THE FEEDING AND SPATIAL ECOLOGY OF CHEETAHS (*Acinonyx jubatus*) AND LIONS (*Panthera leo*) IN THE LITTLE KAROO, SOUTH AFRICA.

Submitted in fulfilment of the academic requirements

for the degree of

MASTER OF SCIENCE

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by

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Supervisor: Prof. R. Bernard

Declaration

I hereby declare that this dissertation, which I submit for the degree Master of Science (MSc) Zoology, at Rhodes University, Grahamstown, is my own work, and has not previously been submitted by me for degree purposes to this or any other tertiary institution.

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Table of Contents

Abstract

The re-introduction of large carnivores into relatively small conservation areas that fall within the historic distribution range of the species is becoming an increasingly common occurrence. The success of such re-introductions depends very much on the quality of the information that is available to guide management decisions, but in many cases, little information is available. The re-introduction of lions and cheetahs to Sanbona created the opportunity to monitor the behaviour of re-introduced predators to a relatively large system that was characterised by a low ungulate stocking density and little standing water. The broad aims were to study the feeding and spatial ecologies of the lions and cheetahs, to collect standard base-line data, and to examine the effects of the low prey density and limited standing water on habitat selection, range size and diet. The diet (data collected from direct observation and faecal analysis) was similar to that reported in previous studies, and lions and cheetahs preferred greater kudu, black wildebeest and springbok. Lions preferred medium to large prey items, and cheetahs preferred medium to small prey items. The hilly and mountainous terrain of much of the reserve meant that only 50% of the total space was available to the predators. Home ranges of most of the predators were focused around the single large body of standing water. This is likely to have been a response to the water, the vegetation, and the prey that was attracted to these. Habitat selection was also influenced by inter and intra-specific interactions at least for a solitary male lion and female cheetahs. Range sizes were larger than on some other reserves and it is suggested that this was a result of the low prey density. These results form the basis for management recommendations including the importance of continuing to monitor the system and opening up additional parts of the reserve to the predators.

Acknowledgements

With great gratitude I acknowledge the guidance and supportive contributions of all those who supported me in the execution of this study. With regard to the relevant field of study, Prof. Ric Bernard of Rhodes University and Mr. Trevor Wolf (Environmental GIS Consultant) needs particular recognition. Their continued professionalism, willingness, friendly encouragement and guidance were indispensable. To Prof. P.J. Vorster, for the constant motivation, interest and the editing, thank you Dad. To the inspiring interest of my colleagues and family, especially my wife Liesl's compassionate support and active assistance in many areas, Thank You.

To the Creator and Father all praise and glory, "Great and marvelous are thy works, Lord God Almighty…" (Rev.15:3).

List of Tables

List of Figures

Chapter 1

Introduction

Since the 1800s, throughout the world, large mammalian carnivores have experienced substantial reductions in range and numbers (Schaller 1972; Anderson 1981; Skead 1987; Caro 1994; Creel & Creel 2002; Sillero-Zubiri *et al*. 2004). This has been primarily due to loss of habitat, as well as direct and indirect persecution by humans (Caro 1994; Creel & Creel 2002; Sunquist & Sunquist 2002). Lions (*Panthera leo*) have undergone a dramatic range contraction and have been extinct in northern Africa since 1920, and the range in the southern parts of the continent has been greatly reduced (Skinner & Chimimba 2005). The lion is listed in CITES Appendix II and is classified as Vulnerable in the IUCN Red Data List (Friedmann & Daly 2004). The cheetah (*Acinonyx jubatus*) has suffered similarly. The species was widespread through Africa, excluding tropical forest and deserts (Sunquist & Sunquist 2002) and the distribution is now highly fragmented with populations in Kenya, Tanzania, Namibia, Botswana and South Africa (Caro 1994; Skinner & Chimimba 2005; R. Klein, Cheetah Conservation Botswana, Pers. Comm.). The number of cheetahs has been reduced from 100 000 in 1900 to between 12 000 and 15 000 (Marker *et al*. 2003a). The cheetah is listed in CITES Appendix I and classified as Vulnerable in sub-Saharan Africa and Endangered in North Africa and Asia (Friedmann & Daly 2004).

The conservation of the few remaining free-ranging populations of predators, such as cheetahs in Namibia and Botswana and wild dogs (*Lycaon pictus*) in South Africa, is a priority, and conservation efforts focus on minimizing and managing the conflict between the predators, humans and livestock (Mills 1991; Mills *et al.* 2001; Marker *et*

al. 2003; Lindsey *et al.* 2004). However, continued habitat loss and population declines have resulted in the restriction of many large mammalian predators to fenced conservation areas (Creel & Creel 2002) and it is important to understand the biology of predators in these, essentially unnatural systems. Furthermore, where large carnivores have been re-introduced to conservation areas in South Africa, these too are typically small (Langholz & Kerley 2006).

The conservation of large mammalian predators in enclosed game reserves is problematic for various reasons. The space requirements of large carnivores are large and they typically occur at low densities (Blackburn & Gaston 1994; Creel & Creel 2002) and these requirements are often difficult to replicate in a closed system. As such, the size of the reintroduction area is an important factor for the successful reintroduction of predators. It has been shown that isolated populations are more likely to go extinct in small habitats than in large habitats (Woodroffe 2001). As an example of the minimum size required, Woodroffe & Ginsberg (1998) proposed that the critical reserve size (the area for which there is a 50% probability of population persistence) for lions is 291km^2. While it may be relatively easy to estimate minimum reserve sizes for different carnivores, providing the land may not be as easy, and setting aside large areas for conservation when land is required for agriculture or settling people can be controversial (Breitenmoser *et al*. 2001; Sillero-Zubiri & Laurenson 2001). As a result of the competition for land, the reserves are often small (<300km^2) and fragmented, creating numerous management problems. These include managing genetic diversity which may be addressed through metapopulation management (Blackburn & Gaston 1994, Woodroffe & Ginsberg 1998, Creel & Creel 2002, Bissett 2007). In small conservation areas there is increased competition for resources at an intra- and inter-

specific level (Ginsberg 2001). This may be exacerbated if stocking rates, or density of species, on the reserve are high, which is often the case to meet the expectations of the paying guests. Where a reserve is established as an ecotourism venture, guests pay large amounts of money to see the members of a complete large carnivore guild. This can set the limits for stocking rates of predators which are likely to be higher than can be supported sustainably in the area available. This in turn requires a certain stocking rate for prey species which may again be above the carrying capacity of the reserve. These factors combine to aggravate inter- and intra-specific competition. The important point is that while small conservation areas may have a role to play in conservation (Caro 1994), there are numerous problems that have to be managed, and management interventions need to be based on reliable information which is often not available.

In South Africa, throughout the last two decades, land use in many areas has changed from agriculture to game farming for hunting, game (venison) meat production, game sales, or for ecotourism. As part of this change, many smaller reserves and conservation areas (<300km^2) have attempted to re-establish large carnivore guilds (Rowe-Rowe 1992, Hofmeyr &Van Dyk 1998, Hofmeyr *et al*. 2003, Hayward *et al.* 2007). This has been done for various reasons, including meeting the expectations of tourists and thus benefiting financially (Van Schalkwyk 1994; Van Dyk 1997; Hunter 1998) and sometimes in an attempt to recreate some aspects of normal ecosystem functioning (Primack 1993; Reading & Clark 1996).

The reintroduction of predators is costly and complex (Griffith *et al.* 1989; Lindsey *et al.* 2005) and not always successful (Anderson 1981; Reading & Clark 1996; Linnell *et al.* 1997; Breitenmoser *et al.* 2001). Reintroductions can result in conflict between

reintroduction sites or reserves and the surrounding communities and farmers (Breitenmoser *et al.* 2001, Sillero-Zubiri & Laurenson 2001) and can lead to the local extinction of prey species (Hunter 1998). Long term monitoring is an essential component of reintroduction programs (Ebenhard 1995). However, in South Africa, post release monitoring has rarely occurred and the reasons for failed re-introductions are poorly understood (Hunter 1998a; Hayward *et al.* 2007).

The reintroduction of large carnivores to Sanbona, a 540km² reserve in the Western Cape Province of South Africa, presented an opportunity to study the biology of lions and cheetahs in a part of their historical range from which they had been absent for about 200 years (Skead 1980). In an attempt to fill some of the gaps left by the lack of post release monitoring at some other sites, the broad aims of this research were to monitor the lions and cheetahs with a particular focus on their feeding and spatial ecologies. It was expected that this information would be used to guide the management of the particular system and also to contribute at a fundamental level to the understanding of the ecology of large carnivores. More detailed aims are presented in each research chapter.

Chapter 2

Study Area and Study Animals

This chapter reports the physical characteristics of the study area as well as the animals found within that area.

LOCATION

Sanbona Wildlife Reserve (from here on referred to as Sanbona) lies in the Little Karoo about 27km northwest of Barrydale, and 49km northeast of Montagu in the Western Cape province of South Africa (Figure 2.1). Sanbona covers an area of 540km² or 54 000 hectares. Three roads enter Sanbona from the R62 arterial road; the Divisional Road 1352 from the south, Divisional Road 1352 from the east and Divisional Road 1381 from the west.

The main rivers flowing into Sanbona, the Kalkoenshoek River and the Gatskraal River, feed the central Bellair Dam from the south. The volume of the Bellair Dam is four million cubic meters when full, and it overflows into the Brakriver, which later joins the Touw River and eventually the Gourits River. Together with these main rivers and large dam, Sanbona has numerous small farm dams and seasonal pans and streams that provide important water sources for the fauna (Figure 2.2).

The surrounding land comprises privately owned farmland and nature reserves. Sanbona was developed from 19 merged farms, which had been used for practices such as wheat and lucerne production, domestic animal farming (sheep and goats), game farming, recreational farming and tourism. About 700km of internal fencing was

removed. Sanbona's 130km of perimeter fence is electrified game fence, in accordance with prescription for South African reserves with dangerous game animals.

Figure 2.1: Sanbona Wildlife Reserve in relation to Barrydale, Montagu and other towns in the Western Cape province of South Africa.

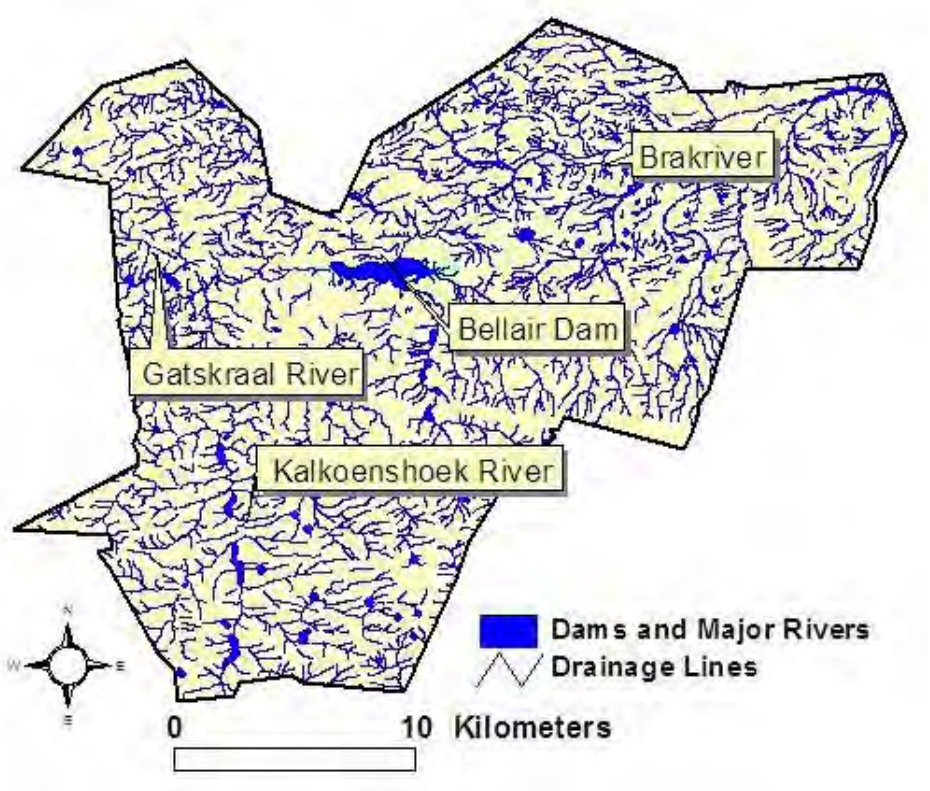


Figure 2.2: The dams, major rivers and drainage lines of Sanbona Wildlife Reserve (Arcview GIS 3.2a, map units: decimal degrees, maps projected to WG21).

MANAGEMENT UNITS

For management purposes, Sanbona is divided into management units (Figure 2.3). Sanbona South forms the largest part of the reserve and covers an area of 382.52km². This is where most of the reserve's tourism activities are focused and Sanbona South is stocked with indigenous mammal species only. Lions and cheetahs were released within this section of Sanbona (details described later) and this is the study site for the research.

Sanbona North was fenced off from Sanbona South at the time of the study and was not part of this research project.

Figure 2.3: The main management units that form part of Sanbona Wildlife Reserve (Sanbona E.M.P. 2007).

TOPOGRAPHY AND GEOLOGY

Geologically, Sanbona consists of sedimentary sandstone, mudstone and siltstone from the Devonian era (Norman & Whitfield 2006) (Figure 2.4). The hard quartzite sandstone of the Table Mountain Group makes up the towering ridges of the Swartberg, Anysberg and the Langeberg. Between these, the softer rocks of the Precambrian formations and much younger late Jurassic formations have been weathered away to form broad valley floors made up of sediments of the Kango and Kansa groups (Norman & Whitfield 2006).

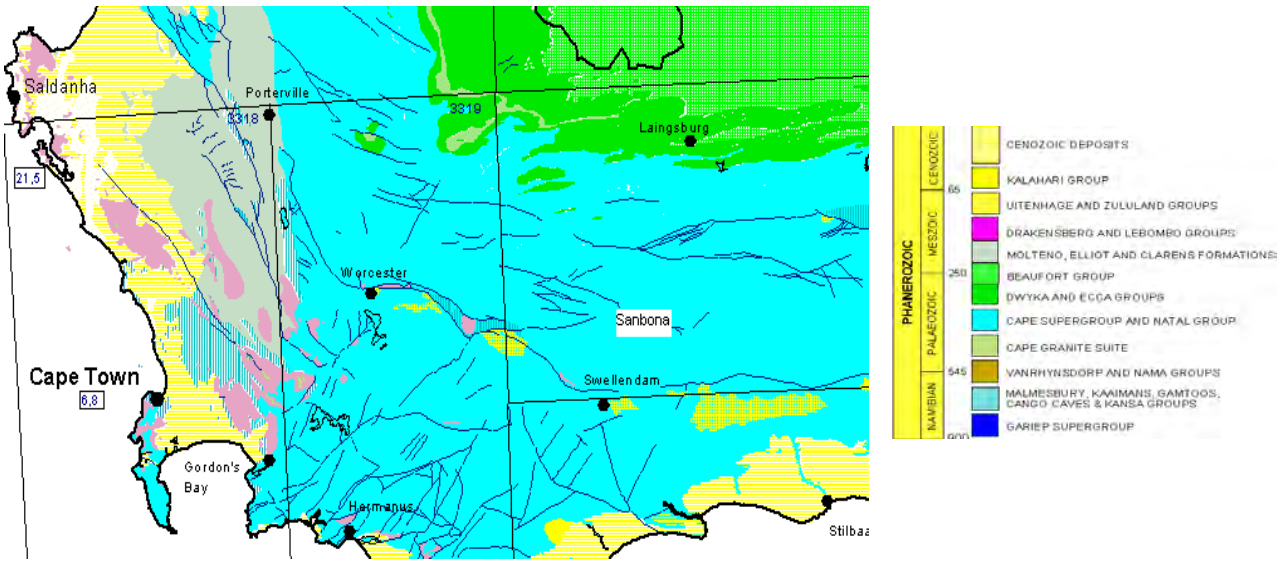


Figure 2.4: Map showing the major geological types of the South Western Cape (http://www.geoscience.org.za/images/stories/rsageology.gif, Simplified geological map of South Africa, 2008).

The topography of Sanbona varies considerably. In the South-eastern parts of the reserve, there are rolling hills and to the southwest, some open plains. Deep river valleys and high mountains dominate the central and western regions of the reserve.

Here the Warmwaterberg is the highest range with a 1344m peak, which forms a natural divide in the reserve between north and south (Figure 2.5). East - west orientated shale ridges cover the northern area of the reserve.

