

**Resource competition between spotted hyaenas, *Crocuta crocuta*, (Erxleben 1777),
and brown hyaenas, *Parahyaena brunnea*, (Thunberg 1820)**

by

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This thesis is dedicated to my late father,
Walter Henry Barker III.

Dad, I hope this will make you proud.

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and brown hyaenas, *Parahyaena brunnea*, (Thunberg 1820)**

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ABSTRACT:

Field data were collected and analysed on the feeding and spatial ecology of spotted hyaenas and brown hyaenas living in the Madikwe Game Reserve. Methods used to estimate the population of spotted and brown hyaenas include audio call-in surveys, photographic records and mark-resighting. The localized convex hull method was used on data collected from latrine surveys, radio-telemetry, sighting records, and camera-trapping to determine the spatial ecology of hyaenas in Madikwe. Faecal analysis and carcass observations were used to determine the prey consumption and dietary components of hyaenas.

Population estimates of spotted and brown hyaenas in Madikwe using the NOREMARK method proved smaller than originally presumed by park officials. The brown hyaena population in Madikwe is critically small at 11 to 13 individuals and needs to be monitored. Spotted hyaenas are slightly more abundant at 20 to 30 individuals, but still merit monitoring of their numbers. The audio call-in survey method is effective when used for the first time or when surveys are separated by extended time periods during long-term monitoring. Hyaenas appeared to become habituated to successive repeated uses of the surveys and the numbers of hyaenas responding to the survey decreased accordingly. Hyaena responses to the audio call-in surveys also fluctuated with respect to the presence or absence of other predators, showing a decrease in response when lions responded to surveys.

Range sizes of spotted hyaenas and brown hyaenas were large and covered nearly the entire reserve, and overlapped considerably with each other. The localized convex hull method is one of the most robust tools used in spatial analysis and was employed to determine the utilization distributions and range sizes of Madikwe's hyaenas based on spatially fixed points of hyaena presence. Utilization distributions obtained from latrine surveys and camera-trap data

indicated seasonal differences in the area use and range sizes of hyenas. Spotted hyaenas had smaller range sizes in the dry season, with larger range sizes in the wet season. Brown hyaenas had larger range sizes in the dry season, which contracted considerably in the wet season. Hyaena utilization distributions overlapped for 581.4km² of the reserve, with an average overlap of 343.0km². The overlapped area was significantly larger than areas which were exclusively used by spotted hyaenas ($\pm 68.8\text{km}^2$) or brown hyaenas ($\pm 92.3\text{km}^2$).

Dietary analysis of hyaenas living in Madikwe depicted a near perfect overlap in food groups and prey remains. Brown hyaenas were shown to exploit a slightly wider dietary breadth than spotted hyaenas, utilizing birds and reptiles in their diets, but both hyaenas exploited larger mammals more often than smaller mammals. Impala and blue wildebeest were the most important food source for hyaenas in Madikwe and other less important food types were seasonally important. Invertebrates featured prominently in hyaena diets in the wet season, while seeds featured prominently in hyaena diets in the dry season. Spotted and brown hyaenas temporally and spatially avoided one another while foraging and at carcasses. Hyaenas often foraged alone or in small numbers in Madikwe, and were never observed to hunt large prey.

The spotted hyaena population in Madikwe appears to be functioning relatively well and not under any immediate threat. However, the low numbers of brown hyaenas presents a concern as to the viability of the population. Competition for the same resources is significant between spotted and brown hyaenas, and efforts to reduce the number of spotted hyaenas through translocation to other reserves may be beneficial in ensuring that brown hyaena populations in Madikwe remain stable. As the lions in Madikwe provide much of the carcasses for hyaenas to feed on, future research may also look at the effect of lions in regulating the spotted hyaena population, and how this may or may not benefit the brown hyaena population.

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- Chapter 1 -

1. INTRODUCTION

1.1 COMPETITION IN CARNIVORES

Animals in situations of high species packing usually undergo niche separation through resource partitioning or resource specialization in order to coexist within the same habitat (MacArthur and Levins, 1967; Yoshiyama and Roughgarden, 1977). However, sympatric guild members who share the same limiting resource will frequently face competition (Linnel and Strand, 2000). This is evident in the case of interspecific competition between carnivores in which competition for prey resources is a limiting ecological factor on their survival (Creel, 2001; Caro and Stoner, 2003). Furthermore, intraguild predation has been documented and is prevalent among communities of mammalian carnivores with interspecific killing accounting for up to 68% of known mortalities in some carnivore species, although their ecological and behavioural factors are poorly understood (Palomares and Caro, 1999). Caro and Stoner (2003) demonstrated that the average African carnivore shares part of its geographic range and habitat with 26 other carnivore species, which suggests a high probability of competition. Carnivores may also have to share food resources with 22 other carnivore species, and may be vulnerable to predation by 15 other species, although they are unlikely to be consumed by other carnivores (Caro and Stoner, 2003). As a result, such high costs of competition and intraguild predation among sympatric guild members can potentially influence species viability through population reduction or extinction. Carnivore population demographics, distributions, individual behaviour and species community structure can be adversely affected by

interactions with other predators (Heithaus, 2001; Tannerfeldt et al., 2002), and can affect populations of other species at lower trophic levels through mesopredator release by limiting or regulating factors of their prey species (Palomares et al., 1995; Crooks and Soulé, 1999; Terborgh et al., 2001).

While predation has been implicated as the major selective force in the evolution of several morphological and behavioural characteristics of animals (Lima and Dill, 1990), greatly influencing their decision-making processes with regards to foraging, sociality, avoiding competition and escaping predators, animals have the ability to assess and behaviourally control their risk of competition/predation. This includes avoidance of larger carnivores in both time and space, and reductions in one species density or even total exclusion from certain habitats or regions (Linnell and Strand, 2000). Local avoidance behaviour of lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) has been exhibited by cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycaon pictus*) (Creel and Creel, 1996; Durant, 1998; 2000a), and kleptoparasitism has been observed between lions, spotted hyaenas and wild dogs (Cooper, 1991; Gorman et al., 1998; Honer et al., 2002). Additionally, several studies have documented the prevalence of competition between carnivores through range and habitat overlaps (Palomares et al., 1996; Fedriani et al., 2000; Tannerfeldt et al., 2002), dietary overlaps (Jones and Barmuta, 1998; Mitchell and Banks, 2005; Azevedo et al., 2006), as well as agonistic interactions between species (Palomares et al., 1995; Venkataraman, 1995; Fedriani et al., 2000); especially among African carnivores (Creel and Creel, 1996; Mills and Gorman, 1997; Gorman et al., 1998; Durant, 2000a; 2000b; Creel, 2001; Honer et al., 2002; Breuer, 2005; Trinkel and Kastberger, 2005; Hayward, 2006).

1.2 DIETARY OVERLAPS

Investigations into the dietary differences among species is fundamental to understanding resource partitioning between species (Nelson et al., 2007) as well as a species' foraging behaviour, population dynamics, habitat use, and social organization (Mills and Gorman, 1997; Jones and Barmuta, 1998; Loveridge and Macdonald, 2003; van Dijk et al., 2008). Flexibility with trophic niches is one of the main components of "ecological plasticity" within a species which in turn is a crucial life-history trait, affording a species phenotypic plasticity or versatility, which affects a species' chance for survival (Crooks, 2002; Rivals et al., 2007). Furthermore, a greater degree of dietary variance reflects a species' ability to occupy an increased variety of habitats (Rivals et al., 2007), and the relevance of what constitutes an animal's diet can also be used as an indicator of habitat partiality (Feranec, 2004). Such variations in a species' diet can be correlated to geographical variation, the availability of prey and/or large-scale environmental factors (Virgós et al., 1999; Roth et al., 2007). Carnivores can potentially avoid further competition with one another by diversifying their dietary preferences, exercising what is known as prey selection so as to minimize competing for the same food resources. This has been demonstrated with the carnivores (tigers, *Panthera tigris* and dholes, *Cuon alpinus*) of the tropical forests of India (Karanth and Sunquist, 1995), as well as between coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis mutica*) in the Northern hemisphere (Nelson et al., 2007). Dietary separation has been further identified in sympatric carnivores (Farrell et al., 2000; Azevedo et al., 2006), with evidence pointing towards resource partitioning of mammalian prey size in relation to predator size (Radloff and du Toit, 2004; Mitchell and Banks, 2005; Carbone et al., 2007).

1.3 *HYAENAS*

Spotted hyaenas and brown hyaenas (*Parahyaena brunnea*) are both large African carnivores with very similar life history strategies and behaviours. They have been studied extensively dating back to 1972 for spotted hyaenas and 1977 for brown hyaenas (Kruuk, 1972; Mills, 1977; Mills, 1989). Both species exist in similar habitats in South Africa, and co-exist in some parts of the region. However, brown hyaenas are largely independent of water and therefore can inhabit more arid regions whereas spotted hyaena distributions are limited to areas with available water sources (Mills and Hofer, 1998; Bothma and Walker, 1999). Spotted and brown hyaenas are mainly nocturnal hunter-scavengers although the spotted hyaena is a more efficient hunter than the brown hyaena, hunting upwards of 50% to 90% of its food (Kruuk, 1972; Henschel and Skinner, 1990), whereas the brown hyaena hunts roughly only 6% of their food (Mills, 1977; Mills, 1990). Although their diets of prey remains overlap to some extent (Mills, 1989), the group hunting behaviour of spotted hyaenas enables them to take larger-sized prey, with the solitary foraging brown hyaenas being more restricted to smaller sized prey or to the carrion of large-sized prey (Kruuk, 1972; Cooper et al., 1999; Burgener and Gusset, 2003). The brown hyaena is considered to be a weaker competitor than spotted hyaenas (Mills, 1989) and spotted hyaenas are thought to have a detrimental effect on brown hyaena densities where they are sympatric due to competitive exclusion (Mills & Hofer, 1998). In the Kruger National Park in South Africa, the decline and eventual extirpation of previously dominant brown hyaenas is correlated with an increase in the spotted hyaena population following the erection of water boreholes (Mills and Hofer, 1998; Bothma and Walker, 1999). A negative association also exists between brown and spotted hyaenas in the Kalahari where both species occur sympatrically and, at kill sites, the

spotted hyaena is the dominant species (Mills, 1990; Mills and Hofer, 1998). Agonistic interactions have been known to occur between brown and spotted hyaenas, with the brown hyaena being attacked and killed by spotted hyaenas, as well as by other carnivores (Mills, 1990). Spotted hyaenas have also been observed to chase brown hyaenas (Kruuk, 1976; Mills, 1990). However, to date, no studies have measured the effects of the results of such interspecific competition between the brown and spotted hyaenas. This study will investigate whether the presence and increasing densities of spotted hyaenas are detrimental for the future survival and viability of the brown hyaenas. Vucetich and Creel (1999) have shown that local extinctions are more likely to occur where competition is intense, and this has been observed in endangered species such as the cheetah and wild dog, which suffer from the consequences of interactions with larger carnivores.

1.4 RESEARCH OBJECTIVES

This has important implications for the sustained conservation of the smaller sized brown hyaena which constantly faces varying degrees of competition with larger predators, including spotted hyaenas over much of its range. The conservation status of the brown hyaena species is currently listed on the 1996 IUCN Red List as Lower Risk: Near Threatened, as recommended by Mills & Hofer (1998). The estimated world population of this species is between 5000 to 8000 individuals, with anywhere between 800 to 2000 individuals in South Africa. In contrast, the spotted hyaena species is classified as Lower Risk: Conservation Dependent with a worldwide population of 27,000 to 48,000 individuals with between 1600 to 5000 individuals in South Africa (Mills and Hofer, 1998). Understanding the role that competition from spotted hyaenas plays on the habitat/range use, activity periods, diet

choices, and behavioural responses of brown hyaenas will aid in an understanding of the animal's behavioural strategies in response to spotted hyaena densities. This may effectively influence the life history strategies of the species in terms of habitat selection, foraging strategies, hunting/scavenging behaviour and clan dynamics that may lead to changes in population dynamics and community structure. Furthermore, knowledge of the importance of dominant predators and their effects on the demographics and habits of other smaller predators may provide the necessary groundwork for the conservation of threatened species and will aid in the management and conservation of multi-species community networks.

Therefore, this study explored whether indirect and/or direct competition exists between the spotted and brown hyaenas. It was hypothesised that spotted hyaenas and brown hyaenas mitigate competition through spatiotemporal segregation by comparing their habitat and range use in sympatric areas, dietary overlaps and observations of behavioural responses towards the other species. A combination of latrine surveys, radio-telemetry tracking and camera trapping were used to test whether brown hyaenas exercised local habitat shifts in response to spotted hyaena densities where they occurred sympatrically, and whether the presence of spotted hyaenas constrained the activity periods and range use of brown hyaenas. Faecal analyses were used to investigate and compare the frequency and types of prey remains in the diets of hyaenas to determine whether hyaena species were exercising prey selection. Behavioural observations at kills or carcasses were examined to determine whether heightened agonistic behavioural responses from each species towards the other occur mainly as increased aggression from spotted hyaenas towards brown hyaenas and increased submission/retreating behaviour of brown hyaenas towards spotted hyaenas.

1.5 STUDY AIMS

The following aims for this study are:

- 1) To estimate current abundances, characterize, and compare density distributions of brown and spotted hyenas in MGR in the context of home ranges, territories, and inter- and intraspecific competitive interactions over time (primarily seasonal) for available host prey species;
- 2) To investigate and ascertain the dietary composition of the brown and spotted hyaenas to determine for differences in hyaena diets and whether hyaenas differ in their choice of prey, and whether hyaena diets differ between seasons;
- 3) To confirm whether brown and spotted hyaenas exercise temporal and/or spatial avoidance towards each other;
- 4) To establish and verify whether spotted hyaenas are aggressive towards brown hyaenas during behavioural interactions, and whether spotted hyaenas are aggressively excluding brown hyaenas from available resources, such as at kills/carcasses.

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- Chapter 2 -

Estimating hyaena population densities in the Madikwe Game Reserve, South Africa, using audio-playback recordings and mark-resighting.

2.1 INTRODUCTION

Carnivore population densities for a given area are often difficult to achieve. Many carnivores occur throughout Africa in dense wooded or bushy areas, and are often nocturnal and cryptic. Carnivores are often wide-ranging and occur at low densities, and are therefore challenging to quantify. Knowledge of a carnivore's population size and trends are necessary for improved management of its' environment and to control for anthropogenic risks. This is especially true for species with little known population and demographical status such as the brown hyaena (*Parahyaena brunnea*) and of heavily persecuted species such as the spotted hyaena (*Crocuta crocuta*) (Mills and Hofer, 1998). For many large carnivores, including hyaenas, accurate and precise estimation of their population numbers are one of the most difficult research questions.

The spotted hyaena population in the Madikwe Game Reserve (MGR) has been estimated at between 40 to 60 individuals, and the brown hyaena population estimated at between 30 to 50 individuals (D. Hofmeyr, pers. comm.). Carnivore population demographics and distributions can be adversely affected by interactions with other predators (Heithaus, 2001; Tannerfeldt et al., 2002), and although the hyaenas in MGR are relatively well-protected within the confines of the park boundaries, they experience competition with other carnivores including lions (*Panthera leo*), leopards (*Panthera pardus*), and wild dogs (*Lycaon pictus*).

Furthermore, brown hyaenas in MGR have even been attacked and killed by both lions and spotted hyaenas (pers. obs.; R. Harrison-White, pers. comm.).

Therefore knowledge of the species' abundance and distribution is of considerable interest for MGR's park management personnel and has important implications for the sustained conservation of the smaller sized brown hyaena. The conservation status of the brown hyaena species is currently listed on the 1996 IUCN Red List as Lower Risk: Near Threatened (Mills & Hofer, 1998) and is suspected to be in population decline with anywhere between 800 to 2000 individuals in South Africa (Wiesel et al., 2008). In addition, the spotted hyaena species is classified as Lower Risk: Conservation Dependent with between 1600 to 5000 individuals in South Africa (Mills and Hofer, 1998).

The techniques used to estimate population size for medium or large carnivores include a wide range of methods. These range from aerial surveys (Gasaway et al., 1992), photographic surveys (Creel and Creel, 1998), thermal imagery (Havens and Sharp 1998), sighting observations along transects (Stander, 1998), spotlighting surveys (Heydon et al., 2000), radio-telemetry (Larivière et al., 2000), using hair snares (Mowat and Strobeck, 2000), camera-trapping (Carbone et al., 2001), audio playback recordings (Mills et al., 2001), mark-recapture methods (Amstrup et al., 2001; Castley et al., 2002), DNA re-captures (Bhagavatula and Singh, 2006), detection of field signs including track counts (Wilting et al., 2006), and measuring the accumulation of faeces (Gruber et al., 2007). Researchers often derive population estimations using a mark-recapture approach on one or more small study areas and extrapolating the results to a larger area (Garshelis and Noyce, 2006), however the large financial costs and repeated disturbances to the animals are two negative aspects of this method (McClintock and White, 2009).

Mark-resight methods constitute a slightly different type of data capture than traditional mark-recapture, but can be used to estimate abundance by modelling encounters (resightings) of marked individuals in a fashion analogous to the closed capture models of Otis et al. (1978). The mark-resight method assumes that some individuals have been marked prior to sampling and each sampling occasion consists of a sighting survey instead of capture periods. As costs associated with capturing animals are generally the most expensive aspects of mark-recapture studies, and capture is also the most hazardous aspect for the animals, the mark-resight method in many ways is a less expensive and a less invasive means for monitoring animal populations (McClintock and White, 2009). With limited funds and resources, mark-resight offers an appealing alternative for researchers as the financial burden of mark-recapture is discouraging for long-term population studies, and the disturbances to the animals from capturing methods may also influence animal behaviour patterns (Minta and Mangel, 1989). Mark-resight can therefore substantially reduce stress to species because the animals can be observed at a distance with minimal disturbance after the initial marking period, and this can be of particular concern when dealing with threatened, endangered or sensitive species.

The mark-resight method requires that animals selected for marking must be equivalent to a simple random sample without replacement, and that marked animals are individually identifiable. Independent sighting trials are not necessary and the number of times animals are sighted must be independent of their mark status, with sighting probabilities varying among individuals (Bowden and Kufeld, 1995). Mark-resight has been used to successfully estimate the populations of California bison (*Bison bison*), North American badgers (*Taxidea taxus*), and Indian crested porcupines (*Hystrix indica*) (Minta and Mangel, 1989). Neal et al. (1993) has used

this method with a joint maximum likelihood estimator to estimate the population of Colorado mountain sheep (*Ovis canadensis canadensis*), while Bowden and Kufeld (1995) estimated the population of Moose (*Alces alces*) in Colorado with 90% confidence intervals. Castley et al. (2002) estimated the lion population in the southwestern Kgalagadi Transfrontier Park using mark-resight with the Lincoln-Petersen method, while Morley and van Aarde (2007) estimated the elephant (*Loxodonta africana*) population in South Africa's Tembe Elephant Park. Both these recent studies found that the Bowden's estimator offered greater precision with narrower confidence intervals.

As acoustic stimulation has often been successful in attracting hyaenas to call stations (Mills and Hofer, 1998), and hyaenas have been successfully attracted with the use of audio playback recordings (Ogutu and Dublin, 1998; Mills et al., 2001; Graf et al., 2009), this method will be used to attract both spotted and brown hyaenas for marking and resighting purposes. The camera-trapping method will be utilized and photographic opportunities will be undertaken whenever possible in order to create an extensive photographic record to individually identify as many hyaena individuals as possible. To date, this study is the first of its kind to combine the use of photographic records together with audio playback recordings in drawing out sympatric hyaena species for resighting to accurately assess and estimate hyaena abundance in MGR. It is predicted that the use of audio playback recordings will increase sightings of brown and spotted hyaenas by attracting hyaenas to call stations. It is also hypothesised that audio playback recordings will also attract other carnivores such as lions to these call stations, and that the presence of lions may deter hyaenas from appearing at these stations during such times. The Bowden's estimator in the

NOREMARK Software will be used to estimate hyaena population numbers for spotted and brown hyaenas in MGR.

2.2 METHODS

2.2.1 STUDY SITE

South Africa's fourth largest game reserve is situated in the north of the Northwest Province in South Africa between latitudes 24°38' to 24°52'S and longitudes 26°08' to 26°31'E, with the north boundary line running adjacent to the Botswana border (Fig. 2.1). The perimeter of the reserve is enclosed by an electrified, 2m high veterinary game fence, with a collective area of approximately 750km². The reserve varies from 19 to 26km in length from north to south and varies from 28 to 36km in width. The varied terrain of the reserve lies between 900m and 1300m above sea level and receives a mean annual rainfall of approximately 520mm, and is distinctly seasonal (D. Hofmeyr, pers. comm.). Most of the precipitation occurs in the summer months from November to March, although it may occur in any month and varies considerably from one year to the next. In summer, the mean maximum temperature is 28°C, while in winter the mean minimum temperature is 14°C (Hudak et al., 2003). Several dams are situated throughout the reserve, which provide water for most of the year but dry up in times of drought. The few permanent dams are supplemented by water pumped from underground.

The reserve has a diverse topography composed of three soil types: black clay, red clay loam and rocky loam (Viljoen and Moore, 2007). MGR's heterogeneous bushveld vegetation is predominantly semi-arid shrubland savannah with important species being *Dichrostachys cinerea* ssp. *africana*, and *Acacia* spp. such as *Acacia mellifera*, *A. tortilis*, *A. erubescens*, *A. gerrandii* and *A. nilotica*, with areas dominated

by *Combretum spp.* and *Boscia foetida* (Hudak et al., 2004). Spotted hyaenas were introduced into MGR through 1994 to 1996 and today are considered common in the reserve (D. Hofmeyr, pers. comm.). MGR supports a large potential prey base as well as a broad spectrum of large carnivores including lions, leopards, wild dogs, cheetahs (*Acinonyx jubatus*) and spotted and brown hyaenas.

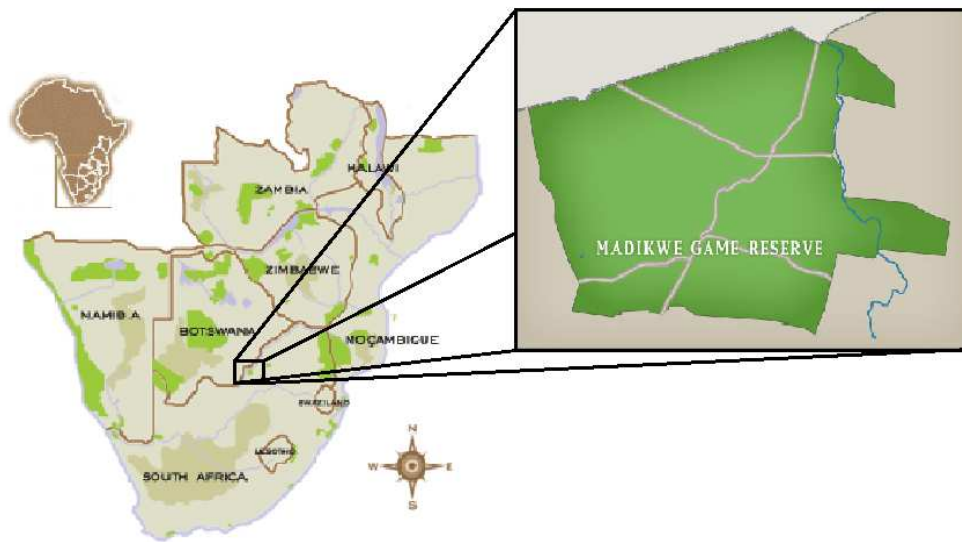


Figure 2.1. The location of the study area, the Madikwe Game Reserve in South Africa.

2.2.2 STUDY SPECIES

2.2.2.1 SPOTTED HYAENA

The spotted hyaena is Africa's second largest carnivore and the most common terrestrial predator in Africa. With a head and body length ranging from 100-180cm and a weight of 40-90kg (Kingdon, 2004), the spotted hyaena is a large, powerfully built, dog-like animal with a sloping back, longer forequarters, long and muscular legs, with a short tail ending in a black and bushy tip. Their feet have four toes with short, blunt, non-retractable claws. The skull is massive, rounded and powerful with a short and blunt muzzle. The ears are broad and round and the long, thick neck complements the powerful tearing and shredding movements of the massive jaws with

robust teeth. The hair is short and coarse with a general sandy, ginger or dull grey to grayish brown colour, with blackish or dark brown spots on the back, flanks, rump, and legs. Yearlings are heavily spotted and spots fade and the colour lightens with age, with the muzzle and tail tip remaining dark (Estes, 1991). Scent glands in the form of anal pouches are situated on either side of the rectum and discharge secretions of a milky substance onto leaves or grass stalks (Mills and Hofer, 1998). Males and females have identically masculine genitalia with the female clitoris being of the same size and shape as the penis, capable of being erected, and is situated at the exact same position as the penis would be in a male (Mills and Hofer, 1998).

Spotted hyaenas are opportunistic and flexible carnivores capable of inhabiting such diverse habitats including semi-deserts, savannahs and open woodlands, dense dry woodlands, and mountainous forests up to 4000m above sea level (Kruuk, 1972; Estes, 1991; Mills and Hofer, 1998). The spotted hyaena, although once widespread throughout Africa south of the Sahara, at present exists primarily concentrated within protected areas and surrounding lands. Spotted hyaenas are highly gregarious and form territorial social clans led and dominated by females, with a social system unlike that of other social carnivores. The spotted hyaena operates on an openly competitive system (instead of co-operation), in where access to resources, mating opportunities, and emigration from natal clans depends mainly on the ability of the individual to dominate other members of its clan (Estes, 1991). Clans usually comprise of philopatric females and their offspring and unrelated immigrant males. Subadult males often emigrate out of their natal clans whereas male offsprings of dominant females remain until they reach sexual maturity in which they subsequently disperse (Frank 1986i & 1986ii; Henschel and Skinner, 1987; Mills, 1990). Clan sizes are primarily limited by available territory size and prey density

and vary throughout the spotted hyaena's range (Mills and Hofer, 1998). Clans may number from as few as three individuals in the southern Kalahari (Mills, 1990) to clans exceeding eighty individuals in the resource-rich Ngorongoro Crater (Kruuk, 1972).

Studies analyzing the diets of spotted hyaenas have shown them to be largely diverse, consuming more non-mammalian food sources than other carnivores (Mills and Biggs, 1993). This is primarily due to its highly opportunistic and flexible foraging nature in which they may scavenge or actively hunt for prey. The diet of spotted hyaenas consists largely of vertebrates, especially ungulates, and is supplemented by invertebrates, reptiles, fruits and seeds. Their ability to extract nutrients from bones and remains of carrion enables them to utilize virtually everything except the rumen contents and horn bosses of their prey (Estes, 1991).

2.2.2.2 BROWN HYAENA

The brown hyaena is a medium-sized, dog-like carnivore, with long legs, strong, well-developed forequarters, long powerful forelegs, shorter hind legs and a sloping back. Head and body length measures between 110-125cm, with a weight ranging between 40-55kg (Kingdon, 2004). The coat is shaggy with the longest hair along the back, and a short tail. Their feet have four toes with short, blunt, non-retractable claws. The skull is robust with long ears that point upwards and a broad, short muzzle with robust teeth adapted for cracking bones. The pelage is dark brown to black, except around the neck and shoulders, which ranges from white to sandy blond. The lower forelegs and hindlegs have alternating brown/black and dark yellow/white stripes in a pattern that differs among individual brown hyaenas. Cubs are gray and maneless, with more stripes on their body and legs. Scent glands in the form of large anal pouches are situated on either side of the rectum and discharge two

secretions of a black substance and a white substance in which they use for scent-marking. Males and females have very little variations between the sexes (Skinner, 1976; Mills, 1983).

Brown hyaenas are hardy species and are capable of inhabiting in desert areas with annual rainfall of less than 100mm (Mills and Hofer, 1998). The brown hyaena inhabits the South West Arid Zone of Africa (Smithers, 1983), and adjacent dry savannah south of the Zambezi River. They are also found along the coast, in semi-deserts, open scrubs and open woodland savannahs. They are independent of drinking water, and seem to favour rocky, mountainous areas with bush cover in the bushveld areas of South Africa. Brown hyaenas also possess the ability to survive close to urban areas and have been seen in the northern districts of the former Transvaal and Cape Provinces (now known as the Gauteng and Northern, Western and Eastern Cape provinces) of South Africa (Estes, 1991; Mills and Hofer, 1998). The brown hyaena is a strictly, solitary, and predominantly nocturnal forager with one of the most elaborate and advanced social system of all carnivores. They live in clans ranging in size from a solitary female and her cubs to groups containing several females and their offspring of different ages. Communal suckling and provisioning of offspring by both males and females occur at the den (Estes, 1991). Males and females have been seen to remain in the natal clan even after reaching sexual maturing at 2.5 years, and adult males either remain with their natal clan, become nomadic, or immigrate into a new clan, and females mate only with nomadic males.

While members of a clan forage alone, several members may come together at a large food source and clan members also come together to defend a common territory (Mills and Hofer, 1998). Clan territories are highly variable in size ranging from as small as 49km² within agricultural lands in the former Transvaal of South

Africa, to between 235 to 480km² in the southern Kalahari (Mills and Hofer, 1998), and are largely determined by the type of food within the territory. Over much of their range, brown hyaenas live in association with other carnivorous mammals and often scavenge from their kills. Brown hyaenas are opportunistic foragers and are primarily scavengers of a wide range of vertebrate remains, and supplement their diets with wild fruits and vegetables, invertebrates, birds' eggs, reptiles, fish, and the occasional small animal that they kill. Hunting in the brown hyaena is unspecialized and opportunistic, directed only at small animals and largely unsuccessful (Mills, 1990). Territorial marking is prevalent in this species through scent-marking behaviour known as pasting. Brown hyaenas will often distribute pastings throughout a territory on an average of 2.6 times per kilometer traveled, and paste with higher frequencies near territorial boundaries (Mills and Hofer, 1998).

2.2.3 DATA ACQUISITION

2.2.3.1 AUDIO-PLAYBACK RECORDINGS

An audio playback recording of sounds known to attract spotted and brown hyaenas (Kruuk, 1972; Mills and Hofer, 1998) was used for the call-in survey. Sounds included a bush pig (*Potamochoerus larvatus*) in distress, wild dogs on a kill, spotted hyaenas calling and brown hyaenas calling. This sound was played through a CD player attached to a 200 W *Mikkai* mobile amplifier and played at full volume (129 decibels) from two 5x8", 30 W horn speakers, connected in series and pointed in four different directions with 90 degree angle rotations on the roof of a 4-wheel drive vehicle.

Prior to the survey, calibration experiments were conducted to test the distance in which hyaenas could hear and react to the playback recordings. This was necessary in order to determine the radius of the audio call-in range to prevent underestimation

or double-counting by calling the same individual twice. This distance was determined to be approximately 3 to 4kms (R. Yarnell, pers. comm.), and Mills et al. (2001) also found that the effect of distance on the response probability was in the 3.2km range. Therefore, in an effort to be conservative and to avoid double-counting, a minimum distance of 5km was decided for the audio call-in sites used in MGR. Using ArcGIS, fifteen sites were chosen throughout the reserve to try to cover as much area of the reserve as possible. These call sites were limited by road access, and were demarcated to have minimal overlap by maintaining a minimum distance of 5kms between sites as well as a 'buffer' boundary of approximately 1 to 2kms from the fence (Fig 2.2).

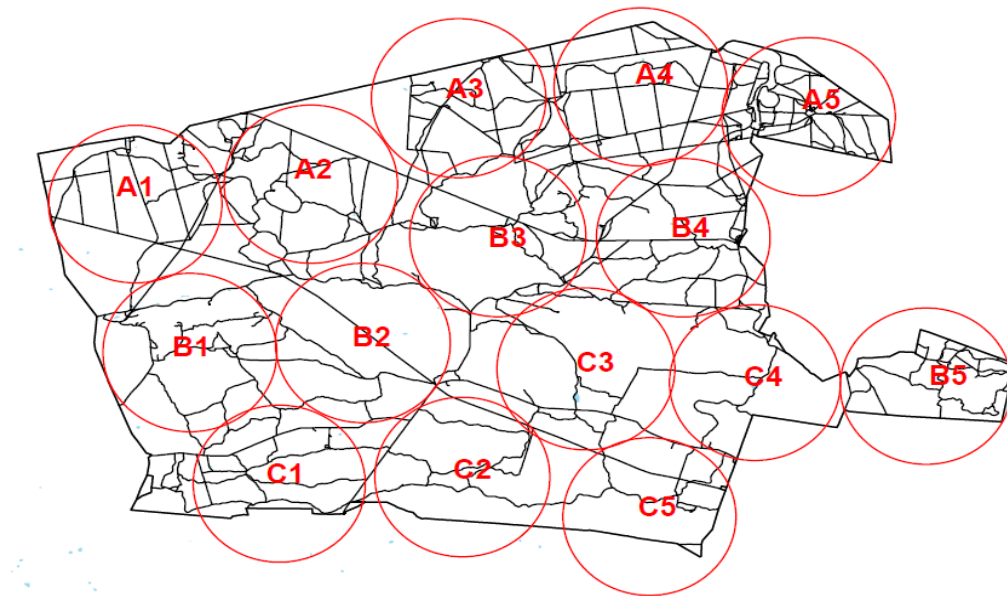


Figure 2.2. The locations of the call-in sites in the Madikwe Game Reserve for the audio playback surveys. Call stations were placed approximately 5km apart, with as minimal overlap, and as maximum coverage as possible. Red circles denote a 5km diameter. (n = 15)

In the span of a five month period, three surveys (April, June, and August) were conducted over a total of five nights using a 4-wheel drive vehicle outfitted with an audio playback recording kit, and utilizing the chosen fifteen sites that allowed for

a sweep of the entire park in as few nights as possible. Once the vehicle had arrived at the designated sites, using as open an area as possible so as to obtain the best visibility, the vehicles then went 'dark' in that the engine was cut, the radio was turned off and the occupants remained silent. Speakers were placed on top of the vehicles pointing in one direction and the sounds were played for three minutes, then stopped for five minutes in which the speakers were rotated 90 degrees and replayed for another three minutes. This continued until all four directions had been covered and after the fourth direction had been played, the vehicles remained for fifteen minutes to allow predators time to come to the site. The area was scanned with a red-filtered spotlight every two minutes for predators. Hyenas are quite easy to identify with a spotlight as *tapetum lucidum* allows the light to be reflected in their eyes, and their sloping backs give them an unmistakable gait. Any hyenas that were seen were carefully monitored so as to prevent double-counting. The number and type of predators were recorded, and every effort was taken to photograph both the lateral sides and anterior view of each hyena individual that had come to the audio call-in site. Environmental conditions were held as constant as possible, especially with regards to wind strength. As the audio call-in sites were at a minimal distance of 5kms from each other, and all fifteen sites were covered in as few nights as possible by a vehicle in a sweep of the park, this decreases the likelihood of double-counting hyena individuals.

2.2.3.2 PHOTOGRAPHIC RECORDS

Photographs were taken of hyena individuals with a Canon EOS Digital SLR camera whenever possible in an effort to build up a reference photo collection in which individuals could be recognized due to their distinct pelage patterns. Photographs are a good source of individual identification as they afford the observer

time to note and match specific characteristics in an animal's pelage, and have been utilized by several camera-trapping studies with other carnivores (Carbone et al., 2001; Henschel and Ray, 2003; Jackson et al., 2005; Soisalo and Cavalcanti, 2006). The characteristics of spot size and placement, scars on ears/faces and ear notches were scrutinized for spotted hyaenas (Fig 2.3), whereas the amount and placement of leg stripes, mane colouration, scars on ears/faces and ear notches were the marking features used for brown hyaenas (Fig 2.4). As brown hyaena markings are bilaterally asymmetrical, a brown hyaena was only considered to be "marked" if it had photographs of each of its lateral sides. Photographs were taken from incidental sightings, spotlighting at night, as well as during audio playback recordings and captures for collaring. Minimal photos were also taken during behavioural observations so as not to disrupt natural behavioural repertoires, and only when an individual was believed to be unknown.

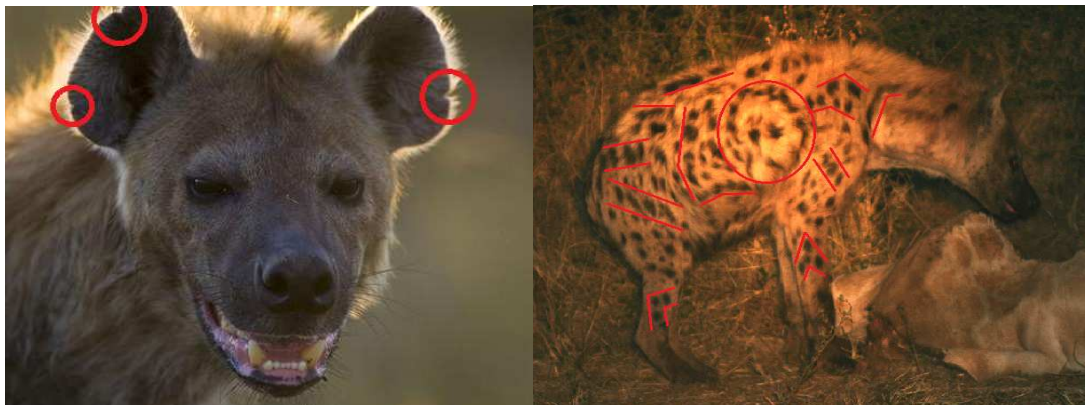


Figure 2.3. Identifying features in spotted hyaenas. Ear notches as depicted by red circles in left photo, and spot patterns as depicted by lines and circles in right photo.

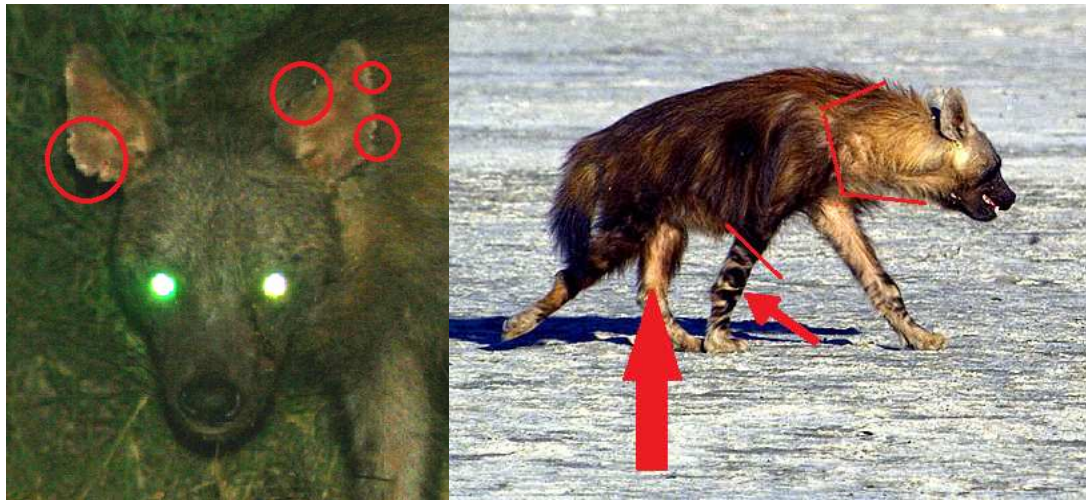


Figure 2.4. Identifying features in brown hyaenas. Ear notches as depicted by red circles in left photo, amount/intensity of blond colouration in mane, and leg stripe patterns as depicted in right photo.

