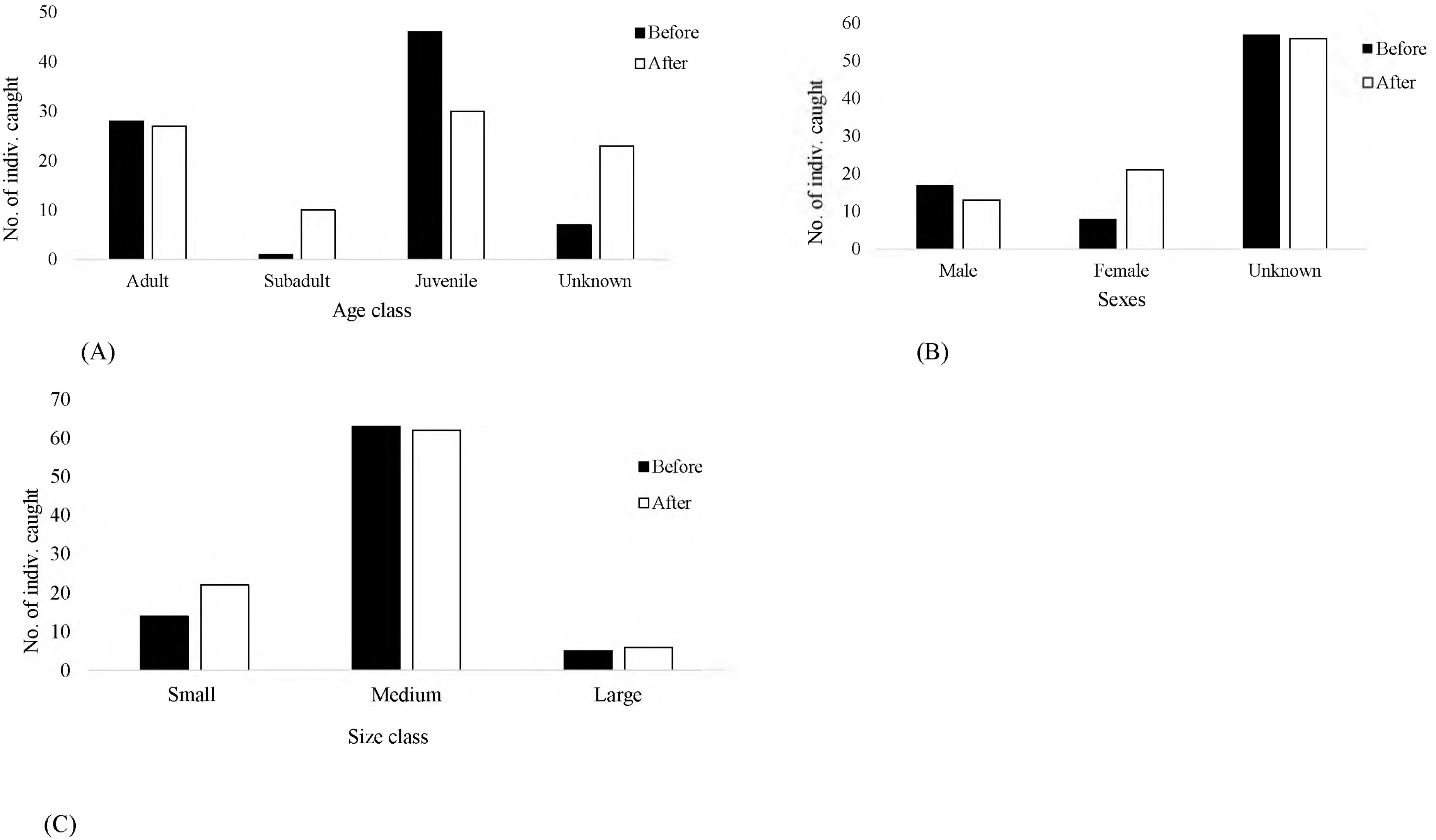


Figure 4.5: Age (A), sex (B) and size classes (C) of cheetah kills before and after the lion re-introduction to MZNP.