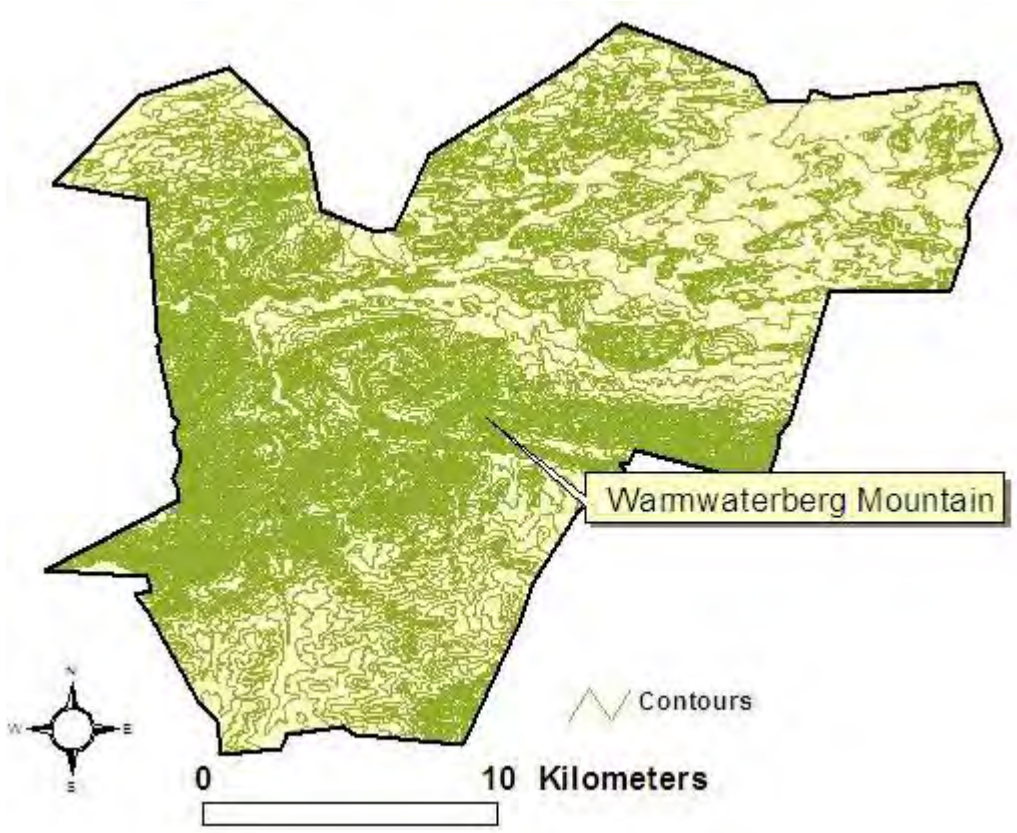


Figure 2.5: The contours of Sanbona Wildlife Reserve (Arcview GIS 3.2a, map units: decimal degrees, maps projected to WG21).

CLIMATE

Sanbona is situated in the Little Karoo and the summer months (December – February) are very hot with the daily temperature often exceeding 45°C (Lovegrove 1993). The hottest month is February with an average daily maximum temperature of 27.1°C. Sanbona has mild to cold winters (June, July and August) with snow often capping the

higher lying areas. The coldest month of the year is July, with an average daily minimum temperature of 4.6°C (Figure2.6).

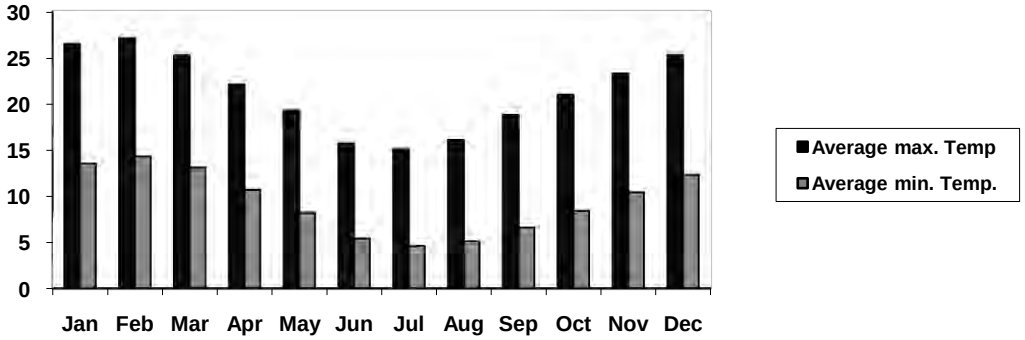


Figure 2.6: The Average monthly minimum and maximum temperatures for the last 20 years (ISCW-Agricultural Research Council 2007). Data from records accumulated on Sanbona, and from an ISCW-Agricultural Research Station just to the south of the reserve.

Sanbona lies within the transition zone of summer and winter rainfall areas of South Africa, with the winter rainfall region of the Western Cape to the south west and typical summer rainfall areas of the Karoo to the north east. Rain falls throughout the year with a slight tendency towards winter rainfall (Figure 2.7). The average rainfall over the past 20 years was 398.3mm per year. The reserve experiences large differences in rainfall due to its large size and the topographical variation. In the south of Sanbona, the temperature is cooler with a higher mean annual precipitation of 401.39mm. The Northern part of the reserve experiences higher temperatures and a lower mean annual precipitation of 173.12mm.

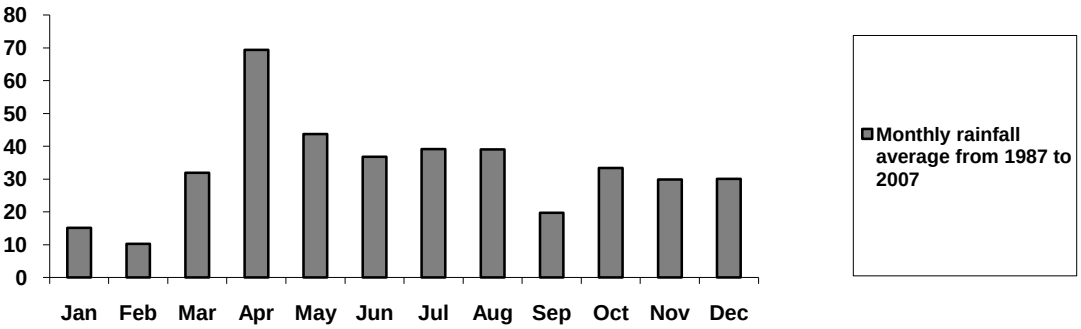


Figure 2.7: Monthly rainfall averages for the last 20 years (ISCW-Agricultural Research Council 2007). Data from records accumulated on Sanbona, and from an ISCW-Agricultural Research Station just to the south of the reserve.

VEGETATION

The vegetation of the Western Cape is well studied and described. Vlok *et al.* (2005) described 369 vegetation variants and of these, 35 occur within the boundaries of Sanbona (Figure 2.8) (Table2.1). To further simplify the vegetation map, these vegetation variants have been combined into six broader categories (the Biome 2 of Vlok *et al* (2005)) being Solid Fynbos, Mosaic Renosterveld, Solid Renosterveld, River and Floodplain, Succulent Karoo and Mosaic Thicket (Table 2.1; Figure 2.9). In the following text, the six vegetation variants are briefly described. The visibility within these vegetation units was not quantified, but was assessed qualitatively as either open (visibility for a predator estimated as greater than 100m), intermediate or dense (visibility less than 10m) (Table 2.2). The intermediate category was further subdivided into intermediate dense and intermediate open. Visibility was estimated at 1m above ground level to represent the approximate shoulder/head height of a lion or cheetah.

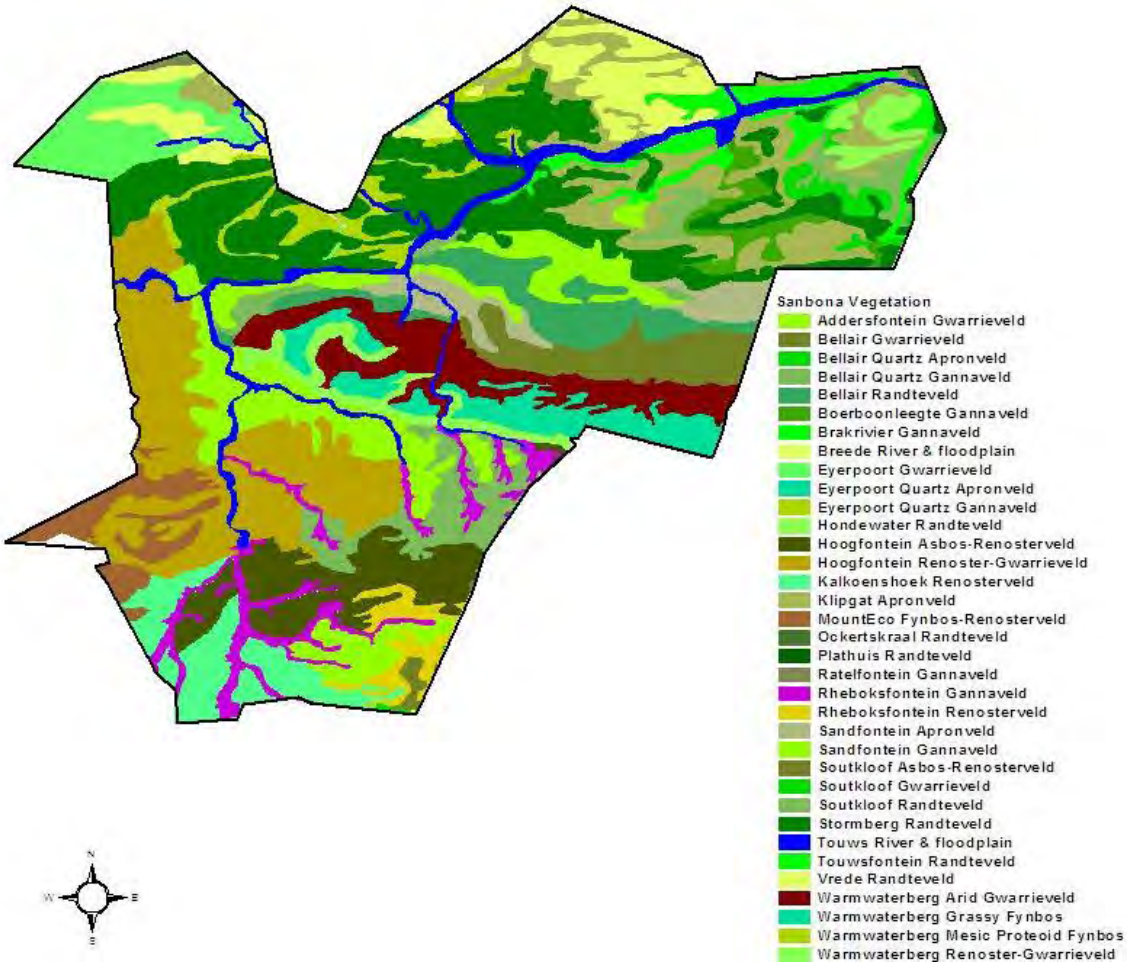


Figure 2.8: A map showing the 35 vegetation variants that occur on Sanbona as described by Vlok *et al* (2005).

Table 2.1: Sanbona vegetation types (Biome 2 (Vlok *et al* 2005)), their variants and the relative size of each vegetation type in hectares.

Vegetation Type (Biome2)	Variant	Size (Ha)
Solid Fynbos	Warmwaterberg Mesic Proteoid Fynbos	
	Warmwaterberg Grassy Fynbos	1907
Mosaic Renosterveld	Soutkloof Asbos-Renosterveld	
	MountEco Fynbos-Renosterveld	1499.9
Solid Renosterveld	Rheboksfontein Renosterveld	
	Kalkoenshoek Renosterveld	
	Hoogfontein Asbos-Renosterveld	5318.7
River & Floodplain	Breede River & floodplain	
	Touws River & floodplain	1927.5
Succulent Karoo	Touwsfontein Randteveld	
	Eyerpoort Quartz Apronveld	
	Plathuis Randteveld	
	Ockertskraal Randteveld	
	Ratelfontein Gannaveld	
	Bellair Quartz Apronveld	
	Hondewater Randteveld	
	Boerboonleegte Gannaveld	
	Bellair Quartz Gannaveld	
	Sandfontein Apronveld	
	Eyerpoort Quartz Gannaveld	
	Sandfontein Gannaveld	
	Soutkloof Randteveld	
	Brakrivier Gannaveld	
	Rheboksfontein Gannaveld	
	Bellair Randteveld	
	Vrede Randteveld	
	Klipgat Apronveld	
	Stormberg Randteveld	27534.1
Mosaic Thicket	Soutkloof Gwarrieveld	
	Warmwaterberg Renoster-Gwarrieveld	
	Eyerpoort Gwarrieveld	
	Bellair Gwarrieveld	
	Warmwaterberg Arid Gwarrieveld	
	Addersfontein Gwarrieveld	
	Hoogfontein Renoster-Gwarrieveld	16235.4
	Total Ha	54422.6

Solid Fynbos (Figure 2.10 & 2.11) consists of Warmwaterberg Mesic Proteoid Fynbos, in which *Leucedendron* species dominate on open slopes, and Warmwaterberg Grassy Fynbos which has a high shrub component including *Merxmuellera arundinacea Chrysanthemoides monilifera, Cullumia bisulca, Erica speciosa, Euryops erectus, Paranomus dispersus, Phylica axillaris)*. The tall *Leucedendron* species and the steeper

slopes on which these occur resulted in quite good visibility in this biome and it was classed as Intermediate Open. Solid Fynbos comprised 5% of the study area.

Mosaic Renosterveld (Figure 2.12) consists of Soutkloof Asbos-Renosterveld and MountEco Fynbos-Renosterveld. In the Soutkloof Asbos-Renosterveld, asbos *(Pteronia incana)* is prominent on deeper loamy soils, with most of the sparsely vegetated shale ridges having karroid shrubs *(e.g. Berkheya cuneata* and *Pteronia paniculata),* some succulents, and a few geophytes. Renosterbos *(Elytropappus rhinocerotis)* is only prominent on south facing slopes, along with some other shrubs *(e.g. Clutia polifoli* and *Passerina obtusifolia).* The MountEco Fynbos-Renosterveld has grasses such as *Ehrharta capensis* and *Merxmuellera spp.* and is less arid than Soutkloof Asbos-Renosterveld. The Fynbos elements are more prominent on the south facing slopes. In some areas the Mosaic Renosterveld is quite dense, but the dominant and low growing karoid shrubs and Renosterbos allowed for greater visibility and the vegetation type was classed as Open. This vegetation type comprised 3.9% of the study area.

Solid Renosterveld (Figure 2.13) consists of Rheboksfontein Renosterveld, Kalkoenshoek Renosterveld and Hoogfontein Asbos-Renosterveld. Renosterbos *(Elytropappus rhinocerotis)* is the dominant shrub but in some sections asbos *(Pteronia incana)* is abundant. Grasses, mostly sour grasses but also some sweet grasses *(e.g. Digitaria eriantha, Ehrharta bulbosa, Ehrharta calycina, Eragrostis capensis,Themeda triandra, Tribolium uniolae),* and some geophytes are present, particularly after fire. Some restios *(e.g. Ischyrolepis capensis, Restio triticeus, Rhodocoma fruticosa*) are present on south facing slopes. The restios and the high density of shrubs reduced the visibility and Solid renosterveld was classed as Intermediate to Dense. This biome comprised 13.9% of the study area.

River and Floodplain (Figure 2.14 & 2.15) consists of Breede River & floodplain and Touws River & floodplain. This unit is easily recognized by the presence of the sweet thorn tree (*Acacia karoo)* which is abundant in the main riverbeds. Trees and reeds such as *Buddleja saligna, Rhus lancea, Tamarix usneoides, Phragmitis australis* and *Typha capensis* are sometimes abundant along the edges of pools and in the riverbeds. Grasses are uncommon, but *Agrostis lachnantha* occurs in moist sites in the riverbeds and *Stipagrostis namaquensis* forms prominent clumps higher up in the floodplains. The visibility within this biome changed seasonally, being reduced after a period of rain when the grass component was longer. The taller and denser vegetation with open sandy riverbeds within these river lines resulted in this vegetation being classed as Intermediate to Dense. River and floodplain comprised only 2.1% of the study area.

Succulent Karoo (Figure 2.16 & 2.17) consists of 19 vegetation variants (Table 2.1) which fall within four broader vegetation groups (Apronveld, Quarts Apronveld, Gannaveld and Randteveld). The Apronveld is located at the base of hills and ridges and never on steep slopes or in valley bottoms. There it is replaced by Gannaveld. The soils are loamy to clayey and surface rocks are abundant. The shrub cover is well developed and gombos (*Pteronia spp*.) and kapokbos (*Eriocephalus spp*.) dominate. Leaf- and stem-succulents, as well as a variety of bulbous plants (geophytes) appear abundantly, but grasses are scarce. Many of the common plant species are palatable and the terrain is easily accessible.

