# POPULATION ASSESSMENT AND FEEDING ECOLOGY OF BROWN HYENAS (*HYAENA BRUNNEA*) IN MOUNTAIN ZEBRA NATIONAL PARK, EASTERN CAPE, SOUTH AFRICA

A thesis submitted in fulfilment of the requirements for the degree of

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by

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# ABSTRACT

The development of many small (<400 km$^2$), enclosed game reserves in the Eastern Cape Province of South Africa over the past 25 years has contributed greatly to the conservation of large carnivores. However, the brown hyena (*Hyaena brunnea*) is one of the least studied large carnivores in South Africa. Nevertheless, the reintroduction of this species (n=3 in 2008) into Mountain Zebra National Park (MZNP) provided the perfect opportunity to broaden our understanding of the role that this carnivore plays in an enclosed system. Camera trap data was collected for just over a year from April 2014 to April 2015 and brown hyena density estimates were calculated using spatially explicit capture-recapture analysis. Left-side images of brown hyenas were used in the analysis and 12 individuals were positively identified. The best model to estimate brown hyena density included a road covariate and estimated brown hyena density to be 6-10 individuals/100 km$^2$ (an absolute abundance of between 12 and 21 individuals), which is higher than densities calculated for brown hyenas in other arid, open systems. In, addition, brown hyena scat samples were collected over a five year period from April 2011 to June 2015 and standard techniques for scat analysis were used to identify prey items. Cheetah (*Acinonyx jubatus*) and lion (*Panthera leo*) kill site data were used to investigate the impacts of these species on the diet of brown hyenas. Before the release of lions brown hyenas predominantly scavenged on medium-sized mammals, which was what the cheetahs mainly killed. However, after the release of the lions, brown hyenas predominantly scavenged on large mammals, which was what the lions primarily killed. The results from my study indicate that brown hyenas are most likely reaching high densities in enclosed systems, due to increased scavenging opportunities provided by other large predators. The rapid increase of brown hyena densities from small founder populations in enclosed reserves could result in inbreeding. Therefore, in order to successfully conserve brown hyenas and other large carnivores in South

Africa, continual post-release monitoring and possible implementation of meta-population management schemes is required.

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# CHAPTER 1

# GENERAL INTRODUCTION

**Brown hyena photographed in the south of Mountain Zebra National Park portraying its long pointed ears and striped legs**

The mammalian order Carnivora consists of over 280 extant species, of which almost all are predators (Treves & Karanth 2003; Karanth & Chellam 2009). Mammalian carnivores are extremely ecologically diverse and have occupied all continents and all major habitat types on Earth (Agnarson *et al.* 2010). In many terrestrial systems, large carnivores occupy the top position of the food web which means that they have the ability to fundamentally alter the structure and function of entire ecosystems through profound influences on biological communities via predation and interspecific competition (Miller *et al.* 2001; Treves & Karanth 2003; Ripple *et al.* 2014). Even medium and small sized carnivores have the potential to be drivers of ecosystem processes despite their relative rarity across landscapes (Gompper *et al.* 2006). Carnivore management has thus become one of the central concerns of conservation biologists (Treves & Karanth 2003).

Over the past two centuries, carnivores across the globe have experienced extreme population declines and are being threatened with extinction due to geographic range contractions, fragmentation of their habitat and human persecution (Abay *et al.* 2011; Ripple *et al.* 2014). The larger and more predatory carnivores appear to be suffering the severest population declines and range contractions (Ripple *et al.* 2014) because of their naturally low population densities, slow population growth rates, expansive spatial requirements and inevitable conflict with humans (Woodroffe & Ginsberg 1998; Hayward *et al.* 2007a; Balme *et al.* 2010). Human-wildlife conflict, which is defined as the scenario where the behaviour of a wild animal negatively affects the needs of humans, is one of the greatest threats to large carnivores across the globe (Treves & Karanth 2003). The most significant cause of human-wildlife conflict is due to the real and perceived depredation threats that large carnivores pose to valuable livestock and game species (Rust & Marker 2013). These threats often result in lethal retaliation by humans, which has contributed greatly to the extirpation of many carnivores from substantial parts of their range (Marnewick *et al.* 2008; Rust & Marker 2013). One way of effectively managing and conserving large, wide-ranging carnivores is to understand their spatial requirements and roles within ecosystems (Marker & Dickman 2005; Terborgh & Estes 2010). For many large carnivores, detailed and reliable knowledge on diet, social organisation, population biology and community ecology is lacking, which is impeding the conservation of these species (Karanth & Chellam 2009).

Collecting accurate biological and ecological data on large carnivores is, however, very difficult because many species are solitary and elusive (Karanth *et al.* 2003; Balme *et al.* 2009). Direct counts of large carnivores are basically impossible and are impractical due to their high time and cost constraints (Schwarz & Seber 1999). Indirect methods such as camera trapping, in conjunction with capture-recapture analysis, have become one of the most efficient ways to collect valuable data on wide-ranging and elusive large carnivores (Karanth 1995; Thorn *et al.* 2009; Gerber *et al.* 2010).

The agricultural and economic development of South Africa in the early 20th century led to the local extinction of many large predators in all but the most uninhabitable areas (Hayward *et al.* 2007a; Skead 2007; Devineau *et al.* 2010). During the past two decades, however, the conversion of uneconomical pastoralism into small (<400 km$^2$), fenced-off national parks and private game reserves in South Africa, particularly the Eastern Cape, led to the reintroduction of locally extirpated populations of wildlife (Hayward *et al.* 2007a; Devineau *et al.* 2010). Although the conservation of large carnivores in South Africa has benefited hugely from the reintroduction of species into private game reserves and national parks, post-release monitoring and evaluation of such programmes rarely occurs (Hayward *et al.* 2007b; Devineau *et al.* 2010). Given the global concern of large carnivores declining, along with their ecological importance and ability to alter ecosystems, documenting the results of their reintroductions is crucial for the development of future conservation and management plans (Estes *et al.* 2011; Hayward *et al.* 2007b; Devineau *et al.* 2010).

In many of these parks and reserves, extirpated carnivores such as lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*) and brown hyenas (*Hyaena brunnea*) have been reintroduced (Hayward *et al.* 2007b). The first carnivore reintroduction into an enclosed reserve in the Eastern Cape was in 1985, where three brown hyena were released into the Great Fish River Complex (Hayward *et al.* 2007b). Since then, several national parks (e.g. Mountain Zebra National Park and Addo Elephant National Park) and private game reserves (e.g. Kwandwe Private Game Reserve and Shamwari Private Game Reserve) have reintroduced brown hyenas along with other large carnivores (Hayward *et al.* 2007b). The brown hyena, which is amongst the least studied of all the charismatic predators found in enclosed reserves of the Eastern Cape, is the focus of the present study.

The family Hyaenidae contains only four extant species of hyena; the striped hyena (*Hyaena hyaena*), spotted hyena (*Crocuta crocuta*), brown hyena and aardwolf (*Proteles cristatus*) (Rohland *et al*. 2005). This family is one of the smallest families among mammalian carnivores but is known for its remarkable social and ecological diversity (Watts & Holekamp 2007). The aardwolf belongs to its own sub-family, Protelinae, and is the only species with a highly specialized diet, feeding exclusively on termites (Rohland *et al*. 2005). The other three species of hyena belong to the sub-family Hyaeninae and are hunters and/or scavengers (Rohland *et al*. 2005).

The brown hyena is a rare animal, endemic to southern Africa, with restricted ranges in Namibia, Botswana, southern Zimbabwe, Mozambique, south-western Angola and South Africa (Fig.1.1; Fig.1.2; Estes 1992; Rothschild & Rothschild 1994; Werdelin & Barthelme 1997). Not only is the brown hyena a rare species, but it also has low genetic diversity, making it susceptible to extinction in the wild (Rohland *et al.* 2005; Thorn *et al.* 2009; Ripple *et al.* 2014).

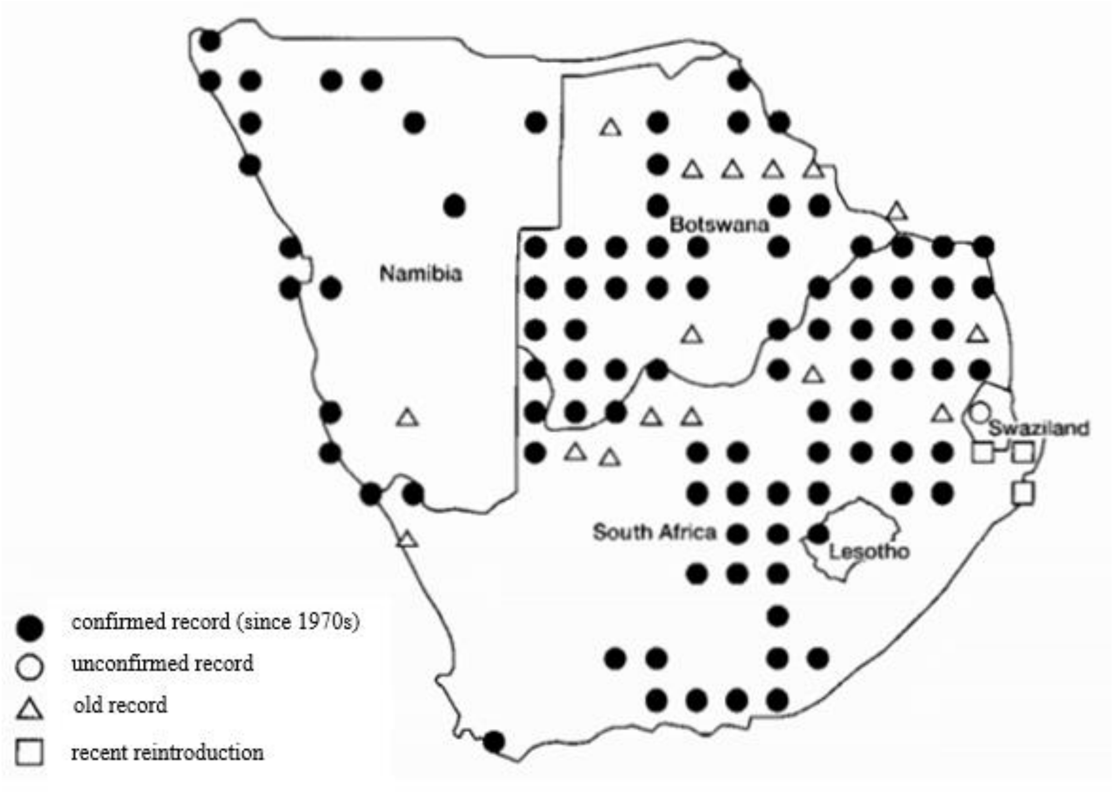

**Figure 1.1:** Distribution of brown hyenas throughout Namibia, Botswana, South Africa, Lesotho and Swaziland (Mills & Hofer 1998).

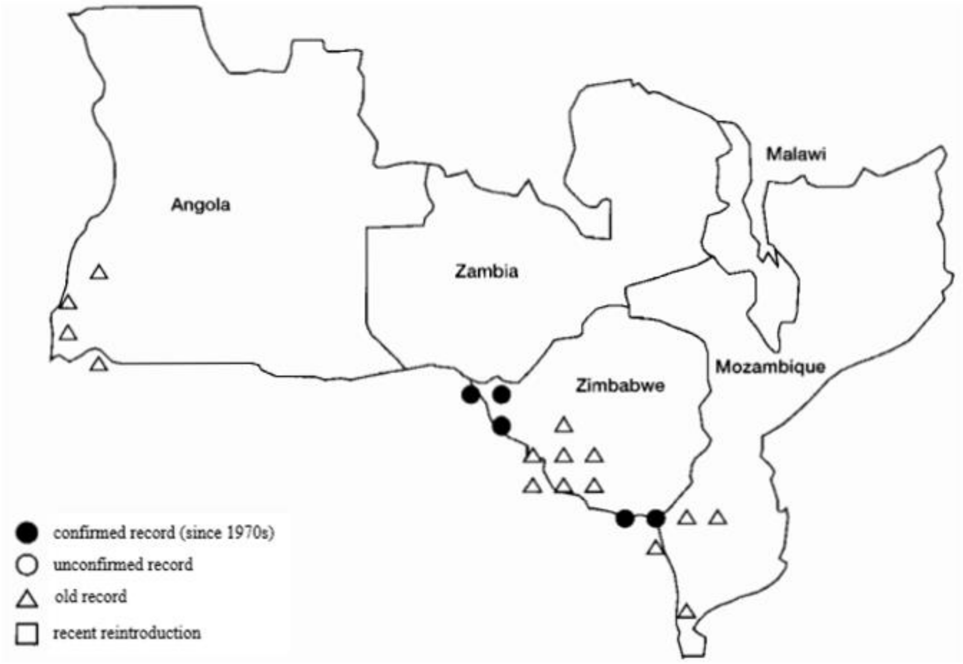

**Figure 1.2:** Distribution of brown hyenas throughout Zimbabwe, Mozambique and Angola (Mills & Hofer 1998).

Brown hyenas are medium to large carnivores with an average weight of 40.7 kg but can weigh anything between 34.2 and 72.6 kg (Owens & Owens 1978; Skinner & Chimimba 2005). Even though there is no clear evidence of sexual dimorphism between male and female brown hyenas, their average mass is listed separately as 47 kg for males and 42 kg for females (Owens & Owens 1978; Skinner & Chimimba 2005). Brown hyenas are almost exclusively nocturnal throughout their range and are most active between sunset and sun-rise (Mills 1984; Hulsman *et al.* 2010). The main characteristics of brown hyenas are their large pointed ears and coarse dark brown shaggy coat, which has hairs that can reach up to 25 cm long, especially around their mantle and tail (Estes 1992; Wiesel 2007). Their mane is lighter in colour (straw-coloured) than the rest of their body and their legs have black stripes (Estes 1992; Wiesel 2007). The teeth of brown hyenas are massive in comparison to many other large carnivores, but it is their upper carnassial tooth which is particularly large and well adapted for crushing bones (Owens & Owens 1978; Skinner & Chimimba 2005). Brown hyenas have a small vocal repertoire with only eight vocalisations; a yell, hoot, two whines and four growls, have been identified (Mills 1984). Their most prominent visual display is pilo-erection of their long back and neck hairs, which usually occurs when there is either the tendency to attack or flee (Mills 1984).

Brown hyenas either live as members of a clan or nomadically (Owens & Owens 1978; Skinner & Chimimba 2005). Small clans usually consist of a single female and her cubs, whereas larger clans consist of extended families, which usually include at least one female, her adult offspring of both sexes and an immigrant male (Owens & Owens 1978; Skinner & Chimimba 2005; Watts & Holekamp 2007). Males that leave their natal clans either adopt a nomadic life style or migrate to a new clan (Watts & Holekamp 2007). Nomadic male brown hyenas are not territorial and therefore do not defend a home range (Owens & Owens 1978; Skinner & Chimimba 2005). Members of a clan not only defend their home ranges, which usually includes the communal den site, satellite dens and the feeding grounds used by the clan, but also feed together on large food items and carry food back to the den for the cubs (Owens & Owens 1978; Skinner & Chimimba 2005). All cubs are raised at den sites and generally stay within close proximity to their dens until they are 15 months old (Mills 1982). For the first three months, the cubs will feed only on their mother’s milk, after which their diet is supplemented by carcasses which have been carried to the den by members of the clan (Mills 1982). Within brown hyena clans there seems to be no dominance hierarchy where clan and home range sizes change according to food availability and climatic conditions (Owens & Owens 1978; Mills 1984; Skinner & Chimimba 2005). Clan size is mainly regulated by food quality and abundance, whereas home range size is mainly regulated by the distribution of food (Mills 1981).

Latrine sites are utilized when defecating and these usually occur at conspicuous landmarks such as junctions, crossroads and rivers or under a tree or large bush (Hulsman *et al.* 2010; Fig.1.3b). Brown hyenas also utilize paste markings (anal sac secretions; Fig.1.3a) which are deposited on grass stalks, bushes or rocks throughout their territory (Owens & Owens 1978; Estes 1992; Skinner & Chimimba 2005; Wiesel 2007; Hulsman *et al.* 2010). The paste markings consist of a white paste which has a long lasting odour and a black paste which has a less long lasting odour (Wiesel 2007; Fig.1.3). Both the latrines and paste markings are used to mark their territories and to communicate between clan members (Owens & Owens 1978; Skinner & Chimimba 2005; Wiesel 2007; Hulsman *et al.* 2010). Behavioural evidence has shown that brown hyenas are able to distinguish between markings made by clan members and those of outsiders (Estes 1992). It is important for brown hyenas to know where other members of the clan have recently foraged, so that time and energy is not wasted foraging in an area which is likely to be unproductive (Mills 1984).

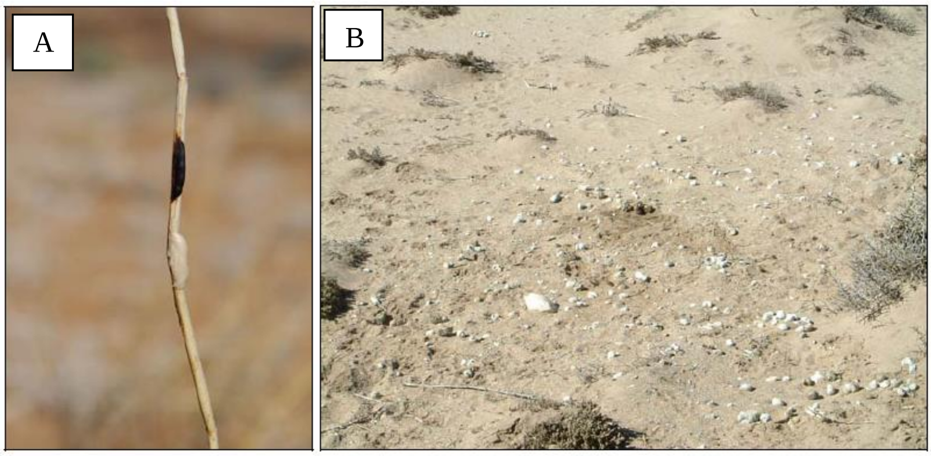

**Figure 1.3:** Example of a brown hyena paste marking (A) and latrine site (B) in Namibia (Wiesel 2007).

Although brown hyenas generally exist in small extended family groups (clans), they usually forage on their own, following previously used trails that have been scent-marked (Owens & Owens 1978; Binder & Van Valkenburgh 2000; Skinner & Chimimba 2005). This is because the food items that are found can typically only sustain one hyena and foraging in a group would not increase their efficiency in finding food (Mills 1984). Brown hyenas are predominantly scavengers, meaning that they feed on carcasses, which neither they, nor others of their species killed (Burgener & Gussett 2003). They have been recorded to kill less than 6% of the biomass of food observed to be consumed in the southern Kalahari (Mills 1984).

Throughout their range, brown hyenas are suspected to be in population decline due to human persecution and habitat fragmentation (Mills & Hofer 1998; Wiesel *et al.* 2008; Thorn *et al.* 2009). In commercial farming areas, brown hyenas have been heavily persecuted (hunting, poisoning and trapping) due to the perceived threat that they pose to livestock (Hofer & Mills 1998; Mills 1998). Currently, brown hyenas are listed as near threatened by the World Conservation Union (IUCN) and if the deliberate persecution of this species continues it could lead to the species being classified as threatened (Wiesel *et al.* 2008).