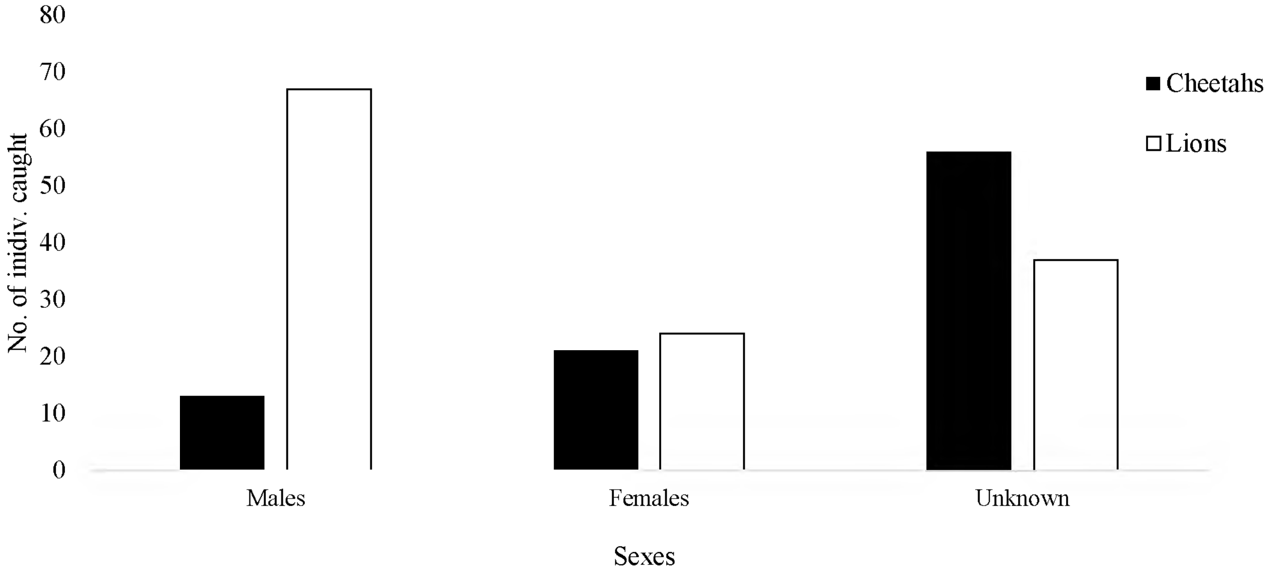
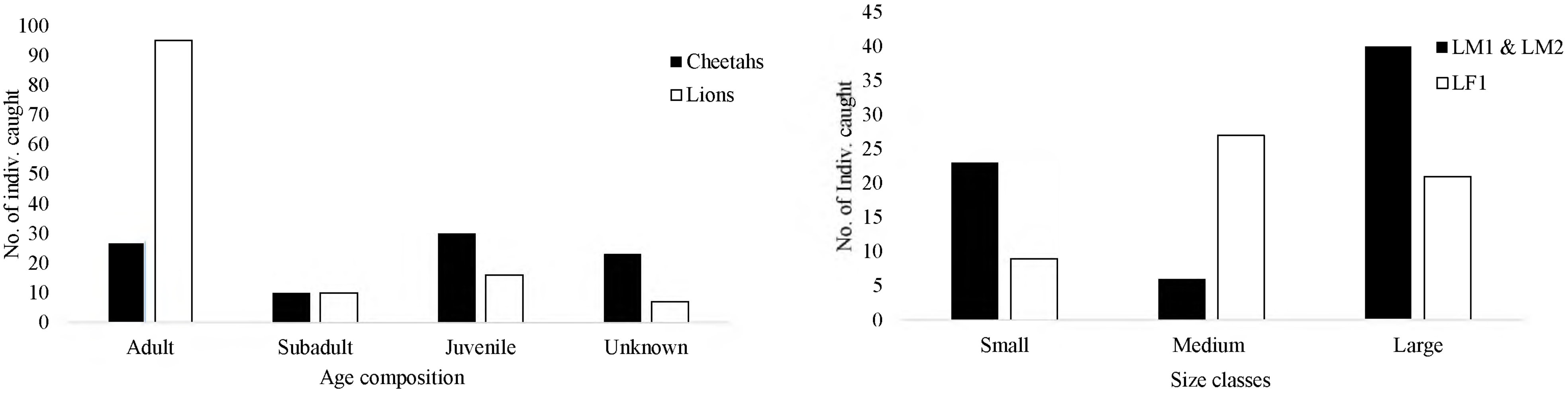


Figure 4.6: A comparison of prey sexes preyed upon by the cheetahs and lions in MZNP.



(A) (B)

Figure 4.7: Age (A) and size classes (B) of prey caught by the cheetahs and lions (LM1 and LM2 and LF1) in MZNP.

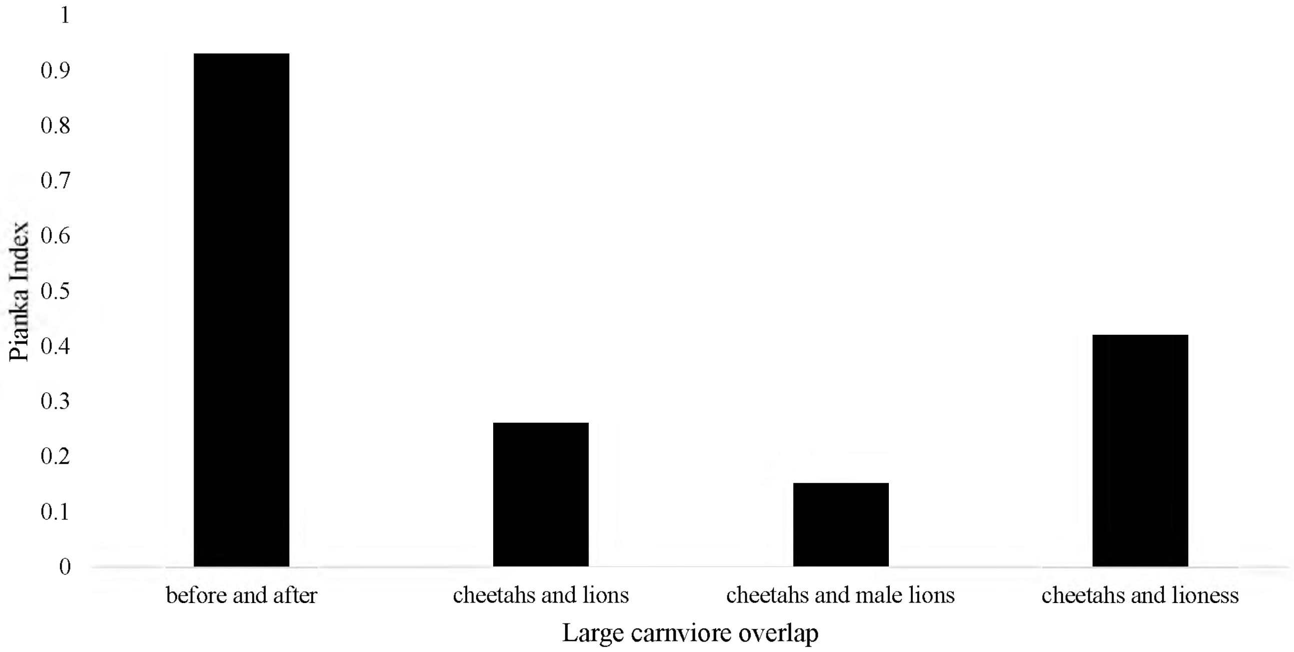


Figure 4.8: The dietary overlap between the cheetahs and lions at the park and individual levels in MZNP. Cheetah diets before and after the lion re-introduction were compared to determine if any dietary shifts had occurred and is presented as before and after.