In restricted areas, patches of white quartz pebbles are present with plant species differing from the surrounding shrubby vegetation (Vlok *et al.,* 2005). A rich variety of small succulents (i.e. *Gibbaeum* spp.) occur within these quartz patches (Vlok *et al.,* 2005).

Gannaveld is located in valley bottoms and often form large open plains just above the River and Floodplain habitat type. The soil is deep, loamy and saline. No trees are present but tall shrubs such as gannabos (*Salsola* spp.) and kriedoring (*Lycium* spp.) are abundant. Many small shrubs (e.g. *Eriocephalus* spp*., Pentzia incana, Pteronia* spp*., Tripteris* spp.) also occur. Quartz Gannaveld is made up of patches of white quartz pebbles with gannabos (*Salsola aphylla*) the most abundant shrub. Leaf succulents are abundant in the quartz patches and most of the species are different from those that occurr in the quartz patches of the Quartz Apronveld. A number of these succulents are localized endemics (Vlok *et al.,* 2005) and Sanbona has one of the highest diversities of *Gibbeaum* spp. in the Little Karoo with up to five species found on its quartz patches (Manning, 2001). Randteveld is a very arid vegetation type and is restricted to south-facing slopes on ridges and hills where the shale derived soils are shallow. The vegetation consists mostly of a sparse cover of small shrubs and compact leaf-succulents (Vlok *et al.,* 2005). There are relatively few bush clumps and tall shrubs within the Succulent Karoo, and it was classed as Open. Succulent Karoo made up 35.9% of the study area.

Mosaic Thicket (Figure 2.18) comprises seven vegetation variants (Table 2.1) and is characterized by scattered bush clumps with koeniebos (*Rhus undulata*) and gwarrie (*Euclea undulata*) as the most abundant trees. *Crassula rupestris* is an abundant shrub and where higher rainfall occurs, *Pteronia incana* is dominant. The scattered bushclumps provide cover while the open area allowed good visibility and this vegetation type was classed as Intermediate. This vegetation type made up 39.4% of the study area.

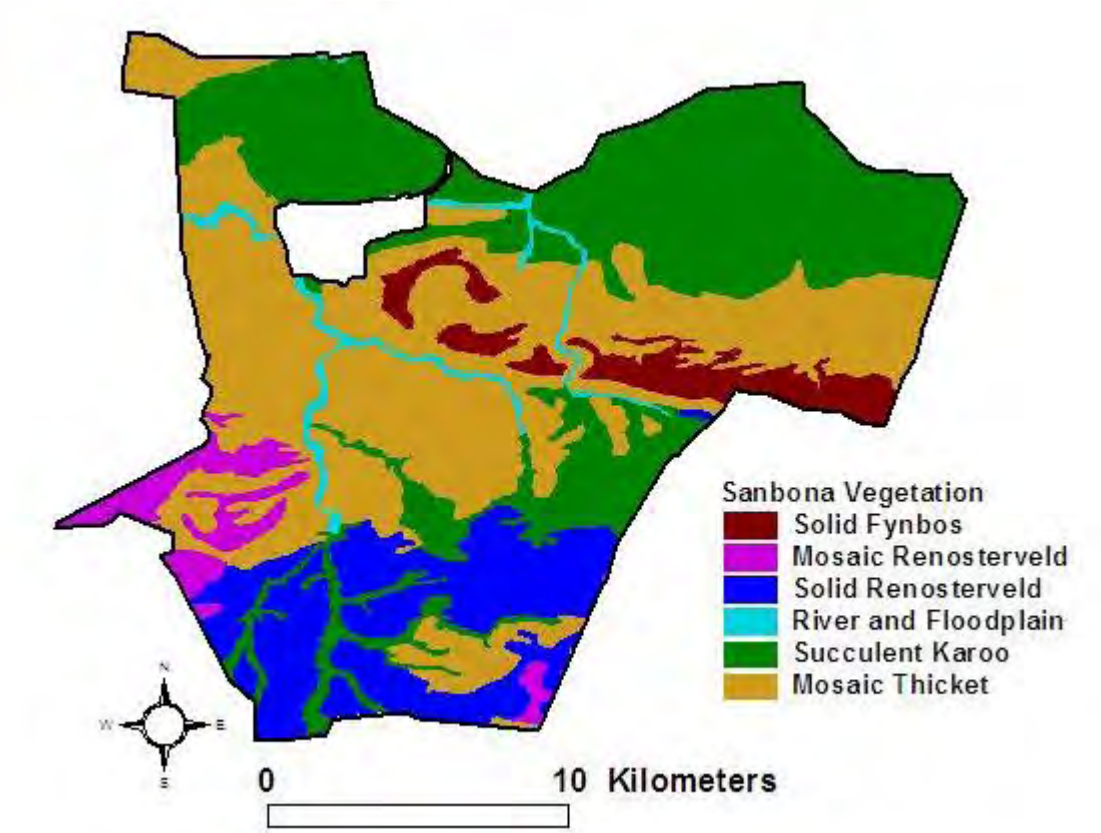


Figure 2.9: Sanbona South (Study Area) vegetation types as described by Vlok *et al* (2005).

Figure 2.10 & 2.11: Solid Fynbos on the higher slopes of the Warmwaterberg.

Figure 2.12: Mosaic Renosterveld.

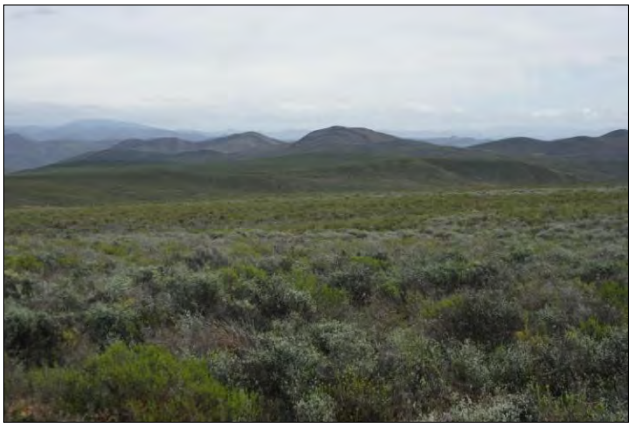


Figure 2.13: Solid Renosterveld.

Figure 2.14: River and Floodplain of the Kalkoenshoek River.

Figure 2.15: River and Floodplain of the Brakrivier.

Figure 2.16: Succulent Karoo

Figure 2.17: The Bellair dam, surrounded by Succulent Karoo.

Figure 2.18: Mosaic Thicket amongst Succulent Karoo.

Table 2.2: The vegetation types of Sanbona South with density of the vegetation type, size (km²) and percentage of the study area.

Vegetation	Density	Size (km²)	Area cover (%)
Solid Fynbos	Intermediate Open	19.11	5
Mosaic Renosterveld	Open	14.89	4
Solid Renosterveld	Intermediate Dense	53.03	14
River and Floodplain	Intermediate Dense	7.9	2
Succulent Karoo	Open	137.03	36
Mosaic Thicket	Intermediate	150.56	39
		382.52	100

MAMMALIAN FAUNA

Prior to 2002, the study site included a number of privately owned farms with a mixture of land uses. Most of the indigenous large mammals had been extirpated but some small and medium sized ungulates were present when Sanbona was established. The ungulate species that were present included cape grysbok, steenbok, grey duiker, klipspringer and grey rhebok. Other mammalian species which had always been on the reserve included chacma baboons, vervet monkeys, small predators like African wild cat, black backed jackal, caracal, spotted genet, black footed cat, brown hyena, honey badger, various mongoose species, rock hyrax and a variety of rodent and bat species. The rare and endangered riverine rabbit also occurred naturally on Sanbona.

To recreate an ecosystem as it was thought to have been 300 years ago and to create a unique game experience for tourists, a range of mammal species were reintroduced onto Sanbona. From 2002, many animals were introduced onto the reserve including plains zebra, springbok, red hartebeest, black wildebeest, greater kudu, gemsbok, eland, elephant, buffalo, giraffe, white rhinoceros, black rhinoceros and hippopotamus. The carrying capacity of the region is low (Erasmus 2007) and as a result, the stocking rate (density of ungulates per hectare; one ungulate per 40 hectares) was low. By comparison the stocking rate on Kwandwe, a reserve in the Eastern Cape Province to which cheetahs and lions had been re-introduced was about one ungulate per four hectares (Bissett 2007).

Initial carnivore re-introductions included six lions, four cheetahs, eight brown hyenas and three leopards. An updated species list of all the mammalian species found on Sanbona, with their common and scientific names is given in Appendix A.

GAME CENSUS (Table 2.3)

Initially, aerial census methods, using a Trike Microlight and Robertson R-44 Helicopter, were tested. However, the high temperatures and mountainous regions caused thermal air movements and only fast and high flying was safe with the Microlight, and game counts were inaccurate. Thus, game counts were done on foot each year.

The reserve was divided into regions, according to dominant geographical structures which limited the movement of animals between the different areas of count. Observers walked between 200 and 600m apart, where possible along higher ridges, to facilitate counting in the valleys. The line of observers advanced through the area recording details (species, group size, age, sex and location) of all animals seen. The size and the nature of the terrain resulted in the counts taking at least seven days to complete.

Table 2.3: Mammal numbers on Sanbona for the years 2003 to 2007. Note that these are total numbers for the whole reserve and are greater than that of the study area alone.

Species	2003	2004	2005	2006	2007
Baboon	0	265	255	275	237
Black backed jackal	0	30	45	76	110
Bontebok	5	5	7	0	0
Brown hyaena	10	8	8	8	10
Buffalo	7	0	12	12	15
Cheetah	4	9	8	8	4
Duiker	200	220	242	190	180
Eland	71	96	186	203	229
Elephant	5	7	7	7	9
Gemsbok	120	94	111	107	126
Giraffe	0	0	6	6	6
Grysbok	50	30	30	18	0
Red hartebeest	56	24	51	41	59
Hippopotamus	0	3	3	6	5
Klipspringer	100	76	81	82	63
Greater kudu	51	78	180	150	154
Leopard	3	5	5	5	4
Lion	3	7	6	4	7
Ostrich	67	35	53	87	11
White rhinoceros	0	0	6	7	8
Grey rhebok	0	30	30	18	0
Springbok	815	770	878	735	671
Steenbok	200	145	158	165	154
Black wildebeest	63	65	15	10	75
Plains zebra	51	47	51	44	42
Total	1883	2052	2438	2270	2182

STUDY ANIMALS

Between September 2003, when the first carnivore re-introduction occurred, and November 2004, eight cheetahs and ten lions were introduced. For identification purposes, all predators were given an alphanumeric identification code that indicated the species and sex, followed by a non-sequential randomly selected number. For example, cheetah male 00 = CM00, lion Male 39 = LM39 and unmarked lion female = LFUn.

Cheetahs (Tables 2.4 & 2.5)

The first four cheetahs, two males (CM00 and CM01) and two females (CF00 and CF01) were brought to Sanbona in September 2003. These animals were kept in a boma for one month and released in October 2003. Subsequent re-introductions occurred in May 2004 and November 2004 (Table 2.5). None of the individual cheetahs released during the study period were ever related. The success of these re-introductions was mixed with animals dying of natural causes, as a result of injury and from unknown causes, and killed by lions (Table 2.4). Three litters were born on the reserve to adult females CF00 (four cubs), CF03 (three cubs) and CF04 (Table 2.4). At the conclusion of this study, four cheetahs (CF04 with her three sub- adult cubs) were present on Sanbona.

Table 2.4: Details of reintroduced cheetah for the study period (September 2003 – December 2007).

(re-introduced cheetahs; cheetahs born on Sanbona)

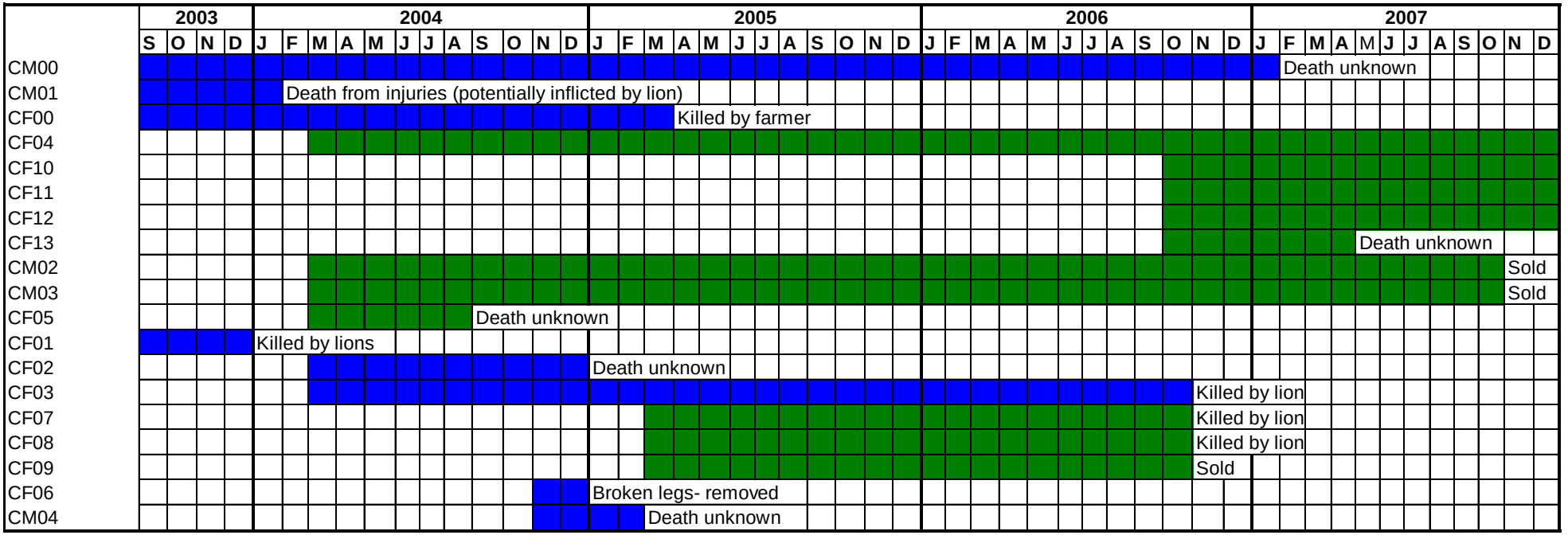


Table 2.5: Details of the cheetahs released on Sanbona from September 2003 until December 2007.

Release	Group Composition	ID	Release Date
1	2 Adult Males	CM00	Sep-03
		CM01	
	2 Adult Females	CF00	Sep-03
		CF01	
2	2 Adult Females	CF02	May-04
		CF03	
3	1 Adult Male	CM02	Nov-04
	1 Adult Female	CF06	

Lions

In 2003, three lions (LM39, LF43, LFUn) were released as a small pride onto Sanbona with further re-introductions in February 2004, February 20005 and September 2005 (Table 2.6). As with the cheetahs, the success of these introductions was mixed and efforts to maintain two prides on the reserve were unsuccessful (Table 2.7). From mid 2006 onwards, Sanbona had one pride of lions; LM47, LF43 and LF32, and one lone male; LM39 (Table 2.8). LM39 moved widely, sometimes entering the core of LM47 territory and even mating with LF43 on occasion. In January 2007, LM39 was badly injured in a fight, was placed in a boma and ultimately removed from Sanbona. Thus, only one pride, LM47 and his pride, remained on Sanbona. LF43 had a litter of four cubs in September 2007. At the conclusion of this study, Sanbona was home to seven lions; three adult lions; LM47, LF32 and LF43 and four cubs.

Table 2.6: Details of the lions released on Sanbona from September 2003 until December 2007.

Throughout the study period, the composition and group structures of the lions changed considerably.

Release	Group Composition	ID	Relatedness	Release Date
1	1 Adult Male 2 Adult Females	LM39 LF43 LFUn	Male unrelated Sisters	Sep-03
2	2 Adult Males 1 Adult Female	LM47 LMUn LF32	2 Brothers and a sister	Feb-04
3	1 Adult Female & 2 Female Cubs &	LF20 LFUn LFUn	Mother and cubs	Feb-05
4	1 Adult Female	LF99	Unrelated	Sep-05

Table 2.7: Details of reintroduced lions for the study period (September 2003 – December 2007).

