The Comparative Ecology of the Brown Hyaena (*Hyaena brunnea*) in Makgadikgadi National Park and a Neighbouring Community Cattle Area in Botswana.

by

Glyn Maude

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Dedication

Dedicated to the continued existence of the Makgadikgadi

as a wilderness area

Brown hyaenas greeting each other at the clans' communal den site

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Glyn Maude

Supervisor: Professor M.G.L. Mills
SAN Parks, Endangered Wildlife Trust and
Mammal Research Institute.
National Parks Board, Kruger National Park
Private Bag X402, Skukuza 1350
South Africa

Co-supervisor: Professor J.T. du Toit
Mammal Research Institute
University of Pretoria
Pretoria 0002
South Africa

Abstract

Field data were collected and analysed on the feeding and spatial ecology of brown hyaenas living in the Makgadikgadi National Park and in an adjacent Wildlife Management Area where local subsistence pastoralists live. The responses of the

pastoralists to a questionnaire designed to document their perceptions of and attitudes towards brown hyaenas and other carnivores that live in the vicinity of their residences, were also analysed.

Brown hyaenas living in the Makgadikgadi National Park have different diets from hyaenas living in the vicinity of pastoralists. In pastoralist areas livestock carcasses were the most important food source and other less important food types were fed on as they became seasonally available. In the Makgadikgadi National Park zebra was the most important food source although several other food types were seasonally important. In the pastoralist areas dietary breadth was similar over the lean and the peak seasons, while in the Makgadikgadi National Park, when food availability was low in the lean season, the brown hyaenas increased their dietary breadth and fed off a greater number of species of food. In the lean season they also changed their foraging behaviour. There was no evidence to suggest that any livestock species were hunted by the brown hyaenas as springhares and Cape hares were the only mammals observed to be hunted, and only occasionally.

Home range sizes were smaller for brown hyaenas living in the vicinity of pastoralists than for hyaenas living in the Makgadikgadi National Park. The size of the home range was found to be dependent on the average distance between the significant food sources. In the Makgadikgadi National Park the seasonal home range size fluctuated greatly due to the variability of seasonal food available, while in the pastoralist areas food availability was less varied and as a consequence seasonal home range size varied less than in the national park.

Although pastoralists believed that black-backed jackals killed the most number of individual livestock animals, lions had the greatest perceived negative economic impact, followed by black-backed jackals, spotted hyaena and then brown hyaena. Wild dog, caracal, cheetah and leopard were also believed to have killed a small number of livestock animals. The general understanding of the brown hyaena is that it is a predator that survived by feeding on hunted livestock. As a consequence of this they were hated and frequently killed by the farmers. In spite of their persecution the brown hyaena populations are viable in the cattle areas and appear not to be under any immediate threat. However, efforts to reduce the number of brown hyaenas killed in the long-term would be beneficial in ensuring that brown hyaena populations in cattle areas remain viable.

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Contents

Page No.

List of Tables

List of Figures

Page No.

List of Appendices

- Chapter 1 -

Introduction

Conflict between people and carnivores worldwide is on the increase (Nowell & Jackson 1996; Frank 1998). This carnivore and human conflict is leading to carnivore population declines in areas where carnivore species and people co-habit or interact temporarily on borders of protected areas (Woodroffe 2000, 2001). As a consequence of this decline many of Africa's large carnivores are presently listed as threatened by the World Conservation Union (Mills & Hofer 1998, IUCN 2003). Intentional killing of carnivores by humans is a major and rising threat to carnivore population viability (Landa *et al*. 1999; Woodroffe 2001). Worldwide, populations of lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted hyaenas (*Crocute crocuta*), tigers (*Panthera tigris*), snow leopards (*Uncia uncia*), jaquars (*Panthera onca*), grey wolves (*Canis lupus)* and wild dogs (*Lycaon pictus*) and several other species continue to decline, primarily due to conflict with people (Ginsberg & Macdonald 1990; Nowell & Jackson 1996; Mills & Hofer 1998; Landa *et al.* 1999; IUCN 2003). As a consequence of this decline, many of Africa's large carnivores are presently listed by the World Conservation Union as threatened. The Ethiopian wolf (*Canis simensis*) is critically endangered, the African wild dog is endangered and the African lion and cheetah are vulnerable. Due to the rapid decline of spotted hyaena populations outside protected areas their status is regarded as lower risk: near threatened. The brown hyaena is listed in the IUCN 2003 red list of threatened species as lower risk: near threatened.

The ecology of many carnivores and the resulting conflict caused by these carnivores living in the African pastoral system has been studied (Frank 1998; Funston

2001; Marker *et al.* 2003; Hemson 2003). However at present there is limited information available on the interactions between pastoralists and brown hyaenas and how the presence of pastoralists and livestock affects the ecology of brown hyaenas. The poisoning, trapping and hunting of brown hyaenas is believed to have had a detrimental effect on their populations and are a threat to the species in some areas (Mills & Hofer 1998). As much of the brown hyaenas' range is outside of protected areas and often coincides with human populations, a study of human and brown hyaena interactions is required in order to increase our understanding of the brown hyaena and to help with efforts to conserve the species (Skinner and Smithers 1990; Mills & Hofer 1998). Brown hyaenas have been extensively studied in the Kgalagadi Transfrontier Park, bordering Botswana and South Africa in the southern Kalahari (Mills 1978a, 1978b, 1982a, 1982b, 1982c, 1983a, 1983b, 1984a, 1989, 1990; Mills & Mills 1977, 1978, 1982; Mills *et al*. 1980). Less intensive studies on the species have been conducted in the Central Kalahari Game Reserve in Botswana, in the agricultural areas in the Gauteng province in South Africa and the Namib Desert in Namibia (Owens & Owens 1978, 1979a, 1979b, 1984; Skinner 1976; Skinner & llani 1979; Skinner & van Aarde 1981; Goss 1986).

1.1 OBJECTIVES

The main objectives of the study are:

1. To compare the ecology of the brown hyaena within and outside a protected area.
2. To add to the existing knowledge of our understanding of brown hyaena ecology in the context of human wildlife interactions.

1.2 KEY QUESTIONS

1. How is the diet and foraging behaviour of the brown hyaena affected by the presence of pastoralists in the area?
2. How is the home range size and spatial ecology of the brown hyaena affected by the presence of pastoralists in the area?

3. Do the brown hyaenas hunt livestock?

3. What are the attitudes of pastoralists towards brown hyaenas and why?

4. Are brown hyaenas persecuted by pastoralists? If so, is the level of persecution a concern and if so, how can it be reduced over the long-term?

1.3 APPROACH

The key questions listed above were answered by collecting and analyzing data on:

1. The diet of brown hyaenas in the Makgadikgadi National Park (MNP) and an adjacent Wildlife Management Area (WMA) where brown hyaenas and pastoralists co-habit (Chapter 3).
2. The foraging behaviour of brown hyaenas in the MNP and the WMA (Chapter 3).
3. The home range sizes of brown hyaenas in the MNP and the WMA (Chapter 4).
4. The utilization of home ranges by brown hyaenas in the MNP and the WMA (Chapter 4).
5. The responses of the pastoralists to a questionnaire designed to document their perceptions of and attitudes towards brown hyaenas and other carnivores that live in the vicinity of their residences.

The M.sc thesis is written up in a style suitable for submission of scientific papers to the South African Journal of Wildlife Research.

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- Chapter 2 -

The Makgadikgadi Pans Study Area and Study Species

2.1 STUDY AREA

The field data were collected in the Makgadikgadi Pans area of northern Botswana between July 2000 to March 2003. The study area incorporated the eastern portion of the Makgadikgadi National Park (MNP) and an adjacent Wildlife Management Area (WMA) to the east of the MNP (Figure 2.1). The Makgadikgadi Pans lie between 20 and 21 degrees south and 20 and 26 degrees east in the eastern central Kalahari region. The MNP is 4 900 km^2 and located on the north and west of Ntwetwe Salt Pan. The MNP was gazetted as a Game Reserve in 1970 and in 1992 increased in size and upgraded to a national park.

The study area is approximately 2 200 km^2 in size, of which 1 200 km^2 is inside of the MNP and approximately 1 000 km^2 outside of the MNP. Part of the study area reached beyond the WMA and into what is either Tribal or State land. In the study area outside of the MNP there are approximately 30 cattle posts. Subsistence livestock ownership in rural Botswana is culturally important, with the primary function of a cattle post being to provide water and good grazing for a herd of cattle while employing traditional livestock husbandry techniques (Shaw 1990). A typical cattle post would consist of four or five traditionally built circular mud huts enclosed by a log fence, with anywhere between two to six adult residents and several children. At each cattle post there is a population of livestock that would typically consist of between 50-300 cattle (*Bos domesticus),* 10-50 goats (*Capra hircus*), 5-10 sheep (*Ovis aries)*, 5-10 donkeys

(*Equus asinus*), and 2-10 horses (*Equus caballus)*. Each cattle post will also usually have five or six dogs (*Canis familiaris*) and 10 to 15 chickens. Crops such as maize, sorghum, millet and melons are cultivated during the rainy season. Subsistence farming is the principal form of agriculture in Botswana, there being in 1997 an estimated 64 707 traditional cattle posts and country wide 2.2 million head of cattle (Botswana Central Statistics Office, Twyman 2001).

2.2 VEGETATION AND CLIMATE

The Makgadikgadi Pans system is part of the Kalahari Desert, which is officially classed as a semi-arid desert (Thomas & Shaw 1991). Rainfall is in the summer with an average of 450 mm falling from November through to April (Meynell & Parry 2002). The rainfall is highly localized and variable with rainfall of between 50mm in drought years to 1 200 mm in the wettest years (Thomas & Shaw 1991). For example in the Makgadikgadi over the duration of the study, in the 1999-2000 rainfall season there was over 1 200 mm of rainfall and in the 2002-2003 rainfall season, less than 200 mm (pers. observations). Rainfall outside of these months is rare and the winter season from May to September, is cold and dry. Annual temperatures can vary from a minimum of – 6 ^{o}C in the winter to a maximum of 42 ^{o}C in the summer (Thomas & Shaw 1991). There are six main vegetation types in the study area as described in Figure 2.1 (Parry 1995).

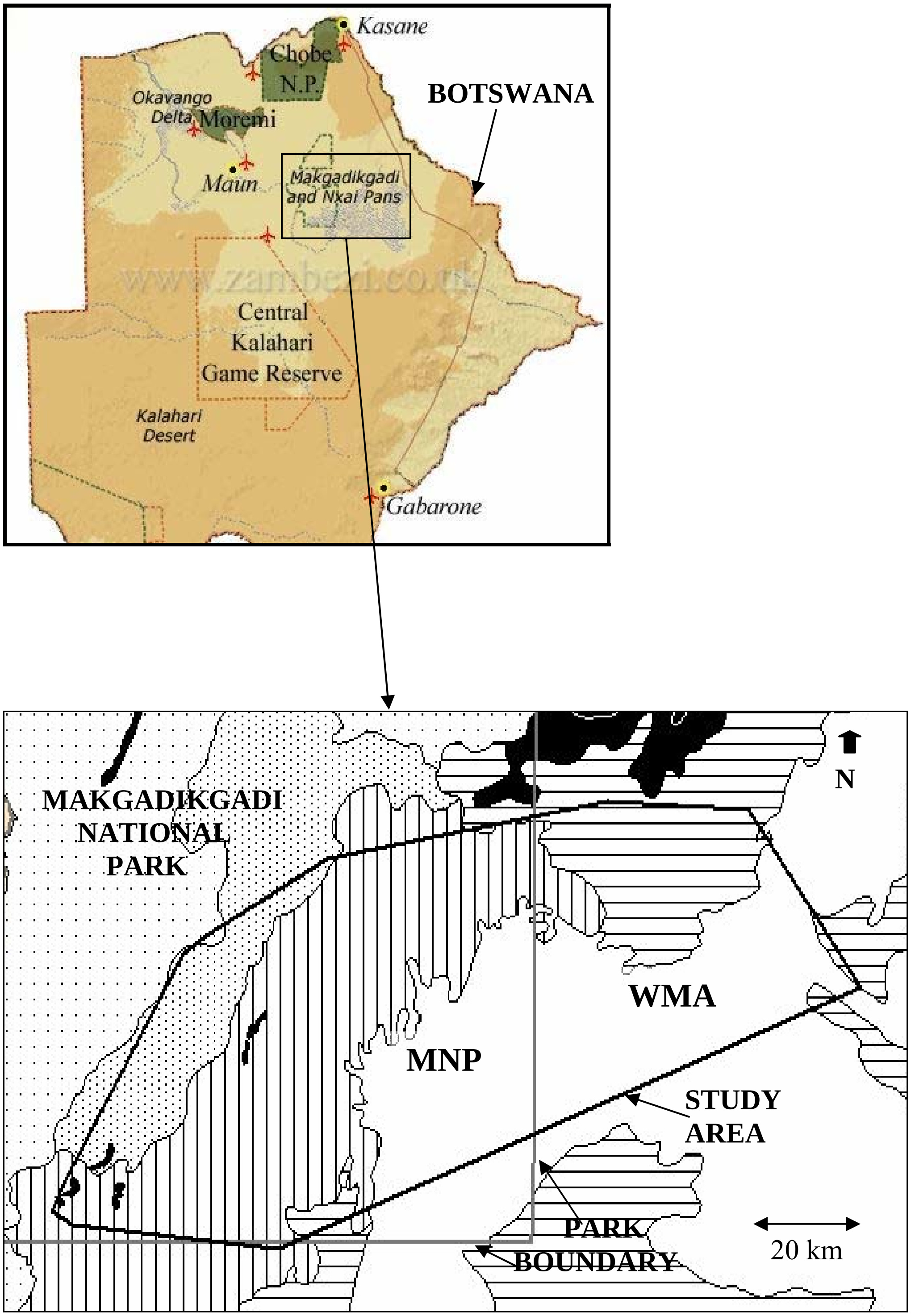

Figure 2.1.The two zones within the study area (MNP and WMA) and the six different habitat types occurring in the area (see key over page). WMA is a cattle area and MNP is the Makgadikgadi National Park

KEY

Ntwetwe Salt Pan. A flat surface that is highly saline with layers of silcrete. Vegetation is limited to saline tolerant green algae.

Small saline pans and short saline tolerant grasses. Dominated by grass species *Sporobolus* and *Oddyssea.*

Saline sands. Short grassland dominated by *Odyssea paucinervis*. More palatable grass species grown in depressions.

Clayey soils on shallow duripan layers. Vegetation is fresh-water grassland with wooded clumps dominated by *Combretum imberbe.*

Old lake terrace. Sandy soils with variable vegetation made up of Mophane woodland and shrublands dominated by *Combretum*, *Acacia* and *Grewia* species. *Hyphaena petersiana* and stands of *Terminalia* species are also common.

Fossil fluvial sand deposits. Deep well drained sands that promote the growth of woody vegetation over grass in the absence of fire. Savanna with typical sandveld species, *Terminalia sericea*, *Burkea africana* and *Peltophorum africanum.*

2.3 STUDY SPECIES

The brown hyaena is a medium sized carnivore with strong forequarters, long powerful forelegs and shorter hind legs. Head to tail an adult measures between 1.26 cm-1.61 cm and stands between 72 cm-88 cm at the shoulder (Skinner 1976; Smithers 1971). Adult back legs measure between 58 cm–64 cm giving the brown hyaena a sloping back. The coat has long, wiry hair that is dark brown in colour with a lighter coloured neck area. Ears are long and pointed upwards and the tail is short. White stripes run around the lower front and hind leg region in a pattern that differs in individual brown hyaenas. Otherwise individual brown hyaenas are very similar in appearance with males and females looking alike. A healthy adult brown hyaena weighs in the region of 40 kg (28-47 kg) with little or no variation between the sexes (Mills 1982a).

The brown hyaena is listed in the IUCN 2003 red list of threatened species as lower risk: near threatened. The global population size is estimated to be a minimum of between 5 070 - 8 020 individuals (Mills & Hofer 1998). Brown hyaenas occur in the southwest arid zone of Africa, with Botswana estimated to have the highest population of approximately 3 900 individuals. Of the total population many live inside protected areas. The largest of these are the Central Kalahari Game Reserve in Botswana, the Kalagadi Transfrontier Park bordering Botswana and South Africa, and the Namib-Naukluft, Skeleton Coast and Etosha National Parks in Namibia. Brown hyaenas are relatively adaptable and many viable populations also exist outside of protected areas in bush and agricultural land alongside human activities.

2.4 POTENTIAL FOOD SPECIES

The Makgadikgadi National Park and the surrounding area support the largest migratory movement of large herbivores in southern Africa (Kgathi & Kalikawe 1993). Approximately 13 000 Burchells zebra (*Equus burchelli*) and 3 000 blue wildebeest (*Connochaetes taurinus*) move seasonally from the west of the MNP where they spend the dry season, to the east of the park into the study area, where they spend the wet season (Department of Wildlife and National Parks aerial survey estimates 2001, 2002; Basis Wint 2000). Depending on rainfall patterns, grazing availability and other factors the zebra and wildebeest move over a wider and less predictable range (Brooks 2003). Other common herbivores in the study area include kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcus marsupilis)*, steenbok (*Raphicerus campestris*) and gemsbok (*Oryx gazelle*). Springhare (*Pedetes capensis*) and Cape hare (*Lepus capensis*) are abundant throughout. Resident carnivores include lion, cheetah, caracal *(Caracal caracal*), African wildcat (*Felis silvestris*), brown hyaena, black-backed jackal (*Canis mesomelas*), aardwolf (*Proteles cristatus*), bat-eared fox (*Otocyon megalotis*) and honey badger (*Mellivora capensis*). Smaller common animals include ground squirrels (*Xerus inaquris),* porcupine (H*ystrix africaeaustralis*), suricate (*Suricata suricatta*), yellow mongoose (*Cynictis penicillata*) and common and large spotted genet (*Genetta genetta & Genetta tigrina*). Aardvark (*Orycteropus afer)* also occurs in the study area.

There are approximately 350 species of migratory and resident birds in the MNP and surrounding area (Newman 1989). The larger resident birds include ostrich (*Struthio camelus*), secretary bird (*Sagittarious serpentarius*) and kori bustard (*Ardeotis kori*), helmeted guinea fowl (*Numida meleagreis)* and black and red-crested korhaan (*Eupodotis* *afraoides & Eupodotis ruficrista)*. Over the wet season the Makgadikgadi pans are an important breeding ground for summer migrants, in particular the waders and aquatic bird species such as cranes and flamingos (Mcculloch *et al.* 2003).

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- Chapter 3 -

The comparative feeding ecology of the brown hyaena (*Hyaena brunnea*) in a cattle area and the adjacent Makgadikgadi National Park, Botswana

3.1 INTRODUCTION

Previous studies on the brown hyaena have shown it to have a wide-ranging diet and primarily be a scavenger of vertebrate remains but also to forage for insects, reptiles, birds' eggs and plants. In the southern Kalahari 58 different food types were identified in faecal samples (Mills & Mills 1978). In the central Kalahari the brown hyaena was found to be an opportunist scavenger, feeding on a wide variety of food types (Owens & Owens 1978). Along the Namib Desert coast the diet of the brown hyaena is much less varied with Cape fur seals (*Arctocephalus pusillus*) making up the bulk of the diet (Skinner & Van Aarde 1981; Siegfried 1984; Goss 1986). Brown hyaenas are inefficient predators and food obtained by hunting is rare. In the southern Kalahari only 4.7 % of hunting attempts were successful and those vertebrates hunted successfully made up only 4.2 % of the total vertebrate diet (Mills 1977, 1978a). All the vertebrates hunted were birds such as korhaans *(Eupodotis* sp) or small mammals such as springbok lamb (*Antidorcus marsupilis*), springhare (*Pedetes capensis*), striped polecat (I*ctonyx striatus*) and bat-eared foxes (*Otocyon megalotis*). In the central Kalahari the remains of kills left by predators were the most important food items in the brown hyaenas' diet (Owens & Owens 1978). Only 2.9 % of the Cape fur seal pups eaten in the Namib Desert coastal area were killed by the brown hyaena (Goss 1986). A brief study conducted in the farming areas of the Gauteng and Limpopo provinces in South Africa indicated, through faecal analysis and inspection of food remains at den sites, that cattle (*Bos domesticus*) and medium sized to small mammal carcasses were the main food source of brown hyaenas (Skinner 1976). From questioning farmers it was speculated that stock killing by brown hyaenas was rare and when it did occur the problem was solved if the individual responsible was removed.

The foraging ecology of large carnivores and the resulting conflict caused by livestock predation has been studied in many areas where carnivores live alongside humans and livestock (Kruuk 1980; Skinner *et al.* 1980; Hoogestein *et al*.1993; Berg 1998; Frank 1998; Karanth *et al.* 1999; Ramussen 1999; Hoogestein 2000; Funston 2001; Marker *et al.* 2003; Hemson 2003). Increasingly this conflict is leading to carnivore population declines in areas where carnivore species and people co-habit or interact temporarily on borders of protected areas (Woodroffe 2001). Intentional killing of carnivores by humans is a major and rising threat to carnivore population viability (Rabinowitz 1986; Landa *et al*. 1999). Worldwide, populations of lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted hyaenas (*Crocute crocuta*), tigers (*Panthera tigris*), snow leopards (*Uncia uncia*), jaguars (*Panthera onca*), grey wolves (*Canis lupus)* and wild dogs (*Lycaon pictus*) and several other species continue to decline, primarily due to conflict with people (Ginsberg & Macdonald 1990; Nowell & Jackson 1996; Mills & Hofer 1998; Landa *et al.* 1999; IUCN 2003). As a consequence of this decline, many of Africa's large carnivores are presently listed by the World Conservation Union as threatened. The Ethiopian wolf (*Canis simensis*) is critically endangered, the African wild dog is endangered and the African lion and cheetah are vulnerable. Due to the rapid decline of spotted hyaena populations outside protected areas, their status is regarded as lower risk: near threatened.

In contrast to most of Africa's large carnivores, there is no evidence of a continuing decline in brown hyaena populations and many viable populations of brown hyaena occur even in areas where humans and livestock coexist (Mills & Hofer 1998, IUCN 2003). In some farming areas in Namibia the populations of brown hyaenas are believed to be on the increase (www.cites.org/eng/cop/11/prop/19.pdf). The brown hyaena's conservation status was down-listed from CITES appendix I to appendix II in 1994. More recently the brown hyaena was deleted from appendix II and is now no longer listed under CITES although is presently classed as lower risk: near threatened under the IUCN. In a cattle area adjacent to the Makgadikgadi National Park in Botswana, the brown hyaena population appears to be viable, inspite of the persecution by farmers (Chapter 5). The objectives of this chapter are: (i) to determine if the brown hyaenas living in the cattle areas benefit from the presence of farmers through feeding off livestock; (ii) to determine if the killing of brown hyaenas by the farmers because of perceived livestock predation by the hyaenas is justified; and (iii) in terms of optimal foraging theory (Taylor 1984), to compare the diets and foraging behaviour of brown hyaenas living in the vicinity of cattle posts to brown hyaenas living in the Makgadikgadi National Park, away from cattle posts.

Optimal foraging theory predicts that for generalist feeders their diet should change between alternative food sources depending on what food sources are seasonally available (Taylor 1984). It also predicts that a generalist feeder will increase dietary diversity in response to a decrease in food availability (Perry & Pianka 1997). Finally an animal could be expected to show seasonal adaptations in foraging behaviour to satisfy its nutritional requirements (Gedir & Hudson 2000). As brown hyaenas are generalist scavengers it might be predicted that their dietary breadth would increase as plentiful food sources that are available over the peak season become less available over the lean season.

This chapter investigates the hypothesis that the diet of brown hyaenas living in a cattle area will be positively influenced by the presence of farmers, as the hyaenas access food by feeding off the remains of livestock carcasses. Prediction 1 is that the diet of brown hyaenas living in a cattle area will be dominated by livestock species. Prediction 2 is that the livestock species identified as food sources will be scavenged and not hunted. Prediction 3 is that due to the presence of livestock, the dietary breadth and number of species eaten by the brown hyaenas in the cattle areas will be less seasonally variable than for hyaenas in the Makgadikgadi National Park.

3.2 METHODS

3.2.1 Study Area

The data were collected in the Makgadikgadi Pans area of northern Botswana between July 2000 and June 2003. The Makgadikgadi Pans lie between 20 and 21 degrees south and 20 and 26 degrees east in the eastern central Kalahari region. The study area incorporated the eastern portion of the Makgadikgadi National Park (MNP) and an adjacent Wildlife Management Area (WMA) bordering the eastern boundary of the Makgadikgadi National Park (WMA, Figure 3.1). The MNP was gazetted as a Game Reserve in 1970 and in 1992 increased in size to 4 900 km^2 and was upgraded to a national park. The study area was approximately 2 200 km^2 in size of which 1 200 km^2 was inside of the MNP and approximately 1 000 km^2 outside of the MNP. In the study area outside of the MNP there are approximately 30 cattle posts. Subsistence livestock ownership in rural Botswana is culturally important, with the primary function of a cattle post being to provide water and good grazing for a herd of cattle while employing traditional livestock husbandry techniques (Shaw 1990). A typical cattle post would consist of four or five traditionally built circular mud huts enclosed by a log fence, with anywhere between two to six adult residents and several children. At each cattle post there is a population of livestock that would typically consist of between 50-300 cattle (*Bos domesticus),* 10-50 goats (*Capra hircus*), 5-10 sheep (*Ovis aries)*, 5-10 donkeys (*Equus asinus*), and 2-10 horses (*Equus caballus)*. Each cattle post will also usually have five or six dogs (*Canis familiaris*) and 10 to 15 chickens. Crops such as maize, sorghum, millet and melons are cultivated during the rainy season. Subsistence farming is the principle form of agriculture in Botswana, there being in 1997 an estimated 64 707 traditional cattle posts and country wide 2.2 million head of cattle (Botswana Central Statistics Office, Twyman, 2001).

The Makgadikgadi Pans system is part of the Kalahari Desert, which is officially classed as a semi arid desert (Thomas & Shaw 1991). Rainfall is in the summer with an average of 450 mm falling from November through to April (Meynell & Parry 2002). Rainfall outside of these months is rare and the winter season from May to September is cold and dry. Annual temperatures can vary from a minimum of – 6 ^{o}C in the winter to a maximum of 42 ^{o}C in the summer (Thomas & Shaw 1991). The Makgadikgadi National

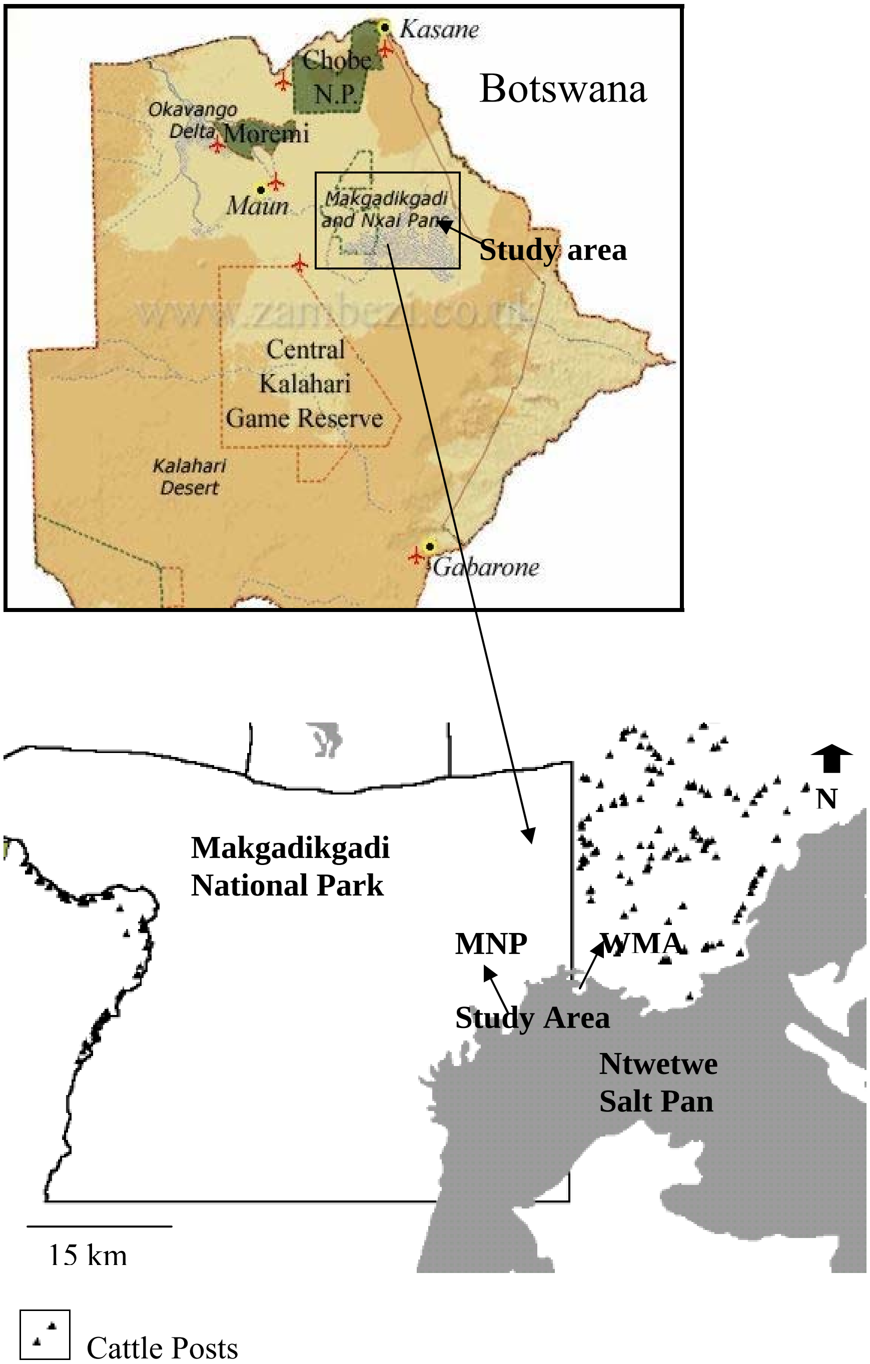

Figure 3.1.The location of the study area, in the eastern portion of the Makgadikgadi National Park (MNP) and in a cattle area (WMA) bordering the eastern boundary of the park.