Extensive studies on brown hyenas have been conducted in the arid regions of southern Africa such as the Kalahari (Mills & Mills 1978; Owens & Owens 1978; Owens & Owens 1979; Mills 1982; Mills & Mills 1982; Owens & Owens 1984), Namib Desert (Skinner & van Aarde 1981; Skinner *et al.* 1995; Wiesel 2007), Makgadikgadi National Park in Botswana (Maude & Mills 2005) and Ghanzi district in Botswana (Kent & Hill 2013). Research has also been conducted in the Pilanesberg National Park (Thorn *et al.* 2009) and the North-West province of South Africa (Thorn *et al.* 2011; Yarnell *et al.* 2013). These studies have generally been conducted in relatively large systems (>500 km$^2$) and only recently have studies been conducted on brown hyenas in small, fenced game reserves (Slater & Muller 2014; Welch *et al.* 2015). In the large, open and arid systems, studies have found that brown hyenas scavenged over large territories, seldom hunted and supplemented their diet in the winter months by feeding on birds, reptiles, insects and fruit (Mills & Mills 1978; Owens & Owens 1979). In these large, open systems, food availability is generally lower and more widespread throughout the reserves than that found in enclosed reserves (Mills 1982; Wiesel 2006).

Thus, in enclosed systems where food availability is higher (Yarnell *et al.* 2013) and the movement of species is restricted, I predicted that the diet of brown hyenas would differ from those found in the arid, open regions of southern Africa. I also predicted that the density estimates of brown hyenas in enclosed systems would be higher than those of the larger, open systems due to the increased abundance of food provided by large predators and because threatening processes such as human persecution are absent (Mills 1984).

The aims of this study were to estimate the density of brown hyenas in an enclosed reserve and to provide information on their distribution and feeding ecology. This was achieved by conducting a comprehensive camera trapping survey and scat analysis.

# CHAPTER 2

# STUDY SITE

**View of the low lying areas of Mountain Zebra National Park**

## STUDY AREA

Mountain Zebra National Park (hereafter MZNP, -32°18’S and 25°24’E) is a South African National Park (SANParks) situated approximately 15 km west of Cradock in the Eastern Cape Province, South Africa (Gaylard *et al.* 2008; Fig.2.1). It was proclaimed in 1937 for the purpose of protecting a remnant population of the Cape mountain zebra (*Equus zebra zebra*) and has since played a principle role in the conservation of the biodiversity of the area (Gaylard *et al.* 2006). The park is classified as being part of the Nama Karoo, but falls in a transitional zone between the arid Nama Karoo bushveld in the west and the drier ‘sweet’ grassveld in the east (Gebeyehu & Samways 2002; Pond *et al.* 2002). The park is approximately 21 000 hectares and measures about 25 km from north to south and about 15.5 km from east to west (Gaylard *et al.* 2006).

## TOPOGRAPHY AND GEOLOGY

The park has a major river, the Wilgeboom (Fig.2.1 & 2.2), flowing through it which is semi-perennial and only flows during the rainy season (Gaylard *et al.* 2006). The wildlife is supplied with water all year round through artificially sourced dams and pans as there are no natural permanent water sources in MZNP (Gaylard *et al.* 2008; Fig.2.1). The park is located on the Northern slopes of the Bankberg mountain range in the Cape Midlands, Eastern Cape and is described as having a cool and arid climate (Gaylard *et al.* 2006; Fig.2.2B).

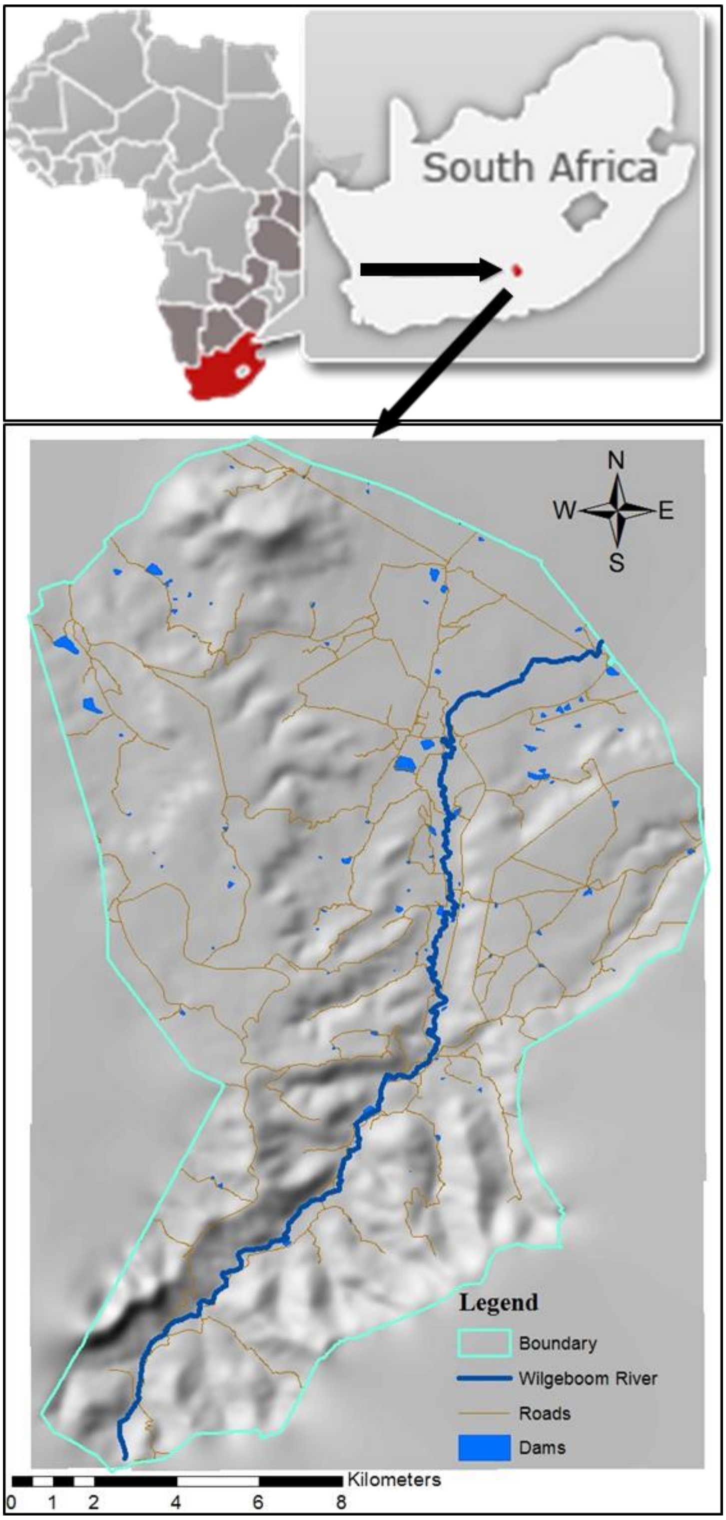

**Figure 2.1:** Map of Mountain Zebra National Park within the Eastern Cape, South Africa, highlighting the major river, dams and road network within the park.

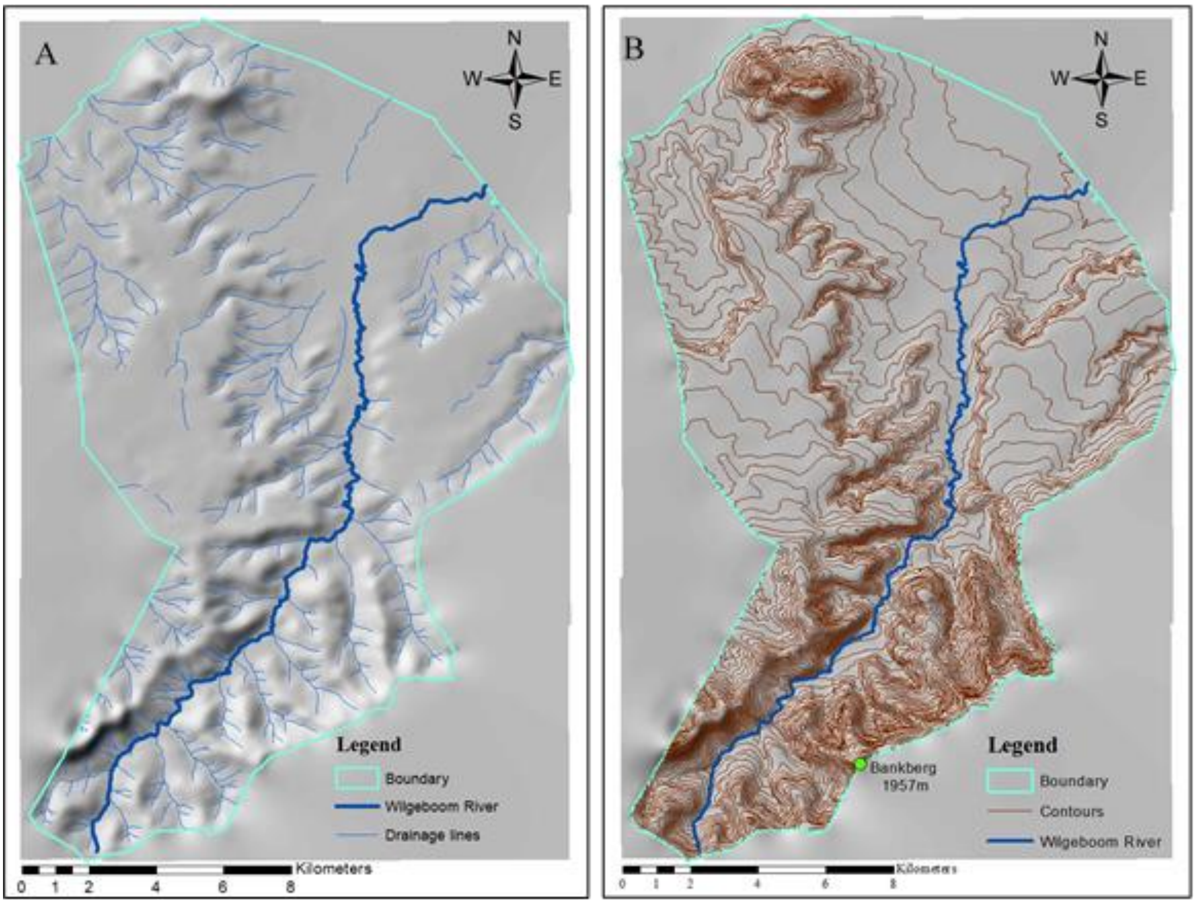

**Figure 2.2:** A map of the Wilgeboom River, drainage lines (A) and the topography (B) of Mountain Zebra National Park.

Mountainous terrain with steep-sided drainage lines (Fig.2.2A), makes up the southern quarter of the park where the highest point is found along the Bankberg Mountain at 1957 m above sea level (Gaylard *et al.* 2006; Fig.2.2B). The lowest part of the park is in the northern section only reaching 1000 m above sea level (Gaylard *et al.* 2006). Although sedimentary rock types such as sandstones, siltstones and mudstones of the Beaufort Series dominate the park, post-Karoo dolerite intrusions are prevalent in certain areas (Gaylard *et al.* 2006). Soil coverage throughout the park is generally shallow (Fig.2.3) and vast parts of the park are rocky with very little to no top soil (Gaylard *et al.* 2006).

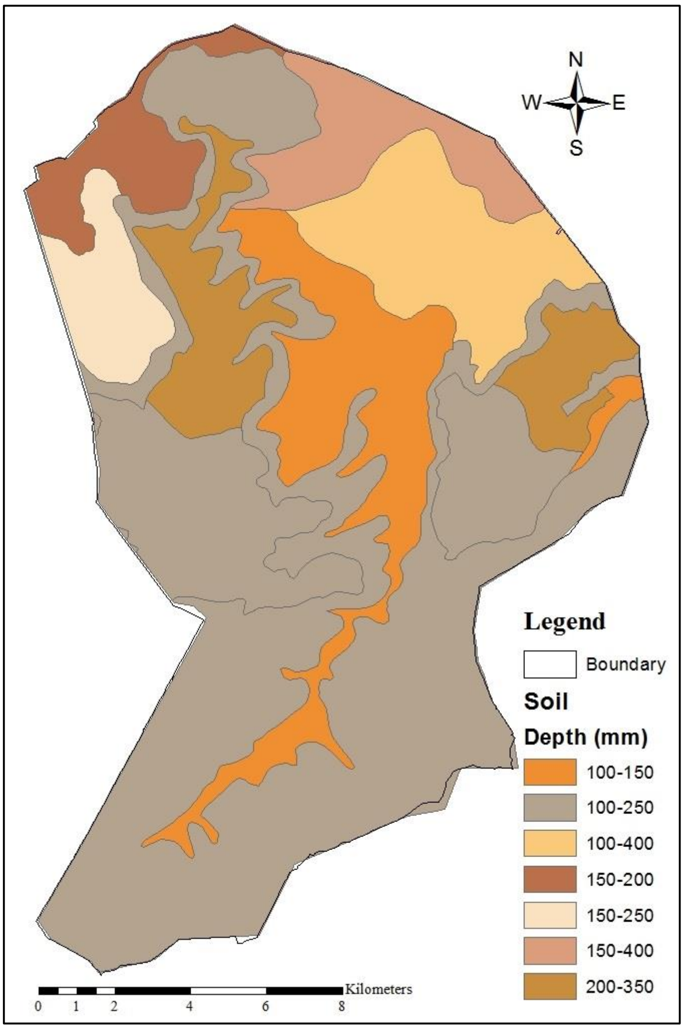

**Figure 2.3:** Map of Mountain Zebra National Park depicting the shallow soil depths.

## CLIMATE

The average monthly temperatures in summer (September to March) vary between a minimum of 6°C and a maximum of 28°C (Figure 2.4), whereas in winter (April to August) the temperature often drops below 0°C and reaches maximums of 20°C (Gaylard *et al.* 2006; Fig.2.4). Rain falls mostly in late summer and autumn (Novellie & Gaylard 2013; Fig.2.5), and the average annual rainfall is 400mm (Pond *et al.* 2002; Gaylard *et al.* 2006; Fig.2.6). The region experiences periodic light snow during the winter months and frost is common between May and October (Novellie & Gaylard 2013).

The mountainous peaks in the southern quarter of the park are exposed to increased cloud cover, extreme temperatures and moisture regimes, resulting in a number of microhabitats due to the local climate variations (Pond *et al.* 2002). The high lying areas in the southern section of the park are the only areas to experience regular snowfall, as the lower lying areas are sheltered and warmer due to the Bankberg Mountain forming a barrier to the cold fronts in winter (Pond *et al.* 2002).

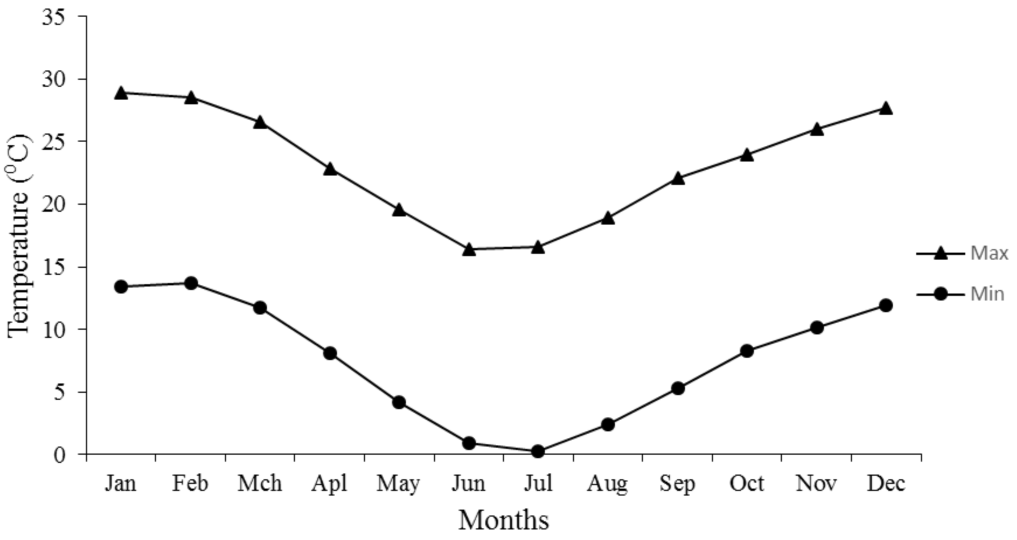

**Figure. 2.4:** The average daily maximum and minimum temperatures for Mountain Zebra National Park over a 30 year period (1983-2013).

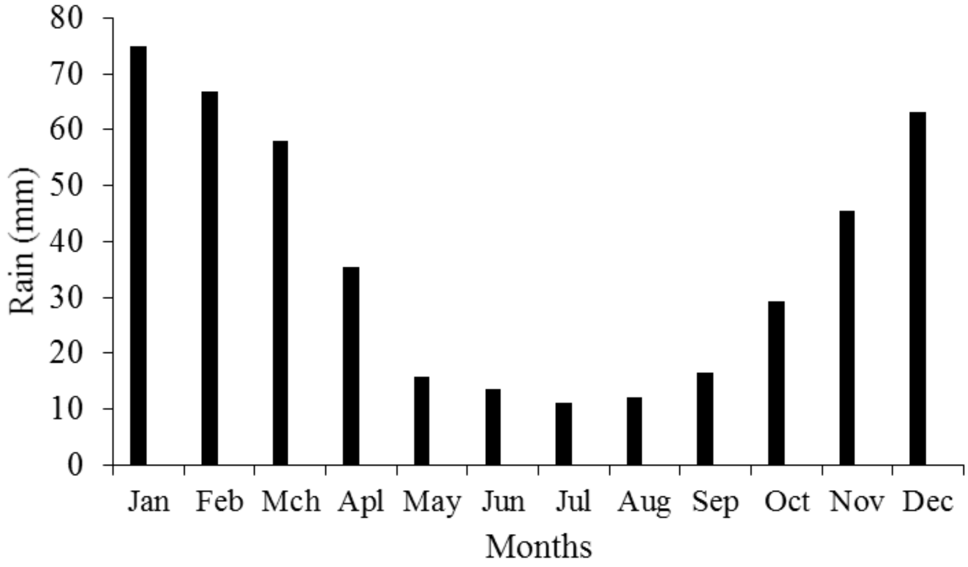

**Figure 2.5:** The average monthly rainfall for Mountain Zebra National Park over a 30 year period (1983-2013).

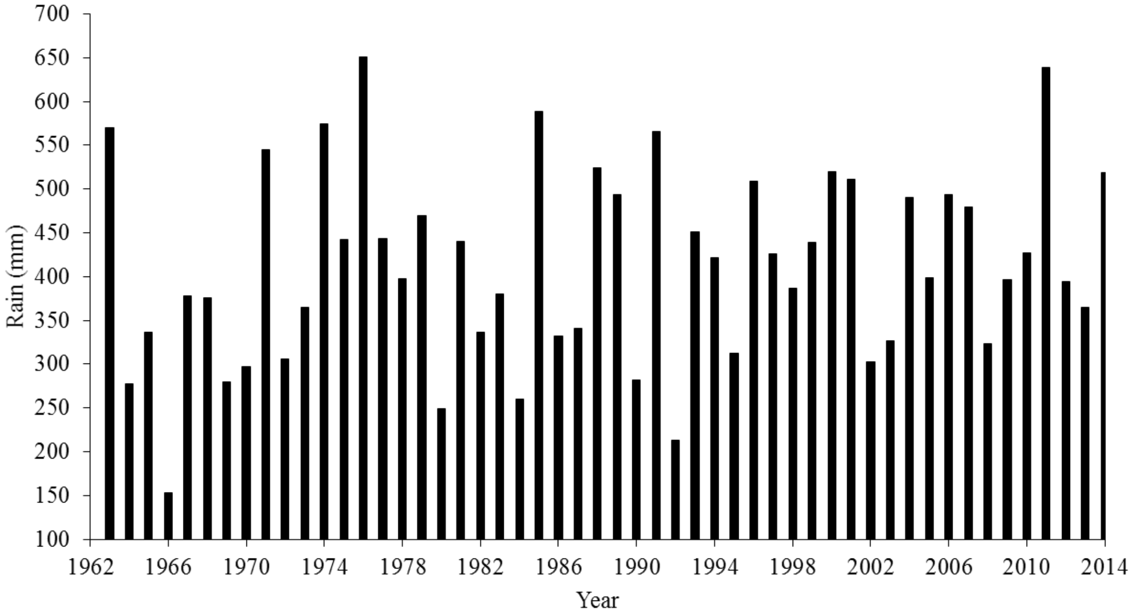

**Figure 2.6:** Annual rainfall for Mountain Zebra National Park over the period 1963 to 2014.

## VEGETATION

Vegetation in the park is subjected to continuous variation in climatic variables due to the influence of an arid climate in the east and a more moderate climate in the west (Pond *et al.* 2002). The three main vegetation types of South Africa found in MZNP are the Karoo Escarpment Grassland (53%), Eastern Upper Karoo (37%) and Eastern Cape Escarpment Thicket (10%) (Gaylard *et al.* 2006; Fig.2.7). The Eastern Upper Karoo is characterized by flat and gently sloping plains interspersed with hills and rocky areas where the dominant flora is dwarf microphyllous shrubs (*Pentzia incana* and *Eriocephalus ericoides*) (Gaylard *et al.* 2006; Mucina & Rutherford 2006). The Karoo Escarpment Grassland is characterized by low mountains and hills with wiry tussock grasslands and mountain wire grass (*Merxmuellera disticia*) being the dominant flora (Mucina & Rutherford 2006). The Eastern Cape Escarpment Thicket is characterized by steeply sloping escarpment and mountain slopes with medium-high and semi-open to closed thicket where the dominant flora is the olive tree (*Olea europaea*) (Mucina & Rutherford 2006).