(re-introduced lions; lions born on Sanbona)

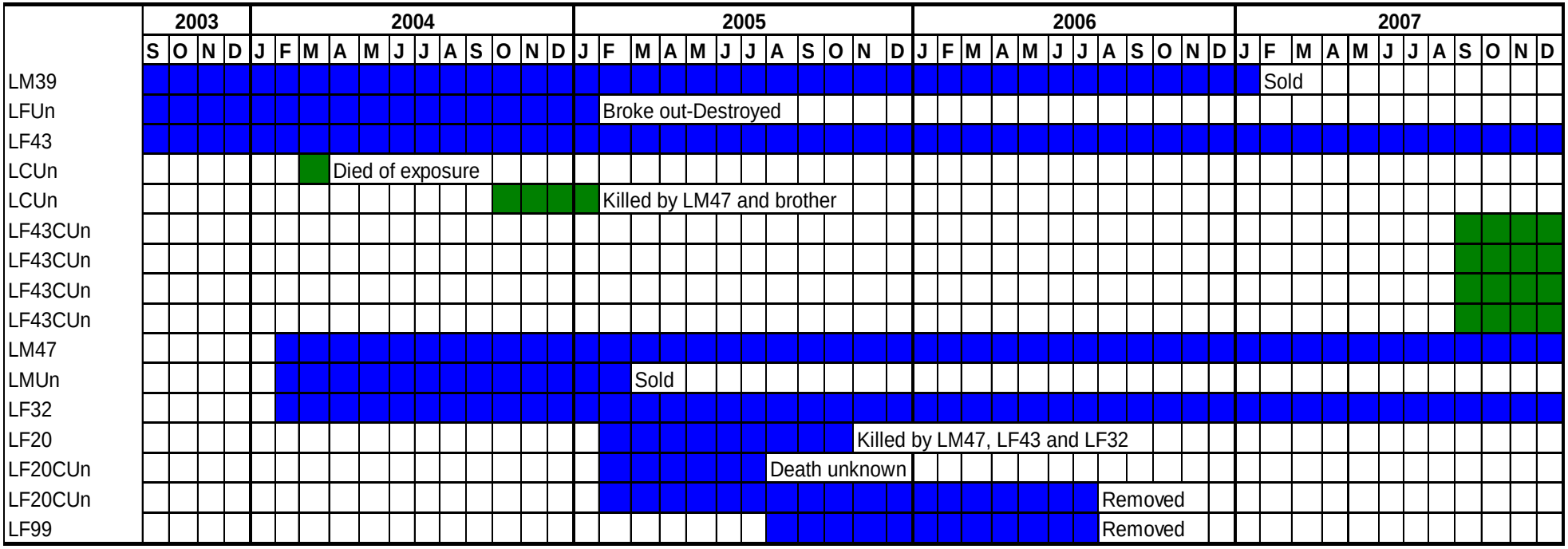
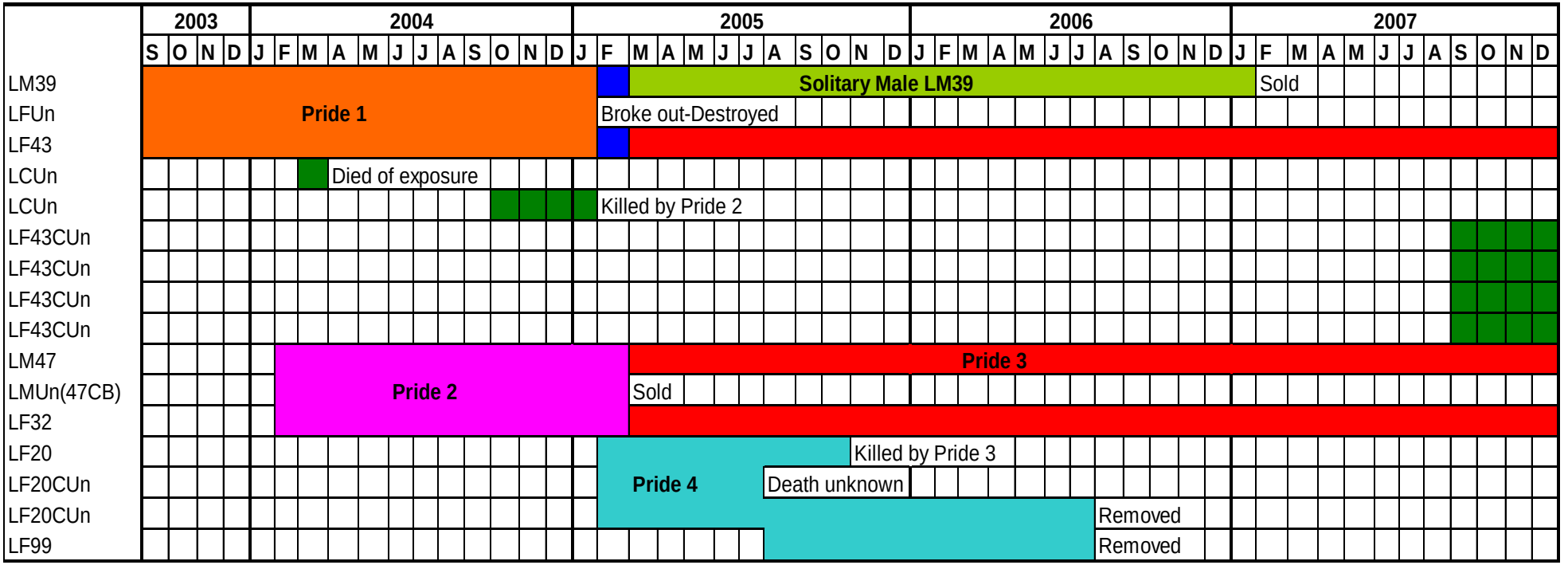


Table 2.8: Lion pride structures for the study period (September 2003 – December 2007).



GENERAL METHODOLOGY

The field work started with the release of the first lions and cheetahs in September 2003, and was concluded in December 2007.

Solitary lions and cheetahs were fitted with radio telemetry collars but not all members of a group or pride were collared. Radio collars and telemetry receivers were provided by African Wildlife Tracking, P. O. Box X1 Groenkloof 1000. The animals were located approximately three times a week, using various telemetry receivers; Telonics TR-4, Icom s/n 902401, and Communication Specialists R-1000. Location points of the animals were recorded using a GARMIN Etrex global positioning system (GPS) and the locations were logged into ArcView 3.2 GIS programme. Where the animals were in thick vegetation or on ridges where visual location was impossible, the position was plotted by triangulation (Kenward 2001). Radio tracking was conducted by foot, motorbike, and various 4-wheel drive vehicles.

Sanbona is a tourism driven operation and game drives are conducted from the various lodges. Qualified tourist guides/rangers operate on Sanbona twice a day: in the mornings and late afternoon or early evenings. Because of the general interest shown by guests in the large carnivores, these animals were in great demand for viewing and were located frequently by the rangers. Where the lions or cheetahs were located, the rangers recorded sightings by giving a description of the exact location, the group composition and activity of the animal/pride. Where possible, these sightings and kill recordings observed by the rangers were confirmed by the researcher. Further details of the methods used are presented in the following chapters.

Chapter 3

Feeding Ecology of Cheetahs and Lions on Sanbona

INTRODUCTION

Predator-prey systems in African terrestrial ecosystems are complex (Owen-Smith & Mills 2008b) and comprise multiple predator and prey species. The sizes of both predator and prey species vary widely, and body size relationships play a central role in shaping these large mammal food webs (Radloff & du Toit 2004; Owen-Smith & Mills 2008b). At a simple level, as predator size increases so does mean prey size (Gittleman 1985; Vezina 1985; Carbone *et al.* 1999). The increase in mean prey size is achieved through an increase in maximum prey size without changing minimum prey size, and consequently larger predators kill a wider range (both species and size) of prey (Sinclair *et al*. 2003; Radloff & du Toit 2004). Large predators typically kill prey items of about their own body mass while predators weighing less than about 21kg typically kill prey items about 45% of their own mass (Carbone *et al*. 1999). The 21kg body mass separates the insectivores and omnivores that mostly weigh less than 21kg from the true carnivores that mostly weigh more than 21kg (Carbone *et al*. 1999). A variety of factors disrupt the body size relationships described above. Pack hunting by wild dogs and cheetahs in Africa and dholes in India allow these species to kill prey that is larger than expected based on the simple relationship between adult body mass and prey size (Creel & Creel 2002; Bissett & Bernard 2007; Karanth & Sunquist 1995). The body size and abundance of prey species in the area will affect diet, and diet will vary from site to site but also within a site over time (Schaller 1972; Dunham 1992; Scheel & Packer 1993; Viljoen 1993). Factors that

affect prey vulnerability such as habitat selection, anti-predator behaviour, group size, age, condition and disease will also affect diet (Kruger *et al*. 1999; Creel & Creel 2002; Radloff & du Toit 2004; Owen-Smith & Mills 2008a). In a typical African terrestrial ecosystem, there are other larger and smaller predators present and the presence of larger predators can affect diet and feeding behaviour in various ways. These would include changing the time of hunting, habitat selection and size of prey killed (Hayward *et al*. 2006; Bissett & Bernard 2007). The range of factors that can affect prey selection, their variation in space and time, and the complexity of their interactions, make analysis of data from multiple sites problematic. Long term studies of members of a large carnivore guild at one site will overcome many of these problems and is the best approach to understand prey selection (Radloff & du Toit 2004; Bissett 2007; Owen-Smith & Mills 2008a,b).

Feeding ecology of cheetahs

The initial studies of cheetah were focused on grassland savannas (Schaller 1972, Durant *et al.* 1988, Fitzgibbon 1990, Caro 1994, Laurenson 1994), and more recently there have been studies in woodland habitats (Marker *et al.* 2003a, Hunter 1998, Purchase & Du Toit 2000, Broomhall *et al.* 2003, Radloff & Du Toit 2004) and Valley Bushveld / Thicket (Bisset 2004, Bisset 2007, Bisset & Bernard 2007). These studies have shown that cheetahs feed predominantly on the most abundant medium sized antelope ranging between 30kg and 65kg in body mass, although they are able to kill both larger and smaller prey (Mills 1996; Hayward *et al.* 2006; Bissett & Bernard 2007). For example, in Phinda Resource Reserve (Phinda) nyala (adult body mass 60-100kg, Skinner & Chimimba 2005) are the most abundant species and the most abundant species in the diet (Hunter 1998); in the Kalahari springbok (30kg, Skinner

& Chimimba 2005) are the most common prey, as well as the most abundant medium sized ungulate (Mills 1984) and in the KNP, impala (40-50kg, Skinner & Chimimba 2005) are the most abundant ungulate and the most preferred prey species (Mills *et al.* 2004). In Kwandwe (Eastern Cape Province, South Africa) the most abundant ungulate is the greater kudu (150-250kg, Skinner & Chimimba 2005) and greater kudu comprise 43% of all cheetah kills (Bissett & Bernard 2007). At the same reserve, 55% of all kills made by a coalition of three cheetahs were of prey items weighing more than 65kg (Bissett & Bernard 2007). Greater kudu are substantially larger than what is regarded as the typical prey mass for cheetahs and on Kwandwe, female cheetahs preferentially killed young and female greater kudu (Bissett & Bernard 2007).

Cheetahs have an unusual social system in which adult females are solitary unless accompanied by their cubs and males may remain alone or form coalitions (Caro 1994). As in lions and other carnivores, group size influences kill size and male coalitions hunt and kill larger prey than lone males or single females (Schaller 1972; Caro 1994; Bissett & Bernard 2007).

The diet of cheetahs is influenced by the presence of other larger, more powerful predators in a number of ways. Cheetahs may be directly affected through aggressive interactions with larger predators (lions and spotted hyaenas) and there are records of cheetahs being wounded and killed (Schaller 1972; Caro 1994; Hunter 1998; Woodroffe & Ginsberg 1998; Bothma & Walker 1999; Durant 2000a, 2000b). Secondly, cheetahs may avoid larger predators by hunting during the day and selecting habitats that are not used by lions (Durant 1998b). Finally, cheetahs lose

kills to larger predators (kleptoparasitism) (Schaller 1972; Mills *et al*. 2004; Radloff & du Toit 2004; Hayward *et al*. 2006).

Feeding ecology of lions

Lions are opportunistic predators (Schaller 1972; Hayward & Kerley 2005), and the diversity of the prey species varies greatly regionally from six to 37 different species (Stander 1992, Hunter 1998, Radloff & du Toit 2004; Hayward & Kerley 2005). Although lions kill a wide range of prey species, a few (three to five) of the most abundant medium to large prey animals (including species such as blue wildebeest, zebra, greater kudu and buffalo) constitute a large proportion of their diet (Kruuk & Turner 1967; Schaller 1972).

Hayward & Kerley (2005) analysed data from 32 studies and concluded that lions prefer prey species with a weight range of 190-550kg, with a most preferred weight of 350kg. Furthermore, they reported that there is no relationship between prey availability and prey preference of lions, but that there is a significant positive relationship between prey size and Jacobs' Index. However, diet must be shaped by the presence and availability of prey species and in areas of low prey density, such as Etosha National Park (Etosha), Namibia, smaller prey species are killed (Stander 1992). Prey preferences are not fixed in space or time but follow seasonal or longer term changes in prey availability (Schaller 1972, Dunham 1992, Scheel & Packer 1993, Viljoen 1993). In the Eastern Cape Province (South Africa) lions switch from killing greater kudu to killing warthog as warthog numbers increase (Bissett 2007; J. O'Brien Shamwari Game reserve, Eastern Cape Province, Pers. Comm.). Similarly, in the Chobe National Park (Botswana), warthog make up a large proportion of kills in

the dry season when larger species have migrated out of the area (Stander 1992; Viljoen 1993, 1997). Clearly, the presence or absence of prey species, the size of those species and their abundance will combine to shape diet. Finally, pride size affects prey selection and members of smaller prides kill smaller prey than members of larger prides (Stander 1992; Schaller 1972).

The selective killing of animals of a specific age class or sex by lions has been well reported although the results are not consistent. In the Kruger National Park (KNP; South Africa), lions select adult blue wildebeest and juvenile zebra (Mills & Shenk 1992) and in the Kalahari Gemsbok National Park (South Africa), adult blue wildebeest and gemsbok form the majority of lion kills, while kills of juvenile gemsbok and springbok are relatively common (Mills 1984). By contrast, in Etsoha (Namibia), lions show no preference for age and sex of blue wildebeest and zebra, but prefer juvenile springbok to adults (Stander 1992). Prey selection at a within prey species level is likely to be driven by factors that affect vulnerability and encounter rate including abundance, body size, group size, and other aspects of behaviour that vary between sexes and age class.

Management implications of predator re-introductions

In large, open ecosystems, where movement is not restricted, predation generally has little effect on migratory prey populations (Kruuk & Turner 1967; Schaller 1972). However, resident populations of herbivores and those within enclosed systems may be more severely influenced by predation. Populations of smaller ungulate species, which are preyed upon by a variety of carnivores (individuals and species) may be controlled by predation or even decline to local extinction (Fryxell *et al.* 1988; Hunter

1998; Sinclair *et al*. 2003). It is clear that the reintroduction of the large carnivores and the development of large carnivore guilds on enclosed reserves can be expected to affect populations of both prey species and more vulnerable members of the carnivore guild. An understanding of predation patterns and feeding ecology is therefore essential.

Small reserves and enclosed conservation areas are often closely managed to ensure a high quality game viewing experience for guests. Introductions and removals of both predators and prey occur but this is often done without any real understanding of how this might affect the ecosystem. Management interventions, such as increasing the abundance of a prey species, create research opportunities that can rarely be recreated in an open system and provide an opportunity to identify and understand some of the factors that affect prey selection.

The re-introduction of cheetahs and lions to Sanbona created an opportunity to study the feeding ecology of these predators in an ecosystem that supports a relatively low density of herbivores. It also created the need for information on feeding ecology that could be used to support management of the reserve. Finally, it created the opportunity to start another long term study looking at the factors that influence diet and feeding ecology of large mammalian carnivores.

The aims of the study have been twofold.

Firstly, to contribute to our understanding of the feeding ecology of cheetahs and lions in an area of low prey density. It was predicted that, as a result of the low prey density, the lions would kill smaller prey than usual, as seen in Etosha. Also that, as in previous studies, the cheetahs would kill the most abundant medium sized prey.

Secondly, to provide information on the diet of the cheetahs and lions that can be used for the management of the reserve.

METHODS

Information on the feeding ecology of lions and cheetahs was collected using two complementary methods. Firstly, through *ad hoc* observations of kills by the researcher, the Sanbona Wildlife Department and by field guides during their routine activities (Chapter 2), and secondly from faecal analysis.