DISCUSSION

Before the re-introduction of lions to MZNP, the cheetahs preyed upon seven different mammalian species but two (kudu and springbok) made up 85.3% of all species preyed upon. Following the re-introduction of lions, the cheetahs still preyed upon the same seven mammalian species, but included two new species, and four avian species. However, kudu and springbok remained the two most important (76.7%) species preyed upon. These findings support a number of other studies which have shown cheetah diets to comprise of only a few, often two – three key species (see Kruuk and Turner 1967, Schaller 1968, Pienaar 1969, Pettifer 1981, Caro 1994, Hunter 1998, Purchase and du Toit 2000, Mills *et al.* 2004, Radloff and du Toit 2004, Hayward *et al.* 2006b, Bissett and Bernard 2007, Marnewick *et al.* 2007, Tambling *et al.* 2014, Mills 2015). Although the cheetah's diets were dominated by only two species, the cheetahs preyed upon species across all weight categories. However, the majority of the species preyed upon were medium sized (30-65 kg) and these findings are also consistent with other studies (Mills *et al.* 2004, Radloff and du Toit 2004, Hayward *et al.* 2006b, Bissett and Bernard 2007, Tambling *et al.* 2014, Mills 2015).

Collectively, the lions in MZNP preyed primarily upon medium (60-120 kg) to large (>120 kg) sized prey. However, at the individual level, the male lions preyed primarily upon both larger and smaller sized prey compared to the lioness. Interestingly, all the species caught by the lions were mammalian. The overall lion diet results are consistent with findings from other studies across Africa (van Orsdol 1984, Mills and Shenk 1992, Hunter 1998, Funston and Mills 2005, Hayward and Kerley 2005, Loveridge *et al.* 2009, Tambling and Belton 2009, Tambling *et al.* 2010, Bissett *et al.* 2012, Mills 2015 and Davies *et al.* 2016).

Within the large carnivore guild in Africa, most predators take similar prey in spite of large differences in carnivore body size (Radloff and du Toit 2004). Thus, larger predators have wider prey options than smaller predators and if the larger predators of the carnivore guild are removed or absent then other members of the guild might be expected to increase their prey size range (Radloff and du Toit 2004). The absence of lions from 2012 till the beginning of 2013 could have resulted in an increased number of larger prey being caught by cheetah. Following the lion re-introduction there could have been a dietary switch back towards smaller sized prey. However, this was not the case with the cheetahs in MZNP. Hayward *et al.* (2006b) found that cheetahs preferentially hunt the most abundant, medium sized prey species in a particular area. Accordingly, the cheetahs of MZNP showed strong preferences for medium sized prey species both before and after the lion re-introduction. The fact that only solitary female cheetahs were studied could skew the dietary findings due to their smaller size and inability to catch larger prey species (Caro 1994). Certainly, Bissett (2007) found that male cheetahs, particularly coalitions of males, kill significantly larger prey than other cheetah social groups. Despite these observations, female cheetahs in MZNP did have the ability to catch larger (> 65 kg) prey but this was found to be a choice of one individual (CF6 caught adult kudu and black wildebeest) as opposed to all the females. This could be due to CF6 being younger and possibly stronger than the other females.

Kudu, particularly juveniles, and grey rhebok were the most preferred prey species hunted by the cheetahs before the lion re-introduction. These results differ (when using the prey sizes proposed by Hunter 1998) from the findings of Mills *et al.* (2004), who found that female cheetahs in the Kruger National Park prey primarily upon small prey species like grey duiker and steenbok. However, McVittie (1979) found cheetahs occurring in habitats devoid of large predators to prey upon larger prey than other cheetahs co-existing within an intact large carnivore guild.

Following the lion re-introduction, kudu, springbok and grey rhebok were the preferred species caught by the cheetahs. Despite the preference for the same species as before the lion re-introduction, there was a slight increase in the number of smaller species (such as steenbok and grey duiker) being caught, and birds were detected in the diet. An increase in smaller prey species can be explained by the work of Hayward *et al.* (2006b), who found that cheetahs kill smaller prey to reduce consumption time and the likelihood of detection by kleptoparasites. Bissett (2007) found cheetahs, particularly females, because of their solitary nature and smaller sizes, to be less likely to defend their prey and themselves against larger members of the carnivore guild. These findings support the findings of female cheetah diets in MZNP. Mills *et al.* (2004) and Mills (2015) also showed that female cheetahs tend to have higher number of smaller prey species in their diet when other large carnivores are present.

The presence or absence of lions did not affect the female cheetah's preferences to select species and the importance of kudu, springbok and grey rhebok presents a unique observation in cheetah hunting ability. Kudu prefer woodland habitats, springbok use open habits and grey rhebok tend to utilize mountainous terrain (Owen-Smith 1994, Skinner and Chimimba 2005). A comprehensive review of cheetah diets by Hayward *et al.* (2006b) came to the conclusion that prey species inhabiting open grassland seemed particularly susceptible to cheetah predation. Hayward *et al.* (2006b) further explained that cheetahs are highly adapted to a grassland niche. The preference of kudu and grey rhebok in MZNP contradict the contention that cheetahs are specialized, grassland hunters and support the findings by Bissett and Bernard (2007). The cheetahs in MZNP showed habitat adaptability by preferentially selecting woodland and mountain inhabiting species, similar to the cheetahs in Kwandwe Private Game Reserve which selected kudu in dense thicket biome (Bissett and Bernard 2007).

Collectively, the lions showed preferences for large and medium sized prey species. However, at the individual level, the male lions preferred buffalo and eland (Funston *et al.* 2001, Hayward and Kerley 2005, Hopcraft *et* al. 2005, Funston and Mills 2005, Hayward and Kerley 2008, Davies *et al.* 2016) and the lioness preferred red hartebeest, grey rhebok and kudu (Funston *et* al. 2001, Loveridge *et al.* 2009, Davies *et al.* 2016). The high prey preference index for grey rhebok should be interpreted with caution because, while it may reflect true preference, it can be artificially elevated because, if a population of a prey species is very small in a park, then a single predation event can produce a very high preference index score (Hayward and Kerley 2005). For example, the lioness in MZNP caught two grey rhebok and the census data showed the total population in the park was only 28 individuals and thus had a preference score of 0.97. Furthermore, the lioness did not spend significant amounts of time in the mountainous regions of the park and this could have been an opportunistic kill.