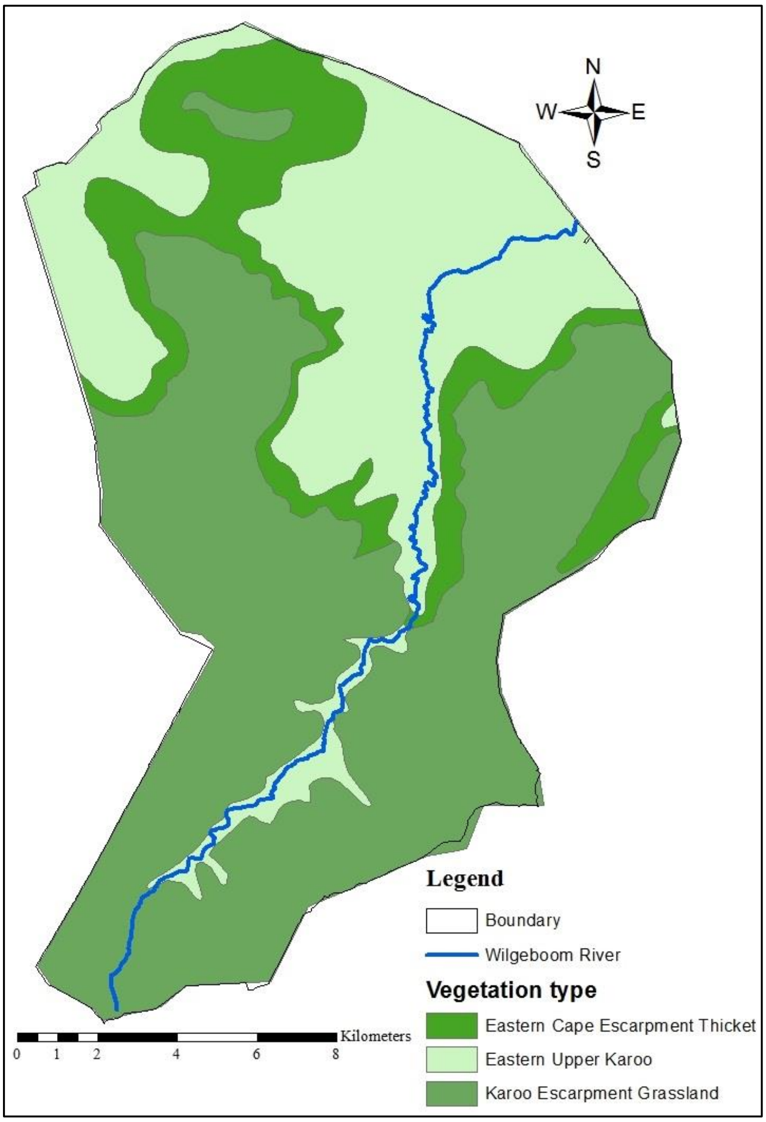

**Figure 2.7:** Distribution of the three main vegetation types of South Africa found in Mountain Zebra National Park.

## MAMMALIAN FAUNA

The habitats within MZNP support a variety of large mammalian species, some of which were present when the park was proclaimed and others which have been reintroduced in accordance with the objective of restoring the diversity of mammals that occurred historically (Gaylard *et al.* 2006). For example, buffalo (*Syncerus caffer*) were reintroduced in 1998 followed by black rhinoceros (*Diceros bicornis bicornis*) and gemsbok (*Oryx gazella*) in 2002. Caracal (*Caracal*

*caracal*) were the primary carnivores in the park until the first large carnivore introduction of four cheetahs (*Acinonyx jubatus*) in 2007. Brown hyenas were reintroduced as the primary scavengers in 2008. Three lions (*Panthera leo*) were introduced in 2013, but just over a year later the female lion was returned to Karoo National Park, leaving only the two male lions which were sourced from Welgevonden Game Reserve (Taplin 2013; Chibba 2013). Since the proclamation of the park, the herbivore guild has been effectively restored and any future reintroductions will be restricted to carnivores (Gaylard *et al.* 2006). Aerial game counts are conducted annually in MZNP by helicopter using standard procedures (Bissett & Bernard 2007). The annual game count figures from 2002 till 2013 (no data for 2007) are represented in Table 2.1 and all mammals found in MZNP are listed in Appendix 1.

## STUDY ANIMALS

Three brown hyenas, an adult male, an adult female and a sub-adult female were released into MZNP in November 2008 (Taplin 2008). All three individuals were translocated from Mafunyane Game Reserve in the North-West Province (Taplin 2008). After three weeks in a boma all three hyenas were released wearing GPS (Global Positioning System)/GSM (Global System for Mobile Communications) collars (Africa Wildlife Tracking, Reitondale, Pretoria, South Africa). However, the collars failed within 3.5-16 months after their release (Welch *et al.* 2015). Therefore, very little information is available on the population of brown hyenas in MZNP.

**Table 2.1:** Mammalian species recorded during aerial censuses at Mountain Zebra National Park from 2002 till 2013 (no data for 2007).

| | | **Total** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Scientific name** | **2002** | **2003** | **2004** | **2005** | **2006** | **2008** | **2009** | **2010** | **2011** | **2012** | **2013** |
| Black-backed jackal | *Canis mesomelas* | 9 | 10 | 9 | 5 | 16 | 16 | 26 | 4 | 14 | 32 | 17 |
| Black wildebeest | *Connochaetes gnou* | 303 | 301 | 368 | 336 | 416 | 599 | 642 | 674 | 590 | 922 | 622 |
| Blesbok | *Damaliscus pygargus phillipsi* | 276 | 226 | 259 | 149 | 219 | 139 | 102 | 168 | 148 | 156 | 30 |
| Buffalo | *Syncerus caffer* | 43 | 78 | 83 | 86 | 126 | 118 | 118 | 104 | 111 | 77 | 84 |
| Burchell's zebra | *Equus burchelli* | 56 | 58 | 28 | 34 | 42 | 34 | 46 | 57 | 60 | 82 | 65 |
| Cheetah | *Acinonyx jubatus* | | | | | | 4 | 12 | 8 | 7 | 8 | |
| Common duiker | *Sylvicapra grimmia* | 5 | 10 | 12 | 11 | 4 | 13 | 8 | 2 | 1 | 5 | 1 |
| Eland | *Tragelaphus oryx* | 199 | 192 | 209 | 242 | 221 | 205 | 200 | 157 | 217 | 260 | 184 |
| Gemsbok | *Oryx gazella* | 0 | 15 | 57 | 68 | 73 | 166 | 147 | 161 | 140 | 212 | 188 |
| Grey rhebok | *Pelea capreolus* | 81 | 57 | 127 | 109 | 108 | 139 | 52 | 102 | 67 | 58 | 9 |
| Klipspringer | *Oreotragus oreotragus* | 14 | 13 | 25 | 9 | 14 | 2 | 3 | 14 | 8 | 3 | 2 |
| Kudu | *Tragelaphus strepsiceros* | 169 | 145 | 191 | 373 | 165 | 292 | 250 | 254 | 249 | 299 | 78 |
| Mountain reedbuck | *Redunca fulvorufula* | 445 | 272 | 699 | 502 | 271 | 592 | 510 | 317 | 164 | 120 | 18 |
| Mountain zebra | *Equus zebra zebra* | 351 | 297 | 300 | 328 | 354 | 469 | 596 | 621 | 672 | 745 | 427 |
| Ostrich | *Struthio camelus* | 104 | 96 | 120 | 119 | 125 | 177 | 113 | 101 | 103 | 105 | 93 |
| Red hartebeest | *Alcelaphus buselaphus* | 235 | 249 | 282 | 326 | 251 | 355 | 326 | 430 | 341 | 427 | 364 |
| Springbok | *Antidorcas marsupialis* | 881 | 818 | 1172 | 1119 | 1147 | 1446 | 1350 | 1226 | 998 | 1003 | 659 |
| Steenbok | *Raphicerus campestris* | 18 | 22 | 8 | 11 | 11 | 5 | 3 | 2 | 1 | 3 | 2 |

# CHAPTER 3

# BROWN HYENA POPULATION ASSESSMENT

**Brown hyena captured along a prominent game path in the northern region of Mountain Zebra National Park**

## INTRODUCTION

For centuries, biologists have been interested in identifying animal species and determining their distributional patterns and behavioural characteristics (Ancrenaz *et al.* 2012). Over the past few decades, however, with the increase in species extinction rates across the globe, it has become more important to determine and understand species composition and population dynamics (e.g. population size, density, trends) (Ancrenaz *et al.* 2012). Reliable population estimates are important as they are crucial baseline parameters for the development of effective wildlife management and conservation strategies (Thorne *et al.* 2004; Gussett & Burgener 2005; Blanc *et al.* 2014).

Many large (>20 kg) African carnivore populations are declining and accurate population estimates for these species are often absent, hindering conservation and management efforts (Thorne *et al.* 2004; Blanc *et al.* 2014). The need for accurate and reliable population estimates is therefore crucial to the survival of these species. Collecting information on large carnivores, however, is often challenging as they are wide-ranging, occur at low densities and have cryptic natures (Thorne *et al.* 2004; Gussett & Burgener 2005). Species such as the brown hyena (*Hyaena brunnea*), which is nocturnal, make data collection even more difficult (Thorne *et al.* 2004). Direct counts of carnivore populations are unrealistic and exceedingly rare because they are expensive and time consuming (Blake & Hedges 2004; Bonesi & Mcdonald 2004; Gussett & Burgener 2005; Balme *et al.* 2009). Indirect methods, however, can be used to reliably estimate carnivore abundance and density through the use of non-invasive survey techniques such as camera trapping (Karanth 1995; Karanth & Nichols 1998), spoor or animal sign counts (Stander 1998; Balme *et al.* 2009), snow-tracking (Drickamer & Stuart 1984) and scat surveys (Koegh 1983; Gompper *et al.* 2006).

Sign-based methods have been criticized due to observer bias and because detection ability varies across environmental conditions (Karanth *et al.* 2003). There is also the issue of observers not being able to reliably identify tracks left by different individuals (Karanth *et al.* 2003). However, camera trap surveys have gained much support as they are non-invasive and have moderately low-labour costs (Pettorelli *et al.* 2010).

Camera trapping of wildlife has been in practice since the early 20th century and has become one of the major tools in conservation and ecology for conducting species inventories (Silveria *et al.* 2003), discovering new species (e.g. Rovero *et al.* 2008) and for determining population dynamics and density estimates (Karanth 1995; Thorne *et al.* 2004; Rowcliffe & Carbone 2008). Density is generally the parameter of interest when conducting camera-trap surveys, as it allows the comparison of estimates across space, especially when comparing sites with different survey areas (Rich *et al.* 2014). Camera trapping is also relatively robust to variation in environmental or climatic conditions and, most importantly, can be used in remote areas to gain information on highly cryptic species, as the cameras do not need to be accessed daily (Stein *et al.* 2008; Pettorelli *et al.* 2010; Ancrenaz *et al.* 2012). Furthermore, the exact locations of camera trap records are known, providing individual encounter history data for animals, which means that the data can also be used for analysing the spatial patterns of species (Royle *et al.* 2009; Ancrenaz *et al.* 2012). Camera traps also provide information on the date and time of when photographs were captured, which can be used to study the general activity patterns of wildlife (Di Betetti *et al.* 2006).

Camera trapping, along with capture-recapture methods, has been used around the world to provide information on abundance and density of individually identifiable carnivores (Maffei *et al.* 2004; Karanth & Nichols 1998; Thorne *et al.* 2004; Rowcliffe & Carbone 2008; Rich *et al.* 2014). Capture-recapture methods estimate population abundance by sampling a proportion of the whole population, while correcting for imperfect detection by accounting for individuals that may not have been detected (Blanc *et al.* 2014). Capture-recapture methods rely on the unambiguous identification of individual animals, either through human-induced markings such as fur-clipping in small mammals (Fullagar & Jewell 1965), ringing in birds (Hjort & Lindholm 1978), or through phenotypical variations in coat patterns (stripes, spots or rosettes) (Royle & Young 2008; Anile & Devillard 2015).

Camera trapping, and the use of capture-recapture principles, was first used by Karanth and Nichols (1998) to monitor tiger (*Panthera tigris*) populations in India. The methodology proved to be such a success that it has since been used to study numerous species such as leopards (*Panthera pardus*) (Henschel & Ray 2003; Balme *et al.* 2009), jaguars (*Panthera onca*) (Silver *et al.* 2004), pumas (*Puma concolor*) (Kelly *et al.* 2008), snow leopards (*Unica unica*) (Jackson *et al.* 2006), ocelots (*Leopardus pardalis*) (Maffei *et al.* 2005), cheetahs (*Acinonyx jubatus*) (Marnewick *et al.* 2008), striped hyenas (*Hyaena hyaena*) (Harihar *et al.* 2009) and brown hyenas (Thorn *et al.* 2009; Kent & Hill 2013).

Capture-recapture methods for closed models have three major assumptions which need to be fulfilled. The first assumption is that the population is both demographically and geographically closed (Pollock 2000). To ensure population closure, studies generally restrict their survey length to a period which is sufficiently short so as to assume that there will be no additions or deletions to the population (Pollock 2000). For large carnivores, survey length is typically between 30 and 90 days (Silver *et al.* 2004). Survey length, however, is usually a trade-off between keeping the sampling period short enough to assume closure and collecting enough data for robust abundance estimation (Tobler & Powell 2013). The second assumption is that no individual animal has a zero probability of being captured (Karanth & Nichols 1998). In order to satisfy the second assumption, the survey design needs to ensure that at least one camera site is placed within the home range of every individual in the study area. Thus, there should be no gaps between camera sites that could accommodate an individual’s home range

(Tobler & Powell 2013). Many studies have used home range estimates from the literature to satisfy this assumption (Silver *et al.* 2004). The final assumption is that the individually identifiable marks on the animals are not lost or overlooked by the observer throughout the duration of the survey (Pollock 2000).

Although conventional capture-recapture methods provide reliable estimates of abundance, several limitations hinder the accuracy of density estimates from such methods (Obbard *et al.* 2010; Gopalaswamy *et al.* 2012; Rich *et al.* 2014). The first limitation is that in order to estimate density, the area from which the study animals are sampled (the effective trapping area) is needed and this is generally unknown (Rich *et al.* 2014). Typically, in the absence of telemetry data, movement data of the study animals collected from the camera traps, is used to determine a buffer area around the trap array to estimate the effective trapping area (ETA) (Borchers & Efford 2008; Foster & Harmsen 2012). Often *ad hoc* approaches such as calculating half mean maximum distance moved (HMMDM) or full mean maximum distance moved (MMDM) by individuals captured at camera stations, are used as ETA's (Otis *et al.* 1978; Karanth & Nichols 1998; Noss *et al.* 2012). Since methods to define the width of the ETA vary, the precise definition of the ETA is uncertain and can result in density estimates that are somewhat arbitrary (Rich *et al.* 2014). The second limitation to conventional capture-recapture methods is that although spatial information from the study area is available, it is not directly incorporated into the analyses (Gopalaswamy *et al.* 2012).

However, a relatively new approach for estimating population density has been developed using spatially explicit capture-recapture (SECR) methods (Borchers & Efford 2008). The problems of conventional capture-recapture methods are addressed in SECR models by incorporating the spatial locations of the camera traps in the analyses, thereby overcoming the problem of estimating the ETA and eliminating the need for *ad hoc* estimations of sampling area (Borchers & Efford 2008; Kent & Hill 2013). SECR models combine information about the capture locations of individuals with their capture probability at point locations (home range centres) to estimate density (Royle & Young 2008). SECR models have also been developed both under maximum likelihood-based estimation (Borchers & Efford 2008) and Bayesian frameworks (Royle & Young 2008). Furthermore, SECR methods have become the preferred method for calculating population estimates and have been applied to a variety of species including birds (Dawson & Efford 2009), black bears (*Ursus americanus*) (Obbard *et al.* 2010) and a number of individually identifiable large carnivores (Royle *et al.* 2009; Foster & Harmsen 2012; Noss *et al.* 2012; Tobler *et al.* 2013).

Translocations of large carnivores is a common phenomenon throughout Africa, however, post-release monitoring in order to determine the success and/or failure of the translocations has rarely occurred (Hayward *et al.* 2007b). The conversion of large areas of agricultural land into game farming and conservation areas in the Eastern Cape, South Africa has led to a large number of predators being reintroduced into various fenced reserves (e.g. Kwandwe Private Game Reserve, Shamwari Private Game Reserve and Mountain Zebra National Park) (Hayward *et al.* 2007b). Brown hyenas are one of the predators which have been reintroduced into the Eastern Cape, and the earliest reintroduction was of three individuals in 1985 into the Great Fish River Complex (Hayward *et al.* 2007b). The most recent reintroduction of brown hyenas into the Eastern Cape was that of three individuals in 2008 into the Mountain Zebra National Park (MZNP) (Taplin 2008). However, no research has been conducted on the success of the reintroduction of these brown hyenas into MZNP.

### Aims

The aim of this chapter was to conduct a comprehensive camera trapping survey, along with SECR analyses, to estimate brown hyena density and distribution in Mountain Zebra National Park.

## METHODS

High levels of precision for estimating population parameters such as density or home ranges require large amounts of data (Ancrenaz *et al.* 2012). Therefore, I ran a camera trapping survey for just over one full year (15 April 2014 to 16 April 2015) to estimate the density of brown hyenas at MZNP. The camera trap setup followed a systematic grid structure which was adapted to the local logistics of MZNP (Ancrenaz *et al.* 2012), to ensure that every brown hyena had a capture probability of greater than zero (Karanth & Nichols 1998; Tobler & Powell 2013).