Ad hoc observations

Although the goal was to locate all study animals at least once every three days, this was not always achieved. In many cases lions and cheetahs were located more frequently but some individuals were located less regularly. When kills were observed, the predator responsible, the prey species, age, sex and location were recorded. Three categories of prey age were used: juvenile being a small and dependent animal; sub-adult being a young, independent animal not fully grown and not sexually mature, and adult being a full grown animal (Hunter 1998; Rapson 2004, Bisset 2007). Very few kills of sub-adult animal were recorded and for the analyses of the influence of prey size on predation, the adult and sub-adult categories were combined. In the analyses of kill size, each kill was categorised as either small, medium or large (Table 3.1; Hunter 1998).

Table 3.1: Prey size categories with typical examples from Sanbona.

Kill Size	Weight Range	Examples
Small	< 30 kg	Grey duiker, steenbok, Cape grysbok, scrub hare, juvenile springbok, juvenile grey rhebok
Medium	30-65 kg	Springbok, grey rhebok, juvenile greater kudu, juvenile red hartebeest, juvenile black wildebeest, bontebok, juvenile gemsbok and ostrich
Large	>65 kg	Greater kudu, black Wildebeest, red hartebeest, gemsbok, plains zebra, eland

Faecal analysis

Ad hoc observations can artificially emphasize the frequency of large kills over expense of small kills. Predators will spend more time on larger kills and are thus more likely to be seen (Bisset 2004, 2007; Owen-Smith & Mills 2008). Faecal analysis compliments the *ad hoc* observations and should provide a more accurate measure of the occurrence of small prey in the diet. Faeces of lions were collected opportunistically throughout the study period. Although efforts were made to locate the faeces of cheetahs, few were found and this analysis is for lions only. On three occasions black backed jackals were observed consuming fresh cheetah scats (faeces) and this may explain this situation. The collected faeces were labelled (date, predator ID, location collected) and frozen. Faecal analyses were done according to procedures of De Marinis & Asprea (2006). Hairs were extracted by soaking the faeces in water until soft. The faeces were then broken open, and hairs were collected from various faecal areas to give a representative sample. The extracted hairs were washed with tap water, filtered and air dried using standard methods (Keogh 1983; Douglas 1989; Bisset 2004). Clean microscope slides were thinly coated with a pre-dissolved gelatin solution (5% in hot water). Ten randomly

selected clean hairs were placed on the slides and allowed to dry for a period of at least 24 hours. Once dry, the hairs were carefully peeled from the slide with forceps, leaving an imprint of the hair scales on the slides (Keogh 1983). In addition, cross sections of hairs were made. Ten to 20 cleaned hairs were selected at random for each faecal sample and placed into the mouth of a disposable plastic pipette. The pipette was then filled with molten wax (Paraclean II, Clinipath BV. Netherlands) and cooled rapidly in a beaker of ice. The plastic pipettes were cut into thin (1-2mm) sections using a scalpel and 15 – 20 sections were fixed onto a microscope slide using drops of the molten wax (method modified from Douglas 1989). A reference collection of scale patterns and cross sections was created using hairs from specimens at the Amathola Museum, King Williams Town in the Eastern Cape Province as well as from carcasses of known prey species on Sanbona. Slides were examined independently by two researchers and where there was disagreement, the slides were re-examined and consensus reached.

Prey preference index

To determine the prey preferences of lions and cheetahs on Sanbona, a preference index D (Jacobs 1974) was calculated for each prey species as follows:

$$D = (r-p)/(r+p-2rp)$$

where r is the proportion of the total kills of a species and p the proportional availability of the species within the study area (Jacobs 1974). The proportional availability of a species was calculated using the mean abundance of the species in the study area (not the whole reserve) for a three year period (2005-2007) relative to the mean abundance of all species preyed on by lions or cheetahs. In calculating the

mean abundance of available prey, species that were not consumed by lions or cheetahs were not included. Abundance data came from the annual game counts (Chapter 2). Jacobs' Index varies from -1 to +1, where -1 indicates maximum avoidance and +1 indicates maximum preference (Jacobs 1974). Because of problems associated with calculating preference indices (to be discussed later), a conservative approach was used in the interpretation of Jacobs' Index. Values greater than +0.3 have been interpreted as selection and values less than -0.3 as avoidance. Values between -0.3 and +0.3 were interpreted as indicating that the prey was utilised according to its abundance on the reserve (Bisset 2007). Prey preference was also calculated by using data from faecal analysis. Proportional availability was as described previously, while *r* was the proportion of scats in which the species was found.

Analyses of prey diversity in the diet

Using the total kill lists for each predator, two measures of prey diversity were calculated. Prey richness was simply the total number of prey species killed while Simpson's Index (D) was used to measure evenness across the kill list:

$$D = \frac{\sum(n-1)}{N(N-1)}$$

where n is the number of individuals of a species and N is the total number of all members of all species.

Simpson's Index (D) varies from zero to one and the index increases with decreasing diversity. Simpson's reciprocal index (1/D) has been used so that the value increases with increasing diversity.

Predator-prey body mass comparison

Body mass data for lions and cheetahs were from Smuts *et al.* (1980); Bothma & Walker (1999) and Skinner & Chimimba (2005), and were from as close to the area of origin of the predators as possible. Body mass for adult males and females of the prey species were taken from Bothma (2002) and Skinner and Chimimba (2005). Sub-adult mass of each sex was estimated by multiplying adult male or female mass by 0.7 and values for juveniles were calculated by multiplying mean adult body mass by 0.3, as suggested by Radloff & du Toit (2004) (Table 3.2).

To allow statistical analysis of the relationship between predator and prey body mass, data for another reserve in the Eastern Cape Province (Kwandwe; Bissett 2007) were used to supplement data from Sanbona. The data at both reserves were generated in the same way.

Data were tested for normality and non parametric tests used where appropriate. Percentages were arcsine transformed before analysis. All statistical analyses were done using Statistica (version 9; StatSoft inc. Tulsa, OK, USA).

Table 3.2: Mass of adult male, female and juvenile prey species for both cheetahs and lions.

	Mass (kg)		
Species	**Male**	**Female**	**Juvenile**
Greater kudu	220	155	56.3
Eland	650	460	166.5
Ostrich	120	120	36
Gemsbok	240	210	67.5
Springbok	41	31	10.8
Black wildebeest	135	115	37.5
Aardvark	45.4	41	13.0
Bontebok	75	67	21.3
Red hartebeest	150	120	40.5
Baboon	30	16	6.9
Leopard tortoise	-	-	-
Brown hyena	40	37	11.6
Buffalo	800	750	232.5
Duiker	17	21	5.7
Grey rhebok	20	20	6.0
Hippopotamus	1490	1321	421.7
Porcupine	12.6	11.7	3.6
Steenbok	11	11	3.3
Yellow mongoose	0.59	0.55	0.2
Zebra	335	290	93.8

RESULTS

General description of carnivore diet

Ninety one kills were recorded for the lions on Sanbona, representing 20 species ranging from leopard tortoise to eland (Table 3.3). Of the 20 species, 13 were large mammalian herbivores and two were carnivores. Greater kudu ranked highest in terms of animals killed, and was the most important prey species, while eland comprised the greatest percentage in terms of prey mass killed (Table 3.3). Five species (greater kudu, eland, ostrich, gemsbok and springbok) constituted 71% of all kills and 82% (9833.4kg) of the total mass of prey killed (Table 3.3). Greater kudu and eland comprised 39% of all kills recorded and 64% of the total mass. Eleven species were recorded as being killed once only and these comprised only 7% of the total mass. Lions did not feed on the brown hyaena or aardvarks that they killed. Of all observed lion kills, 40% were adult males, 50% adult females and 10% juveniles (Table 3.3).

For the cheetahs on Sanbona, 85 kills representing nine species were recorded (Table 3.4). Of the nine species, eight were mammalian herbivores ranging in size from steenbok to adult female eland and the ninth was a scrub hare. Springbok was the most important prey species comprising 66% of all recorded kills and 44% of the total prey mass killed (Table 3.4). Two species (springbok and greater kudu) constituted 81% of all kills observed and 68% of the total mass (Table 3.4). Of all the recorded cheetah kills, 31% were adult males, 34% adult females and 35% juveniles (Table 3.4). The diet of male and female cheetahs differed and this is dealt with later. Springbok and greater kudu were important prey species for cheetahs and lions (Tables 3.3 and 3.4). However, while the lions killed mostly adults (76% adult greater

kudu; 100% adult springbok), the cheetahs killed mostly juvenile greater kudu (69%) and adult (63%) and juvenile (37%) springbok.

Table 3.3: Total kill list for lions on Sanbona, based on *ad hoc* observations. Data include the number and percentage of kills per species, the number of kills in each age and sex class, and total mass per species. u is used to indicate unknown size and sex for kill of that species.

			Age			Total mass killed	
Species	**Kills**	**%**	**AM**	**AF**	**J**	**kg**	**%**
Greater kudu	21	23	4	12	5	2042.05	17
Eland	15	16	8	7	0	5641.4	47
Ostrich	10	12	3	7	0	804	7
Gemsbok	9	10	3	4	2	1127.7	9
Springbok	9	10	6	3	0	268.2	2
Black wildebeest	7	8	3	3	1	536.25	5
Aardvark	4	4	2	2	0	129.6	1
Bontebok	3	3	2	1	0	162.75	1
Red hartebeest	2	2	1	1	0	180.9	2
Baboon	1	1	0	1	0	14.4	0
Leopard tortoise	1	1	u	u	u	-	0
Brown hyena	1	1	1	0	0	30	0
Buffalo	1	1	0	1	0	502.5	4
Duiker	1	1	1	0	0	15.3	0
Grey rhebok	1	1	1	0	0	18	0
Hippopotamus	1	1	0	0	1	235.5	2
Porcupine	1	1	u	u	u	10.53	0
Steenbok	1	1	0	1	0	9.9	0
Yellow mongoose	1	1	u	u	u	0.544	0
Plains zebra	1	1	0	1	0	174	1
Total (%)	91	100	35 (40%)	44 (50%)	9 (10%)	11903.52	100

Table 3.4: Total kill list for cheetahs on Sanbona, based on *ad hoc* observations. Data include the number and percentage of kills per prey species, the number of kills in each age and sex class, and total mass per species.

			Age			Total mass killed	
Species	**Kills**	**%**	**AM**	**AF**	**J**	**kg**	**%**
Springbok	56	66	17	18	21	1251.75	44%
Greater kudu	13	15	0	4	9	679.45	24%
Duiker	4	5	3	1	0	64.8	2%
Steenbok	4	5	2	2	0	39.6	1%
Gemsbok	2	2	1	1	0	301.5	10%
Scrub hare	2	2	1	1	0	7.13	0%
Black wildebeest	2	2	1	1	0	167.5	6%
Eland	1	1	0	1	0	308.2	11%
Bontebok	1	1	1	0	0	56.25	2%
Total (%)	85	100	26 (31%)	29 (34%)	30 (35%)	2876.18	100%

Prey diversity in relation to predator size.

Species richness (the number of different species) in the kill list was greater for lions (20) than cheetahs (9) and species diversity (1/D) for lions (8.84) was four times that for cheetahs (2.18).

Faecal analysis (lions)

Ninety four faecal samples were analysed of which 9 contained hairs from more than one species and 5 contained no identifiable hair. Eleven prey species were identified, nine of which were also recorded through *ad hoc* observation of kills and were thus common to both methods. Faecal analysis added two new species to the kill list, being small mammals (not identified to species level) and black backed jackal (Table 3.5). Eight species for which there was a single observed kill were not detected in the faecal analyses which also failed to detect kills of ostrich, aardvark

and Bontebok (Table 3.5). Greater kudu was most frequently detected by both faecal analysis and *ad hoc* observation but beyond this, the methods generated different results. Some of the small species occurred more frequently in the faeces than in the observations (springbok and duiker) and some of the larger prey species occurred less frequently in the faeces than in the observed kills (eland, gemsbok, black wildebeest; Table 3.5). Zebra hairs were identified in the faecal analysis far more often than zebra kills were observed (Table 3.5).

Table 3.5: Comparison of observed kills and faecal analysis for lions. Major changes were greater than 20%; N: no change; ND: not detected.

Prey Species	**Observed kills**		**Faeces**		**Major changes**
	No.	**%**	**No.**	**%**	
Greater kudu	21	23.1	27	30.7	Up
Eland	15	16.5	4	4.5	Down
Ostrich	10	11.0	0	0	ND
Springbok	9	9.9	18	20.5	Up
Gemsbok	9	9.9	3	3.4	Down
Black wildebeest	7	7.7	2	2.3	Down
Aardvark	4	4.4	0	0	ND
Bontebok	3	3.3	0	0	ND
Red hartebeest	2	2.2	3	3.4	Up
Duiker	1	1.1	18	20.5	Up
Plains zebra	1	1.1	11	12.5	Up
Steenbok	1	1.1	1	1.1	N
Baboon	1	1.1	0	0	ND
Leopard tortoise	1	1.1	0	0	ND
Brown hyena	1	1.1	0	0	ND
Buffalo	1	1.1	0	0	ND
Grey rhebuck	1	1.1	0	0	ND
Hippopotamus	1	1.1	0	0	ND
Porcupine	1	1.1	0	0	ND
Yellow mongoose	1	1.1	0	0	ND
Unidentified small mammals	0	0.0	10	10.6	Up
Black backed jackal	0	0.0	1	1.1	ND
Total	91	100	98	100	

Prey Preference Index

Species which were not consumed (brown hyena, black-backed jackal and aardvark) and those for which no abundance data were available (unidentified small mammals, yellow mongoose, porcupine and leopard tortoise) have been omitted from this analysis. Based on the *ad hoc* observation of kills, lions showed a preference (Jacobs' Index >0.3) for seven species and avoided four species (Table 3.6). The preferred species were mostly of large or medium adult body size while the avoided species were mostly small or medium (Table 3.6). There were exceptions to this trend; zebras were avoided while grey rhebok were selected. There was no significant effect of size on Jacobs' Index (ANOVA; $F_{4,10} = 1.89$; $P>0.05$; Figure 3.1).

Based on the faecal analysis, lions showed a preference for five species and avoided seven species (Table 3.7). Selected species included the small duiker while the avoided species varied in size from small to large (Table 3.7). When *ad hoc* and direct observation methods were compared, black wildebeest and greater kudu were similarly selected and steenbok and springbok similarly avoided (Table 3.7). The largest differences in preference index were for the duiker which had a negative index (-0.2) based on observed kills and a positive index (0.9) based on faecal analysis, and for the plains zebra which had a negative index (-0.6) based on observed kills and a positive index (0.5) based on faecal analysis (Table 3.7). There was no significant effect of prey size class on Jacobs' Index of prey species based on faecal analysis ($F_{4,10} = 1.34$; $P>0.05$; Figure 3.1).

Table 3.6: Prey preference index for lions, showing the kill numbers and size categories of kills made. Note that abundance data are for Sanbona South (the study area) and not the whole reserve. Where two size classes are given, juveniles will be included into the smaller of the class catagories.

Species	Abundance	p	Kill Number	r	D	Size Category
Black wildebeest	5	0.005	7	0.083	0.9	L
Ostrich	12	0.012	10	0.131	0.8	M
Greater kudu	44	0.045	21	0.250	0.8	M/L
Bontebok	7	0.007	3	0.036	0.7	M/L
Grey rhebok	4	0.004	1	0.012	0.5	S/M
Hippopotamus	4	0.004	1	0.012	0.5	L
Eland	76	0.077	15	0.179	0.4	L
Red hartebeest	13	0.013	2	0.024	0.3	M/L
Buffalo	7	0.007	1	0.012	0.3	L
Gemsbok	102	0.104	9	0.107	0.0	M/L
Duiker	17	0.017	1	0.012	-0.2	S
Steenbok	30	0.031	1	0.012	-0.4	S
Plains zebra	45	0.046	1	0.012	-0.6	L
Baboon	81	0.082	1	0.012	-0.8	S/M
Springbok	536	0.545	9	0.107	-0.8	S/M
Total	983		83			

Table 3.7: Comparison of preference index based on observed kills and faecal analysis. Prey species are in the same order as in Figure 3.6. Change is a change in the evenness across the kill list (D); from avoidance (negative) to selection (positive).