Competitive exclusion by large predators has been found to be a limiting factor for cheetah success (Durant 2000a, Hayward and Kerley 2008). However, selective predation has been thought to facilitate the co-existence of carnivores and reduce dietary overlap between interspecific guild members (Hunter 1998, Hayward and Kerley 2008). The presence of lions did not affect the cheetah's diet in relation to prey selection but significant differences were recorded with respect to prey size classes. The cheetahs caught more juvenile than adult animals after the lions were re-introduced. The consumption of smaller species reduced kill retention times, limiting unwanted detection by larger kleptoparasites, in this case lions, but still allowing for energetic demands to be fulfilled by the cheetahs (Hubel *et al.* 2016). Before the lions were introduced, the cheetahs caught more male than female antelope. The preference for male ungulates has been recorded in the Kalahari Gemsbok National Park (Mills 1984), the Serengeti (Fitzgibbon 1990), Kruger National Park (Mills *et al.* 2004), Kwandwe Private Game Reserve (Bissett and Bernard 2007) and Karongwe Private Game Reserve (Tambling *et al.* 2014). The reasoning for male selection was described by Fitzgibbon (1990) who found that male gazelles occur on the periphery of social groups, to be less vigilant and were found in smaller groups than females. Springbok have a similar social structure to Thomson's gazelles (*Eudorcas thomsonii*) and thus males could be more vulnerable to cheetah predation than females.

Following the lion re-introduction, there were no significant differences in the selection of the sexes. Before and after the re-introduction of lions, there was a high percentage of unknown sexes recorded in the cheetah diet due to very few kill remains being found at kill sites, particularly for kudu and springbok (C. Bissett and D. van de Vyver pers. obs.). Kudu are a 'hider species' and kudu calves are hidden for the first two to three months of their lives, after which they will follow their mothers and rejoin the family herds (Owen-Smith 1994). Female cheetahs that inhabited woodland vegetation units (see Chapter 3) could have flushed out hidden calves before catching and killing them. Interestingly, kudu are not the most abundant species in MZNP and the selection of calves in the woodland habitats, re-iterates the adaptability of the cheetah's hunting abilities. Bissett (2007) found that female cheetahs inhabiting thicket vegetation also caught kudu calves but this was thought to be due to kudu being the most abundant species in that reserve (supporting Hayward and Kerley 2006b), as opposed to being preferentially selected. Furthermore, once calves or fawns, joined the herds, they are usually slower and less experienced than the adults which could make easier targets for predators (Bissett 2007).

A comparison of lion and cheetah prey preferences showed a number of differences in overall dietary choices. The variation in prey sizes, sexes and age classes between the lions and cheetahs has been found to be a result of morphological and behavioural adaptations (Hayward and Kerley 2008). Wilson (1975) proposed that competition between species that differed significantly in body mass did not compete. Hayward and Kerley (2008) added that the morphological portioning of body mass amongst Africa's large carnivore guild would reduce dietary overlap and ultimately resource competition. However, interspecific competition can be intensified between large carnivores when enclosed in a reserve and competitors are exposed and forced to compete for the same finite resources (Hopcraft *et al.* 2005, Hayward and Kerley 2008, Lindsey *et al.* 2011, Bissett *et al.* 2012, Jooste *et al.* 2013). A comparison between the cheetah and lion diets at MZNP showed that there was no significant dietary overlap. In addition, finer scale comparisons between the cheetahs and the male lions showed there to be a near zero overlap in dietary preferences. Finally, while the lioness had a higher dietary overlap with the cheetahs, it too was not significant.

Funston *et al.* (1998) found that when male lions hunted in a coalition, not only did they experience higher success rates but they were also able to prey upon larger sized prey. The male lions at MZNP showed strong selection for eland and buffalo, which are the largest bovid species in the park (Skinner and Chimimba 2005). The selection of these species both supports and contradicts the findings made by Hayward and Kerley (2005), who reported that there was no relationship between prey availability and lion prey preference. However, prey body mass and lion pride size was found to be a significant contributor to prey preferences (Funston *et al.* 2001, Hayward and Kerley 2005).

Male lions were initially thought to have lower hunting success rates when compared to lionesses (Funston *et al.* 2001). Male lions were found to obtain most of their food from scavenging from lioness kills or kills from other predators (van Orsdol 1984, Mills and Shenk 1992). There have been several reasons proposed for why male lions have limited hunting success (see Funston *et al.* 2001), but overall size differences between the two lion sexes were thought to inhibit hunting success (Funston *et al.* 2001). However, a review of male lion hunting abilities found them to make use of fine scale adjustments within the landscape to catch prey (Funston *et al.* 2001, Hopcraft *et al.* 2005). Evidence supporting male lion adaptability was found with the selection of eland in MZNP. These findings contest the findings made by Hayward and Kerley (2005) who stated that eland were avoided by lions because of their behavioural adaptations; such as large herd sizes and increased vigilance levels. Even though this may be true elsewhere, the male lions in MZNP showed preference for eland, which have been found to be solitary or in small bachelor herds making them easier to catch (Estes 1991). Buffalo were a preferred prey species for male lions in the Kruger National Park (see Funston *et al.* 1998, 2001). However, the risks involved with preying upon such dangerous animals were outweighed by the energetic gains when successful, compared to hunting smaller, more fleet footed prey species (Funston *et al.* 1998). The male lion's selection for larger prey based on preference rather than abundance was evident at MZNP due to their strong avoidance of black wildebeest and red hartebeest. These two species, which fell within the apparent preferred weight category (Hayward and Kerley 2005), made up a third of the edible biomass available in MZNP and supports the earlier observations of Funston *et al.* (1998).

The lioness preferentially selected red hartebeest and kudu. These findings also support the observations of Funston *et al.* (2001) who found that lioness predation of larger prey was influenced by lion group size. But single lionesses were found to have a higher probability of success than pairs and despite the lioness in MZNP being a solitary hunter, she did have the ability to catch and kill adult eland and buffalo (albeit very rarely). The lioness showed strong avoidance for the prey species selected by the male lions. This could be due to high levels of intraspecific kleptoparasitism between the male lions and lioness (Funston *et al.* 2001). On more than one occasion, the male lions in MZNP kleptoparasited kills made by the lioness, while she was still on the kill (M. Paxton, field guide MZNP, pers. comm.). Thus, the inability of the lioness to defend larger kills from the male lions, coupled with the fact that she had to hunt alone, could have restricted her to only catching medium sized prey species. Interestingly, both the male lions and cheetahs have a high number of kills whose sexes were unknown. These kills whose sexes were unknown can be attributed to the opportunistic nature of male lions who caught juvenile prey (Hopcraft *et al.* 2005) and cheetahs catching small prey which made identification from kill remains difficult (D. van de Vyver, pers. obs., Mills and Mills 2013).