Park and the surrounding area support the largest migratory movement of large herbivores in southern Africa (Kgathi & Kalikawe 1993). Approximately 13 000 burchells zebra (*Equus burchelli*) and 3 000 blue wildebeest (*Connochaetes taurinus*) move seasonally from the west of the MNP where they spend the dry season, to the east of the park where they spend the wet season in the study area (Department of Wildlife and National Parks aerial survey estimates 2001, 2002, Wint 2000). Other common herbivores in the study area include kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcus marsupilis)*, steenbok (*Raphicerus campestris*) and gemsbok (*Oryx gazelle*). Springhare (*Pedetes capensis*) and Cape hare (*Lepus capensis*) are abundant throughout. Resident carnivores include, lion, cheetah, caracal *(Felis caracal*), African wildcat (*Felis silvestris*), brown hyaena, black-backed jackal (*Canis mesomelas*), aardwolf (*Proteles cristatus*), bat-eared fox (*Otocyon megalotis*) and honey badger (*Mellivora capensis*). Smaller common animals include ground squirrels (*Xerus inaquris),* porcupine (H*ystrix africaeaustralis*), suricate (*Suricata suricatta*), yellow mongoose (*Cynictis penicillata*), common and large spotted genet (*Genetta genetta & Genetta tigrina*). Aardvark (*Orycteropus afer)* also occurs in the study area.

3.2.2 Definition of seasons

Two seasons were identified: the peak season, which started when the zebra and wildebeest migration arrived in the study area, and the lean season, which started when the zebra and wildebeest migration left the study area. The arrival and departure of the zebra and wildebeest was established from an ongoing research project monitoring the movement of zebra and wildebeest in the Makgadikgadi using a combination of cues

(Brooks 2003). These included observations made through sightings of radio-collared (both conventional VHF and GPS) and non-collared zebra and wildebeest, detection of fresh tracks and vocalizations, observations made by pilots who flew over the study area regularly and safari operators based in the study area. The start of the peak season coincided with the start of the rains and ended when all the available surface water for drinking had gone. However the timing of the arrival in and departure from each region (MNP and WMA) was often different. Typically the zebra and wildebeest would arrive in the MNP region first and it would then be several weeks before they moved into the WMA. The zebra and wildebeest would leave the MNP first and several weeks later depart from the WMA (Brooks 2003). This was because one water hole located in the WMA often retained water for longer periods after the rains had finished for the season than those in the MNP. The time period used for the peak and lean season in the WMA and the MNP were accordingly slightly different. These time differences were taken into consideration when defining peak and lean season data for the two areas.

3.2.3 Food availability and distribution

A total of 149 strip transects over a distance of 309 km were conducted by driving in a straight line at a constant speed of 20 km/hr and counting and recording carcasses, bones and other potential significant food items for a brown hyaena that were within a corridor of 12 meters (5 m either side of the car plus the width of the car, 2 m). The distance driven for each transect was 1 km, 3.5 km or 5 km. The driver of the car counted and recorded the points on a dictaphone. The location of each transect was determined by ensuring a wide and even coverage of the entire study area. This was achieved by arbitrarily dividing the study area up into 12.3 km^2 grids and by conducting a strip transect in each of the grids in the peak and the lean seasons over a two year period from March 2001 to March 2003. The exact location for the start of each transect within each grid was selected randomly to ensure that there was no bias.

Estimates for the wet and dry season home ranges of the zebra and wildebeest migration were made available by the zebra and wildebeest-monitoring project in the Makgadikgadi. These home range estimates were calculated from data obtained from 15 GPS capable collars and 10 VHF collars, from which over 80 000 locations were obtained (Brooks 2003). These estimates were used to define a "core zebra and wildebeest zone" over the two seasons (Fig. 3.2). A cattle zone, representing the areas in which cattle moved, was established by placing seven GPS collars onto cows at six cattle posts, located within or near the study area, for an average period of 26.9 days for each cow. Each collar was programmed to take a fix every hour for 24 hours a day. A total of 4 233 fixes was obtained over 189 days. Seventy-four of these days were over the peak season and 115 of the days over the lean season. The average straight-line distances that the cattle moved away from their owner's cattle post were established each hour for every 24-hour period that the collars were on each cow. These distances were used to define a "cattle zone" by drawing a buffer around all the cattle posts in the study area (Fig. 3.2). Using the GPS cattle collar data it was calculated that, each cow was on average furthest away from its cattle post at 13:00. The average maximum distance at 13:00 for the seven cows was 6.2 km $\pm$ 1.97 SD, range 5.9. Accordingly a buffer zone of 6.2 km was drawn around each of the cattle posts in the study area and the resulting buffer area was defined

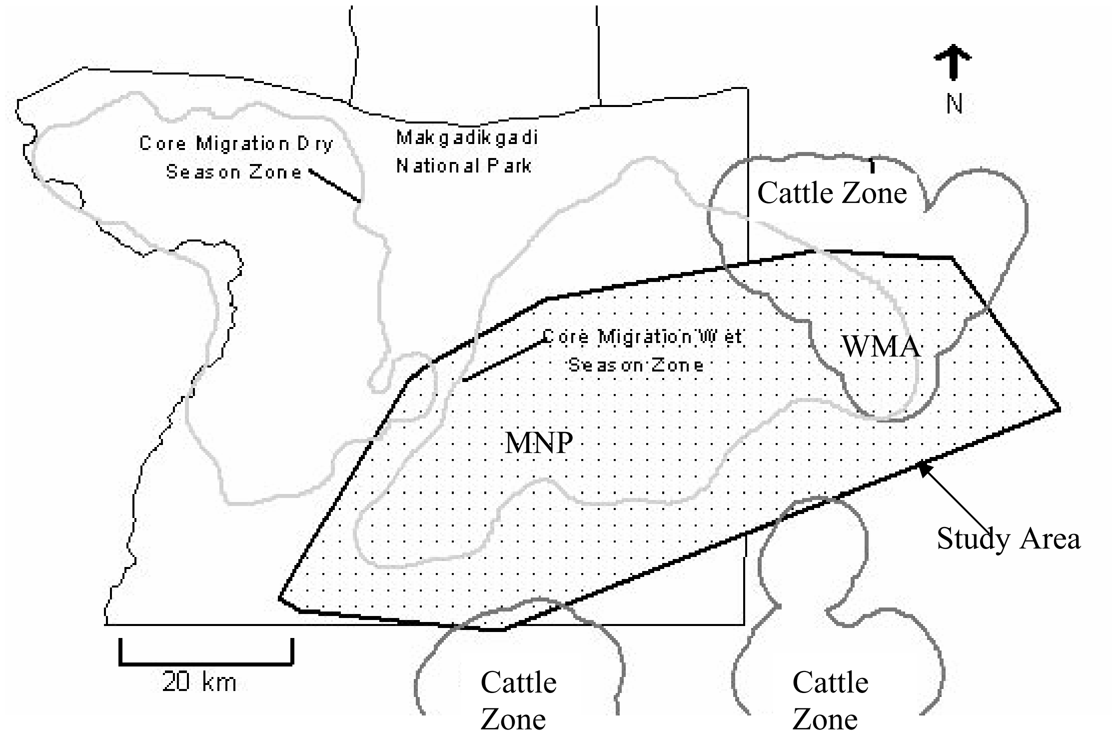

Figure 3.2.The Makgadikgadi National Park and the study area in relation to the areas used by cattle (cattle zone) and the zebra and wildebeest migration (migration zone).

as the “cattle zone” (Fig. 3.2). This cattle zone was considered to be the area that cows most frequently used for both the peak season and lean season. The “zebra and wildebeest zones” over the two seasons are also shown in figure 3.2 (C. Brooks, pers. comm.).

3.2.4 Collection of data on the diet of brown hyaenas

Data on diet and foraging ecology were collected using the following four methods: 1) One hundred and eighty-seven fresh brown hyaena faecal samples, no older than approximately 14 days, were collected from GPS recorded locations and the contents identified. The identification of hair found in faecal samples was done by extracting all the hairs from half (by sun dried weight) of each faecal sample and then cross- sectioning a representative sample of the hairs. A representative sample was selected for analysis by inspecting all the hairs visually from one faecal sample and selecting at least one hair for each size, thickness, colour, length and shape. This maximized the chances of identifying all the different mammal species represented as hair in each faecal sample. The size and shape of the cortex and medulla of each cross section was used to identify the species of mammal from which the hair came from (Keogh 1983; Buys & Keogh 1984). By manually sorting through and inspecting the contents of each faecal sample it was possible to identify the presence of insect and reptile parts, fruit, bone fragments, hair and feathers. 2) 1 444 bones located at five brown hyaena den sites were identified and the proportions of each mammal type represented at the den calculated using minimum the number of individuals (Mills & Mills 1977; Klein & Cruz-Uribe 1984, Lacruz & Maude 2005, appendix F). 3) Four active den sites (with cubs) were inspected regularly and food recently carried in by adult clan members for food provision of cubs was identified. 4) Three VHF collared brown hyaenas were followed at night. Wherever possible food items the brown hyaenas were observed eating was identified, as well as how the food was obtained and the GPS location. Food items were divided into two categories, significant and small. A small food item was smaller than a few centimeters in size and usually consumed in less than a minute. Examples of this would be bone fragments and small-unidentified items that were dug up or eaten off the surface. Anything larger in size or that took longer to eat was defined as a significant food item.

Dietary diversity was calculated using Levin's formula for niche breadth, $N_B = 1 / \sum pi^2$ where *pi* is the proportion of the observations in food category *I* of the diet (Erlinge 1981; Lode 1994). Species richness was represented as the number of species eaten.

3.3 RESULTS

3.3.1 Food distribution

Strip transects in the cattle zone of the WMA counted 38 potential food items for brown hyaenas, 79 % of which were the remains of cattle carcasses, 16 % unknown (unidentifiable partial carcasses with no skin or just bone fragments) and two (5 %) were ostrich (*Struthio camelus*)- one carcass and one egg. Outside of the cattle zone in the WMA only one food item was counted (zebra remains). In the MNP 18 food items were counted, 61 % were zebra, 28 % unknown 6 % gemsbok and 6 % ostrich egg. Cattle remains in the cattle zone were the most common potential food source for brown hyaenas in the WMA and zebra remains in the MNP.

3.3.2 Faecal Analysis

There was a highly significant difference between the occurrences of livestock hairs in the faecal samples in the MNP compared to the WMA ($\chi^2 = 54.82$; df = 1; $P < 0.001$; n = 213, Table 3.1). Livestock hairs were present in a similar high number of faecal samples collected in the WMA during both the peak and the lean season ($\chi^2 = 1.95$; df = 1; $P > 0.05$; n = 93) and similar low numbers of collected in the MNP over the peak and lean season ($\chi^2 = 1.10$; df = 1; $P > 0.05$; n = 94). If the hairs identified in faecal samples are placed into three categories, namely wild residents (all indigenous mammals apart from either zebra or wildebeest), wild migrants (zebra and wildebeest) and domestic (livestock), there was a highly significant difference between the occurrences of wild residents, wild migrants and domestic animals between the MNP and the WMA ($\chi^2 = 54.42$; df = 2; $P < 0.001$; n = 213). For the peak season in the WMA, hairs from livestock were most frequently identified (Fig. 3.3). Over the same time period in the MNP, hairs from wild migrants were identified at a significantly higher frequency than in the WMA ($\chi^2 = 16.83$; df = 1; $P < 0.001$; n = 90). In the lean season in the WMA and the MNP hairs from wild residents were represented in the MNP at a significantly higher frequency than in the WMA ($\chi^2 = 4.71$; df = 1; $P < 0.05$; n = 97, Fig. 3.4).

The occurrence of six categories of items found in the faecal samples from the MNP and the WMA was calculated (Fig. 3.5; Fig 3.6). In both locations the seasonal representation of the six items was similar. Insect remains were found in a significantly higher number of faecal samples collected during the peak season than in the lean season in the WMA ($\chi^2 = 7.45$; df = 1; $p < 0.005$; n = 52) and the MNP ($\chi^2 = 3.87$; df = 1; $p < 0.005$; n = 51). Hairs were found in almost every faecal sample collected and bone fragments were also commonly found. The remains of edible plants were also found in a small percentage of samples from both areas. In the MNP these consisted entirely of melon (*Citrillus* sp) seeds while in the WMA melon and brandy bush seeds (*Grewia* sp) were identified.

3.3.3 Bone accumulations

Using minimum number of individual animals (MNI)(Klein & Cruz-Uribe 1984) cattle, zebra and goat/sheep made up most of the bones from the two dens surveyed in the WMA. Livestock made up 48 % of the accumulation and a total of 13 mammal species was represented (Table 3.2). Carnivores made up 16 % with brown hyaena and black-backed jackal being the most common (Lacruz & Maude 2005). Resident species made up 82 % and migratory species only 19 % (zebra) of the bone accumulations. A high percentage of the juveniles was cattle, with the other juveniles being zebra, brown hyaena or goat/sheep.

Zebra, wildebeest and springbok made up most of the bones from the three dens surveyed in the MNP. Livestock made up a small percentage of the accumulation and a total of 14 mammal species was represented. Carnivores made up 23 % with black-backed jackal, brown hyaena and bat-eared fox being the most common. In the WMA domestic species were the most highly represented and in the MNP both migrants and wild residents were the most abundant (Fig. 3.7). There was a highly significant

Table 3.1. Percentage of faecal samples containing each mammal food type.

Food Type	**WMA**		**MNP**	
	Peak n = 40	**Lean n = 53**	**Peak n = 51**	**Lean n = 43**
Livestock*	72.5	58.5	19.6	11.6
Zebra	20	7.6	62.7	44.1
Wildebeest	2.5	0	5.9	9.3
Kudu	0	1.9	3.9	0
Springbok	0	0	0	4.7
Impala (*Aepyceros melampus*)	0	1.9	0	0
Aardvark	2.5	1.9	0	2.3
Porcupine	2.5	0	0	7
Springhare	7.5	11.3	11.8	11.6
Cape Hare	7.5	13.2	11.8	41.9
Lion	0	1.9	0	0
Black-backed jackal	2.5	11.3	0	2.3
Aardwolf	0	1.9	0	0
Number of Mammals	**8**	**10**	**6**	**9**

* Livestock is recorded as one mammal species

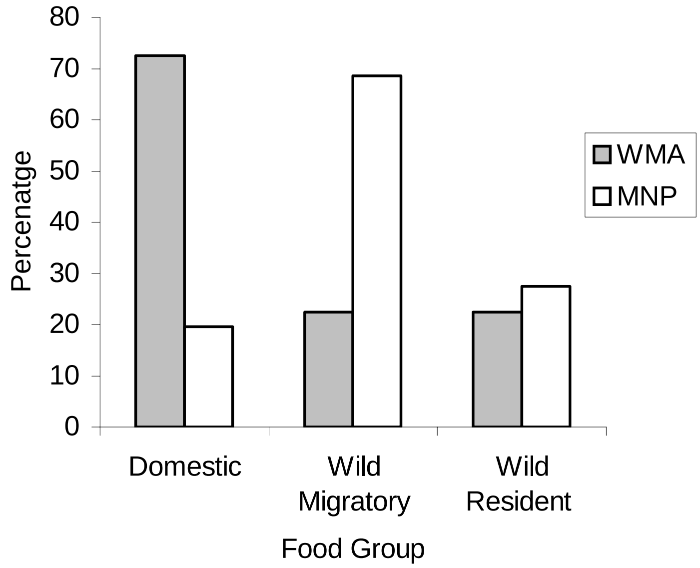

Figure 3.3 The Percentage of hairs for each food group found in faecal samples expressed as a percentage of the total for the peak season in the WMA and the MNP.

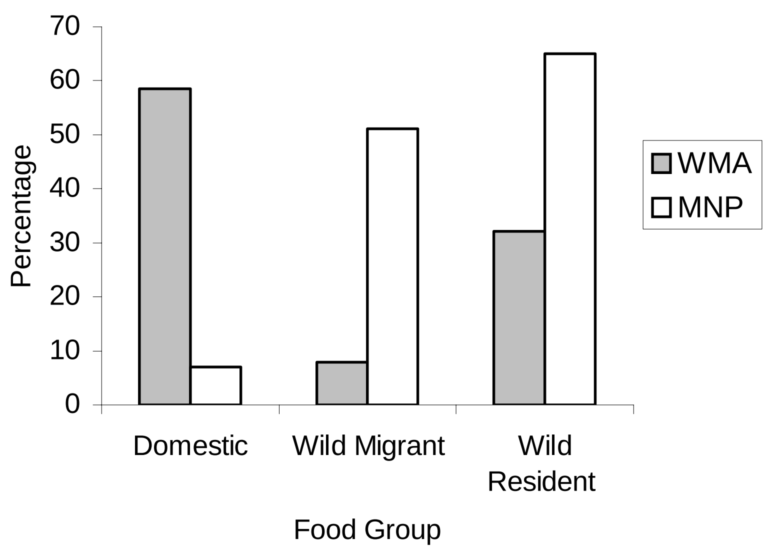

Figure 3.4 Percentage of hairs from three food groups found in faecal samples from the lean season in the WMA and the MNP.

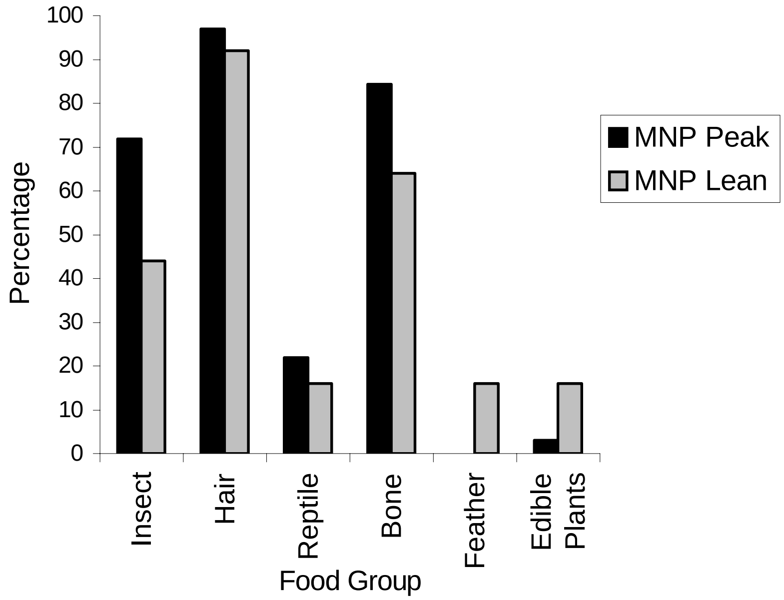

Figure 3.5. The percentage of faecal samples found in the MNP containing each food group over the peak (n = 51) and lean (n = 43) season.

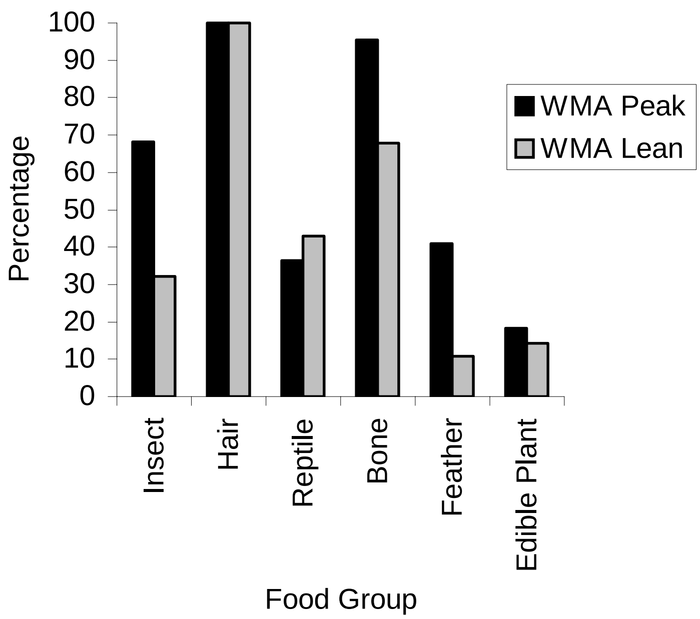

Figure 3.6. The percentage of the faecal samples found in the WMA containing each food group over the peak (n = 40) and lean (n = 53) season.

Table 3.2. Minimum number of individual animals (MNI) represented by the bone accumulations found at five brown hyaena den sites, expressed as a percentage.

Species	Den sites in MNP (N=43)			Den sites in WMA (N=31)		
	MNI	Adults	Juveniles	MNI	Adults	Juveniles
	%	%	%	%	%	%
Zebra	28	19	46	19	19	20
Wildebeest	16	16	15	0	0	0
Springbok	12	13	8	3	5	0
Steenbok	5	6	0	0	0	0
Duiker (*Sylvicapra grimmia*)	2	3	0	3	5	0
Kudu	0	0	0	3	5	0
Aardvark	2	3	0	3	5	0
Cape Fox (*Vulpes chama)*	2	3	0	0	0	0
Aardwolf	2	3	0	0	0	0
Bat-eared Fox	5	6	0	0	0	0
Black-backed Jackal	7	9	0	6	10	0
Brown Hyaena	5	0	15	6	0	20
Honey badger	0	0	0	3	5	0
African Wildcat	7	9	0	0	0	0
Porcupine	0	0	0	3	5	0
Cape Hare	2	3	0	0	0	0
Horse	0	0	0	3	5	0
Donkey	0	0	0	3	5	0
Cattle	5	6	15	29	19	50
Goat/Sheep	0	0	0	13	14	10

* Adults and juveniles are expressed as a percentage of the total number of adults and juveniles recorded.

difference between the minimum number of individual animals (MNI) of livestock in the MNP compared to livestock in the WMA ($\chi^2 = 20.34$; df = 1; $P < 0.001$; n = 73). There was also a significant difference between the MNI of migrants in the MNP compared to the migrants in the WMA ($\chi^2 = 4.97$; df = 2; $P < 0.05$; n = 74). There was no significant difference between the MNI of residents in the MNP compared to the residents in the WMA ($\chi^2 = 6.23$; df = 1; $P > 0.05$; n = 74).

3.3.4 Recorded recent food items at the den sites

Of the 25 types of food found at active den sites in the WMA, the highest percentages were cattle, zebra and goat (Table 3.3). The other 22 types of food item found varied from between only1 % to 6 % of the total recorded number found. Mammal food made up 87 % of all the food types. For the peak season zebra was the most abundant food followed by cattle then goat. Livestock and zebra totaled 66 % of the overall peak season food items found at the den sites. Over the lean season livestock made up 53 % of the food items with the other 47 % being spread between 13 different food types, all of which are each represented at low percentages. There was a highly significant difference between the number of livestock food items recorded in the WMA compared to the MNP ($\chi^2 = 22.94$; df = 1; $P < 0.001$; n = 139). Reptile remains were recorded in the WMA but not in the MNP.

Identified food items at the two active den sites in the MNP showed that of the 17 types of food item the highest percentage was zebra, followed by wildebeest and then porcupine (Table 3.3). The only food remains of a livestock species identified were that of a cow. Over the peak season there were seven food types with zebra and wildebeest

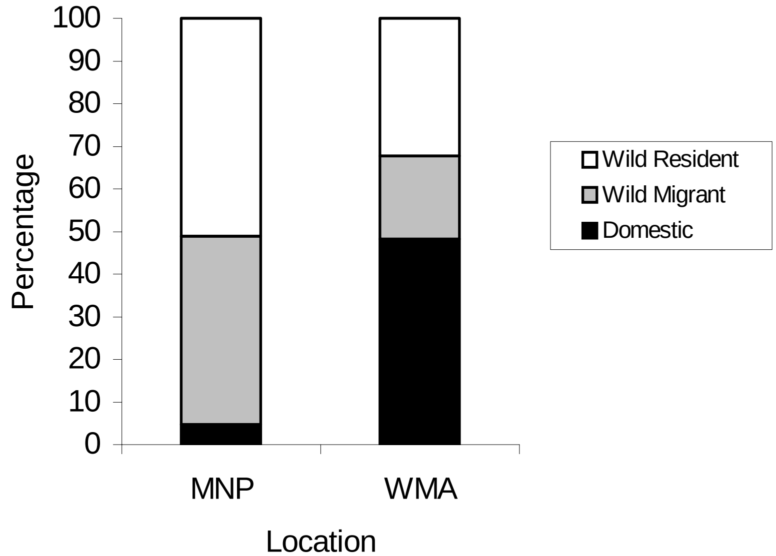

Figure 3.7. MNI represented from bone accumulations identified at den sites in two locations expressed as a percentage and grouped into three food categories.

making up by far the highest percentage of the food items recorded at the two den sites. Over the lean season zebra and wildebeest were not represented. Twelve other food types were represented with the highest being porcupine, springhare and brown hyaena, together making up 45 % of the items found. Nine other food items made up the remainder.

By dividing the food types into three groups, over the peak season in the WMA the remains from domestic animals, wild residents and wild migrants were relatively evenly found at the den sites (Fig. 3.8). In the MNP during the peak season, wild migrant remains were the most common remains found. During the lean season domestic animals and wild residents were the most common in the WMA and in the MNP only wild residents were recorded (Fig. 3.9). An edible plant was recorded as a food item in the MNP but not in the WMA (Table 3.3).

3.3.5 Direct observations of feeding

The two radio-collared brown hyaenas (M 3 and F 1) followed in the WMA were observed to visit the remains of 85 carcasses representing nine mammal species (Table 3.4). Seventy percent of these were visits to livestock carcasses of which almost all were in the cattle zone (Appendix A). There was a highly significant difference in the location of carcasses visited in and out of the cattle zone ($\chi^2 = 112$; df = 2; $P < 0.001$; n = 85). Zebra was the only other species of carcass that was frequently visited and these were mainly located in the cattle zone. Of the 85 carcasses visited, hyaenas were observed feeding on 54 of them. During the peak season brown hyaenas were observed feeding on cattle carcasses most frequently, followed by horse and then zebra (Fig. 3.10). During the lean season brown hyaenas were observed feeding on cattle carcasses most frequently, followed by zebra and then, less frequently, six other mammal species. The number of observations of brown hyaenas feeding on livestock carcasses visited was similar over the peak (24 fed from and 15 only visited) and lean (31 fed from 15 only visited) seasons and are not significantly different ($\chi^2 = 0.32$; df = 1; $P > 0.05$; n = 85). The overall percentage of the types of food did not vary much through the peak and lean seasons. Over the peak season a higher percentage of carcasses was fed on out of the cattle zone than for the lean season (Table 3.5).

Few feeding observations (15) were made when following a radio-collared brown hyaena (F2) in the MNP. These observations were also all made over the peak season (Fig. 3.11). Although not too much can be concluded from this small sample of observations, three food types were recorded that were not recorded in the WMA. These were Guinea fowl eggs (*Numida melwagris*), a black korhaan chick (*Eupodotis afraoides*) and wildebeest. Cattle were represented even though the animal followed has a peak season range that is far into the MNP. If the food types are divided into three groups, in the WMA the proportions of domestic animals, wild residents and wild migrants that the brown hyaenas were observed feeding from were very similar, with domestic being the most common (Fig. 3.12). In the MNP over the peak season wild migrants were the most common with wild residents and domestics also being represented (Fig. 3.13). In only five of the observations of small feeding instances observed in the WMA were a food type identified. These consisted of three insects and two small rodents. The average distance between small feeding instances was less in the peak (2.8 km) than in the lean season (5.3 km) and less out of the cattle zone (2.6 km) than in the cattle zone (5.2 km).

Table 3.3. Recent food items recorded at four active den sites, two in the WMA and two in the MNP, shown as percentages of the total number of food items.