To obtain accurate population estimates, the maximum distance between camera sites should be less than the radius of the smallest home range within the population (Tobler & Powell 2013). Spatial data collected from the GPS satellite collars on the three founder brown hyenas was limited, as the collars failed within 3.5-16 months after their release (Welch *et al.* 2015). These data were therefore considered unreliable for estimating home ranges, as the brown hyenas may still have been trying to settle into their new surroundings and may not have established themselves (Welch *et al.* 2015). Instead, I used home range data collected from three GPS satellite collared brown hyenas at Kwandwe Private Game Reserve, South Africa (1st March 2013 to 28th February 2014), to determine the size of the grid cells (Welch *et al.* 2015). Data on the home ranges of brown hyenas from Kwandwe Private Game Reserve was chosen because it was the closest location to MZNP with reliable data (Welch *et al.* 2015).

Although Shamwari Private Game Reserve also had reliable data on the home ranges of brown hyenas, these data were collected after the start of my study (Welch *et al.* 2015). The smallest home range within a population is usually a breeding female (Ancrenaz *et al.* 2012), but at Kwandwe Private Game Reserve the smallest home range was that of a male (38.64 km$^2$) (Welch *et al.* 2015). Using this home range, a radius of 3.51 km was calculated and used to determine the size of the grid cells (3 km$^2$).

ArcGIS 10.1 (ESRI, Redlands, California, USA) was used to construct the 3 km$^2$ grid system over MZNP (Fig.3.1). From the map, 11 grid cells were chosen so that the number of available cameras, 22 Cuddeback Attack (Fig.3.2) (Non Typical Inc., Green Bay, Wisconsin), could cover the majority of the study area. The markings on brown hyenas are asymmetrical and therefore using two cameras at each site would maximise the likelihood of obtaining simultaneous photographs of both sides of any passing brown hyenas (Karanth & Nichols 1998; Thorn *et al.* 2009; Negrões *et al.* 2010). Three of the camera site locations (sites 5, 7 and 11) were chosen on the basis that they were successful in capturing brown hyenas during a preliminary study in 2011/2012 (Bissett, SANParks Annual Progress Report 2013) and because they fell within one of the 11 chosen grid cells (Fig.3.1). Camera trap sites for the remaining grid cells were pre-selected using aerial photographs of MZNP in ArcGIS (Fig.3.1) (Ancrenaz *et al.* 2012). The GPS co-ordinates of all 11 pre-selected sites were recorded. Once at MZNP, the areas chosen from ArcGIS were scouted on foot for brown hyena activity such as tracks, paste markings or latrines. If signs of brown hyena activity were present, cameras were placed in the direction of activity to maximise the probability of detection. If there were no signs of brown hyena activity, cameras were placed parallel to prominent game paths or roads to maximise brown hyena capture rates (Karanth & Nichols 2002; Thorn *et al.* 2009; Fig.3.3).

Cameras were placed at a height of about 45 cm, which is the average shoulder height of brown hyenas (Thorn *et al.* 2009). At sites where the cameras needed to be attached higher than 45 cm (80 to 100 cm) due to the area and surrounding vegetation, the cameras were angled downwards to ensure that the legs of passing brown hyenas would be photographed. At all sites, the height and angle of the cameras were tested by having someone crawl passed the cameras, to ensure that a passing brown hyena would be captured. Each photographic capture was labelled with supplementary data such as time, date and camera number so that the two corresponding flank images could be linked to develop individual brown hyena identity profiles (Royle *et al.* 2009).

Cameras were set to take high quality (5MP) images and the strobe flash range was set at 10 feet (3.28 m). The cameras used four D-cell batteries to operate, a 2/16GB SD card to store the images captured and a passive infrared sensor to detect heat and motion. Cuddeback Attack cameras have one of the fastest trigger speeds of all trail cameras, which is ¼ second. The cameras were programmed to capture photographs 24h/day with a 30 second interval between consecutive photographs to ensure that as many photographs of passing brown hyenas were captured as possible. No bait or lure was used to attract the brown hyenas to the camera sites. Cameras were checked on a monthly basis to replace batteries if needed, to ensure that they were functioning normally and to download the photographs captured.

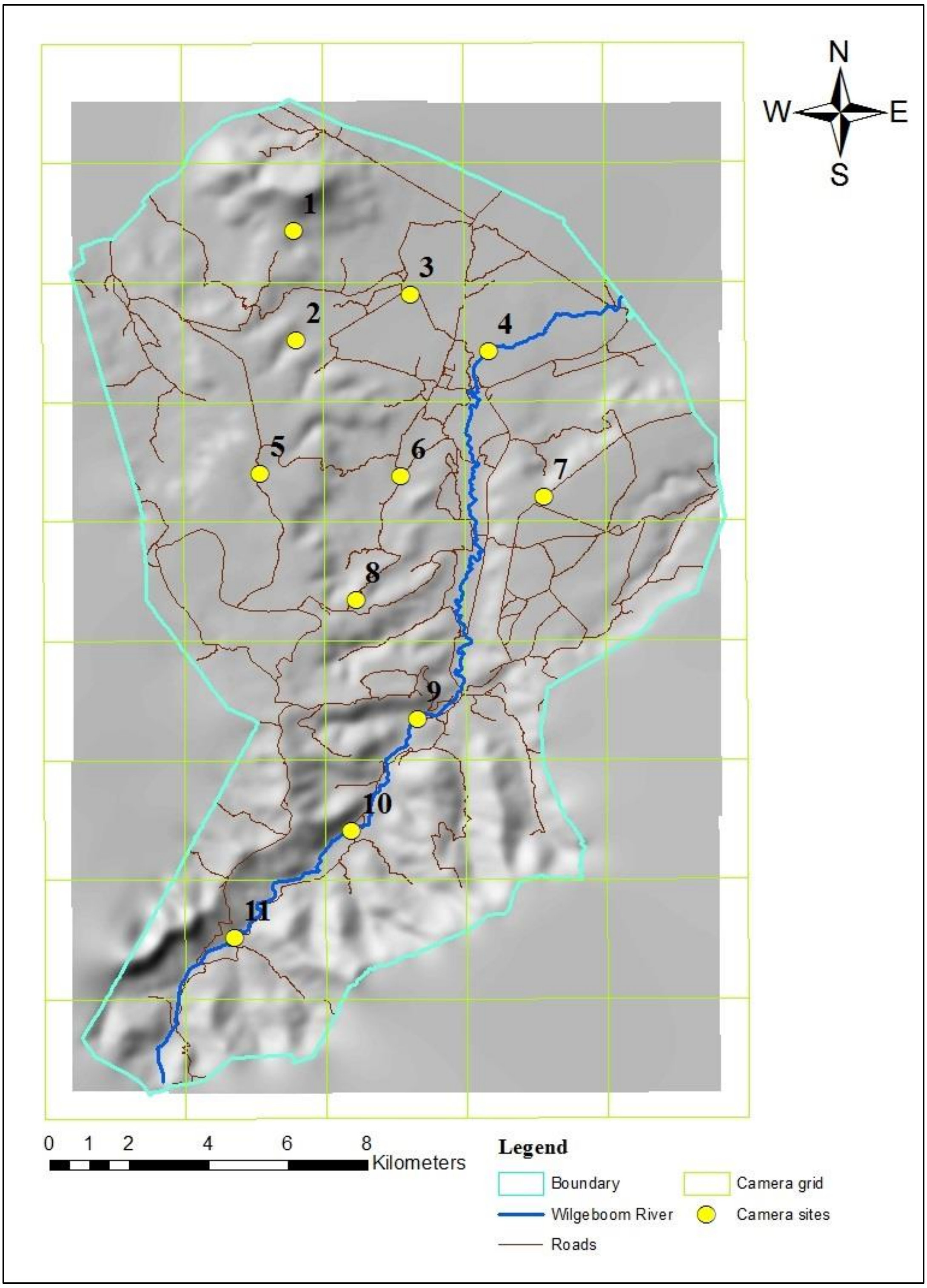

**Figure 3.1:** Location of the grid cells (3 km$^2$) and the 11 camera trap sites within Mountain Zebra National Park.

**Figure 3.2:** Cuddeback Attack camera and protective casing used for the camera trap survey at Mountain Zebra National Park.

**Figure 3.3:** Cuddeback Attack cameras in their protective casings, securely attached to trees on either side of a prominent game path in Mountain Zebra National Park (Site 11).

## Data analysis

The time, date, camera site, camera number and species present in each photograph captured was recorded using the program PhotoGoFer (Rapid Imaging Software, Albuquerque, New Mexico, USA). Brown hyena images were analysed and a general activity pattern was determined by grouping all brown hyena photographs according to their time and date stamp (Cuellar *et al.* 2006). Individual brown hyenas were identified by their unique leg stripes, coat pattern, ear notches or facial scaring (Silver *et al.* 2004; Thorn *et al.* 2009). Brown hyena identity profiles created during the pilot study (Bissett, SANParks Annual Progress Report 2013), along with any newly developed identity profiles were used to assist the identification of individuals captured (Appendix II). An initial capture was determined when an individual could not be matched to any previous images captured (Heilbrun *et al.* 2003). Photographs of poor quality, or where the individually identifiable markings were obscured, were excluded from the analysis (Fig.3.4). A photograph was considered a recapture when the individual was already identified. Trap nights (367 days with 11 camera trap sites equals 4035 trap nights) were not grouped and each trap night was considered to be a separate sampling occasion, where one sampling occasion was defined as a 24 hour period starting at 15h00. This time period was selected to avoid the ‘midnight problem’, which occurs when an individual is photographed before and then again after the midnight cut off time, resulting in two separate occasions rather than being a single occasion like it would be at any other time (Jordan *et al.* 2011). This problem is particularly true for nocturnal species that have high activity patterns around midnight (Jordan *et al.* 2011; Foster & Harmsen 2012). The brown hyena images captured were split into left- and right-sided images from which independent capture events (i.e. images separated by 30 minute intervals (Anile & Devillard 2015)) were determined. From the capture events, detection histories were compiled for each individual for both left- and right-sides (Karanth & Nichols 1998).

The capture events for each side were divided into four sessions, (i.e. four 90 day periods), to comply with population closure assumptions and to minimise demographic changes within the population (Silver *et al.* 2004; Ancrenaz *et al.* 2012; Tobler & Powel 2012). Detection histories were compiled for each individual for both sides and for each session (Efford 2015). All statistical analyses were run separately for each side and session (Efford 2015). An important consideration for session analyses is that sessions are analysed as if they were each sampled from independent populations (Efford 2015).

**Figure 3.4:** Examples of poor quality (A) and partial (B) images of brown hyenas captured in Mountain Zebra National Park that were removed from the density estimation analyses.

Two separate approaches are used for SECR analysis; inverse prediction or likelihood maximization and the Bayesian method (Efford *et al.* 2004). The two models have been found to produce similar results (Noss *et al.* 2012), but the likelihood approach is much faster than the Bayesian method for fitting SECR models. In addition, within certain limits, the likelihood approach is more flexible with respect to model selection and averaging and therefore this approach was used for my study (Kalle *et al.* 2011).

SECR analyses were run in the R language (version 3.1.2, R Development Core Team, 2015) with the use of the package secr (version 2.9.5), which was developed by Efford *et al* (2009) and Efford (2011) to produce full maximum likelihood density estimates. The secr package requires two input files, firstly the trap layout (numbered locations of camera traps; Appendix III) and the capture data (numerical designations for sampling session, animal identification, occasion and trap location; Appendix IV). Additional information is needed with respect to trap layout, such as the detector type, which is set as ‘proximity’ for camera trapping, as it allows for multiple detections of individuals on the same occasion. A usage argument was used to determine each detector’s daily functional state, whereby sites were classified as active if at least one of the two cameras was functioning adequately. The placement of camera traps on roads has shown to be a potential source of bias in camera trap surveys (Sollmann *et al.* 2011) and so the presence of roads was added as a binary covariate in the trap layout file. Presence of predators at the camera site, vegetation type, elevation and slope were also added as trap covariates. For this study, the park was geographically closed with a permanent predator-proof, electrified fence present along the boundary of the park. Therefore, instead of using a buffer value, a habitat mask was defined which spanned within the borders of the park. The sampling area was relatively small and uniform, and I therefore expected the distribution of the home range centres to be homogenous. The detection function was equal to half-normal because I assumed that probabilities of capture increased linearly with the proximity of a camera trap to the home range of an individual. I estimated population size using expected population (E (N)) (Junek *et al.* 2015).

The assumption of demographic closure was tested using tests described by Otis *et al.* (1978) for both the left- and right-side data (Efford 2015). Seven models were employed for both the left- and right-side data: the null model where detection is only affected by the use of space, the learned trap response model and models determining the effects of the trap covariates;

presence of road, presence of predators, vegetation type, elevation and slope. Separate analyses were run for each model.

For each of the analyses, the models were compared with the use of Akaike's Information Criterion (AIC) (Akaike 1974) to test which model was the most appropriate (Symonds & Moussalli 2011). The AIC values are only viable when compared with AIC values from multiple models (Symonds & Moussalli 2011). The model which produces the lowest AIC value, is the model which is most likely to be the correct model (Symonds & Moussalli 2011). When sample sizes are small (n/k <40; n is sample size, k is number of parameters), such as with my study, the corrected AIC (AICc) values are used to compare models (Symonds & Moussalli 2011). Another indication of the best model to use is when the ΔAICc value is less than 2 (Symonds & Moussalli 2011).

## RESULTS

The 11 camera sites covered an area of 212.91 km$^2$ with a mean inter-site distance of 2.9 km (± 0.6 km). The camera trap survey ran over 367 days for a total of 4037 trap nights, during which 19 989 animal photographs were captured (Table 3.1). From these photographs, 39 mammal species were identified, of which 17 were carnivores (Table 3.1). A total of 121 (0.61% of all animal images) adult brown hyena photographs were captured, of which 100 were independent capture events (> 30 minutes apart). No juvenile brown hyenas were captured during the survey period. Overall, brown hyena capture rate was 0.03 captures per trap night, which resulted in a trapping success rate of 3%. Of 119 brown hyena captures recorded when both camera traps at a site were active, only 40 captures were recorded by both cameras, indicating a maximum possible detection failure rate of 66.34%.

Of the 121 brown hyena photographs captured, 43 images were removed from the density estimation analysis due to them either being partial images or of poor quality (e.g. overexposed or individual too far away from camera (Fig.3.4)). The remaining photographs were split into 46 left-side and 29 right-side independent capture events. These images were used for left-side and right-side analyses. The average number of captures per individual for left-side photographs was 3.83 ± 2.08 (sd) and ranged from one to eight. For the right-side photographs, the average number of captures per individual was 2.9 ± 1.90 and ranged from one to five. From the left-side photographs, 12 individuals were positively identified, whereas from the right-side photographs 10 individuals were positively identified (Appendix II).

**Table 3.1:** Summary data from the camera trap survey conducted in Mountain Zebra National Park between 15 April 2014 and 16 April 2015.

| | **n** | **%** |
|---|---|---|
| No. trapping nights | 4037 | 100 |
| Total no. of image captures | 19 989 | 100 |
| Total brown hyena images | 121 | 0.61 |
| Total brown hyena events | 100 | 0.50 |
| No. of individual brown hyenas identified | - | - |
| Left-side | 12 | - |
| Right-side | 10 | - |
| Total mammal species | 39 | - |
| Total carnivore species | 17 | - |

In total, 5 of the 11 (45.45%) camera trap sites were located on roads, the remaining camera trap sites were placed along prominent game paths. The camera sites located on roads captured 57.78% of the left-side brown hyena events and 51.73% of the right-side brown hyena events (Table 3.2), indicating that capture probabilities were higher on roads.

**Table 3.2:** Summary of the brown hyena events captured at Mountain Zebra National Park.

| | **n** | **%** |
|---|---|---|
| No. of brown hyena events | 75 | 100 |
| Left-side | 46 | 61.33 |
| Right-side | 29 | 38.67 |
| | | |
| No. of brown hyena events captured on roads | - | - |
| Left-side | 26 | 57.78 |
| Right-side | 15 | 51.73 |

The Otis *et al.* (1978) test did not reject the closure assumption for the left-side (Z = 0.047, P = 0.52) or the right-side data (Z = 0.25, P = 0.60), but produced a warning message indicating small sample size, which means that the p-value should be interpreted with caution (M. Efford, author of secr, pers.comm).

Closure tests for the left-side data, split into four sessions, did not reject the closure assumption for sessions three (Z = -1.20, P = 0.12) or four (Z = -1.50, P = 0.07) but rejected the closure assumption for sessions one (Z = -3.67, P = 0.0001) and two (Z = -1.61, P = 0.05). Closure tests for the right-side data, split into four sessions, rejected the closure assumption for all four sessions (session one: Z = -2.41, P = 0.008; session two: no result; session three: Z = -1.73, P = 0.04; session four: Z = -1.79, P = 0.04). All four sessions for both left- and right-side closure tests produced a warning message indicating small sample size (Otis *et al.* 1978). Data split into sessions are analysed as if each session was sampled from independent populations, rather than from one population with the same individuals (Efford 2015). Further session analyses were therefore excluded from this study.

Closed population models were used to determine density estimates, despite possible lack of closure because firstly, closed models are more robust than open models (Karanth & Nichols 2000) and secondly, the deviation from population closure was marginal (Karanth *et al.* 2003) despite a long sampling period, due to the population being geographically closed with minimal biological turnover.

Density estimates for both left- and right-side analyses were robust with respect to the inclusion of different trap covariates (Table 3.3 and 3.4). For the left-side analyses, the maximum likelihood model that included a road covariate performed the best, with a weighting of 0.38. This indicates a 38% likelihood that the road model was the correct model (Table 3.3). The $AIC_C$ scores and density estimates for the three best-performing ($AIC_C = < 2$) left-side models (road, vegetation and null) did not differ much, suggesting that these three models fit the data comparably (Table 3.3; Symonds & Moussalli 2011). The combined weighting of the three best-performing models was 0.87, indicating that these models represent the most appropriate models with 87% likelihood. The models which included covariates of predator presence, trap response and slope had $\Delta AIC_C$ values which fell within the range of 2 and 7, meaning that they are less likely to be the best approximating model, but that they should not be discounted (Table 3.3; Richards 2005). The model including elevation as a covariate, had a $\Delta AIC_C$ value greater than 10, meaning that it is extremely unlikely to be the best approximating model and can therefore be ignored (Table 3.3; Richards 2005). The left-side density estimate for the best fit model (road) was 5.97 individuals/100 $km^2 \pm 1.77 \times 10^{-4}$ (Table 3.3). The expected population size for the best fit left-side model (road) was estimated at 12.72 ± 3.77 individuals, with a range of between 7.21 and 22.47 individuals (Table 3.4).

A different pattern was observed for the right-side analyses. The maximum likelihood model which performed the best was the null model with a weighting of 0.70 (Table 3.5). This indicates a 70% likelihood that the null model was the correct model. Although the density estimates and $AIC_C$ scores did not differ much among the right-side models, the null model was the only model with a $\Delta AIC_c$ score of less than 2, indicating that the null model was the best approximating model (Table 3.5). The models which included covariates of predator presence, road, trap response and slope had $\Delta AIC_C$ values which fell within the range of 2 and 7, meaning that they are less likely to be the best approximating model, but that they should not be discounted (Table 3.5; Richards 2005). The model including elevation as a covariate, had a $\Delta AIC_C$ value greater than 10, meaning that it was extremely unlikely to be the best approximating model and can therefore be ignored (Table 3.5; Richards 2005). The right-side density estimate was 5.30 individuals/100 $km^2$ ± 1.75 $x10^{-4}$ (Table 3.5). The expected population size for the best fit right-side model (road) was estimated at 11.27 ± 3.72 individuals, with a range of between 6 and 21.18 individuals (Table 3.6).