Due to variations in morphological adaptations and sheer size, it is not surprising that the cheetahs have such a low dietary overlap with the lions. This finding was further explained by the findings of Donadio and Buskirk (2006). Carnivores that have a high dietary overlap are more likely to have increased encounters or interactions as they hunted the same prey (Hayward and Kerley 2008). These competitive encounters have been found to increase interspecific aggression or killing over the same resources (Donadio and Buskirk 2006). Furthermore, interspecific killing is most likely to occur when an intermediate body size difference exists between two competing carnivores (for example, the larger carnivore is 2-5 times bigger than the other competing species) and at the intermediate body size difference, the larger carnivore (lion) is likely to perceive the smaller carnivore (cheetah) as a sizeable competitor but still small enough to be killed without serious risk to injury (Donadio and Buskirk 2006).

The factors affecting cheetah dietary selections cannot solely be attributed to the re-introduction of the lions. Prey selection by the cheetahs in MZNP may be a result of multiple, interacting factors such as abundance, size and vulnerability (selection of juveniles), prey distribution, habitat selection and presence of other large carnivores (Bissett 2007). Even though the presence of lions did seem to affect the size of prey being caught, the cheetahs did not prey upon the most abundant prey species occurring within the park as proposed by Hayward and Kerley (2006b). This may suggest the cheetahs are not entirely restricted to specific prey sizes. Kudu, grey rhebok, grey duiker and avian species such as the Crowned Lapwing (*Vanellus coronatus*) and Pied Crow (*Corvus albus*) suggest the cheetahs are hunting opportunistically and not selecting the most readily available or most abundant prey. In MZNP, kudu were the most preferred prey species, despite springbok being the most abundant, with the highest Jacob's Index value. Similarly, Pienaar (1969) found common reedbuck (*Redunca arundinum*) to be the most preferred prey in the Kruger National Park despite impala (*Aepyceros melampus*) being the most abundant. Bissett (2007) found blesbok to be the most preferred prey in Kwandwe Private Game Reserve, even though kudu were the most abundant species.

The re-introduction of lions did result in an increase in juvenile prey being caught by the cheetahs. The selection of smaller prey in areas that had thicker cover could be a result of specialization by cheetahs in MZNP to reduce kleptoparasitism in the presence of large carnivores. Single cheetahs feeding on smaller species, killed in thicket vegetation, had longer retention times and avoided unnecessary detection by unwanted, often larger competitors (Bissett and Bernard 2007).

Cheetah populations within protected areas across South Africa do not appear to be affected by the presence of lions (Swanson *et al.* 2014). However, Hayward and Kerley (2008) stated that interference competition was a primary factor affecting success of Africa's large carnivore guild and it was difficult to see cheetahs thriving under continued threat from lions. Furthermore, the clumping of competing predators into confined or restricted spaces (enclosed reserves) may increase the likelihood of interspecific competition which could result in localized extinctions of inferior predators (Hayward and Kerley 2008). However, Hopcraft *et al.* (2005) proposed that identical guilds of predators and prey could have very different hunting and feeding dynamics as a result of fine-scale differences employed across the landscape. The findings in MZNP further challenge a widespread perception that lions suppress cheetah populations (Kelly and Durant 2000, Chauvenet *et al.* 2011) at least when lions are at low densities. By being solitary, as in the case of female cheetahs, and the reduction in visibility by hunting in areas with thicker vegetation (woodland) cover can reduce lion inflicted cheetah mortalities and kleptoparasitism (Mills *et al.* 2004, Bissett and Bernard 2007, Mills and Mills 2013).

Overall, my findings suggest that cheetahs are not specialized hunters of open grassland species but that they are adaptable predators which can adjust their diets to fit the terrain in which they inhabit. The ability to make fine-scale adjustments in response to the re-introduction of lions further challenges the perceived perception of lions negatively affecting cheetah survival rates (Laurenson 1995, Durant 2000a). The responses and adaptations shown by the cheetahs in MZNP support the recent findings of cheetahs being able to co-exist with larger, more aggressive carnivores within an enclosed environment without compromising access to resources (Mills and Mills 2013, Swanson *et al.* 2014). However, more research, over longer time scales, is required across a range of lion and cheetah densities and habitats in order to fully explore this issue.

CHAPTER 5

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The next generation of cheetah cubs to MZNP. Image courtesy of C. Bissett.

The reproductive success of large carnivores ensuring their continued survival in South Africa has been found to vary in response to a number of factors (see Durant *et al.* 2015 and Bauer *et al.* 2016). The survival of large carnivores is dependent on the tolerance levels and intervention methods put in place by humans to ensure their continued existence in varied habitats across South Africa and Africa as a whole (Estes *et al.* 2011, Ripple *et al.* 2014). Furthermore, the presence of large carnivores is crucial to terrestrial ecosystems and understanding all aspects of their ecology provides valuable information with regards to their conservation (Estes *et al.* 2011). It is widely accepted that large carnivores need to be protected by fences but this has been found to present a number of other challenges (Bissett and Bernard 2007, Packer *et al.* 2013). In the Eastern Cape Province of South Africa, the switch in land use practices and the benefits of ecotourism has seen a number of large carnivore re-introductions in the past 25 years (Hayward *et al.* 2007b). The re-introduction of cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*) into small, enclosed reserves, such as Mountain Zebra National Park (MZNP) have contributed greatly to their conservation (Hayward *et al.* 2007b). However, cheetahs, in the presence of lions, have been found to be negatively affected and are often killed or excluded from favourable habitats (Durant 2000a, 2000b).