Food Item	WMA N=100			MNP N=42		
	Both %	Peak %	Lean %	Both %	Peak %	Lean %
Plant	**0**	**0**	**0**	**2**	**0**	**6**
Geophite	0	0	0	2	0	6
Bird	**11**	**10**	**12**	**12**	**11**	**19**
Secretary (*Sagittarious serpentarius*)	0	0	0	2	0	6
Korhaan	1	2	0	0	0	0
Vulture (*Gyps* sp)	2	3	0	2	4	0
Flamingo (*Phoenicopterus* sp)	2	3	0	0	0	0
Guinea fowl	3	2	5	0	0	0
Crow (*Corvus* sp)	1	0	2	5	0	6
Ostrich Egg	2	0	5	2	0	6
Reptile	**2**	**0**	**5**	**0**	**0**	**0**
Snake	2	0	5	0	0	0
Mammal	**87**	**90**	**83**	**86**	**89**	**75**
Zebra	20	32	5	37	55	0
Wildebeest	1	2	0	12	18	0
Kudu	1	0	2	0	0	0
Steenbok	0	0	0	2	0	6
Springbok	1	0	2	2	0	6
Springhare	1	2	0	5	0	13
Cape hare	1	2	0	0	0	0
Aardvark	4	5	2	0	0	0
Porcupine	6	7	5	7	0	19
Striped polecat (*Ictonyx striatus*)	0	0	0	2	0	6
Caracal	0	0	0	5	4	6
Aardwolf	2	0	5	5	4	6
Black-backed jackal	4	4	5	0	0	0
Brown hyaena	1	0	2	5	0	13
Honey badger	1	2	0	2	4	0
Lion	1	0	2	0	0	0
Cow	26	16	38	2	4	0
Goat	10	14	5	0	0	0
Horse	3	2	4	0	0	0
Donkey	3	2	4	0	0	0
Sheep	1	0	2	0	0	0

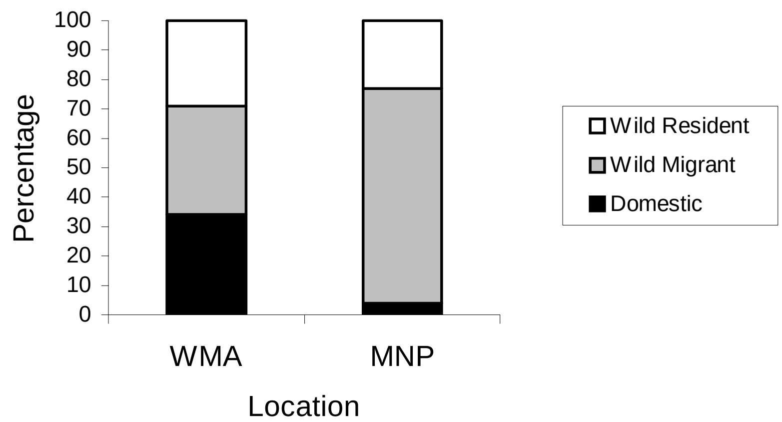

Figure 3.8. Three food groups identified as recent food items found at den sites in the WMA and the MNP over the peak season as a percentage.

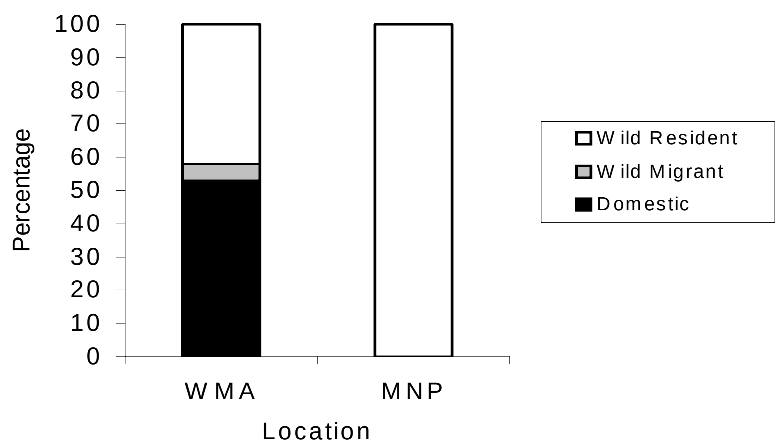

Figure 3.9. Three food groups identified as recent food items found at den sites in the WMA and the MNP over the lean season as a percentage.

Table 3.4. Identified carcasses visited and significant food eaten from observations made on two brown hyaenas foraging in the WMA in and out of the cattle zone, expressed as percentages.

Food type	**In cattle zone % (N =78)**	**Out cattle zone % (N =7)**
Cow	60	2
Horse	7	0
Goat	2	0
Donkey	2	0
Zebra	10	3
Kudu	1	0
Steenbok	1	0
Springhare	1	1
Cape hare	1	1
Unknown	5	2
Total	**91**	**9**

Table 3.5. Recorded carcasses visited and significant food eaten from observations made on two brown hyaenas (M3 and F1) foraging in the WMA (in the cattle zone and out) in the lean and peak seasons expressed as percentages. N = 85.

Food type	Peak season (%)		Lean season (%)	
	In CZ %	Out CZ %	In CZ %	Out CZ %
Cow	39	0	52	3
Horse	22	0	3	0
Goat	0	0	6	0
Donkey	0	0	3	0
Zebra	4	13	16	0
Kudu	0	0	3	0
Steenbok	0	0	3	0
Springhare	0	4	3	0
Cape hare	4	0	0	0
Unknown	4	9	6	0
Total	**74**	**26**	**97**	**3**

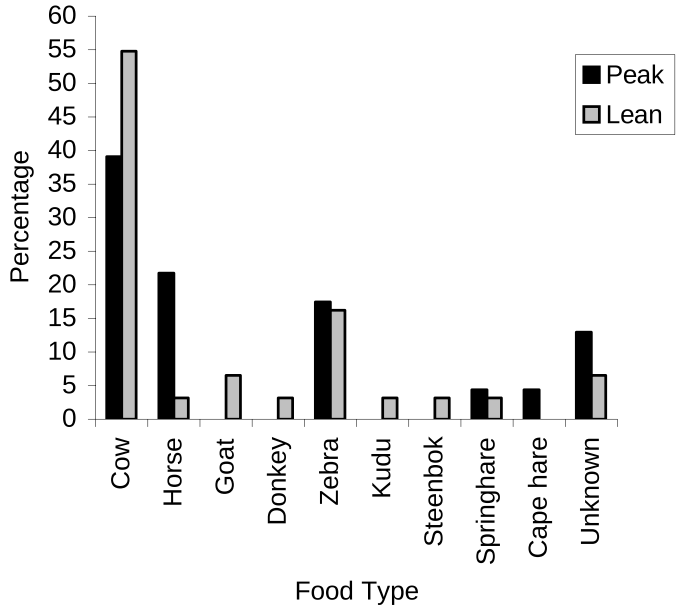

Figure 3.10. The significant food types two brown hyaenas (M 3 and F 1) were observed feeding on in the WMA over the peak and lean season expressed as a percentage.

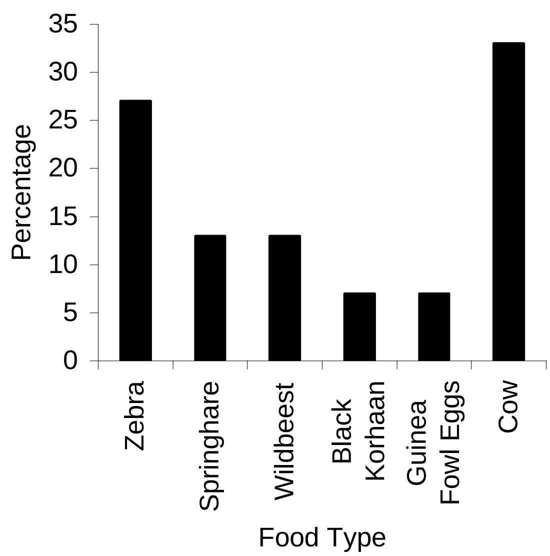

Figure 3.11. The significant food types one brown hyaena (F2) was observed feeding on in the MNP over the peak season expressed as a percentage.

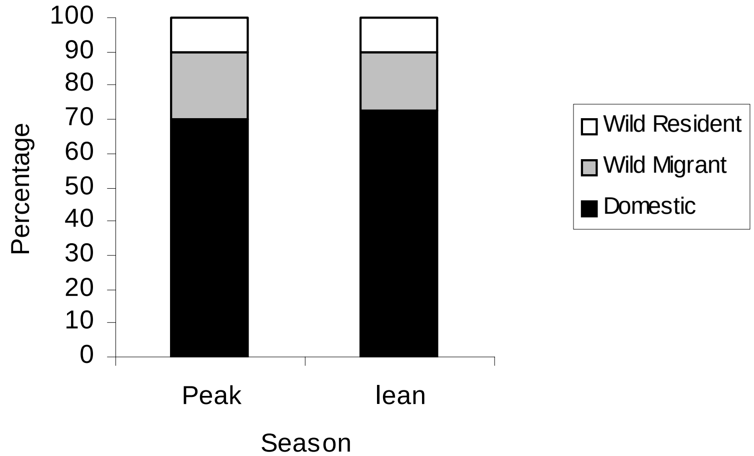

Figure 3.12. Three food groups that brown hyaenas were observed feeding from in the WMA over the peak and lean season as a percentage.

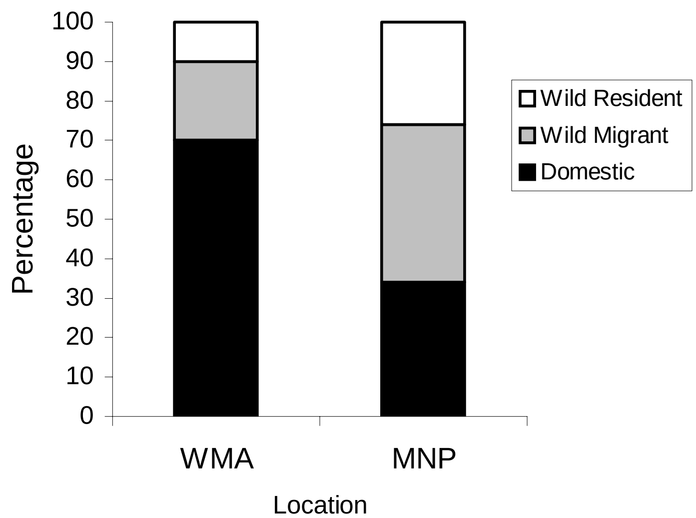

Figure 3.13. Three food groups that brown hyaenas were observed feeding from in the WMA and the MNP over the peak season as a percentage.

3.3.6 Niche breadth and species richness

The niche breadth was calculated using the dietary data from recent food items found at the den sites as this method had data available on the diet of the brown hyaenas over the two seasons in the MNP and the WMA. It was also considered to be the most suitable method for calculating niche breadth as it identified more species eaten by the hyaenas in each season when compared to the other methods. The total number of identified species eaten by the hyaenas in each location (species richness) was calculated using all the methods apart from bone accumulations at the den sites, as there was no seasonal data available from this method. In the WMA the niche breadth was very similar between the peak and the lean seasons and species richness was highest in the lean season (Table 3.6). In the MNP niche breadth was 3.4 times greater in the lean season than the peak season and species richness was highest in the lean season.

3.3.7 Foraging and Hunting Behaviour

In the WMA of the significant feeding observations made, 93 % was on scavenged mammal carcasses, 3.7 % was hunted (one instance of a springhare and one of Cape hare) and the remaining 3.7 % consisted of two instances where the source of food was unconfirmed. One was a suspected kill of a steenbok (*Raphicerus campestris*) that occurred when the brown hyaena emerged from a thick clump of trees with a very bloody steenbok (that appeared to have died very recently) in its mouth. It was however possible that initially the brown hyaena had robbed the steenbok from another predator or discovered it freshly dead and not actually hunted it. Mills (1990) recorded a brown hyaena robbing a caracal (*Caracal caracal*) of fresh carcasses in the southern Kalahari.

On a separate occasion a brown hyaena was observed determinedly chasing a steenbok for a distance of more than 50 m without success. The other instance was a suspected robbery of a springhare from two cheetahs. While foraging the brown hyaena was observed to change direction and run rapidly towards two adult cheetahs at which point visual contact with the brown hyaena was lost. Two minutes later the brown hyaena had a very bloody springhare in its mouth and the cheetah had moved away. There were two recorded instances of hunting non-significant mammal food items. These were on rats or mice. Brown hyaenas were observed interacting with cattle and horses on several occasions. In all cases no hunting behavior (stalking, rapid movement towards or chasing) was shown and in most cases the brown hyaenas changed direction to move away from the livestock. The livestock also did not show any obvious signs of alarm due of the presence of the brown hyaenas. No interactions were seen between brown hyaenas and smaller livestock animals such as goats and sheep. On two occasions a brown hyaena was observed running from dogs. Of the 15 significant feeding events observed in the MNP two were hunted, a black korhaan chick and springhare. A brown hyaena was observed chasing a black-backed jackal on one occasion but this was in an effort to successfully rob the jackal of a springhare.

3.4 DISCUSSION

3.4.1 Diet

The mortality of livestock provided the brown hyaenas in the cattle areas with a reliable, abundant and permanently available food source. Although the overall diet was diverse,

Table 3.6. Seasonal differences in the diversity (Levins niche breadth index) and species richness (number of food species eaten) of the diet in brown hyaenas in the MNP and the WMA, using data from recent food items found at den sites and faecal analysis.

Method of data collection	**Niche breadth and species richness**			
	WMA		**MNP**	
	Peak	**Lean**	**Peak**	**Lean**
Niche breadth	6.1	5.9	2.9	9.8
Species richness	17	22	12	18

scavenged livestock carcasses were the single most important food item eaten in both the peak and the lean season. Large numbers of livestock carcasses were available for the hyaenas in the WMA throughout the year for several reasons. Firstly there was frequent lion predation on livestock in the WMA in both seasons (Hemson 2001). Secondly there was also evidence of high predation by other predators such as spotted hyaena and black-backed jackal in the WMA (Chapter 5). Thirdly livestock carcasses, in particular during drought periods, were frequently found in the WMA where the cause of death as determined by the owner was disease, starvation or old age. Fourthly remains from meals eaten by people were often discarded into the surrounding area around the cattle post and made available for hyaenas to eat.

This plentiful supply of livestock carcasses meant that the difference between peak and lean season food availability to brown hyaenas was small, in particular when compared to the MNP (Chapter 4). As a consequence, in the WMA the lean and peak season diet was similar, as was the dietary breadth over the two seasons. The number of species of food eaten was slightly more in the lean season than in the peak season. This may have been in response to food availability being slightly less over the lean season compared to the peak season as the average distance between foods in the lean season was slightly more than for the peak season (Chapter 4). The arrival of large numbers of zebra into the WMA over the peak season and the availability of zebra carcasses were the main reasons for this.

In the Makgadikgadi National Park, as suggested by the optimal foraging theory, the composition of the diet varied according to the seasonal availability of food resources. Zebra, in the form of carcasses to scavenge, was the most important food source, in particular in the peak season. Lions were often recorded successfully killing zebra in the area over the peak season (Hemson 2003). Overall mortality within the zebra population throughout the Makgadikgadi is high, at 24 % per annum (Brooks 2003).

In the MNP livestock was only a minor food source for the brown hyaenas as only a small number of livestock carcasses were likely to be accessible to the brown hyaenas. Also in agreement with optimal foraging theory, when food availability was low in the lean season, the brown hyaenas increased their dietary breadth and fed off a greater number of species.

Wildebeest was recorded as an important food source in the MNP but not the WMA because a population of approximately 3 000 wildebeest (DWNP aerial survey 2001, 2002) frequented the MNP but were rarely seen in the WMA. In the MNP, zebra and wildebeest were still represented as important food sources over the lean season even though they were almost entirely absent from the area over the lean period (Fig. 3.2). This indicates that the brown hyaena were eating the remains of relatively recently died zebra and wildebeest carcasses over the peak season and then re-utilizing these old carcasses for a period of time over the lean season. It may have been possible for the brown hyaenas to access a small number of fresh carcasses over the lean season to the far west of their home range (Chapter 4). However zebra remains were not recorded being carried into the den sites by adults for the cubs as food over the lean season, even though zebra hair was frequently found in adult faecal samples. This may be because old zebra carcasses, with little soft tissue on them, may have been suitable as a food source for adults but not cubs due to the latter having smaller, less developed teeth than adults.

Fresh zebra remains with plenty of soft tissue remaining were carried to the den site often over the peak season.

Insect remains were found in a much higher percentage of faecal samples from the peak season than the lean season in both the WMA and the MNP, due to the insect population being higher over the hot, rainy peak season compared to the cold and dry lean season. The number of observed small feeding bouts on unidentified items was also more frequent over the peak season than the lean season indicating that many of these unidentified items were insects. However others may have been frogs, small reptiles such as lizards or small edible plants such as brandy bush seeds as identified in some of the faecal samples. Although independently each of these small feeding points must have a limited food value, they were eaten frequently and the combined value of food energy may be important.

3.4.2 Foraging Behaviour and Hunting

Direct observations of brown hyaenas foraging in the Makgadikgadi indicate that it is highly unlikely that brown hyaenas kill livestock. Brown hyaenas were not observed hunting livestock and all the livestock carcasses fed from were scavenged. Successful hunting attempts of any mammal were rare and by weight the largest observed kill was a springhare (approximately 3.5 kg), as has been found in other studies of this species (Mills 1978a). The killing of the brown hyaenas by farmers in retaliation for livestock predation by the hyaenas, therefore, appears to be unjustified.

Brown hyaenas followed at night were often observed visiting a carcass without feeding from it. The brown hyaenas appeared to feed off only the freshest of the carcasses that they found each night of foraging. It is likely that although these carcasses were not feed on while being observed, the hyaena may have visited and fed from them previously when the carcasses were fresher. Brown hyaenas may also visit carcasses for reasons other than food, for example they were frequently observed defecating in latrine sites and pasting on grasses located near old carcasses.

As migratory species made up between half to three quarters of the peak season diet in the Makgadikgadi National Park, optimal foraging theory would suggest a seasonal change in diet and foraging strategy during the lean season. This appeared to be the case, as Cape hare was represented in the lean season diet at a much greater percentage than the peak season. Cape hare carcasses are unlikely to be scavenged frequently, although it is not possible to be conclusive with the available data, it would appear that brown hyaenas in the MNP have adapted to a low level of food availability in the lean season by hunting Cape hares. In the WMA where lean season food resources are higher than in the MNP and carcasses were available all year round, springhares and Cape hare were represented in the diet at low levels equally over the two seasons.

3.4.3 Dietary benefits

Brown hyaenas living in the cattle areas benefited greatly from the presence of farmers through eating livestock carcasses. The fact that there was a viable population of brown hyaenas within the cattle area studied over the study period and stable populations in other cattle areas through southern Africa, would indicate that overall the hyaenas benefit from the presence of farmers in spite of their persecution. The resource dispersion hypothesis predicts that the average distance between food sources will determine home range size and that the amount of food at each point (patch richness) will determine the number of animals in each group or area (Macdonald 1983; Kruuk and Macdonald 1985). The average distance between significant meals was found to influence home range size for the brown hyaenas in the Makgadikgadi and the southern Kalahari (Chapter 4; Mills 1990). In the Makgadikgadi more closely spaced food meant that the home range sizes for hyaenas in the cattle areas were smaller than for hyaenas in the park where food was more widely spaced. In the southern Kalahari increased food patch richness was found to increase the number of brown hyaenas in a clan (Mills 1990). Thus a plentiful food supply in the form of livestock carcasses is likely to reduce the average distance between food patches and also increase the quality of each food patch, resulting in an increase of the number of brown hyaenas in any area associated with the food supply and also a reduction in home range sizes. This is likely to increase the number and density of brown hyaenas in an area. Access to livestock as a food source may, therefore, be an important reason for brown hyaena populations remaining stable outside protected areas.

However in other carnivore populations occurring alongside farmers, the carnivores also obtain a dietary advantage through feeding off livestock and yet populations are still in decline primarily due to persecution (Ogada *et al* 2003; Woodroffe 2001). There could be several reasons for this. Brown hyaenas are almost entirely nocturnal, hiding up in holes or in thick bushes during the day, they are secretive by nature, rarely vocalize and are generally very difficult to find (Mills 1990). As such they might be more difficult to catch and kill than other more conspicuous carnivores such as lion, spotted hyaena, wild dog and cheetah. Brown hyaenas are also very adaptable in their feeding behaviour and will eat almost anything that is not grass or herbage (Mills 1990). This may allow for populations of brown hyaena to exist in marginal areas where food and surface water is scarce and where other large carnivores would not be able to survive. For example brown hyaenas have been recorded living very close to or even in large cities and much of the range of the brown hyaena in southern Africa is in areas where humans and farmers live (Mills & Hofer 1998; M.G.L Mills, pers. Comm.; pers. obs.; Skinner 1976). Although brown hyaena are disliked and persecuted by the farmers in the Makgadikgadi, other carnivores such as lion are hated more and as a consequence possibly persecuted more often (Chapter 5). Brown hyaenas are unlikely to kill livestock so there is a greater chance of some farmers being more tolerant towards them compared to other known livestock predators such as lion, spotted hyaena and wild dog.

The number of people in Botswana and the number of cattle posts has increased substantially since independence in 1966 and this trend is likely to continue over the next few decades not only in Botswana but also in the range of the brown hyaena in southern Africa (central statistics office, Gaborone). Higher human densities are likely to increase the chances of carnivore populations decreasing or becoming extinct (Woodroffe 2000). The brown hyaena is one of the few large carnivores that can survive alongside farmers and still maintain viable populations. It appears to do this by exploiting available food resources by scavenging livestock, while also remaining relatively inconspicuous and avoiding being persecuted by farmers as often as other large carnivores.

3.5 CONCLUSION

Brown hyaenas living in the Makgadikgadi National Park and those in the vicinity of cattle have different diets. In the cattle areas livestock carcasses were the most important food source and other less important food types were fed on as they became seasonally available. In agreement with optimal foraging theory, dietary breadth was similar over both seasons in response to similar food availability in the peak and the lean season, due to the permanent presence of plentiful livestock remains. There was no evidence to suggest that brown hyaenas hunted livestock, thus the persecution of brown hyaenas because of perceived livestock predation by them is unjustified.

In the Makgadikgadi National Park zebra was the most important food source although several other food types were also seasonally important. In the national park, as suggested by the optimal foraging theory, the composition of the diet varied according to the seasonal availability of food resources. Also in agreement with optimal foraging theory, when food availability was low in the lean season the brown hyaenas increased their dietary breadth and fed off a greater number of species of food. In the lean season they also changed their foraging behaviour by regularly hunting Cape hare and reutilized old zebra carcasses.

Clearly brown hyaenas living in the cattle areas derived benefit from the presence of farmers through the reliable, abundant and permanently available food source provided by dead livestock. This influenced their foraging behaviour as the hyaenas took advantage of the presence of livestock carcasses. However, the killing of the brown hyaenas by farmers due to perceived livestock predation by the hyaenas must, to some degree, counter balance these benefits. Even so, the brown hyaenas' ability to take advantage of this plentiful supply of food is likely to be the primary reason that brown hyaena populations appear to be remaining stable in the cattle areas of not only the Makgadikgadi and but also through much of southern Africa (Mills & Hofer 1998, IUCN 2003).

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- Chapter 4 -

Spatial aspects of brown hyaena (*Hyaena brunnea)* ecology in the Makgadikgadi Region, Botswana.

4.1 INTRODUCTION

The spatial ecology of large carnivores that have home ranges that contain human settlements has been studied in many areas around the world (Mech 1970; Skinner 1976; Kruuk 1981; Ikeda *et al.* 1983; Ginsberg & Macdonald 1990; Stander 1991; Campbell & Hofer 1995; Karani *et al.* 1995; Marker *et al.* 1996; Frank 1998; Mladenoff & Sickely 1998; Polisar 2000; Polisar *et al.* 2003). Increasing spatial interaction between large carnivores and humans and the resulting increased predation of livestock by these carnivores has led to increased levels of carnivore and human conflict (Woodroffe 2002). Intentional killing of carnivores by humans is a major and rising threat to carnivore population viability (Rabinowitz 1986; 1986b; Landa *et al*. 1999). This carnivore and human conflict is leading to carnivore population declines in areas where carnivore species and people co-habit or interact temporarily on borders of protected areas (Woodroffe 2001).

Several studies have investigated the spatial ecology of brown hyaenas in protected areas: Mills (1982a, 1990), Mills & Mills (1982) in the southern Kalahari, Owens & Owens (1978) in the central Kalahari and Goss (1986) in the Namib Desert. Only one study, in South Africa, estimated the range of a single translocated brown hyaena in an agricultural area (Skinner & van Aarde 1981).

Many studies of carnivores suggest that the size of a home range is determined by the dispersion of food, with wider resource dispersion leading to greater home range sizes (Mills & Mills 1982, Mills 1982a; Macdonald 1983; Kruuk & Macdonald 1985; Packer 1986; Kruuk & Parish 1987). The dispersion of food resources for scavengers such as brown hyaena *(Hyaena brunnea)* can be expected to be influenced by human land use.

The objectives of this chapter are: (i) to determine if the presence of pastoralists influences the spatial ecology of brown hyaenas occurring in areas used for subsistence cattle production in the Makgadikgadi region; and (ii) to determine if home range sizes for the brown hyaenas can be explained using the resource dispersion hypothesis. Prediction 1 is that, due to greater food availability, primarily in the form of livestock carcasses, the home range sizes of brown hyaenas living in the vicinity of pastoralists will be smaller than those of hyaenas living away from human influences and livestock. Prediction 2 is that foraging patterns of brown hyaenas will be influenced by the presence of pastoralists, with brown hyaenas foraging in the vicinity of human settlements.

4.2 METHODS

4.2.1 Study Area

The data were collected in the Makgadikgadi Pans area of northern Botswana between July 2000 to June 2003. The Makgadikgadi Pans lie between 20 and 21 degrees south and 20 and 26 degrees east in the eastern central Kalahari region. The study area incorporated the eastern portion of the Makgadikgadi National Park (MNP) and an adjacent Wildlife Management Area (WMA) bordering the eastern boundary of the Makgadikgadi National Park (WMA, Figure 2.1). The MNP was gazetted as a Game Reserve in 1970 and in 1992 increased in size to 4 900 km^2 and upgraded to a national park. The study area was approximately 2 200 km^2 in size, of which 1 200 km^2 was inside of the MNP and approximately 1 000 km^2 outside of the MNP. In the study area outside of the MNP there are approximately 30 cattle posts. Subsistence livestock ownership in rural Botswana is culturally important, with the primary function of a cattle post being to provide water and good grazing for a herd of cattle while employing traditional livestock husbandry techniques (Shaw 1990). A typical cattle post would consist of four or five traditionally built circular mud huts enclosed by a log fence, with anywhere between two to six adult residents and several children. At each cattle post there is a population of livestock that would typically consist of between 50-300 cattle (*Bos domesticus),* 10-50 goats (*Capra hircus*), 5-10 sheep (*Ovis aries)*, 5-10 donkeys (*Equus asinus*), and 2-10 horses (*Equus caballus)*. Each cattle post will also usually have five or six dogs (*Canis familiaris*) and 10 to 15 chickens. Crops such as maize, sorghum, millet and melons are cultivated during the rainy season. Subsistence farming is the principal form of agriculture in Botswana, there being in 1997 an estimated 64 707 traditional cattle posts and country wide 2.2 million head of cattle (Botswana Central Statistics Office, Twyman 2001).