**Table 3.3:** Results of the left-side maximum likelihood SECR analyses. The 'Model' column depicts which covariate was used in the analyses, with the density estimate, standard error (SE $x10^{-4}$), 95% confidence interval (95% CI) and the four Akaike's Information Criterion (AIC) scores.

| **Model** | **Density (100 $km^2$)** | **S.E ($x10^{-4}$)** | **95% CI** | **AIC** | **AICc** | **ΔAICc** | **AICc weight** |
|---|---|---|---|---|---|---|---|
| Road | 5.97 | 1.77 | 3.38 – 10.05 | 658.72 | 664.44 | 0.00 | 0.38 |
| Vegetation | 5.95 | 1.77 | 3.37 – 10.52 | 654.76 | 664.76 | 0.32 | 0.32 |
| Null | 5.96 | 1.77 | 3.38 – 10.52 | 663.07 | 666.07 | 1.64 | 0.17 |
| Predators | 5.99 | 1.78 | 3.40 – 10.58 | 661.48 | 667.19 | 2.76 | 0.10 |
| Trap response | 5.77 | 1.71 | 3.27 – 10.19 | 664.29 | 670.01 | 5.57 | 0.02 |
| Slope | 5.96 | 1.77 | 3.38 – 10.53 | 665.07 | 670.78 | 6.35 | 0.01 |
| Elevation | 6.70 | 2.02 | 3.75 – 11.96 | 687.81 | 693.53 | 29.09 | 0 |

**Table 3.4:** Results of the left-side estimates for expected population size (E (N)) with standard error (SE), 95% confidence interval (95% CI) and realised population size (n).

| **Model** | **E (N)** | **S.E** | **95% CI** | **n** |
|---|---|---|---|---|
| Road | 12.72 | 3.77 | 7.21 – 22.47 | 12 |
| Vegetation | 12.68 | 3.76 | 7.18 – 22.39 | 12 |
| Null | 12.69 | 3.76 | 7.19 – 22.41 | 12 |
| Predators | 12.76 | 3.78 | 7.23 – 22.53 | 12 |
| Trap response | 12.30 | 3.64 | 6.97 – 21.70 | 12 |
| Slope | 12.70 | 3.76 | 7.19 – 22.41 | 12 |
| Elevation | 14.26 | 4.31 | 7.99 – 25.25 | 12 |

**Table 3.5:** Results of the right-side maximum likelihood SECR analyses. The ‘Model’ column depicts which covariate was used in the analyses, with the density estimate, standard error (SE x$10^{-4}$), 95% confidence interval (95% CI) and the four Akaike’s Information Criterion (AIC) scores.

| **Model** | **Density (100 km$^2$)** | **S.E (x$10^{-4}$)** | **95% CI** | **AIC** | **AICc** | **ΔAICc** | **AICc weight** |
|---|---|---|---|---|---|---|---|
| Null | 5.30 | 1.75 | 2.82 – 9.95 | 439.06 | 443.06 | 0.00 | 0.70 |
| Predators | 5.34 | 1.76 | 2.84 – 10.00 | 438.10 | 446.10 | 3.05 | 0.15 |
| Road | 5.27 | 1.75 | 2.82 – 9.94 | 440.24 | 448.24 | 5.19 | 0.05 |
| Trap response | 4.96 | 1.64 | 2.64 – 9.32 | 440.40 | 448.40 | 5.34 | 0.05 |
| Slope | 5.30 | 1.75 | 2.82 – 9.94 | 441.00 | 449.00 | 5.94 | 0.04 |
| Vegetation | 5.37 | 1.78 | 2.85 – 10.11 | 436.39 | 451.39 | 8.33 | 0.01 |
| Elevation | 5.70 | 1.96 | 2.96 – 10.97 | 452.77 | 460.77 | 17.71 | 0 |

**Table 3.6:** Results of the right-side estimates for expected population size (E (N)) with standard error (SE), 95% confidence interval (95% CI) and realised population size (n).

| **Model** | **Expected population size** | **S.E** | **95% CI** | **N** |
|---|---|---|---|---|
| Null | 11.27 | 3.72 | 6.00 – 21.18 | 10 |
| Predators | 11.35 | 3.74 | 6.05 – 21.31 | 10 |
| Road | 11.28 | 3.72 | 6.01 – 21.17 | 10 |
| Trap learned response | 10.56 | 3.49 | 5.62 – 19.83 | 10 |
| Slope | 11.27 | 3.72 | 6.00 – 21.17 | 10 |
| Vegetation | 11.44 | 3.79 | 6.07 – 21.52 | 10 |
| Elevation | 12.13 | 4.17 | 6.30 – 23.36 | 10 |

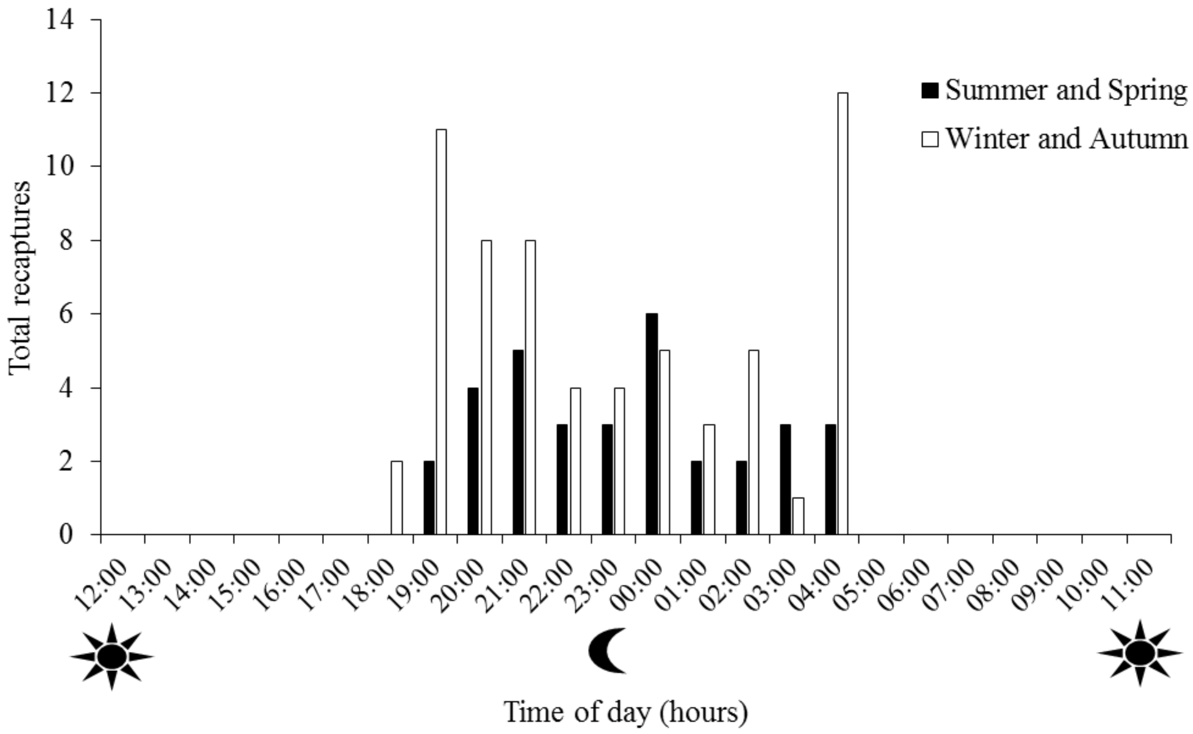

**Figure 3.5:** Summary of the activity patterns of brown hyenas during summer/spring and winter/autumn, based on cumulative camera trap recaptures in Mountain Zebra National Park during the period April 2014 to April 2015.

Figure 3.5 shows that brown hyenas within MZNP are mainly nocturnal, as all images were captured between 18h00 and 04h00. It is evident from the recaptures that the brown hyenas in MZNP are mainly active just after sunset, between 19h00 and 21h00, and just before sun-rise at 04h00 (Fig.3.5). It is also evident that the brown hyenas are considerably more active during the early hours of the evenings (18h00) and later in the mornings (04h00) in winter and autumn than they are in summer and spring (Fig.3.5).

Figure 3.6 illustrates the spatial distribution of the 12 individually identifiable brown hyenas within MZNP. It is evident from the brown hyena recaptures that although the brown hyenas are utilizing the entire park, the majority of the recaptures occurred within the northern region of the park (Fig.3.6). It is also evident that certain brown hyena individuals were either only recaptured in the north (BH M1, BH A, BH B, BH H, BH I and BH J) or the south (BH C, BH E, BH F and BH K), suggesting that there are possibly two separate clans within MZNP (Fig.3.6).

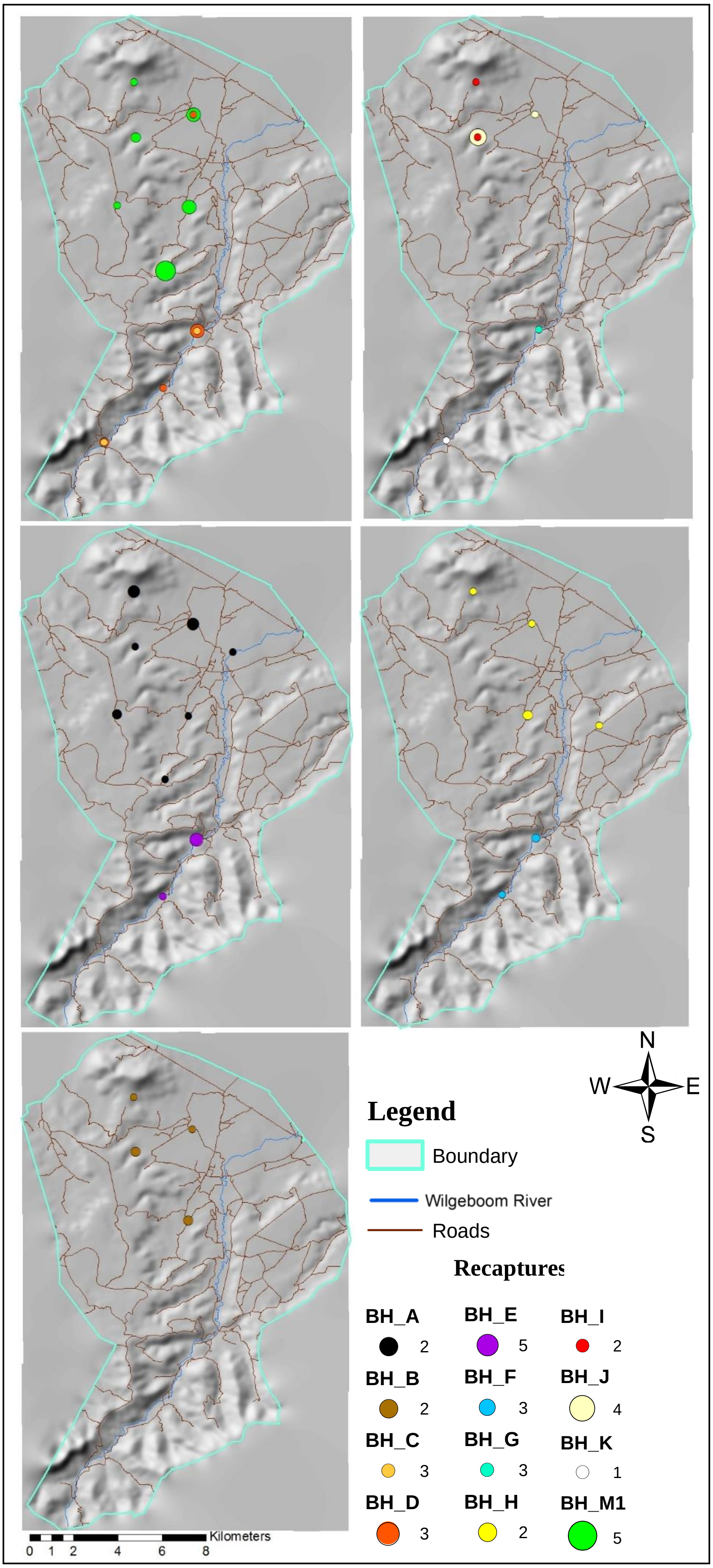

**Figure 3.6:** Maps of Mountain Zebra National Park, illustrating the recaptures of the 12 individually identifiable brown hyenas (BH = brown hyena).

## DISCUSSION

A fundamental requirement of wildlife conservation and management is reliable population estimates of the target species within areas of concern (Harmsen *et al.* 2011). SECR analysis of camera trap data is becoming the conventional method to estimate the abundance of medium to large-sized mammals living at low densities (Harmsen *et al.* 2011). SECR models are found to be unbiased and more accurate than non-spatial models, as study site information and covariates can be included in the analyses (Tobler & Powell 2013). One of the requirements of SECR models is that the study population is both geographically and demographically closed during the survey period (Otis *et al.* 1978). Population closure is, however, rarely realistic and often violated because natural populations cannot be controlled, and in reality a death in the population could occur within the smallest of sampling periods (Karanth 1995; Soisalo & Cavalcanti 2006).

The brown hyena population in MZNP fulfils the assumption of geographic closure, as the park is enclosed by a permanent predator-proof fence (Welch *et al.* 2015). In order to meet demographic closure, it is recommended that studies on large carnivores restrict their survey period to between two and three months (Henschel & Ray 2003; Silver *et al.* 2004; Tobler & Powell 2013). This suggested restriction on survey length, may however, be insufficient for species that occur at very low densities, such as brown hyenas, as it is likely to result in low capture probabilities, which would produce imprecise population estimates in SECR models (Otis *et al.* 1978; Brassine & Parker 2015). Therefore, when captures are low, researches often choose to extend the survey period in order to obtain sufficient captures for analysis (Tobler & Powell 2013). Extending the survey period is particularly appropriate for species with long life expectancies or prolonged breeding cycles (O'Brien & Kinnaird 2011). Brown hyenas fulfil this criterion, as not only do they have long life expectancies but they are also known to be slow breeders with long and erratic intervals between births (Mills 1982). Though the statistical test for closure in the secr program detected no violations for my data, the test is known to produce incorrect results (Soisalo & Cavalcanti 2006). Therefore, although the increased survey length of my study (367 days) makes it possible that the assumption of demographic closure was violated, the use of SECR models for closed populations can be justified.

Population estimates for brown hyenas in MZNP were based on left-side results because more individuals were identified using this set of images. Roads have been found to be important in determining how brown hyenas use their space, as the probability of brown hyena presence increases as the distance to roads decreases (Welch *et al.* 2015). Therefore, it is not surprising that my results revealed that the most appropriate SECR model to use was the model which included a road covariate. Other studies have also found that the addition of a road covariate improved their population estimates (Sollmann *et al.* 2011). According to the most appropriate model, the density estimate for brown hyenas in MZNP was 6 individuals/100 km$^2$ and the expected brown hyena population size in the park was 12 individuals. These population estimates are considered to be a minimum for MZNP, as the estimates are equal to the number of individuals positively identified. It is therefore highly likely that the population estimates will fall within the 95% confidence intervals for the analysis and more reasonable to say that the density of brown hyenas in MZNP falls within 6 to 10 individuals/100 km$^2$. The expected brown hyena population size in the park is thus between 12 and 21 individuals.

The density estimates obtained from my study (6-10 individuals/100 km$^2$), are higher than those recorded for brown hyenas in previously published studies, where densities ranged between 0.4 and 4.4 individuals/100 km$^2$ (Mills & Mills 1982; Mills 1984; Mills 1990; Thorn *et al.* 2009; Hill & Kent 2013). The highest brown hyena density estimates to be recorded were from Kwandwe Private Game Reserve, South Africa where their density ranged between 14 and 20 individuals/100 km$^2$ (Welch *et al.* 2015; Welch & Parker 2016). Several factors such as, land use, predator and prey density, vegetation type and whether or not spotted hyenas

(*Crocuta crocuta*) are present, may account for the differences observed in the brown hyena density estimates across the various studies (Owens & Owens 1978; Skinner & Van Aarde 1981; Balme *et al.* 2009; Kent & Hill 2013).

The size of brown hyena clans has been previously associated with the availability of food resources within their environment (Mills 1984). In areas where spotted hyenas are present, brown hyenas are often rare or absent, because the competitive dominance of the larger spotted hyena results in brown hyenas being deprived of significant amounts of food (Skinner & Van Aarde 1981; Mills & Mills 1982). The absence of spotted hyenas in MZNP could therefore explain why the density estimates of brown hyenas in MZNP (6-10 individuals/100 km$^2$) was higher than those estimated for brown hyenas in the southern Kalahari (1.8-2.81 individuals/100 km$^2$), where spotted hyenas are present (Hill & Kent 2013). In contrast, the presence of other large predators such as lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*), can aid the success of brown hyenas, through facilitating scavenging opportunities (Yarnell *et al.* 2013; Welch 2014). This theory is particularly true for the brown hyena population in MZNP. The abundance of potential food resources in MZNP is relatively higher and the food resources are less patchy than that found in the Kalahari, because in MZNP the migration of species is restricted to within the borders of the park by a predator-proof fence (see Chapter 4). Although lions are known to be more beneficial than detrimental to brown hyenas, antagonistic encounters between the two species are known to occur (Mills 1990). Although no brown hyenas were reported to have been killed by the lions during my study, one was killed by the lions three months after I had completed my field work. It can therefore be assumed that the lions in MZNP have minimal influence in limiting the brown hyena population size in MZNP. The higher abundance of potential food resources in MZNP could therefore, potentially explain why higher brown hyena densities are observed in MZNP compared to the Kalahari.

When assessing the status of a species or evaluating conservation plans for a region, knowledge about the spatial distribution of species is just as important as estimating population size (Henschel & Ray 2003; Tobler *et al.* 2008). The spatial distribution of the 12 individually identifiable brown hyenas in MZNP shows that the brown hyenas are utilising the entire park. It is not surprising that the brown hyenas are utilising both the mountainous and low lying areas of MZNP, as brown hyenas are known to be flexible in their use of habitat at the landscape level (Welch *et al.* 2015). Brown hyenas either live as members of a clan or nomadically, where clans occupy territories which they actively defend against members of another clan (Owens & Owens 1979; Mills 1982). Brown hyenas belonging to a clan are rarely known to leave their clans territory (Owens & Owens 1979). Therefore, from the spatial distribution of the known brown hyenas in MZNP, it can be speculated that the population is made up of at least two separate clans, as individuals were either only recaptured in the northern or southern sections of the park.

The activity patterns of brown hyenas in the enclosed systems of MZNP, Kwandwe Private Game Reserve and Lapalala Wilderness resemble those reported for brown hyenas in the open systems of the central Kalahari and southwest Namibia (Owens & Owens 1978; Hulsman *et al.* 2010; Edwards *et al.* 2015; Welch *et al.* 2015). My results, along with those from Kwandwe Private Game Reserve and Lapalala Wilderness, reiterate the fact that brown hyenas are predominantly nocturnal (Edwards *et al.* 2015; Welch *et al.* 2015). No brown hyenas in MZNP were captured on the cameras after 05h00, which supports Owens and Owens (1978) suggestion that brown hyenas almost always leave a carcass before sun-rise, because they are heat sensitive animals. Temperature is regarded as the most influential factor determining the activity patterns of brown hyenas, because in the central Kalahari it was only on cool, cloudy days that brown hyenas were seen foraging earlier in the evenings (Owens & Owens 1978). A similar pattern could be in seen in MZNP, as the brown hyenas were not only active earlier in the evenings (18h00) during the cooler winter and autumn months, but were also considerably more active in the early mornings (04h00) compared to their activities during the warmer summer and spring months. As seen in MZNP, brown hyenas are usually the most active in the early evening from approximately 19h00 to 21h00 and then have another peak in activity at dawn (Owens & Owens 1978; Edwards *et al.* 2015).