2.2.3.3 CAMERA-TRAPS

Twelve passive infrared camera-traps were placed at various locations easily accessible by roads throughout the reserve for a duration of five weeks in the wet season (Fig. 2.5). Eight Deer Cam DC300 (Non Typical Inc., Park Falls, WI, U.S.A.; <http://www.deercam.com>) and four Camtrakker™ (CamTrakker, Watkinsville, GA, U.S.A.; <http://www.Camtrakker.com>) 35 mm camera units were attached to trees using lanyard and nylon ropes at a height of about 45 to 50 cm above the ground (approximately shoulder height for hyaenas; Karanth and Nichols, 2002; Thorn et al., 2009). Camera-traps were set for 24 hour operation with a time delay of 3 minutes between consecutive photographs because although hyaenas are nocturnal, brown hyaenas were often sighted during the daytime in MGR (N. Barker, pers. obs.). The date and time were set to be imprinted on the photographs and the standard sensitivity mode was used for all camera-traps. The camera trap sites were placed near brown and spotted hyaena latrines in order to maximize the chances of detection (Karanth and Nichols, 2002; MacKenzie et al., 2006). At the end of the 5-week survey, ten

camera-trap units and ten rolls of film were retrieved with two Camtrakker™ units either lost or destroyed.

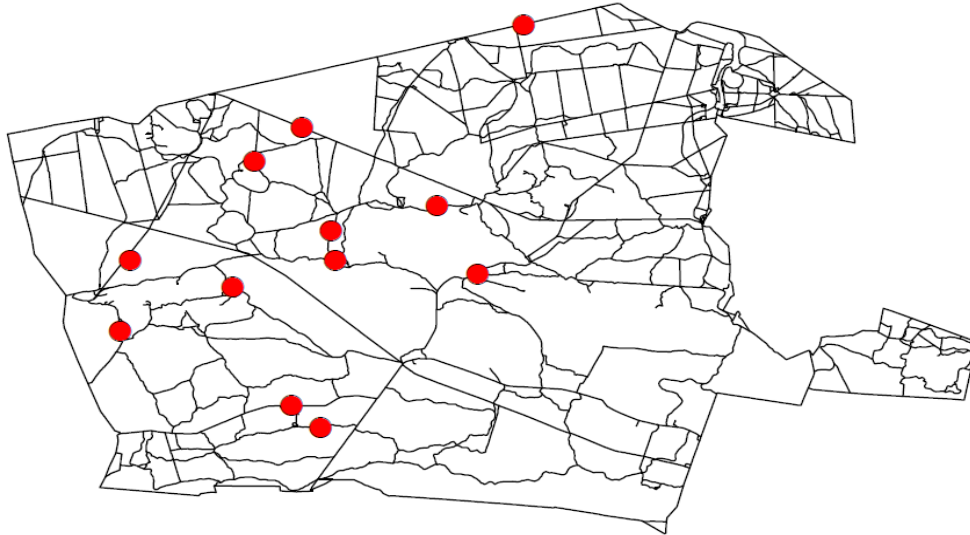


Figure 2.5. The locations of the camera-traps set in the study area during the wet season at Madikwe Game Reserve. Camera-traps were placed beside roads at hyaena latrines. (n = 12)

Additionally, twenty-one camera-traps were used over a period of five weeks in the dry season (Fig. 2.6). This survey used 12 Deer Cam DC300, two Camtrakker™, and seven Leaf River (Leaf River Outdoor Products, P.O. Box 557, Taylorsville, MS 39168, USA. www.myleafriver.com) 35 mm camera units. Camera-traps were used on a 5-day rotating basis and placed at 60 locations throughout the park according to a 9km² grid created with ArcGIS 9.3.1. Camera-traps were also attached to trees and set in the same fashion as for the wet season. However, instead of placing the camera-traps at latrines as was previously done for the wet season, the camera-traps were instead placed at 9km² grid intersections throughout the reserve. At the end of this survey, 29 rolls of film had been retrieved.

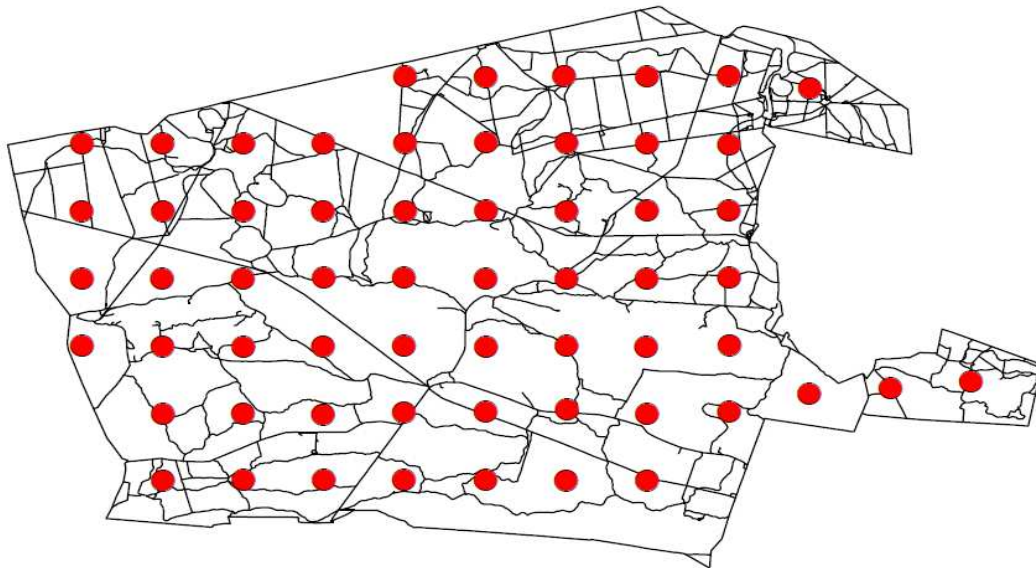


Figure 2.6. The locations of the camera-traps set in the study area during the dry season at Madikwe Game Reserve. Camera-traps were placed based on a 9km² grid. (n = 60)

2.2.4 DATA ANALYSIS

2.2.4.1 AUDIO-PLAYBACK RECORDINGS

Principal component analyses, using STATISTICA 8.0 (StatSoft, Inc. 1984-2008), were employed to examine for the effects of cloud cover, grass height, visibility, soil and vegetation on hyaena responses to audio call-in sites, and to test for the effect of trial numbers on hyaena responses to audio playback recordings. The PCA also examined for other effects, which included predator and lion responses, as well as predator and lion counts on hyaena response, species response, and hyaena counts. The PCA helped narrow down the myriad of effects to the main important contributing factors, on which further regression and chi-square analyses were undertaken. Regression analyses were used to investigate for a relationship between the counts of hyaenas that responded to audio call-in sites with the counts of predators or lions that also responded to the sites. The chi-square statistic was used to determine whether hyaena response to audio call-ins occurred more often than when other predators or lions responded to the call-ins as well. The chi-square was also

used to determine whether brown and spotted hyaenas responded differently to audio call-ins based on predator and lion responses to the sites. Trend analyses were also employed using the Minitab Student Release 12.0 software to investigate whether habituation by both hyaenas and predators to the audio playback recordings was occurring over time.

2.2.4.2 POPULATION ESTIMATION

Hyaena population estimates were calculated from individual photographs and video footage of hyaena individuals which assisted in identifying specific individuals due to their distinct pelage patterns. Identified individuals were “marked” (known) and given an encounter history in which binary values indicated a resighting of a marked individual with “1” indicating a resight during the sampling occasion and “0” indicating non-sighting. As all hyaenas were not initially marked at the same time, but were marked only at first sightings and subsequently “re-captured” through the resighting method over a period of many nights, this study utilized an extended capture and recapture period. Therefore a number of the models used for population estimates such as the Jolly-Seber Model and the classic Lincoln-Petersen method were deemed inappropriate, as these models were developed for open populations and time-series recaptures, or for simple two sample capture-recapture experiments (Otis et al., 1978; Seber, 1982; Arnason et al., 1991; Chao, 2001). The encounter histories of both spotted and brown hyaenas were analyzed with the NOREMARK program (White, 1996i) to determine hyaena population densities with a 95% confidence interval. Of the four methods available in NOREMARK, the Bowden’s estimator (Bowden and Kufeld, 1995) allows for heterogeneity within each animal’s sighting probability, and that sampling can be with or without replacement. Two additional and important assumptions of the NOREMARK program follow that the number of

marked animals is known and that marked animals are a representative sample of the population (White, 1996ii). As the study area is in a fenced reserve, it follows the assumption of a geographically closed population and so the resulting estimate is the total population of the animals within the reserve, and not the average density of animals.

2.3 RESULTS

2.3.1 AUDIO-PLAYBACK RECORDINGS

A total of three call-in surveys were conducted using 15 call-in sites over five nights within a five-month period in 2008 with the surveys occurring in April, June, and August. A total of 61 carnivores responded to the call-in surveys, which consisted of 6 different carnivore species (Table 2.1). The principal component analyses of all factors with respect to the call-in surveys (cloud cover, grass height, visibility, soil and vegetation, survey trial number, predator and lion response, predator and lion counts) demonstrated the importance of predator and lion response, as well as predator and lion counts on hyaena and species responses, and hyaena counts (Fig 2.7a,b).

Table 2.1. Results of the audio-playback call-up surveys in the Madikwe Game Reserve.

SURVEY TRIAL	SPECIES RESPONSE	INDIVIDUAL COUNT
Survey 1	Spotted hyaena (<i>Crocuta crocuta</i>)	9
	Brown hyaena (<i>Parahyaena brunnea</i>)	4
	Lion (<i>Panthera leo</i>)	8
	Leopard (<i>Panthera pardus</i>)	3
	Jackal (<i>Canis mesomelas</i>)	1
	Caracal (<i>Felis caracal</i>)	1
Survey 2	Spotted hyaena (<i>Crocuta crocuta</i>)	9
	Brown hyaena (<i>Parahyaena brunnea</i>)	6
	Lion (<i>Panthera leo</i>)	8
	Jackal (<i>Canis mesomelas</i>)	2
Survey 3	Spotted hyaena (<i>Crocuta crocuta</i>)	4
	Brown hyaena (<i>Parahyaena brunnea</i>)	1
	Lion (<i>Panthera leo</i>)	3
	Leopard (<i>Panthera pardus</i>)	1
	Jackal (<i>Canis mesomelas</i>)	2

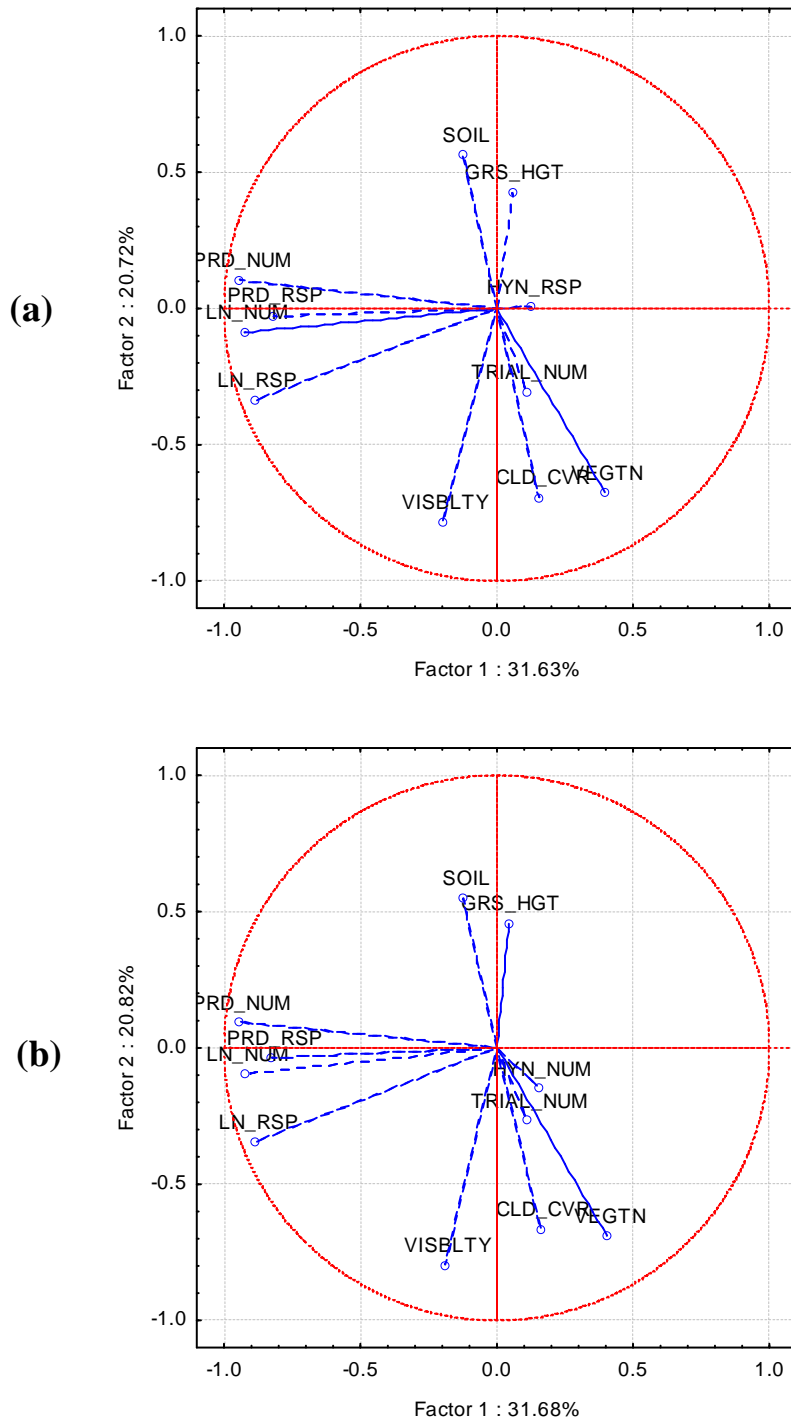


Figure 2.7. Principal components analyses indicating importance of factors on (a) hyaena species' response and (b) hyaena counts in response to audio call-in surveys. Predator and lion counts, predator and lion responses are the furthest points from the center of the circle, demonstrating their heightened effects on hyaena species' response and hyaena counts to audio call-ins over soil, grass heights, trial numbers, visibility, cloud cover and vegetation.

Hyaena counts from animals that responded to the call-in surveys did not demonstrate a relationship with respect to predator counts or lion counts that responded to surveys (predator counts $r^2 = 0.0128$; $df = 43$; $p\text{-value} = 0.460$; lion counts $r^2 = 0.0249$; $df = 43$; $p = 0.300$). However, hyaenas responded to the call-in surveys significantly more often when there were no predators and no lions responding to the surveys (predators $\chi^2 = 7.172$; $df = 1$; $p = 0.007$; lions $\chi^2 = 5.202$; $df = 1$; $p = 0.023$). Additionally, when separating for species, both brown and spotted hyaenas exhibited the same results in that both species also responded to the call-in surveys significantly more often when there were no predators and no lions responding to the surveys (predators $\chi^2 = 11.500$; $df = 2$; $p = 0.003$; lions $\chi^2 = 15.500$; $df = 2$; $p < 0.001$). There were no significant differences between the two species with respect to responding to the call-in surveys ($t\text{-value} = 0.2555$; $df = 88$; $p\text{-value} = 0.799$). Brown hyaenas responded to 10 of the 45 call-in surveys, or 22.2% of the time. Spotted hyaenas responded to 9 of the 45 call-in surveys, or 20.0% of the time.

With respect to the three trials of the call-in surveys, hyaenas exhibited a decreasing trend in responding to the call-in surveys over time (Fig. 2.8a), and this was also true when analyzing the trends in responses for the two hyaena species separately (Fig. 2.8b). Furthermore, while a slight decrease in response to the surveys over time was seen for lions (Fig 2.8c), predator response to the surveys were seen to increase over time (Fig. 2.8d). The numbers of hyaenas also decreased in response to the surveys over time (Fig. 2.8e), and this was also seen for the numbers of lions and other predators, which also decreased in response to call-in surveys over time (Fig. 2.8f & Fig. 2.8g).

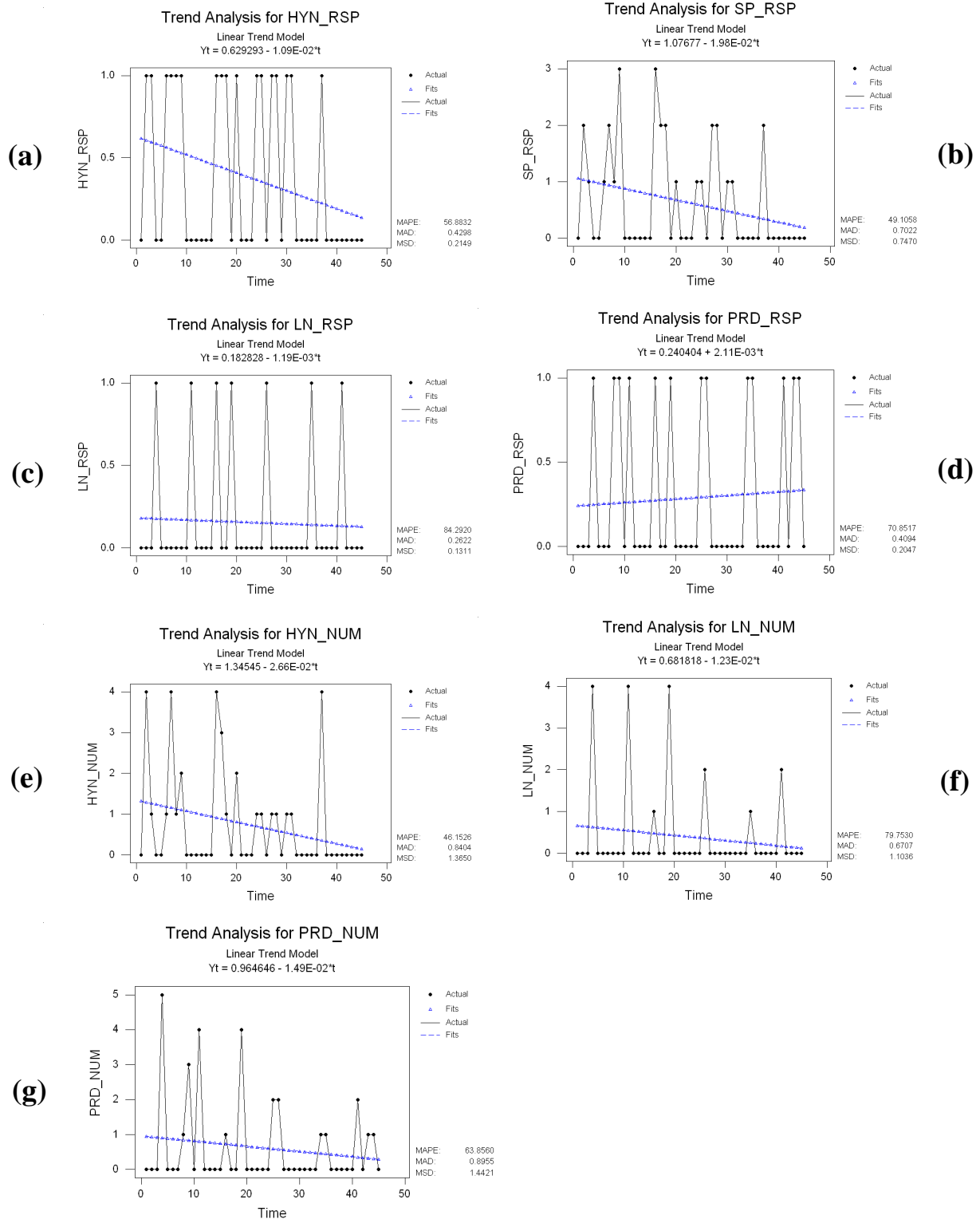


Figure 2.8. Linear trend analyses of the responses to the audio call-in surveys over time at Madikwe Game Reserve. **(a)** Hyaenas, **(c)** lions, and **(d)** other predators; 0 indicates no responses, and 1 indicates a response. **(b)** Hyaena species; 0 = no hyaenas responded, 1 = brown hyaena responded, 2 = spotted hyaena responded, and 3 = both species responded. **(e)** Numbers of hyaenas, **(f)** numbers of lions, and **(g)** numbers of other predators; 0 indicates no animals responded, and 1, 2, 3, or 4 are the numbers of animals that responded to the survey. Number of surveys, $n = 45$.

2.3.2 CAMERA-TRAPPING

Throughout a total of 583 days of camera trapping, 306 independent photographs were obtained. The wet season yielded 141 independent photographs from 283 trap days while the dry season yielded 165 independent photographs from 300 trap days. Seventy of these were of carnivore species, including both spotted and brown hyaenas. Fifty were of small ungulates, other small mammals and birds, 82 were of medium-sized ungulates, 46 were of larger ungulates, and fifty-eight were of mega-herbivores. Of the hyaena photographs obtained, 36 were of spotted hyaenas and 18 of brown hyaenas. The hyaena photographs that could be identified against the marked individuals were deemed “re-sighted”, whereas photographs that could not be identified were “un-marked”.

2.3.3 POPULATION ESTIMATION

The MGR hyaena population estimates were determined by individual identification from 1304 hyaena photographs, with 1017 photographs of spotted hyaenas and 287 photographs of brown hyaenas. Eighty-one minutes of video-recorded footage of hyaenas were also used to assist with the process of identifying individuals. As a result of these records, 25 spotted hyaenas have been identified and “marked”, with 11 brown hyaenas also identified and “marked”. This information was analyzed in NOREMARK using the Bowden’s estimator, which gave the population estimate for spotted hyaenas as 27 with a 95% confidence interval of 25-30, while the population estimate for the brown hyaenas is 11 with a 95% confidence interval of 11-13 (Table 2.2).

Table 2.2. Population estimates of the brown and spotted hyaenas in the Madikwe Game Reserve, South Africa using the Bowden's estimator in NOREMARK.

SPECIES	POPULATION ESTIMATE	95% CI
Brown Hyaena	11	11 – 13
Spotted Hyaena	27	20 – 30

2.4 DISCUSSION

2.4.1 *AUDIO-PLAYBACK RECORDINGS*

As both hyaena species exhibited similar behaviours in their responses to the call-in surveys, responding between 20-22% of the time, and showing a decreasing trend over time, the audio call-in survey can be deemed as an unbiased selector for attracting hyaenas. However, while the audio-playback recording has also been utilized by other studies to attract carnivores for the purpose of estimating population densities (Mills, 1985; Ogutu and Dublin, 1998; Mills et al., 2001; Graf et al., 2009), it is not without faults as the hyaenas in MGR exhibited inconsistent variation in their responses to the audio calls, especially when other predators or lions were in the vicinity of the area or had responded to the call-in sites themselves. Additionally, Ogutu and Dublin (1998) found that lions did not respond to call-in sites when they were in possession of a carcass, and this may also hold true for MGR's hyaenas in that if they were in possession of some food source then this may affect their propensity to respond to the surveys. Mills et al. (2001) strengthened the ability to correctly estimate the population densities of the spotted hyaenas in the Kruger National Park (KNP), South Africa, by correcting for non-response, but this was not undertaken in this study due to the low trial numbers during the surveys. Another issue of caution with the use of call-in surveys is that the hyaenas quickly become habituated to the sounds of the recordings as portrayed by the decreasing trends seen in the responses of the hyaenas' and lions' responses to the call-ins (Figures 2.8–2.14), and in the obvious decrease of carnivore numbers that responded to the surveys over time. This results in a very limited capacity for the repeatability of this method

and such surveys are suggested to not be repeated in the same area more than twice per year (Mills and Hofer, 1998).

Although the audio playback recordings should not be used as the only source of resighting hyaenas, it has provided a useful method in attracting carnivores especially when used for the first time in a study area and/or in conjunction with food rewards. Audio playback recordings can prove a useful aid in drawing out elusive carnivores for the purpose of resighting as was the goal of these surveys for this study, and in giving the observer a rough idea of the numbers and types of carnivores there exists within a study area. Hyaena resighting occurred not only from the call-in surveys but also from camera-traps, spotlighting at night as well as observing kills and carcasses or incidental sightings. The amount of hyaena sightings, and the ability to obtain photographic records were only intensified with the use of the call-in surveys.

2.4.2 THE USE OF PHOTOGRAPHIC RECORDS

The use of photographic records has proven to be an effective means of obtaining population estimates of individually identifiable animals. Karanth and Nichols (1998) and Carbone et al. (2001) used camera-traps to identify individual tigers (*Panthera tigris*) in India to assist with estimating population densities. Camera-trapping has also given individually identifiable photographic records for leopards, snow leopards (*Panthera uncia*) and jaguars (*Panthera onca*), which served a useful tool in determining their population densities (Henschel and Ray, 2003; Jackson et al., 2005; Soisalo and Cavalcanti, 2006). Additionally, photographs have also been used to identify and count lions and wild dogs in the Selous in Tanzania (Creel and Creel, 1998), and for wild dogs in the Hluhluwe-Umfolozi Park in South Africa (Maddock, 1999).

The first studies which utilized photographic records of hyaenas were actually used for behavioural observations of the social organizations for spotted hyaenas (Kruuk, 1972) and in the foraging behaviour of brown hyaenas in the Kalahari (Mills, 1977). More recently, Engh et al. (2005) used photographs to identify spotted hyaena individuals for a behavioural study in the Masai Mara, Kenya. Additionally, the demographical information of brown hyaenas in the Pilanesberg National Park (PNP), South Africa, has been ascertained with the use of camera-traps (Thorn et al., 2009). Therefore the use of photographic records has proven to be an effective and efficient method for individual identification and is consequently a valuable asset for behavioural and demographical studies. It is however not without faults as the photographic records of a species group within a region are rarely complete and there will invariably be at least one or a few individuals that have not been photographed. There also needs to be a certain amount of repeatability in the photographic records to ensure that all the individuals of an area have been identified.

2.4.3 MARK-RESIGHTING POPULATION ESTIMATION

This study provided insights on the population densities of the brown and spotted hyaenas in MGR, which are considerably lower than originally assumed (D. Hofmeyr, pers. comm.). Mark-resighting estimates are widely influenced by the proportion of marked animals in the sample. A population underestimation occurs when more than 30% of the population has been marked, while marking less than 30% of the population gives an overestimation (Bartmann et al., 1987). Minta and Mangel (1989) concluded that when a marking event does not affect the resighting probability, then the catchability is independent, and the Bowden estimator is strengthened by the lack of its assumption of an equal probability of resighting for individual animals. Additionally, heterogeneity in capture or survival probabilities

can bias population estimates (Seber, 1982), while sampling heterogeneity causes a substantial bias in the estimators that assumes equal catchability (Chao, 1989). A sampling heterogeneity may result from the “trap-happiness phenomenon” exhibited by some animals which results in a higher probability of resighting marked animals, thereby underestimating the population size (Arnason et al., 1991).

Certain hyaena individuals were seen more often than others which may be because re-sighting efforts were largely concentrated along the roads in MGR while the thicker and impenetrable bush areas were relatively neglected. Bowden and Kufeld (1995) found that sighting probabilities can vary among individuals and may depend on other factors such as group size and vegetational cover. Re-sighting of hyaenas in MGR were also largely dependent on the home ranges of the various clans, and those clans whose home ranges overlapped with the more accessible road areas may have a greater chance of being seen.

It has been proposed that when a population is composed of several subpopulations, then the combined total of subpopulation size estimators may be more accurate than the complete population size estimator (Bowden and Kufeld, 1995). The brown and spotted hyaena populations in MGR are composed of identifiable clans, and the mark-resighting method could be utilized on each clan to estimate the whole population. This however would require that each clan contains both marked and unmarked animals which may not be feasible when the goal of the photographic record is to individually identify as many individuals of the population as possible. Designing or planning for a mark-resighting method that ensures that at least one animal is marked in each clan (i.e. with the use of radio-collars) rather than the continuous marking of all individuals may provide a more robust estimate of the hyaena population.

2.4.4 POPULATION ESTIMATION METHODS: AUDIO PLAYBACK VS MARK-RESIGHT

Studies that have utilized the methods of audio playback recordings, individual identification, and mark-resighting on the same population have resulted in very similar population estimates. In the Maasai Mara National Reserve, Kenya, lion densities were estimated to be between 0.2 – 0.4 lions/km² from the mark-resighting method (Ogutu and Dublin, 2002), and 0.37 lions/km² using the audio playback method (Ogutu et al., 2005). In the KNP, lion density was estimated at 0.13 lions/km² using the mark-resight method (Funston et al., 2003), with a lion density of 0.10 lions/km² from the audio playback method (Ferreira and Funston, 2010). In South Africa's Tembe Elephant Park, mark-recapture methods using the Bowden's estimator gave a population estimate of 67 bull elephants with a 95% confidence interval of 60-74 individuals. This model yielded estimates closest to the actual registration count of 65 bull elephants in the park, which had been previously individually identified (Morley and van Aarde, 2007). In the Kgalagadi Transfrontier Park, the mark-resight method estimated a lion density of 0.012 lions/km² (Castley et al., 2002). This was confirmed by spoor counts and individual identification of lions which estimated lion densities at 0.008 lions/km² for the dune-savannas and 0.016 lions/km² for the tree-savannas (Funston, 2011), giving an average density of 0.012 lions/km². Although hyaena densities have been previously estimated using either the audio playback recording, or the mark-recapture method, these methods have never been applied to the same population. Spotted hyaena densities in the KNP were estimated at 0.12 hyaenas/km² with the audio playback method (Mills et al., 2001). Brown hyaena densities have been estimated at 0.03 hyaena/km² with the mark-recapture method in the PNP, South Africa (Thorn et al., 2009).

2.4.5 ALTERNATIVE METHODS FOR POPULATION ESTIMATION

The population sizes of terrestrial carnivores have been estimated using a variety of methods (Wilson and Delahay, 2001). The track classification method was used to estimate the density of tigers and leopards in northern India (Johnsingh and Negi, 2003), as well as the population size of clouded leopards (*Neofelis nebulosa*) in northeastern Borneo (Wilting et al., 2006). Track counts have also been used to estimate the population density of spotted hyaenas in Ethiopia (Engeman and Evangilista, 2006), and Lewison et al. (2001) found that individual identification could be ascertained from tracking mountain lion (*Felis concolor*) tracks.

Road transect track counts of lions, leopards and wild dogs in homogenous landscapes in Namibia proved to be a useful tool in determining density estimates (Stander, 1998), and the distance sampling method was used to estimate badger (*Meles meles*) abundance (Hounscome et al., 2005). Population parameters could also be derived from presence/absence qualitative data with the use of occupancy models and detection probabilities (Nichols et al., 2008). Further advances in population estimation could utilize DNA-based capture-recapture studies in which an individual's genotype acts as the tag as in a standard tagging study where the researcher affixes a unique tag to the animal (Lukacs and Burnham, 2005). A study on Bengal tigers in India was able to use DNA information from faecal samples of tigers for the purpose of population estimation (Bhagavatula and Singh, 2006).

An alternative and increasingly popular method is the use of camera-trapping for population density estimate studies. Camera trapping has been used the world over for a variety of elusive, cryptic and rare carnivores. Camera trapping studies have ranged from Africa, India, Nepal, Thailand, Malaysia, Indonesia (Carbone et al., 2001), to the Brazilian Pantanal (Soisalo and Cavalcanti, 2006) and to Japan (Yasuda,

2004). Camera trapping has proven a valuable tool in the population estimate studies of leopards in African rainforests (Henschel and Ray, 2003), tigers in India (Karanth et al., 2004), snow leopards in the Himalayas (Jackson et al., 2005), jaguars in Amazon rainforests (Soisalo and Cavalcanti, 2006), and brown hyaenas in South Africa (Thorn et al., 2009). de Leaniz et al. (2006) has taken the field of camera-trapping one step further by using submerged infrared technology to monitor the activity of Eurasian otters (*Lutra lutra*).

When camera-trapping is not possible, sighting surveys have been shown to yield accurate group size estimates (Davies, 2000). Sighting surveys may also be the only means possible for a researcher to estimate a carnivore population, especially for extremely mobile or highly sociable species (Lindsey, 2003). Sighting records may also be coupled with field-interview surveys of local pastoralists/hunters or game ranchers and wildlife researchers to provide a better understanding of the population dynamics of certain species in the area. Field-interview surveys in Kenya and Tanzania proved useful in determining the distribution and abundance of cheetahs (Gros 1998; 2002) while hunter surveys and radio-tracking data estimated the densities of gray wolves (*Canis lupus*) in eastern Canada (Larivière et al., 2000).

Yet another method that could be used in combination with the photographic and sighting surveys is the audio playback recordings, or acoustic stimulation, attracting animals to fixed calling points. It has proven a useful tool in estimating the population densities of spotted hyaenas (Kruuk, 1972; Ogutu and Dublin, 1998; Mills et al., 2001), and lions (Smuts et al., 1977; Ogutu and Dublin 1998), and has been attempted with wild dogs (Robbins and McCreery, 2003). The use of audio playback recordings has provided an excellent source for obtaining photographic records of hyaenas for this present study. Audio playback recordings or acoustic stimulation can

be especially useful where road networks are limited or a thick habitat effectively restricts off-road driving such as was the case experienced in several areas in MGR.

2.4.6 *IMPLICATIONS OF RESEARCH FOR MANAGEMENT*

As carnivores mitigate trophic processes and play a role in the regulation of ecosystems, knowing and understanding the distribution and abundance of carnivores within a given area is a valuable research asset as it allows for informed and appropriate management decisions regarding the reserve. Carnivores are also extremely difficult to study due to their cryptic, behaviourally elusive, and nocturnal natures. The huge home ranges of many carnivores also makes it likely to overestimate the true population value. Therefore, advances in a variety of methodological techniques can prove useful tools in estimating carnivore population densities.

The two benefits of the mark-resighting survey allows for reduced costs and reduced disturbances to the animals of study which makes it an advantageous alternative over the traditional mark-recapture experiments (McClintock and White, 2009). The photographic records used for a mark-resighting survey provides an invaluable resource base with which identified individuals can be compared and contrasted against many re-sights for the remainder of the animal's life, and as the photographic record aims to identify all individuals of a population or as many as possible, this decreases the likelihood for population overestimation. Camera-trapping provides an excellent method from which to obtain a photographic record, or at least of re-sights which will aid in determining population estimates. Tourists who frequent the parks or reserves can also be enticed to submit their photographs of the species of study which provides for a relatively cheap and vast resource base, considering the large volume of tourists who frequent many of Africa's parks and

reserves every year. A photographic contest complete with prizes could be held as an added incentive to encourage tourists to submit their photographs. Where animals cannot be detected, a variety of other means such as radio-telemetry, latrine surveys, spotlighting transects, or acoustic stimulation may also be utilized in combination with the photographic record in order to supplement and give more information on the population.

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- Chapter 3 -

The comparative spatial ecology of spotted hyaena and brown hyaena in the Madikwe Game Reserve, South Africa.

3.1 INTRODUCTION

Sympatric guild members who share the same limiting resource frequently face competition (Linnel and Strand, 2000). Competition and intraguild predation among sympatric guild members can potentially influence species viability through population reduction or extinction (Heithaus, 2001). Interspecific competition and resource exploitation has important effects for several carnivores and is a limiting ecological factor on their survival (Creel, 2001; Caro and Stoner, 2003). In the face of decreasing viable habitat, which is one of the main factors contributing towards the loss of biodiversity and global species extinction (Crooks, 2002), such complex interactions among mammalian carnivores has severe implications for successful wildlife management (Glen and Dickman, 2005). Carnivore population demographics, distributions, individual behaviour and species community structure are often adversely affected by interactions with other predators (Tannerfeldt et al., 2002).

Although predation has been implicated as the major selective force in the evolution of several morphological and behavioural characteristics of animals (Lima and Dill, 1990), the intensity of predation may influence the degree of overlap and intensity of competition between competing species (Roughgarden and Feldman, 1975). Furthermore, interspecific differences in strategies of resource use or of predator avoidance may permit species coexistence (Levins and Culver, 1971). The

coexistence of large carnivores has been facilitated by selective predation, as exhibited by tigers (*Panthera tigris*), leopards (*Panthera pardus*) and dholes (*Cuon alpinus*) in India (Karanth and Sunquist, 1995; Andheria et al., 2007). Behavioural avoidance of carnivores in both time and space as a result of localized habitat shifts or temporal avoidance has also contributed to the coexistence of sympatric carnivores (Palomares et al., 1996; Fedriani et al., 2000; Linnell and Strand, 2000; Tannerfeldt et al., 2002; Loveridge and MacDonald, 2003; Mitchell and Banks, 2005). Furthermore, coexistence between competing species results in the weaker competitor occurring at low densities relative to competing carnivores (Durant, 1998; Jones and Barmuta, 1998; Creel and Creel, 2002). An understanding of how species are able to coexist within an area has implications for the maintenance of diversity in multi-trophic communities, and can assist in the natural regulation of populations (Amarasekare, 2007).

Brown hyaenas (*Parahyaena brunnea*) and spotted hyaenas (*Crocuta crocuta*) exist sympatrically in the Madikwe Game Reserve (MGR) and are thought to utilize much of the same habitats and resources (D. Hofmeyr, pers. comm.). Spotted hyaenas face high levels of competition with lions (*Panthera leo*) over much of their range (Mills and Hofer, 1998; Trinkel and Kastberger, 2005; Hayward, 2006), while the brown hyaenas occur at low densities and exist outside protected areas (Mills and Hofer, 1998; Maude and Mills, 2005). As brown and spotted hyaenas share similar foraging tactics in that they are both scavengers (Mills, 1990; Mills and Hofer, 1998), they will likely be utilizing the same areas in search of carrion. Theoretical studies looking at animal distributions between areas of different levels of profitability predict that animals should redistribute themselves from less profitable to more profitable foraging areas (MacArthur and Levins, 1964; MacArthur and Pianka, 1966;

Krebs 1977). However, recent models describe how local rules of movement and interaction together with the pressure exerted at territorial boundaries are what determine an animal's territory shape and size (Adams, 2001). It has previously been determined that the spatial distribution of spotted and brown hyaenas are directly influenced by the exploitation of resources (Kruuk, 1972; Mills, 1990), and the distribution and abundance of prey is what positively drives the locations and movements of hyaenas within their home ranges (Kruuk, 1972; Mills, 1977; Mills, 1978; Skinner and van Aarde, 1980; Mills, 1983; Tilson and Hamilton, 1984; Frank, 1986ii; Cooper, 1990; Mills, 1990; Hofer and East, 1993). Therefore, an investigation into the spatial ecology of the brown and spotted hyaenas at MGR will demarcate whether hyaenas are utilizing the same areas, and if so, whether they avoid competition with each other on a temporal and spatial scale.

Various field methodologies can be used to determine the presence of, or location of an animal's movement over time, which can then be used to estimate a species' range and distribution. Both brown and spotted hyaenas mark their territory by depositing faeces regularly at specific areas until they accumulate into latrines (Owens and Owens, 1978; Mills, 1990; Estes, 1991). As hyaenas often create latrine sites along roads (Stuart and Stuart, 1994), which are easily distinguished by their conspicuously white-coloured faeces, these latrine deposits are relatively easy to spot in the field (Estes, 1991), and provide a useful tool for establishing the presence of hyaenas. Latrine surveys have been found to be an important and useful method in determining for the presence of a species, especially where direct observations are difficult or nearly impossible (Gese, 2001; Gruber et al., 2007). Radio-telemetry tracking of collared individuals is typically used to pinpoint the locations of animal movements over time, and this information is useful in establishing a species' home

range or range use. This radio-telemetry method of determining a species' range has been employed for several studies of African carnivores, including striped hyaenas (*Hyaena hyaena*) (van Aarde et al., 1988), leopards (Jenny, 1996), forest mongooses (*Herpestes naso* and *Atilax paludinosus*) (Ray, 1997), wild dogs (*Lycaon pictus*) (Andreka et al., 1999; van Dyk and Slotow, 2003), cheetahs (*Acinonyx jubatus*) (Broomhall et al., 2003; Durant et al., 2004), lions (Loveridge et al., 2009; Tumenta et al., 2010), spotted hyaenas (Henschel and Skinner, 1987; Purchase and Du Toit, 2000; Boydston et al., 2003; Honer et al., 2005; Kolowski and Holekamp, 2007), and brown hyaenas (Skinner, 1976; Mills and Mills, 1978; Mills, 1983; Skinner and Van Aarde, 1987; Owens and Owens, 1996; Maude and Mills, 2005). Sighting surveys in which a sighted animal's location is recorded, may also be used to estimate an animal's range or distribution. This is possible in areas with excellent visibility, such as in open savannahs or grassland, as was done with cheetahs in Kenya and Tanzania (Gros, 1998; 2002), and brown hyaenas in the Kalahari (Owens and Owens, 1978). Camera-trap surveys are especially useful in sighting highly elusive or cryptic carnivores and can be used to determine the occupancy of a species and whether they exist in a particular area or range (Linkie et al., 2007; Nichols et al., 2008). These surveys have been undertaken with tigers in India (Carbone et al., 2001; Karanth et al., 2004), jaguars (*Panthera onca*) in Brazil (Soisalo and Cavalcanti, 2006), and brown hyaenas in South Africa (Thorn et al., 2009).