The Makgadikgadi Pans system is part of the Kalahari Desert, which is officially classed as a semi-arid desert (Thomas & Shaw 1991). Rainfall is in the summer with an average of 450 mm falling from November through to April (Meynell & Parry 2002). Rainfall outside of these months is rare and the winter season from May to September is cold and dry. Annual temperatures can vary from a minimum of – 6 ^{o}C in the winter to a maximum of 42 ^{o}C in the summer (Thomas & Shaw 1991). The Makgadikgadi National Park and the surrounding area support the largest migratory movement of large

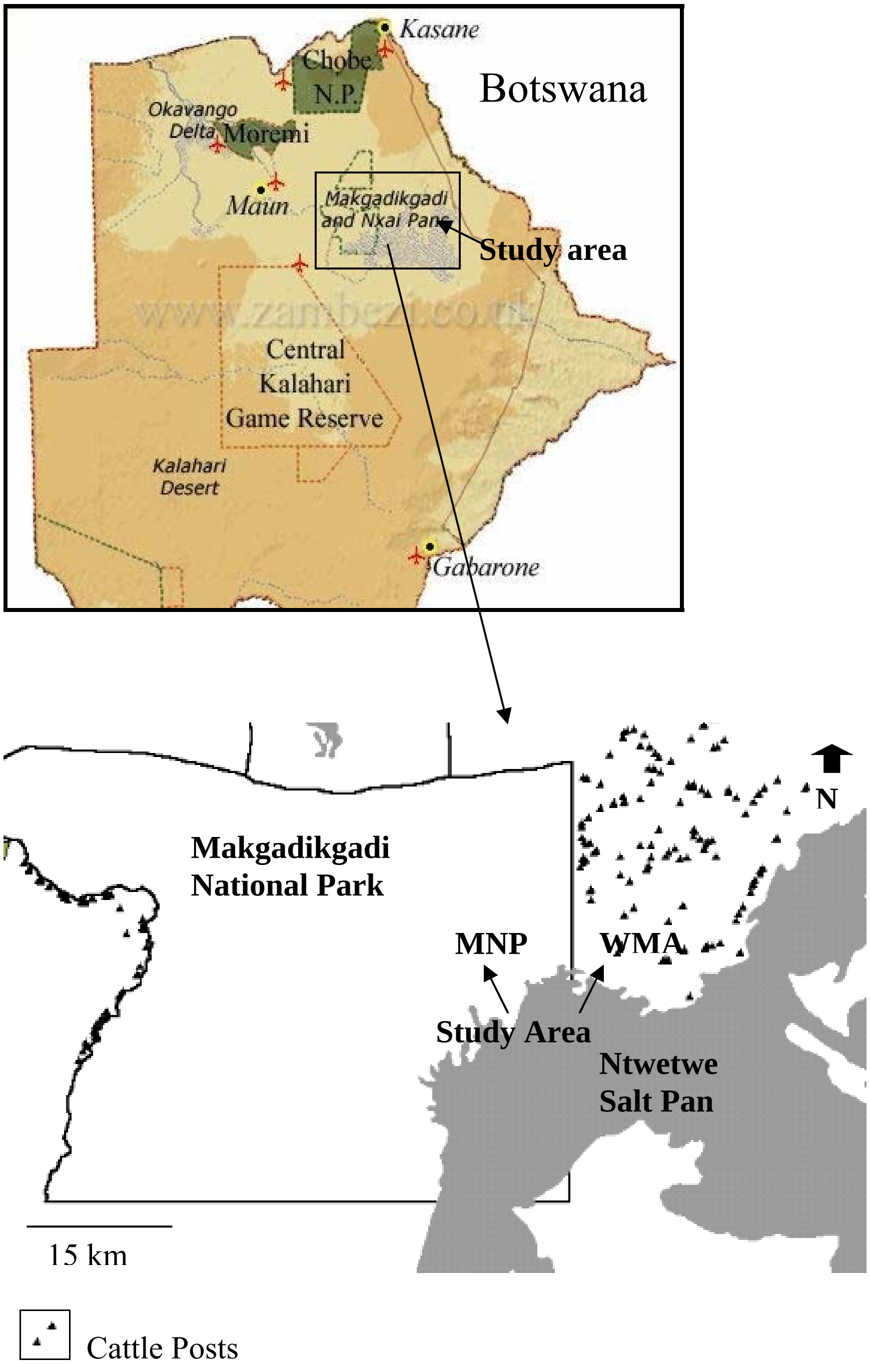


Figure 4.1.The location of the study area, in the eastern portion of the Makgadikgadi National Park (MNP) and in a cattle area (WMA) bordering the eastern boundary of the park.

herbivores in southern Africa (Kgathi & Kalikawe 1993). Approximately 13 000 burchells zebra (*Equus burchelli*) and 3 000 blue wildebeest (*Connochaetes taurinus*) move seasonally from the west of the MNP where they spend the dry season, to the east of the park where they spend the wet season in the study area (Department of wildlife and National Parks aerial survey estimates 2001, 2002). Other common herbivores in the study area include kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcus marsupilis)*, steenbok (*Raphicerus campestris*) and gemsbok (*Oryx gazelle*). Springhare (*Pedetes capensis*) and Cape hare (*Lepus capensis*) are abundant throughout. Resident carnivores include lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), caracal *(Felis caracal*), African wildcat (*Felis silvestris*), brown hyaena, black-backed jackal (*Canis mesomelas*), aardwolf (*Proteles cristatus*), bat-eared fox (*Otocyon megalotis*) and honey badger (*Mellivora capensis*). Smaller common animals include ground squirrels (*Xerus inaquris),* porcupine (H*ystrix africaeaustralis*), suricate (*Suricata suricatta*), yellow mongoose (*Cynictis penicillata*)and common and large spotted genet (*Genetta genetta & Genetta tigrina*). Aardvark (*Orycteropus afer)* also occurs in the study area.

4.2.2 Definition of seasons and zones

Two seasons were identified. The peak season, which started when the zebra and wildebeest migration arrived in the study area, and the lean season, which started when the zebra and wildebeest migration left the study area. The arrival and departure of the zebra and wildebeest was established from an ongoing research project monitoring the movement of zebra and wildebeest in the Makgadikgadi using a combination of cues (Brooks 2003). These included observations made through sightings of radio-collared (both conventional VHF and GPS) and non-collared zebra and wildebeest, detection of fresh tracks and vocalizations, observations made by pilots who flew over the study area regularly and safari operators based in the study area. The start of the peak season coincided with the start of the rains and ended when all the available surface water for drinking had gone. However the timing of the arrival in and departure from each region (MNP and WMA) was often different. Typically the zebra and wildebeest would arrive in the MNP region first and it would then be several weeks before they moved into the WMA. The zebra and wildebeest would leave the MNP first and several weeks later depart from the WMA (Brooks 2003). This was because one water hole located in the WMA often retained water for longer periods after the rains had finished for the season than those in the MNP. The time period used for the peak and lean season in the WMA and the MNP were accordingly slightly different. These time differences were taken into consideration when defining peak and lean season data for the two areas.

Estimates for the wet and dry season home ranges of the zebra and wildebeest migration were made available by the zebra and wildebeest-monitoring project in the Makgadikgadi. These home range estimates were calculated from data obtained from 15 GPS capable collars and 10 VHF collars, from which over 80 000 locations were obtained (Brooks 2003). These estimates were used to define a "core zebra and wildebeest zone" over the two seasons (Fig. 4.2). A cattle zone, representing the areas in which cattle moved, was established by placing seven GPS collars onto cows at six cattle posts, located within or near the study area, for an average period of 26.9 days for each cow. Each collar was programmed to take a fix every hour for 24 hours a day. A total of 4 233 fixes was obtained over 189 days. Seventy-four of these days were over the peak season and 115 of the days over the lean season. The average straight-line distances that the cattle moved away from their owner's cattle post were established each hour for every 24-hour period that the collars were on each cow. These distances were used to define a "cattle zone" by drawing a buffer around all the cattle posts in the study area (Fig. 4.2). Using the GPS cattle collar data it was calculated that each cow was on average furthest away from its cattle post at 13:00. The average maximum distance at 13:00 for the seven cows was 6.2 km $\pm$ 1.97 SD, range 5.9. Accordingly a buffer zone of 6.2 km was drawn around each of the cattle posts in the study area and the resulting buffer area was defined as the "cattle zone" (Fig. 3.2). This cattle zone was considered to be the area that cows most frequently used for both the peak season and lean season. The "zebra and wildebeest zones" over the two seasons are also shown in figure 3.2 (C. Brooks, pers. comm.).

4.2.3 Distribution of food

A total of 149 strip transects over a distance of 309 km were conducted by driving in a straight line at a constant speed of 20 km/hr and counting and recording carcasses, bones and other potential significant food items for a brown hyaena that were within a corridor of 12 meters (5 m either side of the car plus the width of the car, 2 m). The distance driven for each transect was 1 km, 3.5 km or 5 km. The driver of the car counted and recorded the points onto a dictaphone. The location of each transect was determined by ensuring a wide and even coverage of the entire study area. This was achieved by arbitrarily dividing the study area up into 12.3 km^2 grids and by conducting a strip transect in each of the grids in the peak and the lean seasons over a two year period from

March 2001 to March 2003.. The exact location for the start of each transect within each grid was selected randomly to ensure that there was no bias.

4.2.4 Data collection on spatial ecology

Seven radio collared brown hyaenas were observed for varying time periods from July 2000 to July 2003. Five of the hyaenas were fitted with VHF collars and two were fitted with geographical positioning system (GPS) capable collars that recorded GPS locations automatically and stored these locations on the collar (Table 4.3). Two of the VHF collared males (M1 and M2) and one of the GPS males (M4) were known sub-adult individuals (they had been observed regularly at den sites from the time they were small cubs) with fully erupted teeth but not fully-grown at the time of collaring. The remaining animals were adults. M5 and F2 were caught inside the MNP while all the others were caught in the WMA. M1a and M1b are home range estimates from the same individual male hyaena, before dispersal as a sub-adult (M1a) and after dispersal as an adult (M1b). Two types of observation were made on hyaenas wearing VHF collars. Firstly: the hyaenas were located through radio tracking and their positions recorded as a GPS co-ordinate. To ensure that the locations used for estimating home range incorporated all of the brown hyaenas movement patterns, each hyaena was located at time periods throughout the night and also on occasion during the daytime. Of all the locations obtained by tracking VHF collared brown hyaenas, 40 % of the locations were from between 18:00 to 22:00, 30 % were from between 22:01 to 02:00, 10 % were from between 02:01 to 06:00 and 20 % from between 06:01 to 17:59.

Each collared hyaena was usually located at least once every week through the peak and the lean seasons. Secondly, direct observations were performed on three brown hyaenas, when a hyaena was followed continuously (Table 4.1). Here movement was recorded with a GPS that was programmed to record points every 25 meters along with the corresponding time. The duration and/or distance over which certain activities were performed were recorded. Activities recorded were feeding, hunting and interaction with other animals as well as brown hyaenas.

The two GPS capable collars were programmed to take a GPS position every hour from 18:00 to 07:00 daily (14 fixes every night). A total of 2 332 fixes was obtained from the two GPS collars out of a programmed 2 506 over a total period of 181 days (Table 4.4). This shows a 7 % failure rate of fixes, most of which were at sunrise and sunset when the brown hyaena was likely to be down a deep hole resting.

4.2.5 Home range estimators

Home range sizes of seven hyaenas were determined using the GIS software package Arc-View. Only one fix per 24 hr period (defined as from 12:00 to 11:59 the following day) was used in the analysis to ensure independence of locations (Harris *et al.* 1990; Kenward 1992). For the VHF collars, if more than one location was available for a hyaena in a 24 hr period then the location used for home range analysis was the one where there were fewest locations available for that time period. For example, if I already had 30 locations for a brown hyaena, most of which were from between18:00 to 24:00 or between 02:00 to 06:00, then the 31st location I would select, given the choice, would be the location that was between 24:00 to 02:00. This ensured that locations from through the night were used when calculating home range size. For the GPS collars, as there were many locations available for each 24 hr period, locations were selected as follows: from day one the 18:00 location was used, from day two the 19:00 location, from day three the 20:00 location and so forth. If for one of the days a location was not available for the required time period then the next nearest time period was used. After the 07:00 location was used then for the next day the 18:00 was used again and the same pattern continued. This ensured that locations from all time periods through the night were used and any bias is avoided. The number of fixes was plotted against home range size to determine the number required to estimate a home range accurately, by assuming that an asymptote indicates sufficient fixes (Kenward 1992). This was achieved for each set of fixes for each hyaena by running the data through the Arc-View program MCP Bootstrap.

Minimum convex polygons (MCP) were used to estimate home range size (Jenrich & Turner 1969). Minimum convex polygons are heavily influenced by outlying points and may include large unused areas (Harris *et al.*1990). To reduce the effects of outlying points, 5 % of them were removed and the figure is presented as MCP (95 %). Straight-line distance is calculated by working out the straight-line distances between each consecutive GPS location recorded by the GPS collars and then adding the results for any given time period. There is much overlap in the use of the terms “home range” and “territory” (Wilson 1975). For the sake of clarity the area that the individual brown hyaenas utilized is described as a home range. As the observed behaviour of the brown hyaenas studied in each clan meets the criteria for a territorial system, the area that the entire clan utilized is described as a territory (Davies 1978).

To determine the activity profiles of the hyaenas tracked, fixes (GPS locations) obtained for each animal were grouped into three categories: (1) all (2) resting or (3) foraging. The analysis showed that the generalized pattern of activity for the hyaenas was to be active from sunset to sunrise with occasional resting periods through the night. Accordingly the fixes for the GPS collars were programmed to capture this active period by taking GPS locations on the hour from 18:00 to 07:00. All of the fixes were used when looking at overall utilisation of home range. For resting fixes the nearest fix to sunset (the first fix of the night, usually at 18:00 or 19:00) was used. If no sunset fix was available then a sunrise fix was used from the same day (06:00 or 07:00). The sunrise fix and sunset fix from the same day were almost always within a short distance of each other. The foraging fix for the GPS collars was taken to be the midnight- fix or the nearest fix to midnight as this was the fix that was midway through the night.

For the VHF collars any fix that was between 06:00 and 20:00 was classed as a resting location and a fix between 22:00 and 02:00 was classed as a foraging location. The nearest fix to midnight was used when there was more than one foraging fix between 22:00 and 02:00 and the fix closest to midday (12:00) was used if there was more than one resting fix between 06:00 and 20:00. To estimate the distance moved per night for each of the GPS collared hyaenas, the observed distance moved by three VHF collared hyaenas that were followed was compared to the straight line distance (367 km straight line distance = 572 km actual distance moved for 39 one- hour time periods). Hence for the GPS data for M4 and M5, based on the above, the calculated actual distance traveled per night was the straight-line distance per night multiplied by 156 %.

To calculate the total distance moved per night for the VHF collared hyaenas that

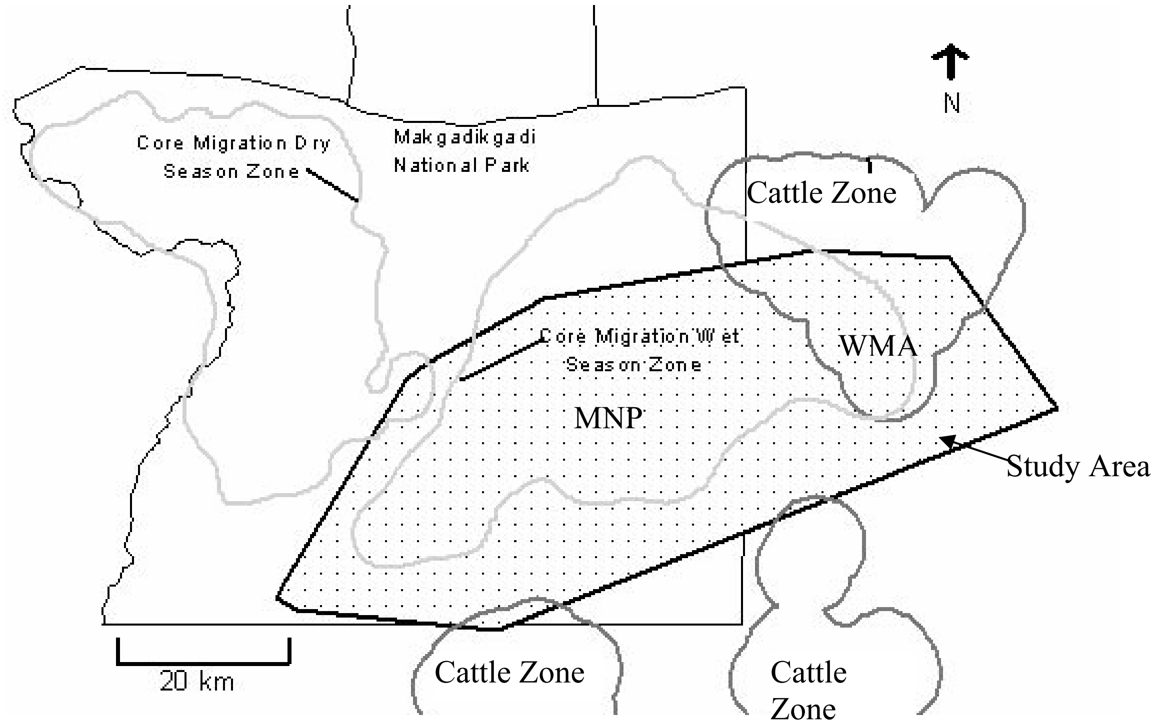


Figure 4.2.The Makgadikgadi National Park and the study area in relation to the areas used by cattle (cattle zone) and the zebra and wildebeest migration (migration zone).

Table 4.1. Summary of distances followed and duration of night follows done on three brown hyaenas F1, F2 and M3 (M = Male and F = Female) with VHF collars.

Brown Hyaena I.D	Number of follows	Season	Distance followed (km)		Time (Hours and minutes)	
			Total	Mean per follow	Total	Mean per follow
F1	21(+2)*	Both	300.3	15.8	88h 53m	4h 12m
	11	Peak	135.5	12.3	49h 23m	4h 29m
	10(+2)*	Lean	164.8	16.5	39h 30m	3h 57m
F2	7	Peak	99.2	14.2	45h 23m	6h 29m
M3	21(+1)*	Both	325.7	15.5	86h 23m	4h 07m
	7	Peak	97.9	13.9	28h 06m	4h 01m
	14(+1)*	Lean	227.8	15.2	58h 17m	4h10m
Total	**49(+3)***	**Both**	**725.1**	**14.8**	**220h 39m**	**4h 30m**

***(+)** Shows the number of follows where distance and time was not recorded but other data from the follow have been used.

were only followed for part of the night, the following was done: GPS collar M4 was typically found to become active between 18:00 and 20:00 and to rest for the day between 05:00 and 07:00. It can be reasonably concluded that a typical night of activity for a hyaena in the WMA began at approximately 19:00 and ended at 06:00, a period of 11 hours. Accordingly the average distance moved per hour for each of the VHF collars was multiplied by 11 hrs to estimate the distance moved per night.

4.3 RESULTS

4.3.1 Distribution of food

Strip transects in the WMA showed that the average distance between food items out of the cattle zone was 17 times greater than in the cattle zone (Table 4.2). In the MNP the lean season average distance between significant foods was 2.3 times greater than for the peak season. The average distance between food items in the cattle zone of the WMA over the peak season was similar to the peak season in the MNP. However over the lean season in the MNP the average distance was 2.3 times greater than for the lean season in the cattle zone. However if the number of food points counted per kilometer is calculated for every strip transect conducted in each area, there is no significant difference in the number of food points found per 1 kilometer, per transect between in the cattle zone of the WMA and in the MNP (Mann-Whitney U test: $U = 5335$; $n_1 = 61$; $n_2 = 111$; $P > 0.05$) or between in the peak and the lean season in the MNP (Mann-Whitney U test: $U = 1063$; $n_1 = 32$; $n_2 = 29$; $P > 0.05$). There is no significant difference between the number of food points found per 1 kilometer, per transect in the cattle zone of the WMA and the MNP over the peak season (Mann-Whitney U test: $U = 1063$; $n_1 = 32$; $n_2 = 29$; $P > 0.05$) or between the lean season in the MNP and the lean season in the cattle zone of the WMA (Mann-Whitney U test: $U = 1175$; $n_1 = 52$; $n_2 = 29$; $P > 0.05$). Due to the low number of food points counted out of the cattle zone in the WMA it is not possible to compare statistically between this area and any other area.

Food items are significantly more abundant nearer the cattle posts than further away as, close to the cattle posts (within 1 km), the average distance between food items counted was 1.5 km, but in the rest of the cattle zone (more than 1 km away), the average distance between food items was 4.3 km. There is a significant difference between the number of food points found per 1 kilometer, per transect within 1 km of a cattle post than more than 1 km from a cattle post but still within the cattle zone (Mann-Whitney U test: $U = 629$; $n_1 = 14$; $n_2 = 56$; $P < 0.05$)

In the cattle area in the Makgadikgadi (WMA) the average distance traveled by brown hyaenas, between feeding on significant food items, was 1.3 times further in the lean season than the peak season (Table 4.3). The average distance between carcasses visited and significant food eaten was far greater out of the cattle zone than inside the cattle zone. On average a brown hyaena had to travel 2.7 times further between significant feeding events out of the cattle zone than in the cattle zone. The average distance over the peak season between carcasses visited in the MNP was 5.9 km and food eaten was 6.2 km. In the WMA in the peak season these distances were 4.6 km and 8.3 km respectively (Table 4.3).

4.3.2 Home range size and location

When the calculated home range size (using MCP 95 %) was plotted against the total number of fixes for each hyaena, an asymptote was reached for six of the eight home range estimates (Appendix B). The number of fixes required to reach an asymptote varied from 18 (M1a) to 47 (M1b). No asymptote was reached for M4 or M5. The reason for this may have been due to the method of data collection (GPS as opposed to VHF). GPS collars record all of the outlying movements, where as when radio tracking VHF collared hyaenas, many of the outlying movements are likely to be missed. This means that many more locations are likely to be required to reach an asymptote for GPS data as compared to VHF data. It may also be due to the fact that the locations used from the 2 GPS collars (M4 and M5) are from shorter time periods than for the locations used from the VHF collars.

Observations made over the study period showed that the hyaenas F1, M1a, M2, M3 and M4 were all part of the same clan. Over the duration of the study M3, M4 and F1 had similar home range sizes and large home range overlaps. M1a had, as a sub-adult hyaena from July 2000 to July 2001, a very similar home range size and area to M3, M4 and F1, and at that time was part of the same clan (Fig. 4.3). After that time period the home range moved to the east (M1b) and it appeared that he had integrated into another clan (Fig. 4.4). As a sub-adult M2 also had a similar home range to M3, M4 and F1 and was also considered to be part of the same clan until July of 2001 (Fig. 4.4.) After July of 2001 the home range for M2 also extended to the east but the animal disappeared a short time afterwards when it had only been radio tracked on a few occasions. In the cattle areas the home range size for individual hyaenas using MCP (95 %) varied from between 135 km^2 to 221 km^2 (Table 4.4). For the peak season home range size was 103 km^2 to 145 km^2 and for the lean season between 128 km^2 to 183 km^2. Home range size for hyaenas in the WMA over the lean season was approximately 1.3 times greater than the peak season. By combining all the fixes for the hyaenas in the WMA, the estimate for the territory size (MCP 95 %) of the clan in the cattle area is 245 $km^{2.}$

GPS collar M5 (in the MNP) moved over a much greater area than GPS collar M4 (in the cattle area) and had a considerably larger home range (Table 4.4, Fig. 4.5). Observations made over the study period also showed that F2 and M5 were part of the same clan that lived in the MNP (Appendix C). The home range estimate for the VHF collar, F2 (176 km^2) in the MNP is not meaningful and likely to be too small. This is because F2 was frequently not located while radio tracking, and when F2 was found it was often a biased location as it was in the vicinity of a den site where F2 had cubs and outlying locations were not obtained. Part of the reason for this was that there was no road network in MNP thus limiting the area that could be searched for F2 each night and over the rainy season much of the MNP was inaccessible. F2 was trapped and collared far out of her estimated home range, further indicating that the home range estimate is too small (Appendix D). The home range estimate for M5 is considered more meaningful than for F2 (Table 4.4). M5 had a GPS collar and the home range estimate was based on many more locations than for F2 and included all the outlying locations. The home range estimated for the peak season can be treated with some caution because it is from movement data that covered only 18 continuous days. The overall home range size for the hyaena inside the MNP was approximately 2.3 times greater than for the hyaenas in the WMA. This was calculated by dividing the home range estimate for M5 (447 km^2) by the mean of the home range sizes for the hyaenas in the WMA (192 km^2). In the MNP lean season home range was approximately 2.2 times greater than peak season home range. In the WMA there was little difference between the home range sizes for the seasons with the lean season home range being about 1.3 times greater than that of the peak season home range.

4.3.3 Home range spatial use and overlap with cattle posts

The hyaenas with home ranges in the WMA- M1a, M1b, M2, M3, M4 and F1 all had a large overlap (24 % - 98 %, mean 58 %) of total home range with the cattle zone area (Table 4.5). The cattle zone was located in the north and east of the home ranges for the hyaenas (Fig. 4.3). The percentage of the home range inside the cow zone did not vary much for all the hyaenas between the peak and the lean seasons. There is no significant difference between the percentage of the home range in the cattle zone between the peak and the lean seasons (Mann-Whitney U test: $U = 11$; $n_1 = 3$; $n_2 = 3$; $P > 0.05$). The hyaenas with home ranges inside the MNP had no overlap with the cattle zone using MCP at 95 %. For those animals in the WMA with sufficient data, a lower percentage of resting fixes were in the cattle zone compared to foraging fixes (Table 4.6). The percentage of resting fixes in the cattle zone is significantly less than for foraging fixes in the cattle zone (Mann-Whitney U test: $U = 6$; $n_1 = 3$; $n_2 = 3$; $P < 0.05$). A similar pattern occurred through the peak and lean season. There was a gradually higher percentage of fixes in the cattle zone for every successive hour from 18:00 up until 01:00 for M4 (Fig.

Table 4.2.The average distance between food items counted in strip transects conducted in the study area.

Location	Total Distance of transects (km)	Number of food points	Average distance between food points (km)
WMA	**221**	**39**	**5.7**
In cattle zone	153	38	4.0
Peak season	102	26	3.9
Lean season	51	12	4.3
Out cattle zone	68	1	68.0
Peak season	57	1	57.0
Lean season	11	0	**
MNP	**92**	**18**	**5.1**
Peak season	63	15	4.2
Lean season	29	3	9.7

Table 4.3. The average distance, in kilometers, between significant food sources over the two seasons and in and out of the cattle zone.

Season	Average distance (km) between significant:		
	Carcasses Visited	Food Eaten	Hunted Food Eaten
Total	5.6	9.9	113.8
Peak	4.6	8.3	82.9
Lean	6.7	11.2	144.8
Location			
In cattle zone	5.3	8.0	78.1
Out cattle zone	13.6	21.4	149.0

Table 4.4. Eight home range estimates in km^2 for hyeanas using MCP (95 %), M = Male and F = female.