Very little data has been published on the success or failure of brown hyena reintroductions in South Africa (but see Welch *et al.* 2015). Monitoring reintroductions and how the numbers of reintroduced populations change over time is fundamental to the future development of conservation and management plans for this species (Wegge *et al.* 2004; Hayward *et al.* 2007b). The results from my study show that the reintroduction of brown hyenas into MZNP can be viewed as being successful, because not only was there survival of the release generation (i.e. one of the original male's) but there was also evidence that both the release generation and their offspring were breeding as the population has grown from three individuals in 2008 to between 12 and 21 in 2015.

In small (<440 km$^2$) protected areas like MZNP, where carnivores are not threatened by human persecution and food availability is high, populations of reintroduced species can increase rapidly (Smith 2006; Welch & Parker 2016). In less than a single decade, the brown hyena population in MZNP increased by at least 400% which is comparable to the 367% increase in the brown hyena population within a decade in Kwandwe Private Game Reserve (Welch & Parker 2016). The restriction of movement in fenced reserves prevents natural ecological processes such as emigration and immigration, which can have huge genetic implications such as inbreeding depression and reduction in heterozygosity (Caro 2000; Lindsey *et al.* 2009). Therefore, even though reintroductions are deemed successful, it does not imply an end-point as further research and monitoring is needed to make informed decisions about issues such as the relocation or new releases of individuals into areas where inbreeding could be an issue (Seddon 1999; Welch & Parker 2016).

Obtaining reliable population estimates for shy and secretive species is particularly challenging as capture rates are bound to be low. Capture rates were low in my study and in order to improve capture rates, I would recommended that future research includes the use of scent lures. The function of a scent lure is to keep the animal stationary in front of the cameras so that clear images of both sides of the animal are captured to produce a full profile (Negrões *et al.* 2010; Ancrenaz *et al.* 2012). The use of scent lures can therefore increase the number of individuals identified in the study area and potentially reduce the number of poor quality images captured. When determining density estimates using camera traps, the use of scent lures is more appropriate than bait, because scent lures do not draw in individuals from outside their home ranges (Ancrenaz *et al.* 2012).

The results from my study demonstrate that camera trapping with an extended survey period is a successful method to use to obtain population estimates for species with low capture rates. My study also shows that camera trapping is a successful method to use for obtaining information on the activity patterns and spatial distributions of a nocturnal and secretive species such as the brown hyena.

# CHAPTER 4

# FEEDING ECOLOGY OF BROWN HYENAS

**Original male captured carrying the remains of a zebra carcass in Mountain Zebra National Park**

## INTRODUCTION

Large carnivores play a key role in regulating the function of terrestrial ecosystems and are of vital importance for the conservation and management of biodiversity (Yarnell *et al.* 2013; Ripple *et al.* 2014). According to ecological theory, carnivores control herbivore abundance, which can lead to changes in the structure of communities at most trophic levels (Steneck 2005). Simultaneously, the result of interactions between carnivores may be important in controlling their own abundance (Ritchie & Johnson 2009). The coexistence and ecological relationships of large terrestrial carnivores (>20 kg) has been widely studied in the Serengeti Plains and the woodland savanna regions of southern Africa (Durant 1998; Radloff & Du Toit 2004; Hayward *et al.* 2007a; Cozzi *et al.* 2013). These studies have reinforced the concept that African ecosystems are predominantly characterised by the predatory and competitive dominance of large, apex carnivores, such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), while the subordinate positions are filled by smaller carnivores, especially cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*) (Mills 2015).

During the early 20th century in South Africa, large predators such as lions, cheetahs and hyenas, were extirpated from most of their range mainly due to human persecution. However, from the early 1990s, large areas of agricultural land, particularly in the Eastern Cape, were transformed into economically viable game farming and conservation areas (Hayward *et al.* 2007a). In order to restore the historic diversity of mammals, conserve threatened species and maximise ecotourism, many fenced reserves in South Africa (e.g. Mountain Zebra National Park (MZNP), Shamwari Private Game Reserve, Kwandwe Private Game Reserve) began reintroducing predators (Gaylard *et al.* 2006; Hayward *et al.* 2007a; Yarnell *et al.* 2013). Although the relocation of large predators is common in the Eastern Cape, very little to no post-release monitoring of these species has been conducted (Hayward *et al.* 2007a). Besides the need for post-release monitoring, the reintroduction of predators brings about the opportunity for research to be conducted on the ecological impacts of large predators (Yarnell *et al.* 2013). While the impacts of predators on prey populations has been well studied in South Africa (Hayward *et al.* 2007a; Hayward *et al.* 2007b), little is known about their impact on the foraging behaviour of other carnivores, such as brown hyenas (*Hyaena brunnea*) (Hayward & Kerley 2009; Yarnell *et al.* 2013).

Previous studies on brown hyenas have shown that they are generalist and opportunistic scavengers, and take advantage of any food source that becomes available to them (Owens & Owens 1978; Binder & Van Valkenburgh 2000). They feed mainly on the remains of fresh kills left by other predators, but their diet may be supplemented year round, especially in the dry months, by hunting small mammals, birds, insects, reptiles and feeding on fruits (Owens & Owens 1978; Binder & Van Valkenburgh 2000; Kuhn *et al.* 2010). In the southern Kalahari, the hunting behaviour of brown hyenas is unspecialised and completely opportunistic (Mills 1984). Their chases usually last no longer than 100m and their main prey items include springbok lambs (*Antidorcus marsupialis)*, springhares (*Pedetes capensis*), bat-eared foxes (*Otocyon megalotis*) and ground nesting birds such as Korhaans (Mills 1984).

The opportunistic scavenging and hunting behaviour of brown hyenas means that they play a key role in removing the remains of old carcasses from the environment (Mills 1982). The importance of this behaviour is that carcasses, if left to decay on their own, may act as breeding grounds for many parasites and diseases (Mills 1982). By feeding on fruits in the dry months, brown hyenas also act as seed dispersers for many plants through defecation (Owens & Owens 1978). Brown hyenas are also known to alter the predation frequencies of carnivores, such as cheetahs and leopards (*Panthera pardus*) by stalking them during hunts and sometimes driving them off their kills (Owens & Owens 1978; Ripple *et al.* 2014). Therefore brown hyenas are ecologically important as they can alter ecosystems along multiple food web pathways (Ripple *et al.* 2014).

Brown hyenas were reintroduced into MZNP in 2008, after the park’s first predator reintroduction of cheetahs during 2007 (Taplin 2008). The park’s most recent predator reintroduction was of three lions in 2013 (Taplin 2013). Studies on the feeding ecology of the cheetahs and the lions in MZNP began in 2011 and 2013 respectively, whereas no studies had been conducted on the feeding ecology of brown hyenas in MZNP. In fact, there is a general lack of knowledge on the diet of brown hyenas across most of its distributional range (but see Slater & Muller 2014). The handful (n=5) of papers which do provide detailed information on the feeding ecology of brown hyenas are mostly limited to arid environments (Owens & Owens 1978; Mills & Mills 1978; Skinner & Van Aarde 1981; Mills 1989; Mills 1990). In the Kalahari, brown hyena populations thrive on the remains of the kills of large predators such as cheetahs and lions (Estes 1992). It would therefore be interesting to see if brown hyenas in MZNP are benefiting from the reintroduction of the lions.

A fairly simple means of gaining valuable information on the role of a carnivore in an ecosystem is through studying their diet (Klare *et al.* 2011). Analyses of diet can assist in understanding the impacts that carnivores have on prey populations or other carnivores (Ruhe *et al.* 2008; Klare *et al.* 2011). Diet analyses can thus have far reaching impacts especially on the development of carnivore management plans where either economically important or endangered species are involved (Klare *et al.* 2011). Historically, diet analyses of a wide variety of mammals relied on the highly invasive technique of studying their stomach contents (e.g. Spalding 1964; Perez & Bigg 1986; Trites & Joy 2005). Analyses of stomach contents is often not a viable option and so alternative methods of determining the diet of animals include; field observations (Hilderbrand *et al.* 1996; Wilson & Delahay 2001), stable isotopes (Hilderbrand *et al.* 1996) and scat analyses (Burns *et al.* 1998). Satisfactory results are often difficult to obtain through direct observations, particularly regarding smaller food items and especially for shy and secretive carnivores (Kaunda & Skinner 2003). Stable isotope analysis is a fairly new technique, which has been used in recent dietary studies but has a major drawback, as it can only differentiate between broad food categories (Klare *et al.* 2011). Scat analysis, on the other hand, gains a large amount of support because it is a basic, non-invasive technique which has low costs. It is also particularly attractive because scats can be easily collected in the field and stored to be analysed at a time convenient for researchers (Mukherjee *et al.* 1994; Foran 1997; Wiesel 2007; Ruhe *et al.* 2008). Consequently, scat analysis has become the most commonly used method to assess the diets of terrestrial carnivores, especially for species which are rare and elusive, such as brown hyenas (Kaunda & Skinner 2003; Klare *et al.* 2011).

Scat analysis is the identification and quantification of undigested parts of prey that have passed through the digestive system of mammals (Pierce & Boyle 1991; Trites & Joy 2005). Prey species can be reliably identified from scats through the cuticular and medullary characteristics of hair, as the hair of prey is relatively undamaged in carnivore scats (Mukherjee *et al.* 1994; Ramakrishnan *et al.* 1999). Small mammals can also be identified from bones and cranial structures that survive the digestive process (Trites & Joy 2005). Insects consumed can be identified through their exoskeletons and plants can be macroscopically identified either from cellular characteristics or from fruits and seeds that pass through the digestive system (Trites & Joy 2005). It is important to note that scat analyses cannot determine prey preference of carnivores, as hair frequency does not necessarily correlate with prey volume (Wiesel 2010). Scat analyses can also not be used to differentiate between killed and scavenged prey (Klare 2010; Wiesel 2010).

The reintroduction of large predators into an ecosystem is said to have large effects on other carnivore species through both density- and behaviourally-facilitated interactions (Wikenros *et al.* 2013). For example, the presence of other large predators is likely to influence the diet of brown hyenas, as their diet will adjust according to the availability of food (Kaunda & Skinner

2003; Klare *et al.* 2010). Detailed quantitative data on the diet of brown hyenas is required to obtain a better understanding of the functional role that brown hyenas play in ecosystems. The structured reintroduction of predators into MZNP presented the opportunity to research not only the feeding ecology of brown hyenas in a semi-arid region, but also to evaluate how the presence of large predators such as lions and cheetahs, influence the feeding ecology of brown hyenas.

### Aims

The aim of this chapter was to determine the diet of brown hyenas in MZNP through scat analysis, and to investigate whether the presence of other large predators such as lions and cheetahs influenced this diet in any way.

## METHODS

Brown hyena scat samples were collected opportunistically from April 2011 to June 2015 while either walking or driving through the park. Brown hyena scats could be identified by their size and shape along with their obvious white or grey colouration (Hulsman *et al.* 2010). In the field, scats were placed in air-tight zip-lock plastic bags for storage. Each scat sample was labelled with details about the scat site such as date, location and GPS coordinates. All scats found in the field were collected except for ones which were extremely decomposed and brittle. Collected scats were then stored in a freezer until they could be processed.

Each scat was placed in pieces of nylon stocking that were tied at both ends (Klare *et al.* 2011). The stockings were placed into beakers of water in a hot water bath (± $45^0$ Celsius). The scats were left to soak in the water for up to 48 hours until soft. After soaking, the scats were removed and carefully washed and strained under running water and over a 1mm mesh sieve to separate dietary remains such as hair, bones and teeth from other organic matter (Karanth & Sunquist 1995; Do Linh San *et al.* 2009). Dietary remains (hair, bones, seeds etc.) from each scat were placed onto paper towel and allowed to air-dry for approximately 36 hours. Once dry, all dietary remains were placed into labelled plastic bags.

Cross sections of mammalian hair found in the scats were prepared using the method proposed by Douglas (1989), whereby a random selection of between 10 and 20 hairs (ensuring that all hair types present in the scat were represented) from each scat sample were placed inside a disposable plastic pipette (Reynolds & Aebischer 1991). Hot paraffin wax (Paraplast Plus, Sherwood Medical Co., St Louis, Missouri, USA) was sucked up into the pipette filled with hair and then cooled in a beaker of crushed ice. Once cooled, the pipette was cut into between six and eight sections which were 1-2 mm thick. These sections were fixed onto labelled microscope slides using a drop of paraffin wax.

Hair samples were identified to the lowest taxonomic level by comparing the prepared slides to the Rhodes University mammal hair reference collection of all potential prey species found in MZNP (Appendix I) (Karanth & Sunquist 1995; Spaulding *et al* 2000; Wiesel 2007). Hair slides for potential prey species that were missing from the reference collection, were prepared from hair samples collected from museum specimens (Amathola Museum, King Williams Town, Eastern Cape Province) prior to the analysis. The presence of a species was recorded for each scat sample.

Kill sites of the cheetahs and lions in MZNP were used to compare the diets of the cheetahs and the lions with the diet of the brown hyenas. Kill site data for the cheetahs were collected from three males and four females (between April 2011 and September 2015; Appendix V) and kill site data for the lions were collected from two males and one female (between April 2013 and September 2015). Kill sites for both the lions and the cheetahs were either located opportunistically by tracking the animals using VHF (Very High Frequency) signal from the collars or were opportunistic kills reported by MZNP management or staff. The majority of the kill sites however, were located using GPS clusters. The collars on the cheetahs and lions were programmed to send four GPS locations (set of co-ordinates) per day via satellite to a secure data service website from which the data could be downloaded onto a computer. The GPS data obtained from the fixes of all seven cheetahs and the three lions were used to determine where GPS aggregation clusters (hereafter, clusters) were, and therefore where potential kill sites were (Anderson *et al.* 2003; Sand *et al.* 2005; Tambling *et al.* 2010). The downloaded GPS co-ordinates were used to conduct cluster analyses in ArcGIS, so that cluster sites could be visually identified. A cluster of locations was defined as being two or more consecutive recorded fixes within a 100m radius of each other (Sand *et al.* 2005; Tambling *et al.* 2010). The co-ordinates of clusters were programmed into a handheld Garmin GPSmap 62s, where a 50m radius from the central point of the tightest cluster was examined on foot for any prey remains (Tambling *et al.* 2010). GPS points surrounding the central point were often examined if remains were not found surrounding the central point (Tambling *et al.* 2010). A kill site was identified from the presence of prey stomach contents, bones, horns, hair, feet, hooves and teeth. The remains of prey were used to identify the prey species as well as to age and sex the prey species where possible (Anderson *et al.* 2003; Sand *et al.* 2005; Tambling *et al.* 2010).

### Data analyses

The importance of each food item found in the brown hyena scat samples was determined by calculating the relative frequency of occurrence. This was calculated as a percentage using the number of scats containing the item as a function of the number of occurrences of all items found (Juarez & Marinho-Filho 2002; Phillips *et al.* 2007). The prey items found in the brown hyena scat samples were also divided into four broad categories: small mammals (<30 kg), medium mammals (30-90 kg), large mammals (>90 kg) and other (birds, unknown, etc.) (Kruger *et al.* 1999). The prey items found in the diet of the lions and cheetahs both before and after the release of the lions were divided into the same four categories. Reducing the large number of prey species consumed into categories allows for the simplification of descriptions and comparisons of diet (Trites & Joy 2005).

Chi-square goodness-of-fit tests were conducted in the R language (version 3.1.2, R Development Core Team, 2014) to examine the overall differences in the proportional contribution of the major prey categories among the diets of the lions, cheetahs and brown hyenas (Fedriani *et al.* 2000). The proportional contribution of the major prey categories for the brown hyenas (both before and after the release of the lions) were used as the observed values and the proportional contribution of the major prey categories for the lions and cheetahs (both before and after the release of the lions) were used as the expected values for the chi-square tests (Phillips *et al.* 2007). Significance of chi-square tests was based on a probability level of $P \leq 0.05$. Niche overlap of the major prey categories between cheetahs and brown hyenas (before the release of the lions) was calculated using the Pianka index (Pianka 1973) in the EcoSim Software v7.72 (Gotelli & Entsminger 2004). The amount of overlap between the prey categories of cheetahs and brown hyenas (after the release of the lions) was also calculated, as was the dietary overlap between brown hyenas and lions.

## RESULTS

In total, 118 brown hyena scats were collected between April 2011 and June 2015 (Fig.4.1). Seven scats were excluded from the analyses as they did not contain any dietary remains. An additional 15 scats were also excluded because they fell within a six month period after the release of the lions. I excluded these scats to ensure that the scat samples being analysed were definitely deposited after the release of the lions. Thus, a total of 96 brown hyena scats were analysed, 12 of which were collected before the release of the lions and 84 after (Fig.4.2). The analysis of the 96 brown hyena scats is viable, as Trites and Joy (2005) indicate that a minimum of 94 scat samples are needed when comparing diets so that reasonable effects can be distinguished over time or between areas.

In the 96 brown hyena scat samples analysed, 25 dietary items were found; 10 were found in the scat samples before the release of the lions and 23 were found after (Fig.4.1). Vegetation remains (e.g. leaves and grass) were found in the scat samples, but were not included in the analyses as they were considered to be consumed to aid digestion instead of for nutritional value (Vieira & Port 2007). No remains of birds, insects or reptiles were found in the brown hyena scat samples (Fig.4.1 & 4.3). One seed was found in a scat before the release of the lions and two were found afterwards (Fig.4.1). A total of nine mammalian species were identified in the brown hyena scat samples collected before the release of the lions and 22 mammalian species were found after the lions were released (Fig.4.3). Analyses revealed a mean of 1.46 ± 0.78 (sd) prey items per scat sample before the release of the lions and 1.34 ± 0.48 after their release.

Ungulates made up the biggest portion of the diet of brown hyenas both before (54%) and after (70%) the release of lions into MZNP (Fig.4.3). Kudu (*Tragelaphus strepsiceros*) was by far the most frequent prey species occurring in the brown hyena scat samples both before (33%) and after (22%) the release of the lions (Fig.4.3). Primates (babbons 5%, vervet monkey 1%) accounted for 6% of the occurrences in the scat samples of brown hyenas after the release of lions and none were found before (Fig.4.3). Carnivore remains were found in the scats of brown hyenas both before (17%) and after (12%) the release of lions (Fig.4.3). Species such as the western rock elephant shrew (*Elephantulus rupestris*) and the rock hyrax (*Procavia capensis*) were only found in the scats of brown hyenas before the release of the lions (Fig.4.3).