These field methodologies in the form of latrine surveys, radio-telemetry tracking, sighting records, and camera-trapping will be undertaken for the purposes of this study. To my knowledge, this study is the first of its kind to compare and analyze the spatial use patterns of sympatric hyaenas. It is hypothesized that sympatric brown and spotted hyaenas utilize the same areas and habitats within the boundaries of the

reserve. The data obtained from the above surveys will be used to create a known range of areas utilized by each hyaena species throughout the reserve. It is predicted that these utilized areas will result in a high degree of overlap, and is therefore proposed that this overlapping area will be mitigated by either a spatial or temporal avoidance of mutually exclusive areas. This study will investigate whether brown and spotted hyaenas are occupying the same places at different times, or are utilizing different places at the same time to determine whether hyaenas are exhibiting temporal or spatial avoidance of each other.

3.2 METHODS

3.2.1 STUDY SITE

South Africa's fourth largest game reserve is situated in the north of the Northwest Province in South Africa between latitudes 24°38' to 24°52'S and longitudes 26°08' to 26°31'E, with the north boundary line running adjacent to the Botswana border (Fig. 3.1). The perimeter of the reserve is enclosed by an electrified, 2m high veterinary game fence, with a collective area of approximately 750km². The reserve varies from 19 to 26km in length from north to south and varies from 28 to 36km in width. The varied terrain of the reserve lies between 900m and 1300m above sea level and receives a mean annual rainfall of approximately 520mm, and is distinctly seasonal (D. Hofmeyr, pers. comm.). Most of the precipitation occurs in the summer months from November to March, although it may occur in any month and varies considerably from one year to the next. In summer, the mean maximum temperature is 28°C, while in winter the mean minimum temperature is 14°C (Hudak et al., 2003). Several dams are situated throughout the reserve, which provide water

for most of the year but dry up in times of drought. The few permanent dams are supplemented by water pumped from underground.

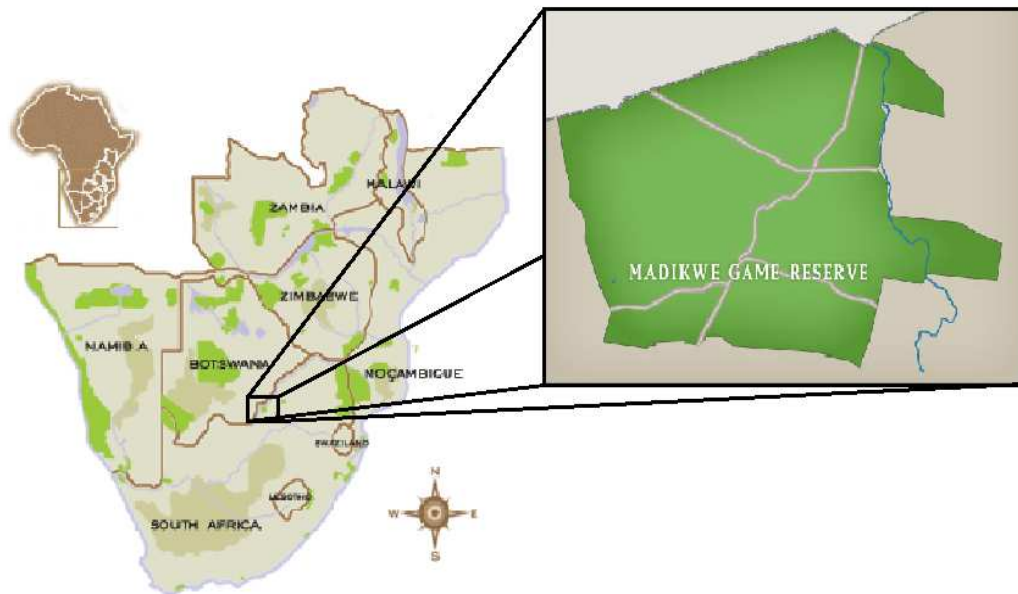


Figure 3.1. The location of the study area, the Madikwe Game Reserve in South Africa.

The reserve has a diverse topography composed of three soil types: black clay, red clay loam and rocky loam (Viljoen and Moore, 2007). MGR's heterogeneous bushveld vegetation is predominantly semi-arid shrubland savannah with important species being *Dichrostachys cinerea* ssp. *africana*, and *Acacia* spp. such as *Acacia mellifera*, *A. tortilis*, *A. erubescens*, *A. gerrardii* and *A. nilotica*, with areas dominated by *Combretum* spp. and *Boscia foetida* (Hudak et al., 2004). Spotted hyaenas were introduced into MGR through 1994 to 1996 and today are considered common in the reserve (D. Hofmeyr, pers. comm.). MGR supports a large potential prey base as well as a broad spectrum of large carnivores including lions, leopards, wild dogs, cheetahs and spotted and brown hyaenas.

3.2.2 STUDY SPECIES

3.2.2.1 SPOTTED HYAENA

Spotted hyaenas are opportunistic and flexible predators capable of inhabiting such diverse habitats including semi-deserts, savannahs and open woodlands, dense dry woodlands, and mountainous forests up to 4000m above sea level (Kruuk, 1972; Estes, 1991; Mills and Hofer, 1998). The spotted hyaena operates on an openly competitive system (instead of co-operation), in where access to resources, mating opportunities, and emigration from natal clans depends mainly on the ability of the individual to dominate other members of its clan (Estes, 1991). They are often highly gregarious and form territorial social clans which are led and dominated by females (Frank, 1986ii; Mills, 1990). Spotted hyaena clans are fission-fusion societies usually comprising multiple adult females, their offspring, and unrelated adult immigrant males. Females are generally philopatric while males disperse. Male offsprings of dominant females will remain with their natal clans, and disperse only after they reach sexual maturity, whereas low-ranking subadult males emigrate (Kruuk, 1972; Frank 1986i & 1986ii; Henschel and Skinner, 1987; Mills, 1990; Estes, 1991). Clan sizes are primarily limited by available territory size and prey density (Mills and Hofer, 1998), and may number from as few as three individuals in the southern Kalahari (Mills, 1990) to clans exceeding eighty individuals in the resource-rich Ngorongoro Crater (Kruuk, 1972).

Spotted hyaenas will often target whichever prey species is locally abundant (Kruuk, 1972; Cooper, 1990; Hayward, 2006), and have defended territories as small as 9km² in the Ngorongoro Crater (Honer et al., 2005) or as large as 130km² in the Kruger National Park (KNP), South Africa (Henschel and Skinner, 1987) and over 1000km² in the Kalahari (Mills, 1990). As the spotted hyaena's social system is one

of rank-related access to food resources in the territory, hyaenas with a low social status will forage more often outside their territory and therefore utilize a wider range area than higher ranking hyaenas (Honer et al., 2005). Previous studies have shown female spotted hyaena territory sizes to be typically 25 to 30km² (Kruuk, 1972; Purchase and du Toit, 2000; Honer et al., 2005), while a male spotted hyaena was found to utilize a territory of 53.2km² (Purchase and du Toit, 2000).

3.2.2.2 BROWN HYAENA

Brown hyaenas are predominantly solitary nocturnal foragers with one of the most elaborate and advanced social system of all carnivores. They are a hardy species and are capable of surviving in desert areas with an annual rainfall of less than 100mm (Mills and Hofer, 1998). The brown hyaena inhabits the southwest arid zones of Africa (Smithers, 1983), and adjacent dry savannahs south of the Zambezi River. They are also found along the coast, in semi-deserts, open scrubs and open woodland savannahs. They are independent of drinking water, and seem to favour rocky, mountainous areas with bush cover in the bushveld areas of South Africa. Brown hyaenas also possess the ability to survive close to urban areas and have been seen in the northern districts of the former Transvaal and Cape Provinces (now known as the Gauteng and Northern, Western and Eastern Cape provinces) of South Africa (Estes, 1991; Mills and Hofer, 1998).

Brown hyaenas live in clans ranging in size from a single female and her cubs to groups containing several females and their offspring of different ages (Estes, 1991). Males and females have been seen to remain in the natal clan even after reaching sexual maturing at 2.5 years, and adult males either remain with their natal clan, become nomadic, or immigrate into a new clan, and females mate only with nomadic males. Although members of a clan forage alone, several members may

come together at a large food source and clan members also come together to defend a common territory (Mills, 1977; Mills and Hofer, 1998). Clan territories are highly variable in size ranging from as small as 5.5km² within agricultural lands in the former Transvaal of South Africa, to between 235 to 480km² in the southern Kalahari (Mills, 1977; Skinner and van Aarde, 1987; Mills, 1990), and are largely determined by the availability and type of food within the territory.

3.2.3 DATA ACQUISITION

3.2.3.1 LATRINE SURVEYS

During this study, latrine surveys were conducted on all primary and many of the secondary game roads. Roads were surveyed as transects and roads that were likely to become impassable due to deterioration or weather conditions were avoided. Surveys were carried out throughout the wet season (November to March) and again throughout the dry season (June to August). Vehicles were driven at continuous speeds of 15-25 km/h while observers searched the area beside roads up to 3m from the edge of the road for latrines. Special attention was paid to culverts, junctions and intersections, as these often serve as boundary-marking areas.

Upon detection of a latrine, the appearance of the latrine and faeces were scrutinized in order to classify the latrine as either belonging to a spotted or brown hyaena. Latrines were classified as *Unknown* when faeces were heavily deteriorated or indistinguishable, and classified as *Mixed* when both brown and spotted faeces were found within the same latrine. While both brown and spotted hyaena faeces are similar in colour and appearance, there are a few notable differences that help to differentiate between the two species. A spotted hyaena latrine is usually large, sometimes covering an area of several hundred square metres with fairly dispersed droppings while a brown hyaena latrine is nearly always in a slight depression with

the droppings much closer together (Stuart and Stuart, 1994). The droppings of the spotted hyaenas are usually larger than a brown hyaena's, 150g and 50g respectively. However, a small spotted hyaena's dropping may be quite similar to a large brown hyaena's, and therefore indistinguishable. Another identifying feature that helped to differentiate which species the faeces belonged to was the visual appearance of the faeces. Faeces of the spotted hyaena are usually smoothly rounded pellets (Fig. 3.2a), whereas a brown hyaena's faeces would often have squiggly or wavy lines on the surface of the faeces (Fig. 3.2b).

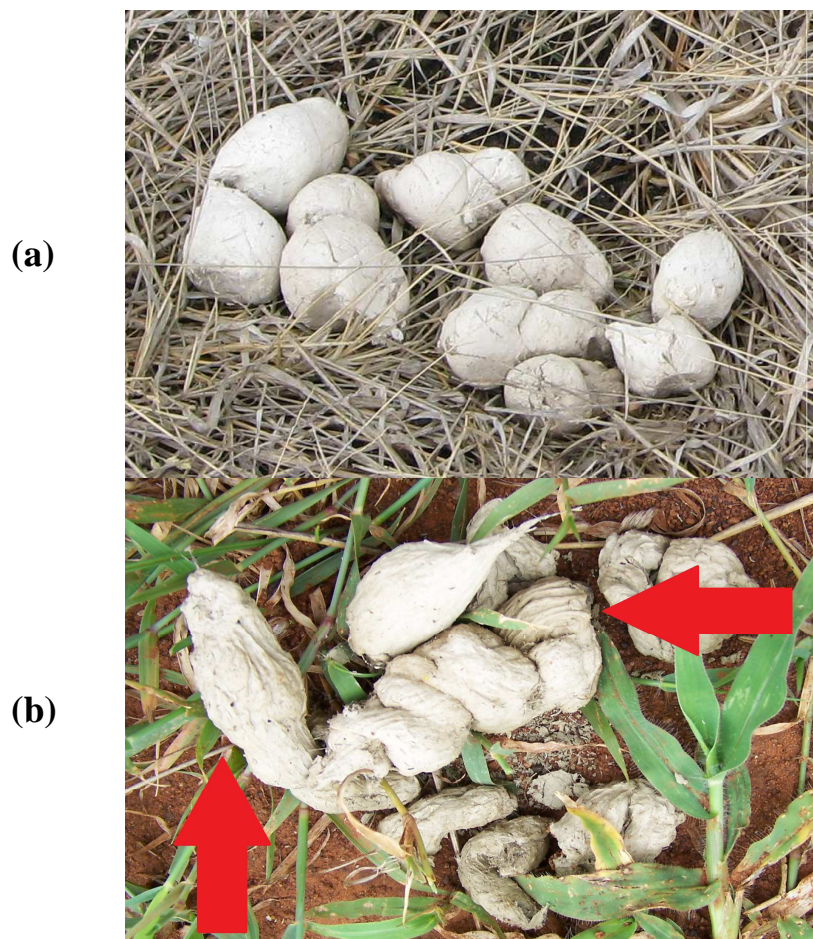


Figure 3.2. (a) An example of spotted hyaena faeces. Note the smoothly rounded pellets. (b) An example of brown hyaena faeces. Arrows indicate the wavy, squiggly lines which are often prevalent in brown hyaena faeces.

Latrines and faeces were identified as belonging to a particular species only when confidence in all criterias had been met. If uncertainty was encountered at anytime with respect to a latrine or hyaena faeces, it was classified as unknown. Along with a confident species identification of latrines, the GPS location, transect code, frequency count for that transect, number of faecal clusters within the latrine, age estimate range of faeces in latrine (ranked from 12 hours to over a month), altitude above sea level and general habitat of area were all recorded. Fresh faecal samples were collected whenever possible to be used for the faecal analysis of prey remains (see chapter 4). Latrine surveys from the two seasons (wet and dry) were compared to determine for differences between the range and habitat use of the two hyaena species, as well as to determine whether seasonal variation existed between the two species' range use within the reserve.

3.2.3.2 RADIO-TELEMETRY

Ethics clearance and permits were obtained from MGR and NorthWest Parks Board for capturing and handling of the animals. Darting stations were chosen in various locations in the reserve and consisted of open areas with few trees. Bait, consisting of zebra, wildebeest and kudu, were planted with Dormicum 15mg tablets and tied to trees. Hyaenas were attracted to darting stations using audio recordings playing calls of a Wildebeest calf in distress (see chapter 2, Methods). Once hyaenas had eaten some of the bait and appeared to be sedated, red filtered lights allowed the darter to visualize and dart hyaenas, aiming for the flank/shoulder area. Hyaenas were darted with the tranquilizer gun DAN INJECT MOD JM No.3027 with Zoletil 100 using 5mg/kg body mass. When hyaenas were anaesthetized, blood and tissue samples were taken for DNA analysis, ear notches were made for easier visual

identification in the field, faecal samples were obtained for parasitology studies, and VHF telemetry collars were affixed to hyaenas. Anterior and lateral photographs were taken of all darted hyaenas, and both lateral sides for the brown hyaena as brown hyaenas are bilaterally asymmetrical. Hyaenas were then left to recover and monitored until a full recovery was made. A radio-telemetry receiver was then used to locate and obtain fixes on hyaenas. Radio-telemetry fixes were used to map and examine species' range use within the reserve and to determine for a home range size.

3.2.3.3 SIGHTINGS

Over a period of one year from February 2008 to March 2009, all hyaena sightings were reported over the radio by the MGR's park personnel and field rangers. Tau Lodge recorded the date, time and location of reported sightings, as well as hyaena species and the number of hyaenas seen. For the purpose of this study, all sightings between the hours of 6:00am to 17:29pm were classified as 'day sightings', while sightings between the hours of 17:30pm to 5:59am were classified as 'night sightings'. This set time-frame was chosen for ease of comparison across seasonal patterns, as game drive times did not vary seasonally. This information was also helpful in localizing a species' range use within the reserve by their sighting data.

3.2.3.4 CAMERA TRAPS

Twelve passive infrared camera-traps were placed at various locations easily accessible by roads throughout the reserve for a duration of five weeks in the wet season (Fig. 3.3). Eight Deer Cam DC300TM (Non Typical Inc., 860 Park Ln, Park (CamTrakker, 1050 Industrial Drive, Watkinsville, GA, 30677, U.S.A.; <http://www.Camtrakker.com>) 35 mm camera units were attached to trees using lanyard and nylon ropes at a height of about 45 to 50 cm above the ground

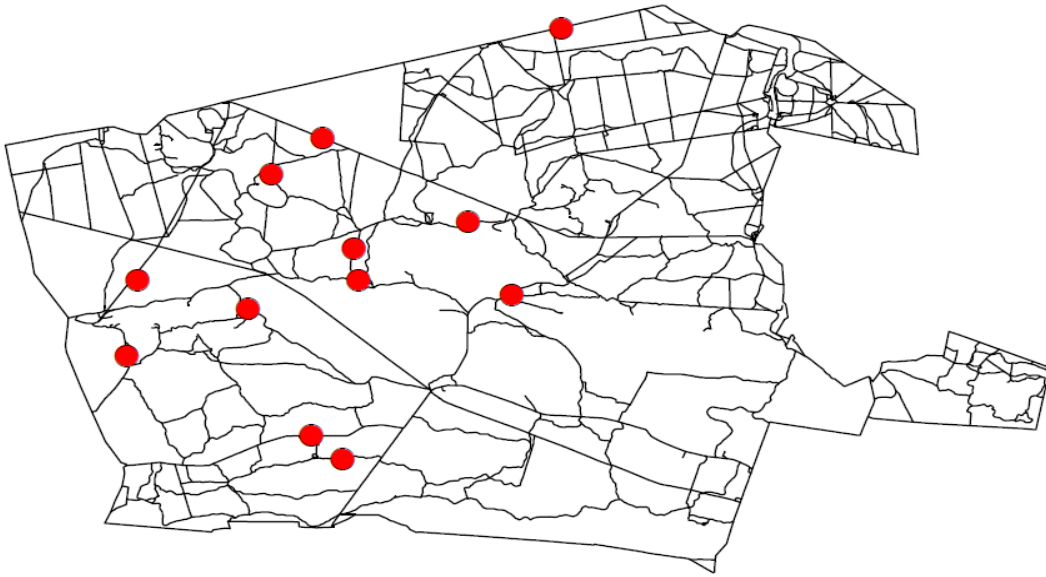


Figure 3.3. The locations of the camera-traps set in the study area during the wet season at Madikwe Game Reserve. Camera-traps were placed beside roads at hyaena latrines. (n = 12) Falls, WI, 54552-9167, U.S.A.; <http://www.deercam.com>) and four Camtrakker™

(approximately shoulder height for hyaenas; Karanth and Nichols, 1998; Thorn et al., 2009). Camera-traps were set for 24 hour operation with a time delay of 3 minutes between consecutive photographs because although hyaenas are nocturnal (Mills, 1990), brown hyaenas were often sighted during the daytime in MGR (N. Barker, pers. obs.). The date and time were set to be imprinted on the photographs and the standard sensitivity mode was used for all camera-traps. The camera trap sites were placed 12m away from brown and spotted hyaena latrines in order to maximize the chances of detection (MacKenzie and Royle, 2005; MacKenzie et al., 2006). At the end of the 5-week survey, ten camera-trap units and ten rolls of film were retrieved with two Camtrakker™ units either lost or destroyed.

Additionally, twenty-one camera-traps were used over a period of five weeks in the dry season (Fig. 3.4). This survey used 12 Deer Cam DC300™, two

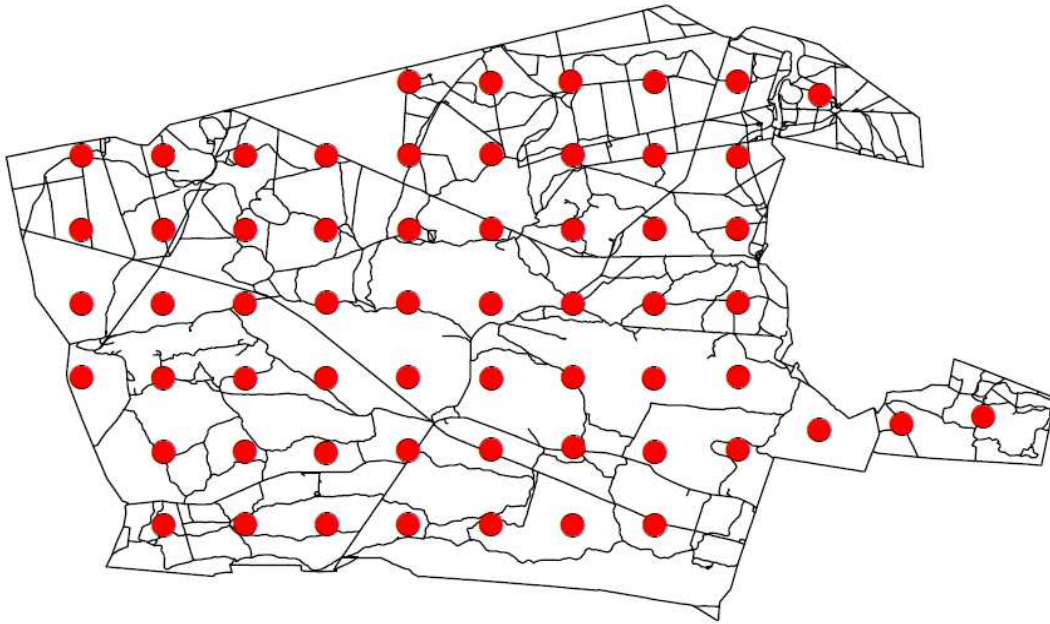


Figure 3.4. The locations of the camera-traps set in the study area during the dry season at Madikwe Game Reserve. Camera-traps were placed based on a 9km² grid. (n = 60)

Camtrakker™, and seven Leaf River (Leaf River Outdoor Products, P.O. Box 557, Taylorsville, MS, 39168, U.S.A.; <http://www.myleafriver.com>) 35 mm camera units. Camera-traps were used on a 5-day rotating basis and placed at 60 locations approximately 3km apart (≥ 1 camera/9 km²) throughout the park according to a 9km² grid created with ArcGIS 9.3.1. Camera-traps were also attached to trees and set in the same fashion as for the wet season. However, instead of placing the camera-traps at latrines as was previously done for the wet season, the camera-traps were instead placed at 9km² grid intersections throughout the reserve. At the end of this survey, 29 rolls of film had been retrieved.

Camera trap locations were assumed to be independent as the detection probability at each site of each species was unlikely to be biased by the presence of other non-intrusive camera traps (Linkie et al., 2007; Thorn et al., 2009). Both surveys were also limited to a period of 5 weeks to adhere to the assumption that no changes in occupancy occurred during the study period (MacKenzie et al., 2006;

Thorn et al., 2009). Camera-trap data from the two seasons were analyzed and compared to determine for seasonal variation between the range and habitat use of the hyaena species, as well as to determine for species' range utilization in the reserve.

3.2.4 DATA ANALYSIS

3.2.4.1 LATRINE SURVEYS

All subsequent analyses examined for the effects of habitat and range use on species' latrine placement within the reserve. All statistics were carried out using the STATISTICA 10.0 (StatSoft, Inc. 1984-2011) software. The chi-square analyses checked for seasonal variations and species differences on latrine placement between the core and periphery of the reserve. Latrines placed less than 2.5km from the reserve fence were grouped as 'periphery', while latrines more than 2.5km from the reserve fence were grouped as 'core'. The main effect analysis of variance was used to examine for the effects of habitat on species' latrine placement, looking at the effects of season, soil and vegetation. The t-test statistic examined for differences in the cluster size of the latrines between the two species and whether a seasonal variation existed in the cluster size of latrines. Regression analyses were undertaken to determine whether a relationship existed between the increasing cluster sizes of the latrines with increasing distance from the reserve fence. The chi-square test statistic was again used to examine for differences between species' latrine placement against a 'mixed' neighbouring latrine, consisting of both brown and spotted hyaena faeces. The t-test statistic also tested whether elevation influenced species' latrine placement between seasons, while the one-way ANOVA examined for the effect of elevation on hyaena species latrine. Regression correlations were used to examine for the presence of a relationship in latrine placement between species and among seasons. The GPS locations of the latrines of the brown and spotted hyaenas were then plotted with the

R program using the k-NNCH (nearest neighbour convex hull) method to generate a localized convex hull of their respective ranges in the reserve.

3.2.4.2 RADIO-TELEMETRY

A radio-telemetry receiver was used by field rangers to obtain the GPS location of radio-collared hyaenas. The date and time, as well as two GPS positions were recorded per hyaena location, as well as the compass heading degrees from North. Using MapSource 6.13.7, the two GPS positions for each hyaena location were mapped and a straight line was drawn from each point according to the compass heading. The intersecting point of the two straight lines was deemed to be the location of the hyaena and the GPS co-ordinate of this intersecting point was obtained and recorded as the precise location of that hyaena at that specific date and time. Using ArcGIS 9.3.1, the distance from the GPS location of the hyaena to the nearest road, nearest water source, and nearest infrastructure were all measured and recorded. Soil and vegetation type of the hyaena's location were also noted. The radio-telemetry points of the collared hyaenas were plotted with the R program using the k-NNCH method to generate a localized convex hull of the hyaena's range as indicated by the radio-telemetry data.

3.2.4.3 SIGHTINGS

Based on the sighting data collected from the rangers and field guides, the chi-square test statistic confirmed whether brown and spotted hyaenas were more often seen by themselves or with conspecifics rather than with the other species. The chi-square also analyzed if spotted hyaena group size had an affect on whether brown hyaenas were seen in association with them. Regression analyses investigated for a relationship between the time of hyaena sighting and which species was sighted. The

t-test was used to compare for differences in the times of sightings between brown and spotted hyaenas. The GPS locations of the hyaena sightings were then plotted with the R program using the k-NNCH method to generate a localized convex hull of the two hyaena species based on the sighting data.

3.2.4.4 CAMERA TRAPS

Analysis of covariance was used to investigate for the effects of elevation, distance to nearest road, distance to nearest water source, distance to nearest infrastructure, and the interaction between soil and vegetation on the detection of hyaenas by camera-traps. Further analyses using the principal component analysis examined for the importance of seasonal effects, time of detection, as well as soil and vegetation in the detection of hyaenas by camera-traps. These factors were also analyzed using the main effects ANOVA to determine to a finer scale the significant effect each factor had on the detection of hyaenas. The locations of the camera-traps which resulted in photos of hyaenas were plotted with the R program using the k-NNCH method to generate the localized convex hull of the hyaena's range as shown by the camera-traps.

3.2.4.5 RANGE SIZES AND AREA UTILIZATIONS

Hyaena range distributions were obtained using the data from latrine surveys, radio-telemetry, hyaena sightings, and camera-trap sighting records. GPS positions from latrine deposits, radio-telemetry fixes, sightings from park personnel and camera-traps were analyzed with R version 2.12.0 using the local nearest neighbour convex-hull construction (LoCoH; see Getz and Wilmers, 2004 for details). The k nearest-neighbour convex hull, or the k-NNCH method, depends on a user-selected nearest-number-of-neighbours parameter, k . The method then constructs a utilization

distribution from the union of local convex hulls associated with each point and its $k-1$ nearest neighbours, and constructs isopleths by merging these local polygons (Getz and Wilmers, 2004). To determine the potential ranges utilized by hyaenas, this method was repeatedly run for k values from 3 to 8 and 11 (camera-trap data), 3 to 18 (radio-telemetry data), and 3 to 25 (latrine data) to find the plateau that gives the most stable area value across a range of k values to represent the area of the home range (see appendix). If the analysis results in several plateaus occurring, then choosing the correct k value represents a trade-off between errors of type I and type II. A low k value will fail to represent areas that hyaenas might occupy between the observed points, and a high k value will overestimate the area of their range. The LoCoH method has proven superior over other methods as it converges to an estimate with the addition of data points, uncovers areas of avoidance, and uses isopleth analyses to create high-use areas, especially when the data is multi-modal, topologically complex and reflects the existence of real boundaries (Getz and Wilmers, 2004; Ryan et al., 2006). The localized convex hulls were converted into shapefiles and using ArcGIS, hyaena range distributions were measured in square kilometres. A t -test determined for significant differences between the range sizes of brown hyaenas and spotted hyaenas, and also with ranges of overlapping areas. The differences in the total areas utilized by brown and spotted hyaenas, as well as overlapping areas were analyzed using the chi-square analyses.

3.3 RESULTS

3.3.1 LATRINE SURVEYS

Latrine surveys were conducted on a total of 58 roads, totaling 362.5km for the wet season. This survey resulted in 264 marked latrines, with 110 spotted hyaena

and 65 brown hyaena latrines. The remaining 33 were classified as ‘mixed’, consisting of both brown and spotted hyaena faeces, while the other 56 latrines were marked as ‘unknown’ (Fig. 3.5). The dry season latrine surveys were conducted on 62 roads, totaling 375.5km, and resulted in 480 marked latrines. Of these 480 latrines, 237 belonged to the spotted hyaena and 135 belonged to the brown hyaena. The remaining 29 were mixed with 79 classified as unknown (Fig. 3.6). Consequently, 744 hyaena latrines have been observed and recorded, with 347 spotted hyaena and 200 brown hyaena latrines, 62 mixed and 135 unknown latrines (Fig. 3.7).

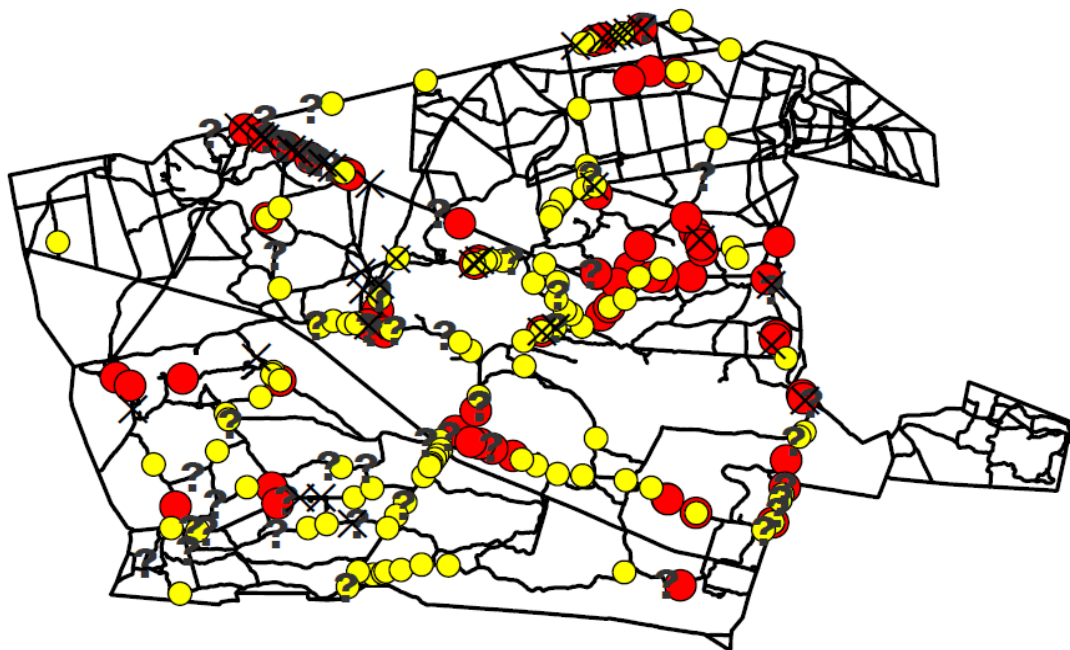


Figure 3.5. Mapped results of latrine survey findings during the wet season from the Madikwe Game Reserve. Red circles = brown hyaena latrines, Yellow circles = spotted hyaena latrines, Question mark = unknown latrines, X = mixed latrines.

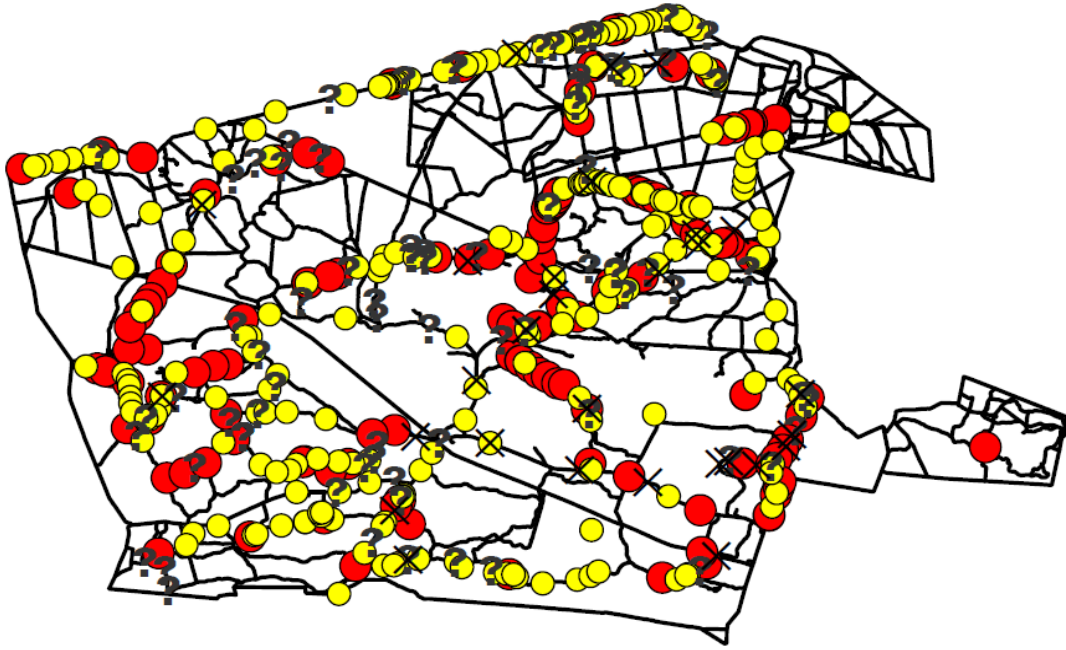


Figure 3.6. Mapped results of latrine survey findings during the dry season from the Madikwe Game Reserve. Red circles = brown hyaena latrines, Yellow circles = spotted hyaena latrines, Question mark = unknown latrines, X = mixed latrines.

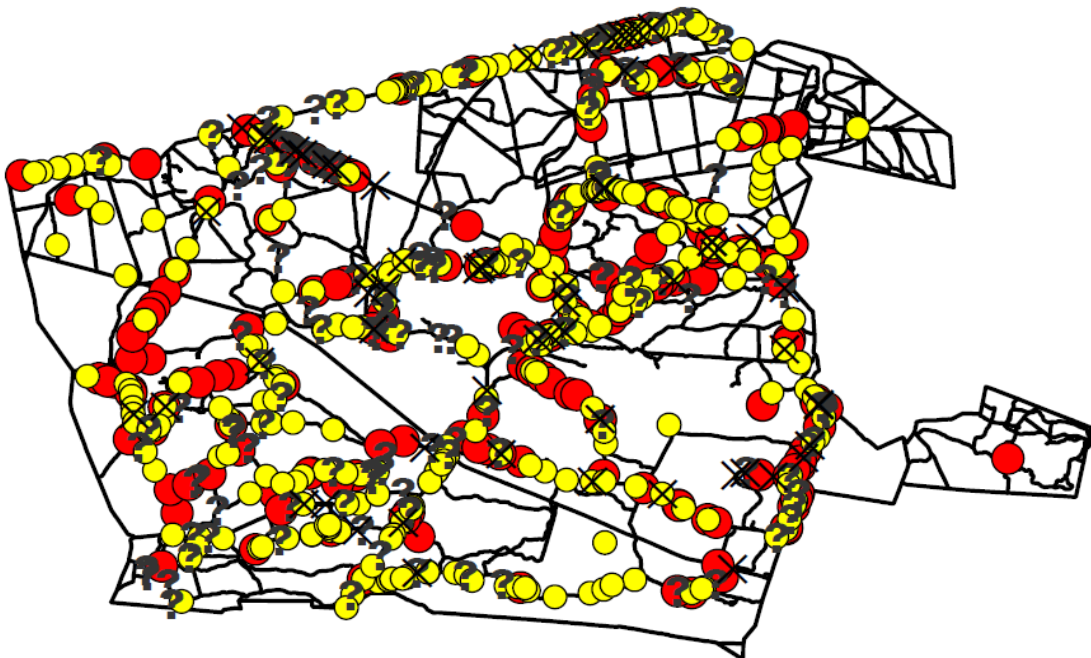


Figure 3.7. Mapped results of overall latrine survey findings from the Madikwe Game Reserve. Red circles = brown hyaena latrines, Yellow circles = spotted hyaena latrines, Question mark = unknown latrines, X = mixed latrines.

Both brown and spotted hyaenas deposited significantly more latrines in the core of the reserve during the wet season than in the dry season (brown $\chi^2 = 5.554$; $df = 1$; $p = 0.018$; spotted $\chi^2 = 19.236$; $df = 1$; $p < 0.001$). Spotted hyaenas were also found to have significantly more latrines overall than brown hyaenas for both the periphery and core areas of the reserve (periphery $\chi^2 = 18.782$; $df = 1$; $p < 0.001$; core $\chi^2 = 20.779$; $df = 1$; $p < 0.001$). When examining for the differences between the core and periphery of the reserve, both brown and spotted hyaenas were found to deposit significantly more latrines in the core than the periphery (brown $\chi^2 = 3.920$; $df = 1$; $p = 0.048$; spotted $\chi^2 = 4.844$; $df = 1$; $p = 0.028$). Vegetation was shown to be the most important main effect of habitat on species latrine placement, while soil and season had no effect (Vegetation $F = 1.903$; $df = 15$; $p = 0.021$; Soil $F = 1.202$; $df = 4$; $p = 0.309$; Season $F = 0.023$; $df = 1$; $p = 0.879$).

Hyaena latrines had various cluster sizes, often ranging from 1 to 26 with a mean of 3.3 clusters for brown hyaenas, or ranging from 1 to 89 with a mean of 7.6 clusters for spotted hyaenas. Spotted hyaena latrines were found to have significantly larger cluster sizes than brown hyaena latrines ($t = -6.409$; $df = 545$; $p < 0.001$; Fig. 3.8). Spotted hyaena latrines were also found to have significantly larger clusters in the wet season than for the dry season ($t = -0.265$; $df = 370$; $p < 0.001$; Fig. 3.9). There were no significant relationships between increasing cluster size of hyaena latrines and increasing distance from the reserve fence ($r^2 = 0.001$; $df = 545$; $p = 0.393$). Both brown and spotted hyaenas did not exhibit any significant differences in whether they preferred to deposit latrines beside a ‘mixed’ neighbouring latrine rather than a conspecific’s latrine ($\chi^2 = 0.258$; $df = 1$; $p = 0.611$).

Spotted hyaena latrines were placed at higher elevations significantly more often in the wet season than in the dry season ($t = 2.192$; $df = 345$; $p = 0.029$; Fig.