My findings have shown that cheetahs are able to co-exist with lions in a small, enclosed reserve without suffering from landscape-scale displacement while the lion density is low (Lindsey *et al.* 2011). These findings are similar to those of Broekhuis *et al.* (2013), Darnell *et al.* (2014) and Swanson *et al.* (2014). The cheetahs in MZNP did not avoid vegetation units or areas with a high likelihood of encountering lions but rather made fine-scale adjustments in their use of space in the presence of lions (Broekhuis *et al.* 2013). Smaller carnivores have been found to minimize negative encounters with larger carnivores by utilizing areas with fewer competitors or with lower prey densities (Broekhuis *et al.* 2013). However, this was not the case with the cheetahs in MZNP, as they still selected and utilized the same home range locations before and after the lion re-introduction. The presence and risk of encountering lions was an important factor in determining how the cheetahs used the available space within MZNP. The cheetahs maintained a mean distance of > 500 m away from the lions suggesting that the cheetahs may have the ability to assess the level of risk posed by the lions and adjusted their behaviour accordingly (Broekhuis *et al.* 2013, Swanson *et al.* 2014, Bissett *et al.* 2015). Despite my findings supporting more recent studies challenging the perception that cheetahs require areas with a low lion density or no lions to survive, there are still a number of unanswered questions, such as: how do cheetahs respond to lions over a 24 hour period? How long are cheetah kill retention times? What are the levels of kleptoparasitism? Answers to these questions will improve our understanding of how cheetahs respond to the presence and/or re-introduction of lions in enclosed reserves (Broekhuis *et al*. 2013, Vanak *et al*. 2013, Swanson *et al*. 2014).

All the female cheetahs and the lions in MZNP overlapped at the home range and core areas levels. However, apart from the lioness, all the female cheetahs and the male lions had multiple core areas within their home ranges. The high levels of home range and core area overlap may allow the cheetahs to cope with changes in lion numbers without suffering from competitive exclusion from preferred habitats as the lion population grows in MZNP. The selection of vegetation units by cheetahs changed before and after the lion re-introduction and generally the cheetahs preferred a combination of open and closed areas. The use of cover also changed after the lion re-introduction with cheetahs avoiding areas with the thickest cover which were selected by the lions. Bissett (2007) found that cheetah space use changed when females had cubs and den sites were selected close to water, in thick cover and considerable distances away from lions. Considering that the cheetahs are currently breeding in MZNP, the positions of their den sites in relation to lions could improve our understanding of their breeding requirements within enclosed reserves.

The cheetah diets were also similar to those reported from other studies, with small to medium sized prey comprising the majority of kills (Hayward *et al*. 2006b). However, the cheetahs in MZNP did not select the most abundant prey within the proposed prey range (see Hayward *et al*. 2006b) but selected kudu (*Tragelaphus strepsiceros*) calves which comprised 65.8% of all kudu killed by cheetahs before and after the lion re-introduction. The selection of prey did not vary dramatically before and after the lion re-introduction but the incorporation of different species suggests that cheetahs are opportunistic hunters and that their hunting may not necessarily be dictated by prey availability (Hayward *et al*. 2006b, Bissett and Bernard 2007). The preference for the same prey species in the cheetah's diet opposes the perception of smaller carnivores being excluded to areas of poor-prey availabilities in the presence of lions (Broekhuis *et al*. 2013).

The lions in MZNP had relatively smaller home ranges compared to elsewhere (see Loveridge *et al.* 2009). However, core areas were positioned in areas that afforded the greatest cover (along the Wilgerboom River) and increase the probability of successfully catching prey (Hopcraft *et al.* 2005). The preference of buffalo (*Syncerus caffer*) and eland *(Tragelaphus oryx*) by the male lions re-iterates how lion space use is influenced by 'catchability' within the landscape as opposed to abundance (Spong 2002, Hayward and Kerley 2005, Hopcraft *et al.* 2005).

Bissett (2007) stated that meta-analytical studies that showed prey species and sizes class preferences for a range of predators (see Hayward and Kerley 2005, Hayward *et al.* 2006b) created the impression that prey selection and preference was fixed at a predator level and did not vary in time and space. Indeed, the results of the large carnivore diets in MZNP have shown the adaptable nature of cheetahs and lions. Large carnivore diets should therefore be analysed separately within a specific region, as the influences of other carnivores and effects of predation can vary both spatially and temporarily (Smuts 1978, Bissett 2007, Valiex *et al.* 2009a).

Management implications

Darnell *et al.* (2014) suggested that when large carnivores are forced to co-exist at high densities in an enclosed reserved, it is the smaller carnivores most at risk to extinction. The information collected during this study has shown that cheetahs are able to make fine-scale adjustments in response to a lion re-introduction. However, if enclosed reserves are to continue to make a contribution to large carnivore conservation, long term assessments of predator-predator and predator-prey interactions are required (Hayward and Kerley 2009).

Two of the most influential factors affecting large carnivore success in enclosed reserves are carrying capacity and prey biomass (Hayward and Slotow 2009). Despite the cheetahs showing fine-scale avoidance of lions in MZNP, the small population of lions decreases the chances of cheetahs having negative encounters with lions (Vanak *et al.* 2013). Bissett (2007) added that understanding spatial requirements in response to changing carnivore numbers and the level of interspecific competition was equally important in ensuring long-term large carnivore success within enclosed reserves. Since the completion of this study, the lion population in MZNP has grown from three to seven (D. van de Vyver pers. obs.). Cheetah densities have been shown to have an inverse relationship with lion densities (Durant 2000a. 2000b). Thus, the changes in the carnivore populations require careful management, with particular emphasis on guild structure and composition (Hayward and Slotow 2009).

However, large carnivore compositions is often influenced by their tourism value, as opposed to their ecosystem contributions (Lindsey *et al.* 2007). For example, lions, particularly coalitions of males and females with cubs, rank highly amongst the viewing preferences of tourists (Lindsey *et al.* 2007). In enclosed reserves, incorrect large carnivore guild structure can have adverse effects on prey because of higher encounter rates causing localized extinctions due to selective predation (Hayward and Kerley 2005, Funston and Levendal 2015).