Brown Hyaena I.D	Season	Number of nights tracked	No.of fixes used	Home Range Estimate MCP (95 %)
M1a#	Both	49	49	172
	Peak	34	34	137
M1b#	Both	19	19	216
M2	Both	22	22	221
	Peak	12	12	***
	Lean	10	10	***
M3	Both	52	52	204
	Peak	12	12	***
	Lean	40	40	179
M4**	Both	133	133(1732)*	135
	Peak	41	41 (520)*	103
	Lean	92	92(1212)*	128
M5**	Both	48	48(579)*	447
	Peak	18	18(221)*	230
	Lean	30	30(358)*	505
F1	Both	61	61	202
	Peak	23	23	145
	Lean	38	38	183
F2	Both	28	28	176
	Peak	10	10	***
	Lean	18	18	***

* Total fixes selected from
** GPS collars
*** Not sufficient data
\# Same individual over two time periods, before (a) and after (b) dispersal

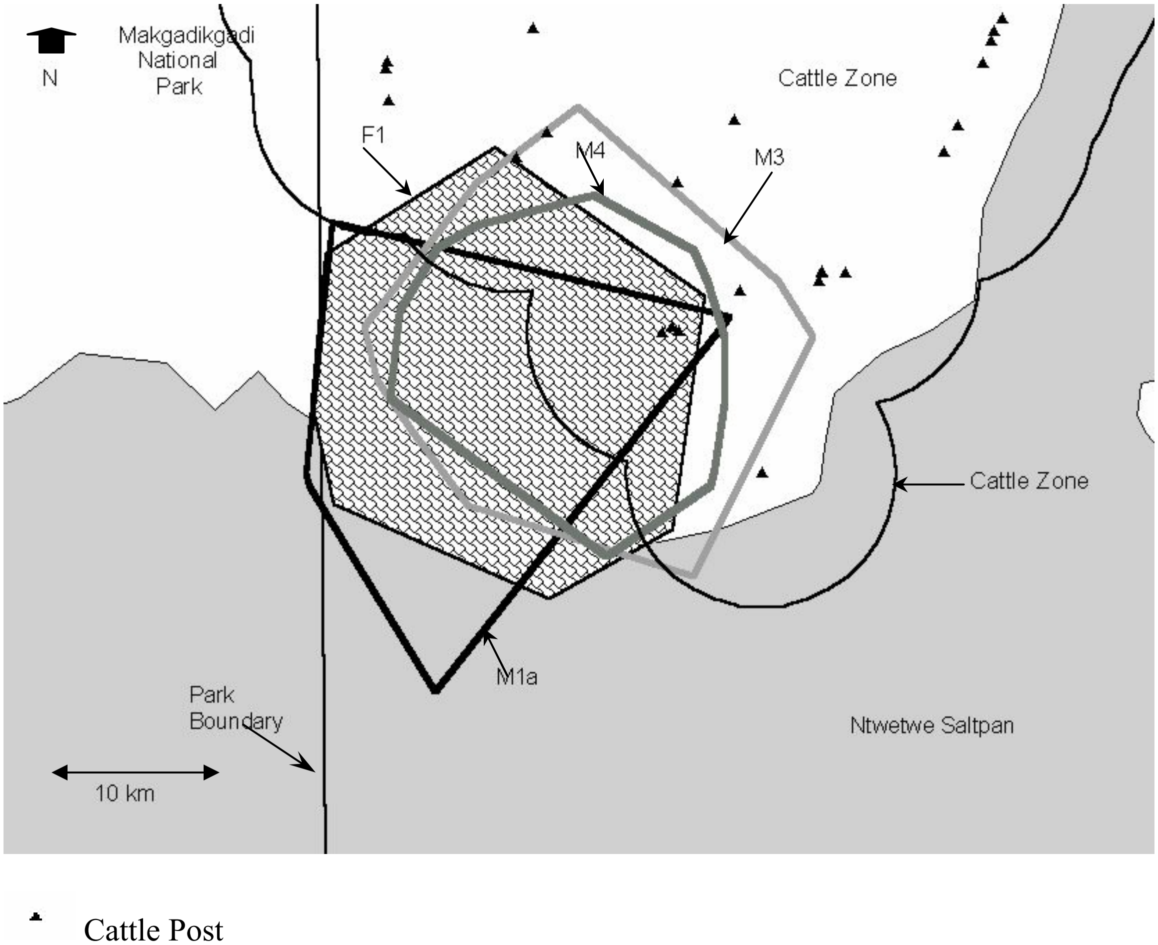
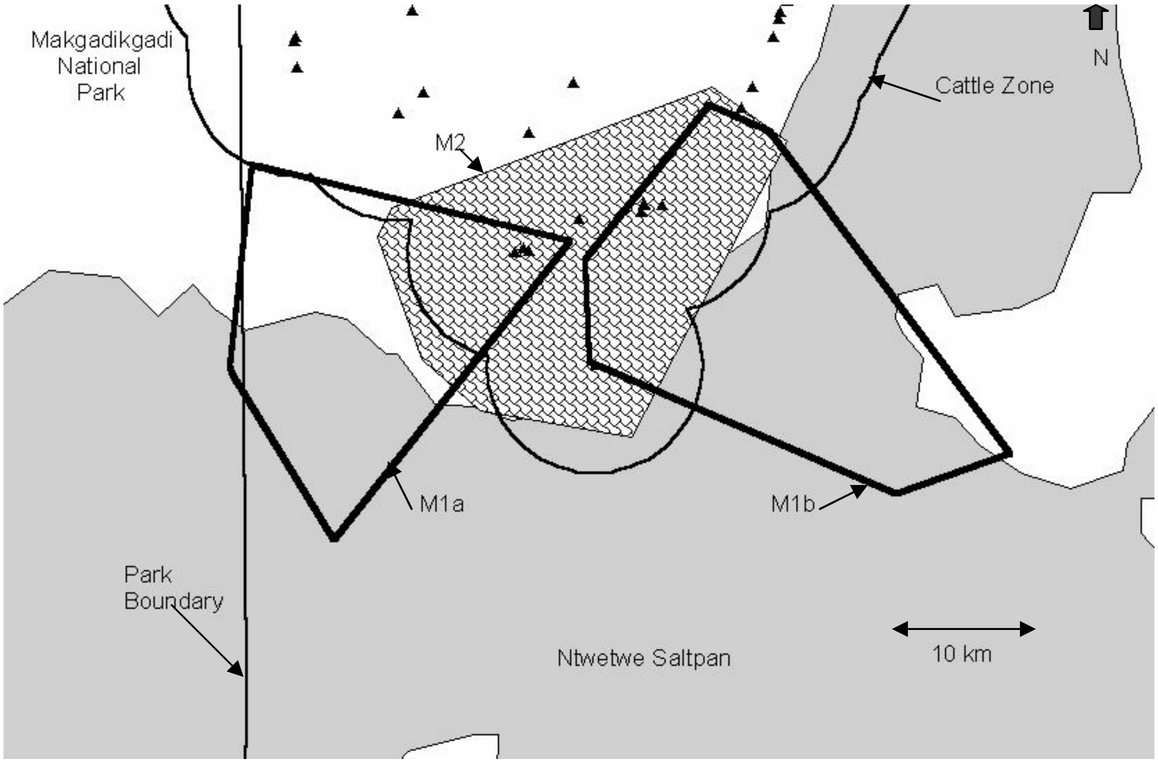


Figure 4.3. Home range estimates for four brown hyaenas in the WMA and overlap with each other and the cattle zone.



M1a = Home range from 22/09/00 to 07/07/01
M1 b = Home range from 07/09/01 to 04/0702

Figure 4.4. Home range (MCP 95 %) of M1 in the WMA, shown over two different time periods, M1a (pre dispersal) and M1b (post dispersal).

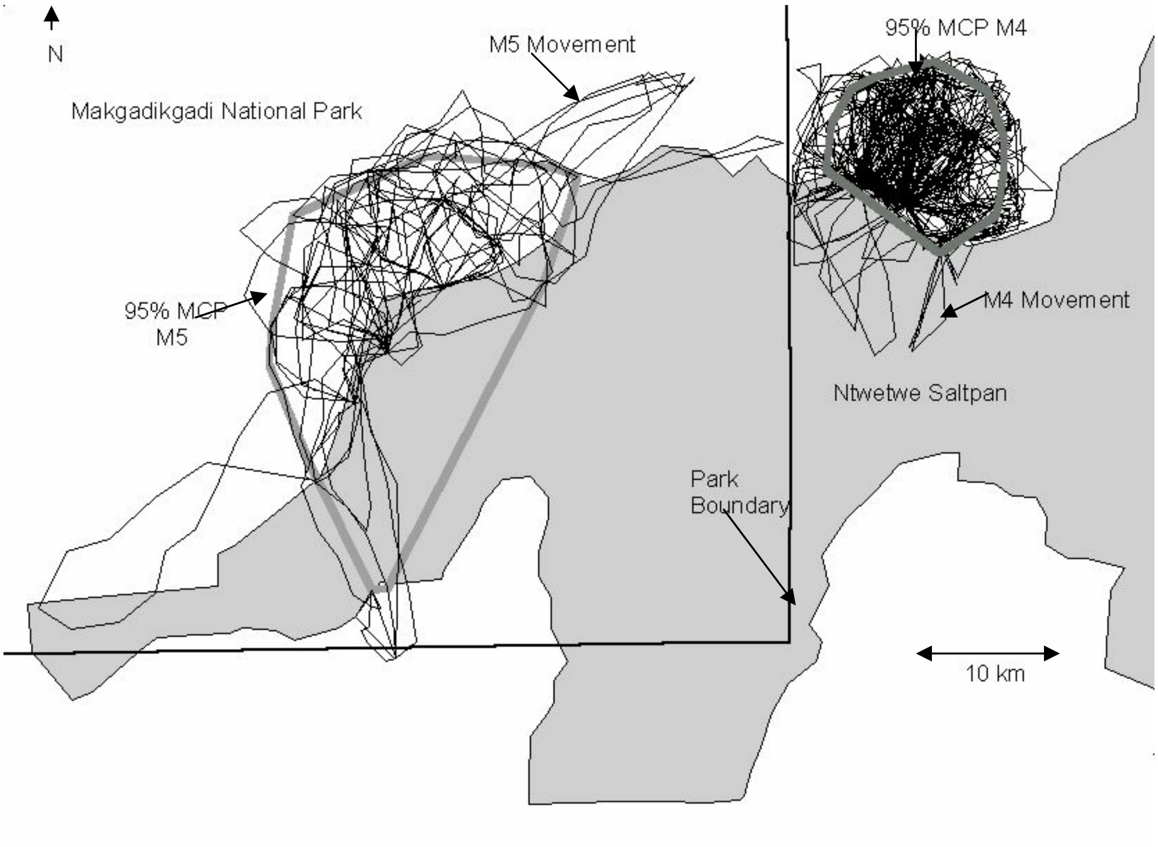


Figure 4.5. The 95 % MCP and recorded movements for M4 and M5, the two GPS collars.

4.6). From 01:00 to 07:00 there is a gradually descending percentage of fixes in the cattle zone. The pattern is similar for the peak and the lean season. M5 had a very small percentage of fixes in the cattle zone only over the lean season (3 % for resting and 7 % for foraging). This is due to the fact that although the total home range estimate is inside the MNP and out of the cattle zone, a few outlying fixes were in the cattle zone out of the park to the south.

M4 visited the clans' den site on average once every two days and M5 did so once every 6.7 days. M5's visits to the den were less frequent than those of M4 because the den in the MNP was not permanently active with cubs over the duration of M5's movement data. Foraging to within close vicinity of the cattle posts is arbitrarily decided as occurring if there is a fix within 1 km of a cattle post (Fig. 4.7). For M4 at 18:00, 19:00 and 07:00, no fixes were within 1 km of a cattle post. The highest percentage of fixes within1 km were between 01:00 and 03:00 and over the two seasons the pattern was similar. Over the peak season M4 was, on average, closest to the cattle posts between 23:00 to 03:00 and furthest away near sunset and sunrise (Fig. 4.8). No clear pattern of movement was present over the lean season (Fig. 4.8). The mean distance that M4 was away from the nearest cattle post for the peak season was 5.1 km and for the lean season 5.5 km.

The average straight-line distance traveled per night, was calculated for M4 and M5 (Table 4.7). Over the period of GPS data collection M5 in the MNP traveled on average per night highly significantly further (29.8 km) than M4 (22.1 km) (Mann-Whitney U test: $U = 10403$; $n_1 = 133$; $n_2 = 47$; $P < 0.001$). For M5 the average distance covered per night did not vary significantly between the lean (28.5 km) and the peak (32

Table 4.5. The percentage of each brown hyaena's home range, using MCP at 95 %, that was in the defined cattle zone.

Brown Hyaena I.D	**Season**	**% of home range in cow zone**
M1a	Both	24
	Peak	03
M1b	Both	41
M2	Both	98
M3	Both	72
	Lean	72
M4	Both	62
	Peak	68
	Lean	62
M5	Both	0
	Peak	0
	Lean	0
F1	Both	49
	Peak	48
	Lean	50
F2	Both	0

Table 4.6. Percentage of fixes in the defined cattle zone for: 1) all fixes; 2) resting fixes; 3) foraging fixes. Data were from three brown hyaenas.

Brown Hyaena I.D	**Season**	**% Fixes in the cow zone**		
		All	**Resting**	**Foraging**
M3	Both	73	25	68
M4	Both	60	39	75
	Peak	66	49	76
	Lean	57	34	74
M5	Both	2	2	4
	Peak	0	0	0
	Lean	3	3	7
F1	Both	57	26	59

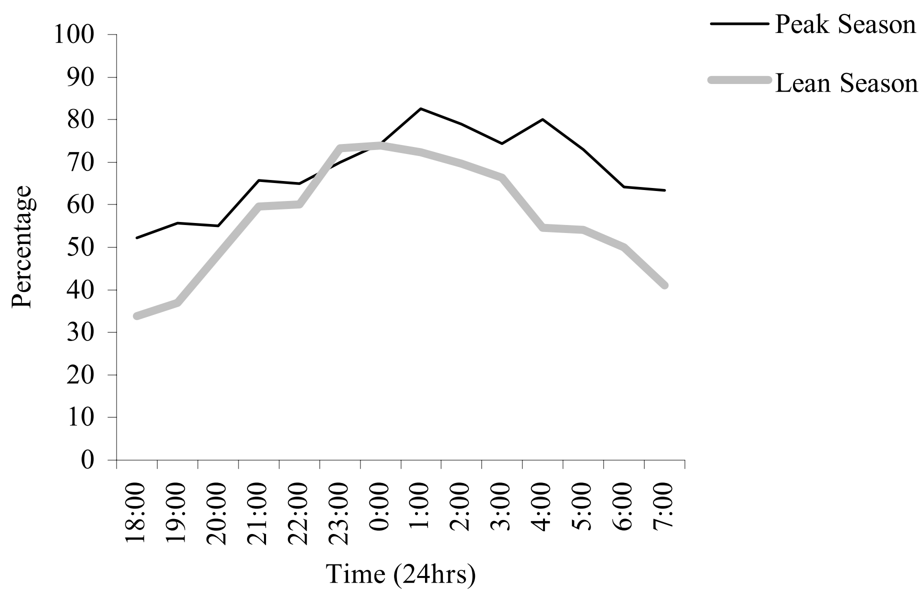


Figure 4.6. The percentage of fixes, for each time period, that were in the cattle zone for M4.

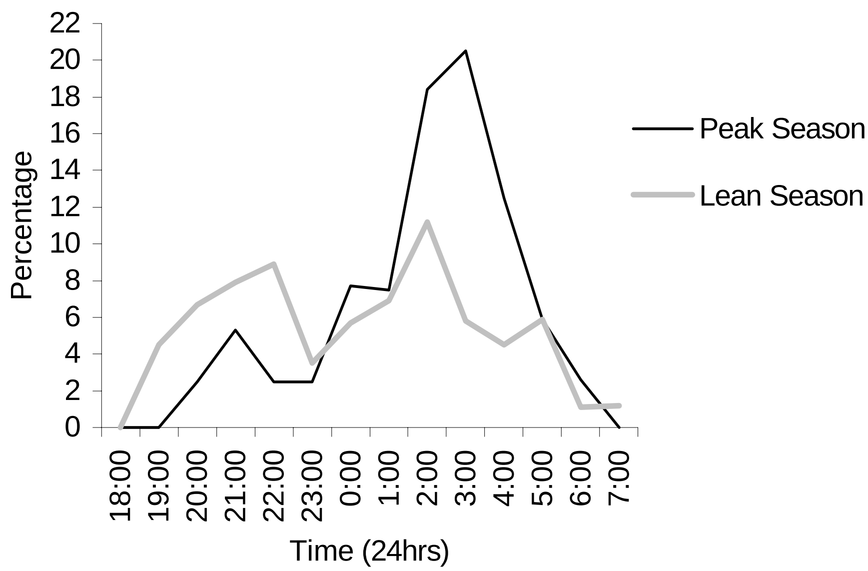


Figure 4.7. The percentage of fixes, for each time period, that were within 1 km of a cattle post for M4.

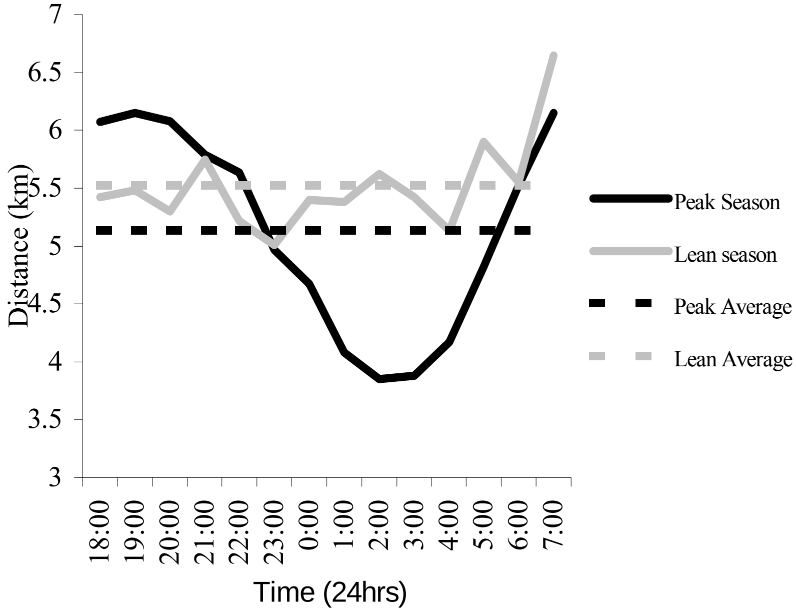


Figure 4.8. The average distance that M4 was from the nearest cattle post for each time period over the peak season and the lean season.

Table 4.7. Straight line distances foraged per night for the GPS collars and per hour for all collars.

Brown Hyaena I.D	Season	Mean Distance* per night (km)	Hour blocks covered	Mean distance* per hour (km)
M4	Both	22.1	1754	2.4
	Peak	19.3	518	1.5
	Lean	23.3	1211	1.8
M5	Both	29.8	578	2.4
	Peak	32.0	221	2.6
	Lean	28.5	358	2.3
M3	Both	**	65	2.5
	Peak	**	18	2.1
	Lean	**	47	2.6
M1	Both	**	19	2.5
F1	Both	**	64	3.0
	Peak	**	33	2.5
	Lean	**	31	3.6
F2	Peak	**	39	1.7

* = Straight line distance

Table 4.8. Calculated distances foraged per night for the 2 GPS (M4 and M5) collars and 3 VHF collars. M5 is located in the MNP.

Brown Hyaena I.D	**Season**	**Mean Distance Per Night (km)**
F1	Both	37.0
	Peak	30.1
	Lean	45.9
M3	Both	41.4
	Peak	38.5
	Lean	42.9
M4*	Both	34.5
	Peak	30.1
	Lean	36.3
M5*	Both	46.2
	Peak	49.9
	Lean	44.4

km) seasons (Mann-Whitney U test: U = 655; n_1 = 30; n_2 = 17; P > 0.05). M4 moved on average a straight-line distance of 23.3 km per night over the lean season and 19.3 km over the peak season. The distance moved per night over the lean season is highly significantly greater than for the peak season (Mann-Whitney U test: U = 1 871; n_1 = 93; n_2 = 40; P < 0.01).

Over a night of foraging, M5 moved significantly further than M4 over the lean (Mann-Whitney U test: U = 2 327; n_1 = 93; n_2 = 30; P < 0.01) and peak seasons (Mann-Whitney U test: U = 781; n_1 = 40; n_2 = 17; P < 0.001). The straight-line distance traveled per hour for the four hyaenas in the WMA varied from between 2.5 km/hr (M3) to 3.01 km/hr (F1). In all cases the average distance traveled per hour over the lean season was higher than the peak season (mean of 40.3 % higher). For M5 in the MNP the average distance traveled per hour was 2.6 km over the peak season and 2.3 km over the lean season. F2 in the MNP traveled, on average, 1.7 km per hour in the peak season. The calculated actual distances (not straight-line) moved by each hyaena over a night are shown in table 4.8.

4.4 DISCUSSION

4.4.1 Home range size

The home range sizes for the brown hyaenas in the cattle area were smaller than for the hyaenas in the Makgadikgadi National Park. The resource dispersion hypothesis predicts that territory size is determined by the dispersion pattern of food patches (Macdonald 1983; Kruuk and Macdonald 1985). Food patches closely distributed will tend towards smaller territories and food patches widely spaced will tend to larger territories. For example, the home range size for spotted hyaenas and brown hyaenas studied in the southern Kalahari, was predominantly determined by the average distance between food sites (Mills 1982a). This was also the case with red foxes (*Vulpes vulpes*) (Macdonald 1981) and European badgers (*Meles meles*) (Kruuk & Parish 1987).

In the cattle areas of the WMA food was more closely distributed than in the MNP in both the peak and lean seasons. The main reason for this is that in the cattle areas the mortality of livestock provides the brown hyaenas with an abundant and closely distributed food source throughout the year. However in the Makgadikgadi National Park, due to the absence of livestock, food is more widely distributed and more seasonally variable. As a consequence, as predicted by the resource dispersion hypothesis, the home range size for the brown hyaena in the MNP was larger than for the hyaenas in the cattle area.

In the cattle area in the Makgadikgadi (WMA), there is a response of increasing lean season home range size as the distance between food eaten increases and the resource dispersion hypothesis is supported. Factors other than the distance between each significant food item may also be playing a role in home range size. The distances between the less significant food items fed on by hyaenas such as insects, reptiles and melons, must also influence food availability and distribution and correspondingly home range size. The location of almost all the significant food items in one section of the hyaenas' home ranges, the cattle zone, may also play a role as the hyaenas in the WMA had to forage in the north and east of their home range for most of the significant food.

In the MNP the resource dispersion hypothesis is also supported as more widely spaced food is causing an increase in home range size. There is also likely to be a severely reduced patch quality over the lean season as although still present, almost all of the carcasses are old due to the zebra and wildebeest migration having left the area along with the most common large predator the lion (Hemson 2003). However the resource dispersion hypothesis predicts that patch quality will be correlated with group size and not home range size (Macdonald 1983).

In the southern Kalahari territory estimates for brown hyaena clans were between 215 km^2 and 461 km^2, with a mean of 308 km^2 (Mills1978a). These are larger than for individual brown hyaenas in the WMA of the Makgadikgadi, which have a mean size home range estimate of 192 km^2 and they are smaller than the home range estimate for M5 in the MNP, which was 447 km^2. However the estimate for the territory size of clan in the WMA in the Makgadikgadi is 245 km^2, which is very similar to three of the six-clan territory size estimates in the southern Kalahari. The other three clans had larger territories. For the three territory estimates in the southern Kalahari that were similar in size to hyaenas in the WMA, the average distance between feeding on significant food items was also similar to that of the WMA. In the central Kalahari the average dry season home range estimate per individual brown hyaena was 40 km^2 while the average clan territory size was 170 km^2 (Owens & Owens 1978, 1979b). Due to these small home range size and clan territory estimates the resource dispersion hypothesis would predict that food at the time of the study in the central Kalahari was closely distributed when compared to the southern Kalahari and the Makgadikgadi. In the Namib Desert, along the coast, the estimate for a clan's territory was 220 km^2 (Goss 1986). As most of the food was obtained from a rich supply of scavenged Cape fur seal pups (*Arctocephalus pusillus*) along a short stretch of coast the home range size is excessively large and cannot be explained in terms of food availability and distribution. Goss explained this large territory in terms of the hyaenas defending an area where food resources were available in the past and may become available again in the future. The present access to abundant food provides the hyaenas with sufficient energy for them to maintain a large home range even though there is little immediate food benefit in doing so.

4.4.2 Home range utilization

All of the hyaenas caught in the WMA had a large territory overlap with the defined cattle zone. Farmers set traps to catch and kill brown hyaenas as they enter the cattle areas scavenging for livestock carcasses (Chapter 5). Most of the hyaenas' resting locations were away from the cattle areas and a high percentage of them were located on the edge of Ntwetwe Salt Pan. Most of the foraging locations were concentrated in the cattle zone. The most common strategy adopted by hyaenas was to rest away from the cattle posts, usually down aardvark holes during the day time, and then move into the cattle post areas to forage at night. This may have evolved to minimize human contact and disturbance while resting and to maximize access to feeding opportunities while foraging. This strategy was adopted through both the peak and the lean seasons. Most of the significant food items eaten were located in the cattle zone through both seasons (Chapter 3).

The arrival of the zebra migration into the WMA over the rainy season did not noticeably change foraging patterns and areas selected for resting by the hyaenas. This was partly due to the fact that a large part of the core range for the zebra migration was in the cattle zone (Brooks 2003). Close approaches to cattle posts (within 1 km or less) were mainly between 01:00 and 03:00 and likely to be for purposes of scavenging on food that had been discarded by the residents such as remains from meals and rubbish (Chapter 3). These approaches were timed over the period when the residents and dogs are most likely to be asleep, making an encounter with them least likely. The two active den sites over the duration of the study in the WMA were both located out of the defined cattle zone along the edge of Ntwetwe Salt Pan. This may have also been to avoid disturbance from humans.

The overall distance traveled by M5 in the MNP was considerably greater than for the hyaenas in the WMA. This may be a reflection of the large disparity between food availability in the two areas year round. In the MNP the mean distance traveled every night was similar over the peak and the lean seasons even though over the lean season food is much more widely distributed. This may be because data available for M5 in the wet season are limited to only 18 nights at the start of the season. Movement data over a longer time period might show different results. The distance covered per hour for F1, who was followed continuously in the MNP the middle of the peak season, was considerably less than the distance per hour for M5 over the peak season. It is possible that as the peak season continued the average distance for M5 would have decreased as food availability increased. For the hyaenas in the WMA the mean distance traveled every night was greater over the lean than the peak season and may have been a response to the average distance between significant food items being greater in the lean than the peak season.

Factors other than food may also influence hyaena movement patterns, for example the location of the clan den. The den site is the focal point for all clan members where social interactions and meetings often take place (Mills 1983b; Owens & Owens 1979a). The mother of any cubs at the den site would need to visit frequently for the suckling of cubs and food provision. Other adult clan members also help with food provisioning of cubs and visit the den site often (Mills 1990). Territorial behaviour that involves patrolling and scent marking would influence overall movement. Mating behaviour, such as seeking a mate, may also be a factor in influencing movement patterns.

When the actual distances traveled per night by hyaenas in the Makgadikgadi are compared to other brown hyaenas studied in other areas, the distances are greater in the Makgadikgadi. In the Makgadikgadi in the WMA hyaenas moved an average of 37.6 km per night and in the MNP 46.2 km. In the central Kalahari the distances traveled by hyaenas per night were between 10 km – 20 km over the wet season and 20 km - 30 km over the dry season (Owens & Owens 1978) In the southern Kalahari hyaenas moved an average of 31.1 km per night and in the Namib Desert between 12.3 km and 21.9 km (Goss1986; Mills 1978, 1990). This may be a reflection of the various levels of food available and its distribution in the different areas. For example in the southern Kalahari the average distance moved between significant food sources was very similar to that in the WMA of the Makgadikgadi, and to the average distance traveled by the hyaenas in both areas. In the central Kalahari and the Namib Desert food is more closely distributed resulting in hyaenas traveling shorter distances on average every night.

4.5 CONCLUSIONS

When looking at the earlier predictions it can be concluded that the home range size and movement patterns of brown hyaenas are significantly influenced by the presence of pastoralists. There is a spatial benefit for brown hyaenas living in a cattle area. The size of the brown hyaenas' home ranges was determined by the dispersion of food, with wider resource dispersion leading to greater home range sizes as predicted by the resource dispersion hypothesis. Home range sizes were smaller for brown hyaenas living in the vicinity of cattle than for hyaenas living in the Makgadikgadi National Park. This was because the size of the home range was found to be dependent on the average distance between the significant food sources. In the cattle areas, due to the presence of abundant livestock carcasses, food was more closely distributed than in the Makgadikgadi National Park where there was no permanent livestock. In the national park the seasonal home range size fluctuated greatly due to the variability of seasonal food availability .The lean season home range size was larger than for the peak season. This was because food availability over the lean season was much more widely spaced than for the peak season. In the cattle areas food distribution was similar in the peak and the lean season thus seasonal home range size varied less. In the cattle area the brown hyaenas further benefited through the presence of pastoralists and livestock carcasses, as they traveled shorter distances foraging every night compared to the hyaenas in the national park.

The presence of cattle posts and livestock had an influence on the utilization of home ranges by the brown hyaenas. Movement patterns were to rest away from the cattle areas during the daytime and to forage in the cattle areas during the night. This pattern of movement may have evolved to minimize any chance of an encounter with potentially hostile humans and to maximize foraging opportunities. Home range sizes and areas selected for resting and foraging were consistent through the lean and the peak seasons.

As much of the range of the brown hyaena overlaps with pastoralists and commercial cattle farming, these findings are important when looking at the likely ways in which brown hyaenas have adapted spatially to the presence of people. The presence of pastoralists in an area occupied by brown hyaenas increases the availability of food resources by reducing the average distance between foods and thus decreases the size of the home ranges of the hyaenas living in the same area.

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- Chapter 5 -

Traditional attitudes and behaviour towards brown hyaenas (*Hyaena brunnea*) and other carnivores by subsistence pastoralists in the Makgadikgadi Region, Botswana.

5.1 INTRODUCTION

Predation of livestock causes significant conflict between predators and pastoralists worldwide. Studies on conflict between carnivores and humans in Africa have shown that carnivores may cause significant economic damage through livestock predation and in retaliation are often destroyed (Skinner 1976; Kruuk 1980; Skinner *et a*l. 1980; Berg 1998; Frank 1998; Mills 1998; Karanth *et al.* 1999; Leakey *et al.* 1999; Hoogestein 2000; Funston 2001; Hemson 2003; Mordecai 2003). This intentional killing of carnivores by humans is a major and rising threat to carnivore population viability (Rabinowitz 1986; Woodroffe & Ginsburg 1998).

In the Laikipia District of northern Kenya, in retaliation for livestock killings, farmers killed a higher number of lions, leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*) and spotted hyaenas (*Crocuta crocuta*) where the predators were found to kill a high number of livestock (Ogada *et al.* 2003). Fewer predators were killed if the number of livestock animals killed by the predators was low. In Lothagam, northern Kenya the Turkana people believed that striped hyaenas (*Hyaena hyaena*) regularly visited their homesteads to kill goats and sheep and occasionally to kill human babies (Leakey *et al.* 1999). However the closely related and ecologically similar brown hyaena (*Hyaena brunnea*) has not been recorded as being responsible for the killing of livestock in the Makgadikgadi region (Chapter 3). Brown hyaenas are generally regarded as inefficient hunters of small prey scavenging most of their food (Mills & Mills 1978; Owens & Owens 1978). There has been speculation that brown hyaenas may occasionally be responsible for small livestock killings, although these incidences are believed to be rare and isolated occurrences that are solved when the individual responsible is removed (Skinner 1976; Mills 1990). In spite of this, poisoning, trapping and hunting of brown hyaenas, in retaliation for perceived livestock predation, is believed to have had a detrimental effect on their populations and are a threat to the species in some areas (Hofer & Mills 1998).