Species	Kill Number	Faecal Number	Kill D	Faecal D	Size Category	Change
Black wildebeest	7	2	0.9	0.6	L	/
Ostrich	11	0	0.8	-1.0	M	Down
Greater kudu	21	27	0.8	0.8	M/L	/
Bontebok	3	0	0.7	-1.0	M/L	Down
Hippopotamus	1	0	0.5	-1.0	L	/
Grey rhebok	1	0	0.5	-1.0	S/M	/
Eland	15	4	0.4	-0.3	L	Down
Red hartebeest	2	3	0.3	0.4	M/L	/
Buffalo	1	0	0.3	-1.0	L	/
Gemsbok	9	3	0.0	-0.5	M/L	Down
Duiker	1	18	-0.2	0.9	S	Up
Steenbok	1	1	-0.4	-0.5	S	/
Plains zebra	1	11	-0.6	0.5	L	Up
Baboon	1	0	-0.8	-1.0	S/M	/
Springbok	9	18	-0.8	-0.6	S/M	/
Totals	84	87				

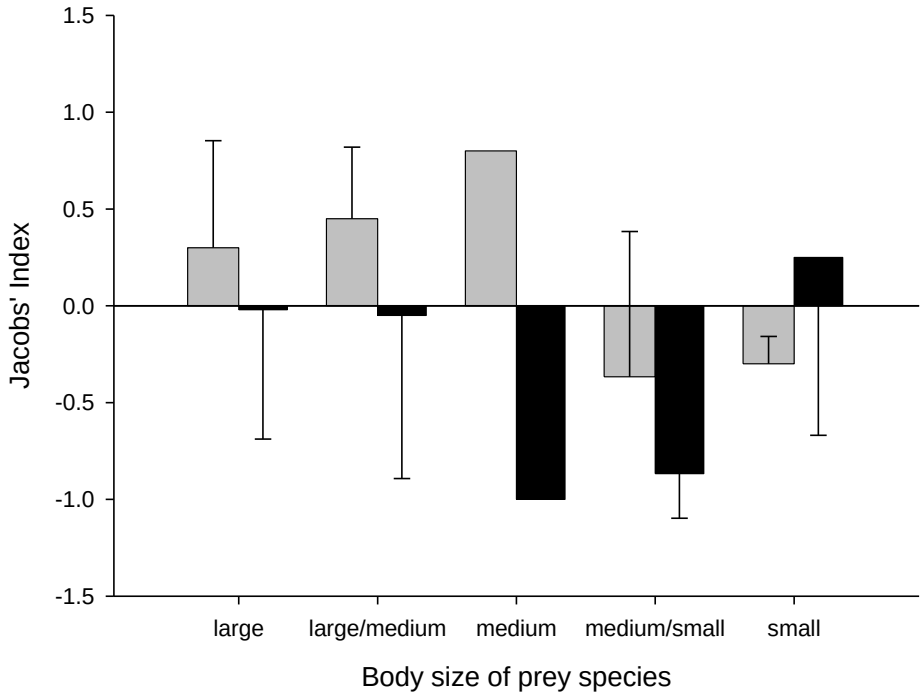


Figure 3.1: Mean Jacobs' Index (±1sd) for lions, for prey species of different body size. Grey bars are for *ad hoc* observations; black bars are for faecal analysis.

Cheetahs showed a preference for three species and avoided two (Table 3.8). The avoided species were of large adult body size and the preferred were medium or small. Large species such as red hartebeest and zebra were not killed by cheetahs and were thus also avoided. There was no significant effect of size class on Jacobs' Index ($F_{3,4} = 1.10$; $P>0.05$; Figure 3.2).

Table 3.8: Prey preference index for cheetahs, showing the kill numbers and size categories of kills made. Note that abundance data are for Sanbona South (the study area) and not the whole reserve.

Species	Abundance	p	Kill Number	r	D	Size Category
Black wildebeest	5	0.005	2	0.024	0.6	M/L
Greater kudu	44	0.047	13	0.157	0.6	M/L
Duiker	17	0.018	4	0.048	0.5	S
Bontebok	7	0.007	1	0.012	0.2	M/L
Springbok	536	0.568	56	0.675	0.2	S/M
Steenbok	30	0.032	4	0.048	0.2	S
Gemsbok	102	0.108	2	0.024	-0.7	M/L
Eland	86	0.091	1	0.012	-0.8	L
Total	944		83			

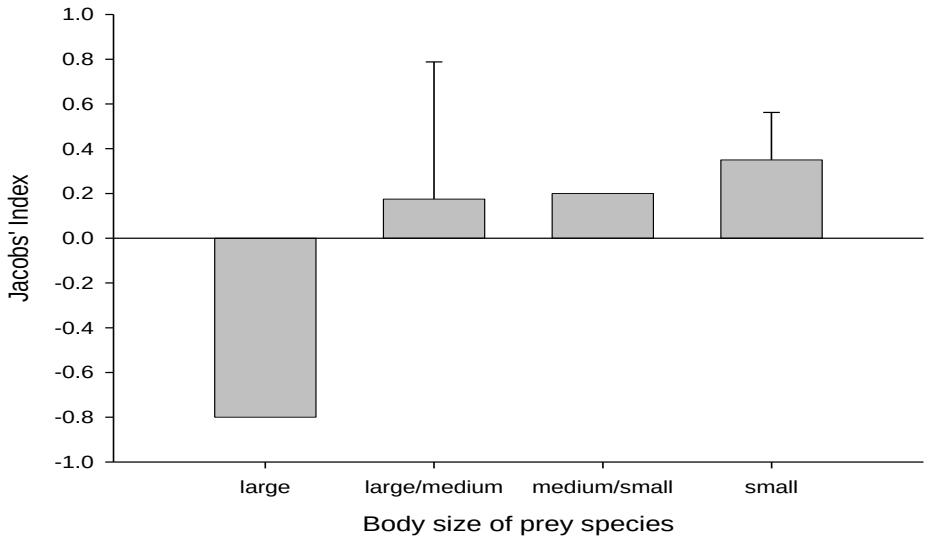


Figure 3.2: Mean Jacobs' Index (±1sd) for cheetahs, for prey species of different body size.

Prey size in relation to predator size

This analysis is not at the species level but rather recognises that animals of different ages of the same species may fall into different size classes. Nearly three quarters (73%) of all the kills recorded for the lions were in the large prey size category, whereas just over half of all kills (52%) for cheetahs were within the medium prey size category (Table 3.9). Lions were rarely observed on small kills (5%), while cheetahs were rarely observed on large kills (12%). Male and female cheetahs both killed mostly medium sized prey, but males killed more large (25%) than small prey (14%) and females more small (47%) than large (2%) prey (Table 3.9).

For all the predators, the proportions of items of different sizes was different from expected where the expected was simply the number of kills divided equally between the three size classes (lions; $\chi^2 = 66.6$; df = 2; $P<0.05$; male cheetahs; $\chi^2 = 9.9$; df = 2; $p<0.05$; female cheetahs; $\chi^2 = 25.7$; df = 2; $P<0.05$; all cheetahs; $\chi^2 = 25.9$; df = 2; $P<0.05$).

Table 3.9: Numbers and percentage of prey in each of the three size categories for male and female cheetahs and lions.

Kill Sizes	Cheetah Males	Cheetah Females	Cheetah Total	Lions Total
Small	4 (14%)	27 (47%)	31 (36%)	5 (5%)
Medium	17 (61%)	29 (51%)	46 (52%)	20 (22%)
Large	7 (25%)	1 (2%)	8 (12%)	66 (73%)
Total	28	57	85	91

There was a significant effect of predator on mean prey mass (one-way ANOVA; $F_{3,257} = 22.95$; $P<0.05$) and lions killed significantly heavier prey items than the other predators (Tukey post hoc tests; $P<0.05$ for all pairs). There was no significant

difference in mean prey mass between male and female cheetahs (P>0.05; Table 3.10). For both species, and for male and female cheetahs, the standard deviations were large and this reflects the wide range of prey sizes killed (Table 3.10). The maximum prey size of lions (750kg) was slightly greater than that of cheetahs (650kg), and the prey to predator mass ratio was slightly greater for lions than for cheetahs (Table 3.10). The prey to predator body mass ratio for male cheetahs was greater than that of females (Table 3.10).

Table 3.10: Descriptive statistics for the body mass (kg) of prey killed by lions and cheetahs, and by male and female cheetahs. Predator mass was 158kg (lions), 54kg (male cheetahs), 44kg (female cheetahs) and 48kg (cheetahs combined).

		Prey body mass (kg)		Prey: Predator mass ratio	
	N	**mean±1sd**	**range**	**Mean**	**Max**
Lion	91	194.7± 193.3	0.54-750	1.23 : 1	4.7:1
Cheetah	85	49.1± 79.5	3.2-650	1.02 : 1	13.5:1
Cheetah Male	28	96.5±74.0	11-240	1.79 : 1	4.4:1
Cheetah Female	57	44.8±90.8	3.2-650	1.04 : 1	14.7:1

Using additional data from Kwandwe, there was a significant relationship between predator mass and mean prey mass (linear regression; $r^2 = 0.86$; $F_{1,6} = 38.1$; $P<0.05$), but not predator size and minimum prey size ($r^2 = 0.03$; $F_{1,6} = 0.22$; $P>0.05$) or maximum prey size ($r^2 = 0.38$; $F_{1,6} = 3.69$; $P>0.05$) (Figure 3.3).

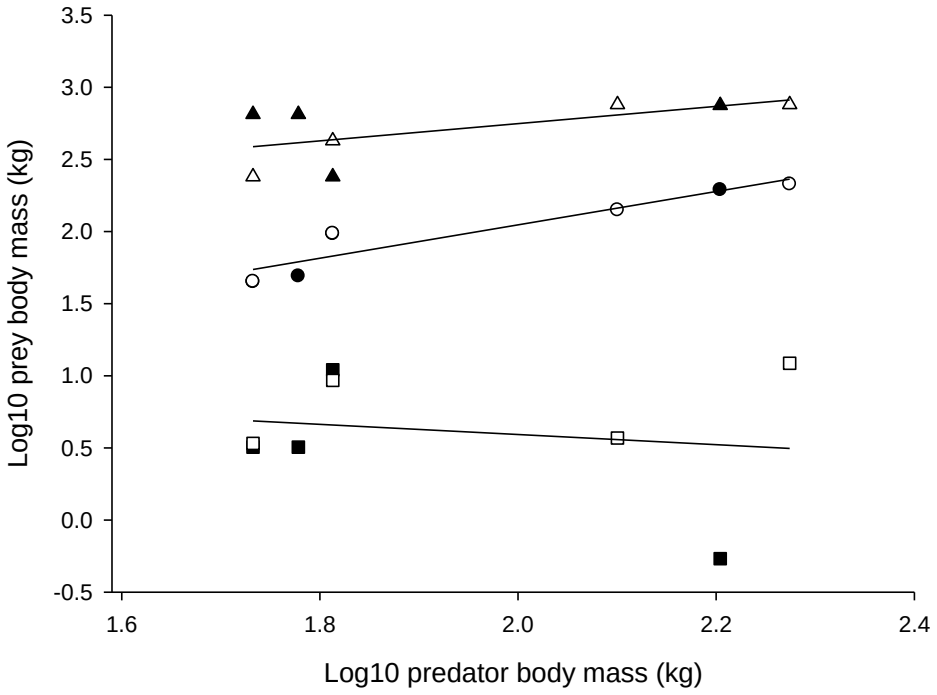


Figure 3.3: Predator-prey body mass relationships showing minimum (square symbols), mean (circular symbols) and maximum (triangular symbols) prey body mass (Log10 transformed) against predator body mass (Log10 transformed). Regressions: Y mean = -0.264 + 1.15*x; Ymin = 1.29 – 0.35* x; ymax = 1.55+ 0.59*x. Solid symbols are for data from Sanbona and open symbols for data from a similar study on Kwandwe.

Prey selection at within species level

Differences in the mean size of kills made by male and female cheetahs (Table 3.10) can be explained by differences in the prey age and species (Table 3.11). Adult greater kudu, gemsbok, black wildebeest and bontebok contributed to the large and medium kills of the cheetah males. Springbok was the most regularly killed prey species by male and female cheetahs, and a greater percentage of the kills made by female cheetahs were small juveniles (Table 3.11). Of 28 kills recorded for male cheetahs, 22 were large or medium, and 6 were small. Of 57 kills by female cheetahs, 32 were large or medium and 25 were small (Table 3.11).

Table 3.11: Kills made by male and female cheetah according to species, size and age.

	Adult body size	Male		Female		Total
Prey species		kills	% juveniles	kills	% juveniles	% juveniles
Duiker	S	1S	0	1S	0	0
Springbok	M	10M; 2S	17	25M; 19S	43	37.5
Greater kudu	L	4L; 6M	60	3M	100	69.2
Gemsbok	L	1L	0	1M	100	50
Scrub hare	S	0	/	2S	0	0
Eland	L	0	/	1L	0	0
Black wildebeest	L	2L	0	0	/	0
Bontebok	M	1M	0	0	/	0
Steenbok	S	1S	0	3S	0	0
Total		28		57		

There was no significant effect of adult size of a prey species on the percentage of juveniles killed of that species (two-way ANOVA with cheetah sex and prey size category as independent variables; $F_{2,8} = 0.97$; $P>0.05$).

DISCUSSION

A number of recent studies have used observational records from ecotourism reserves to establish predator diet (Radloff & du Toit 2004. Bissett 2007; Owen-Smith & Mills 2008). These observations are made by tourist guides while taking tourists on game drives (Radloff & du Toit 2004) or by conservation staff on the reserve (Owen-Smith & Mills 2008) or a combination of these (Bissett 2007). In all cases, the observations are relatively unstructured and do not highlight kills of small prey species. Small kills will be quickly and completely consumed reducing the likelihood of recording the kill or any remnants of a carcass (Mills 1984; Radloff & du Toit 2004; Owen-Smith & Mills 2008). Nevertheless, the early morning and late afternoon game drives that take place on ecotourism reserves are an excellent platform for the collection of data on the feeding biology (and other aspects of biology) of large predators (Radloff & du Toit 2004). The severity of the bias against recording kills of small prey species has been questioned and Radloff & du Toit (2004) argue that where the observation effort is high, as is likely to be the case on ecotourism reserves, the bias should be low. Furthermore, in Mala Mala and the adjacent Kruger National Park (KNP), observations by field rangers, periods of continuous observation, and game drives gave similar prey proportions for lions (Mills & Biggs 1993; Radloff & du Toit 2004; Owen-Smith & Mills 2008a). Sanbona is larger than some of the private game reserves and observation effort, while not quantified, will not have been as great as on Mala Mala or Kwandwe. There are two methods that can be used to complement *ad hoc* observations and these are continuous observations where an animal or group of animals is followed continuously for several weeks and all kills recorded, and faecal analysis. Continuous

observations do not share the bias towards large kills that is a characteristic of *ad hoc* observations, but they are labour intensive and require a comprehensive network of reserve roads from which the predators can be followed. The network of roads on Sanbona was not sufficient to allow continuous observations and the reserve management policy did not allow driving off the roads. Faecal analysis is not biased in the same way as *ad hoc* observations but may suffer from other biases. Identification of prey species from hair cross sectional shape and scale pattern was easier for some species (e.g. springbok) than others, and the less easily identified species may have been undercounted. It is also possible that one scat may contain hair from more than one prey species and if one prey item is large and the other small, the hair from the large item may "dilute" the hair from the small item to such an extent that the small item goes undetected. In spite of these drawbacks, the use of two methods rather than reliance on one is more likely to produce an accurate picture of diet.

The data from Sanbona tend to support the suggestions that kills of small prey species will be undercounted in *ad hoc* observations. Kills of four medium and large prey species (ostrich, eland, gemsbok and aardvark) were less frequently detected in the scat analysis than the *ad hoc* observations, while two small prey species (springbok and duiker) and unidentified small mammals were detected more often in scats. An exception to this pattern was that zebra were recorded more frequently in scats than in *ad hoc* observations. It is possible that the lions were killing young zebra and this would have reduced the likelihood of kills being recorded in the *ad hoc* observations while hairs would be present in the scats. However, zebra is a preferred species for lions (Hayward & Kerley 2005) and it is unlikely that the lions would not

have killed adult animals on Sanbona. Faecal analysis failed to detect 11 species that had been recorded by the *ad hoc* observations. This represents a serious weakness in the method which could be overcome by increasing the sample size. Since the *ad hoc* observations and faecal analysis generated different frequencies for kills, they also generated different values for Jacobs' Indices which were more negative for some large species and more positive for some small prey species.

Real preference for a prey species is challenging to demonstrate, unless direct observations of the selection are made when hunting predators are presented with a choice of prey (Stander 1992). While measures of prey preference have some value, they must be interpreted with care. The record of kills, be it from *ad hoc* observation or faecal analysis, that is used to calculate prey preference, is not a simple measure of preference, but is the end product of a range of factors and decisions. The latter includes where and when to hunt, whether or not to initiate a chase, whether or not to continue with a chase after a certain distance, whether or not the chase was successful and others (Stander 1992; Owen-Smith & Mills 2008a). The way in which the relative abundance of a prey species is estimated is also important and the inclusion of a species that is not consumed (perhaps a megaherbivore) will result in an artificially elevated preference index.