3.10), while brown hyaena latrines were placed at higher elevations significantly more often during the dry season than the wet season ($t = -2.294$; $df = 198$; $p = 0.022$; Fig. 3.11). Comparing between the two hyaena species, both species are shown to use similar elevations for latrine placement although the brown hyaena utilizes a wider range of elevation differences (Fig. 3.12). However, in the wet season spotted hyaena latrines were found to be placed at significantly higher elevations than brown hyaena latrines ($t = -2.748$; $df = 173$; $p = 0.007$). Conversely, the one way analysis depicted no significant effects of elevation on hyaena species latrine ($F = 1.001$; $df = 226$; $p = 0.494$), while the regression correlation exhibited a significant relationship in the elevation of latrines for brown and spotted hyaenas only for the dry season ($r^2 = 0.246$; $df = 133$; $p < 0.001$).

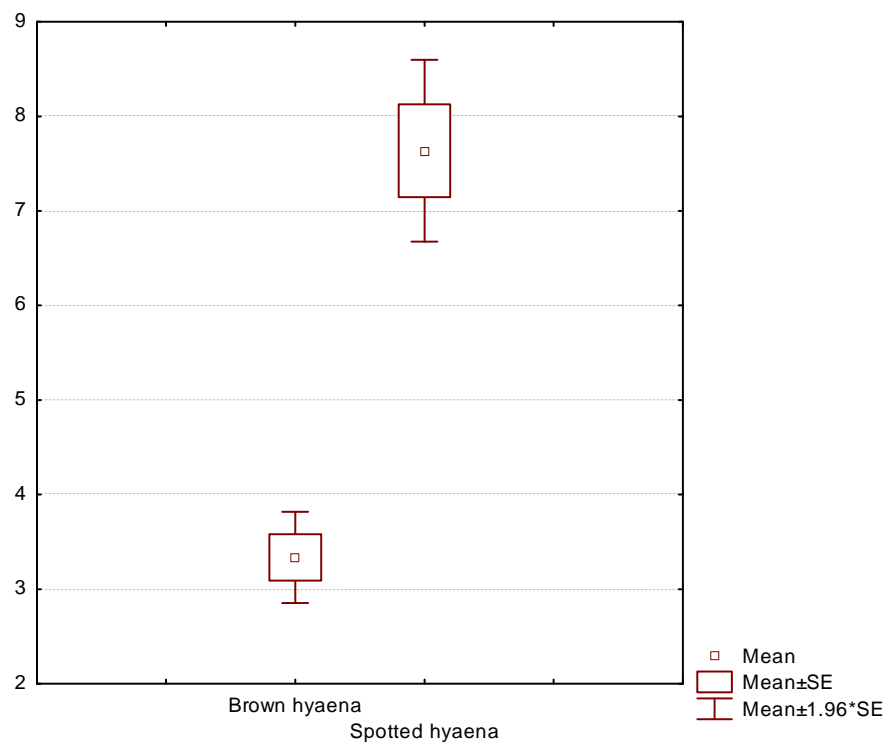


Figure 3.8. Comparison of cluster sizes of hyaena latrines from the Madikwe Game Reserve. Cluster sizes were determined by counts of faeces within a latrine.

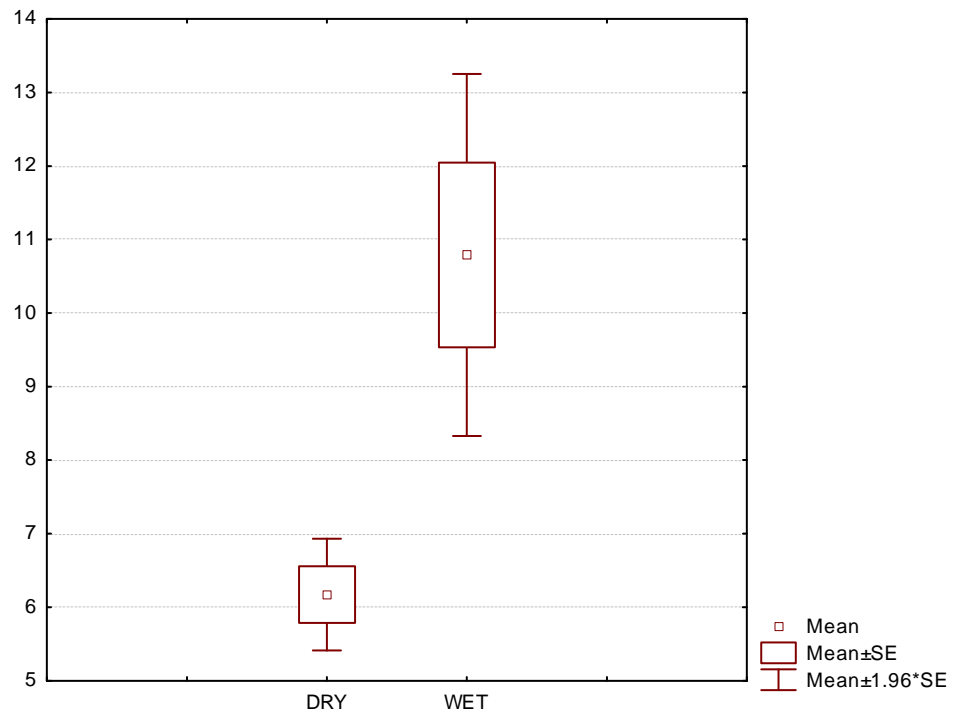


Figure 3.9. Comparison of cluster sizes across two seasons for spotted hyaena latrines from the Madikwe Game Reserve. Cluster sizes were determined by counts of faeces within a latrine.

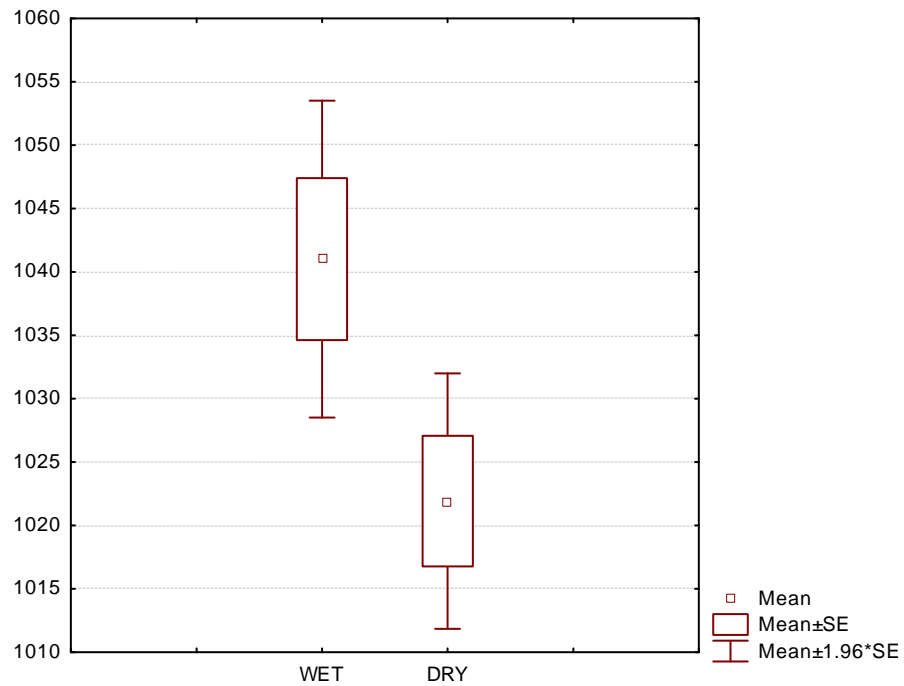


Figure 3.10. Comparison of elevation differences between wet and dry seasons for spotted hyaena latrines in the Madikwe Game Reserve.

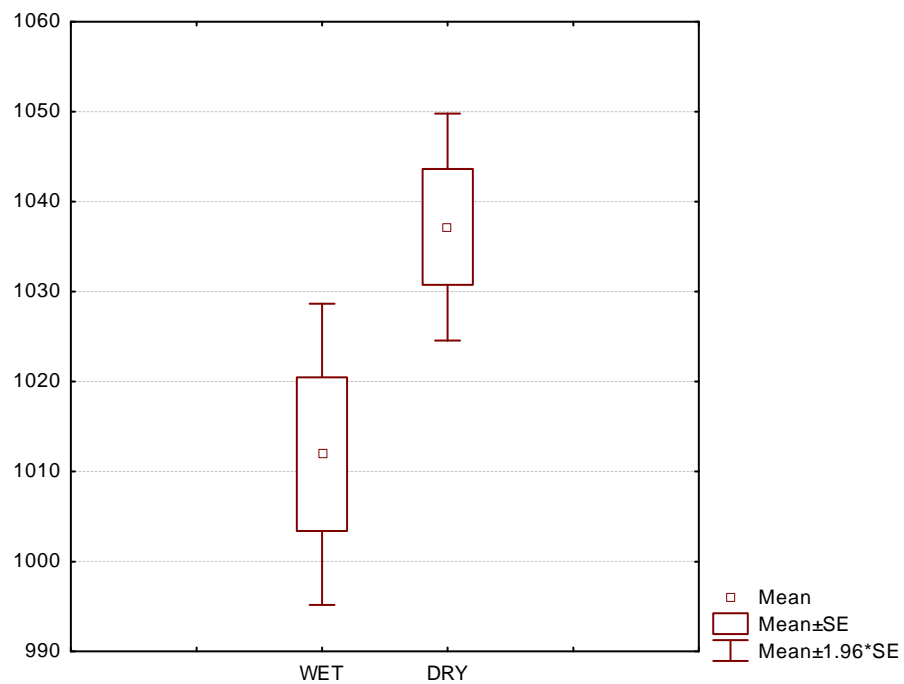


Figure 3.11. Comparison of elevation differences between wet and dry seasons for brown hyaena latrines in the Madikwe Game Reserve.

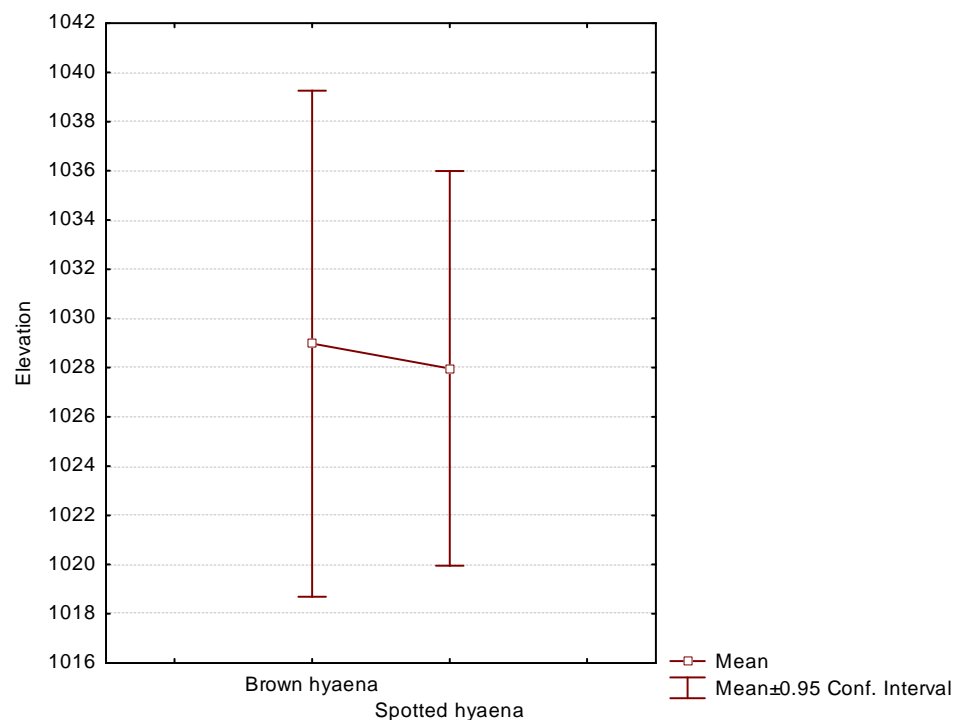


Figure 3.12. Elevation ranges where hyaena latrines were found in the Madikwe Game Reserve. 0 = brown hyaena latrines, 1 = spotted hyaena latrines.

The localized convex hull method on the latrine depositions of hyaenas estimates the range utilization of the brown hyaena species to be 466.4km^2 in the dry season and 343.9km^2 in the wet season (Fig. 3.13), with an overall range utilization estimation of 415.7km^2 (Fig. 3.14). The spotted hyaena's range utilization is estimated at 427.5km^2 in the dry season and 422.8km^2 in the wet season (Fig. 3.15), with an overall range utilization estimation of 422.0km^2 (Fig. 3.16). Evidently, both brown and spotted hyaenas are utilizing much of the same areas when it comes to depositing latrines, as is portrayed by the overlapping areas (Fig. 3.17 & Fig. 3.18).

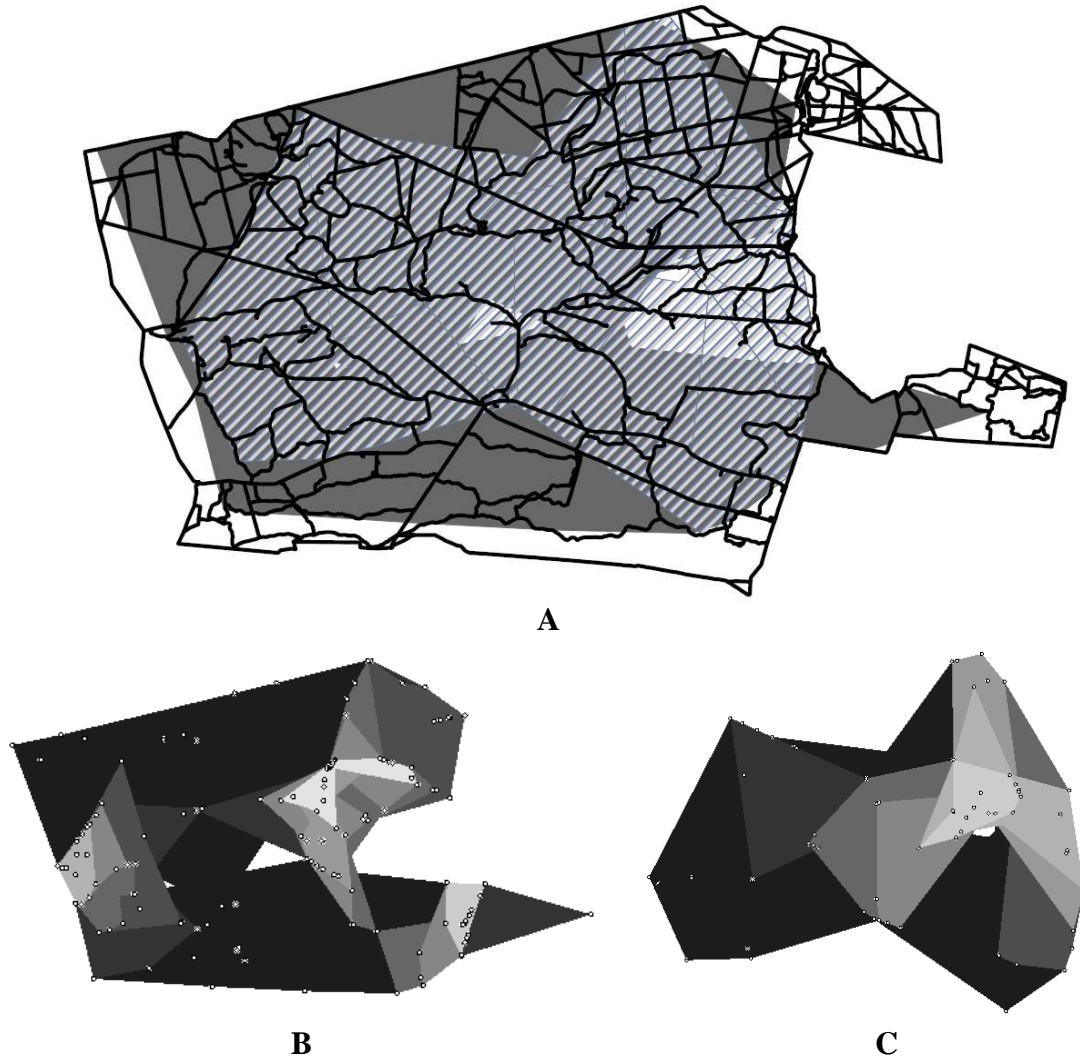
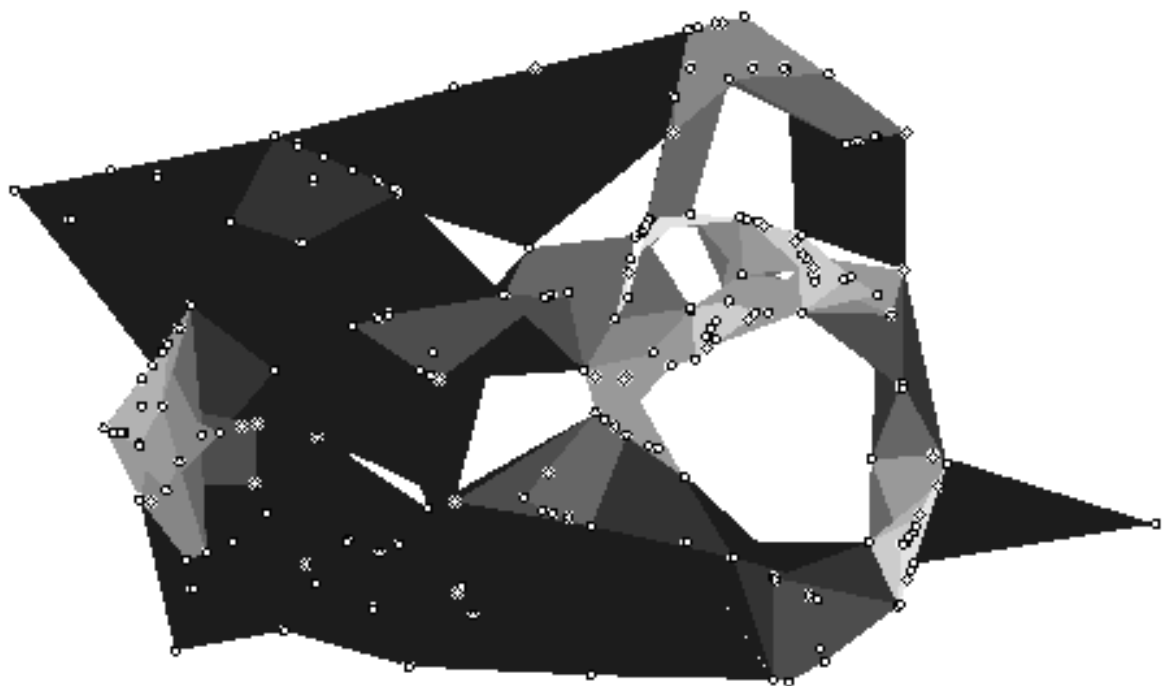


Figure 3.13. Seasonal area utilization of brown hyaenas in the Madikwe Game Reserve as determined by latrine surveys. (A): solid grey colour = dry season range use, grey hatched bars = wet season range use. (B): LoCoH representation of dry season range use, lighter shades represent heavier use. (C): LoCoH representation of wet season range use, lighter shades represent heavier use.



A



B

Figure 3.14. (A): Area utilization of brown hyaenas in the Madikwe Game Reserve as determined by latrine surveys. (B): LoCoH representation of range use, lighter shades represent heavier use.

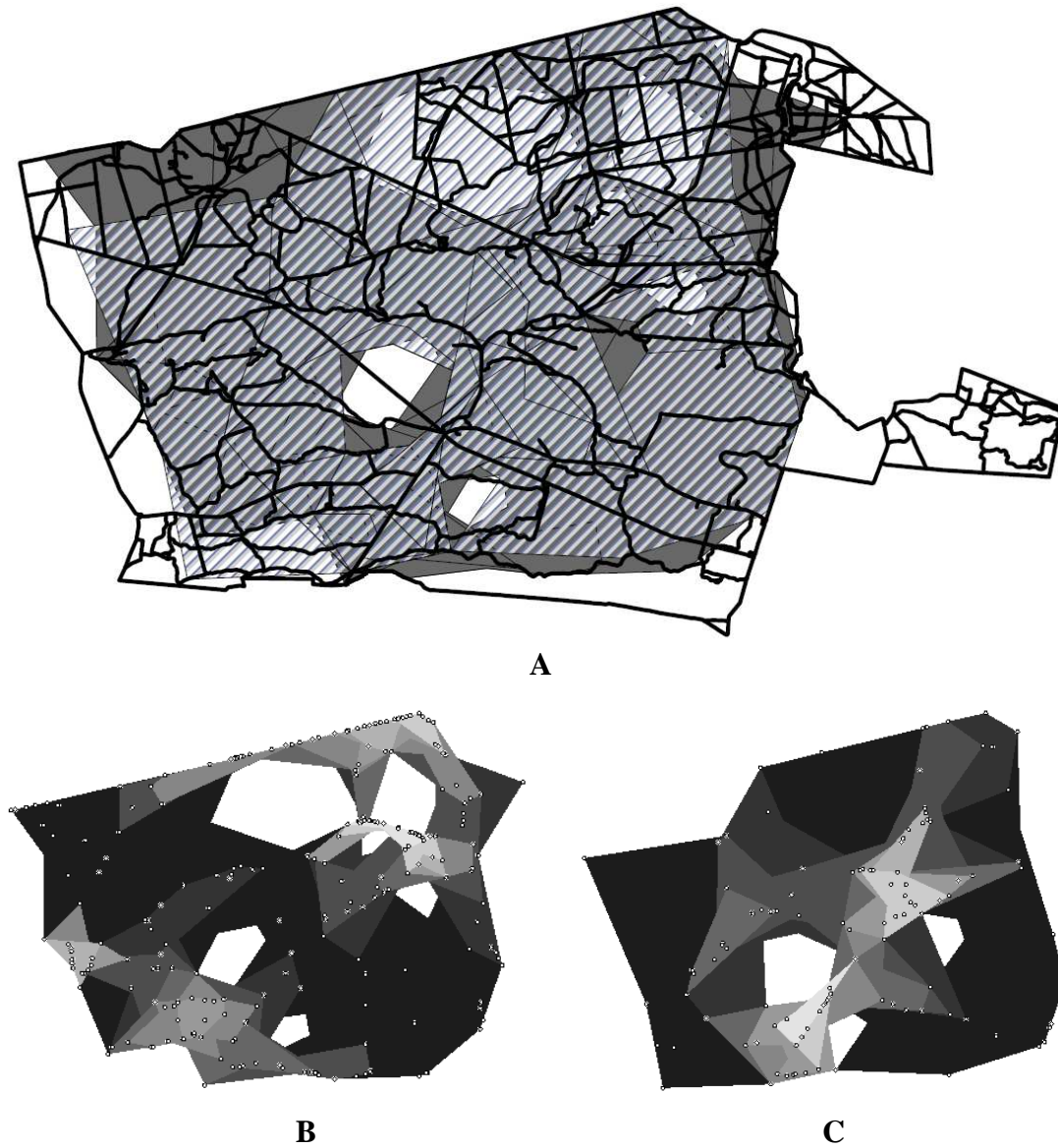
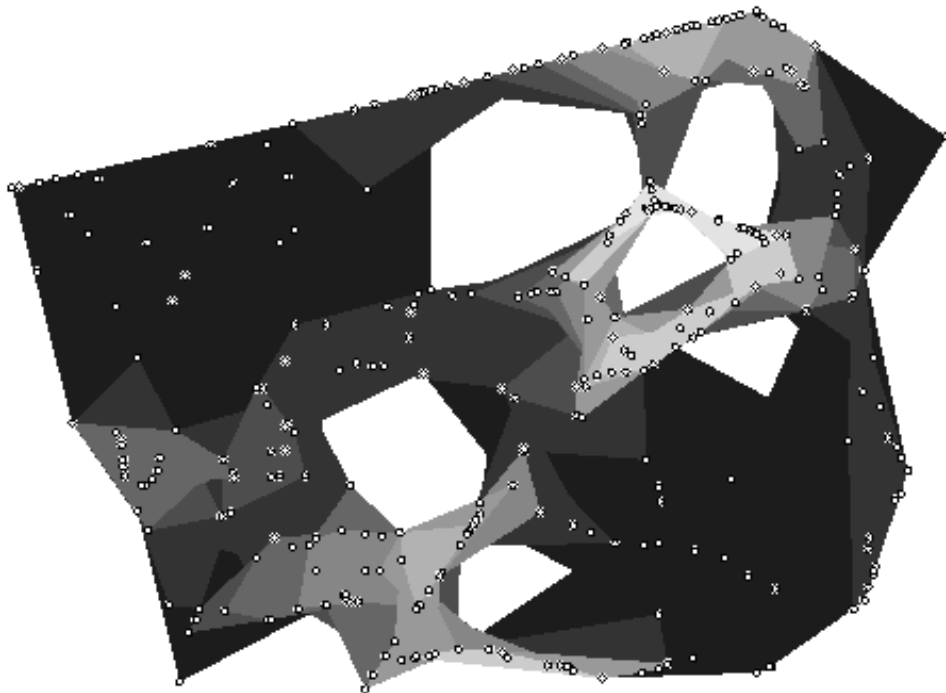


Figure 3.15. Seasonal area utilization of spotted hyaenas in the Madikwe Game Reserve as determined by latrine surveys. (A): solid grey colour = dry season range use, grey hatched bars = wet season range use. (B): LoCoH representation of dry season range use, lighter shades represent heavier use. (C): LoCoH representation of wet season range use, lighter shades represent heavier use.



A



B

Figure 3.16. (A): Area utilization of spotted hyaenas in the Madikwe Game Reserve as determined by latrine surveys. (B): LoCoH representation of range use, lighter shades represent heavier use.

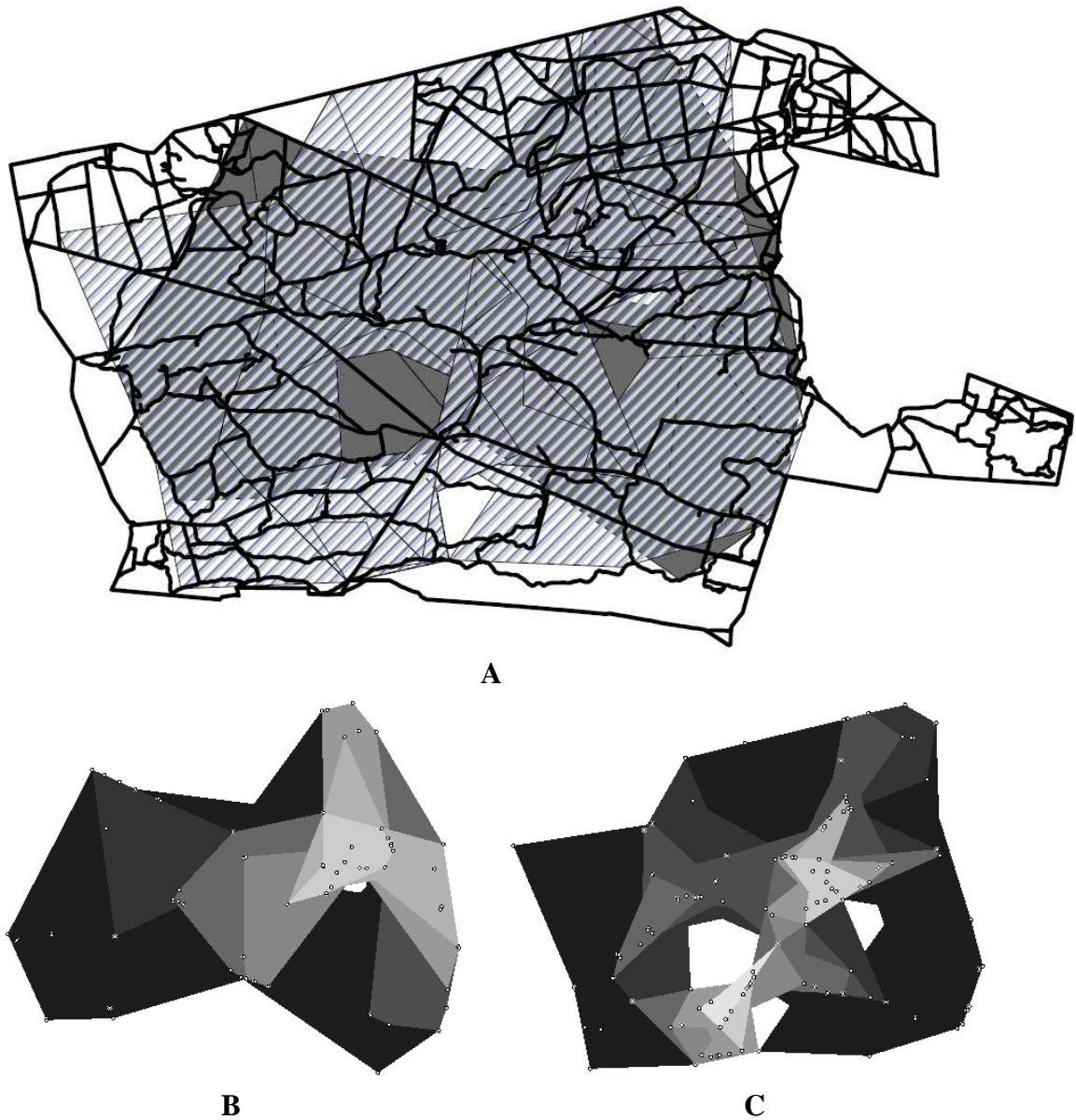


Figure 3.17. Comparison of hyaena area utilization during the wet season in the Madikwe Game Reserve as determined by latrine surveys. (A): solid grey colour = brown hyaena range use, grey hatched bars = spotted hyaena range use. (B): LoCoH representation of brown hyaena range use, lighter shades represent heavier use. (C): LoCoH representation of spotted hyaena range use, lighter shades represent heavier use.

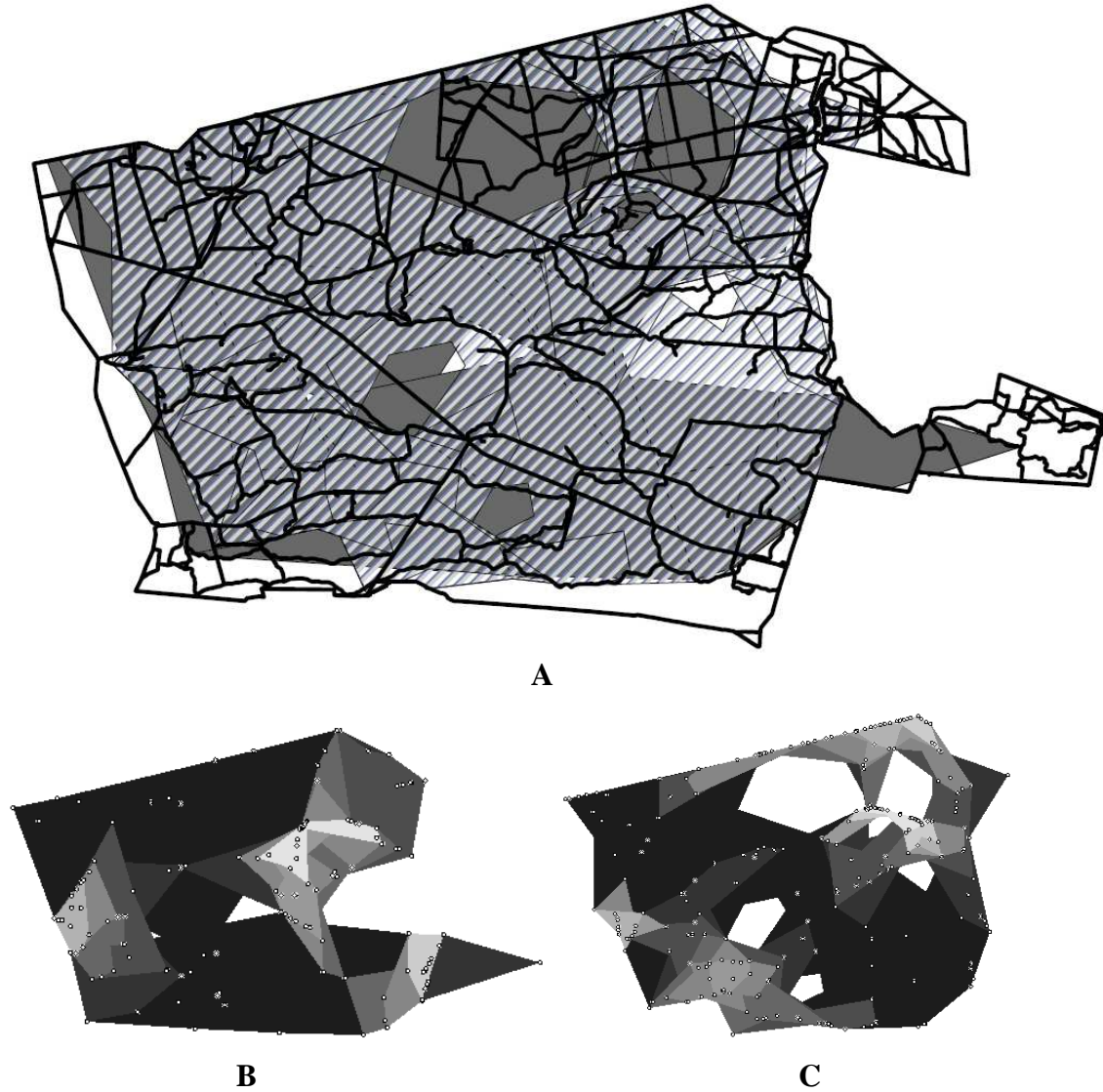


Figure 3.18. Comparison of hyaena area utilization during the dry season in the Madikwe Game Reserve as determined by latrine surveys. (A): solid grey colour = brown hyaena range use, grey hatched bars = spotted hyaena range use. (B): LoCoH representation of brown hyaena range use, lighter shades represent heavier use. (C): LoCoH representation of spotted hyaena range use, lighter shades represent heavier use.

3.3.2 RADIO-TELEMETRY

Two VHF collars were affixed to a male spotted hyaena and to a male brown hyaena. One VHF collar was placed on a dominant female spotted hyaena. Attempts to obtain support or funding for more VHF collars were unsuccessful. Tau Lodge's field guides had agreed to obtain a radio-telemetry fix on collared hyaenas nightly for the duration of the study. However, mitigating factors beyond the scope of this study only allowed the field guides to obtain radio-telemetry fixes on only one hyaena for between 1 to 4 nights per month throughout the study period. This resulted in 22 radio-telemetry fixes for a single brown hyaena. These 22 GPS co-ordinates were then plotted using the localized convex hull method to generate a range distribution of this brown hyaena, which resulted in a total of 22.4km² (Fig. 3.19).

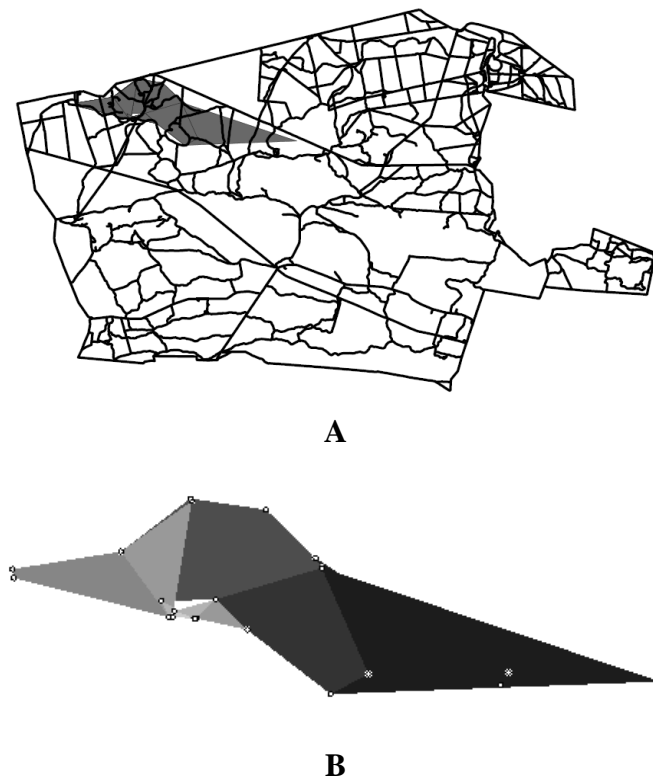


Figure 3.19. Area utilization of a collared brown hyaena in the Madikwe Game Reserve as determined by radiotelemetry surveys. (A): Brown hyaena range use in relation in the game reserve. (B): LoCoH representation of range use, lighter shades represent heavier use.

3.3.3 SIGHTINGS

A total of 528 hyaena sightings were recorded throughout the study period, with 269 sightings for brown hyaenas and 259 sightings for spotted hyaenas. Brown and spotted hyaenas were seen more often alone or with conspecifics rather than with the other species ($\chi^2 = 476.283$; $df = 1$; $p < 0.001$). An increase in group size of spotted hyaenas had an adverse effect on whether brown hyaenas were seen with them ($\chi^2 = 117.000$; $df = 8$; $p < 0.001$; Fig. 3.20), whereas a spotted hyaena was seen only on one occasion with a group of three brown hyaenas out of 37 brown hyaena group sightings.

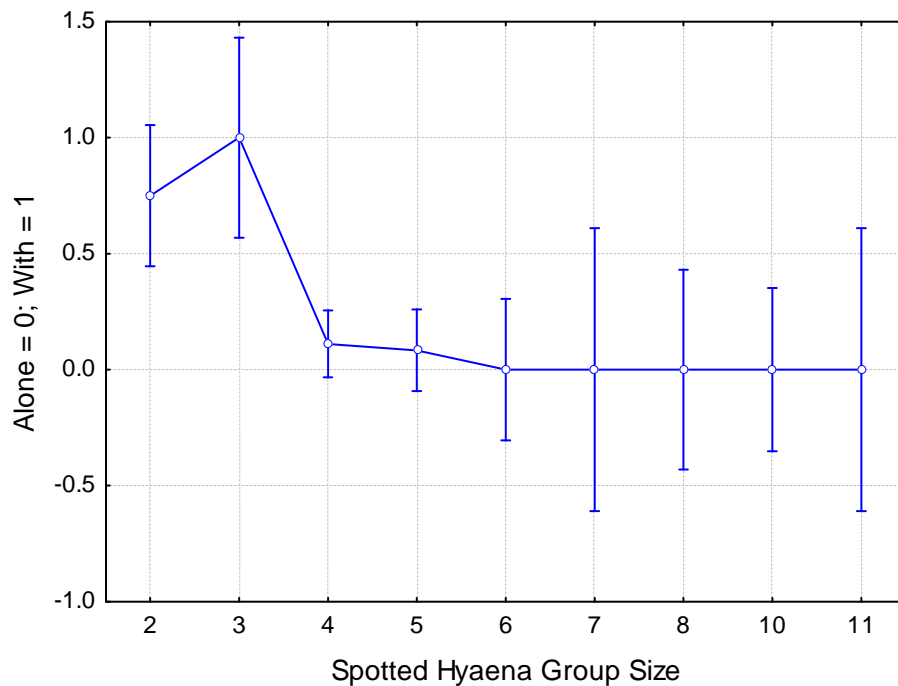


Figure 3.20. Brown hyaena association with spotted hyaenas of increasing group sizes with 95% confidence intervals. 0 = No association, 1 = association with spotted hyaenas.

Both hyaena species were seen significantly more often during the night than in the day (brown $\chi^2 = 25.610$; $df = 1$; $p < 0.001$; spotted $\chi^2 = 13.440$; $df = 1$; $p < 0.001$).