In this chapter the understanding of and attitudes towards the brown hyaena and other carnivores by subsistence pastoralists in the Makgadikgadi are documented and assessed. There are several objectives which are: i) to determine which carnivores are considered to be livestock predators by the pastoralists and to examine the attitudes of the pastoralists towards these carnivores; ii) to determine if brown hyaenas are persecuted by the pastoralists in the Makgadikgadi region and if so, why; iii) to establish if the persecution of brown hyaenas is likely to be a reason for concern when considering brown hyaena population occurring in cattle areas; iv) to determine if educational information will lead to a better understanding of the non-predatory behaviour of the brown hyaena and correspondingly a reduction in the number of brown hyaenas killed by the pastoralists; and v) to determine the attitudes of the pastoralists towards tourism and to assess whether tourism could play a role in reducing the number of carnivores killed by the pastoralists.

5.2 METHODS

5.2.1 Study area

The study area is located to the east of the Makgadikgadi National Park and north of the Makgadikgadi salt pans (Fig. 5.1). The Makgadikgadi Pans lie between 20 and 21 degrees south and 20 and 26 degrees east in the eastern central Kalahari region. The Makgadikgadi Pans system is part of the Kalahari Desert, which is officially classed as a semi-arid desert (Thomas & Shaw 1991). Rainfall is in the summer with an average of 450 mm falling from November through to April (Meynell & Parry 2002). Rainfall outside of these months is rare and the winter season from May to September is cold and dry. Annual temperatures can vary from a minimum of – 6 ^{o}C in the winter to a maximum of 42 ^{o}C in the summer (Thomas & Shaw 1991).

Subsistence pastoralist people live and farm in the study area and reside at cattle posts. A typical cattle post would consist of four or five traditionally built circular mud huts enclosed by a log fence, with anywhere between two to six adult residents and several children. At each cattle post there is a population of livestock that would typically consist of between 50-300 cattle (*Bos domesticus),* 10-50 goats (*Capra hircus*), 5-10 sheep (*Ovis aries)*, 5-10 donkeys (*Equus asinus*), and 2-10 horses (*Equus caballus)*. Each cattle post will also usually have five or six dogs (*Canis familiaris*) and 10 to 15 with the chickens. Crops such as maize, sorghum, millet and melons are cultivated during the rainy season. Subsistence livestock ownership in rural Botswana is culturally important, with the primary function of a cattle post being to provide water and good grazing for a herd of cattle while employing traditional livestock husbandry techniques (Shaw 1990).

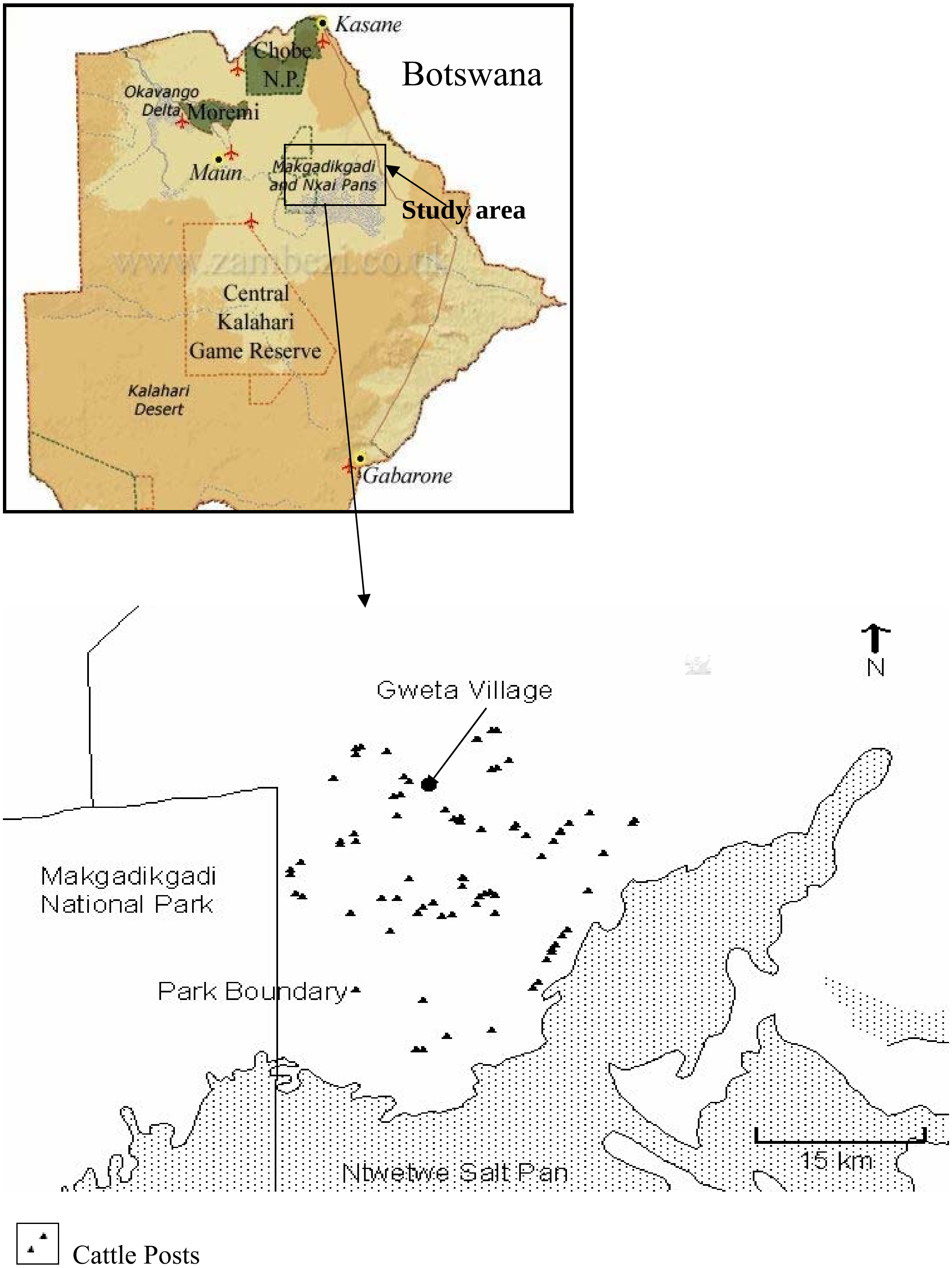

Figure 5.1.The location of the cattle posts to the east of the Makgadikgadi National Park, where the residents were questioned for the study.

Subsistence farming is the principal form of agriculture in Botswana, there being in 1997 an estimated 64 707 traditional cattle posts and country wide 2.2 million head of cattle (Botswana Central Statistics Office, Twyman 2001).

5.2.2 Data Collection

A questionnaire comprising 129 questions in 33 subject areas (appendix E) was answered by 138 subsistence Kalanga pastoralist people living in 94 cattle posts located in the eastern Makgadikgadi region (Fig. 5.1). The cattle posts varied from 1 km to 36 km away from the eastern boundary of the Makgadikgadi National Park. Each of the 138 people questioned (61 females and 77 males) represented one sampling unit. However when the question referred to predation of livestock by each carnivore species at each cattle post residence, then a single cattle post was taken as one sampling unit (appendix E, question 14).

A Kalanga translator asked the questions and recorded the responses. To ensure independence of responses each person was questioned alone. The questions were designed to obtain information in five broad categories: (1) background information such as name, age and sex of the person interviewed; (2) the perceived number and types of livestock animals killed at each cattle post per year, by each of the carnivore species; (3) the level of knowledge and understanding the person had of brown hyaenas; (4) the attitude of the person towards brown hyaenas and other carnivores, and (5) the attitude of the person towards tourism in the area.

Three types of evidence were gathered to determine if the subsistence pastoralists trapped or killed brown hyaenas over the duration of the study in the Makgadikgadi. (1)

Regular observations of 11 radio-collared brown hyaenas were made in order to determine if they were trapped, killed or injured by the pastoralists. (2) A series of questions contained within the questionnaire were about the trapping and killing of brown hyaenas by the pastoralists. (3) Miscellaneous observations of such things as baited traps discovered in the bush, gin traps present at the cattle posts and observations of dead or injured un-collared brown hyaenas.

When determining the average economic loss per cattle post of livestock to predators the values are given in US dollars. The exchange rate of 6.1 Botswana pula to the US dollar was used as this was the relative value of the currencies at the time the questionnaire was conducted. The value of each livestock species was determined by asking the pastoralists at several cattle posts what the present value for each species of livestock was. There was variability in the value of each livestock species depending on the sex, age and condition of each individual animal. However the general consensus was that an approximate value for each livestock species in US dollars was: horse \$ 330, cow \$ 217, goat or sheep \$ 33, donkey \$ 25 and a chicken \$ 5.2.

5.3 RESULTS

5.3.1 Perceived livestock predators

At the 94 different cattle posts people were asked to rank brown hyaenas, lions and black-backed jackals as killing most, plenty, some, few or none of their livestock. Brown hyaenas and lions were blamed to a similar level as regards responsibility for killing of livestock (Fig. 5.2). This does not reflect the number of actual livestock animals perceived killed by the two species. Jackals were blamed for a significantly greater percentage of livestock killings than were brown hyaenas ($\chi^2 = 49.51$; df = 1; $P < 0.001$; n = 121) and lions ($\chi^2 = 33.33$; df = 1; $P < 0.001$; n = 121). There was also a significant difference between lions being regarded as responsible for livestock killing within a 15 km location of the Makgadikgadi National Park and further than 15 km from the Makgadikgadi National Park ($\chi^2 = 8.23$; df = 1; $P < 0.01$; n = 117). Within 15 km of the MNP boundary 34.8 % of people questioned believed that lions killed some of their livestock. More than 15 km from the MNP 14.5 % believed that lions had killed some of their livestock. Actual average perceived numbers of animals killed by lions per year is 1.8 animals per cattle post, worth a total of approximately $ 221 within 15 km of the MNP boundary. More than 15 km from the MNP boundary the average is 0.4 animals killed by lions per cattle post, worth a total of approximately $ 65. There is no such variability depending on the distance from the MNP boundary for all the other cattle posts for the other perceived livestock predators. Of the carnivores, black-backed jackals were perceived to have killed the most livestock animals by a big margin (Table 5.1; Fig. 5.3). Spotted hyaenas, brown hyaenas and lions were perceived to have killed a similar number. Lions were perceived as the biggest culprit for cow and horse killings, black-backed jackals for goat/sheep killings, and spotted hyaenas for donkey killings. Of the animals brown hyaenas were blamed for killing, goats were the most common.

Of the 94 cattle posts surveyed, 63 % of them reported livestock killed by black-backed jackal, 38 % by spotted hyaena, 22 % by lion, 22 % by brown hyaena, 11 % by wild dog, 8 % by leopard and 1 % by cheetah. However the value in US dollars of the livestock believed to be killed shows that lions have the greatest economic impact

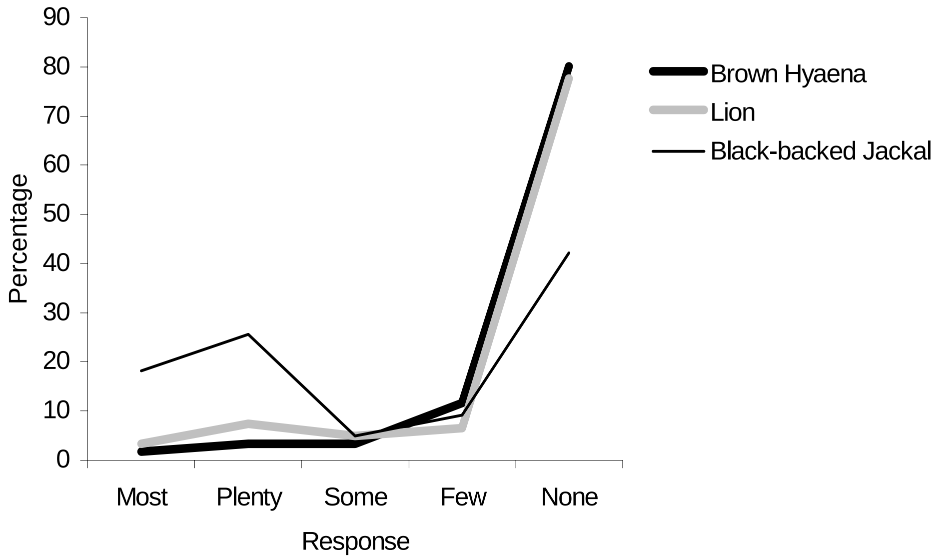

Figure 5.2. The percentage of responses to the question: Of your livestock that has been killed by predators how much has been killed by each of the three species?

Table 5.1. The perceived numbers of each livestock species killed for each carnivore and the value in US dollars ($) of livestock killed expressed as an average per cattle post.

Predator	**Perceived Number of Livestock Species Killed and Value**											
	Cow		**Donkey**		**Horse**		**Goat/Sheep**		**Chicken**		**Total**	
	N	$	N	$	N	$	N	$	N	$	N	$
Brown Hyaena	0.2	41	0.01	0.3	0	0	1.6	52.3	0	0	1.8	94
Lion	0.7	152	0.1	2.5	0.2	63	0.5	17	0	0	1.5	235
Black-backed Jackal	0	0	0	0	0	0	5.5	183	0	0	5.5	183
Spotted hyaena	0.3	59	1.2	30	0.1	20	0.5	18	0	0	2.1	127
Wild Dog	0.3	59	0.04	1	0	0	0.1	4	0	0	0.4	64
Caracal	0	0	0	0	0	0	0.5	17	0.1	0.3	0.6	17
Leopard	0.02	4	0	0	0.01	3.3	0.4	14	0	0	0.5	21
African Wild Cat	0	0	0	0	0	0	0	0	0.4	2	0.4	2
Cheetah	0	0	0	0	0	0	0.02	0.7	0	0	0.02	1
Total	1.5	315	1.3	33.6	0.3	86.3	9.2	306	0.4	2.2	12.7	744

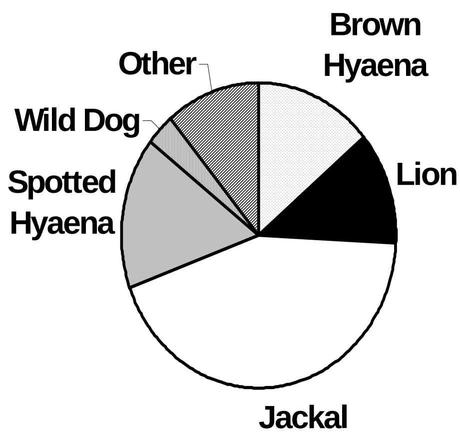

Figure 5.3. Five carnivore species and the percentage of the average number of livestock perceived to be killed per cattle post over a 12-month period.

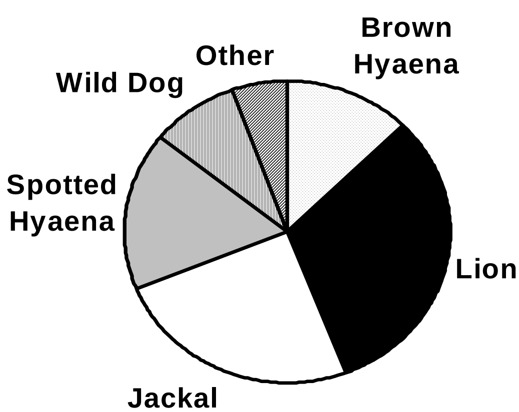

Figure 5.4. Five carnivore species and the percentage of the average cost of livestock perceived to be killed per cattle post over a 12-month period.

followed by black-backed jackals, spotted hyaena and then brown hyaena (Fig. 5.4). There is an average loss per cattle post of \$ 744 in a 12-month period of which over half is due to lions killing cows and horses and black-backed jackals killing goats/sheep. Other perceived significant costs are through spotted hyaenas and wild dog killing cows and brown hyaenas killing goats/sheep (Table 5.1). A significant correlation was found between the cost of perceived livestock killed by brown hyaenas at cattle post and the negative attitude towards the brown hyaena (Spearman rank correlation: $r_s = 0.248$; $n = 138$; $P < 0.01$).

5.3.2 Understanding of brown hyaenas by the pastoralists

When asked to name the species of hyaena occurring in the vicinity of their cattle post, 59.4 % of the people questioned answered that they were aware of the existence of the brown hyaena and 68.1 % of the spotted hyaena. However many of the people questioned (49.3 % of the total), in particular the women (62.3 %), did not mention both spotted and brown hyaena as the two species of hyaena occurring in the area (Fig. 5.5). Only 46.4 % of the people questioned claimed to have seen a brown hyaena and of these 40 % had seen a brown hyaena on one or two occasions and 60 % on more than two occasions. Of these sightings 83 % were near the cattle post and 40.7 % of them were within the last two years. Of the people who claimed to have seen a brown hyaena before, only 44.7 % could describe its appearance with some degree of accuracy. Of all people asked 56.1 % gave a roughly correct estimate as to the weight of a brown hyaena. Of the people questioned 79.1 % were aware that brown hyaenas were nocturnal and foraged at night. When questioned on the diet of brown hyaenas, 54.8 % said that they ate meat, 11.1 %

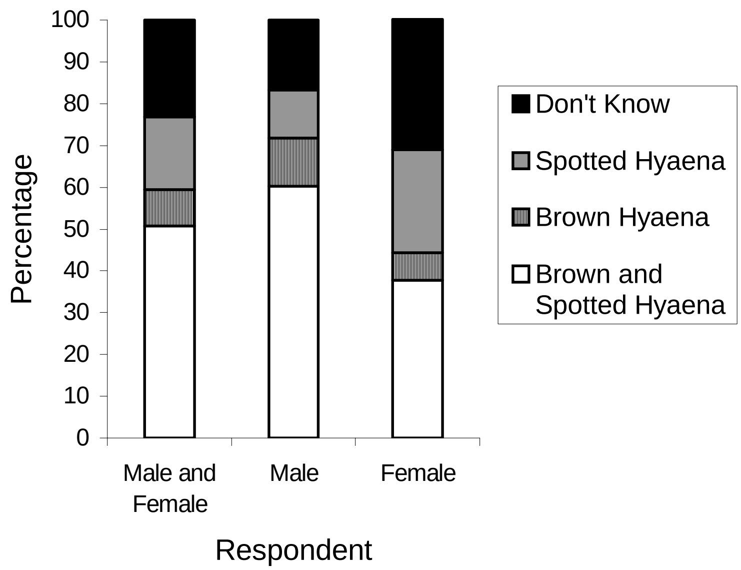

Figure 5.5. Responses to the question of which types of hyaena there are in the area, expressed as a percentage of the total number of people questioned in each respondent class.

livestock, 13.3 % both meat and livestock, 4.4 % carrion, 3.7 % melons and 2.2 % small game. It was believed by 60.3 % of the people questioned that brown hyaenas live in the bush or in the salt pans, 5.9 % down holes and 29.4 % did not know. Of those questioned 55.5 % said that brown hyaena cubs lived down holes.

5.3.3 Attitudes towards brown hyaenas and other carnivores

All the people questioned believed that brown hyaenas visited their cattle post at regular intervals: 44.7 % believed that brown hyaenas visited their cattle post every few days, 11.8 % every few weeks and 22.4 % every few months. Of those questioned 87.8 % thought the reason for these visits was to destroy their property by killing livestock or eating cultivated melons from their gardens. Of the people asked whether brown hyaenas should be allowed live in the same area as their cattle posts, 79 % said no and 16.7 % said yes. Of those questioned 66.7 % questioned felt that brown hyaenas did "bad things" and 10.1 % felt that brown hyaenas did something good.

The overall attitude towards brown hyaenas, black-backed jackals and lions was one of hate (responded with "hate" or "hate very much", Fig. 5.6). When those people who hated brown hyaenas were asked why they hated them, the responses varied: 66.3 % said they hated them because they killed their livestock; 8.9 % because they ate their melons; 9.9 % because they killed livestock and ate their melons; 5.9 % because they were troublesome and destructive; 3 % because they harmed people; 2 % because they hate all predators; 1 % because they live in the bush; and 1 % because they hated the law preventing them from killing brown hyaenas. Of the people questioned who mentioned that brown hyaenas killed livestock and /or ate cultivated melons (group one) a high percentage hated brown hyaenas (Fig. 5.7.). Of those who did not mention that brown hyaenas killed livestock and/or ate cultivated melons (group two) a low percentage hated brown hyaenas. The number of people hating brown hyaenas (responding with hate and hate very much) in group one was significantly different from group two ($\chi^2 = 12.6$; df = 1; $P < 0.001$; n = 127).

When comparing the attitudes of the people towards brown hyaenas, lions and jackals (the number of people who responded with like very much, like, indifferent, hate and hate very much for the three species) there was a significant difference ($\chi^2 = 42.4$; df = 1; $P < 0.001$; n = 355). Of the people questioned 30.4 % were either indifferent towards brown hyaenas or liked them. The percentages for the others were only 8.1 % for lions and 1.1 % for black-backed jackals. The reasons given for liking brown hyaenas were because they were not as troublesome as other predators (90.7 %), it was possible to coexist with them (6.1 %) and the tourists liked them (3 %). Of the respondents who hated lions, 84.4 % hated them because they killed livestock and 9.4 % because they were considered dangerous to humans. The primary reasons given for hating jackals were because they either killed livestock (66.7 %), or they ate melons (6.4 %) and they ate melons and killed livestock (24.4 %). Reasons given for liking lions were, because they were nature's resources (60 %), they were attractive (20 %) and they were the totems of the person questioned (20 %). No one questioned liked black-backed jackals.

Of the 21 cattle posts (22 %) where any livestock had been perceived as killed by brown hyaenas over the last 12 months, 95.2 % of the people questioned hated brown hyaenas. Of the cattle posts where no livestock was believed to have been killed by brown hyaenas over the last 12 months 65.8 % of the people questioned hated brown

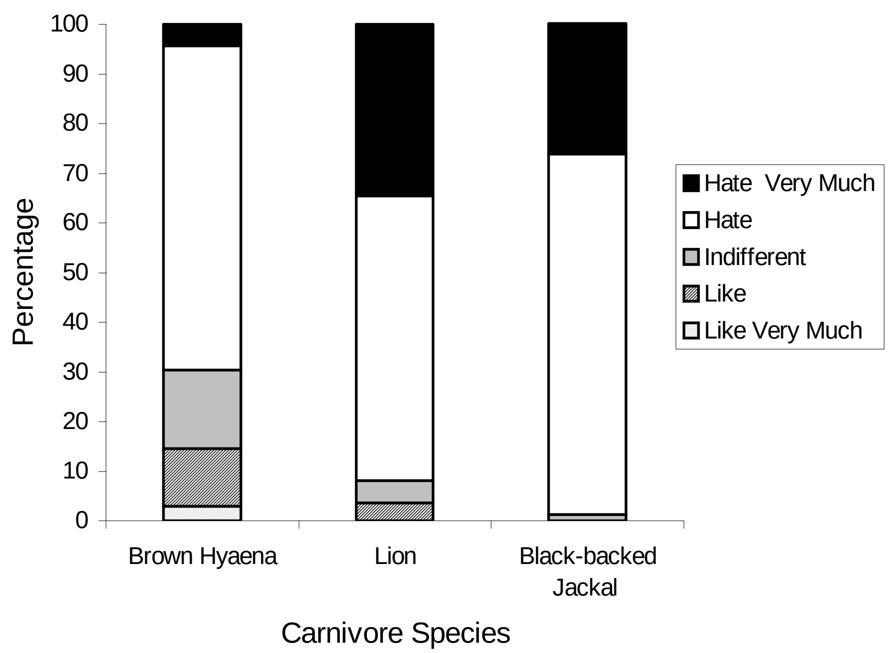

Figure 5.6. The attitude of subsistence cattle post farmers towards three carnivore species living in the same area as the farmers.

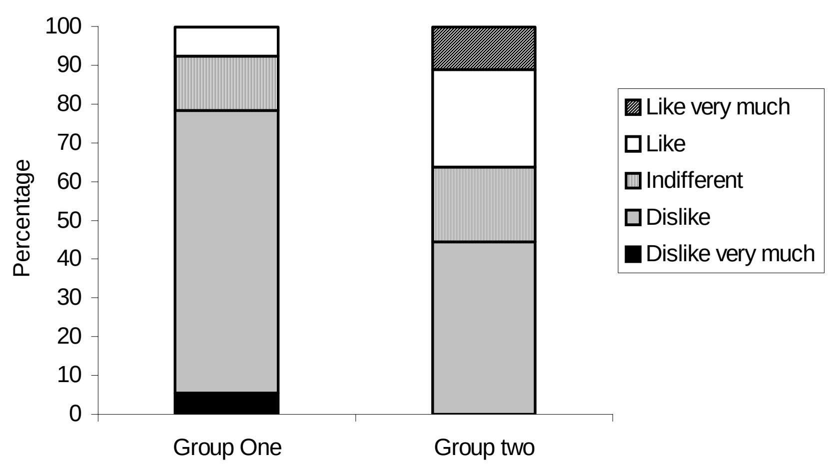

Figure 5.7. The attitude of two groups of people towards brown hyaenas. Group One is people who mentioned brown hyaenas as livestock killers and cultivated melon eaters. Group two is people who did not believe that brown hyaenas did anything bad.

hyaenas. Of the people questioned 64.5 % felt that there were more brown hyaenas around at present than there were 20 years ago and 4.4 % fewer than 20 years ago. Many people (72.2 %) wanted fewer brown hyaenas in the area and only 9 % wanted more. In order to achieve fewer brown hyaenas 52.9 % (of the people who wanted fewer) advocated the killing of them and 26.4 % favoured moving the brown hyaenas out of the area.

5.3.4 Persecution of brown hyaenas and other carnivores

Of the people questioned 31.1 % said that they would attempt to kill a predator if it were known to be killing their livestock. Of these 70.4 % said that they would shoot the predators and 20 % would use a gin trap. No other methods of killing were mentioned. Of the people who had seen a dead brown hyaena (11.6 % of those questioned), 31.1 % believed these deaths were caused by deliberate attempts to kill the brown hyaena by humans. Other reasons given for death were killed by a car, sickness or reason not known. Of those people who said that they would not kill the predator 72.6 % said that they would report the incidence of livestock killing to the Department of Wildlife and National Parks and 24.7 % would chase away the predator with guns and dogs. Of all the people questioned only 5.8 % (five men and three women) said that they had attempted to kill predators before. On two other occasions people said that they had seen another person set traps. All these cases also involved only the use of gin traps. Brown hyaena was the target species on four occasions, black-backed jackal on four occasions, lion on three occasions and spotted hyaena on one occasion.

Of the seven brown hyaenas that were collared living in the vicinity of the cattle areas two were confirmed as killed by farmers, a third was badly injured by a gin trap (broken leg) and wire snare around its neck and would have died without intervention and a forth hyaena disappeared in suspicious circumstances. Thus over the 3 years duration of the field study, there was confirmed direct evidence that at least 43 % of the collared hyaenas were either killed or injured badly by the farmers. One other brown hyaena with no collar was found dead with a wire noose around its leg and a second un-collared brown hyaena was observed with a broken front leg likely to have been caused by a gin trap. Although not quantified, gin traps were also regularly found stored at cattle posts although the residents in all cases stated that the gin traps had not been used for many years. However a gin trap was found near a den site with a toe bone from a brown hyaena caught inside and two traps were found (one gin trap and one snare) in the bush a short distance from a cattle post. Lions and wild dogs have been recorded as killed by farmers in the Makgadikgadi through the use of gin traps, snares, guns and poisons (Hemson 2003, pers. obs).

Of the four brown hyaenas collared in the Makgadikgadi National Park two of them died over the duration of the study. There was no evidence to suggest that the hyaenas had been killed by farmers. Over the duration of the study no traps were found in the Makgadikgadi National Park, nor brown hyaenas discovered that may have been killed or injured by farmers.

5.3.5 Attitudes towards tourism

When the farmers were asked why tourists come to the Makgadikgadi 50 % said that tourists come to see the animals. However 72 % still wanted there to be fewer brown hyaenas in the area. Of those questioned 74.0 % felt that there were more brown hyaenas around than there were 20 years ago, the main reason for this being that they were breeding and not being killed. Of the people questioned 52 % said that to reduce the number of brown hyaenas in the area some should be killed. Only 13 % of the people questioned felt any personal benefit from local tourism but 63 % wanted more tourists to come to the Makgadikgadi primarily because tourism provided jobs.

5.4 DISCUSSION

The pastoralist people living in the Makgadikgadi persecute brown hyaenas. Over a three-year period three of seven brown hyaenas that were captured and collared in the cattle area, were killed or injured by the pastoralists. Gin traps and snares were found in the vicinity of cattle posts and some of the people questioned admitted to having set traps in an attempt to kill brown hyaenas and other carnivores. It is likely that the actual number of people who had set traps was greater than those who admitted that they had. This is because many people would probably have avoided admitting to the killing of carnivores due to the fear of repercussions from the Department of Wildlife and National Parks (DWNP). Although the killing of some carnivores is legal in Botswana if in defense of livestock or personal safety, the use of gin trapping, poisons and wire snares are illegal. Gin trapping was the most common method used to kill carnivores. Lion, cheetah and wild dog are protected species and it is illegal to kill them even if in defense of livestock. Only a few people admitted to killing carnivores while more people did admit that they would kill a carnivore if the carnivore were known to be responsible for livestock killings. This might be more representative of the actual numbers of people who had attempted to kill carnivores rather than of those who actually admitted doing so.