On Sanbona, faecal analyses did contribute to developing a more accurate prey profile and it is recommended that faecal analyses is used in conjunction with *ad hoc* observations to identify predator diet.

Large mammalian predators typically kill a range of prey species with the number of species killed increasing with increasing body size of the predator (Gittleman 1985; Cohen *et al*. 1993; Sinclair *et al*. 2003; Durant *et al*. 2009). Lions, for example, kill a

greater range of prey species than do cheetahs or African wild dogs on Mala Mala (Radloff and du Toit 2004), the Kruger National Park (Mills 1984; Owen-Smith & Mills 2008b), Kwandwe (Bissett 2007). In the present study lions killed 20 species while cheetahs killed nine. It is argued that larger species cannot just capture and overcome larger prey, but also travel greater distances and thus have access to a wider range of habitats with a greater diversity of species (Durant *et al*. 2009). The long kill lists, irrespective of predator size, probably reflect the opportunistic nature of most large predators (Schaller 1972; Radloff & du Toit 2004; Hayward & Kerley 2005) and the diversity of prey species (ungulates and small mammals such as lagomorphs and rodents) in most African terrestrial ecosystems. It is also the case that a small number of prey species comprise the majority of kills (Schaller 1972; Rudnai 1974; Funston *et al.* 1998; Power 2003; Radloff & du Toit 2004; Bissett 2007; Owen-Smith & Mills 2008). In Phinda, for example, nyala comprise 49% and impala 34% of all kills made by cheetahs (Hunter 1998). Three to five species comprise 80 to 90% of all kills made by lions (Smuts 1979; Mills 1990; Stander 1991, 1992; 1997; Funston *et al*. 1998, 2001; Radloff & du Toit 2004). The same pattern was seen on Sanbona where greater kudu and eland comprised 39% of all lion kills and springbok 66% of all cheetah kills. Kill lists with many species (high species richness) but where one or two species comprise the majority of kills, result in low levels of diversity, a measure that incorporates both species richness and evenness in the diet (Radloff & du Toit 2004). Whether or not there is a relationship between predator size and diversity in the kill list is not clear. In the present study, prey diversity was much lower for cheetahs than for lions, but on Mala Mala there was no significant relationship (Radloff & du Toit 2004). The preference for killing certain species from

a long kill list will be the result of a variety of interacting biotic and abiotic factors. These would include abundance and size of the prey species. Lions are expected to prefer large or medium sized prey species (Hayward & Kerley 2005) but this is influenced by abundance. In the Kalahari, small mammals and juveniles (calves of gemsbok) comprise more than 50% of the diet (Eloff 1973). Habitat selection by both predator and prey species may make one prey species more or less vulnerable or a species may be encountered more often. Leopards in Mala Mala kill woodland species and avoid ungulate species that use the open grasslands (Radloff & du Toit 2004).

The presence of other larger predators may affect diet in a number of ways. Kleptoparasitism may result in the selection of smaller prey species or items that can be quickly consumed (Hayward, Hofmeyr *et al*. 2005). Larger predators may displace smaller species to less optimal habitats with a different prey species composition and finally smaller predator species may change the time at which they hunt to avoid larger predator species (Sunquist & Sunquist 1989; Carbone *et al*. 1999; Creel & Creel 2002; Mills & Gorman 1997; Pole *et al*. 2004; Bissett & Bernard 2007).

Drought and disease may affect one prey species more than another and increase its vulnerability to predation. For example, in the Mana Pools National Park (Zimbabwe), buffalo were the most important prey species of lions in the 1980s. However, following droughts in 1983 and 1984, the numbers of buffalo in the riverine woodland, which is the favored habitat for hunting, declined and the lions switched to killing other large ungulates (Dunham 1992). Drought also affected the diet of lions in the KNP, but quite differently from that in Mana Pools. In the KNP, drought differentially affected the vulnerability of three favored prey species; the

vulnerability of buffalo increased and prey selection for buffalo increased (Owen-Smith & Mills 2008a). Thus the diet of predators is influenced by many factors, and because these change with time and space, it is not surprising that different studies have reported quite different diets for the same species. On Kwandwe, for example, greater kudu comprise 43% of all recorded kills for cheetahs (Bissett & Bernard 2007) while on Phinda, nyala comprise 49% of all kills (Hunter 1998). In the KNP, impala comprise 78% of kills made by leopards (Pienaar 1969b) while in the Matobo National Park (Zimbabwe), hyrax, hares and klipspringers comprise more than 50% of all kills (Grobler & Wilson 1972). The diet of lions is highly variable both in time and space. In Chobe National Park (Botswana), Buffalo and zebra comprise 70% of kills in the wet season while in the dry season warthogs comprise 43% of kills (Viljoen 1993). By contrast, in Phinda, blue wildebeest and nyala comprise 80% of the diet of lions (Hunter 1998).

The results from the present study support the previously reported patterns. Lions killed more species than cheetahs and, with the exception of springbok, killed the most abundant medium to large ungulate species. The initial prediction that the lions on Sanbona would tend to kill smaller species, as seen in Etosha, was not fully supported. Three large and relatively rare prey species (greater kudu, eland and gemsbok) comprised the greatest number of kills and total mass killed, while the small and abundant springbok comprised 10% of kills, but only 2% of total mass killed. The preferred species for lions (Jacobs' Index >0.3) were mostly large or medium sized, while the avoided species (Jacobs'Index <-0.3) were small or medium sized. The most preferred species was the black wildebeest (Jacobs' Index 0.9), which reflected the low relative abundance of the species and the previously reported

preference for wildebeest (Hayward & Kerley 2005). The kill list of cheetahs was less diverse (lower 1/D) than that of lions because species richness was lower and a single species (springbok) comprised 66% of all recorded kills.

The relationship between prey species size and the diet of cheetahs was not as clear as it was for the lions and the initial prediction was poorly supported. Cheetahs selected species that were small, medium and large and similarly avoided small, medium and large prey species. The selection of large prey species is counter intuitive but is explained by the fact that particularly female cheetahs killed juveniles of the larger prey species. This selection of small prey items by female cheetahs has been reported in previous studies (Bissett & Bernard 2007). Male cheetahs occur in functional groups (coalitions) and members of a coalition have been reported to hunt cooperatively (Bissett & Bernard 2007; personal observations). Male cheetahs are also larger than females and a combination of the larger body size and cooperative hunting probably explains why prey size is larger (Caro 1994; Hunter 1998; Mills 1998; Mills *et al*. 2004). By contrast, female cheetahs are solitary and smaller and in addition are less able to defend a carcass from a potential kleptoparasite (McVittie 1979). These factors could explain the selection of small prey items by female cheetahs. Prey selection at a within species level has been reported in a number of other studies where predators select for a particular age or sex of a prey species (Fitzgibbon 1990; Mills 1990, 1984; Mills & Shenk 1992; Stander 1992; Owen- Smith 1993; Hunter 1998; Bissett & Bernard 2007). Such selection will be driven by sex or age based differences in size, vulnerability, abundance, habitat choice and behaviour of the prey animals. Hunter (1998) found that in species where males are often solitary or form small bachelor herds, the males are at greater risk of

being caught due to the smaller numbers and reduced vigilance by not having the 'many eyes' of the larger herds. Male Thomson's gazelles tend to occur on the periphery of herds, have a greater nearest neighbour distance, are less vigilant and occur in smaller numbers than females and this may explain why they are selected by cheetahs in the Serengeti (Fitzgibbon 1990). Springbok show a similar social structure to Thomson's gazelle, and this may explain why they are selected by male cheetahs (Mills *et al*. 2004).

The body size of the adult large mammalian predators on Sanbona ranged from 43 kg (cheetah female) to 158 kg (lion male) and this was reflected in the differences in the prey profile. In general, the larger predators (the lions and male cheetahs) killed larger individuals from the larger prey species, while all predators killed similar sized small prey items. There was a significant positive relationship between predator size and mean prey size but not between predator size and minimum or maximum prey size. The lack of effect of predator size on maximum prey size is interesting and contrary to what has been reported in some previous studies (Radloff & du Toit 2004). The most likely explanation is that in the present study, lions killed no very large prey items (the largest was 750kg) compared to over 1000kg on Mala Mala where there was a significant relationship between predator size and maximum prey size (Radloff & du Toit 2004). These results are typically interpreted as indicating that larger predators have greater predatory options than the smaller predators (Gittleman 1985; Cohen *et al*. 1993; Radloff & du Toit 2004; Bisset 2007) and this is supported by the results of this study.

In conclusion, the results for the feeding biology of lions and cheetahs on Sanbona support the broad patterns that have been described previously. Both lions and

cheetahs preferred greater kudu and black wildebeest and the combined predation pressure may represent a threat to the viability of these species on Sanbona. This will be discussed further in chapter 5.

Chapter 4

Spatial Ecology of Cheetahs and Lions on Sanbona

INTRODUCTION

Use of space and home range size vary widely between different species of mammalian carnivores, and within and between populations of the same species (Caro & Macdonald 1986; Spong 2002; Sillero-Zubiri *et al.* 2004). The space used, both in terms of the size of the area used and where it is located, is influenced by a suite of interacting factors. These include the availability of suitable prey and its distribution, the body mass, group size and population density of the predator, and aspects of the physical environment, including availability of cover (for hunting and predator avoidance and for denning sites), water availability and topography (Clutton-Brock & Harvey 1978; Macdonald 1983; Reiss 1988; Mills & Knowlton, 1991; Caro 1994; Laurenson 1995; Mizuntani & Jewel 1998; Oli *et al.* 2002; Spong 2002; Sunquist & Sunquist 2002; Jetz *et al.*2004; Grassman *et al.* 2005; Marker & Dickman 2005; Benson *et al.* 2006). In addition, since large mammalian predators are typically part of a large carnivore guild, the presence of carnivores with a greater relative competitive ability will affect spatial ecology (Carbone & Gittleman 2002).

Typically, there is a negative relationship between the size of the space used, and environmental productivity and resource density (Marker & Dickman 2005). It has been suggested that carnivores generally maintain a space that is just sufficient for the requirements of the species and, or sex (Caro 1994; Delahay *et al*. 2006). The positive relationship between body size and home range size reflects the fact that absolute energy requirements increase with increasing body size (McNab 1963; Jetz

et al. 2004) and a greater area is required to meet these needs. For the same reason, increasing group size in species such as lions and African wild dogs is associated with increased home range size (Spong 2002).

The availability of cover, particularly for hunting, and water are important determinants of space use by carnivores. Habitat selection and the size of the area used by females is often set by food availability and the availability of suitable denning sites, while the space used by males is determined more by the female distribution (Caro 1994; Mizutani & Jewell 1998; Sunquist & Sunquist 2002).

The preceding discussion has excluded any effect of inter or intra-specific competition and assumes that an individual within a single species will settle where expected fitness is highest (Ideal Free Distribution of Fretwell & Lucas 1970; Cressman *et al*. 2004). However, where more than one species of large mammalian carnivore is present, it is very likely that interference competition will result in modified space use for one or more of the species (Woodroffe 2001). Interference competition may take the form of kleptoparasitism, harassment and killing and can result in population reduction, displacement and competitive exclusion from an area (Linnell & Strand 2000; Carbone & Gittleman 2002)

Social system and space use by lions and cheetahs

Lions and cheetahs are more social than many other felids (Schaller 1972; Caro & Collins 1986; Hunter 1998; Funston *et al.* 2001). Lions live in prides comprising related adult females, their cubs and one or two attendant adult males. This typically excludes unrelated adult females although overlap between home ranges of adjacent prides may occur where territories are large (van Orsdol *et al*. 1985; Hanby *et al.* 1995; Hunter 1998; Sunquist & Sunquist 2002). Home range size of prides is

dependent on factors such as pride size, availability of food and water, and the availability of denning sites (Sunquist & Sunquist 1989; Packer *et al*. 1990). Male lions may associate with more than one group of females and therefore male home ranges are often larger than those of females (Spong 2002). In large, open systems with migratory prey, home ranges may be as large as 2000km^2 (Etosha, Stander 1991) and in smaller, fenced systems with higher prey abundance, home ranges may be as small as 53km^2 (Phinda, Hunter 1998). Home range size varies both in space and time and there is an inverse relationship between range size and prey availability in the lean season (van Orsdol *et al*. 1985).

Habitat selection by lions is affected by the abundance of suitable prey, cover for hunting and denning, and water (Schaller 1972; Spong 2002). Lions tend to select regions with more dense vegetation often preferring riverine thickets and riparian forest where requirements for water and cover may be met (Schaller 1972; Hunter 1998; Funston *et al*. 2001; Spong 2002; Bissett 2007).

The social system of cheetahs is unique amongst the felids. Adult females are solitary unless accompanied by their dependent young, while adult males are either solitary or live in groups called coalitions comprising two to four, often related animals. Independent adolescents of both sexes remain together for up to six months before separating from their mother (Caro 1994; Bissett 2004; 2007; Bissett & Bernard 2007). Cheetah males that live in coalitions are more sedentary than the females and have territories that are smaller than those of the females (Caro 1994; Bissett 2007). The home range sizes of cheetahs vary considerably from 1500km^2 in Namibia (Marker *et al*. 2003) to 29km^2 in Matusadona National Park, Zimbabwe (Purchase & du Toit 2000). Home range size is affected by the range of factors described earlier.

While home ranges of females often overlap, cheetahs typically maintain separate core areas (Broomhall *et al*. 2003; Bissett 2007). The home range of a male or of a coalition often overlaps with those of several females (Caro 1994; Bissett 2007), possibly to increase mating opportunities.

Habitat selection by cheetahs varies regionally and between the sexes. In the Kruger National Park (Broomhall *et al*. 2003) and Kwandwe in the Eastern Cape Province of South Africa (Bissett & Bernard 2007; Bissett 2007) female cheetahs use a denser woodland or thicket habitat while males hunt in more open savannas. In the Serengeti (Caro 1994) both sexes use the more open savannas but ranges include plains or woodland border which will provide necessary cover for hunting and denning.

Management implications of understanding space use and habitat preference

An understanding of the spatial requirements of a species is essential for its conservation and management (Herfindal *et al.* 2005) and this is particularly true for small, fenced reserves. Since spatial requirements vary in time and space (as discussed earlier) information is site specific and this requires that information has to be collected from the particular site. Thus, a key aim of this chapter is to report on the size of the space used and the habitat features selected by cheetahs and lions on Sanbona. It is predicted that home ranges of the lions and cheetahs will be larger than those on other reserves in the region on which stocking rates are higher. It is further predicted that, in view of the low annual rainfall, space use by the carnivores will be focussed around streams, dams and streamlines.

This information will be discussed in the context of the existing considerable data for lions and cheetahs where emphasis will be placed on an analysis of factors that may

affect spatial ecology. In Chapter 5 the information will be discussed in terms of management of the reserve.

METHODS

Information on the spatial ecology of lions and cheetahs was collected through *ad hoc* observations by the researcher, the Sanbona Wildlife Department and by field/tourist guides during their routine activities (Chapter 2). For all sightings of large predators, the species, individual ID, activity, date, time and location were recorded on to a central data base. Where direct sightings of an animal or group was impossible, for example if the animals were in thick vegetation, triangulation, using radio telemetry, was used to identify the exact location (Kenward 2001).

Data analysis

Location points for the period between September 2003 and December 2007 were used for the home range analyses and where the predators were located more than once a day, only one reading was taken to ensure the independence of data fixes (Mizutani & Jewell 1998; Broomhall *et al*. 2003). The home range sizes were determined by using the non-parametric Fixed Kernel Utilisation Distribution (UD) method (Worton 1989; Powell 2000; Bisset 2004) in ArcView 3.2, with the Animal Movement Extension Package (Hooge & Eichenlaub 1997). Kernel Utilisation Distributions are thought to reflect habitat use and home range size more accurately than non-parametric methods (Harris *et al* 1990; Worton1995; Seaman & Powell 1996; Nilsen *et al.*2007). In addition, UDs are now widely used for the analysis of home range patterns in large carnivores (Seaman & Powell 1996; Bothma *et al.* 1997; Bissett 2007). The use of UDs in this study allowed for easy comparison with results

from similar studies. The 50% and 95% UDs were selected as they are regularly used to indicate an animal's core area and home range size (Mizutani & Jewell 1998). The Almond Farm on Sanbona formed an inaccessible island and where 95% and 50% UDs included some of the Almond Farm or extended beyond the boundaries of the reserve, these areas were clipped (ArcView 3.2) to the reserve boundary, and the remaining area of UD recalculated. A smoothing factor (H) of 1800 was used throughout for determining of the 50% and 95% UDs.