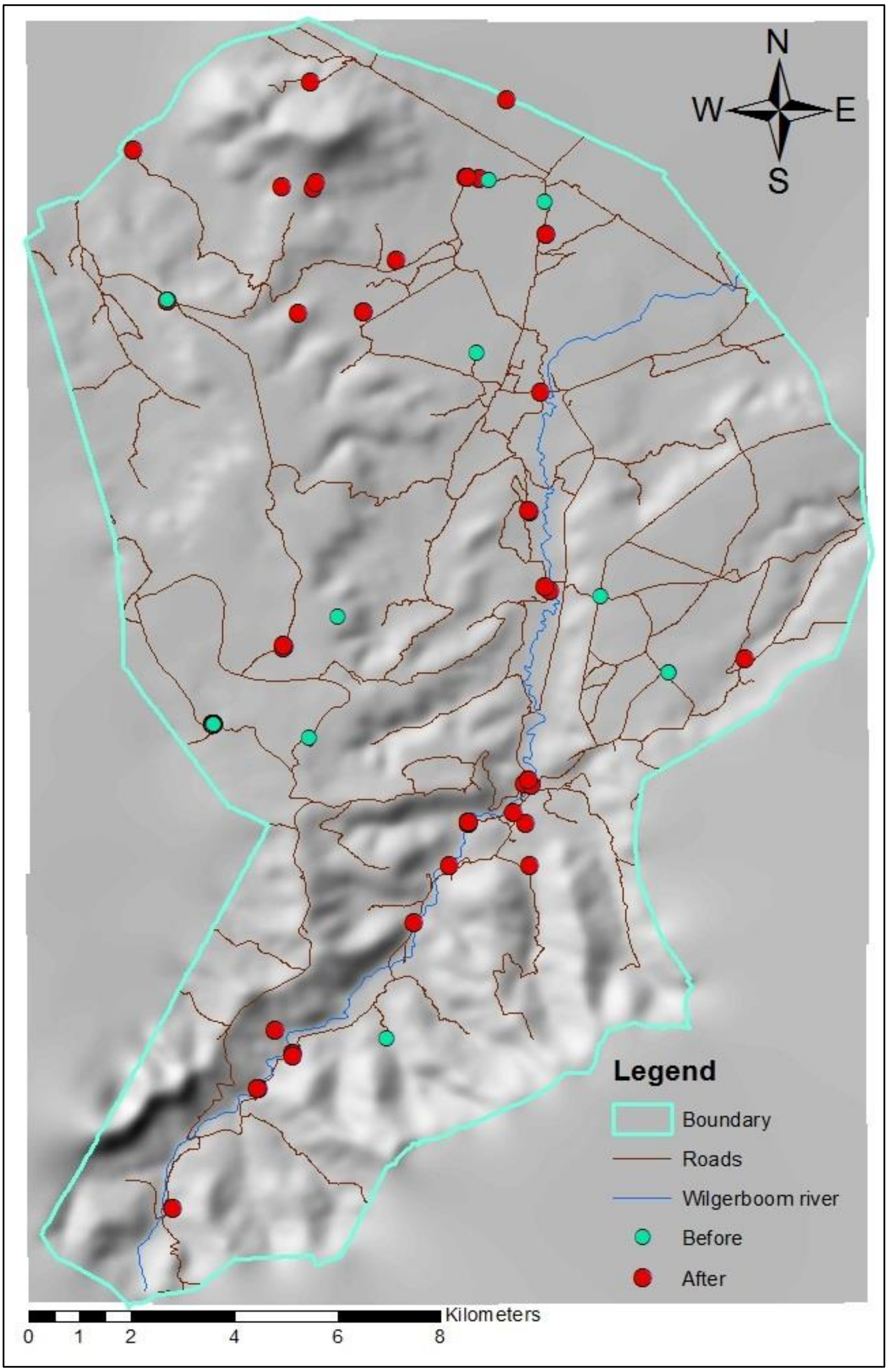

**Figure 4.1:** Location of the brown hyena scat samples collected at Mountain Zebra National Park before (n=12) and after (n=84) the release of the lions.

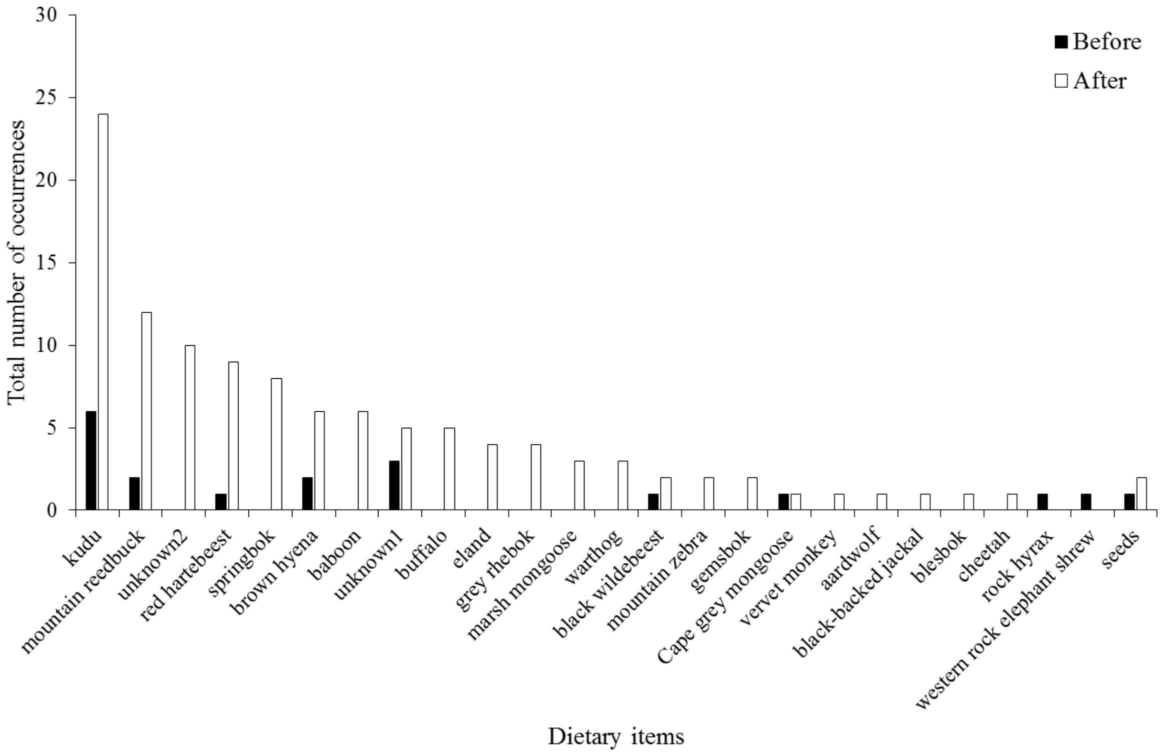

**Figure 4.2:** The total number of occurrences of dietary items found in scats of brown hyenas before and after the release of the lions into Mountain Zebra National Park.

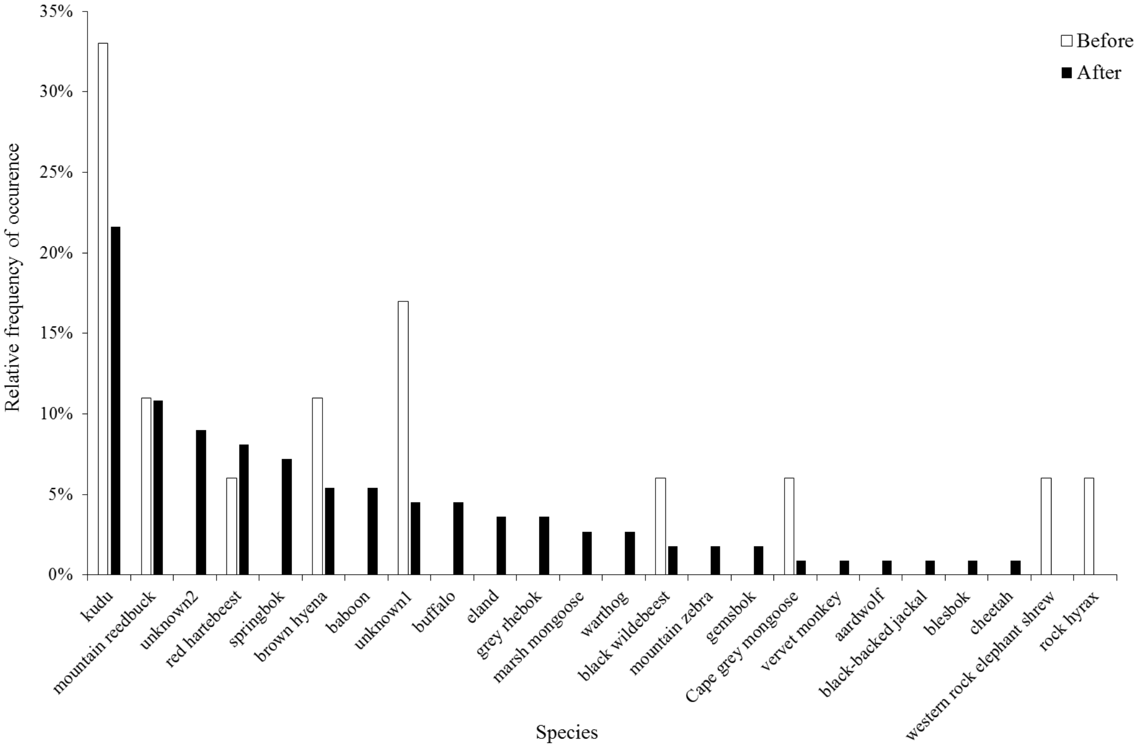

**Figure 4.3**: Relative frequency of occurrence of dietary items in the scats of brown hyenas before (n=12 scats) and after (n=84 scats) the release of the lions into Mountain Zebra National Park.

In total, data for 272 cheetah kill sites (114 before and 158 after the release of the lions) and 183 lion kill sites were recorded. A total of 14 prey species were identified for the cheetahs whereas a total of 12 prey species were identified for the lions. Interestingly the lions and the cheetahs had seven prey species in common (eland (*Tragelaphus oryx*), kudu, red hartebeest (*Alcelaphus buselaphus*), black wildebeest (*Connochaetes gnou*), gemsbok (*Oryx gazella*), grey rhebok (*Pelea capreolus*) and common duiker (*Sylvicapra grimmia*)).

Ungulates dominated the diet of the cheetahs both before (94%) and after (92%) the release of the lions into MZNP (Fig.4.4). The diet of lions in MZNP also predominantly consisted of ungulate species (93%, Fig.4.5). Kudu (46%) was the most frequent prey species recorded in the diet of the cheetahs before the release of lions, whereas springbok (36%) was the most frequent species after the release of the lions (Fig.4.4). Eland (20%) and buffalo (*Syncerus caffer*) (20%) where the most frequent prey species recorded in the diet of the lions (Fig.4.5). Vervet monkey (*Cercopithecus pygerythrus*) (1%) was only recorded in the diet of cheetahs before the release of lions whereas scrub hare (*Lepus saxatilis*) (1%) was only recorded after the release of the lions (Fig.4.4). Neither of these two species were recorded in the diet of the lions (Fig.4.5). The only rodent to be recorded in the diet of the lions was porcupine (*Hystrix africaeaustralis*) (Fig.4.5).

Medium mammal remains were the most frequently recorded prey category in the brown hyena scat samples before the release of the lions, whereas large mammal remains were the most frequent after the release of the lions (Fig.4.6). Large mammals were the prey category most frequently recorded in the diet of lions (Fig.4.6), whereas medium mammal remains were recorded most frequently for cheetahs (Fig.4.6).

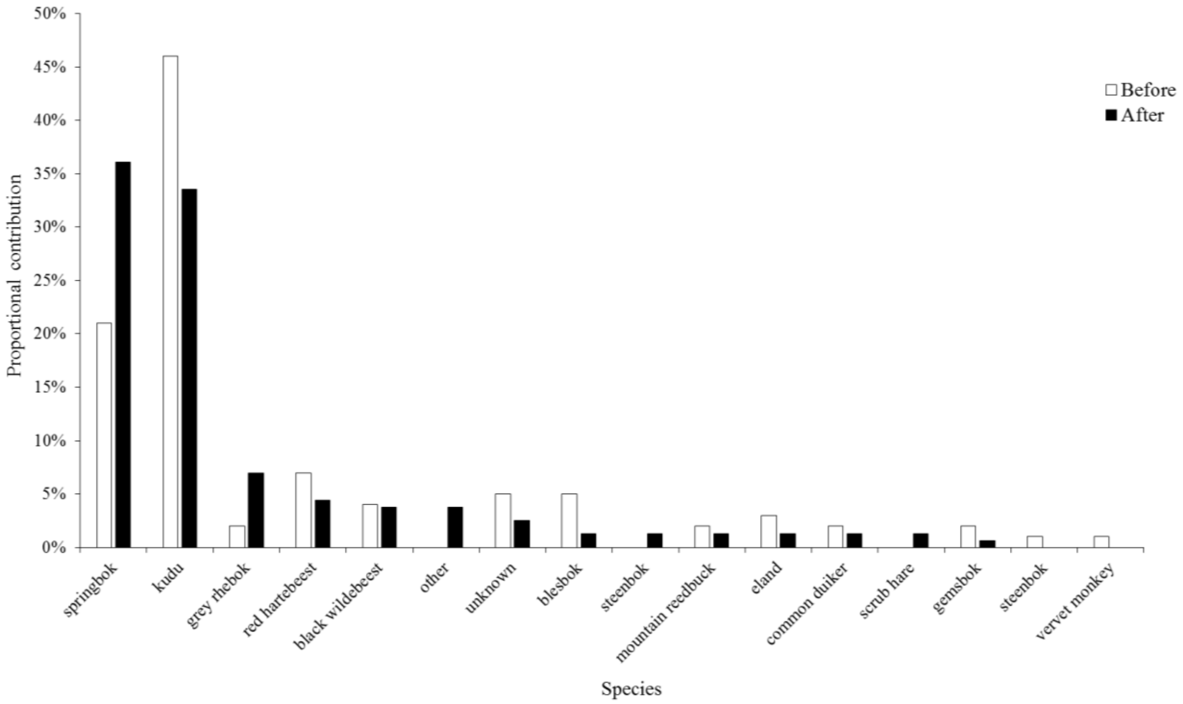

**Figure 4.4:** Proportional contribution of prey species found at cheetah kill sites before and after the release of lions in Mountain Zebra National Park.

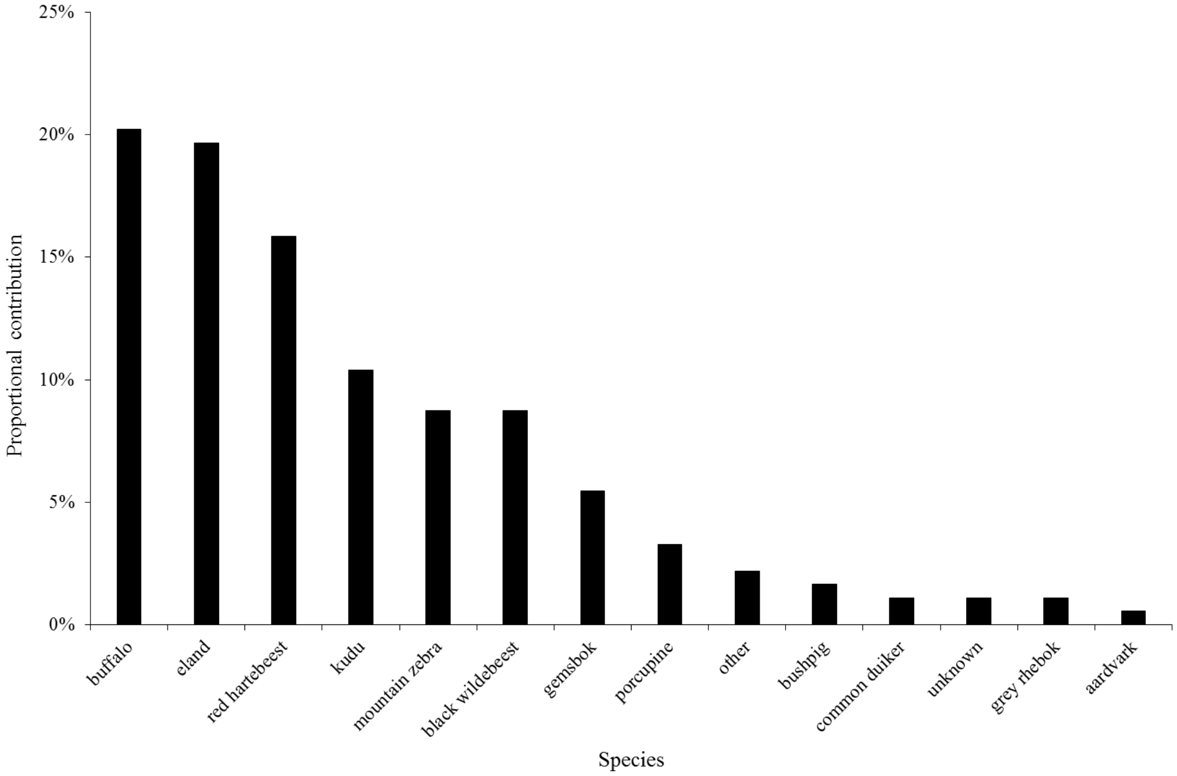

**Figure 4.5**: Proportional contribution of prey species found at lion kill sites in Mountain Zebra National Park.

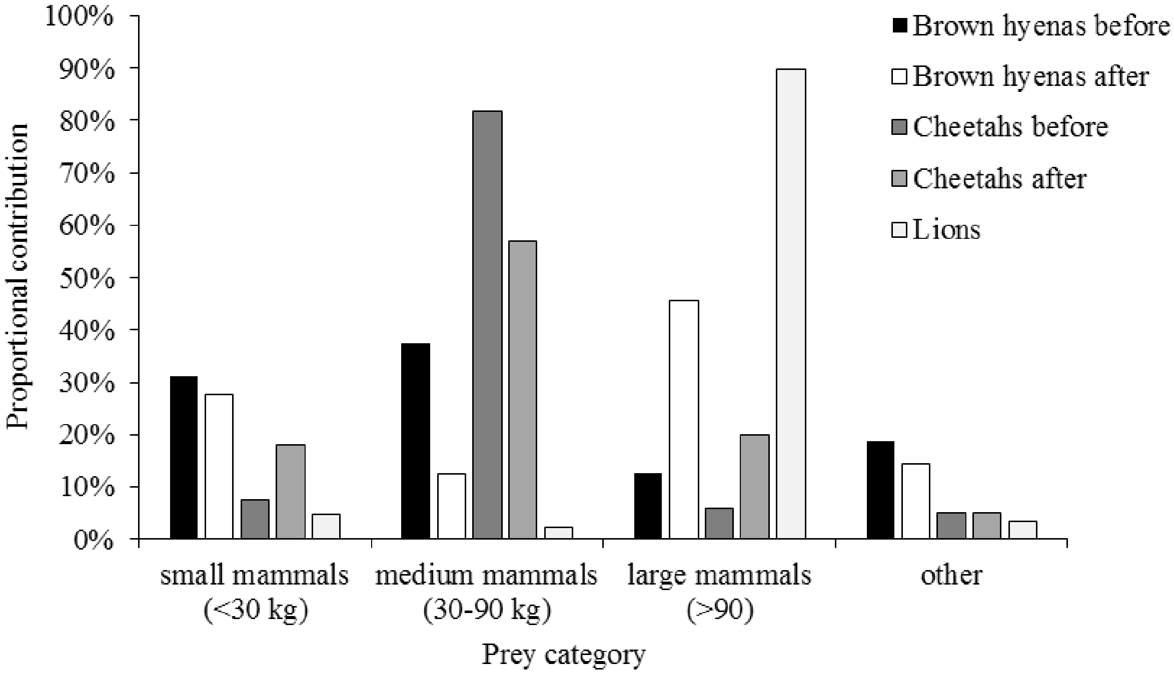

**Figure 4.6:** Proportional contribution of the major prey categories that made up the diets of brown hyenas, cheetahs (before and after the release of the lions) and lions in Mountain Zebra National Park.

A significant relationship ($\chi^2 = 19.59$; d.f. = 1; $P<0.05$) was found between the major prey categories recorded for brown hyenas and cheetahs before the release of the lions. Both species' diets contained more medium mammals (cheetahs before = 82%, brown hyenas before = 38%) than small mammals (cheetahs before = 8%, brown hyenas before = 31%; Fig.4.6). A significant relationship ($\chi^2 = 224.61$; d.f. = 3; $P<0.05$) was found between the major prey categories recorded for brown hyenas and the lions. The lion and brown hyena diets predominantly consisted of large mammals (lions = 90%, brown hyenas = 46%) and, in both species' diets, medium sized mammals contributed the least (lions = 2%, brown hyenas = 12%; Fig.4.6). The major prey categories for brown hyenas and cheetahs after the release of lions was also found to have a significant relationship ($\chi^2 = 94.65$; d.f. = 3; $P<0.05$). Although the diet of the cheetahs contained a considerably higher proportion of medium sized mammals than the brown hyenas (cheetahs = 57%, brown hyenas 12%), both species' diets contained similar proportions of small sized mammals (cheetahs = 18%, brown hyena = 28%; Fig.4.6). The niche overlap index revealed a high level of dietary overlap between brown hyenas and cheetahs before the release of the lions ($O$ =0.96). After the release of the lions, the dietary overlap between brown hyenas and cheetahs decreased, but remained high ($O$ = 0.80). Dietary overlap between the brown hyenas and the lions was relatively high ($O$ = 0.79), but not as high as the overlap between the brown hyenas and cheetahs.