The pastoralists trapped and killed brown hyaenas primarily because they believed that they killed their livestock. However observations indicated that the livestock eaten by the brown hyaenas living in the cattle areas of the Makgadikgadi were scavenged and not hunted (Chapter 3). Livestock killings blamed on brown hyaenas are more likely to be from known livestock predators such as lion, spotted hyaena or black-backed jackal (Frank 1998; Ogada *et al.* 2003). Predation of livestock by carnivores other than brown hyaena, and the incorrect assumption that brown hyaenas also prey on livestock regularly, are likely to be the primary reasons why the pastoralists kill them. Gin traps, wire snares and poisons are fairy indiscriminate and brown hyaenas may be killed when another carnivore is the target species. Brown hyaenas are likely to eat cultivated melons from the cattle post gardens and this is one of the reasons given for trapping them (Chapter 3).

Brown hyaenas may be incorrectly blamed for killing livestock regularly for a variety of reasons: (1) From the responses to some of the questions it is clear that many people were not entirely sure what a brown hyaena is. This means that the attitudes formed towards brown hyaenas and the responses to the questions from a high number of people are likely to be based not on the behaviour of brown hyaenas, but possibly on spotted hyaenas or on a grouped perception of carnivores that live in the area. (2) The presence of recent brown hyaena spoor near a livestock carcass may also lead to the owner of the animal wrongly believing that a brown hyaena was responsible for the death of the animal. Spotted hyaena and brown hyaena spoor are very similar, which may also lead to the misidentification of the predator of the livestock. (3) In some areas brown hyaenas are believed to be occasionally responsible for isolated occurrences of the killing of small livestock animals (Skinner 1976, Mills and Hofer 1998). It may also be that rare incidences may occur when brown hyaenas do kill a small livestock animal. As a result brown hyaenas are blamed for many other killings for which they are not responsible.

Brown hyaenas were hated primarily because they were perceived to be killers of livestock but also because they were believed to eat melons from the gardens. There was however, a belief that brown hyaenas did not kill as many livestock animals as other predators such as lion and black-backed jackal. Lions, black-backed jackals and spotted hyaenas were actually perceived to kill and probably do kill, more livestock animals worth more money than brown hyaenas do. This might explain why brown hyaenas were not hated by as many people as black-backed jackals and lions were. The belief that the number of brown hyaenas living in the area around their cattle post was presently higher than in the past and that there was no benefit to the farmers from their presence, is likely to have added to the farmers' hatred of them. Even though it was acknowledged that tourists came to the area to see animals, the fact that most people believed that local tourism did not benefit them personally, meant that there was no incentive not to kill brown hyaenas as they had no value to them. The average perceived cost to the livestock owner caused by livestock predation was high and likely to influence the tolerance of any carnivore in the area.

The level of persecution of brown hyaenas by the pastoralists is high. Of the people who admitted to trying to kill carnivores, brown hyaenas were targeted as often as jackals and more often than lions and spotted hyaenas. Over the duration of the study, inspite of their persecution, the number of brown hyaenas in a clan located in the cattle area appeared to be viable. A single adult female who was part of the study had a minimum of 17 cubs over a period of 4 years and 6 months. Only four of these 17 cubs died before they reached the age of a sub-adult (15 months, Mills 1990) at which point their long- term fate was unknown (pers. obs). Two other adults, one male and one female, were recorded as permanently part as of the same clan and observed regularly at the clan den site (Chapter 4). At varying time periods all of the surviving 13 cubs were also regularly observed as sub-adults and adults in the area and at the clan den site. However none of them appeared to remain within the clan over the long-term (chapter 4). Five other identified adult individual brown hyaenas were sighted in the same area as the WMA clan's home range (chapter 4). As resident clan adults were observed fighting with these individuals and chasing them out of the immediate area it is assumed that they were not part of the same clan. The numbers of brown hyaena observed as part of the clan in the cattle area are similar to the numbers of brown hyaena recorded in clans in the southern and central Kalahari (Mills 1990; Owens & Owens 1979b). For that reason, inspite of the killing of brown hyaenas by subsistence pastoralists the brown hyaena population can be considered to be viable. In the Makgadikgadi the benefits gained by the brown hyaenas through the presence of pastoralists (Chapters 3 and 4) would appear to be greater than the negatives caused by their persecution. The present level of persecution of the brown hyaenas by the pastoralists in the Makgadikgadi does not appear to be of immediate concern as the brown hyaena populations in the cattle areas are not threatened.

However as the levels of persecution do appear to be high in the cattle area, over the long-term any increase in these levels of persecution could be a reason for concern. This could be caused by a variety of factors such as a greater number of pastoralists moving into an area or greater conflict caused by increased livestock predation by other carnivores such as lion, jackal and spotted hyaena. Over the long-term efforts to reduce the level of conflict between brown hyaenas and pastoralists would be beneficial to ensure that brown hyaena populations living in cattle areas remain viable. It has been recommended that areas in South Africa already designated for extensive cattle production could also be designated as brown hyaena conservation areas (Stuart *et al.* 1985). A major effort would be required for the rational management of the brown hyaena in these areas (Mills & Hofer 1998). A similar recommendation could be made for the brown hyaenas living in cattle areas in Botswana. This might partially be achieved through a process of communication with the farmers and provision of information on the non-predatory nature of the brown hyaena. Attitudes towards brown hyaenas may change and if brown hyaenas are accepted as not being common livestock killers, then the targeted killing of brown hyaenas is likely to be reduced or at least remain stable. Certainly fewer people were found to hate brown hyaenas if the people believed that the brown hyaenas did not kill their livestock than if they believed that they did. A significant correlation was also found between the cost of perceived livestock killed by brown hyaenas at a cattle post and the negative attitude towards the brown hyaena. In areas where tourism, pastoralists and brown hyaenas co-exist, tourism should be developed to generate a direct personal benefit to the pastoralists. This could be used as a lever to reduce the number of killings of brown hyaenas and other carnivores by the pastoralists, in particular if the economic gain from tourism was considered to be greater than the economic loss of livestock to predators.

5.5 CONCLUSION

The pastoralists in the Makgadikgadi appeared to have a confused and largely incorrect understanding of what a brown hyaena is and also how it behaves. The general understanding was that brown hyaenas are predators that survive by feeding off hunted livestock. The farmers hated brown hyaenas primarily because they were believed to kill livestock but also because they eat cultivated melons from gardens. These were the main reasons given by people who had attempted to kill brown hyaenas. It was found that the subsistence pastoralists in the Makgadikgadi do persecute brown hyaenas and other carnivores mainly by trapping and then killing them. Evidence indicated that the level of persecution against brown hyaenas in the cattle areas was high. The killing of brown hyaenas may have been as a result of targeted killing of brown hyaenas but also indiscriminate killings where traps or poisons may have been set for other carnivores.

Inspite of their persecution the brown hyaena populations are viable in the cattle areas and not under any immediate threat. However efforts to reduce the number of brown hyaenas killed in the long-term would be beneficial in ensuring that brown hyaena populations in cattle areas remain viable. This could be done through a process of communication with the farmers and information provision as to the non-predatory nature of the brown hyaena. In areas where tourism, pastoralists and brown hyaenas co-exist, tourism should be developed to generate a direct personal benefit to the farmers as this could be used as a lever to reduce the number of killings of brown hyaenas and other carnivores by the pastoralists.

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- Chapter 6 -

Synthesis

Most of the information available on brown hyaena ecology is from studies conducted in areas where there is little or no farming or permanent human presence. As a result our current understanding of brown hyaena ecology in the presence of farming and humans is limited. The aim of this study is to increase our knowledge and understanding of brown hyaena ecology in the context of human wildlife interactions. In order to achieve this data were collected and analysed on: (i) the diet of brown hyaenas living inside the Makgadikgadi National Park (MNP) and in an adjacent Wildlife Management Area (WMA) where brown hyaenas and local subsistence pastoralists co-habit (Chapter 3); (ii) the foraging behaviour of brown hyaenas in the MNP and the WMA (Chapter 3); (iii) the home range sizes of brown hyaenas in the MNP and the WMA (Chapter 4); (iv) the utilization of home ranges by brown hyaenas in the MNP and the WMA (Chapter 4); and (v) the responses of the pastoralists to a questionnaire that incorporated 33 different subject areas designed to document their perceptions of and attitudes towards brown hyaenas and other carnivores that live in the vicinity of their residences (Chapter 5). This study has increased our knowledge and understanding of the interaction between brown hyaenas and humans and the more general ecology of the species in several areas as described below.

6.1 KEY FINDINGS

6.1.1 Chapter 3

(1) The diet of the brown hyaenas was influenced by the presence of pastoralists in the area as hyaenas living in the Makgadikgadi National Park and in the vicinity of cattle have different diets.

- In the cattle areas livestock carcasses were the most important food source and other less important food types were fed on as they became seasonally available.
- In the Makgadikgadi National Park zebra was the most important food source although several other food types were seasonally important.

(2) The dietary benefit derived by the brown hyaenas through the presence of subsistence pastoralists and their livestock carcasses is likely to be the primary reason that brown hyaena populations in cattle areas appear to be viable not only in the Makgadikgadi but in other agricultural areas in southern Africa.

- The brown hyaenas living in the cattle areas derived benefit from the presence of pastoralists through the reliable, abundant and permanently available food source provided by livestock carcasses.

(3) There was no direct evidence to suggest that any of the livestock species were hunted by the brown hyaenas. Thus any persecution of brown hyaenas because of perceived livestock predation by them is unjustified.

- In the cattle post areas springhares and Cape hares were the only mammals observed to be hunted, and only occasionally.

(4) The findings of the study are in agreement with optimal foraging theory.

- In the cattle areas dietary breadth was similar over both seasons in response to similar food availability in the peak and the lean season due to the permanent presence of plentiful livestock remains.

- In the Makgadikgadi National Park, as suggested by the optimal foraging theory, the composition of the diet varies according to the seasonal availability of food resources. Also in agreement with optimal foraging theory, when food availability was low in the lean season the brown hyaenas increased their dietary breadth and fed off a greater number of species of food. In the lean season they also changed their foraging behaviour by regularly hunting Cape hare and re-utilized old zebra carcasses.

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6.1.2 Chapter 4

(5) The presence of pastoralists and livestock had an influence on the spatial ecology of the brown hyaenas. The presence of pastoralists did influence the way the brown hyaenas utilized their home ranges.

- Movement patterns of the brown hyaenas were to rest away from the cattle areas during the daytime and to forage in the cattle areas during the night. This pattern of movement may have evolved to minimize any chance of an encounter with potentially hostile humans and to maximize foraging opportunities.

- There was an increase in distance foraged per night over the lean season, which may have been a response to a reduced level of food availability. Foraging strategy was to visit the same areas frequently and may have evolved because of a plentiful food supply all year round in the form of livestock carcasses.

(6) The presence of pastoralists and livestock had an influence on the home range size of the brown hyaenas through the resource dispersion hypothesis.

- Home range sizes were smaller for brown hyaenas living in vicinity of pastoralists than for hyaenas living in the Makgadikgadi National Park.

- The size of the home range was found to be dependent on the average distance between the significant food sources. In the cattle areas food was closely distributed mainly due to the presence of abundant livestock carcasses. Home range sizes were correspondingly smaller in the cattle areas than in the Makgadikgadi National Park where there was no permanent livestock and a much greater distance between significant food sources.

- Seasonal home range sizes fluctuated depending on the level of food availability. In the Makgadikgadi National Park the seasonal home range size fluctuated greatly due to the variability of seasonal food availability. In the cattle areas food availability was less varied than in the national park during the peak and the lean season and as a consequence seasonal home range size did vary but by less than in the national park.

6.1.3 Chapter 5

(7) Of the perceived livestock predators, black-backed jackals were believed to have killed the most livestock animals. Spotted hyaenas, brown hyaenas and lions were believed to have killed a similar number. Wild dog, caracal, cheetah and leopard were also believed to have killed a small number of livestock animals. However the economic value of the livestock believed to be killed, shows that lions have the greatest negative economic impact followed by black-backed jackals, spotted hyaena and then brown hyaena.

- Lions were perceived as the biggest culprit for cow and horse killings, black-backed jackals for goat/sheep killings, spotted hyaenas for donkey killings. Of the animals brown hyaenas were blamed for killing, goats were the most common.

(7) Pastoralists in the Makgadikgadi appeared to have a confused and largely incorrect understanding of what a brown hyaena is and how it behaves.

- The general understanding was one of the brown hyaena being a predator that survived by feeding on hunted livestock.

(8) As a consequence of this misunderstanding of how a brown hyaena behaves they were disliked and frequently killed by the farmers.

- Brown hyaenas were largely disliked by the farmers primarily because they were believed to kill livestock.

- This may have been as a result of targeted killing of brown hyaenas but also indiscriminate killings where traps or poisons may have been set for other predators. This is partly due to incidences of predation on livestock (by lion, spotted hyaena and black-backed jackal) that are blamed on brown hyaenas.

(9) In spite of their persecution the brown hyaena populations are viable in the cattle areas and appear not to be under any immediate threat. However efforts to reduce the number of brown hyaenas killed in the long-term would

be beneficial in ensuring that brown hyaena populations in cattle areas remain viable.

- This could be done through a process of communication with the pastoralists and information provision as to the non-predatory nature of the brown hyaena.

- In areas where tourism, pastoralists and brown hyaenas co-exist, tourism should be developed to generate a direct personal benefit to the farmers as this could be used as an economic lever to reduce the number of killings of brown hyaenas and other carnivores by the pastoralists.

6.2 MANAGEMENT IMPLICATIONS

The findings of this study may be useful in reducing and managing conflict between brown hyaenas and subsistence farmers. The range of the brown hyaena in southern Africa overlaps greatly with both subsistence farming and large scale commercial livestock farming (IUCN 2003, Skinner 1976). As a result conflict is very common between farmers and brown hyaenas with farmers blaming brown hyaenas for livestock killings, in particular of young sheep and goats (Skinner 1976). In the Makgadikgadi it can be seen that viable populations of brown hyaenas live in subsistence farming areas inspite of the killing of them by the pastoralist. This would appear to be the case in other agricultural areas of southern Africa (Mills & Hofer 1998; Skinner 1976). However efforts to reduce the number of brown hyaenas killed would be beneficial in ensuring that brown hyaena populations in cattle areas remain viable over the longer term.

The findings of this study show that brown hyaenas are unlikely to kill livestock regularly and there should be minimal conflict between brown hyaenas and farmers over livestock predation. In order to address the problem of brown hyaena and farmer conflict it is first necessary to address the widespread misconception that brown hyaenas kill livestock regularly. A process of communication with the farmers and information provision on the non-predatory nature of the brown hyaena is likely to have some success in reducing the persecution of brown hyaenas. Farmers should be informed that the killing of brown hyaenas is unlikely to reduce the number of their livestock animals killed by carnivores.

The close proximity of the to the brown hyaenas studied in a cattle area to the Makgadikgadi National Park, does mean that caution must be observed when interpreting and implementing the findings of this study to brown hyaena populations living in areas well away from National Parks, Game Reserves and other protected areas. For example it may be that the Makgadikgadi National Park acts as a source population with brown hyaenas dispersing from the park into the adjoining cattle areas. Even so the findings of this study should be incorporated into overall policies and specific strategies for dealing with issues of brown hyaena and human conflict in Africa. The laws in Botswana governing the circumstances under which brown hyaenas and other carnivores (apart from lion, cheetah and wild dog) can be killed only include acting in defense of livestock or when the farmer's own safety is threatened by the animal. Gin trapping, the use of poisons and wire snaring are illegal methods of killings carnivores. This study suggested that the most common method used to kill a brown hyaena is by gin trap. This is probably due to the elusive and nocturnal nature of the brown hyaena making attempts to kill it by using a gun and dogs unlikely to be successful. The use of a gun and dogs is permitted and the killing of a carnivore must be reported at a Department of Wildlife and National Parks (DWNP) office within 7 days. Brown hyaenas have been found only to scavenge livestock in the Makgadikgadi and there have been no recorded cases of brown hyaenas posing a threat to human safety. Effectively according to Botswana law any case of brown hyaenas being killed by farmers is likely to be unjustified. It would be useful for the DWNP to clarify with the farmers the circumstances under which brown hyaenas can be killed as firm enforcement of the law will help reduce the number of brown hyaenas killed by the farmers.

In any area where tourism, pastoralists and brown hyaenas co-habit, the tourism operator should be encouraged via the management plan to invest in the local community so that a direct economic benefit is felt by farmers in the area because of the presence of tourism and the associated wildlife that brings tourists to the Makgadikgadi. If farmers were to feel more direct economic benefit from tourism they would be likely to be more tolerant of livestock loss to predators, and incidences of carnivore killings by farmers will be reduced.

The number of people in Botswana and the number of cattle posts has increased substantially since independence in 1966 (Central Statistics Office, Gaborone). In spite of the potential effects of AIDS and urbanization, this trend is likely to continue over the next few decades not only in Botswana but in the rest of southern Africa. This is likely to cause an increase in the interaction between brown hyaenas and subsistence farmers, leading to further conflict. The brown hyaena is in fact likely to be one of the few large carnivores that can co-exist with farmers in relative peace if efforts are made to ensure that farmers are aware of the true non-predatory nature of the brown hyaena. It has been recommended that areas in South Africa already designated for extensive cattle production could also be designated as brown hyaena conservation areas (Stuart *et al.* 1985). A major effort would be required for the rational management of the brown hyaena in these areas (Mills & Hofer 1998). A similar recommendation could be made for the brown hyaenas living in cattle areas in Botswana. Brown hyaenas have large home ranges and occur at low population densities. The maintenance of viable populations of brown hyaena in southern Africa living outside of protected reserves alongside farmers, is essential in order to avoid a decline in the brown hyaena population and to at least maintain or improve its current status as a lower risk: near threatened species.

6.3 FUTURE RESEARCH

At present the estimates available for the total population of brown hyaenas in southern Africa and for the individual populations within the brown hyaena's range are very limited. Any study that provides further estimates of the number of individual brown hyaenas in the various populations and the patterns of dispersal and movement between these populations would also be very useful. In particular further information on the foraging and spatial ecology and population numbers of brown hyaenas outside of protected areas would also be useful. Further investigation into the possibility of livestock predation by brown hyaenas in cattle area other than the Makgadikgadi would be relevant. At present there is limited information available on genetic issues such as relatedness and paternity both within brown hyaena clans and connected populations. More information on sub-adult dispersal would be also invaluable.

Within the Makgadikgadi, partially in order to reduce carnivore and human conflict, a substantial game- proof fence is being constructed around the Makgadikgadi National Park. A study on how the fence influences the ecology of the brown hyaena in the MNP and the surrounding area would be invaluable. The extent to which the ecology of brown hyaena populations may be affected by the fence is dependent on two main factors:

1) The effectiveness of the fence in preventing any movement of mammals in and out of the park. This will depend on several factors including, how well the fence is built and how effective and regular the maintenance of the fence is.
2) The influence that the fence has on the populations of mammal species that are important food sources for the brown hyaenas, in particular the number of zebra and wildebeest in the area.

If the fence remains as a relatively affective barrier, the ecology of the brown hyaenas in the Makgadikgadi National Park is likely to be influenced in several areas. Food available is likely to decrease, as in the long run it might be expected the fence will impact negatively on the zebra and wildebeest migration, causing a reduction in population size and consequently a reduction in the number of zebra and wildebeest carcasses available for the brown hyaenas to feed off. However, due to the likely negative impact of the fence on the zebra and wildebeest migration, in the short term food availability may increase as zebra and wildebeest die. As livestock animals will be prevented from entering the park, the number of number of livestock carcasses available as food for the brown hyaenas living within the fenced national park will also reduce. Consequently a reduction in the quantity and quality of food availability is, through the resource dispersion hypothesis, likely to cause larger home range sizes and a reduction in group sizes and thus a decline in the numbers of brown hyaena in the MNP.

Brown hyaenas living outside of the fenced area in close vicinity to park boundaries are likely to be influenced by a reduction in food availability as zebra and wildebeest carcasses are no longer accessible as a food source. There may also be a reduced level of mortality of livestock animals as populations of predators such as lion in particular in the cattle areas reduce. As with the brown hyaenas in the MNP, a reduction in the quantity and quality of food availability is, through the resource dispersion hypothesis, likely to cause larger home range size and a reduction in group size and a decline in the numbers of brown hyaena in the cattle areas adjacent to the MNP. A decline in the availability of food, might also lead to brown hyaenas coming into more conflict with farmers as they rely more on food accesses through the presence of cattle posts and livestock. This may lead to increased persecution of the brown hyaenas by the farmers and higher levels of mortality of the brown hyaenas.

The extent of this decline in the numbers of brown hyaena is difficult to predict, although it is likely to be small in both areas as the reduction in food availability will probably be relatively small. It is also likely that in the long run the fence will not prevent periodic movement of brown hyaenas in and out of the park thus reducing the negative impacts of the fence on their ecology.

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SUMMARY

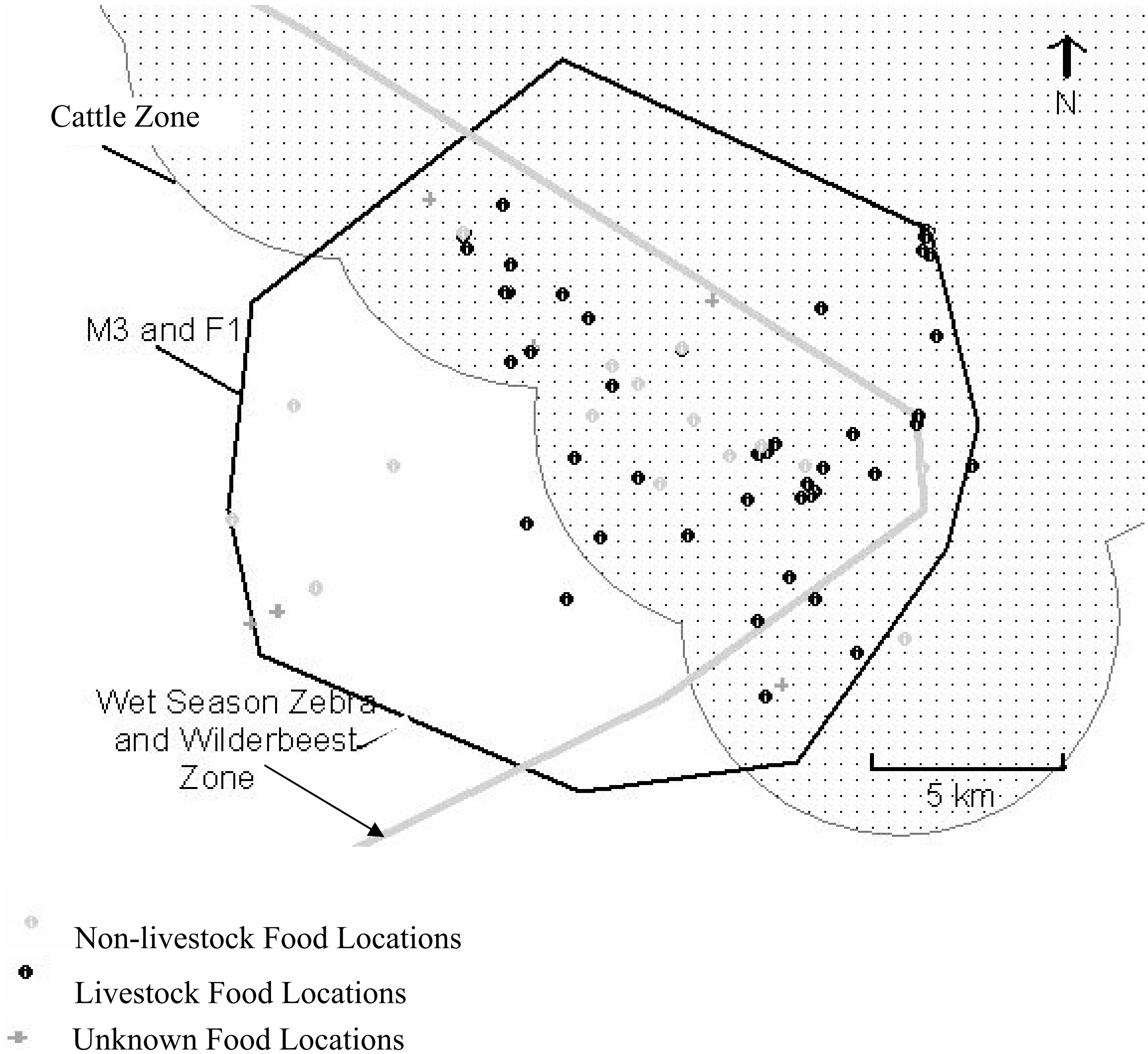
The lack of knowledge on the interaction between the brown hyaena (*Hyaena brunnea)* and pastoralists and its vulnerable conservation status were the motivating factors behind this study. The majority of information available on brown hyaena ecology is from studies conducted in areas where there is little or no agriculture, cattle farming, or permanent human presence. As a result our current understanding of brown hyaena ecology in the presence of farming and humans is limited. The aim of this study was to increase our knowledge and understanding of brown hyaena ecology in the context of human wildlife interactions.

The diet of the brown hyaenas was influenced by the presence of pastoralists, as hyaenas living in the Makgadikgadi National Park and in the vicinity of pastoralists have different diets. The brown hyaenas living in the cattle areas derived benefit from the presence of pastoralists through reliable, abundant and permanently available food source provided by livestock carcasses. The dietary benefit derived by the brown hyaenas through the presence of subsistence pastoralists and their livestock carcasses, is likely to be the primary reason that brown hyaena populations in cattle areas appear to be viable not only in the Makgadikgadi but also in other agricultural areas in southern Africa.

There was no direct evidence to suggest that any of the livestock species were hunted by the brown hyaenas. Thus any persecution of brown hyaenas because of perceived livestock predation by them is unjustified. The findings of the study are in agreement with optimal foraging theory. The presence of pastoralists and livestock had an influence on the spatial ecology and the utilization of the brown hyaenas' home ranges through the resource dispersion hypothesis.

Of the perceived livestock predators, black-backed jackals were believed to have killed the most livestock animals. Spotted hyaenas, brown hyaenas and lions were believed to have killed a similar number. Wild dog, caracal, cheetah and leopard were also believed to have killed a small number of livestock animals. However the economic value of the livestock believed to have been killed, shows that lions have the greatest negative economic impact, followed by black-backed jackals, spotted hyaena and then brown hyaena. Pastoralists in the Makgadikgadi appeared to have a confused and largely incorrect understanding of what a brown hyaena is and how it behaves. As a consequence of this misunderstanding they are disliked and frequently killed by the farmers. Inspite of their persecution the brown hyaena populations are viable in the cattle areas and appear not to be under any immediate threat. However efforts to reduce the number of brown hyaenas killed in the long-term would be beneficial in ensuring that brown hyaena populations in cattle areas remain viable.

- Appendix A -



Location of all significant recorded feeding instances and carcasses visited from observations made on two brown hyaenas (M3 and F1, combined 95 % MCP) foraging in the WMA.

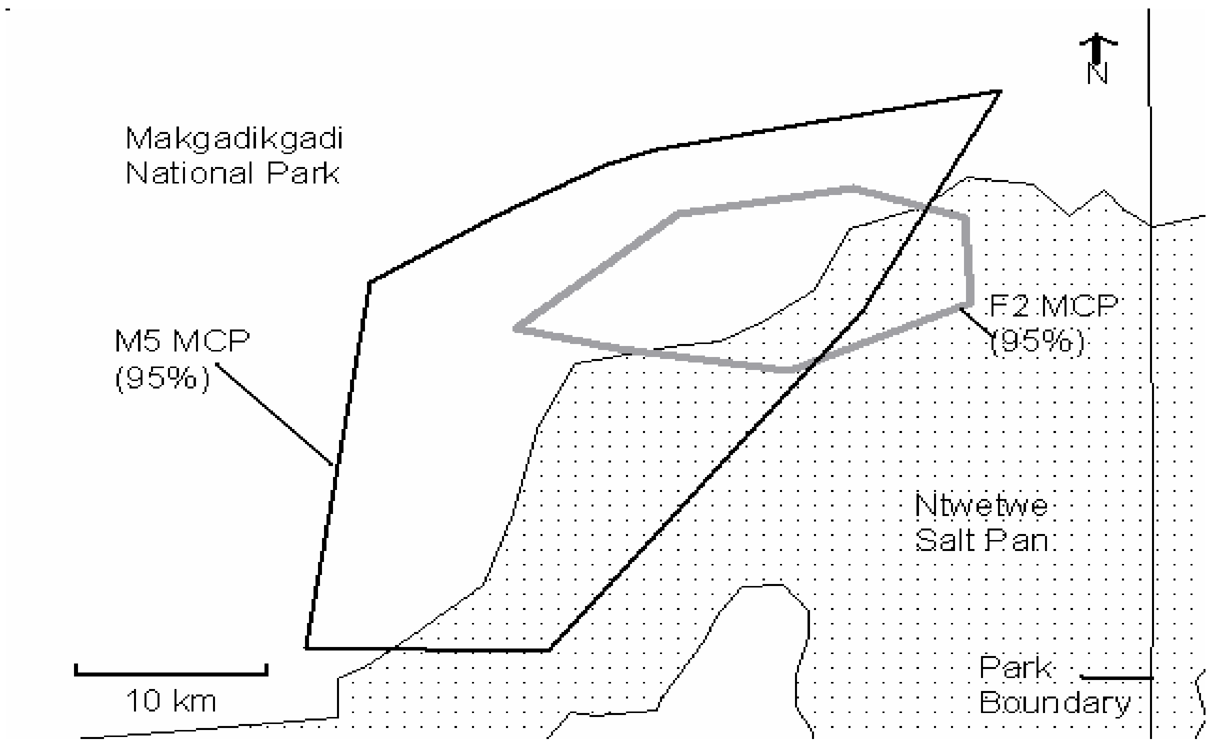
- Appendix B -

The total number of fixes used to estimate home range size using MCP (95 %) and if and when an asymptote was reached.