0.001), although there were no significant differences between the sightings of hyaena species for either the day or night sightings (day $\chi^2 = 0.254$; $df = 1$; $p = 0.614$; night $\chi^2 = 0.863$; $df = 1$; $p = 0.353$). No significant relationships were exhibited for the times of hyaena sighting and which species was sighted ($r^2 = 0.009$; $df = 257$; $p = 0.132$). There were also no significant differences between the times of brown and spotted hyaena sightings ($t = 1.500$; $df = 525$; $p = 0.134$; Fig. 3.21).

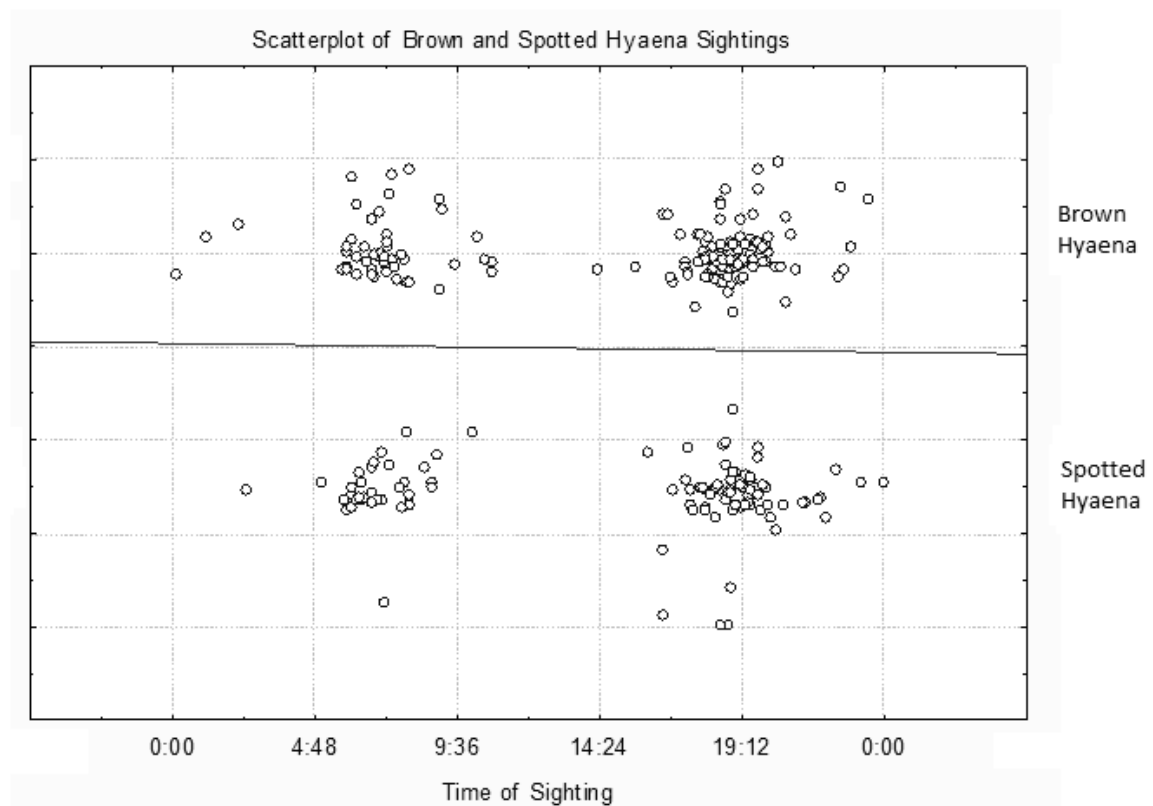


Figure 3.21. Times of brown and spotted hyaena sightings over a 24 hr period for the 2007-2008 study period in the Madikwe Game Reserve.

The sightings of the brown hyaena resulted in a localized convex hull estimate of the species' range use to be 510.4km² (Fig. 3.22). Alternatively, the range distribution for the sightings of the spotted hyaena species is 470.4km² (Fig. 3.23). Additionally, the sighting records portray a high degree of overlap in areas where brown and spotted hyaenas are sighted (Fig. 3.24).

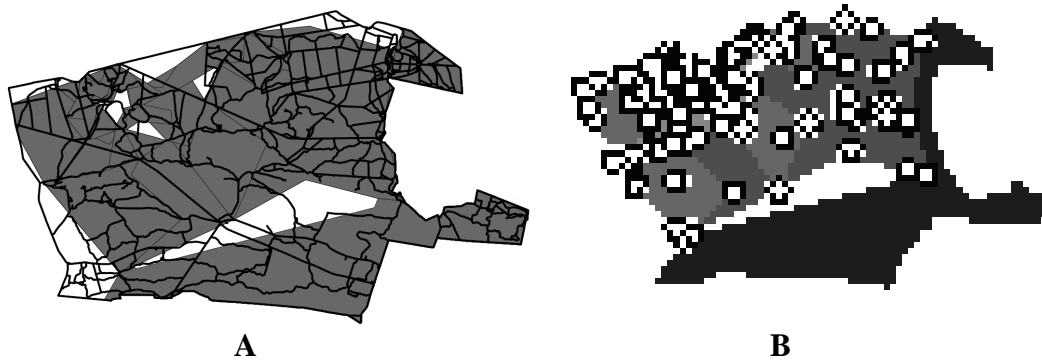


Figure 3.22. (A): Area utilization of brown hyaenas in the Madikwe Game Reserve as determined by sighting surveys. (B): LoCoH representation of range use, lighter shades represent heavier use.

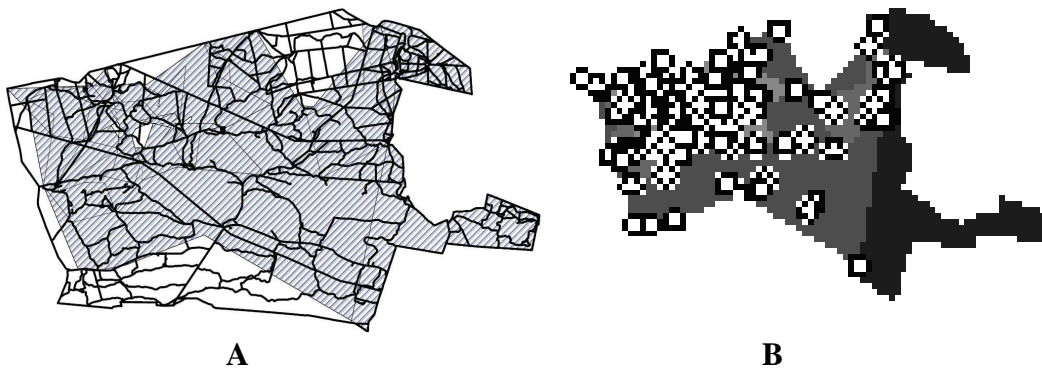


Figure 3.23. (A): Area utilization of spotted hyaenas in the Madikwe Game Reserve as determined by sighting surveys. (B): LoCoH representation of range use, lighter shades represent heavier use.

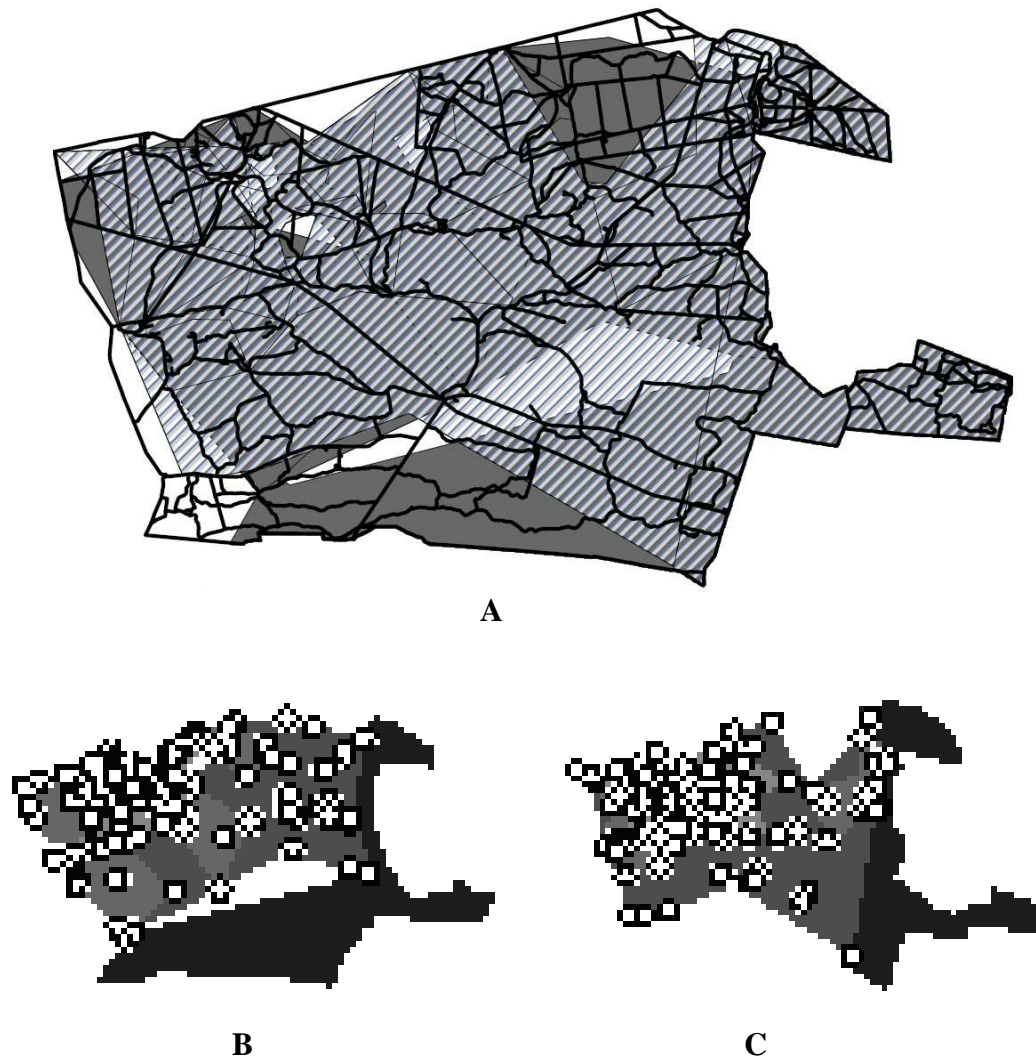


Figure 3.24. Comparison of hyaena area utilization in the Madikwe Game Reserve as determined by sighting surveys. (A): solid grey colour = brown hyaena range use, grey hatched bars = spotted hyaena range use. (B): LoCoH representation of brown hyaena range use, lighter shades represent heavier use. (C): LoCoH representation of spotted hyaena range use, lighter shades represent heavier use.

3.3.4 CAMERA-TRAPS

Camera-traps used over a period of 283 trap days at 12 sites in the wet season yielded a total of 238 photographs, from which 141 independent photographs could be obtained. Camera-traps from 300 trap days at 60 sites in the dry season yielded 562 photographs, from which 165 independent photographs could be obtained. This resulted in 306 independent photographs from a total of 583 camera-trap days. Seventy of these were of carnivore species, which included 36 photographs of spotted hyaenas and 18 of brown hyaenas. Fifty were of small ungulates, other small mammals and birds, 82 were of medium-sized ungulates, 46 were of larger ungulates, and fifty-eight were of mega-herbivores. A camera-trap detection history for the two species was created across the two seasons from the hyaena photographs obtained. There were 24 occurrences of detection from the wet season with 27 photographs of spotted hyaenas and 9 photographs of brown hyaenas. For the dry season, there were 15 occurrences of detection with 9 photographs for each of the brown and spotted hyaenas.

Detection of hyaenas by camera-traps were not influenced by any of the factors of elevation, distance to nearest road, distance to nearest water source, distance to infrastructure, or soil and vegetation. However, the analysis of variance showed the time of detection to be the most important factor in the detection of hyaenas by camera-traps with a significant majority of hyaena photos being taken at night ($F = 115.412$; $df = 2$; $p < 0.001$). A seasonal effect was also an important factor in the detection of hyaenas by camera-traps ($F = 6.149$; $df = 1$; $p = 0.017$).

The locations of successful camera-trap detection of brown hyaenas resulted in a localized convex hull estimate of a range size of 385.0km^2 for the dry season and 403.9km^2 for the wet season (Fig. 3.25). Conversely, the range size estimates for the

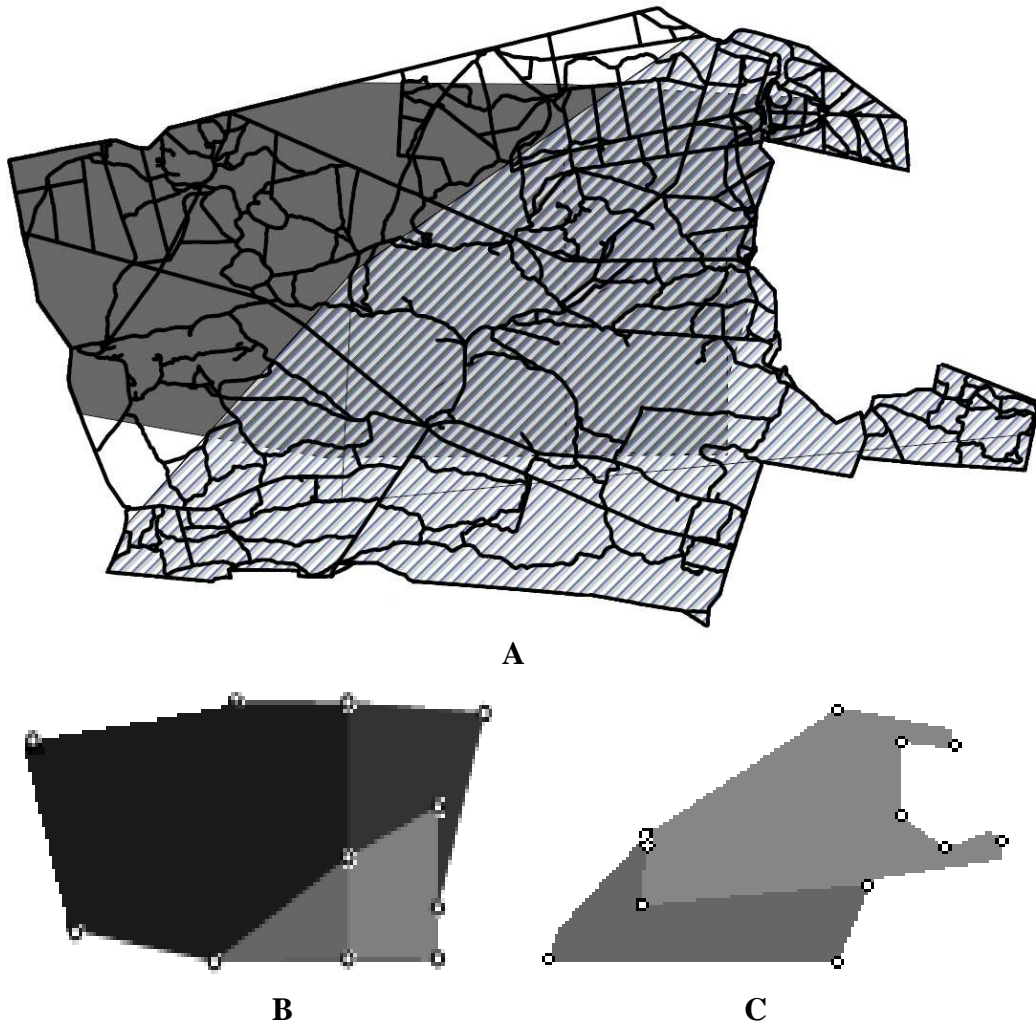


Figure 3.25. Seasonal area utilization of brown hyaenas in the Madikwe Game Reserve as determined by camera-trap surveys. (A): solid grey colour = dry season range use, grey hatched bars = wet season range use. (B): LoCoH representation of dry season range use, lighter shades represent heavier use. (C): LoCoH representation of wet season range use, lighter shades represent heavier use.

spotted hyaenas were smaller with 112.2km^2 for the dry season and larger at 519.1km^2 for the wet season (Fig. 3.26). Seasonal overlaps in certain areas of the reserve used by both brown and spotted hyaenas have also been depicted (Fig. 3.27 & Fig. 3.28).



Figure 3.26. Seasonal area utilization of spotted hyaenas in the Madikwe Game Reserve as determined by camera-trap surveys. (A): solid grey colour = dry season range use, grey hatched bars = wet season range use. (B): LoCoH representation of dry season range use, lighter shades represent heavier use. (C): LoCoH representation of wet season range use, lighter shades represent heavier use.

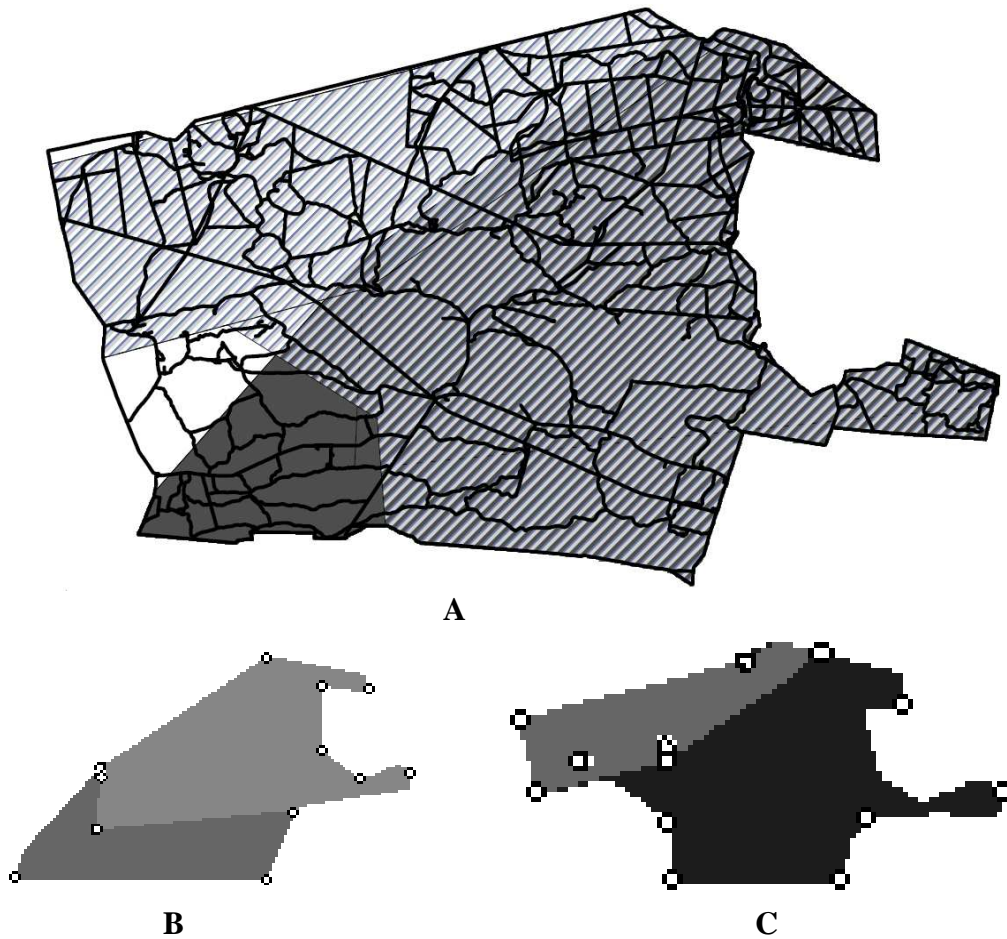


Figure 3.27. Comparison of hyaena area utilization during the wet season in the Madikwe Game Reserve as determined by camera-trap surveys. (A): solid grey colour = brown hyaena range use, grey hatched bars = spotted hyaena range use. (B): LoCoH representation of brown hyaena range use, lighter shades represent heavier use. (C): LoCoH representation of spotted hyaena range use, lighter shades represent heavier use.

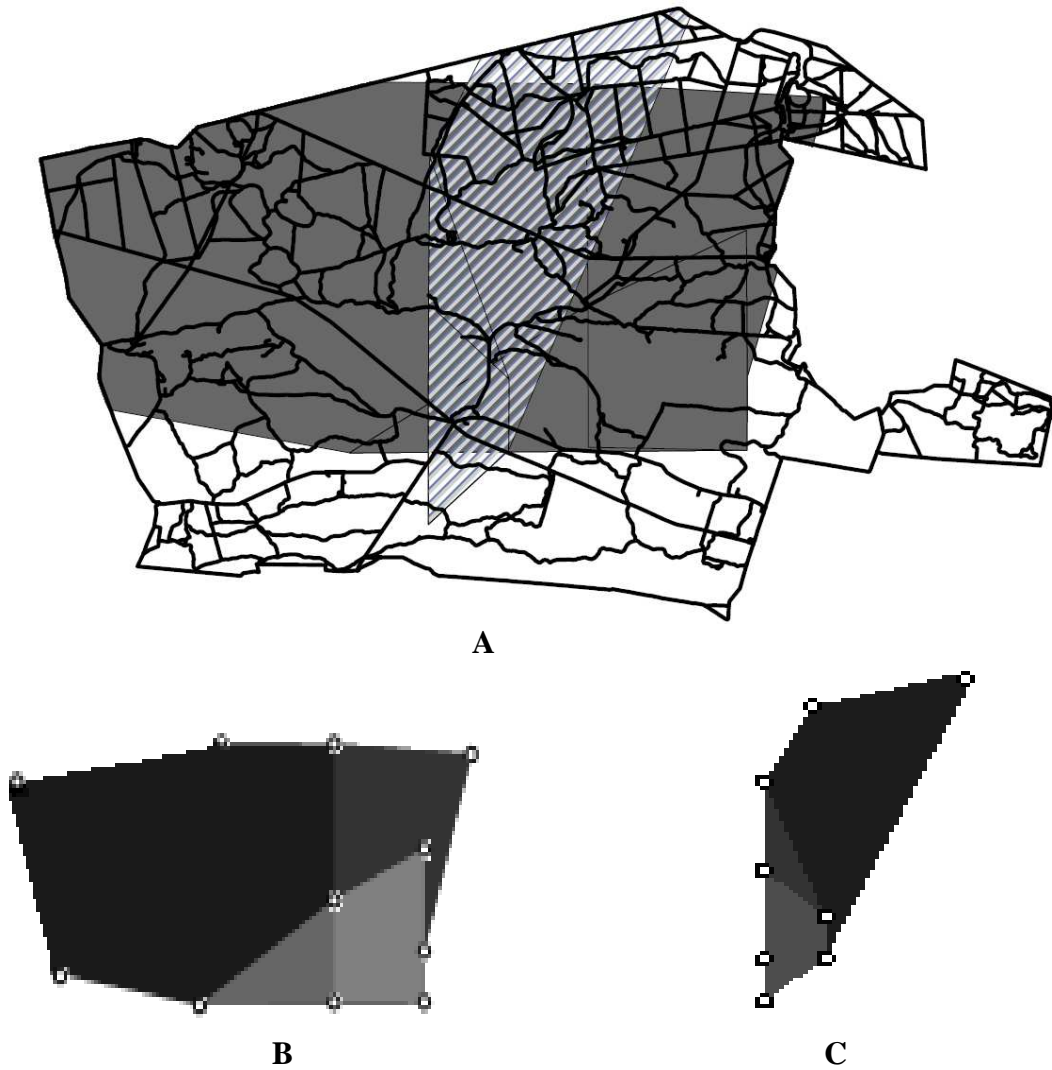


Figure 3.28. Comparison of hyaena area utilization during the dry season in the Madikwe Game Reserve as determined by camera-trap surveys. (A): solid grey colour = brown hyaena range use, grey hatched bars = spotted hyaena range use. (B): LoCoH representation of brown hyaena range use, lighter shades represent heavier use. (C): LoCoH representation of spotted hyaena range use, lighter shades represent heavier use.

3.3.5 RANGE SIZES AND AREA UTILIZATIONS

The localized convex hull method estimated the range sizes and the average total area used by hyaenas in MGR. Table 3.1 shows no significant differences in the range sizes of the two hyaena species when they occupied exclusively used areas without the other species ($t = 0.568$; $df = 12$; $p = 0.581$). Furthermore, the range sizes of overlapping areas, which consisted of both species, were significantly larger than the range sizes of exclusively used areas for each hyaena species (brown $t = -3.802$; $df = 12$; $p = 0.003$; spotted $t = -4.598$; $df = 12$; $p = 0.001$).

The average total area which was exclusively utilized by only brown hyaenas in the reserve was estimated at 92.3km^2 . The average total area which was exclusively utilized by only spotted hyaenas was estimated at 68.8km^2 (Fig. 3.29). The average total overlap area in the reserve that was utilized by both brown and spotted hyaenas was estimated at 343.0km^2 (Fig. 3.29). Using the chi-square analysis, the average sizes of the exclusively utilized areas were not significantly different between the brown and spotted hyaenas ($\chi^2 = 3.432$; $df = 1$; $p = 0.064$). In contrast, the area of overlap, which was the average area utilized by both hyaena species, were significantly larger than the average area utilized by each species alone ($\chi^2 = 275.081$; $df = 2$; $p < 0.001$).

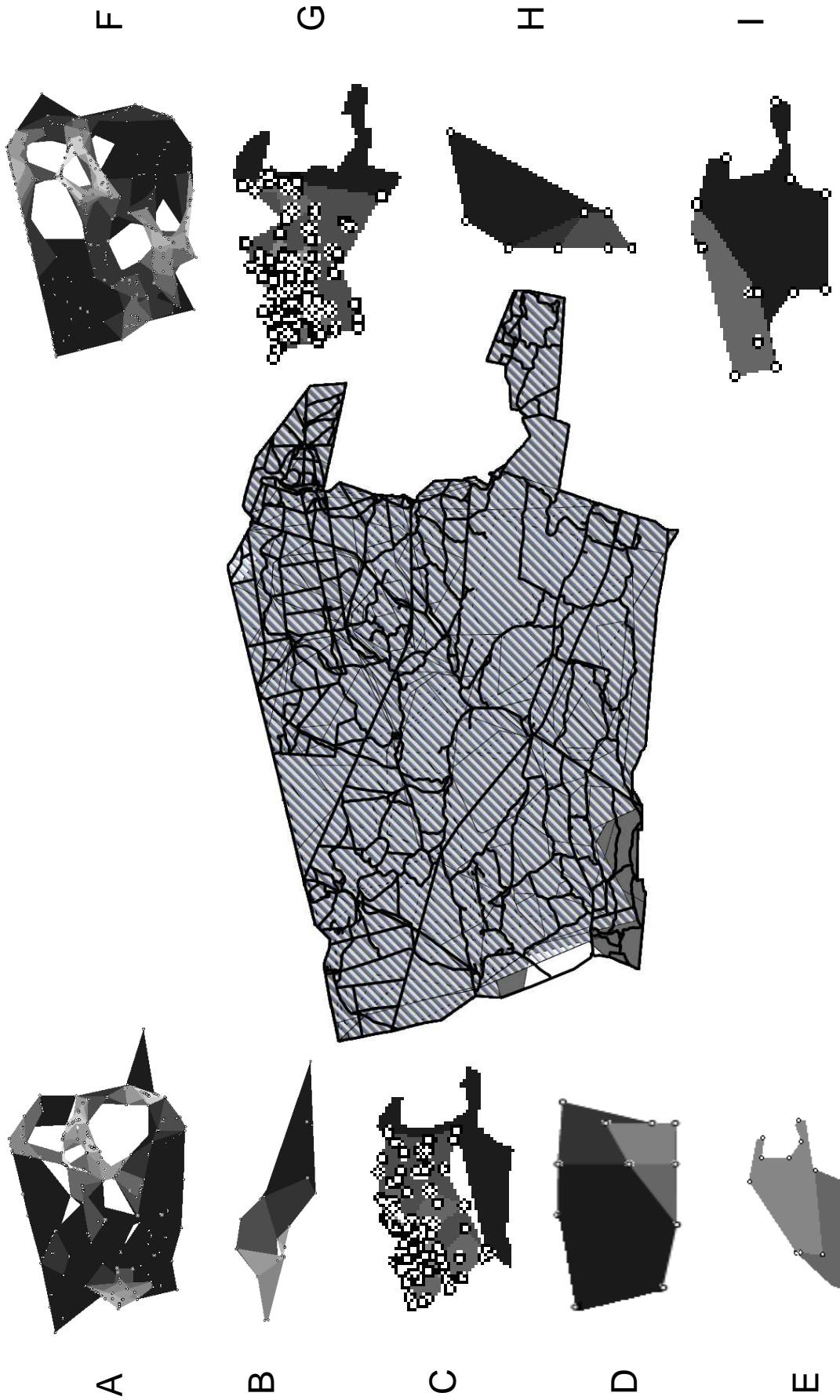


Figure 3.29. Area utilization and range use of brown and spotted hyaenas in Madikwe Game Reserve. Central figure: solid grey colour = brown hyaena range use, grey hatched bars = spotted hyaena range use. A – I are LoCoH representation maps of hyaena range use. Brown hyaena range use based on: A = latrines, B = radiotelemetry, C = sightings, D = camera-trapping in dry season, E = camera-trapping in wet season. Spotted hyaena range use based on F = latrines, G = sightings, H = camera-trapping in dry season, I = camera-trapping in wet season.

Table 3.1. Home range estimators in km² using the localized convex hull method based on various surveys in the Madikwe Game Reserve, South Africa.

SURVEYS	BROWN HYAENA AREAS ONLY	SPOTTED HYAENA AREAS ONLY	OVERLAP AREAS
All combined	14.8	3.5	581.4
Cameratrap Overall	73.2	19.2	501.6
– <i>Dry Season</i>	295.0	21.1	90.7
– <i>Wet Season</i>	53.0	169.6	350.9
Sightings (incl. radiotelemetry)	91.7	51.5	421.8
Latrines Overall	69.7	74.5	348.6
– <i>Dry Season</i>	87.8	48.6	316.0
– <i>Wet Season</i>	34.0	112.5	291.9
Average total area	92.3	68.8	343.0

3.4 DISCUSSION

3.4.1 *HYAENA RANGE SIZES*

In MGR, the areas utilized by spotted and brown hyaenas overlap extensively and are significantly larger than exclusively utilized areas. The smallest exclusively utilized area for brown hyaenas were 14.7km² and 3.5km² for spotted hyaenas. The camera-trap and latrine surveys indicate that brown hyaenas have larger exclusive areas during the dry season, with larger exclusive areas for the spotted hyaena in the wet season. In addition, the sighting and radiotelemetry surveys revealed a larger exclusive area for brown hyaenas, but neither of these areas were large enough to be substantial. Furthermore, all surveys consistently portray huge overlapping areas for both hyaenas ranging from 90.7km² to 581.4km². The absence of any significant differences in the sizes of exclusively utilized areas between brown and spotted hyaenas points towards the potential for a high degree of competition, especially when all overlapping areas are significantly larger than exclusive areas. It is difficult to determine which area is exactly exclusive to only brown or spotted hyaenas when there is so much overlap between the two species. This is further exacerbated by the fact that brown and spotted hyaena clans are likely to behaviourally defend their territories from conspecifics, and such behaviour will effectively influence the home range sizes of hyaenas by either increasing or constraining individual ranges based on their interactions with conspecifics. However, it is evident that both hyaena species are utilizing most of the, if not the entire, 750km² reserve.

Kruuk (1972) reported that the territories of several spotted hyaena clans in the Serengeti varied between 14km² and 48km² with a mean of 27.6±13.9km². Honer et al. (2005) has also determined variations in the territories of the Ngorongoro Crater's spotted hyaena clans to be between 9km² and 40km² with a mean of 23.8±11.6km².

In Zimbabwe's Matusadona National Park, Purchase and du Toit (2000) established the home range for a spotted hyaena female at 23km^2 , with the home ranges for two males at 11km^2 and 53.2km^2 . In a region of the Masai Mara in Kenya, a clan of 60 to 80 hyaenas was observed to defend a territory of 62km^2 (Boydston et al., 2003), while a group of 5 spotted hyaena females increased their home range from 10.9km^2 to 13.9km^2 following the closure of a refuse pit within their territory (Kolowski and Holekamp, 2007). However, in the KNP, a clan of 11 spotted hyaenas defended a territory of 130km^2 (Henschel and Skinner, 1987), and in the Kalahari, spotted hyaena territories were over 1000km^2 (Mills, 1990).

Furthermore, space use patterns of spotted hyaenas have been found to be clearly influenced by their social relationships and anthropogenic disturbances (Frank, 1986; Kolowski and Holekamp, 2007). Lower ranking individuals were often found to forage in areas outside their territory (Honer et al., 2005), and home range size increased while the core area decreased after removal of an anthropogenic food source (Kolowski and Holekamp, 2007). Additionally, Boydston et al. (2003) found a 60% increase in the home range size of a spotted hyaena female following disturbance from pastoralists and livestock grazing. Females were found to travel farther, to have larger home ranges, were more nocturnal and to occur in smaller groups.

Brown hyaenas have also exhibited wide differences in their ranging behaviour. As they often exist in arid regions with sparse prey resources, they are capable of covering huge distances in one night and normally cover between 20 to 30km while foraging at night in the Kalahari (Owens and Owens, 1978) and have huge home ranges from 235 to 544km^2 (Mills, 1977; 1981). However, in agricultural areas, which could be regarded as optimal habitat, brown hyaenas utilize a mere fraction of their range, utilizing as small an area as 5.5km^2 (Skinner and van Aarde,

1987), or having upwards of three individuals utilizing a given small area (Skinner, 1976). Maude (2005) estimated the territory size for a brown hyaena clan in a cattle area to be 245km², and found that the overall home range size for brown hyaenas in protected areas was 2.3 times greater.

Mills (1981) determined that brown hyaenas' home ranges varied under different conditions depending on the distribution of food and that the number of animals inhabiting the home range was dependent on the quality of food in the area. There is also extensive overlapping in the home ranges of brown hyaenas as all members of the group utilize coincidental ranges (Mills, 1981; Skinner and van Aarde, 1987). Brown hyaenas use specific common pathways within a network which they often scent-mark by pasting and encounter one another for socializing and grooming purposes (Owens and Owens, 1978). Although each home range is shared by a group of mainly closely related individuals, the home ranges of neighbouring groups overlap slightly and members of neighbouring groups are often aggressive toward one another (Mills, 1977; 1981). As the MGR hyaenas share much of their home ranges with both conspecifics and the other species, a finer-scale analysis is required. By using GPS or VHF telemetry collars on more individuals from each species, this data would be helpful in determining the exact range use of individuals and clans on a temporal and spatial scale. This information would be critical in understanding how spotted and brown hyaenas deal with such high degrees of overlap in this area.

3.4.2 SPATIAL OVERLAPS

Overlaps in habitat utilization for the brown and spotted hyaenas are clearly demonstrated in this study. While the presence of a hyaena latrine in a particular area confirms the presence of hyaenas in that given area (Wilson and Delahay, 2001), it

gives little or no information to the possible interactions experienced between conspecifics or species. In MGR, spotted hyaena latrines were typically larger with more faecal depositions than brown hyaena latrines, likely because spotted hyaenas usually forage in clans of two or more individuals, while the brown hyaena is normally a solitary forager (Mills, 1990). In the Kalahari, Owens and Owens (1978) never observed more than one brown hyaena utilizing the same latrine, but 8.3% of the latrines found in MGR contained both brown and spotted hyaena faeces. Further analysis revealed that differences in vegetation was a habitat's main effect on species latrine placement, but there were also no preferences between brown and spotted hyaenas in whether they utilized a latrine next to a conspecific's or a mixed latrine. This indicates that hyaenas are exploiting the same areas and habitats, but it is likely that they are most probably depositing their faeces in these latrines at different times.

Significantly more latrines from both hyaena species were deposited in the core of the reserve, which indicates a preference for the core area by both species. There was also a higher prevalence of latrines in the core during the wet season than the dry season, although this could simply be attributed to a higher resource base available during the wet season, allowing for increased consumption of resources resulting in a higher frequency of defecations. As a higher prevalence of latrines in the core was evident by both species, this spatial overlap may have been alleviated by utilizing a similar range of elevation areas at different times. Spotted hyaena latrines were often found at higher elevations during the wet season, while brown hyaena latrines were often found at higher elevations during the dry season. This indicates that the hyaenas' spatial competition for the core may have been mitigated temporally by utilizing different elevations in different seasons.

In addition, MGR's hyaena sighting data points towards evidence of avoidance towards the other species. Both brown and spotted hyaenas were seen more often at night, with no notable differences between day and night sightings, and with no notable differences between the times of sightings. This indicates that both hyaena species are usually seen in MGR at night, roughly at around the same times. This is also corroborated by the detection history as recorded by the camera-traps. The time of detection, in this case being night, was the most important factor in detecting hyaenas by camera-traps, with more of the photos being taken at night. However, while both brown and spotted hyaenas were often seen at night at around the same times, they were seen more often either alone or with conspecifics than they were seen in the presence of the other hyaena species. This demonstrates that both brown and spotted hyaenas' are utilizing the park on a similar temporal scale, but actively avoiding one another spatially.

Spatial avoidance has been exhibited in mongooses (*Herpestes ichneumon*) and foxes (*Vulpes vulpes*) who avoid areas utilized by lynxes (*Felis pardina*) (Palomares et al., 1996), in gray foxes (*Urocyon cinereoargenteus*) who avoid habitats with increased coyote (*Canis latrans*) densities (Fedriani et al., 2000), in arctic foxes (*Alopex lagopus*) who avoid areas with red foxes (Tannerfeldt et al., 2002), and in sympatric jackals (*Canis mesomelas*) who favoured different habitats and did not utilize the same areas (Loveridge and MacDonald, 2003). Conversely, Mitchell and Banks (2005) found no differences in the distribution of the Australian wild dogs (*Canis lupus dingo*) and foxes, and point towards temporal avoidance or localized habitat shifts for their continued coexistence. The hyaenas in MGR share many of the same habitat resources, and are in competition for the same areas

especially within the core of the reserve. They appear to mitigate these limiting ecological factors by avoiding the other species both temporally and spatially.

Durant (1998) in her study on cheetahs in the Serengeti found that cheetahs were more strongly associated with each other than with their competitors and that they utilized areas with low-density prey. Cheetahs also exhibited local avoidance behaviour towards lions and hyaenas, both temporally and spatially. Durant postulates that the prevalence of cheetahs in the ecosystem, although widely distributed, occurs at low densities due to the cheetah's heightened mobility in seeking out 'competition refuges', areas with low densities of competing predators such as lions and hyaenas. This behavioural characteristic of seeking out 'competition refuges' may be why MGR's brown hyaenas occur at low densities, but continue to coexist with spotted hyaenas and lions and be widely distributed throughout the reserve. An understanding of how species are able to coexist within an area has implications for the maintenance of diversity in multi-trophic communities, and can assist managers with the natural regulation of populations.

3.4.3 LIMITATIONS OF SURVEYS

In estimating a species range, latrine surveys are a useful tool as they provide a series of data points throughout a given area with which GPS coordinates can be affixed to assist with the construction of localized convex hulls. However, sometimes an older latrine may act as an outlier, as it is more than a few weeks old and may not have been recently utilized by the animal. Adding this data point to the assimilation of the hull may result in an *overestimation* by including more points to create a larger area than actually exists. A way around this would be to sample a subset of the study area extensively and only to include latrines with fresh faecal deposits not more than

48 hours old, with the intention of extrapolating the results towards the surrounding study area.

In contrast, camera-trap surveys provide an excellent tool in estimating a species' range by portraying where and when a species was detected, however the low detection probability may result in an *underestimation* of a species' range by making it smaller than what it actually is. In one instant during this study, a camera-trap was set and upon returning five days later, a fresh hyaena faecal deposit was made directly behind the tree to which the camera-trap was affixed to, but the film revealed no photographs of said hyaena. As well, camera-traps were situated at known places frequented by hyaenas during the wet season, and placed in a 9km² grid in the dry season, resulting in more photographs of hyaenas in the wet season. Increasing the efficacy of detection probabilities by camera-traps can be improved by increasing the density of camera-traps in the sampling area (Carbone et al., 2001), or by using baits or lures to attract the animals to camera-traps (Thorn et al., 2009).