## DISCUSSION

One of the most crucial factors affecting the survival and occurrence of carnivores in a specific habitat is food availability (Wiesel 2007). In MZNP, brown hyenas fed on a wide variety of mammals. Similar diets for brown hyenas have been documented in the southern Kalahari (Mills & Mills 1978), central Kalahari (Owens & Owens 1978) and in reserves in the North-West (Yarnell *et al.* 2013) and Limpopo (Burgener & Gusset 2003) provinces of South Africa. Brown hyenas along the Namib Desert coastline, however, exhibit a far more restricted diet and feed almost exclusively on Cape fur seals (*Arctocephalus pusillus*) (Skinner & van Aarde 1981; Weisel 2007). One of the major differences between my findings and those of brown hyenas in the Kalahari and Northern provinces of South Africa is that brown hyenas in MZNP were not found to be supplementing their diet with insects, reptiles or fruit.

In the arid Kalahari, brown hyenas supplement their diet in the dry season by eating wild melons, insects or reptiles because fresh food resources become widely dispersed when the lions increase their range in response to their migrating prey (Owens & Owens 1978). At this time, the brown hyenas feed mainly on the wild melons as they are an essential source of moisture during the dry season (Owens & Owens 1978). In MZNP, the wildlife are supplemented with water all year round through artificially sourced dams and pans (± 14) and migration of species is restricted due to the reserve being surrounded by predator-proof fencing (Gaylard *et al.* 2008). Brown hyenas in MZNP are therefore less likely to supplement their diet with fruit or insects as water is readily available and food resources are more likely to be obtained from the kill remains of the lions and cheetahs.

Medium mammals were recorded the most frequently for cheetahs because even though kudu (a large mammal) were recorded as one of the most frequent species in their diet, the cheetahs were predominantly killing the juveniles, which fall into the medium size prey category (Mills *et al.* 2004). Although I was unable to determine the age of the dietary remains found in the scat samples of the brown hyenas or whether they were obtained by scavenging or hunting; the high proportion of kudu remains in the diet of the brown hyenas before the release of the lions was most likely in response to the scavenging opportunities provided by the cheetahs. Therefore, the occurrences of kudu in the diet of the brown hyenas before the release of the lions were classified as medium mammals, which was the most frequently recorded prey size category for the brown hyenas. The occurrence of kudu in the scats of brown hyenas after the release of the lions was classified as large mammals as both the lions and the cheetahs preyed on kudu.

The dietary composition of mammalian carnivores is often determined by the abundance and dispersion of prey resources (Klare *et al.* 2010). The results from my study support this ecological theory, as the introduction of lions into MZNP led to changes in the dietary composition of brown hyenas. Large mammals became the prey category contributing the greatest proportion to the diet of the brown hyenas, instead of medium mammals as was seen before the release of the lions. Changes in foraging behaviour of brown hyenas in response to increased carcass availability have also been documented in the Kalahari (Owens & Owens 1978). The lions increased the scavenging opportunities of brown hyenas, especially of buffalo and eland, which were the lions most prominent prey species and which only occurred in the scats of brown hyenas after the release of the lions. Eland were present in the diet of cheetahs in MZNP, but occurred a great deal less frequently. Studies on the prey preferences of lions have shown that lions predominantly kill large mammals as they are morphologically adapted to kill prey their own size or larger (Hayward & Kerley 2005). Hunting is almost irrelevant for brown hyenas and they usually only hunt small mammals (Owens & Owens 1978), which makes the high occurrence of medium (before release of lions) and large (after release of lions) mammal remains in their scats to be indicative of scavenging (Slater & Muller 2014). The change in the feeding ecology of brown hyenas in my study highlights the important role that large predators play in providing scavenging opportunities for brown hyenas and other species in the ecosystem (Yarnell *et al.* 2013). Similar results of large predators facilitating the scavenging behaviour of brown hyenas were found in the Pilanesberg National Park in the North West Province and Shamwari Game Reserve in the Eastern Cape of South Africa (Yarnell *et al.* 2013; Slater & Muller 2014).

Examples of large predators influencing the foraging behaviours of scavengers can be seen in species outside of Africa. In Yellowstone National Park (YNP), United States, for example, the reintroduction of grey wolves (*Canis lupus*) influenced the scavenging behaviour of coyotes (*Canis latrans*), which are highly dependent on carrion in the winter (Wilmers *et al.* 2003). Just like the lions in MZNP, the wolves in YNP play an important role in providing scavenging opportunities for scavengers in the ecosystem (Wilmers *et al.* 2003).

The presence of carnivore remains such as those found in the scats of brown hyenas in MZNP (Cape grey mongoose (*Galerella pulverulenta*), black-backed jackal (*Canis mesomelas*) and brown hyena) are not uncommon and similar dietary results were found for brown hyenas in Shayamanzi Game Ranch in the Limpopo Province of South Africa (Burgener & Gusset 2003). The occurrence of Cape grey mongoose is most likely the result of brown hyenas hunting in MZNP, as they are known to opportunistically hunt small mammals, and neither the lions nor cheetahs were recorded preying on such species. Although neither the lions nor cheetahs were recorded preying on black-backed jackal, apex predators such as lions are known to occasionally kill black-backed jackals (Yarnell *et al.* 2013). Therefore, the occurrence of black-backed jackal remains in the brown hyena scat samples could be because the brown hyenas scavenged on black-backed jackal carcasses either due to predation by the lions or due to other factors such as disease and old age (Burgener & Gusset 2003; Yarnell *et al.* 2013). The occurrence of brown hyena hair in their own scats is most likely the result of either auto- or allogrooming (Owens & Owens 1978; Mills 1983). Although the occurrence of cheetah, which was found in one of the brown hyena scat samples (after release of the lions) is an uncommon occurrence it can be explained, as one of the female cheetahs in MZNP was found dead in the field (D. Van de Vyver, MZNP staff member, pers.comm). Park management suspected that the cheetah was killed by the lions, as GPS data from the collared lion, showed that they were in the same area as the cheetah when she died. Therefore, the rare occurrence of cheetah found in the brown hyena scat sample was most likely the result of a scavenging opportunity. Finding brown hyena scats with no dietary remains is not an unusual phenomenon, as Mills and Mills (1978) stated that many of the vertebrate remains that brown hyenas feed on are bones devoid of hair. These bones that are fed on are completely digested leaving only dry bone powder in the scat, which cannot be identified (Mills & Mills 1978).

Various studies have shown that although the diets of large carnivores overlap significantly, factors such as preferred habitat and hunting periods can lead to ecological separation (Breuer 2005). My data supported this concept as Pianka’s indices showed that the diets of the brown hyenas, cheetahs and lions overlapped substantially. The opportunistic hunting and scavenging behaviour of the brown hyena makes it highly unlikely that they are competing with the cheetahs or lions for prey. Instead, the substantial niche overlap between the brown hyenas and the lions and cheetahs at MZNP, means that these large predators are facilitating the scavenging behaviour of the brown hyenas.

My study shows that scat analysis was an appropriate method to use to gain insight into the feeding ecology of brown hyenas from the previously unstudied area of MZNP. My analyses also supported the ecological theory that apex predators can influence the diet of brown hyenas. However, further research is needed to determine the long term impacts that apex predators such as lions can have on brown hyenas, as lion are known to attack, kill or maim brown hyenas (Mills 2015).

# CHAPTER 5

## SYNTHESIS AND CONCLUSIONS

**Brown hyena caught carrying the head of a black wildebeest in the northern section of MZNP**

Although southern Africa is recognised globally for its rich biodiversity, most of it is heavily threatened by human activity (Dalerum *et al.* 2008). The large carnivore guild, is a particularly important group of animals for the African continent as a whole, as it includes some of the most charismatic and well-known species in the world (Dalerum *et al.* 2008). Large carnivores are known to be crucial components of functional terrestrial ecosystems and often act as 'umbrella species' for the conservation of numerous other local species (Terborgh *et al.* 1999; Ray *et al.* 2005; Dalerum *et al.* 2008; Estes *et al.* 2011). Understanding aspects of large carnivore ecology and behaviour could therefore provide valuable information on multiple trophic levels and benefit ecosystem management (Gittleman *et al.* 2001).

Conservation of large carnivores is crucial to their survival as not only have they been extirpated from many parts of the world, but their existing habitat is being rapidly reduced and fragmented by the ever increasing human population (Gittleman *et al.* 2001; Holmern *et al.* 2007). In the Eastern Cape, South Africa the reintroduction of large carnivores, such as brown hyenas (*Hyaena brunnea*) into small, enclosed game reserves over the past 25 years has contributed greatly to their conservation (Hayward *et al.* 2007a). The findings of my study, along with those from Kwandwe Private Game Reserve, reveal that small, enclosed reserves are able to support larger populations of brown hyenas compared to the larger, open reserves in the more arid areas of southern Africa (Mills 1990; Thorn *et al.* 2009; Welch 2014). My findings also revealed that brown hyenas are successful generalist scavengers which in enclosed, small reserves do not need to supplement their diets by feeding on fruits, insects or reptiles, as much as they do in the arid regions of the southern Kalahari (Mills & Mills 1978; Owens & Owens 1979). Although my study provides valuable information on the density and dietary composition of brown hyenas in a small, enclosed reserve there are still a number of gaps in our understanding of the ecology of this species in enclosed systems.

The camera trap survey from my study revealed that brown hyenas were utilizing the entire park and that there appeared to be two separate clans, but detailed information of their use of space (home ranges), behaviour and social interactions could not be determined from the photographs captured. Knowledge of factors influencing space use and habitat selection by brown hyenas is essential in developing appropriate management strategies, especially in enclosed reserves where their use of space is restricted (Mills 1991; Wiesel *et al.* 2008, Welch *et al.* 2015). The majority of our knowledge about the ecology of brown hyenas is based on data collected in the large, open regions of the Kalahari and the Namib Desert (Mills & Mills 1978; Owens & Owens 1978; Owens & Owens 1979; Skinner & van Aarde 1981; Mills 1982; Mills & Mills 1982; Mills 1984; Owens & Owens 1984; Skinner *et al.* 1995; Wiesel 2007) and as seen in my findings, differences between regions can occur, which means that extrapolating data from open systems for management purposes in enclosed reserves is precarious (Mills 1991). The need for continual and careful monitoring of brown hyena and other carnivore populations in enclosed systems is heightened by the fact that natural processes such as immigration and emigration are prevented, which can lead to issues such as genetic inbreeding (Caughley 1994; Hayward *et al.* 2007a; Hayward & Kerley 2009).

Although protected areas are sheltered from most human activities, very few of the existing reserves in South Africa are large enough or have adequate resources to meet the extensive spatial requirements of the carnivore populations they are intended to protect (Linnell *et al.* 2001; Brashares *et al.* 2001; Holmern *et al.* 2007). Space use assessments of reintroduced carnivores are therefore imperative to the successful conservation of carnivore species (Owens & Owens 1996). Data collected on the space use of brown hyenas in three small, fenced reserves in the Eastern Cape, South Africa (Mountain Zebra National Park (MZNP), Kwandwe Private Game Reserve and Shamwari Private Game Reserve), revealed that brown hyenas are fairly non-specific with regards to their habitat requirements but that distance to roads was a major driver of space use within their home ranges (Welch *et al.* 2015). An extensive proportion of brown hyena populations live outside protected areas in southern Africa where they suffer from both deliberate and accidental persecution from livestock farmers (Hofer & Mills 1998, Wiesel *et al.* 2008). If brown hyenas outside protected areas resemble similar uses of roads as they do within protected areas, it could present an additional threat to the species through road-related mortality (Collinson *et al.* 2015, Welch *et al.* 2015). In the Greater Mapungubwe Transfrontier Conservation Area, two brown hyena individuals were found to be victims of roadkill (Collinson *et al.* 2015). Therefore, the use of space, particularly the relationship between brown hyenas and their use of roads should be of just as much importance within enclosed reserves as it is outside of protected areas.

The home ranges of brown hyenas from MZNP were considerably larger compared to the other two enclosed sites, however this could have been because the brown hyena population in MZNP had not fully established within one year of reintroduction (Welch *et al.* 2015). The occurrence and abundance of other large predators was not taken into account when determining the space use of the brown hyenas, limiting the full understanding of what ultimately drives their space use patterns (Welch *et al.* 2015). Therefore, in order to gain a better understanding of the factors potentially influencing brown hyena space use in enclosed reserves, future research should be conducted to determine the impacts that various apex predator assemblages and densities have on established brown hyena populations.

Knowledge on the space use of brown hyenas in relation to various other predators could also broaden our understanding of the feeding ecology of brown hyenas in small, enclosed systems. The only detailed reference available on the hunting behaviour of brown hyenas is from the observations of individuals in the southern Kalahari, where hunting accounted for less than 6% of their consumed biomass (Mills 1984). As it stands, we assume that brown hyenas are predominantly scavengers in MZNP because the large predators in the park were found to be facilitating their scavenging behaviour and very little evidence of them hunting small mammals was found in their scat samples. Therefore, future research conducted on the movements of brown hyenas in small, enclosed reserves via GPS collars, should look into how their movements overlap with the movements of other large predators and their kill sites to try and determine if brown hyenas are indeed predominantly scavengers with minimal hunting abilities.

Although small, fenced reserves individually contribute to the conservation of large carnivores such as brown hyenas, their contribution is sometimes limited because species are being managed in isolation (Slotow & Hunter 2009). It would therefore be beneficial for reserves to work together in order to make their conservation efforts more significant across a regional scale. Brown hyenas are clearly highly successful scavengers and if the pattern of high densities is consistent across all small fenced reserves, the ecological ramifications for isolated high density populations needs to be considered in the management of such species. Meta-population management schemes, where individuals are moved between reserves, should be implemented in South Africa to ensure greater genetic variability within isolated carnivore populations (Caughley 1994). The genetic structure of reintroduced brown hyena populations throughout South Africa is unknown and should be the focus of future research. Not knowing the genetic diversity of brown hyenas could be detrimental to the already ‘near threatened’ species as the probability of inbreeding in small, enclosed reserves is high.

# APPENDICES

**Appendix I:** List of mammals found in Mountain Zebra National Park.

### ORDER INSECTIVORA
South African hedgehog *Erinaceus frontalis*

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

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

### ORDER HYRACOIDEA
Rock hyrax *Procavia capensis*

### ORDER TUBLIDENTATA
Aardvark *Orycteropus afer*

### ORDER RODENTIA
Porcupine *Hystrix africaeaustralis*
Ground squirrel *Xerus inauris*
Springhare *Pedetes capensis*
African pygmy mouse *Mus minutoides*

### ORDER PERISSODACTYLA
Cape mountain zebra *Equus zebra zebra*
Plains zebra *Equus quagga*
Black rhinoceros *Diceros bicornis bicornis*

### ORDER ARTIODACTYLA

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

### ORDER LAGOMORPHA

Scrub hare *Lepus saxatilis*
Cape hare *Lepus capensis*
Natal red rock rabbit *Pronolagus cassicaudatis*
Smith’s red rock rabbit *Pronolagus rupestris*

**Appendix II:** Identity profiles of brown hyenas used to determine recaptures.

BH M1 – original male

BH A

BH B

BH C

BH D

BH E

BH F

BH G

BH H

BH I

BH J

BH K

**Appendix III:** Example of a trap layout format used in the package secr to estimate density. The table shows the trap identification along with the associated X and Y co-ordinates (UTM). Numbers 1 – represent occasions, where “1” represents that at least one camera was active at the site.

| **#trap ID** | **X coordinate** | **Y coordinate** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| C1 | 352332 | 6445201 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C2 | 352441 | 6442477 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C3 | 354850 | 6443647 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C4 | 356552 | 6442259 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C5 | 351719 | 6439111 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C6 | 354725 | 6439095 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C7 | 357768 | 6438620 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C8 | 353797 | 6435951 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C9 | 355154 | 6432990 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C10 | 353782 | 6430160 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| C11 | 351344 | 6427450 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

**Appendix IV:** Example of a capture matrix for left-side images of brown hyenas captured during the camera survey at Mountain Zebra National Park. BHM1 to BH K represent the brown hyena individuals captured. Numbers 1 – 20 represent sampling occasions and "1" represents that an individual was captured and "0" represents that an individual was not captured.

| **# id** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BHM1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHA | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHB | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHC | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHD | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHE | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHF | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHH | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHI | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHJ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BHK | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**Appendix V:** An example of the kill site data recorded for cheetahs (and lions) at Mountain Zebra National Park (Sex: M = Male, F = Female, U = Unknown).

| Latitude | Longitude | Species killed | Age | Sex | Date |
|---|---|---|---|---|---|
| -32.145200 | 25.511310 | springbok | adult | M | 24/04/2011 |
| -32.181800 | 25.476830 | springbok | adult | M | 01/05/2011 |
| -32.173900 | 25.479170 | ostrich | adult | M | 13/05/2011 |
| -32.140800 | 25.433530 | springbok | adult | M | 30/06/2011 |
| -32.136100 | 25.483350 | springbok | adult | U | 03/07/2011 |
| -32.126000 | 25.464870 | springbok | adult | F | 27/07/2011 |
| -32.094080 | 25.421503 | kudu | adult | F | 28/07/2011 |
| -32.148850 | 25.510440 | red hartebeest | juvenile | U | 29/07/2011 |
| -32.163200 | 25.486530 | ostrich | adult | F | 13/08/2011 |
| -32.203410 | 25.495630 | springbok | adult | F | 09/11/2011 |
| -32.188108 | 25.414381 | blesbok | adult | F | 01/12/2011 |
| -32.136720 | 25.468680 | springbok | adult | M | 13/01/2012 |
| -32.164767 | 25.488433 | kudu | juvenile | U | 08/01/2012 |
| -32.174480 | 25.492050 | kudu | juvenile | U | 21/02/2012 |
| -32.200790 | 25.450630 | kudu | juvenile | F | 21/02/2012 |
| -32.189410 | 25.429430 | kudu | juvenile | U | 22/02/2012 |
| -32.191440 | 25.479350 | steenbok | adult | M | 23/02/2012 |
| -32.203660 | 25.459460 | kudu | juvenile | U | 24/02/2012 |
| -32.251183 | 25.470183 | kudu | juvenile | U | 17/03/2012 |
| -32.148650 | 25.463150 | kudu | juvenile | U | 17/03/2012 |
| -32.249233 | 25.464500 | kudu | juvenile | U | 21/03/2012 |
| -32.218167 | 25.415967 | blesbok | adult | M | 24/03/2012 |
| -32.153733 | 25.460567 | red hartebeest | subadult | M | 24/03/2012 |
| -32.153717 | 25.460617 | kudu | juvenile | M | 25/03/2012 |
| -32.243650 | 25.488133 | kudu | juvenile | U | 26/03/2012 |
| -32.263160 | 25.448010 | kudu | juvenile | U | 29/03/2012 |
| -32.219020 | 25.435530 | black wildebeest | juvenile | U | 31/03/2012 |
| -32.193417 | 25.488967 | red hartebeest | juvenile | U | 22/04/2012 |
| -32.238231 | 25.475650 | kudu | juvenile | U | 04/06/2012 |

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