Although the availability of space is an important factor in the management of large carnivore guilds in enclosed reserves, the presence of large predators is also likely to affect prey populations (Radloff and du Toit 2004). The lion diets in MZNP showed that a small number of lions can kill a substantial number of animals on an annual basis. Lehmann *et al.* (2008b) found that a coalition of male lions killed a larger number of animals than a single male. For example, in MZNP, the male lions killed four animals in three days in September 2013 and five animals in seven days in November 2016 (D. van de Vyver pers. obs.). Thus, reserves need to be able to ensure that the preferred prey base is large enough to sustain a lion population as well as other members of the large carnivore guild (Lehmann *et al.* 2008b). A true reflection of large carnivore diets is therefore needed to accurately determine their overall effects on their prey (Lehmann *et al.* 2008b).

The quantification of the large carnivore diets in MZNP, especially for cheetahs, was difficult when using the GPS cluster method with a spatial resolution of six hour intervals. Many kills were missed because cheetahs killed between fix times or moved off within one to two hours after catching their prey (C. Bissett and D. van de Vyver pers. obs.). The successful location of cheetah kills from the GPS clusters in MZNP before the lion re-introduction was 23.6% and 21.3% after the lion re-introduction compared to 80.7% for lion kills. Previous studies have shown there is bias with *ad hoc* observations, as they under-represent small prey species (Mills 1984). Continuous observations or an increase in GPS fix resolution would improve the ability of locating cheetah kills (Radloff and du Toit 2004, Tambling *et al.* 2010).

Continuous observations can provide additional information in helping determine the factors affecting decisions to hunt and the measurement of Daily Energy Expenditure of cheetahs and lions in MZNP (Bissett 2007). Hilborn *et al.* (2012) found that prey size and the availability of vulnerable prey were the important factors affecting a cheetahs decision to hunt. Differences in ages have also been found to affect hunting success, with young carnivores relying on small prey due to their inexperience in perfecting different hunting techniques (Hilborn *et al.* 2012). The differences in hunting abilities of carnivores of varied ages can result in differential predation pressures on prey, causing unexpected population collapses (Power 2002, Hilborn *et al.* 2012). In MZNP, cheetahs prey upon kudu calves and lions prey upon the adults and continued predation pressure could result in the collapse of the kudu population (Hilborn *et al.* 2012). Miller *et al.* (2016) suggested that reserve managers routinely manage their carnivore populations through translocations every three years to simulate natural emigration and prevent excess killing of selected prey or contracepting females as they became sexually mature to limit population growth. Trinkel *et al.* (2008) proposed translocations to be an important adaptive management tool as populations of large carnivores become fragmented or exceed the reserves carrying capacity.

Often, large carnivores re-introduced into enclosed reserves are managed to limit population growth and maintain genetic variability and diversity (Funston and Levendal 2015). However, when carnivores are allowed to breed, problems can arise when reserve carrying capacities are exceeded and this can be further complicated by a lack of suitable reserves that are able to support these 'excess' carnivores (Bauer *et al.* 2015). Van der Merwe *et al.* (2016) stated that a scientifically-based national metapopulation management plan should be implemented for all large carnivores in South Africa. This approach would effectively allow for gene flow to be maintained between reserves that have large carnivores (van der Merwe *et al.* 2016). Funston and Levendal (2015) stated that although the management of a metapopulation was an intensive and potentially costly process, it did ensure the continued survival of fragmented populations and reduced the chances of inbreeding.

The translocations of cheetahs into reserves with unfamiliar terrain or without any experience of larger carnivores, particularly lions, has been found to be unsuccessful (Lindsey *et al.* 2011). The majority of reserves seeking cheetahs, require lion habituated individuals (van der Merwe 2014).

However, the results from my study suggest that cheetahs do not need to be lion habituated before they can survive within a large carnivore guild. However, due to the spatial resolution of GPS fix downloads it was not possible to determine the effects of cheetah activity patterns before and after the lion re-introduction. Bissett *et al.* (2015) found that there were significant differences in the activity patterns of cheetahs, particularly females, in reserves with and without lions. Furthermore, cheetahs in reserves where lions were absent, were active throughout the 24 hour day (Bissett *et al.* 2015). In contrast, in the presence of lions, cheetahs were found to be primarily crepuscular with little to no activity occurring at night suggesting a shift in cheetah behaviour in response to lions (Bissett *et al.* 2015). Further studies addressing cheetah activity patterns after the lion re-introduction in MZNP could thus add additional information on how cheetahs respond to the presence of lions over a 24 hour period.

The cheetahs showed temporal avoidance in response to lions by reducing their activities at night (Bissett *et al.* 2015). The changes in activity patterns are thought to have evolved to maximize hunting success, minimize the effects of inter-guild competition but still maintain some degree of behavioural flexibility (Bissett *et al.* 2015). Behavioural flexibility allows smaller carnivores to respond to the natural changes in prey species responding to the effects of predation and the top-down pressures of superior carnivores through interference competition and kleptoparasitism (Bissett *et al.* 2015).

Smaller carnivores are particularly susceptible to the effects of kleptoparasitism from larger carnivores which can result in competition displacement (Scantlebury *et al.* 2014). In the Kalahari, Scantlebury *et al.* (2014) found that cheetahs were subjected to kleptoparasitism from brown hyaenas (*Hyaena brunnea*) and lions. Cheetahs were found to be able to cope with kleptoparasitism rates of 25% or less within large systems with an intact carnivore guild (see Scantlebury *et al.* 2014).