Radio-telemetry fixes from a single collared brown hyaena established the range size of this particular hyaena to be 22.4km². Such fixes were usually obtained at around the same time once a night over several evenings. In order for such data to be useful and to increase the accuracy and integrity of the data, several fixes need to be obtained throughout the night over several evenings for a set period of time in order to establish the movement of the animal throughout the duration of its activity periods (Claridge et al., 2005; Broquet et al., 2006; Huck et al., 2008). Tau Lodge, together in conjunction with MGR park personnel also provided the hyaena sighting data for this study. These sightings were collected mainly during game drive times in the park, which occurred mainly in the mornings between 05h00 to 09h00 and in the evenings between 16h30 to 21h00. Incidental sightings were also recorded

throughout the day, but several days in the sighting logs are unaccounted for. This lends itself to a biased sampling effort, occurring mainly during game drive time and heavily favoured towards tourist response, in that certain areas of the park with known high animal concentrations would be frequented more often, rather than a random uniform sampling effort.

Although there has been considerable debate about the best way of deriving home range estimates, the k-NNCH, or fixed k LoCoH, is a relatively new and powerful method for creating home ranges and area distributions, with density indices to accurately represent animal location and movements. LoCoH is a superior advancement over the MCP and kernel methods, and has performed consistently better than fixed kernel methods (Huck et al., 2008). LoCoH is especially appropriate for patchy study areas where an animal's home range contains frequent inaccessible areas (Ryan et al., 2006). Finding the correct k-value for the dataset requires knowledge of the topology of the area and experience with the software. A current working knowledge of the topology of MGR, in combination with extensive analyses of isopleth graphs proved to be useful in determining k-values for the dataset associated with this study. Ongoing research and applications using the k-NNCH method will be necessary to determine whether the range sizes and area utilization of the brown and spotted hyaenas in MGR change over time or with changes in predator and prey numbers.

3.4.4 IMPLICATIONS OF RESEARCH FOR MANAGEMENT

This study is the first of its kind to provide insight into how temporal and spatial avoidance of the other species may be allowing the two hyaena species to continue to co-exist within this reserve. Further research into this type of behaviour may divulge how such behaviour choices are made by not only the hyaenas, but by

other co-existing species. Knowledge into this type of behavioural plasticity may prove crucial for the conservation of coexisting species and the promotion of biodiversity, especially in the light of ongoing habitat destruction and fragmentation.

As remaining habitats are often subjected to increasing land-use competition, coupled together with insufficient funding for conservation efforts, the need to conserve a maximum number of species diversity is further constrained by the available minimum areas (Gurd et al., 2001; Restani and Marzluff, 2002). Therefore, area considerations are of paramount importance for the effective conservation planning of carnivores, whose large spatial requirements have made them most susceptible to habitat loss, and equally difficult to conserve (Linnell et al., 2001; Lindsey et al., 2004). A myriad of factors need to be considered with determining the spatial use patterns of large carnivores.

Spatial use patterns of large carnivores are determined by the availability of water and prey resources, available cover for den sites, refuges from predators or climate, and interspecific or intraspecific competition (Mills and Knowlton, 1991; Hofer and East, 1993). Carnivore population densities, movements, and home range sizes are also influenced by anthropogenic resources (Craighead and Craighead, 1971; Fedriani et al., 2001; Hidalgo-Mihart et al., 2004), and may result in heightened human-carnivore conflict. Human-carnivore conflict may occur as a result of increasing carnivore densities (Yom-Tov et al., 1995), or animals relocating towards human-dominated areas (Beckmann and Berger, 2003). Kolowski and Holekamp (2007) demonstrated how hyaena space use patterns were altered in the face of even small sources of human refuse.

The behavioural plasticity of hyaenas allows them to respond quickly to changing ecological conditions, affording them the ability to adapt and survive in the

face of increasing anthropogenic pressure, even when other carnivore species have shown significant population declines (Gittleman et al., 2001). Consequently, marked behavioural changes in the hyaena's ranging behaviour and habitat preferences may be a key indicator of degradation or a serious deficiency in an ecosystem (Kolowski and Holekamp, 2007). Such findings may provide vital information towards the conservation of biodiversity within a protected area.

3.5 REFERENCES

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- Chapter 4 -

The comparative feeding ecology of two sympatric hyaena species in the Madikwe Game Reserve, South Africa.

4.1 INTRODUCTION

Among carnivores, similar foraging strategies for the same food resources invariably leads to competition (Caro and Stoner, 2003; Hayward and Kerley, 2008). Carnivores can potentially avoid further competition with one another by diversifying their dietary preferences, exercising what is known as prey selection to minimize competition for the same food resources. This has been demonstrated with the carnivores (tigers, *Panthera tigris* and dholes, *Cuon alpinus*) of the tropical forests of India (Karanth and Sunquist, 1995), as well as between coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis mutica*) in the Northern hemisphere (Nelson et al., 2007). Prey selection can lead to dietary separation among members of a guild, and has been identified in sympatric carnivores (Farrell et al., 2000; Azevedo et al., 2006), with evidence pointing towards resource partitioning of mammalian prey size in relation to predator size (Radloff and du Toit, 2004; Mitchell and Banks, 2005; Carbone et al., 2007).

Investigations into the dietary differences among species is fundamental to understanding resource partitioning between species (Nelson et al., 2007) as well as a species' foraging behaviour, population dynamics, habitat use, and social organization (Mills and Gorman, 1997; Jones and Barmuta, 1998; Loveridge and Macdonald, 2003; van Dijk et al., 2008). Ecological plasticity influences resource partitioning, as it provides phenotypic plasticity and versatility. Flexibility to use a variety of habitats

is therefore a key life-history trait (Crooks, 2002; Rivals et al., 2007). Furthermore, a greater degree of dietary variance reflects a species' ability to occupy an increased variety of habitats (Rivals et al., 2007), and the components of an animal's diet can also be used as an indicator of habitat partiality (Feranec, 2004). Such variations in diet can be correlated to geographical variation, the availability of prey and/or large-scale environmental factors (Virgós et al., 1999; Roth et al., 2007).

The brown hyaena (*Parahyaena brunnea*) is regarded primarily as a scavenger of mammalian food remains, supplementing its diet with invertebrates, reptiles, birds and their eggs, fruits and vegetables (Mills and Mills, 1978; Owens and Owens, 1978). In the southern Kalahari, Mills and Mills (1978) identified 58 different food items in the faecal samples of brown hyaenas, while Owens and Owens (1978) found brown hyaenas to feed on a wide variety of food types in the central Kalahari. Along the Namib Desert coast, the diet of brown hyaenas is much less varied as they feed predominantly on Cape fur seals (*Arctocephalus pusillus*) and scavenge other marine organisms that have washed up on the shore (Skinner and van Aarde, 1981; Siegfried, 1984). Brown hyaenas have also been found to scavenge domestic livestock in the form of carrion from agricultural lands (Skinner, 1976; Maude and Mills, 2005), but they are inefficient predators and rarely obtain their food by hunting. Only 4.7% of hunting attempts were successful for the brown hyaenas of the southern Kalahari, and those vertebrates hunted successfully made up only 4.2% of the total diet (Mills, 1977; 1978; 1990). Most hunts were directed towards small animals such as springhare (*Pedetes capensis*), springbok lamb (*Antidorcus marsupilis*), bat-eared foxes (*Otocyon megalotis*), and korhaan species (*Eupodotis sp.*) (Mills, 1990). Brown hyaenas of the Namib Desert coast killed only 2.9% of the Cape fur seals that they

consumed (Goss, 1986). Clearly, brown hyaenas exhibit wide degrees of dietary variance, thereby allowing them to occupy an increased variety of habitats.

In contrast, the spotted hyaena (*Crocuta crocuta*), once widely regarded to be primarily a scavenger, is an efficient hunter capable of killing large prey weighing up to 350kg (Kruuk, 1972; Cooper et al., 1999). Spotted hyaenas are opportunistic predators/scavengers and often hunt whatever is locally abundant ranging from blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*), to buffalo (*Syncerus caffer*) and giraffes (*Giraffa camelopardalis*), to smaller prey such as scrub hares (*Lepus saxatilis*) and rodents (Kruuk, 1972; Cooper, 1990; Mills, 1990; Sillero-Zubiri and Gottelli, 1992; Di Silvestre et al., 2000). In addition, the spotted hyaena exploits carrion as a food source and scavenges from other predators' kills, and has also been found to utilize non-mammalian remains such as invertebrates, reptiles, fruits and vegetables, although to a smaller extent than the brown hyaena (Kruuk, 1972; Bearder, 1977; Smuts, 1979; Tilson et al., 1980; Henschel and Skinner, 1990; Mills, 1990; Mills and Biggs, 1993; Mills and Hofer, 1998). Spotted hyaenas forage and hunt co-operatively in large groups called clans in East Africa (Kruuk, 1972; Honer et al., 2005), and are often seen foraging in smaller groups and/or alone within the southern parts of its range (Bearder, 1977; Smuts, 1979; pers. obs.).

As both brown and spotted hyaenas are capable of exploiting carrion as a food source and often scavenge from the kills of other predators, they are utilizing and appropriating similar resources. However, as spotted hyaenas are physically larger, exist in social clans of several individuals and defend their territories (Kruuk, 1972; Mills, 1990; Honer et al., 2005), spotted hyaenas are thought to have a detrimental effect on brown hyaena densities where they are sympatric due to competitive exclusion (Mills and Hofer, 1998). In the Kruger National Park (KNP), South Africa,

the decline and eventual extirpation of previously dominant brown hyaenas is correlated with an increase in the spotted hyaena population following the erection of water boreholes (Mills and Hofer, 1998; Bothma and Walker, 1999). A negative association also exists between brown and spotted hyaenas in the Kalahari where both species occur sympatrically and, at kill sites, the spotted hyaena is the dominant species (Mills, 1990; Mills and Hofer, 1998). Agonistic interactions also occur between brown and spotted hyaenas, with the brown being attacked and killed by other carnivores, including spotted hyaenas (Kruuk, 1976; Mills, 1990). Aside from Mills' (1990) study on sympatric Kalahari hyaenas, this study is the first to investigate the feeding ecology of sympatric brown and spotted hyaenas within a heterogeneous bushveld habitat in a southern African protected area.

The identification of food remains found in faeces is the most common and practical method for analyzing the food habits of carnivores and is useful in determining a basic description of a carnivore's diet (Mills, 1990; Mills, 1996). Faecal analysis has been used in numerous past studies on the feeding habits of brown and spotted hyaenas (Kruuk, 1972; Bearder, 1977; Mills and Mills, 1978; Owens and Owens, 1978; Tilson et al., 1980; Henschel and Skinner, 1990; Sillero-Zubiri and Gottelli, 1992; Skinner et al., 1992; Maddock, 1993; Burgener and Gusset, 2003; Maude and Mills, 2005), and serves as a reasonable approximation of dietary composition, especially when other types of observations prove to be difficult or impossible (Bearder, 1977; Putman, 1984; Mills, 1996). As the faeces of both brown and spotted hyaenas are used to mark territories through regular deposition at specific or predicted sites along roads and pathways, and have a characteristic appearance being distinctively white in colour, this makes them relatively easy to spot in the field and for collecting samples (Estes, 1991; Stuart and Stuart, 1994).

This chapter investigates the hypothesis that sympatric brown and spotted hyaenas experience competition from each other through the direct or indirect exploitation of similar food resources. It is hypothesised that ascertaining the dietary compositions of each hyaena species will result in a high degree of overlap in prey categories and/or prey items consumed. It is also hypothesised that brown and spotted hyaenas will exhibit spatial or temporal avoidance of each other or behaviourally exclude the other species from available food sources at kills/carcasses. Furthermore, the behaviour observations of brown and spotted hyaenas at kills/carcasses are believed to reveal the ecological dynamics between sympatric hyaenas through the prevalence of agonistic interactions.

4.2 METHODS

4.2.1 STUDY SITES

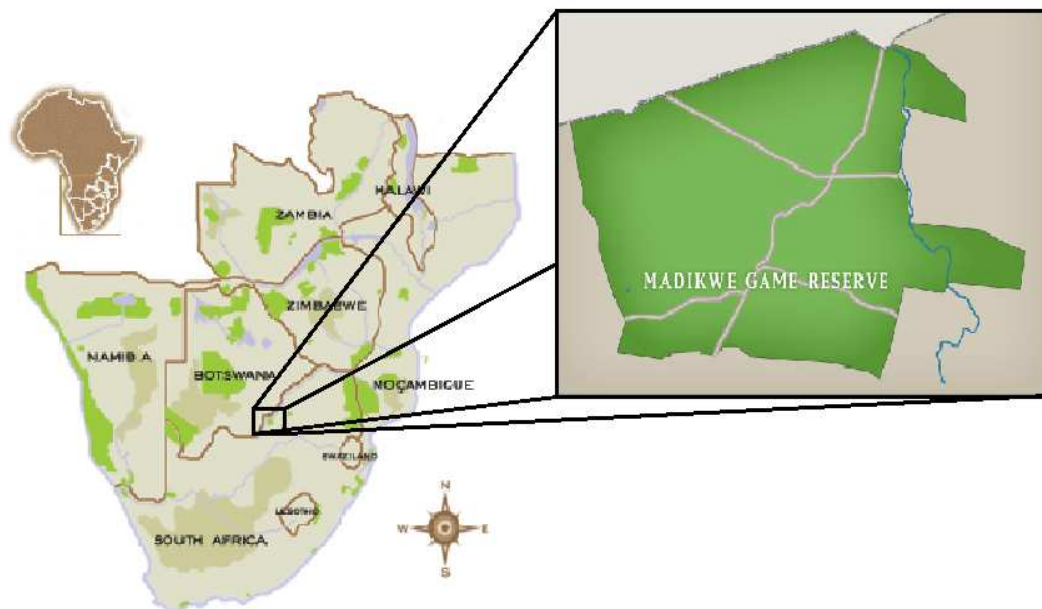


Figure 4.1. The location of the study area, the Madikwe Game Reserve in South Africa.

Field work was conducted within the bushveld region of South Africa in the Madikwe Game Reserve (MGR) between the years of 2007 and 2008, including both the wet and dry seasons. MGR is situated in the Northwest province, in the transition zone of the arid Kalahari Desert and the Lowveld (Figure 4.1), and encompasses an area of approximately 750km².

4.2.1.1 MADIKWE GAME RESERVE

South Africa's fourth largest game reserve is situated in the north of the Northwest Province in South Africa (24°38' to 24°52'S; 26°08' to 26°31'E), with the north boundary line running adjacent to the Botswana border. The reserve has a diverse topography composed of three soil types: black clay, red clay loam and rocky loam (Viljoen and Moore, 2007). MGR's vegetation is predominantly semi-arid shrubland savannah with important species being *Dichrostachys cinerea* ssp. *africana*, and *Acacia* spp. such as *Acacia mellifera*, *A. tortilis*, *A. erubescens*, *A. gerrandii* and *A. nilotica*, with areas dominated by *Combretum* spp. and *Boscia foetida* (Hudak et al., 2004). Mean annual rainfall is approximately 520mm for MGR, and is distinctly seasonal with most of the rains falling largely during the summer (November to March). In winter, the mean minimum temperature is 14°C, while the mean maximum temperature in summer is 28°C (Hudak et al., 2003). Spotted hyaenas were introduced into MGR through 1994 to 1996 and today are considered common in the reserve (D. Hofmeyr, pers. comm.). MGR supports a large potential prey base as well as a broad spectrum of large carnivores including lions (*Panthera leo*), leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*) and spotted and brown hyaenas. The perimeter of the reserve is enclosed by an electrified fence.

4.2.2 STUDY SPECIES

4.2.2.1 SPOTTED HYAENA

The spotted hyaena is Africa's second largest carnivore and the most common terrestrial predator in Africa. With a head and body length ranging from 100-180cm and a weight of 40-90kg (Kingdon, 2004), the spotted hyaena is large and powerfully built. Spotted hyaenas are opportunistic and flexible carnivores capable of inhabiting such diverse habitats including semi-deserts, savannahs and open woodlands, dense dry woodlands, and mountainous forests up to 4000m above sea level (Kruuk, 1972; Estes, 1991; Mills and Hofer, 1998).

The spotted hyaena, although once widespread throughout Africa south of the Sahara, at present exists primarily concentrated within protected areas and surrounding lands. Spotted hyaenas are highly gregarious and form territorial social clans led and dominated by females, with a social system unlike that of other social carnivores. The spotted hyaena operates on an openly competitive system (instead of co-operation), where access to resources, mating opportunities, and emigration from natal clans depends mainly on the ability of the individual to dominate other members of its clan (Estes, 1991). Clan sizes are primarily limited by available territory size and prey density and vary throughout the spotted hyaena's range (Mills and Hofer, 1998). Clans may number from as few as three individuals in the southern Kalahari (Mills, 1990) to clans exceeding eighty individuals in the resource-rich Ngorongoro Crater (Kruuk, 1972).

The diets of spotted hyaenas are diverse, and they consume more non-mammalian food sources than other carnivores (Mills and Biggs, 1993), due to its opportunistic and flexible foraging strategy whereby they scavenge and actively hunt for prey. The diet of spotted hyaenas consists largely of vertebrates, especially

ungulates, and is supplemented by invertebrates, reptiles, fruits and seeds. Their ability to extract nutrients from bones and remains of carrion enables them to utilize virtually everything except the rumen contents and horn bosses of their prey (Estes, 1991).

4.2.2.2 BROWN HYAENA

The brown hyaena is smaller than the spotted hyaena with head and body length measures between 110-125cm, with a weight ranging between 40-55kg (Kingdon, 2004). Brown hyaenas are hardy species and are capable of inhabiting in desert areas with annual rainfall of less than 100mm (Mills and Hofer, 1998). Consequently, the brown hyaena inhabits the South West Arid Zone of Africa (Smithers, 1983), and adjacent dry savannah south of the Zambezi River. They are also found along the coast, in semi-deserts, open scrubs and open woodland savannahs. They are independent of drinking water, and seem to favour rocky, mountainous areas with bush cover in the bushveld areas of South Africa. The brown hyaena is a strictly, solitary, and predominantly nocturnal forager with one of the most elaborate and advanced social system of all carnivores. They live in clans ranging in size from a solitary female and her cubs to groups containing of several females and their offspring of different ages.

While members of a clan forage alone, several members may come together at a large food source and clan members also come together to defend a common territory (Mills and Hofer, 1998). Clan territories are highly variable in size ranging from as small as 49km² within agricultural lands in the former Transvaal (now known as the Gauteng province) of South Africa, to between 235km² to 480km² in the southern Kalahari (Mills and Hofer, 1998), and are largely determined by the type of food within the territory. Over much of their range, brown hyaenas live in association

with other carnivorous mammals and often scavenge from their kills. Brown hyaenas are opportunistic foragers and are primarily scavengers of a wide range of vertebrate remains, and supplement their diets with wild fruits and vegetables, invertebrates, birds' eggs, reptiles, fish, and the occasional small animal that it kills. Hunting in the brown hyaena is unspecialized and opportunistic, directed only at small animals and largely unsuccessful (Mills, 1990).

4.2.3 DATA ACQUISITION

4.2.3.1 SAMPLE COLLECTION

Hyaena faecal samples were collected from latrines in MGR. All of the primary and many of the secondary game roads were driven as transects and roads that were likely to become impassable due to deterioration or weather conditions were avoided. Surveys were carried out throughout the wet season (November to March) and again throughout the dry season (June to August). Vehicles were driven at continuous speeds of 15-25 km/h while observers searched the area beside roads up to 3m from the edge of the road for latrines. Special attention was paid to culverts, junctions and intersections, as these often serve as boundary-marking areas.

Upon detection of a latrine, the appearance of the latrine and faeces were scrutinized in order to classify the latrine as either belonging to a spotted or brown hyaena. Latrines were classified as *Unknown* when faeces were heavily deteriorated or indistinguishable, and classified as *Mixed* when both brown and spotted faeces were found within the same latrine. A spotted hyaena latrine is usually large, sometimes covering an area of several hundred square metres with fairly dispersed droppings while a brown hyaena latrine is nearly always in a slight depression with the droppings much closer together (Stuart and Stuart, 1994). The droppings of the

spotted hyaenas are usually larger than a brown hyaena's, 150g and 50g respectively. However, a small spotted hyaena's dropping may be quite similar to a large brown hyaena's, and therefore indistinguishable. Another identifying feature that helped to differentiate which species the faeces belonged to was the visual appearance of the faeces. Faeces of the spotted hyaena are usually smoothly rounded pellets (Figure 4.2a), whereas a brown hyaena's faeces would often have squiggly or wavy lines on the surface of the faeces (Figure 4.2b). Criteria used to aid in species identification of hyaena latrines included the total size of the area utilized for the latrine, the estimated average distance between faeces within the latrine, the estimated average size of the faeces in the latrine, and the appearance of the faeces within the latrine. Latrines and faeces were identified as belonging to a particular species only when confidence in all criteria had been met. Along with a confident species identification of latrines, the GPS location, transect code, frequency count for that transect, number of faecal clusters within the latrine, age estimate range of faeces in latrine (ranked from 12 hours to over a month) and general habitat of area were all recorded. Fresh faecal samples were collected whenever possible to be used for the faecal analysis of prey remains. Faecal samples used for analysis were only collected from confidently identified or known latrines. A subset of 60 faecal samples for each of the brown and spotted hyaenas were randomly selected from the collected total of brown and spotted hyaena faeces from each of the wet and dry seasons. This gave a total of 120 faecal samples per species for analysis, as it was determined that 59 faecal samples were enough to assess a species' dietary composition (Trites and Joy, 2005).

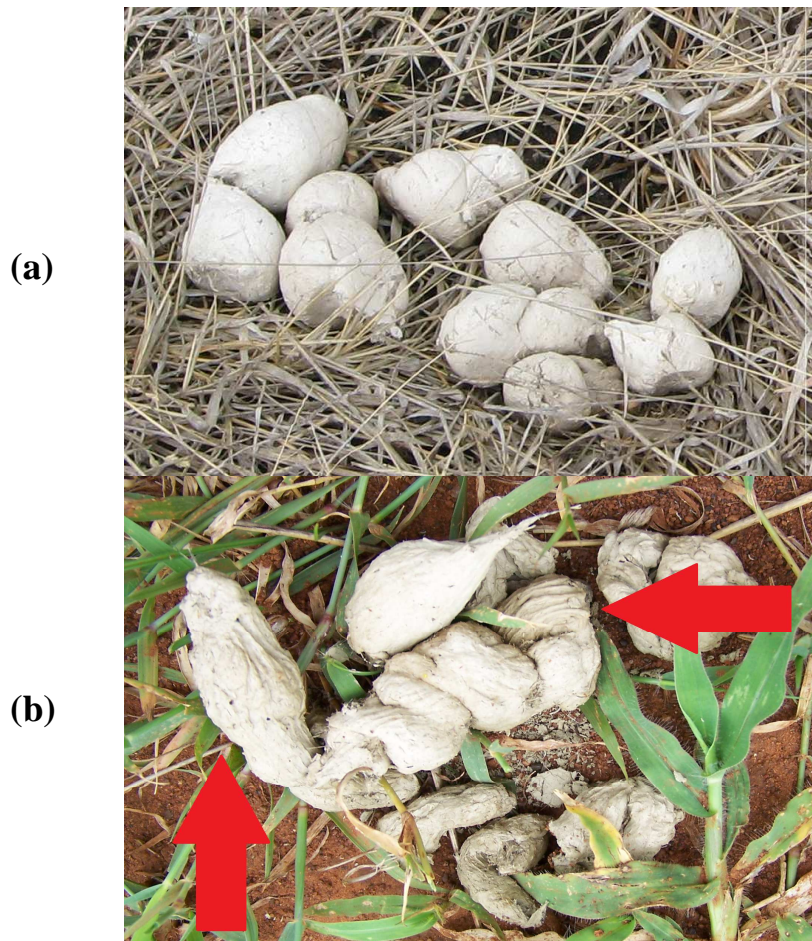


Figure 4.2. (a) An example of spotted hyaena faeces. Note the smoothly rounded pellets. (b) An example of brown hyaena faeces. Arrows indicate the wavy, squiggly lines which are often prevalent in brown hyaena faeces.

4.2.3.2 FAECAL ANALYSIS

Faeces were collected and stored in brown paper bags and labeled with the date of collection as well as the latrine code, and were allowed to air-dry. Samples were then transported to the laboratory for analysis. Faeces were soaked in boiling water for at least 24 hours and then broken up with a mortar and pestle. The faeces were continually washed with tap water over a fine mesh net until all the undigested material had been extracted. The extracted material was then stored in labeled plastic containers and allowed to air-dry for further analysis. Each sample was analyzed

macroscopically and faecal contents were separated into eleven discrete dietary categories: bone, feathers, hair, invertebrates, keratin in the form of hooves, quills, reptile, seeds, stones, vegetation, and anthropogenic materials. While stones and vegetation are not usually considered a dietary staple for hyaenas, the vegetation was present in most samples and was recorded, and stones were noted in many of the samples. Anthropogenic materials were recorded, although they are not considered as dietary items, as an indication of the anthropogenic impact in the diets of the hyaenas within MGR.

Hair was identified to species level and subsequently divided into categories of small and large mammals. Large mammals were defined as prey items over 45 kg (Sinclair et al., 2003) and, while rodent teeth found in samples were not identified to species level, they counted towards the presence of small mammals in samples. Samples with hairs were further analyzed microscopically with the use of the cross-sectioning method (Maddock, 1993; Di Silvestre et al., 2000; Maude and Mills, 2005) and subsequently identified to species level using published keys (Keogh, 1979; Keogh 1983; Buys and Keogh, 1984) and a reference collection. Cross-sections of hairs were made by placing hairs into short, transparent plastic straws which were sealed at one end (Douglas, 1989), and filled with heated paraffin wax using syringes. The tubes were then allowed to solidify and using surgical razor blades, 5 cross-sections were taken from each straw and placed onto a glass slide for microscopic analysis. Cross-sections were examined under a diaphan slide microscope (© Leitz) and identified to species level with the aid of Motic McCamera and Motic Images Plus version 2.0 (Motic®). Further investigations of the hairs were sometimes required for species identification in which case cuticular scale patterns of hairs were examined under a light microscope (Short, 1978). Where there was any doubt,

especially with attempts in identifying hairs of small carnivores, the sample was left as “unidentified”. Invertebrate remains consisted of insect exoskeletons while reptile remains consisted of unidentified reptile skin or tortoise (*Stigmochelys pardalis*) carapaces. The characteristic markings on bird feathers were used to identify to species level with the aid of species keys (Sinclair et al., 2002). Brown and spotted hyaena hairs were often present in faeces but were disregarded as they were most likely from either allo- or auto-grooming (Owens and Owens, 1978; Mills, 1983).

4.2.3.3 KILLS

The presences of kills or carcasses were often discovered by MGR personnel patrolling the study area or by field researchers following radio-collared jackals (*Canis mesomelas*). All discovered kills were reported to the field ecologist for game census purposes and were made available for this study. Hyaenas were also followed whenever encountered in MGR at night which sometimes led to kills or carcasses. As hyaenas were usually sighted at some point at all reported kills and carcasses, GPS locations and prey species as well as which predator responsible for the kill (if possible) were recorded. Hyaena species and count as well as time of sighting at kills were also recorded. A subset of these reported kills/carcasses were used for further extensive behavioural observations of hyaenas’ feeding behaviour.

4.2.3.4 BEHAVIOURAL OBSERVATIONS AT KILLS/CARCASSES

The behaviours of both spotted and brown hyaenas were assessed while carrying out direct feeding observations of hyaenas at kills/carcasses in the MGR during the 2007/2008 study period. As brown hyaenas are notoriously shy and elusive, behavioural observations mainly consisted of arriving at kills/carcasses before dark and waiting for predators to appear. Upon arriving at the kill/carcass, the vehicle

was parked approximately 15 to 30m away depending on the visibility of the area and the motor was turned off. Every effort was made to minimize observer/vehicle noise and disturbance. A spotlight with a red filter was used sparingly to check for species identification of newcomers and for behavioural observations of interactions between individuals. In the case of observations, the spotlight with the red filter was held high so that only the peripheral beam of light shone on the animals with the stronger, central glare of the light pointing upwards and away from the animals so as to minimize the amount of light shining on the hyaenas during observations. Photographs were also taken for identification purposes only after hyaenas appeared to have become accustomed to the red glow of the spotlight and to the presence of the observer. And even then, only minimal photos were taken.

Information recorded included GPS locations of kills/carcasses, what was killed (if distinguishable), who killed it (if known), hyaena species and count at kills/carcasses, time of arrival and departure of hyaena species, and behaviour for the duration hyaenas were in view of the observer. Behaviours were recorded using the focal animal sampling method in which all occurrences of behaviour were recorded for the hyena group feeding at kills/carcasses (Altmann, 1974). This allowed for the latency, duration, and frequency of behaviours to be recorded, including vigilance (alert ears directionally sensing with a cocking of the head and a searching of the periphery with the eyes and ears), aggression (tensing of the body, arching of the tail, lunging, baring of the teeth, snapping, biting, chasing, displacing, pushing, standing over, and piloerection of hairs along the spine only in brown hyaenas), and submission (lowering of the head in response to approach from conspecific, tail between the legs, ears flattened back against skull, body lowered and bent, 'carpal' crawl, retreating, running away, exposing one's flank or rolling onto one's back in

response to approach from conspecific) (Kruuk, 1972; Owens and Owens 1978; Mills, 1983; Holekamp and Smale, 1998).

4.2.3.5 AVAILABILITY OF PREY SPECIES

The numbers of herbivorous mammals were calculated from ground and aerial censuses carried out in the study area from 1995 to 2005 by MGR personnel (D. Hofmeyr, pers. comm.). Therefore recent prey counts from the years 2003 to 2005 have been included in this study to estimate the available prey base (Table 4.1). Species such as bushbuck (*Tragelaphus scriptus*), mountain reedbuck (*Redunca fulvorufula*), common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) are most likely to have been underestimated because of inaccuracies and difficulties in counting these species due to their small size, shyness, active avoidance of roads, and tendency to “freeze” in response to threats.

Table 4.1. Prey species count data for the years 2003, 2004, and 2005 as carried out by ground and aerial censuses in Madikwe Game Reserve, South Africa. (A hyphen indicates years when no data was collected for that species)

SPECIES	2003	2004	2005
Blue wildebeest (<i>Connochaetes taurinus</i>)	1610	1213	1870
Buffalo (<i>Syncerus caffer</i>)	310	314	332
Common duiker (<i>Sylvicapra grimmia</i>)	-	8	5
Eland (<i>Taurotragus oryx</i>)	194	105	75
Elephant (<i>Loxodonta africana</i>)	424	450	450+
Gemsbok (<i>Oryx gazella</i>)	246	147	191
Giraffe (<i>Giraffa camelopardalis</i>)	158	118	129
Impala (<i>Aepyceros melampus</i>)	1406	837	1084
Kudu (<i>Tragelaphus strepsiceros</i>)	526	435	429
Mountain Reedbuck (<i>Redunca fulvorufula</i>)	-	6	5
Red Hartebeest (<i>Alcelaphus buselaphus</i>)	435	190	189
Rhinoceros, Black (<i>Diceros bicornis</i>)	-	32	40
Rhinoceros, White (<i>Ceratotherium simum</i>)	-	128	134
Sable (<i>Hippotragus niger</i>)	-	3	2
Springbok (<i>Antidorcas marsupialis</i>)	-	22	34
Steenbok (<i>Raphicerus campestris</i>)	-	7	23
Tsessebe (<i>Damaliscus lunatus</i>)	-	11	13
Warthog (<i>Phacochoerus africanus</i>)	-	372	461
Waterbuck (<i>Kobus ellipsiprymnus</i>)	366	220	156
Zebra (<i>Equus burchelli</i>)	1260	787	965

4.2.4 DATA ANALYSIS

4.2.4.1 FAECAL ANALYSIS

A total of 240 samples from MGR were analyzed, 120 from each species. The subset of 60 samples was selected from 151 spotted hyaena faeces and 105 brown hyaena faeces for the wet season. For the dry season, 163 spotted hyaena faeces and 123 brown hyaena faeces were collected, from which a subset of 60 samples were also randomly selected from each species group for analysis.

The percentage occurrence and relative percentage frequency was calculated for each dietary category and prey item in the total number of faeces for each species as an indication of the frequency that each species fed on each dietary component (Loveridge and Macdonald, 2001). The relative percentage frequency is the number of times a food item is encountered as a percentage of the total occurrence of all species and indicates the importance of each dietary item to the overall diet (Loveridge and Macdonald, 2003). Student's t-test was utilized to test for significant differences between the diets of brown and spotted hyaenas between and across seasons.

The amount of niche overlap between brown and spotted hyaenas was calculated using Pianka's index (α) (Pianka, 1973) for the dietary categories, which consisted of eleven food groups, and for the prey remains, which consisted of nine categories including the subdivision of hairs into large and small mammals. Pianka's index is calculated by

$$\alpha = \frac{\sum p_i q_i}{\sqrt{\sum p_i^2 \sum q_i^2}}$$

where $\alpha = 1$ indicates complete overlap and $\alpha = 0$ indicates no overlap, and p_i is the dietary item i for predator p and q_i is the dietary component i for predator q .

Furthermore, niche breadth for each of the brown and spotted hyaena was also determined to evaluate for the extent of exploitation among dietary categories and prey items for each species. Niche breadth (B_A) equals 1 when dietary categories are exploited in equal frequencies, and results in values close to 0 when extensive exploitation of one or a few dietary categories is experienced (Levins, 1968; Krebs, 1989). Niche breadth is calculated from the standardized Levin's index equation, $B_A = (B - 1) / (n - 1)$, where B_A is standardized by the number of items (n), $B = 1 / \sum p_i^2$ and p equals the relative percentage frequency of the dietary category i (Loveridge and Macdonald, 2003).

4.2.4.2 KILLS/CARCASSES

The chi-squared statistic was used to determine whether the two hyaena species were seen alone or together more often at kills/carcasses, and to demonstrate whether kills/carcasses belonged exclusively to one hyaena species or whether they were often shared between the two species. The chi-squared was also used to determine whether both hyaena species were present at most of the kills/carcasses. Analysis of variance was utilized to determine whether spotted hyaena group size at kills/carcasses had an effect on whether or not brown hyaenas would associate together with them at kills/carcasses; and to determine whether time had a significant effect on which hyaena species would be at kills/carcasses. The t-test was used to determine whether there existed a significant difference in the times hyaena species were sighted at kills/carcasses, and regression was used to investigate for the existence of a relationship between which hyaena species was present at specific

times at kills/carcasses, as well as to determine whether there existed a relationship between spotted hyaena group size and the times hyaenas were at kills/carcasses. Binary logistic regression was used to demonstrate whether time had an effect on whether brown and spotted hyaenas would be alone or associating with each other at kills/carcasses.

4.2.4.3 BEHAVIOURAL OBSERVATIONS

The percentage occurrence and relative frequency per unit time was calculated for hyaena behaviours as an indication of the prevalence of certain types of behaviours hyaenas exhibited towards one another at kills/carcasses. The t-test was used to determine for significant differences among the behaviours exhibited by hyaena species, and to test for whether the amount of time spent at kills/carcasses or latency to arrival at kills/carcasses differed significantly between brown and spotted hyaenas. The chi-square test was used to determine whether agonistic interactions occurred significantly more often among conspecifics or between species at kills/carcasses. The binary logistic regression examined whether spotted hyaena group size had a significant affect on whether agonistic interactions occurred or not between hyaenas at kills/carcasses.

4.3 RESULTS

4.3.1 FAECAL ANALYSIS

Among dietary categories, bones, hair, and vegetation were prevalent in all faeces with more than 80% occurrence across seasons (Figure 4.3). Keratin (hooves), stones, and anthropogenic materials featured nearly equally across species and seasons, with between 25-30% occurrence of keratin and stones and between 8-13%

occurrence of anthropogenic materials in hyaena faeces (Figure 4.3). Feathers were present only in brown hyaena dry season faeces while parts of undigested porcupine (*Hystrix africaeaustralis*) quills were present in both brown and spotted hyaena faeces for only the wet season (Figure 4.3). Reptilian remains, which consisted of undigested reptilian skin and tortoise carapaces, were present in only the brown hyaena wet season faeces, but were present in both seasons for spotted hyaena (Figure 4.3). Invertebrates had a percentage occurrence of approximately 20% for the dry season, which increased dramatically to between 60-80% for the wet season, whereas

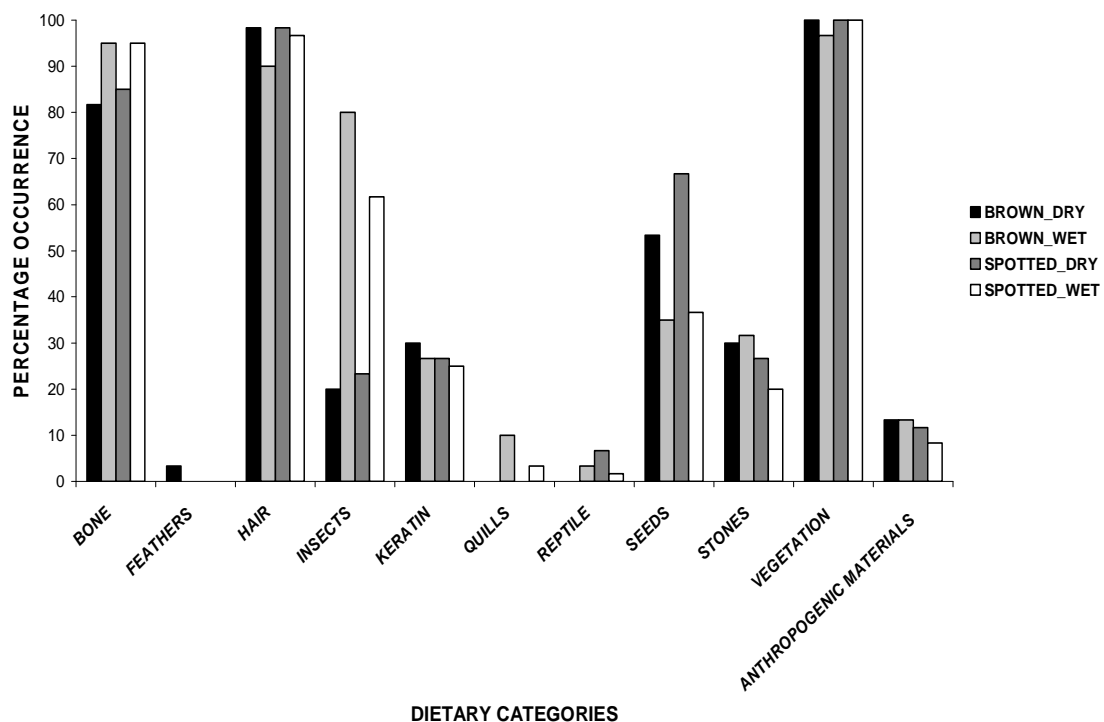


Figure 4.3. Percentage occurrence of distinct dietary categories as determined by faecal analysis of brown and spotted hyaena faeces collected from two seasons (dry and wet) in the Madikwe Game Reserve.

seeds had a lower percentage occurrence in the wet season (approximately 35%), which increased to between 50-60% in the dry season (Figure 4.3). In addition, the dietary composition of both brown and spotted hyaenas reveals that large mammals were consumed significantly more often than small mammals in both brown and spotted hyaenas (brown: Figure 4.4; $\chi^2 = 22.458$; $df = 1$; $p < 0.001$; spotted: Figure 4.5; $\chi^2 = 60.976$; $df = 1$; $p < 0.001$). Large mammals had a 90-100% occurrence in the faeces of both hyaena species as compared to 27-40% occurrence of smaller mammals (Figure 4.6). Impala (*Aepyceros melampus*) and blue wildebeest featured prominently in the diets of both species across seasons with a percentage occurrence of 35-37% and 19-20% respectively (Table 4.2). For smaller prey, mountain reedbuck had a 5% occurrence in the diet of brown hyaena with common duiker a nearly 6% occurrence in the spotted hyaena diet (Table 4.2).