Brown	Total No. of Fixes	No. Fixes before asymptote is reached
M1a	49	Yes (47)
M1b	19	Yes (18)
M2	22	Yes (21)
M3	52	Yes (40)
M4*	133(1732)**	No
M5*	48(579)**	No
F1	61	Yes (38)
F2	28	Yes (25)

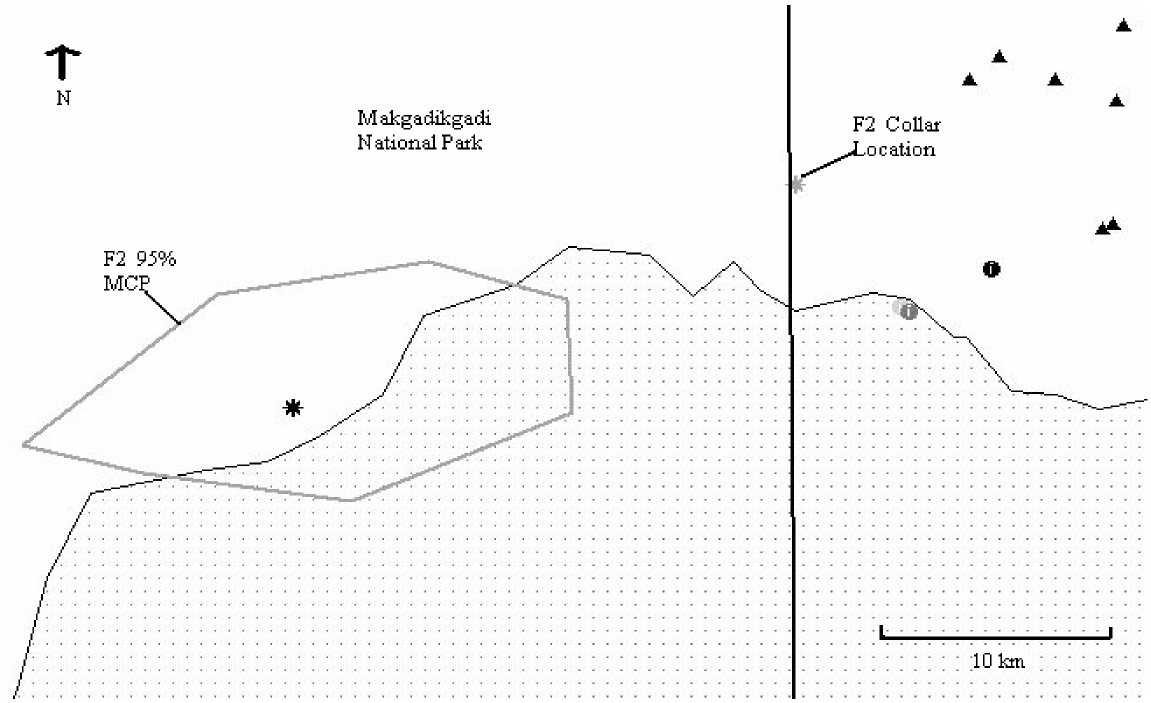
* GPS collars
** (Total fixes)

- Appendix C -



The home range estimates (MCP 95 %) for F2 and M5.

- Appendix D -



The location where F2 was trapped and collared and the home range estimate for F2 using MCP (95 %).

- Appendix E -

Questionnaire template used for chapter 5.

Name of cattle post:
Owner:
Year built:
Tribe:
Name of person interviewed:
Age:
Sex:
G.P.S Coordinates:

1. How many types of hyaena are there here in the Makgadikgadi?
    a) Name them -Spotted
        -Brown
        -Aardwolf
        -Don't know

2. Have you ever seen a brown hyaena?
    a) How many times?
    b) Where?
    c) When?
    d) What does a brown hyaena look like? How heavy is it?
        Heavy like a goat
        Heavy like young boy (14 years)
        Heavy like a lion
        Heavy like a cow

3. What noises do they make?
    a) Brown
    b) Spotted
    c) Aardwolf

4. Do brown hyaenas come to your cattle post?
    a) When?
    b) How often? Every day
        Every few days
        Every Week
        Every Month
        Every 6 months
        Every Year
    c) Why?

5. Do spotted hyaenas come to your cattle post?

a) When?
b) How often? Every day
Every few days
Every week
Every month
Every 6 months
Every year
c) Why?

6. Do you like or hate lions?
1 like very much; if so why?
2 like; if so why?
3 don't care; if so why?
4 hate; if so why?
5 hate very much; if so why?

7. Do you like or hate brown hyaenas?
1 like very much; if so why?
2 like; if so why
3 don't care; if so why?
4 hate; if so why?
5 hate very much; if so why?

8. Do you like or hate Jackals?
1 like very much; if so why?
2 like; if so why?
3 don't care; if so why?
4 hate; if so why?
5 hate very much; if so why?

9.Have you set traps for or shot predators?
a) Which?
b) Why?
c) What sort of trap?

10. Have you seen other people set traps or shoot predators?
a) Which?
b) Why?
c) What sort of trap?

11. Would you set traps or shoot a predator if they were eating your livestock?

12. Have you ever seen a dead brown hyaena?
a) How many?
b) When?
c) How did it/they die?

13. Should brown hyaenas live here near your cattle post? If not then where?

14. Which predators are most responsible for killing your livestock? How many and which animals killed in the last 12 months?

Cow	Goat	Donkey	Horse	Dog	Chickens

Total for cattle post

Predator
- Lion
- Leopard
- Cheetah
- Jackal
- Caracal
- African wildcat
- Spotted hyaena
- Brown Hyaena
- Domestic Dog
- Other

a) Which predators kill your livestock starting with the one that kills the most to the one that kills the least? (Tick the above starting no 1 for highest etc)

b) Of the livestock killed Lions kill
- 1- most of my livestock
- 2- plenty of my livestock
- 3- some of my livestock
- 4- a few of my livestock
- 5- none of my livestock

c) Of the livestock killed Jackals Kill
- 1- most of my livestock
- 2- plenty of my livestock
- 3- some of my livestock
- 4- a few of my livestock
- 5- none of my livestock

d) Of the livestock killed brown hyaenas kill
- 1- most of my livestock
- 2- plenty of my livestock
- 3- some of my livestock
- 4- a few of my livestock
- 5- none of my livestock

15. Do brown hyaenas do anything bad?
    a) What?

16. Do they do anything good?
    a) what?

17. Can brown hyaenas kill animals?
    a) If so which?

18. Where do brown hyaenas live?

19. When do brown hyaenas look for food?

20. Where do they keep their cubs?

21. What do brown hyaenas eat?

22. How many brown hyaenas are there here in this area? Ct 11 (Not including the park)

23. How many brown hyaenas are there in the Makgadikgadi National Park?

24. Do you think that there are more or fewer brown hyaenas now than there were 20 years ago?
    1 many more; why are there many more?
    2 more; Why are there more?
    3 same; why are there the same?
    4 less; why are there less?
    5 much less; why are there much less?

25. Would you like there to be more brown hyaenas here or less?
    1 many more; if so how can we get many more?
    2 more; if so how can we get more?
    3 same; if so how can we keep the same?
    4 fewer; if so how can we get fewere?
    5 much fewer; if so how can we get much fewer?

26. Why do tourists come to the Makgadikgadi?

27. Do you or your family benefit from tourists coming here?
    a) If so, who?
    b) How?

28. Would you like the number of tourists that visit the Makgadikgadi (Gweta) to be?
    1. many more: why?
    2. more: why?
    3. the same: why?
    4. less: why?
    5. none: why?

29. What stories do you know about hyaenas?
    a) Who told you the stories?

30. Can the body of a brown hyaena be used for anything?
    a) If so what?

31. What else can you tell us about brown hyaenas e.g. cultural beliefs, more stories, encounters with, what you would like to happen to them in the Makgadikgadi, etc

32. Are brown hyaenas dangerous?
    a) If so why?

33. Have you heard about the fence?
    a) If yes, is it a good thing?

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Bone Accumulations at Brown Hyena (*Parahyaena brunnea*) Den Sites in the Makgadikgadi Pans, Northern Botswana: Taphonomic, Behavioral and Palaeoecological Implications

Rodrigo Lacruz *
Palaeoanthropology Unit for Research and Exploration, School of GeoSciences, University of the Witwatersrand. P. Bag 3, WITS 2050. South Africa.

Glyn Maude
Mammal Research Institute, University of Pretoria.

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Bone accumulations at five brown hyena den sites representing two clans in the Makgadikgadi Pans region of northern Botswana were studied. Our intent was to assess the correlation between the taxonomic abundance at these den sites and the local faunas. Our statistical interpretation shows that such accumulations significantly correlate with the local fauna. A previously proposed criterion which suggested a carnivore representation of 20 % or more of the total Minimum Number of Individuals (MNI) at hyena-accumulated assemblages is re-assessed. The use of this criterion is important to assess the involvement of hyenas as accumulating agents in bone assemblages of unknown origin. We suggest that bone accumulations created by different hyena species may not always meet the proposed criterion. This is probably because of behavioral differences between hyena species. In agreement with other studies, we observed that juvenile brown hyenas are widely represented in the accumulations and that there is a high percentage of bones showing carnivore damage. We conclude that fossil assemblages purportedly accumulated by brown hyenas do provide information about the predominant ungulate taxa in the area and thus, the overall habitats.

Keywords: BROWN HYENA, BONE ACCUMULATIONS, MNI, NISP, LOCAL FAUNA

* E-mail: lacruzr@science.pg.wits.ac.za

Introduction

The contribution of hyenas to the accumulation of southern African Plio-Pleistocene fossil assemblages has been a subject of study for over 50 years. However, the lack of behavioral studies on hyena species at the time, which led to the perception of all hyenas as a group of behaviorally similar carnivores, negatively influenced interpretations of their role as a contributing agent in cave assemblages (e.g. Hughes, 1954).

Modern hyaenids are represented by four genera: *Parahyaena, Proteles, Crocuta* and *Hyaena* (Werdelin & Solounias, 1991). Besides important differences in morphology and biogeography, these four genera display unique behaviors (e.g. Kingdon, 1997; Mills & Hofer, 1998). Thus, understanding the variability in the behaviour of modern hyaenid taxa is important for interpretations of fossil assemblages purportedly accumulated by the different hyenas.

More recent studies on hyena accumulations identified a number of features which could be used as guidelines to assess the involvement of hyenas in a given accumulation (Cruz-Uribe, 1991). However, these were based on studies of bone assemblages for which the accumulating agent was not known with certainty. This led Pickering (2002) to re-evaluate Cruz-Uribe's (1991) proposal. Pickering's analysis was based on accumulations of known (hyena-derived) origin collected during field work conducted by wildlife biologists. A reduced list of three criteria was subsequently proposed to distinguish hyena accumulations (Pickering, 2002). These are: 1) high percentage of hyena damaged bones 2) high representation of long bones lacking epiphyses 3) carnivore minimum number of individuals (MNI) ≥ 20% of the total MNI.

The present study was conducted on five brown hyena accumulations in the Makgadikgadi region of Northern Botswana to test the criteria proposed by Pickering (2002). Additionally, comparisons between the ungulate species and abundance derived from the analyses of the bone accumulations were made with census data on ungulate populations obtained from the Department of Wildlife and National Parks authorities to assess the degree of correlation between these data sets. This information was interpreted in the context of fossil accumulations.

The present study was possible through an ongoing field study on the ecology of *Parahyaena* in northern Botswana conducted by one of the authors (GM). Thus, there was conclusive evidence as to the accumulating agent of the bones. The osteological remains were studied during three visits to the sites over a period of 18 months by RL. Each visit dealt with different dens to avoid overlap in the analysis of the bones. The osteological data recorded during this study has not been included here but forms the basis of a subsequent publication.

Study area

The Makgadikgadi Pans represent the remnants of Palaeo-lake Makgadikgadi and are located in the north eastern Kalahari region between 20^{o} and 21^{0} S and 20^{0} and 26^{0} E. The Makgadikgadi National Park (MNP) is 4900km^{2} in size and located to

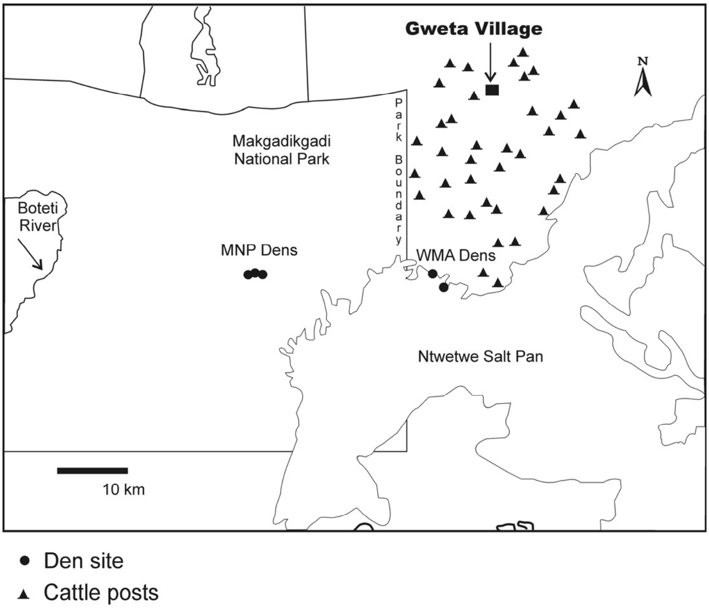

Figure 1. Map indicating the location of the brown hyena dens studied. The vertical line labelled as National Park boundary marks the divide between the Makgadikgadi National Park (MNP) and the Wildlife Management Area (WMA). See legend in the figure for more details.

the north west of the salt pan system (Figure 1). The Makgadikgadi National Park and the surrounding area (Nxai Pan) support the largest migratory movement of herbivores in southern Africa. Between 10 000 and 15 000 zebra (*Equus burchellii*) and 3 000- 6000 blue wildebeest (*Connochaetes taurinus*) move seasonally from the west of the MNP in the Boteti region (Figure 1), where they spend the dry season, to the east of the MNP into the study area referred to as the Wildlife Management Area (WMA) where they spend the wet season (Brooks, 2003; Kgathi & Kalikwe, 1998).

The maternity den sites used by brown hyenas in both MNP and WMA were originally burrows excavated by aardvarks into the relatively soft pan sediments. Some of these burrows are several meters long and in places nearly a meter wide.

Materials and methods

The study areas were divided into the Wildlife Management Area (WMA) and the Makgadikgadi National Park (MNP) (Figure 1). Two of the den sites are located in the WMA and three in the MNP. The three dens in the MNP are located within 1 km of each other and were used by breeding females from one clan. Only one of the den sites was active at any one time and periodically the cubs were moved from one den site to another (Maude, 2004). For this reason the bone accumulations from these three den sites were combined and analyzed as the MNP accumulation. The two den sites in the WMA were located four kilometers away from each other but the data were combined for the same reasons given for the MNP clan. Three visits were made to these areas by RL and most of the skeletal remains collected from the surface were identified *in situ*. No bones were extracted from inside the holes as most of these were occupied by brown hyena cubs at the time our study was conducted. Records of each specimen included identification of skeletal element and taxon from which it derived. The number of identified specimens (NISP) and the minimum number of individuals (MNI) per taxon was calculated. Carnivore damage was assessed on the basis of the presence of tooth scratches, chewed edges and punctures following Newman (1993). Specimens that could not be identified with certainty *in situ* were brought to the University of the Witwatersrand for comparison with modern osteological collections housed at that institution.

Ungulate taxa represented at the MNP and WMA dens area were compared with the ungulate census data compiled by the Botswana Department of Wildlife and National Parks (DWNP) available as the Botswana Aerial Survey Information Systems (BASIS). To increase the reliability of the DWNP population estimates, we have averaged the most recent ungulate census data for the period 2001 and 2002 in the Makgadikgadi

Table 1. BASIS data on ungulate species and abundance found in the MNP and at the WMA areas. Only those species identified in the vicinity of the brown hyena dens were included.

Taxa	**Population MNP**	**% Population MNP**	**Population WMA**	**% Population WMA**
Zebra (*Equus burcheli*)	13103	51,3	14332	20,7
Wildebeest (*Connochaetes taurinus*)	3752	14,7	0	0
Springbok (*Antidorcas marsupialis*)	2334	9,2	44	0,1
Cow *(Bos taurus*)	3516	13,8	37999	54,9
Steenbok (*Raphicerus campestris*)	331	1,3	239	0,4
Common duiker (*Sylvicapra grimmia*)	45	0,2	72	0,1
Kudu (*Tragelaphus strepsiceros*)	514	2,0	650	0,9
Horse (*E. caballus*)	30	0,1	1846	2,7
Donkey (*E. asinus*)	74	0,3	3667	5,3
Goat/Sheep (*Capra/Ovis*)	292	1,1	10318	14,9
Gemsbok (*Oryx gazella*)	1528	6,0	0	0

Table 2. Species list derived from the analysis of bones accumulated in the Wildlife Management Area (WMA). The first two columns indicate the Minimum Number of Individuals (MNI) represented at each of the dens. The last two columns reflect the total number of identified specimens and total MNI's for all WMA dens combined.

		WMA MAIN	WMA-E	TOTAL	TOTAL
	Taxa	**MNI**	**MNI**	**NISP**	**MNI**
Equidae	*Equus burchelli*	6	0	66	6
	E. asinus	0	1	3	1
	E. caballus	0	1	2	1
Bovidae	*Tragelaphus strepsiceros*	1	0	2	1
	Sylvicapra grimmia	1	0	1	1
	Antidorcas marsupialis	1	0	2	1
Domestic	*Bos*	6	3	74	9
	Caprinae *(*goat/sheep*)*	3	1	13	4
Carnivora	*Parahyaena brunnea*	2	0	8	2
	Canis mesomelas	2	0	3	2
	Mellivora capensis	1	0	1	1
Other	*Hystrix africaeaustralis*	1	0	1	1
	Orycteropus afer	1	0	1	1

National Park (Table 1). Only the ungulate fauna found within the home ranges of the hyena clans studied here were included (Maude, 2004). Normality test (Anderson Darling) indicated that data was not normally distributed and Spearman's rank correlation coefficient was then used to assess the similarity between the relative abundance of percentages of NISP per taxon, and the values of the MNI. Additionally, both NISP and MNI values are compared with the percentages of the ungulate faunas in each area.

Results

Bone accumulations at the WMA

Two den sites were studied in the WMA. A species list and MNI is presented in Table 2. The bulk of the identified material corresponds to domestic cattle (50%) followed by zebra (18%). Carnivores represent 16% of the total identified fauna of which brown hyenas represent 40%. All hyena individuals represented are cubs (P^4 or M_1 not fully unerupted). The total numbers of bones showing carnivore activity is nearly 61% for the two den sites studied in the WMA (69% and 53% respectively).

Bone accumulations at the MNP

A species list from the bones identified at the three den sites within the MNP are presented in Table 3. Carnivores comprise 24% of the total MNI and brown hyenas represent about 18% of the carnivores. Two brown hyena individuals were identified, one of which was a cub and the other a sub-adult (see Mills, 1990: 8) with complete permanent dentition but showing unfused cranial sutures. The percentage of bones showing carnivore-induced damage is 65% for the three MNP den sites (55%, 73% and 68% respectively). The most abundant taxa are zebra, wildebeest and springbok all of which are usually found in open grasslands (Skinner & Smithers, 1990) in similar environments to those near the dens (Figure 2).

Table 3. Species list derived from the analysis of bones accumulated in the Makgadikgadi National Park (MNP). The first three columns indicate the Minimum Number of Individuals (MNI)represented at each of the dens. The last two columns reflect the total number of identified specimens and total MNI's for all MNP dens combined.

		GUS DEN	BH4	BH5	TOTAL	TOTAL
	Taxa	**MNI**	**MNI**	**MNI**	**NISP**	**MNI**
Equidae	*Equus burchelli*	5	3	4	217	12
Bovidae	*Connochaetes taurinus*	3	1	3	45	7
	Antidorcas marsupialis	3	1	1	14	5
	Raphicerus campestris	1	1	0	2	2
	Sylvicapra grimmia	1	0	0	2	1
Domestic	*Bos*	1	1	0	9	2
Carnivora	*Otocyon megalotis*	1	1	0	7	2
	Canis mesomelas	1	1	0	23	2
	Parahyaena brunnea	0	2	0	7	2
	Proteles cristatus	1	0	0	2	1
	Felis lybica	0	0	1	7	1
	Vulpes chama	1	0	0	2	1
Other	*Orycteropus afer*	1	0	0	1	1
	Lepus capensis	0	0	1	1	1

Figure 2. A general view one of the den sites in the National Park during the dry season showing the scatter of bones near the den. A brown hyena and a zebra skull can be seen in this picture. The dens were still active at the time this study was conducted, and to avoid disturbing the cubs, only the bones located on the surface and not those inside the dens were analysed.

Correlations between bone accumulations and local environments

Data on ungulate taxa recovered from the MNP and WMA den sites represented as percentages of the NISP and MNI shown in Tables 2 and 3 were statistically tested to assess the degree of similarity with the percentages of the local faunas shown in Table 1. Spearman's rank correlation coefficient shows a highly significant correlation between percentage of bones per taxon of the NISP category and the MNI in the WMA ($N = 8$; $r_s = 0.891$; $P < 0.01$), between the MNI and the local population in the WMA, ($N=8$; $r_s = 0.878$; $P < 0.01$) and between NISP and the local population in the WMA ($N = 8$, $r_s = 0.957$, $P < 0.01$). When Spearman's rank is applied to the MNP area, similar results are obtained: NISP/MNI ($N = 7$; $r_s = 0.956$; $P < 0.01$); NISP/ Population ($N = 7$; $r_s = 0.973$; $P < 0.01$) and MNI/ Population ($N = 7$; $r_s = 0.899$; $P < 0.05$). Therefore, the percentages of taxa represented at the bone accumulations identified at both den sites and the percentage of the ungulate component in the local faunas of each area

Table 4. Proportion of carnivore remains recorded in hyena den accumulations as measured by the percentage of the total Minimum Number of Individuals (MNI) from each site. Only macromammals were included. It must be noted that in the cases where the MNI values are low, this probably affects the results. In Skinner & Van Arde (1991), the highest MNI was that of seals (58 out of 105 individuals), which were not included. If this marine carnivore is included the percentage is higher than shown in this table. The figure used in Kuhn's (2001) is an average given for five different dens.

Hyena species		**Each study**	**Mean per species**
Spotted hyena dens	Lim (1992)	4%	
	Hill (1989)	9%	
	Bunn (1983)	4%	
	Mills & Mills (1977)	0%	**spotted 4%**
Brown hynea dens	Skinner & Van Arde (1991)	74%	
	Lacruz & Maude MNP dens	20%	
	Lacruz & Maude WMA dens	16%	
	Mills & Mills (1977) Kasperdraai dens	69%	
	Mills & Mills (1977) Kannaguass den	22%	
	Mills & Mills (1977) Rooikop dens	36%	
	Mills & Mills (1977) Kwang dens	56%	
	Mills & Mills Botswana dens	30%	**brown 40%**
Striped hyena dens	Kruuk (1976)	0%	
	Kuhn (2001)	21%	
	Skinner et al. (1980) area A	13%	
	Skinner et al. (1980) area B	25%	
	Leakey et al. (1999)	26%	**striped 17%**

are highly correlated, whether using MNI or NISP.

Carnivore representation in hyena bone accumulations

For small carnivores, census data in BASIS only indicates the presence of jackals. However, direct observations on the populations of small carnivores in both areas do not indicate significant differences between the WMA and the MNP areas, except for bat-eared foxes which are more abundant in the MNP (Maude pers. obs.). It appears then that the probability of the representation of carnivore taxa in both areas is similar. Although the WMA dens reflect a high percentage of carnivores in the MNI (16%), this number is slightly lower than the previously proposed ≥20%. At the MNP carnivores represent 24% of the MNI. However, it would be useful to contextualize this information. As shown in Table 4, means of the percentages of carnivores represented at 17 hyena dens (four dens of spotted, eight of brown and five of striped hyena) indicates highly variable results for each hyena species as previously noted by Potts (1988) and Cruz-Uribe (1991). It must be noted that the percentages may be influenced in some cases by the total values of MNI represented at each case study. For example, the stripped hyena study by Kruuk (1976) and the one on spotted hyenas by Mills & Mills (1977) each had an MNI of just four. However, a general trend from these case studies indicates that carnivores are usually highly represented at *Parahyaena* and *Hyena* dens, but the same cannot be said for *Crocuta* accumulations. These differences probably reflect variation in the behavioral ecology of each species. *Crocuta* is regarded as a more active hunter than *Parahyaena* and *Hyaena* which are mostly scavengers (Skinner & Smithers, 1990). In addition, even for the same species, there is a degree of variability across their geographical ranges (Table 4).

The high representation of carnivores at the *Parahyaena* dens studied here is not correlated with the abundance of carnivores in the local faunas, and yet its high representation is intriguing. In the southern Kalahari brown hyenas were observed on 18 occasions attempting to hunt small-sized carnivores but were only successful once when a bat-eared fox was killed (Mills, 1978). No successful hunts on small carnivores by brown hyenas were observed in the Makgadikgadi, the Central Kalahari and the Namib Desert (Goss, 1986; Maude, 2004; Owens & Owens, 1978). This information may suggest that brown hyenas are rarely successful hunters of small carnivores but will frequently scavenge on their remains.

Conclusions

Studies on the associations between how well the bones accumulated at brown hyena den sites reflect the immediate environment have been lacking. The present study conducted on *Parahyaena* den sites in northern Botswana indicated that assemblages accumulated by this carnivore can be used to infer general features of the large mammalian community. There is a clear correlation between the abundance of ungulate faunas and their representation in the osteological remains recovered from *Parahyaena* dens as indicated by NISP and MNI in these case studies. Therefore, it appears that when studying bone accumulations of *Parahyaena*-derived origin in palaeontological assemblages, the predominant habitat type can be broadly inferred by the presence of the ungulate taxa represented. It is obviously necessary to establish the involvement of brown hyenas first.

Both Cruz-Uribe (1991) and Pickering (2002) suggested that there are high numbers of bones showing hyena damage recovered in hyena accumulations. This study recorded a mean of 63.6% (min = 53%, max = 73%, sd = 8.99) of bones showing hyena damage in agreement with previous studies.

As noted by others (Cruz-Uribe, 1991; Potts, 1988), differences exist between *Crocuta*, *Hyaena* and *Parahyaena* accumulations. It appears that high representation of carnivores is a diagnostic feature of *Parahyaena* and *Hyaena* accumulations, not of *Crocuta*. Thus, the use of a minimum carnivore remains representation of 20% of the total MNI in a given accumulation as a defining criterion for hyena involvement needs to be regarded with caution. In addition, as aptly noted by Pickering (2002), the presence of juvenile or subadult brown hyenas and hyena scats in the bone accumulations is a strong indication that brown hyenas are involved, a feature confirmed by the present study. Brown hyena cubs are abundantly represented at the Makgadikgadi dens with three cubs of the four specimens identified, the other one being a sub-adult. This indicates cub mortality at the dens.

The variability in carnivore representation shown in hyena accumulations is indicative of their opportunistic behaviour. However, in the cases where correlations have been made between bone accumulations and local faunas, (Hill, 1989) for *Crocuta* and this study for *Parahyaena*, results show that these accumulations broadly represent the ungulate faunas (domestic or wild) in the immediate surroundings.

Finally, the information presented here derives from the analysis of bones in areas of very different geomorphological and ecological context, past and present, to that of the South African Plio-Pleistocene caves in the Sterkfontein Valley. However, we consider that the variables that influence bone accumulations at brown hyena dens sites are primarily the scavenging and opportunistic behaviour of this species. Therefore, it is to be expected that the ungulate species represented by osteological remains at brown hyena dens, regardless of their geological context (and time) represent the faunas making use of the local environment.

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