However, the effects of brown hyaenas on cheetahs within enclosed reserves is poorly understood and recent research has found that brown hyaenas do exceptionally well in enclosed reserves (see Welch 2014 and Comley 2016). Furthermore, the presence of large predators within enclosed reserves can aid in the success of brown hyaenas, through an increase in scavenging opportunities (Yarnell *et al.* 2013). This theory was found to be true for the brown hyaena population in MZNP

(Comley 2016). The abundance of readily available food sources has been thought to facilitate a high brown hyaena population (Yarnell *et al.* 2013). However, Mills (2015) found that the relationship between brown hyaenas and lions was unusual because the smaller hyaena derived considerable benefit from the presence of the larger lion. Brown hyaenas scavenging from lion kills were able to gain large amounts of food, as they were usually large ungulates (Mills 2015). Mills (2015) concluded that brown hyaenas gained more than they lost from the presence of lions in the Kalahari. The brown hyaena population has already experienced a 400% increase in size in MZNP since their re-introduction in 2008 (see Comley 2016) and the presence of lions has been found to be beneficial to their existence (Mills 2015). Thus, future research and management interventions should focus on determining hyaena movements via GPS collars set to the same download times as the lions and cheetahs. Mills (2015) found that cheetahs were an important food contributor to the brown hyaena. However, only 6% of observed cheetah kills were kleptoparasitized by the brown hyaenas in the Kalahari and the extent of kleptoparasitism on cheetahs in MZNP is yet to be determined (Mills 2015, Comley 2016).

Lindsey *et al.* (2011) presented a range of scenarios to help reserve managers make the most informed decisions with regard to cheetah re-introductions in order for them to be successful but acknowledged the challenges imposed by small, enclosed reserves with competing carnivores. The management of metapopulations requires innovative strategies to either increase carrying capacities or reserve sizes to sustain their large carnivore guilds (see Lindsey *et al.* 2011, van der Merwe *et al.* 2016). Broekhuis *et al.* (2013) stated that to better understand the mechanisms facilitating large carnivore co-existence, spatial resolution, temporal variations and environmental complexity needed to be analysed both independently and collectively. Thus, a holistic and integrated approach, which incorporates a variety of ecological processes and a number of participating reserves is required to ensure the continued existence of large carnivores, not only within MZNP but all enclosed reserves across South Africa (Miller *et al.* 2016, Pooley *et al.* 2016, van der Merwe *et al.* 2016).

APPENDICES

Appendix 1: The mammal list of Mountain Zebra National Park.

ORDER RUMINANTIA
Black wildebeest *Connochaetes gnou*
Blesbok *Damaliscus pygargus phillipsi*
Bushpig *Potamochoerus larvatus*
Cape buffalo *Syncerus caffer*
Eland *Tragelaphus oryx*
Gemsbok *Oryx gazella*
Grey duiker *Sylvicapra grimmia*
Grey rhebok *Pelea capreolus*
Klipspringer *Oreotragus oreotragus*
Kudu *Tragelaphus strepsiceros*
Mountain reedbuck *Redunca fulvorufula*
Red hartebeest *Alcelaphus buselaphus*
Springbok *Antidorcas marsupialis*
Steenbok *Raphicerus campestris*
Warthog *Phacochoerus africanus*

ORDER CARNIVORA
Aardwolf *Proteles cristatus*
African striped weasel *Poecilogale albinucha*
African wild cat *Felis lybica*
Bat-eared fox *Otocyon megalotis*
Black-backed jackal *Canis mesomelas*
Black-footed cat *Felis nigripes*
Brown hyaena *Hyaena brunnea*
Cape clawless otter *Aonyx capensis*
Cape fox *Vulpes chama*
Cape grey mongoose *Galerella pulverulenta*
Caracal *Caracal caracal*
Cheetah *Acinonyx jubatus*
Honey badger *Mellivora capensis*
Large-spotted genet *Genetta tigrina*
Lion *Panthera leo*
Small-spotted genet *Genetta genetta*
Striped polecat *Ictonyx striatus*
Suricate *Suricata suricatta*
Marsh mongoose *Atilax paludinosus*
Yellow mongoose *Cynctis pencillata*

ORDER HYRACOIDEA
Rock hyrax *Procavia capensis*

ORDER MACROSCELIDEA
Cape rock sengi *Elephantulus edwardii*
Eastern rock sengi *Elephantulus myurus*
Smith's rock sengi *Elephantulus rupestris*

ORDER EULIPOTYPHLA
South African hedgehog *Erinaceus frontalis*

ORDER LAGOMORPHA
Cape hare *Lepus capensis*
Natal red rock rabbit *Pronolagus crassicaudatus*
Scrub hare *Lepus saxatilis*
Smith's red rock rabbit *Pronolagus rupestris*

ORDER PERISSODACTYLA
Black rhinoceros *Diceros bicornis bicornis*
Cape mountain zebra *Equus zebra zebra*

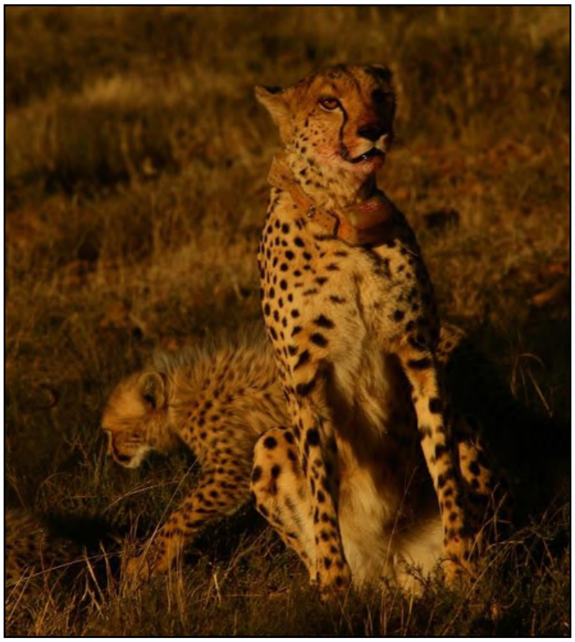
ORDER PRIMATES
Chacma baboon *Papio ursinus*
Vervet monkey *Cercopithecus pygerythrus*

ORDER RODENTIA
African pygmy mouse *Mus minutoides*
Four-stripped grass mouse *Rhabdomys pumilio*
Ground squirrel *Xerus inauris*
Karoo bush rat *Otomys unisulcatus*
Porcupine *Hystrix africaeaustralis*
Springhare *Pedetes capensis*

ORDER TUBLIDENTATA
Aardvark *Orycteropus afer*

Appendix 2: Study animals in Mountain Zebra National Park. Images by D. van de Vyver and C. Bissett.

CF3



CF4

CF6

CF35

LM1 and LM2

LF1

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