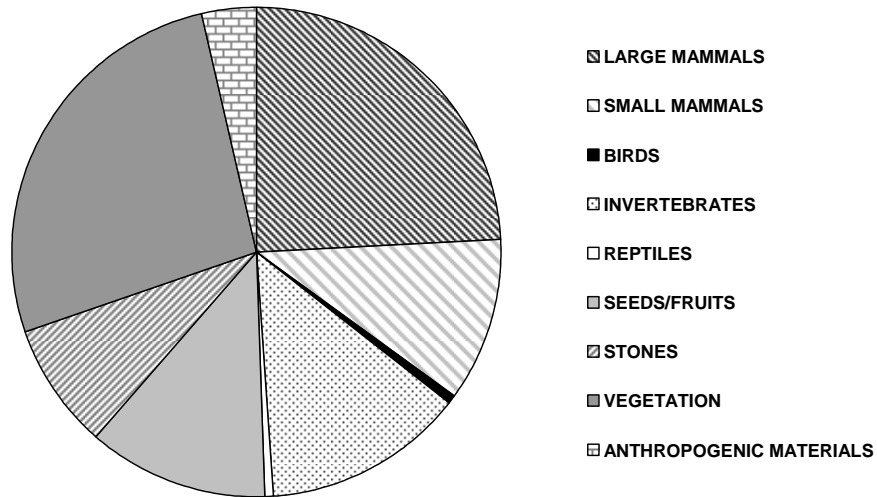


Figure 4.4. Composition of brown hyaena diets as determined from faeces of brown hyaenas from the Madikwe Game Reserve.

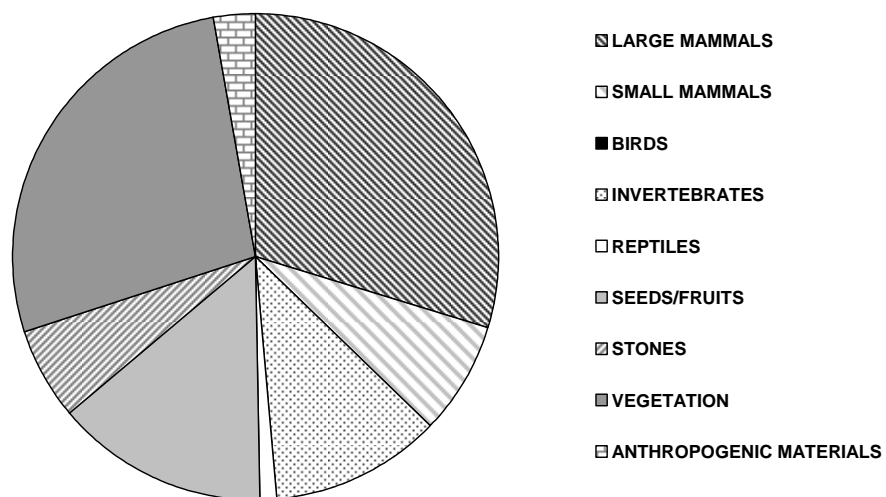


Figure 4.5. Composition of spotted hyaena diets as determined from faeces of spotted hyaenas from the Madikwe Game Reserve.

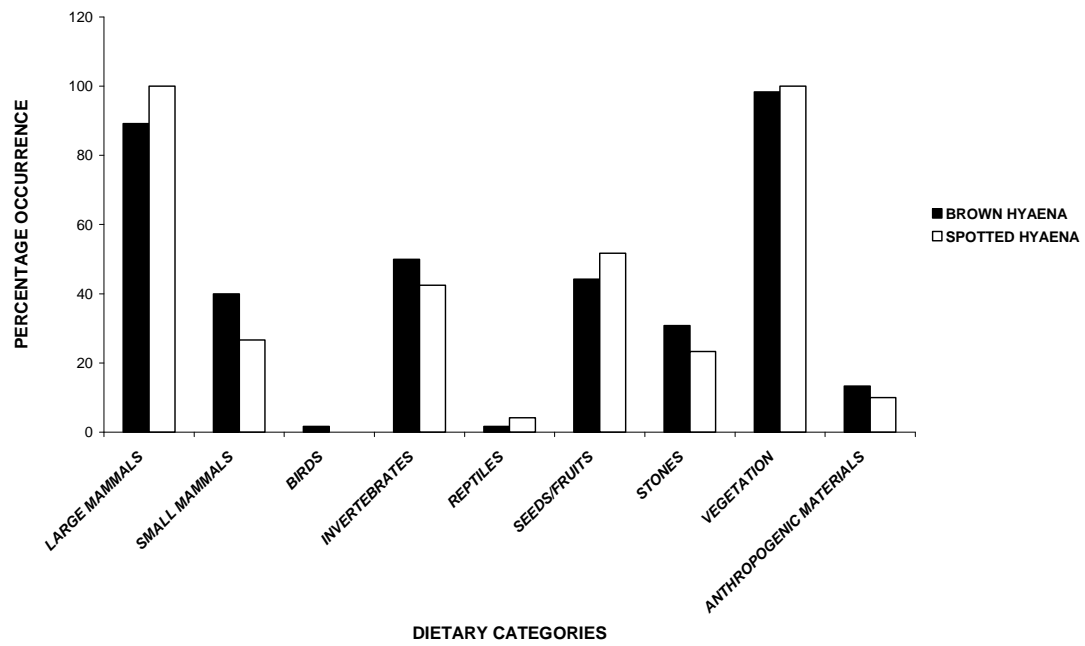


Figure 4.6. Overall percentage occurrence of dietary categories as determined by faecal analysis of brown and spotted hyaena faeces collected from the Madikwe Game Reserve.

Table 4.2. Percentage occurrence of prey remains in brown and spotted hyaena faecal samples collected from MGR, South Africa in 2007–2008.

PREY	HYAENAS	BROWN HYAENA	SPOTTED HYAENA	BROWN HYAENA		SPOTTED HYAENA	
				DRY	WET	DRY	WET
Baboon (<i>Papio ursinus</i>)	0.42	0.83	0	1.67	0	0	0
Blue wildebeest (<i>Connochaetes taurinus</i>)	19.58	20	19.17	18.33	21.67	23.33	15
Buffalo (<i>Syncerus caffer</i>)	2.92	2.5	3.33	1.67	3.33	5	1.67
Bushbuck (<i>Tragelaphus scriptus</i>)	2.08	0.83	3.33	1.67	0	1.67	5
Bushpig (<i>Potamochoerus larvatus</i>)	2.5	1.67	3.33	0	3.33	1.67	5
Common duiker (<i>Sylvicapra grimmia</i>)	4.17	2.5	5.83	3.33	1.67	8.33	3.33
Eland (<i>Taurotragus oryx</i>)	0.42	0	0.83	0	0	1.67	0
Elephant (<i>Loxodonta africana</i>)	0.42	0	0.83	0	0	0	1.67
Gemsbok (<i>Oryx gazella</i>)	0.42	0	0.83	0	0	1.67	0
Giraffe (<i>Giraffa camelopardalis</i>)	4.17	1.67	6.67	0	3.33	5	8.33
Impala (<i>Aepyceros melampus</i>)	36.25	37.5	35	53.33	21.67	45	25
Kudu (<i>Tragelaphus strepsiceros</i>)	5.42	3.33	7.5	5	1.67	10	5
Mongoose, Banded (<i>Mungos mungo</i>)	1.25	1.67	0.83	0	3.33	1.67	0
Mongoose, Dwarf (<i>Helogale parvula</i>)	0.83	1.67	0	0	3.33	0	0
Mongoose, Selous' (<i>Paracynictis selousi</i>)	1.25	0.83	1.67	1.67	0	1.67	1.67
Mongoose, Slender (<i>Herpestes sanguinea</i>)	0.83	1.67	0	1.67	1.67	0	0
Mountain reedbuck (<i>Redunca fulvorifula</i>)	4.58	5	4.17	1.67	8.33	6.67	1.67
Hartebeest (<i>Alcelaphus buselaphus</i>)	3.33	2.5	4.17	0	5	3.33	5
Sable (<i>Hippotragus niger</i>)	2.08	0.83	3.33	0	1.67	0	6.67
Scrubhare (<i>Lepus saxatilis</i>)	2.92	4.17	2.5	0	8.33	3.33	0
Springbok (<i>Antidorcas marsupialis</i>)	2.5	0.83	4.17	1.67	0	3.33	5
Springhare (<i>Pedetes capensis</i>)	1.67	2.5	0.83	0	5	1.67	0
Steenbok (<i>Raphicerus campestris</i>)	4.17	4.17	4.17	8.33	0	3.33	5
Ground squirrel (<i>Geosciurus inauris</i>)	2.92	3.33	2.5	1.67	5	0	5
Tsessebe (<i>Damaliscus lunatus</i>)	5.42	5	5.83	5	5	8.33	3.33
Warthog (<i>Phacochoerus africanus</i>)	2.08	2.5	1.67	3.33	1.67	0	3.33
Waterbuck (<i>Kobus ellipsiprymnus</i>)	4.58	5.83	3.33	8.33	3.33	1.67	5
Zebra (<i>Equus quagga</i>)	5.42	4.17	6.67	5	3.33	1.67	11.67
Insufficient/no hair	6.25	7.5	5	1.67	13.33	1.67	8.33
Unidentified	6.25	6.67	5.83	5	8.33	1.67	10
n	240	120	120	60	60	60	60

Brown and spotted hyaenas consumed a high proportion of bones, hair, and vegetation with 19-23% relative frequency of occurrence in their diet. Invertebrates and seeds also made up a large proportion of their diet with 14-17% relative frequency of occurrence for invertebrates in the wet season and 12-15% relative frequency of occurrence for seeds in the dry season (Figure 4.7). Brown and spotted hyaenas also consumed a higher proportion of large mammals in their diets than smaller mammals with 24-29% relative frequency and 7-10% relative frequency of occurrence respectively (Figure 4.8). Impala and blue wildebeest were the most abundant prey choice in the diets of hyaenas (25-28% and 13-15% relative frequency of occurrence), with waterbuck (*Kobus ellipsiprymnus*), tsessebe (*Damaliscus lunatus*), zebra, and kudu (*Tragelaphus strepsiceros*) following for brown hyaenas (4.43%, 3.8%, 3.17%, and 2.53% relative frequency of occurrence, Table 4.3). Kudu, giraffe, zebra, and tsessebe were the next most abundant prey choice for spotted hyaenas (5.26%, 4.68%, 4.68%, and 4.09% relative frequency of occurrence, Table 4.3).

Out of the fifty-seven comparisons, six significant seasonal differences were found with four significant seasonal differences for brown hyaenas among the categories of bones, invertebrates, quills, and seeds and two significant seasonal differences for spotted hyaenas among the categories of invertebrates and seeds (Table 4.4). Significant differences were exhibited in two dietary categories between hyaena species for invertebrates in the wet season and reptiles in the dry season. The similarity between the diets of the brown and spotted hyaena is clearly evident in the near complete niche overlap as exhibited by the Pianka's index ($\alpha = 0.997$ for food groups and $\alpha = 0.987$ for prey items, Figure 4.9). Niche breadth (B_A) was also found to be quite similar between the two hyaena species with the brown hyaena exhibiting

a wider niche breadth ($B_A = 0.534$ food groups, $B_A = 0.562$ prey items, Figure 4.10), and the spotted hyaena a slightly narrower niche breadth ($B_A = 0.497$ food groups, $B_A = 0.482$, Figure 4.10).

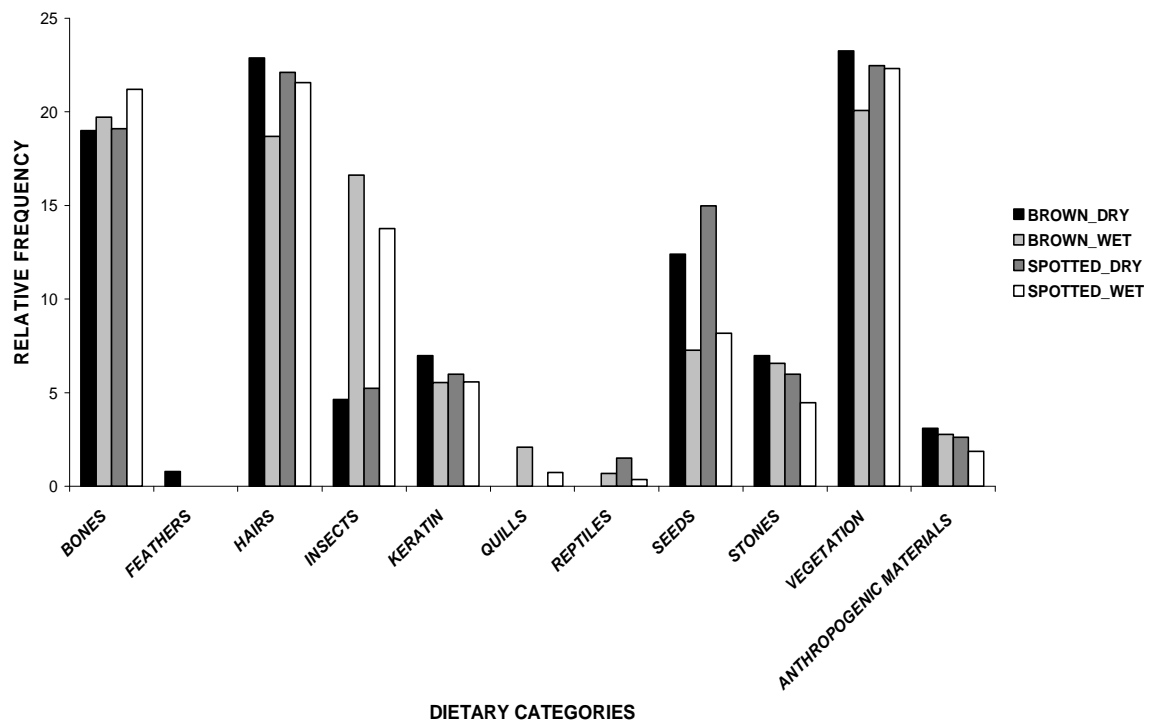


Figure 4.7. Relative frequency of occurrence of distinct dietary categories as determined by faecal analysis of brown and spotted hyaena faeces collected from two seasons (dry and wet) in the Madikwe Game Reserve.

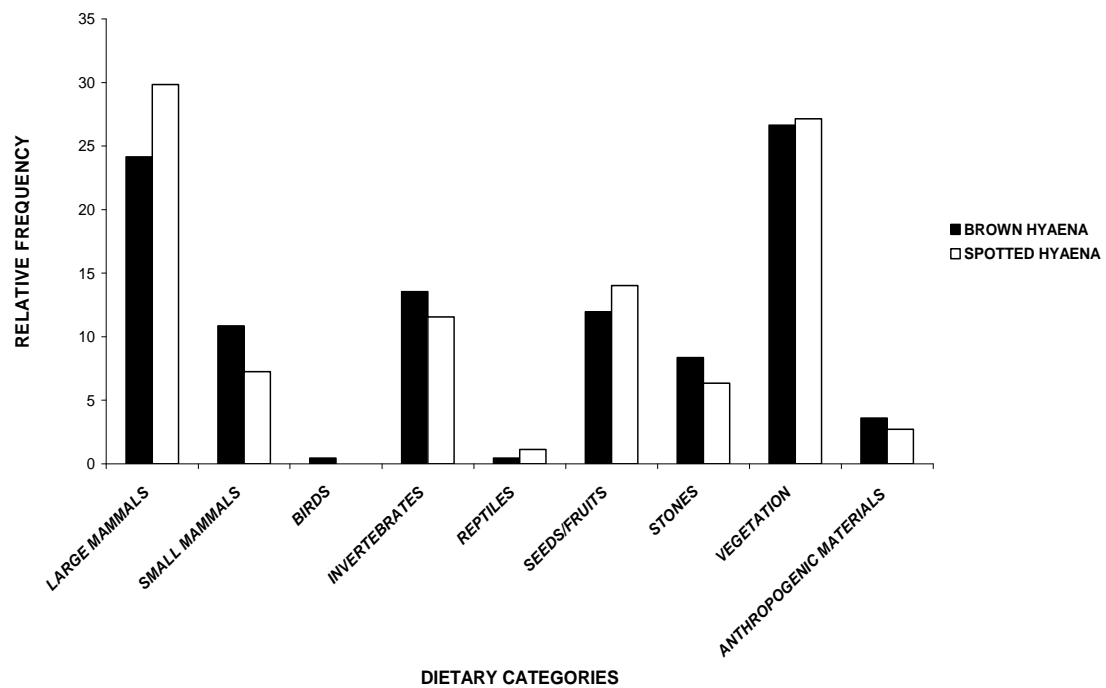


Figure 4.8. Overall relative frequency of occurrence of dietary categories as determined by faecal analysis of brown and spotted hyaena faeces collected from the Madikwe Game Reserve.

Table 4.3. Relative frequency of prey remains in brown and spotted hyaena faecal samples collected from the MGR, South Africa in 2007-2008.

PREY	HYAENAS	BROWN HYAENA	SPOTTED HYAENA	BROWN HYAENA		SPOTTED HYAENA	
				DRY	WET	DRY	WET
Baboon (<i>Papio ursinus</i>)	0.3	0.63	0	1.28	0	0	0
Blue wildebeest (<i>Connochaetes taurinus</i>)	14.29	15.19	13.45	14.1	16.25	16.28	10.59
Buffalo (<i>Syncerus caffer</i>)	2.13	1.9	2.34	1.28	2.5	3.49	1.18
Bushbuck (<i>Tragelaphus scriptus</i>)	1.52	0.63	2.34	1.28	0	1.16	3.53
Bushpig (<i>Potamochoerus larvatus</i>)	1.82	1.27	2.34	0	2.5	1.16	3.53
Common duiker (<i>Sylvicapra grimmia</i>)	3.04	1.9	4.09	2.56	1.25	5.81	2.35
Eland (<i>Taurotragus oryx</i>)	0.3	0	0.59	0	0	1.16	0
Elephant (<i>Loxodonta africana</i>)	0.3	0	0.59	0	0	0	1.18
Gemsbok (<i>Oryx gazella</i>)	0.3	0	0.59	0	0	1.16	0
Giraffe (<i>Giraffa camelopardalis</i>)	3.04	1.27	4.68	0	2.5	3.49	5.88
Impala (<i>Aepyceros melampus</i>)	26.44	28.48	24.56	41.03	16.25	31.4	17.65
Kudu (<i>Tragelaphus strepsiceros</i>)	3.95	2.53	5.26	3.85	1.25	6.98	3.53
Mongoose, Banded (<i>Mungos mungo</i>)	0.91	1.27	0.59	0	2.5	1.16	0
Mongoose, Dwarf (<i>Helogale parvula</i>)	0.61	1.27	0	0	2.5	0	0
Mongoose, Selous' (<i>Paracynictis selousi</i>)	0.91	0.63	1.17	1.28	0	1.16	1.18
Mongoose, Slender (<i>Herpestes sanguinea</i>)	0.61	1.27	0	1.28	1.25	0	0
Mountain reedbuck (<i>Redunca fulvorifula</i>)	3.34	3.8	2.92	1.28	6.25	4.65	1.18
Hartebeest (<i>Alcelaphus buselaphus</i>)	2.43	1.9	2.92	0	3.75	2.33	3.53
Sable (<i>Hippotragus niger</i>)	1.52	0.63	2.34	0	1.25	0	4.71
Scrubhare (<i>Lepus saxatilis</i>)	2.13	3.17	1.17	0	6.25	2.33	0
Springbok (<i>Antidorcas marsupialis</i>)	1.82	0.63	2.92	1.28	0	2.33	3.53
Springhare (<i>Pedetes capensis</i>)	1.22	1.9	0.59	0	3.75	1.16	0
Steenbok (<i>Raphicerus campestris</i>)	3.04	3.17	2.92	6.41	0	2.33	3.53
Ground squirrel (<i>Geosciurus inauris</i>)	2.13	2.53	1.75	1.28	3.75	0	3.53
Tsessebe (<i>Damaliscus lunatus</i>)	3.95	3.8	4.09	3.85	3.75	5.81	2.35
Warthog (<i>Phacochoerus africanus</i>)	1.52	1.9	1.17	2.56	1.25	0	2.35
Waterbuck (<i>Kobus ellipsiprymnus</i>)	3.34	4.43	2.34	6.41	2.5	1.16	3.53
Zebra (<i>Equus quagga</i>)	3.95	3.17	4.68	3.85	2.5	1.16	8.24
Insufficient/no hair	4.56	5.7	3.51	1.28	10	1.16	5.88
Unidentified	4.56	5.06	4.09	3.85	6.25	1.16	7.06
n	240	120	120	60	60	60	60

Table 4.4. Summary of results of t-tests comparing variations between species; seasonal variations within a species; and seasonal variations between species. A single asterisk denotes significance at < 0.05 , and a double asterisk denotes significance at < 0.005

CATEGORY	SPECIES GROUP OR SEASON	VARIABLE(S) COMPARED	T-VALUE	df	P-VALUE	SIGNIFICANCE
Bone	Brown hyaena	Spotted hyaena	-0.41379	238	0.67940	*
	Brown hyaena	Dry season vs Wet season	-2.30615	118	0.02285	
	Spotted hyaena	Dry season vs Wet season	-1.83615	118	0.06885	
	Dry season	Brown hyaena vs Spotted hyaena	-0.48629	118	0.62767	
	Wet season	Brown hyaena vs Spotted hyaena	0.00000	118	1.00000	
Feathers	Brown hyaena	Spotted hyaena	1.42019	238	0.15686	
	Brown hyaena	Dry season vs Wet season	1.42635	118	0.15641	
	Dry season	Brown hyaena vs Spotted hyaena	1.42635	118	0.15641	
Hair	Brown hyaena	Spotted hyaena	-1.29122	238	0.19789	
	Brown hyaena	Dry season vs Wet season	1.96244	118	0.05207	
	Spotted hyaena	Dry season vs Wet season	0.58064	118	0.56259	
	Dry season	Brown hyaena vs Spotted hyaena	0.00000	118	1.00000	
	Wet season	Brown hyaena vs Spotted hyaena	-1.46474	118	0.14565	
Insects	Brown hyaena	Spotted hyaena	1.16361	238	0.24575	
	Brown hyaena	Dry season vs Wet season	-8.14709	118	0.00000	
	Spotted hyaena	Dry season vs Wet season	-4.56913	118	0.00001	
	Dry season	Brown hyaena vs Spotted hyaena	-0.43982	118	0.66087	
	Wet season	Brown hyaena vs Spotted hyaena	2.23670	118	0.02719	
Keratin	Brown hyaena	Spotted hyaena	0.43412	238	0.66460	
	Brown hyaena	Dry season vs Wet season	0.40205	118	0.68838	
	Spotted hyaena	Dry season vs Wet season	0.20684	118	0.83649	
	Dry season	Brown hyaena vs Spotted hyaena	0.40205	118	0.68838	
	Wet season	Brown hyaena vs Spotted hyaena	0.20684	118	0.83649	
Quills	Brown hyaena	Spotted hyaena	1.43860	238	0.15158	*
	Brown hyaena	Dry season vs Wet season	-2.56038	118	0.01172	
	Spotted hyaena	Dry season vs Wet season	-1.42635	118	0.15641	
	Wet season	Brown hyaena vs Spotted hyaena	1.46474	118	0.14565	

CATEGORY	SPECIES GROUP OR SEASON	VARIABLE(S) COMPARED	T-VALUE	df	P-VALUE	SIGNIFICANCE
Reptiles	Brown hyaena	Spotted hyaena	-0.71697	238	0.47410	*
	Brown hyaena	Dry season vs Wet season	-1.76218	118	0.08063	
	Spotted hyaena	Dry season vs Wet season	1.36979	118	0.17335	
	Dry season	Brown hyaena vs Spotted hyaena	-2.05287	118	0.04230	
	Wet season	Brown hyaena vs Spotted hyaena	1.01296	118	0.31315	
Seeds	Brown hyaena	Spotted hyaena	-1.16133	238	0.24667	* **
	Brown hyaena	Dry season vs Wet season	2.04027	118	0.04356	
	Spotted hyaena	Dry season vs Wet season	3.41827	118	0.00087	
	Dry season	Brown hyaena vs Spotted hyaena	-1.49212	118	0.13834	
	Wet season	Brown hyaena vs Spotted hyaena	-0.18887	118	0.85057	
Stones	Brown hyaena	Spotted hyaena	1.30649	238	0.19265	
	Brown hyaena	Dry season vs Wet season	-0.19605	118	0.84491	
	Spotted hyaena	Dry season vs Wet season	0.85878	118	0.39220	
	Dry season	Brown hyaena vs Spotted hyaena	0.40205	118	0.68838	
	Wet season	Brown hyaena vs Spotted hyaena	1.46068	118	0.14676	
Vegetation	Brown hyaena	Spotted hyaena	-1.42019	238	0.15686	
	Brown hyaena	Dry season vs Wet season	1.42635	118	0.15641	
	Wet season	Brown hyaena vs Spotted hyaena	-1.42635	118	0.15641	
Anthropogenic materials	Brown hyaena	Spotted hyaena	0.80202	238	0.42334	
	Brown hyaena	Dry season vs Wet season	0.00000	118	1.00000	
	Spotted hyaena	Dry season vs Wet season	0.60442	118	0.54672	
	Dry season	Brown hyaena vs Spotted hyaena	0.27380	118	0.78471	
	Wet season	Brown hyaena vs Spotted hyaena	0.87661	118	0.38248	
Prey remains	Brown hyaena	Spotted hyaena	-0.21409	58	0.83123	
	Brown hyaena	Dry season vs Wet season	-0.05261	58	0.95823	
	Spotted hyaena	Dry season vs Wet season	0.02945	58	0.97658	
	Dry season	Brown hyaena vs Spotted hyaena	-0.18197	58	0.85625	
	Wet season	Brown hyaena vs Spotted hyaena	-0.19519	58	0.84593	

SPECIES	VARIABLE	VARIABLE(S) COMPARED	χ^2	df	P-VALUE	SIGNIFICANCE
Brown hyaena	Large mammals	Small mammals	22.458	1	0.000	**
Spotted hyaena	Large mammals	Small mammals	60.976	1	0.000	**

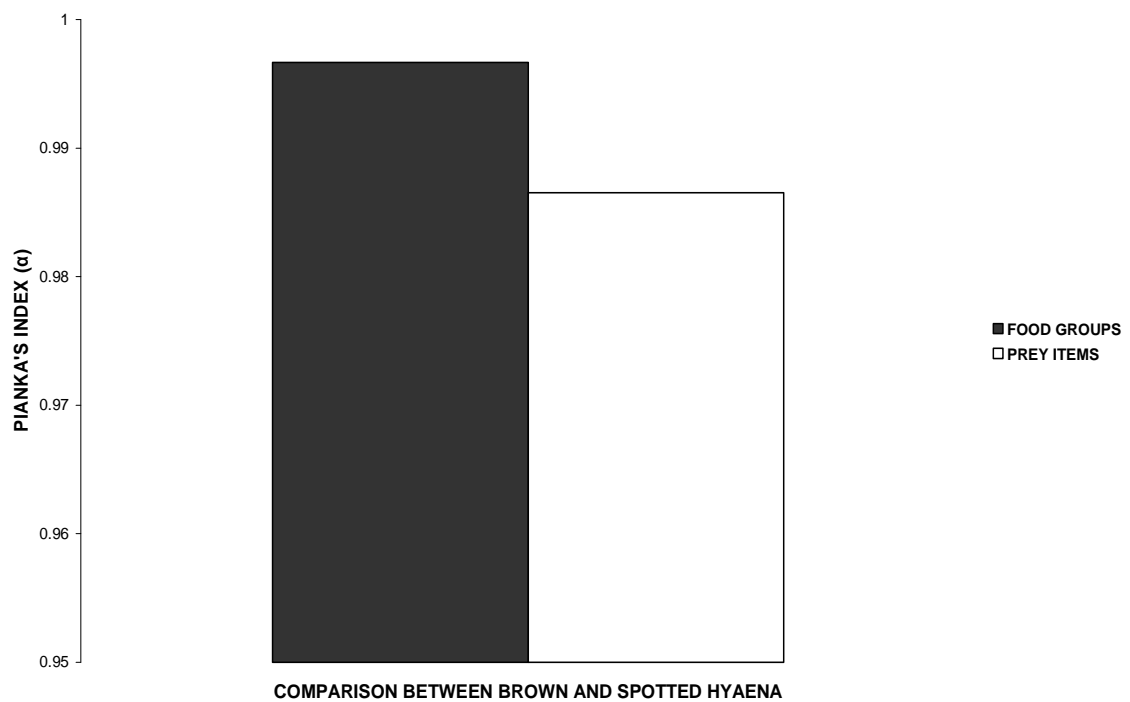


Figure 4.9. Comparison of food groups and prey items between brown and spotted hyaenas as found in their diets, using Pianka's index (α). Faecal analyses were performed on hyaena faeces from the Madikwe Game Reserve.

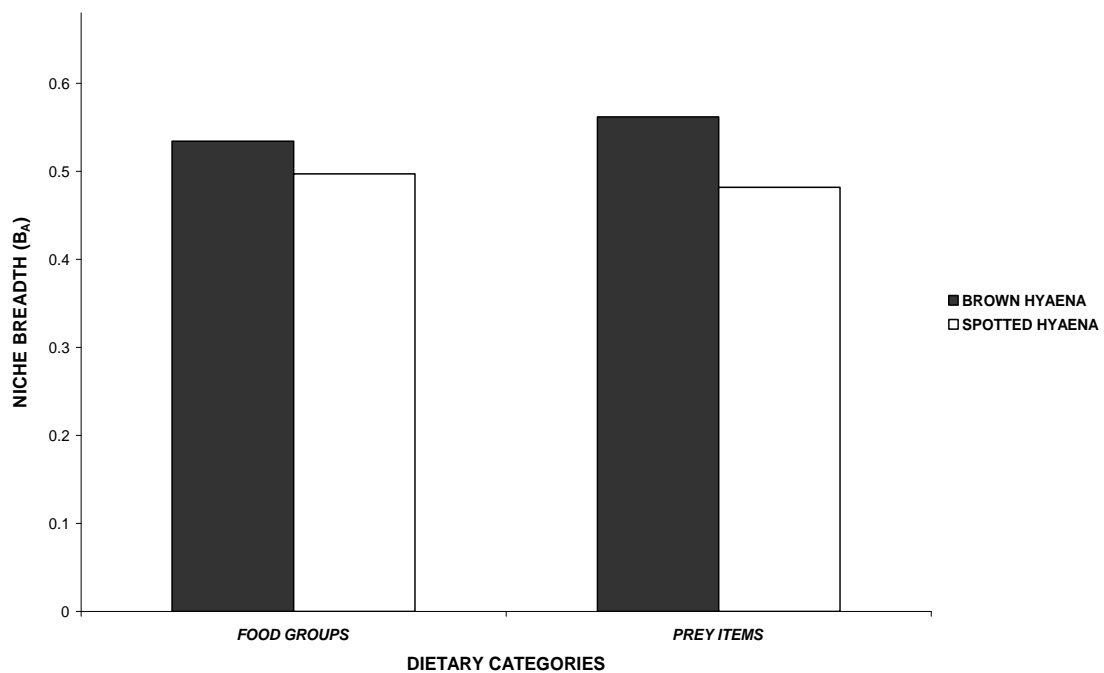


Figure 4.10. Niche breadth (B_A) in the dietary categories of food groups and prey items between brown and spotted hyaena diets. Faecal analyses were performed on hyaena faeces from the Madikwe Game Reserve.

4.3.2 KILLS / CARCASSES

A total of 31 cases were reported in which hyaenas were present at kills/carcasses. Out of these 31 cases, brown and spotted hyaenas were seen significantly more often either alone or with conspecifics at kills/carcasses than associating with the other hyaena species ($\chi^2 = 5.452$; $df = 1$; $p = 0.019$). Kills/carcasses did not belong exclusively to one hyaena species but were shared significantly more often than not between both species ($\chi^2 = 54.871$; $df = 3$; $p < 0.001$). Both hyaena species were also significantly present at most of the kills/carcasses ($\chi^2 = 27.832$; $df = 2$; $p < 0.001$). Spotted hyaena group size had a significant effect on whether brown hyaenas would associate together with them or

not, in that brown hyaenas were more likely to not associate with spotted hyaenas of group sizes larger than three ($F = 5.093$; $df = 5$; $p = 0.003$; Figure 4.11). Time was

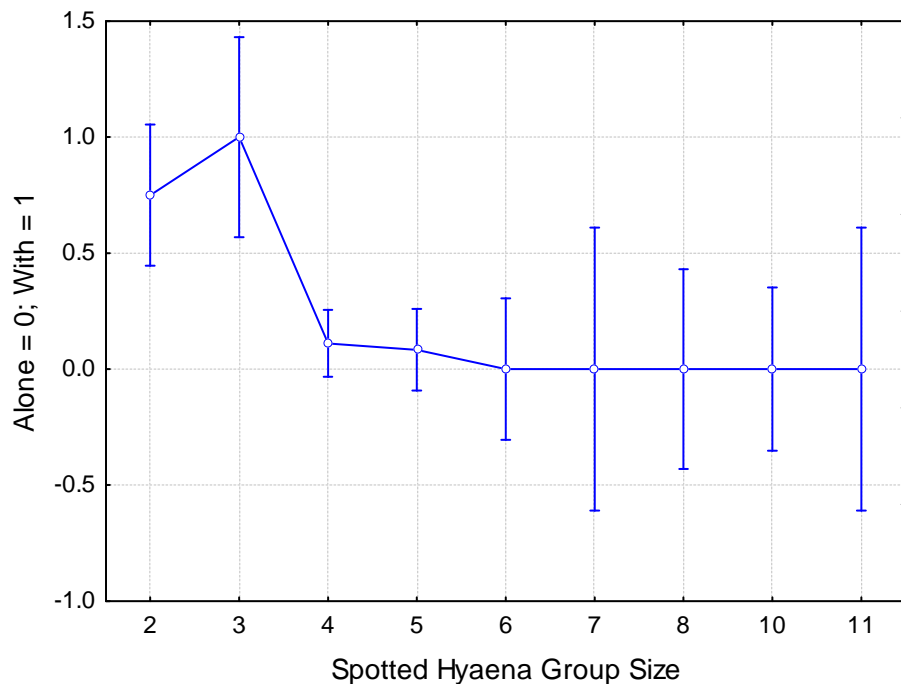


Figure 4.11. Brown hyaena association with spotted hyaenas of increasing group sizes with 95% confidence intervals. 0 = No association, 1 = association with spotted hyaenas.

found to have had no significant effect on which hyaena species would be present at kills ($F = 0.909$; $df = 49$; $p = 0.619$). There were no significant differences between the two species in the times hyaenas were sighted at kills ($t = -0.632$; $df = 59$; $p = 0.529$), and there were no significant relationships found between time and which species were present at kills/carcasses, or between time and the group size of hyaenas at kills/carcasses ($r^2 = 0.019$; $df = 26$; $p = 0.488$; and $r^2 = 0.033$; $df = 59$; $p = 0.162$). Time also did not have a significant effect on whether hyaena species would associate

with each other or only with conspecifics at kills/carcasses (Wald Stat = 0.379; $df = 1$; $p = 0.538$).

4.3.3 BEHAVIOURAL OBSERVATIONS

A total of 146.5 hours of behavioural observations were logged over 21 nights at kills/carcasses, resulting in a total of 55 hours of hyaena activity recorded over 14 nights. Aggressive behaviours occurred in both brown and spotted hyaenas with 33% and 38% occurrence, accounting for 11% and 17% relative frequency per unit time, respectively (Figure 4.12). However, vigilant behaviours were much more prevalent with 67% occurrence (26% relative frequency per unit time) for brown hyaenas, and 100% occurrence (64% relative frequency per unit time) for spotted hyaenas (Figure 4.12). Pasting behaviour at kills/carcasses were non-existent in spotted hyaenas but were prominent in brown hyaenas with 89% occurrence which accounted for 29% relative frequency per unit time (Figure 4.12).

Aggressive behaviours did not differ significantly between brown and spotted hyaenas ($t = -0.906$; $df = 94$; $p = 0.367$), whereas spotted hyaenas exhibited significantly more vigilant behaviours than brown hyaenas ($t = -3.821$; $df = 94$; $p < 0.001$), and brown hyaenas exhibited significantly more pasting behaviour than spotted hyaenas ($t = 4.810$; $df = 94$; $p < 0.001$). The amount of time spent at kill/carcasses, or duration, did not differ significantly between hyaena species ($t = -1.452$; $df = 94$; $p = 0.149$), nor did latency to arrival at kills/carcasses differ between the two species ($t = -0.391$; $df = 94$; $p = 0.697$). The chi-square demonstrated that spotted hyaenas exhibited agonistic behaviours at kills/carcasses significantly more towards their conspecifics than they did towards brown hyaenas ($\chi^2 = 6.800$; $df = 1$; $p = 0.009$), and agonistic behaviours occurred in brown hyaenas at kills/carcasses significantly more than not ($\chi^2 = 4.00$; $df = 1$; $p = 0.045$) although they were nearly

always observed to be feeding at kills/carcasses alone. Spotted hyaena group size was found to have had no significant effect on whether aggression or agonistic behaviours occurred between hyaenas at kills/carcasses (Wald Stat = 1.461; $df = 1$; $p = 0.227$).

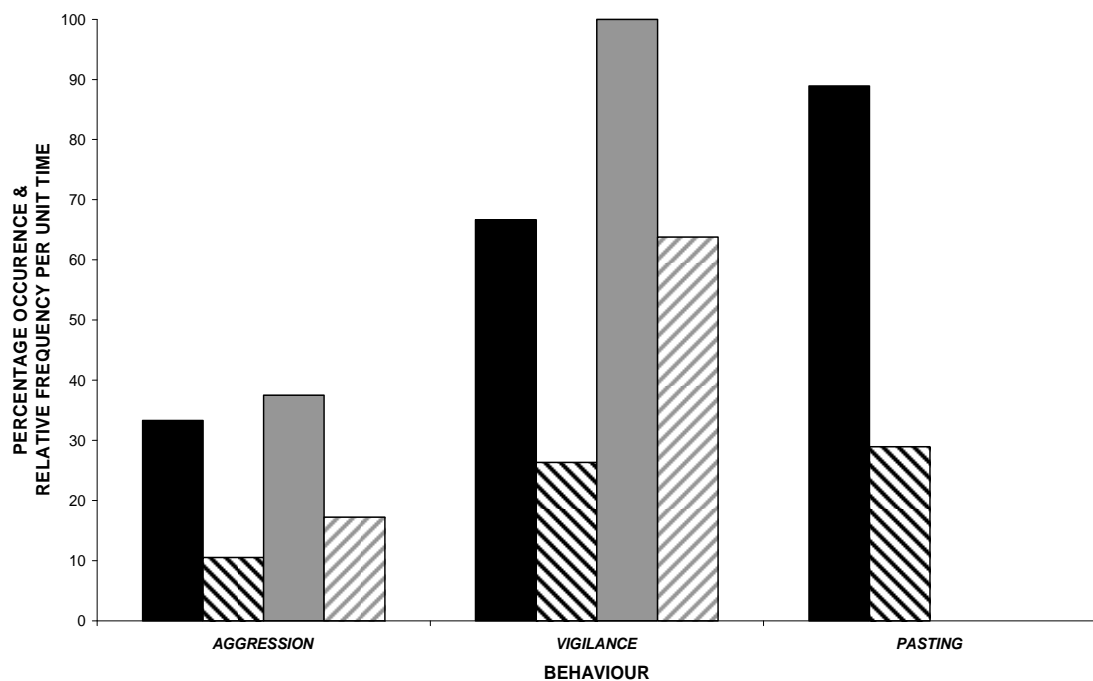


Figure 4.12. Percentage occurrence and relative frequency of behavioural observations of brown and spotted hyaenas observed at kills/carcasses in the Madikwe Game Reserve. Solid colours = percentage occurrence of behaviours observed per unit time. Hatched bars = Relative frequency of behaviours observed per unit time. Black = brown hyaenas, grey = spotted hyaenas.

4.4 DISCUSSION

4.4.1 *HYAENA DIETS*

This study shows that the brown and spotted hyaenas of MGR are both generalist and opportunistic carnivores, utilizing whatever food sources are readily available, including human refuse pits. The presence and high frequency with which large game were found in hyaena faeces are probably the result of predation by other carnivores such as lions, leopards, and wild dogs as hyaenas were often observed feeding on the kills of other predators. Although brown hyaenas in the Kalahari would hunt small animals, usually with a low success rate, this would only occur when carrion was not widely available (Owens and Owens, 1978; Mills, 1990). Similarly, Mills and Mills (1978) found that 95.8% of all vertebrate food items consumed by brown hyaenas during direct observations in the southern Kalahari were scavenged. While Kruuk (1972) found spotted hyaenas to be formidable predators in East Africa where they formed clans of upwards of eighty individuals, and Cooper (1990) found the spotted hyaenas of the Savuti in Botswana to be opportunistic hunters; spotted hyaenas were found to forage solitarily more often than together in the Lowveld region of South Africa (Bearder, 1977; Smuts, 1979), and this was also observed in this present study with the spotted hyaenas in MGR.

Mills (1982) demonstrated in his study in the southern Kalahari of the brown hyaena that the most common ungulate prey species were the most common prey items consumed in the diets of brown hyaenas. Skinner et al. (1992) found the occurrence of large antelopes in the diets of spotted hyaenas in southern African game reserves to be directly related to the availability of prey. In Senegal, Di Silvestre et al. (2000) demonstrated the relationship between the compositions of the diet of the

spotted hyaena to the composition of ungulate populations in that the prey within the study area were exploited in proportion to their availability. This follows from the optimal foraging theory that the diets of generalist feeders alternates between food sources depending on what food sources are seasonally available (Taylor, 1984), and generalist feeders have also been shown to increase the diversity of its diets in response to a decrease in food availability (Perry and Pianka, 1997). Gedir and Hudson (2000) demonstrated that a generalist feeder would be expected to adapt its foraging behaviour to changes in seasonal fluctuations in order to satisfy its dietary and nutritional requirements.

This holds true for the brown and spotted hyaenas of MGR in that the composition of their diets varied between seasons in accordance to the seasonal availability of food sources. Both hyaena species primarily fed on mammals, as indicated by the high occurrence of mammalian remains in their faeces, as well as on a range of other vertebrates. Both species exhibited plasticity in their dietary choices and clearly demonstrated a lack of preference for any one particular prey species, instead utilizing whatever carrion was available either through the kill from other predators, or death from other causes (i.e. intraspecific competition). The results from the faecal analysis of both hyaena species demonstrated a tendency for feeding on abundant prey items (blue wildebeest and impala), which may be indicative of a functional response to the availability of prey species as found for spotted hyaenas from other studies (Kruuk, 1972; Honer et al., 2002; Hayward, 2006). Bone remains occurred in the faeces of both species at high proportions, which corresponds with the findings of other studies that much of the hyaenas' food consists of scraps from carrion and small pieces of bone (Skinner and Smithers, 1990). The high prevalence of vegetation found in hyaena faeces also conforms to the results from other studies in

which the conventional assumption is that the grass, leaves and seeds in hyaena faeces originates from the rumen contents of ungulate prey or has been accidentally ingested while feeding on carrion, rather than through direct consumption (Tilson et al., 1980; Henschel and Skinner, 1990).

During the dry season, brown hyaenas used other food sources such as birds, while spotted hyaenas showed a significant increase in reptilian remains (i.e. tortoise carapaces) over brown hyaenas. There was also a significant increase of seeds in the diets of both species for the dry season. The presence of invertebrates in diets significantly increased during the wet season for both hyaena species, as well as the presence of porcupine remains. While the diets of brown hyaenas featured significantly more invertebrates than spotted hyaenas in the wet season, the diets of both hyaena species overall were very similar across all seasons and this is evident in the high dietary overlap as demonstrated by the Pianka's index calculation across all dietary categories.

The brown and spotted hyaenas of MGR apparently adhere to the well-documented pattern of scavenging carrion from other predators' kills as well as opportunistically consuming whatever is readily and easily available (Bearder, 1977; Mills and Mills, 1978; Owens and Owens, 1978; Mills and Biggs, 1993). MGR's hyaenas consumed a significantly higher proportion of large mammals than small mammals in their diets, although this difference was insignificant between the two species. This significant prevalence of large mammals over small mammals in their diet, together with a frequent occurrence of other food items such as invertebrates and seeds/fruits coincides with other studies that have looked at the diets of brown and spotted hyaenas through the use of faecal analysis.

4.4.2 GEOGRAPHICAL VARIATION IN DIETS

Small mammals were consumed less by the brown hyaenas in the Pilanesberg National Park (PNP), South Africa, whereas large mammals (notably impala and blue wildebeest) were found to be the most important dietary component, with the hair of large mammals in more than 50% of the brown hyaena faeces (I. van der Merwe et al., pers. comm.). Preliminary investigations into the faeces of spotted hyaenas collected recently from the KNP reveal impala to be a significant contributor to their diet (Ryan et al., unpubl. thesis). Henschel (1986) found impala and buffalo to be major contributors to the diets of KNP's spotted hyaenas, and Smuts (1979) found that spotted hyaenas in the KNP fed mainly on impala, zebra, and wildebeest, as well as on a variety of insects, reptiles, vegetation and various bits of refuse found along tourist areas.

Invertebrates figured prominently in the diets of brown and spotted hyaenas as well with a 45% frequency of occurrence for PNP's brown hyaenas, and an average of 40% occurrence for the KNP's spotted hyaena clans. Although hyaenas in MGR were observed to purposely consume invertebrates, such as licking termites off the ground, the high prevalence of invertebrates in hyaena diets is most likely a result from incidental ingestion while feeding on carrion (Mills, 1977). The presence of seeds/fruits were also observed in PNP's brown hyaenas and KNP's spotted hyaenas, although to a lesser extent than what was seen in the hyaenas of the Kalahari in where fruits play a central role in water provisioning (Mills and Mills, 1978; Owens and Owens, 1978; Mills, 1990).

As found in other studies, brown hyaenas are seen to consume large mammals and small mammals on a nearly equivalent basis except for when in arid areas or during lean times when large game have migrated, when they supplement their diet

with other food items such as invertebrates, birds, and reptiles (Skinner, 1976; Mills and Mills, 1978; Owens and Owens, 1978; Maddock, 1993; Burgener and Gusset, 2003; Maude and Mills, 2005). In contrast, the spotted hyaena's diet is more specialized towards large mammals than small mammals, and although they supplement their diet with other food items, they do so less than brown hyaenas (Kruuk, 1972; Bearder, 1977; Tilson et al., 1980; Sillero-Zubiri and Gottelli, 1992; Skinner et al., 1992; Di Silvestre et al., 2000).

Artiodactyls, being the most abundant animals in MGR, figured prominently in the diets of brown hyaenas in this study. Similarly in other studies in South Africa, artiodactyls were the most important mammalian food source for brown hyaenas with common duiker the most frequent prey item in faeces (Burgener and Gusset, 2003). However, in the central Karoo where large predators are absent, medium-sized ungulates predominated in the diet of brown hyaenas with mountain reedbuck and common duiker appearing frequently in faeces (Maddock, 1993). In the Makgadikgadi National Park, zebras were the most important prey item for brown hyaenas (Maude and Mills, 2005), whereas the most abundant large mammal in the Southern Kalahari, the gemsbok (*Oryx gazella*), was the most important prey item for brown hyaenas (Mills and Mills, 1978). Yet, in the central Kalahari where giraffes also occur, they figured prominently together with gemsbok in the diet of brown hyaenas (Owens and Owens, 1978).

Artiodactyls, namely impala and wildebeest, also figured prominently in the diets of spotted hyaenas in this study. Impala and wildebeest, as well as giraffes, were also the most important mammalian food source for spotted hyaenas in the Timbavati Game Reserve bordering the KNP in South Africa (Bearder, 1977), while buffalo, hartebeest (*Alcelaphus buselaphus*), and warthog (*Phacochoerus africanus*) figured

prominently in the faeces of spotted hyaenas from the Niokolo Koba National Park in Senegal (Di Silvestre et al., 2000). Additionally, wildebeest and zebra were the most important prey item for the spotted hyaenas of East Africa (Kruuk, 1972), whereas bushbuck, suni (*Neotragus moschatus*), and buffalo were the most important food items for spotted hyaenas from the Aberdare National Park in Kenya, and were also the most common prey species in the study area (Sillero-Zubiri and Gottelli, 1992). Furthermore, in the Namib Desert and in the Kalahari Gemsbok National Park of southern Africa, the gemsbok was the most important prey item for the spotted hyaenas (Tilson et al., 1980; Henschel and Tilson, 1988; Mills, 1990).

4.4.3 COMPETITION BETWEEN HYAENAS

The diets of the brown and spotted hyaenas in MGR exhibit a high degree of overlap, and both hyaena species show a tendency for feeding on abundant prey items (blue wildebeest and impala), with no specific preference for a particular prey item. This may be indicative of a functional response by both the brown and spotted hyaenas to the available prey base (Honer et al., 2002; Hayward, 2006). Although an overlap in resource use among species does not always necessarily necessitate competition between species (Slobodchikof and Schulz, 1980), an examination of the feeding behaviour exhibited by the brown and spotted hyaenas around kills/carcasses in MGR suggests that the hyaenas at MGR compete directly for the same resources and seem to relieve this competition through temporal and spatial avoidance of each other.

The brown and spotted hyaenas at MGR significantly share most of the kills and are seen alone at kills significantly more often than together, even though they are sometimes present at kills together. As both hyaena species were often present at most kills, kills were not found to exclusively belong to a particular species. When

observed at kills/carcasses together, hyaena species are tolerant of one another, or feign ignorance towards each other and rarely display aggression towards the other species. Aggression was seen to occur in agonistic interactions among conspecifics within spotted hyaena clans feeding at kills/carcasses, and it may be for this reason that brown hyaenas will more often than not associate with spotted hyaena clans of more than three individuals. While there were no temporal differences between species at kills/carcasses, hyaenas at kills clearly depicted behavioural avoidance of one another either spatially or temporally by actively walking away when sighting one another or waiting at a distance for the other species to leave before embarking onto a kill/carcass. On one occasion of observing a kill/carcass, a single brown and spotted hyaena individual were seen to alternate feeding bouts on a carcass for two hours lasting approximately two to three minutes each before one individual would tear off a piece of the carcass and move away several metres to feed on it while the other hyaena individual would come in for its turn at the carcass.

As latency to arrive on a kill/carcass and duration at a kill/carcass did not differ between hyaena species, hyaenas were seen to exhibit very similar behaviours with respect to kills/carcasses. On several occasions hyaenas showed a “first come, first serve” type of behaviour in that the first hyaena individual on the scene would have first rights to the carcass. Brown hyaenas and solitary spotted hyaenas will often grab pieces of the carcass and run, and would feed from the carcass only after it had hoarded or cached a food supply for itself. Spotted hyaenas in groups of two or more remained at the carcass and feed from it and would rarely carry off pieces of the carcass. Spotted hyaenas foraging in groups were more likely to “guard” the carcass by remaining within close proximity of it although no longer feeding. As this often happened, brown hyaenas in the periphery would wait patiently, even lying down in

the grass for hours for the spotted hyaenas to disperse, after which it would arrive at the carcass for a quick feed and to run off with a piece of it. Spotted hyaenas in groups not only ward off intrusion from brown hyaenas but also from jackals, and were also more likely to exhibit mobbing behaviour towards lions.

An extensive analysis of observations in hyaena behaviour at kills/carcasses further revealed slight and distinct differences between species' behaviour. Pasting, the act of depositing secretions from the anal glands onto grass stalks, was inherent in all observations of brown hyaenas at kills/carcasses whereas spotted hyaenas never pasted. Aggression was seen to occur more often within conspecifics than between species, since the hyaena species avoided each other as much as possible. Spotted hyaenas in groups would consistently have some form of agonistic interactions occurring, as is presumably inherent to a highly social carnivore with a dominant hierarchy. Brown hyaenas were very rarely observed feeding together with conspecifics although there was one occasion of five brown hyaenas feeding together at one carcass, in which all individuals were very placid and tolerant of one another. As brown hyaenas usually forage alone, their aggressive behaviours at kills/carcasses (i.e. piloerection, arching of tail, baring of teeth) was directed mainly to unknown threats.

Spotted hyaenas were more wary than brown hyaenas around kills/carcasses, and exhibited a high degree of vigilant behaviours. Spotted hyaenas' main competition were lions, as lions were often seen chasing spotted hyaenas away from kills/carcasses and spotted hyaenas were behaviourally more cautious around lions at kills. Kruuk (1972) found that spotted hyaenas lose up to 5% of their kills in the Serengeti, or up to 20% of their kills in the Ngorongoro Crater mostly to lions, and are often killed by lions in agonistic encounters with them. Furthermore, the dietary

niche breadth of the spotted hyaena was found to be very similar to that of the lion (Hayward, 2006), and in the KNP, spotted hyaenas scavenged a substantial amount of food from lions (Mills and Biggs, 1993). In addition, spotted hyaenas in Etosha National Park, Namibia, suffer from high mortality because of lions (Trinkel and Kastberger, 2005). However in MGR, brown hyaenas were much more bolder and seemingly much more tolerated by lions at kills/carcasses than spotted hyaenas were, although occasions of attacks by lions have occurred to brown hyaenas, resulting in one known death (R. Harrison-White, pers. comm.).

4.4.4 LIMITATIONS OF FAECAL ANALYSIS

Although faecal analysis can be used for inter- and intraspecific comparisons of diets and is a helpful tool in providing a basic description of a carnivore's diet, it is subject to some limitations and should be supplemented with data from other sources. Kruuk (1972) in his study of the spotted hyaena in East Africa was able to establish a close correlation between faecal analysis and direct observations in correctly estimating the diet of spotted hyaenas, in light of discrepancies such as the overrepresentation of Thomson's gazelle (*Gazella rufifrons*) and an underrepresentation during observations of species consumed. In the KNP, Henschel and Skinner (1990) also concluded that discrepancies existed between the diets of spotted hyaenas determined by faecal analysis and the diet estimated by direct observation in that large, scavenged mammals were often overestimated while medium-sized ungulates were often underestimated.

There are further limitations with the use of faecal analysis due to the difficulties associated with identifying the hair of species, which is often difficult and time-consuming. In addition, the relative biomass of each food item cannot be determined and can only be scored on a presence or absence basis. As well, smaller

mammals such as rodents, shrews, and lagomorphs are hairier than other species and may be overrepresented in the samples. It is also nearly impossible to differentiate between the hairs of adults and juveniles, as well as to determine whether prey was scavenged or killed (Kruuk, 1972; Mills, 1996).

4.4.5 PRESENCE OF ANTHROPOGENIC MATERIALS

While the overall amounts of anthropogenic materials found in the faeces of MGR's hyaenas were small, the presence of such materials in itself is problematic in that it creates a source for potential future conflicts through the provision of a reliable and abundant food source which would likely attract carnivores, including hyaenas (Beckmann and Berger, 2003; Hidalgo-Mihart et al., 2004; Kolowski and Holekamp, 2007). Pienaar (1969) and Smuts (1979) often found anthropogenic refuse in the stomach contents of spotted hyaenas that scavenged around human settlements in the KNP. As a result of the hyaena's scavenging and opportunistic nature, anthropogenic materials are ingested by brown and spotted hyaenas as they scavenge from refuse pits which were a nearly daily recurrence around the many lodges' refuse pits throughout MGR. The need to scavenge from refuse pits may also be an imposed modification of the hyaena's natural foraging behaviour due to the restrictions imposed by the limited total available area within fenced reserves on home range sizes (van Dyk and Slotow, 2003; Lehmann et al., 2008; Hayward et al., 2009).

Recurring human-wildlife conflicts results from the utilization of anthropogenic refuses by opportunistic carnivores, and this has drastic effects on the behavioural and ecological morphology of carnivores (Gilchrist and Otali, 2002; Otali and Gilchrist, 2004). Hidalgo-Mihart et al. (2004) demonstrated how anthropogenic food sources have facilitated a reduction in the home range sizes of the coyote, and the availability of human refuse has been shown to affect the spatial use patterns of

spotted hyaenas (Kolowski and Holekamp, 2007). Anthropogenic influences has been documented in grizzly bears (*Ursus arctos*), maned wolves (*Chrysocyon brachyurus*), coyotes, dingoes (*Canis familiaris dingo*) and has shown to result in behavioural and ecological modifications including increased body mass, reductions in home range sizes, increased population densities relative to baseline levels, and depopulation from wild areas (Craighead and Craighead, 1971; Aragona and Setz, 2001; Fedriani et al., 2001; Thompson et al., 2003; Beckmann and Berger, 2003).

Evidence of ingestion of anthropogenic items was common in brown hyaena faeces collected from within PNP, but not in faeces from outside the park (I. van der Merwe et al., unpubl. thesis, pers. comm.). Furthermore, anthropogenic materials were prevalent in spotted hyaena faeces from the KNP with the majority of faeces from a single clan representing the highest proportion of anthropogenic materials ever recorded for a spotted hyaena clan living within a protected reserve (Ryan et al., unpubl. thesis). There is an emerging global pattern of human refuse consumption by opportunistic carnivores within natural areas as these areas are more commonly frequented by tourists; and as the wildlife tourism industry continues to increase, interactions between humans and wildlife will occur with greater frequency as well, increasing the potential for human-wildlife conflict (Craighead and Craighead, 1971; Aragona and Setz, 2001; Thompson et al., 2003).

4.4.6 IMPLICATIONS OF RESEARCH FOR MANAGEMENT

As the faecal analysis of the hyaenas in MGR revealed a close dietary overlap, and the behaviour of the hyaenas at kills/carcasses appears to demonstrate temporal and spatial avoidance of one another, it is likely that the brown and spotted hyaenas experience competition with one another for food resources. However, several of these food items are carrion and it is unlikely that the brown hyaena has actively

hunted large game (Mills, 1977; Owens and Owens, 1978). While the spotted hyaena is capable of hunting large game in East Africa (Kruuk, 1972), and are opportunistic hunters within the Savuti region in the Chobe National Park in Botswana (Cooper, 1990), this has rarely been seen in the KNP in South Africa (Bearder, 1977; Mills and Biggs, 1993), and was never observed in this study. Therefore, the rationale for the continued persistence of the brown hyaenas in MGR in light of their heightened competition with the spotted hyaenas may be attributed to the large prevalence of lions (upwards of 70 individuals) in the park, which is presumably the regulating factor of spotted hyaenas through direct and indirect competition. As the lions pose a more competitive threat to spotted hyaenas, this may provide a benefit for the sustainability and viability of the brown hyaenas and this should be taken into consideration when management tactics include culling or removal of large predators from the park.

As the relationship between lions and spotted hyaenas is a sensitive one (Mills, 1990), with lion populations recovering rapidly with the spotted hyaena population continuing to flounder seven years later (Henschel, 1986; Mills and Biggs, 1993), caution would be necessary in determining how to best manage such populations of large predators. Further studies would be crucial in looking at the dynamics between these predators by determining the effect on population demographical changes of the brown hyaena with increases and decreases of the lion population in the park. This would be especially valuable with assisting in wildlife management decisions as culling and/or removing lions from MGR may not only warrant more game viewing for tourists, but may also decimate a small population of brown hyaenas that have so far managed to co-exist with the spotted hyaenas by surviving off of the abundance of food resources from lions' kills.

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- Chapter 5 -

5.1 SYNTHESIS

Much of the information available on hyaenas is from studies conducted in areas where only spotted hyaenas or brown hyaenas are found. Even in the Kalahari, where Mills (1990) conducted his well cited studies of the hyaenas, the range use of the brown and spotted hyaeans rarely overlapped and both species exploited different niches. As a result, our current understanding of the factors contributing to the co-existence of the spotted and brown hyaenas in the Madikwe Game Reserve (MGR) is limited. The aim of this study was to increase our knowledge and understanding of hyaena ecology in the context of the competition hypothesis, and whether the sympatric co-existence of the hyaenas in MGR results in competition or co-existence through resource partitioning. In order to achieve this, data were collected and analyzed on: (i) the population numbers of spotted and brown hyaenas in the MGR (Chapter 2); (ii) the responses of spotted and brown hyaenas to audio-playback recordings (Chapter 2); (iii) the spatial patterns and range sizes and area utilizations of the hyaenas in MGR (Chapter 3); (iv) the diets of spotted and brown hyaenas in the MGR (Chapter 4); and (v) the foraging behaviour of the spotted and brown hyaenas in MGR (Chapter 4). This study has increased our knowledge and understanding of the interaction between spotted and brown hyaenas in an enclosed area, and the competition experienced by sympatric hyaena species for the same resources.

5.2 KEY FINDINGS

5.2.1 CHAPTER 2

(1) The responses of hyaenas to the audio call-in surveys were influenced by the presence of lions and other predators.

- Hyaenas responded to the call-in surveys significantly more often when there were no predators and no lions responding to the surveys.

(2) The responses of hyaneas to the audio call-in surveys were influenced by the number of surveys, indicating habituation.

- Hyaenas exhibited a decreasing trend in responding to the call-in surveys over time.
- The number of hyaneas also decreased in response to the surveys over time.

(3) Population estimates were obtained for spotted and brown hyaenas in the MGR, using Bowden's estimator in NOREMARK.

- The spotted hyaena population was estimated at 27 with a 95% confidence interval of 25-30.
- The brown hyaena population was estimated at 11 with a 95% confidence interval of 11-13.

5.2.2 CHAPTER 3

(1) Spotted hyaena latrines were more abundant than brown hyaena latrines in the MGR.

- There were significantly more spotted hyaena latrines than brown hyaena latrines overall, and spotted hyaena latrines had larger cluster sizes than brown hyaena latrines.

(2) There were seasonal and habitat influences on the placement of hyaena latrines in the reserve.

- During the wet season, more hyaena latrines were deposited in the core of the reserve.
- During the wet season, spotted hyaena latrines were placed at higher elevations than brown hyaena latrines.
- During the dry season, brown hyaena latrines were placed at higher elevations than their latrines in the wet season.
- Overall, more hyaena latrines were deposited in the core more often than in the periphery of the reserve.
- Habitat vegetation was the most important effect on hyaena species' latrine placement.

(3) Hyaena range and distribution in the MGR were determined by the placement of latrines.

- In the wet season, spotted hyaena range was estimated at 422.8km^2 and brown hyaena range was estimated at 343.9km^2 .
- In the dry season, spotted hyaena range was estimated at 427.5km^2 and brown hyaena range was estimated at 466.4km^2 .
- The total range which consisted of exclusively spotted hyaena latrines was estimated at 74.5km^2 , while the total range consisting of exclusively brown hyaena latrines was estimated at 69.7km^2 .
- The total range that consisted of both spotted hyaena and brown hyaena latrines was estimated at 348.6km^2 .

(4) Home range size of a collared brown hyaena was determined with the k-NNCH localized convex hull method (LoCoH).

- The home range size of a collared brown hyaena in MGR was estimated at 22.4km^2 .

(5) Hyaena sightings in the MGR were influenced by each other, the size of the group and the time of day.

- Both hyaena species were seen more often either alone or with conspecifics rather than with each other.
- An increase in the group size of spotted hyaenas had an adverse effect on whether brown hyaenas were seen with them.
- Both hyaena species were seen significantly more often during the night than in the day.

(6) Hyaena range and distribution in the MGR were determined by the sighting records.

- Spotted hyaena range was estimated at 470.4km^2 , and brown hyaena range was estimated at 510.4km^2 .
- The estimated total range where only spotted hyaenas were sighted was 51.5km^2 , and where only brown hyaenas were sighted was 91.7km^2 .
- The estimated total range where both hyaena species were sighted was 421.8km^2 .

(7) The detection of hyaenas by the camera-traps were influenced by the time of day and locations of the traps.

- Hyaenas were detected by the camera-traps significantly more often at night.
- Hyaenas were detected by the camera-traps significantly more often in the wet season when camera-traps were placed at latrine sites.

(8) Hyaena range and distribution in the MGR were determined by a combination of latrine surveys, radio-telemetry, sighting records, and camera-trapping.

- The total average area utilized by only spotted hyaenas in MGR was 68.8km^2 .
- The total average area utilized by only brown hyaenas in MGR was 92.3km^2 .

- The total average area utilized by both spotted and brown hyaenas in MGR was 343.0km².

5.2.3 CHAPTER 4

(1) The diets of the spotted and brown hyaenas in MGR showed no discriminating differences and exhibited large degrees of overlap in both food groups and prey remains.

- Both hyaena species consumed bones, hair, vegetation, keratin (hooves), stones, anthropogenic materials, porcupine quills, reptiles, and tortoise carapaces.
- Feathers were found in the diets of brown hyaenas only.
- The presence of invertebrates increased significantly in the diets of both species for the wet season.
- The presence of seeds increased significantly in the diets of both species for the dry season.
- Both hyaena species consumed a higher proportion of large mammals than small mammals in their diets.
- Impala and blue wildebeest were the most important prey items in hyaena diets.
- The diets of the spotted and brown hyaenas in MGR demonstrated a near complete overlap in both food groups and prey items.
- Brown hyaenas exploit a slightly wider niche of resources in their diets than spotted hyaenas.

(2) The kills/carcasses in the MGR were shared and utilized by both hyaena species.

- Both hyaena species were seen more often at kills/carcasses either alone or with conspecifics rather than with each other.
- The kills/carcasses in MGR were utilized by both hyaena species significantly more often than by only one hyaena species.
- Brown hyaenas were more likely to not associate at kills/carcasses with spotted hyaenas of group sizes larger than three.

(3) The hyaenas in MGR exhibited similar behavioural repertoires at kills/carcasses.

- Aggressive behaviours were prevalent in both hyaena species at kills/carcasses.
- Spotted hyaenas exhibited aggressive behaviours towards their conspecifics more often than towards brown hyaenas.
- Vigilant behaviours featured prominently in the behavioural repertoires of both hyaena species at kills/carcasses.
- Pasting behaviours in the vicinity of kills/carcasses were exhibited by the brown hyaenas only.

5.3 IMPLICATIONS OF RESEARCH FOR MANAGEMENT

5.3.1 *POPULATION ESTIMATES*

As carnivores mitigate trophic processes and play a role in the regulation of ecosystems, knowledge of and understanding the distribution and abundance of carnivores within a given area is a valuable research asset as it allows for informed and appropriate management decisions. Carnivores are also extremely difficult to study due to their cryptic, behaviourally elusive, and nocturnal natures. Many carnivores have huge home ranges which also makes it likely to overestimate the population of carnivore species. Consequently, advances in the methodological techniques for studying carnivores can prove useful tools in estimating carnivore population densities.

The mark-resighting survey allows for reduced costs and reduced disturbances to the animals of study which makes it an advantageous alternative over the traditional mark-recapture experiments (McClintock and White, 2009). The photographic records used for a mark-resighting survey provides an invaluable resource base with which identified individuals can be compared and contrasted against many re-sights for the remainder of the animal's life, and as the photographic record aims to identify all individuals of a population or as many as possible, this decreases the likelihood for population overestimation. Camera-trapping provides an excellent method from which to obtain a photographic record, or at least of re-sights which will aid in determining population estimates (Karanth et al., 2004; Soisalo and Cavalcanti, 2006). Tourists who frequent the parks or reserves can also be enticed to submit their photographs of the species of study which provides for a relatively cheap and vast resource base, considering the large volume of tourists who frequent many of Africa's parks and reserves every year. A photographic contest complete with prizes

could be held as an added incentive to encourage tourists to submit their photographs. Other methodologies including radio telemetry, latrine surveys, spotlighting transects, or acoustic stimulation may also be utilized in combination with the photographic record in order to supplement and give more information on the population (Honer et al., 2005; Maude and Mills, 2005; Gese, 2001; Heydon et al., 2000; Mills et al., 2001).

5.3.2 SPATIAL ECOLOGY

This study is the first of its kind to provide insight into how temporal and spatial avoidance of the other species may be allowing the two hyaena species to continue to co-exist within this reserve. Further research into this type of behaviour may divulge how such behaviour choices are made by not only the hyaenas, but by other co-existing species. Knowledge into this type of behavioural plasticity may prove crucial for the conservation of coexisting species and the promotion of biodiversity, especially in the light of ongoing habitat destruction and fragmentation resulting in decreasing available areas for conservation. Remaining habitats are often subjected to increasing land-use competition, coupled together with insufficient funding for conservation efforts, the need to conserve a maximum number of species diversity is further constrained by the available minimum areas (Gurd et al., 2001; Restani and Marzluff, 2002). Therefore, area considerations are of paramount importance for the effective conservation planning of carnivores, whose large spatial requirements have made them most susceptible to habitat loss, and equally difficult to conserve (Linnell et al., 2001; Lindsey et al., 2004).

Spatial use patterns of large carnivores are determined by a myriad of factors, including the availability of water and prey resources, available cover for den sites, refuges from predators or climate, and interspecific or intraspecific competition (Mills

and Knowlton, 1991; Hofer and East, 1993). Carnivore population densities, movements, and home range sizes are also influenced by anthropogenic resources (Craighead and Craighead, 1971; Fedriani et al., 2001; Hidalgo-Mihart et al., 2004), and may result in heightened human-carnivore conflict. Human-carnivore conflict may occur as a result of increasing carnivore densities (Yom-Tov et al., 1995), or animals relocating towards human-dominated areas (Beckmann and Berger, 2003).

The behavioural plasticity of hyaenas allows them to respond quickly to changing ecological conditions, affording them the ability to adapt and survive in the face of increasing anthropogenic pressure, even when other carnivore species have shown significant population declines (Gittleman et al., 2001). Consequently, marked behavioural changes in the hyaena's ranging behaviour and habitat preferences may be a key indicator of degradation or a serious deficiency in an ecosystem (Kolowski and Holekamp, 2007). Such studies looking into these findings may provide vital information towards the conservation of biodiversity within a protected area.

5.3.3 FEEDING ECOLOGY

In this study, it is likely that the brown and spotted hyaenas experience competition with one another for food resources, as the faecal analysis of the hyaenas in MGR revealed a near perfect dietary overlap, and the behaviour of the hyaenas at kills/carcasses appears to demonstrate temporal and spatial avoidance of one another. Several of these food items were carrion and it is unlikely that the brown hyaena has actively hunted large game in the course of this study (Mills, 1977; Owens and Owens, 1978). While the spotted hyaena is capable of hunting large game in East Africa (Kruuk, 1972), and are opportunistic hunters within the Savuti region in the Chobe National Park in Botswana (Cooper, 1990), this has rarely been seen in the KNP in South Africa (Bearder, 1977; Mills and Biggs, 1993), and was never observed

in this study. Both hyaenas were seen to utilize similar prey items, feeding on large mammals more often than small mammals. In spite of such heightened competition between the hyaenas for the same resources, the continued persistence of the brown hyaenas in MGR may be a consequence of the high numbers of lions in the park (numbering to upwards of 70 individuals). As the lions pose a more competitive threat to spotted hyaenas, the lions are presumably the regulating factor of spotted hyaenas through direct and indirect competition. If this conclusion is correct, then the presence of the lions may be providing a benefit for the sustainability and viability of the brown hyaenas and this should be taken into consideration when management tactics include culling or removal of large predators from the park.

As the relationship between lions and spotted hyaenas is a sensitive one (Mills, 1990), with lion populations recovering rapidly with the spotted hyaena population continuing to flounder seven years later (Henschel, 1986; Mills and Biggs, 1993), caution would be necessary in determining how to best manage such populations of large predators. Further studies would be crucial in looking at the dynamics between these predators by determining the effect on population demographical changes of the brown hyaena with increases and decreases of the lion population in the park. This would be especially valuable with assisting in wildlife management decisions as culling and/or removing lions from MGR may not only warrant more game viewing for tourists, but may also decimate a small population of brown hyaenas that have by far managed to co-exist with the spotted hyaenas by surviving off of the abundance of food resources from lions' kills.

5.4 FUTURE DIRECTIONS

The current available estimates for the total population of brown hyaenas in southern Africa and for the individual populations throughout the brown hyaena's

range are very limited. Studies that can provide further estimates of the numbers of individual brown hyaenas in various populations, as well as the patterns of movement and dispersal between these populations would be of importance. Information on the population numbers as well as the foraging and spatial ecology of brown hyaenas existing outside of protected areas is likely to be valuable. Competition between carnivores has been seen to cause larger home range sizes and a reduction in group sizes, thus triggering a decline in the number of individuals (Durant, 2000; Boydston et al., 2003). Therefore, a study examining the effects of how the fence influences the ecology of the brown and spotted hyaenas in the MGR would be especially valuable, considering the extent to how effective the fence acts as a barrier in preventing the movement and dispersals of hyaenas and other mammals, as well as the influence that the fence has on the social dynamics of the hyaena populations.

Future studies might also look to increase the efficiency of the methodologies utilized in this present study. Designing a mark-resighting method in which one animal is marked in each clan (with the use of collars or identifying tags), coupled together with sighting surveys and field-interview surveys (Davies, 2000; Lindsey, 2003) may provide a more robust estimate of the hyaena population. A DNA-based capture-recapture study based on track counts (Lukacs and Burnham, 2005; Engeman and Evangelista, 2006), or visitation rates to latrine sites (Gruber et al., 2007) may provide information on the genetic relatedness and paternity within hyaena clans and connected populations, as well as information on dispersal between clans. The efficacy of camera-traps can be improved by increasing the density of camera-traps in the sampling area (Carbone et al., 2001), by using baits or lures (Thorn et al., 2009) or by using infrared technology to monitor the activity of the animals (de Leaniz et al., 2006). A finer-scale analysis would be required to further elucidate the hyaena spatial

patterns in MGR. Utilizing GPS collars on individuals from each species would be helpful in determining the exact range use of individuals and clans on a temporal and spatial scale, and can provide further observations into shifts in hyaena activity periods in response to presence of competitors or other predators. Field-intensive behavioural observations would contribute to supplement the diets of hyaenas and to determine whether prey was scavenged or killed, and can obtain data on food that is entirely digested and not represented in faeces (Kruuk, 1972; Henschel and Skinner, 1990). Further studies may also look at the effects of anthropogenic food availability on hyaena spatial patterns and social dynamics (Kolowski and Holekamp, 2007). This information would be critical in understanding how brown and spotted hyaenas deal with such high degrees of overlap and how hyaena range uses and distributions changes over time or with changes in predator and prey numbers.

5.5 SUMMARY

Due to the brown hyaena's vulnerable conservation status, the lack of knowledge on the interaction between sympatric spotted and brown hyaenas was the main motivating factor behind this study. Much of the information available on spotted and brown hyaena ecology comes from areas where one species exists without the other or in areas where both species are not sympatric. As a result, our current understanding of the factors contributing to the co-existence of the spotted and brown hyaenas in a protected area is limited. The aim of this study was to increase our knowledge and understanding of hyaena ecology in the context of the competition hypothesis, and whether the sympatric co-existence of the hyaenas in MGR results in competition or co-existence through resource partitioning.

The number of spotted hyaenas and brown hyaenas in the MGR were both lower than originally reported by Park personnel. The spotted hyaena population was

originally thought to be at around 40 to 50 individuals, with the estimated number at 27 with a 95% confidence interval of 25-30. Whereas the brown hyaena population was originally thought to be at around 20 to 30 individuals, this study showed their estimated number to be much lower at 11 with a 95% confidence interval of 11-13. The responses of the hyaenas to the audio playback recordings for the call-in surveys were favourable at first, but then declined over time, indicating habituation to the calls. Hyaena numbers and responses were also influenced by the presence of lions and other predators responding to the call-in surveys. Hyaenas would sometimes respond when jackals or leopards did, but never responded when lions were in the vicinity of the area.

While spotted hyaena latrines were more abundant than brown hyaena latrines throughout MGR, there were significantly more latrines from both hyaena species in the core area than in the periphery of the reserve. The most important factor in determining whether hyaenas would create a latrine site in a specific location was because of the surrounding vegetation, and both hyaena species were seen to create latrines at different elevation levels during different seasons. Range sizes consisting of only spotted hyaena latrines and of only brown hyaena latrines were insignificantly small, while the area consisting of both species' latrines was considerably large. Camera-traps used in this study detected hyaenas more often at night, and more often at latrine sites rather than at random locations. Spotted and brown hyaenas were seen more often at night, and were often seen either alone or with conspecifics rather than with each other. Larger groups of spotted hyaenas nearly always guaranteed non-association with brown hyaenas. Range sizes where only spotted hyaenas or only brown hyaenas were sighted were of very small sizes, while the overlapping area in where both hyaena species were sighted was incomparably large. Overall, the

methodologies in determining hyaena range use for this study included a combination of latrine surveys, radio-telemetry, sighting records and camera-trapping. The overlapping areas utilized by both hyaena species were a little more than three and a half sizes larger than the exclusively used areas by each species alone.

The diets of the hyaenas in MGR showed no discriminate differences in dietary components and prey remains. Both spotted and brown hyaenas consumed a higher proportion of large mammals than small mammals in their diets, and exhibited large degrees of overlap in both food groups and prey remains. Both hyaena species consumed bones, hair, vegetation, keratin in the form of hooves, stones, anthropogenic materials, porcupine quills, reptiles, and tortoise carapaces. Invertebrates featured prominently in hyaena diets in the wet season, while seeds were prominent in the dry season. Although feathers were found in the faeces of brown hyaenas only, both species were seen to utilize a number of similar prey items, with both impala and blue wildebeest featuring prominently in their diets.

The foraging ecology of the spotted and brown hyaenas in MGR also exhibited many similarities in that the kills/carcasses in the reserve were utilized by both species and in several occasions shared between both species. Spotted and brown hyaenas were seen more often at kills/carcasses either alone or with conspecifics rather than with each other. Furthermore, when hyaenas were sharing the same kill with the other species, they were often tolerant and placid towards one another. Brown hyaenas were more likely to not be present at a kill/carcass when it was frequented by a spotted hyaena group of larger than three individuals. Both hyaena species displayed vigilant and aggressive behaviours at kills/carcasses with spotted hyaenas displaying aggression towards conspecifics more often than towards brown

hyaenas. However, pasting behaviours in the vicinity of kills/carcasses were displayed by brown hyaenas only.

As a consequence of the high prevalence of overlap between the spotted and brown hyaenas in MGR, with respect to the areas of the reserve utilized with much considerable overlap in the range use of both species, and with respect to the high overlap in the diets of both species, it is clear that the hyaenas in MGR are in competition for the same limiting resources. A further fine-scale analysis of the spatial use patterns and activity periods of both species would provide further lucidity in how the two species manage to exist sympatrically in light of such heightened competition. As MGR provides one of the few places in which to study the effects of sympatry on hyaena ecology, efforts to substantiate the reasons for co-existence of hyaenas in this area would prove valuable for the further management and continued viability of these species.

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