Since the spatial requirements of animals are likely to vary with age, sex and group size of the predator, the space use of different social groups was analysed separately if the data allowed for it. For cheetahs, the groups included single adult males (CM00, CM01 and CM02), single adult females (CF00 and CF01), a single female with cubs at a den (CF00 Den) and a single adult female with mobile cubs (CF00 Mobile Cubs). These individuals and groups had been on the reserve for different periods of time and were sighted at different times (Table 4.1).

Table 4.1: Cheetah individuals and social groups showing months on Sanbona and number of GPS fixes.

Cheetah	Months	Fixes
CM00	41	114
CM01	8	24
CM02	44	56
CF00	19	56
CF01	4	22
CF 00 Den	2	20
CF 00 Mobile cubs	14	41

The lions formed small prides, the structure of which changed through the study (Table 4.2). The single exception was a male lion (LM39), who was a member of

pride1 up to January 2005, but from February 2005 onwards was solitary and nomadic. The prides had been on the study area for different lengths of time and were sighted different numbers of times (Table 4.2).

Table 4.2: Pride structure of the lions on Sanbona showing the number of months each pride was present and the number of GPS fixes.

Pride ID	Animal ID	Time as a pride	Months	Fixes
Pride 1	LM39			
	LFUn	Sept 2003 - Jan 2005		
	LF43		17	618
Pride 2	LM47			
	LMUn	Feb 2004 - Feb 2005		
	LF32		13	226
Pride 3	LM47			
	LF32	Feb 2005- Dec 2007		
	LF43		34	589
Pride 4	LF20			
	LF99	Feb 2005 - Jul 2006	18	137
Solitary male	LM39	Jan 2005 - Dec 2007	23	218

Habitat use and preference

The vegetation of Sanbona was fully described in Chapter 2. The reserve has six vegetation types (Figure 4.1), of which Solid Fynbos, Mosaic Renosterveld and River and Floodplain made up only 11.0% of the study area. The greater part of the reserve was covered by Solid Renosterveld (13.9%); Succulent Karoo (35.8%) and Mosaic Thicket (39.4% of the study site). The simplified vegetation map, with six vegetation types, was used to determine available habitat and the proportion of the vegetation types in each home range and core area of the lions and cheetahs (ArcView 3.2).

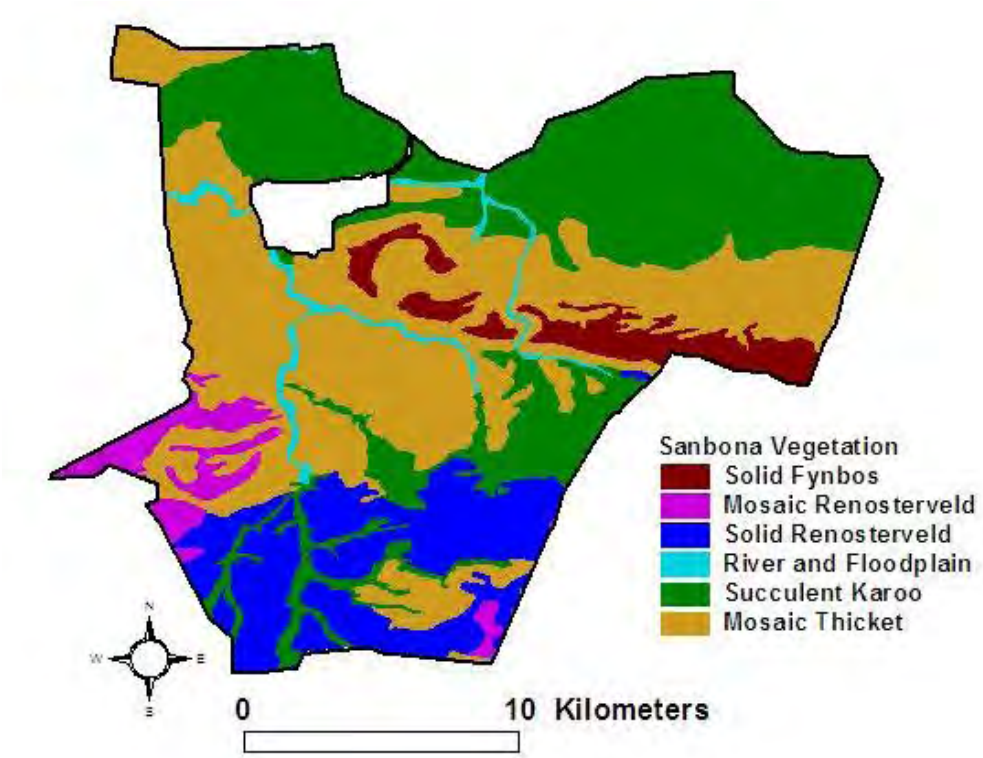


Figure 4.1: Vegetation types of Sanbona South (study area), as described by Vlok *et al* (2005).

To determine whether the predators preferred certain vegetation types, a preference index for vegetation was calculated using Jacobs' Index:

$$D = (r-p)/(r+p-2rp)$$

where r is the proportion of the total sightings in a vegetation type and p is the proportional availability of the vegetation type in the study area (adapted from Jacobs 1974). The proportional availability of each vegetation type on the reserve was calculated by creating an overlay of 2000 random points, using the Arcview Random Point Generator extension and counting the number of points in each vegetation type. The area of each vegetation type in the home range was calculated

in ArcView 3.2 and the number of sightings in each vegetation type counted manually.

The effect of gradient on habitat use

The gradient at each sighting was determined using the 3D Analyst extension in Arcview 3.2. Each slope was allocated to a slope class where slope class 1 equals a gradient of 0° to 9°, slope class 2 gradients of 10° to 19° and so on. These slope class values were then used to determine the mean slope class for each individual or group of animals. The average slope for Sanbona was calculated using the 2000 random points and allocating a slope value to every random point as described above. The highest slope value for the 2000 random points was 6, including gradients of 50° to 59°. Slopes with steeper gradients occurred on the reserve, but none of the random points fell on such slopes.

Proximity to water

The distance of every lion and cheetah sighting to the nearest dam and small body of water was calculated in ArcView 3.2 using the join tables feature. This was repeated for the random points and the mean distances compared using an ANOVA.

RESULTS

Cheetahs

Home range and core area sizes

In this analysis data for cheetah male 01 (CM01) was omitted because there were only 24 fixes. Female 00 (CF00) occupied two separate home ranges at different times and these were dealt with separately.

The mean sizes of the core areas of male and female cheetahs were 14.0± 0.28km² and 21.6 ±1.8km² respectively, covering 3.7% and 5.6% of the reserve (Table 4.3). The mean sizes of the home ranges of male and female cheetahs were 162.7± 20.3km² and 94.6±3.3km² respectively, covering 42.5% and 24.7% of the reserve (Table 4.3). The smallest home range was that of the female with cubs in a den (65.0km^2) and the largest belonged to an adult male (177.1km^2). In a two-way ANOVA with social group and female reproductive status (adult male, adult female, adult female with cubs at a den, and adult females with mobile cubs) and space type (home range or core area) as the independent variables, there was a significant effect of social group ($F_{3,6} = 20.53$; $P<0.05$) on the area of the space used, and a significant interaction between social group and space type ($F_{3,6} = 21.6$; $P<0.05$). As expected, home ranges (95% UDs) were significantly greater than core areas (50% UDs; $F_{1,6} = 370.4$; $P<0.05$). However, using the Tukey post hoc test, the core area of the female with cubs in a den was not significantly different from the home range of the female with cubs at the den ($P>0.05$). There were no significant differences between the sizes of the core areas of the different social groups (Tukey post hoc test; $P>0.05$ for all pairs). The home range of male cheetahs was significantly larger than that of single females and the female with cubs at a den. The home range of the

adult female with mobile cubs was significantly larger than that of the single female and the female with cubs at a den (Tukey post hoc tests; $P<0.05$ for all pairs).

Table 4.3: Space use by cheetahs on Sanbona showing the sizes of the home ranges and core areas (km^2) and the percentage of the study area utilised by each group.

	Area (km^2)		% of Reserve	
Cheetah	**50% UD**	**95% UD**	**50% UD**	**95% UD**
Male 00	14.2	148.4	3.7	38.8
Male 01	11.7	45.1	3.1	11.8
Male 02	13.8	177.1	3.6	46.3
Mean male	14.0 ±0.28	162.7 ±20.3	3.7	42.5
Female 00a	19.6	98.3	5.1	25.7
Female 00b	22.2	93.8	5.8	24.5
Female 01	23.1	91.9	6.0	24.0
Mean female	21.6±1.8	94.6 ±3.3	5.6	24.7
Female 00 at Den	12.6	65.0	3.3	17.0
Female 00 with mobile cubs	25.8	144.0	6.7	37.6

Home ranges and core area locations

Male cheetahs

The core areas of two of the male cheetahs (CM00 &CM01) were located in the north of the reserve and overlapped slightly, whereas the core area of the third cheetah male (CM02) was more central and to the east of the reserve (Figure 4.3A). There was no overlap between the core area of CM02 and the other two males. The home range of CM00 occurred in several separate sections located on either side of the Warmwaterberg (Figure 4.3B). The home range of CM02 was also in separate sections with the majority south of the Warmwaterberg, and a section to the north of the mountain range (Figure 4.3B). These home ranges overlapped extensively. Two components of the home range of CM00 in the northeast of the reserve did not overlap with any part of the home range of CM02.

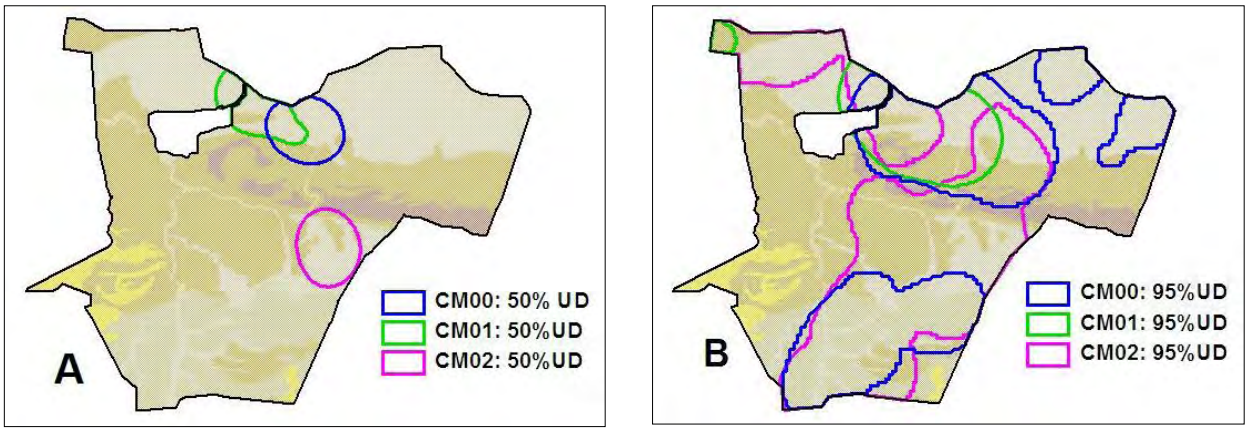


Figure 4.3: Core areas (A) and home ranges (B) for male cheetahs CM00, CM01 and CM02.

Female cheetahs

The core area of CF01 occurred in two sections, both located in the north of the reserve. The core areas for CF00, a single adult, occurred in three sections; two in the north, and one in the south of the reserve (Figure 4.4A). There was extensive overlap of the core areas of CF01 and CF00 in the north of the reserve but the core area of CF00 in the South did not overlap with any of the core areas of CF01. The home range of CF01 was located to the north of the Warmwaterberg while that of CF00, as a single adult, occurred in three separate sections, two to the north and one to the south of the Warmwaterberg (Figure 4.4B). In the north of the reserve, the home ranges of CF01 and CF00 overlapped extensively (Figure 4.4B).

The core area of CF00 with cubs at a den overlapped very slightly with her core area as a single female (Figure 4.4 C) while the core area of CF00 with mobile cubs overlapped extensively with the southern core area of CF00 as a single female

(Figure 4.4 C). The home range of CF00 with cubs at the den fell within her home range as a single female in the south of the reserve, and when the cubs were mobile, the home range was in several sections, both north and south of the Warmwaterberg (Figure 4.4 D).

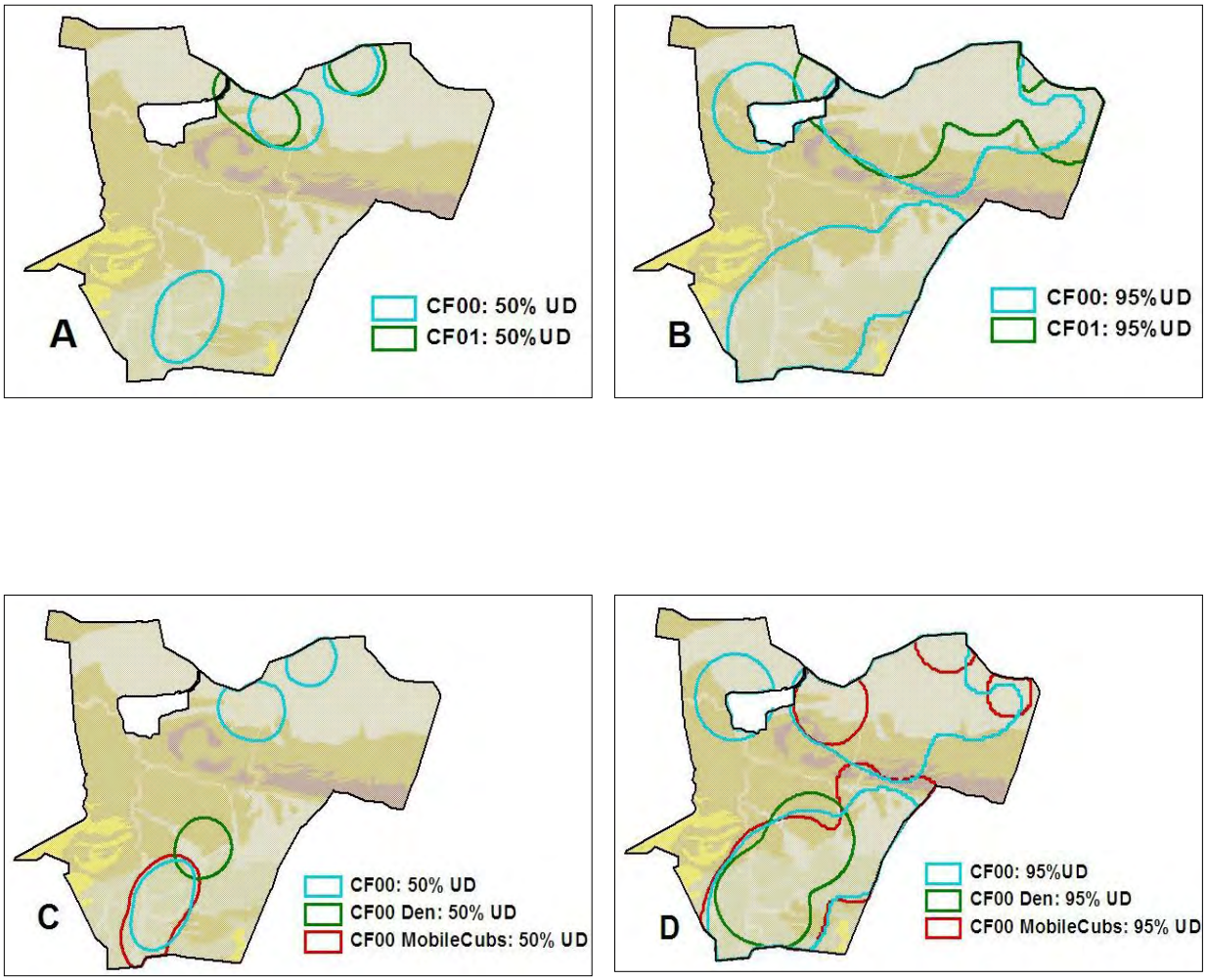


Figure 4.4: Core areas (A & C) and home ranges (B & D) of single adult female cheetahs CF00, CF01 (Figs 4.4 A & B) and CF 00 as a single adult, with cubs at a den and with mobile cubs (Figs 4.4 C and D).

The core areas of the two single adult females overlapped extensively with the core area of the original adult male CM00. There was no overlap with the core area of CM02 (Figure 4.5). The pattern of overlap was different at the home range scale and the home range of CM02 overlapped with the home ranges of both adult females.

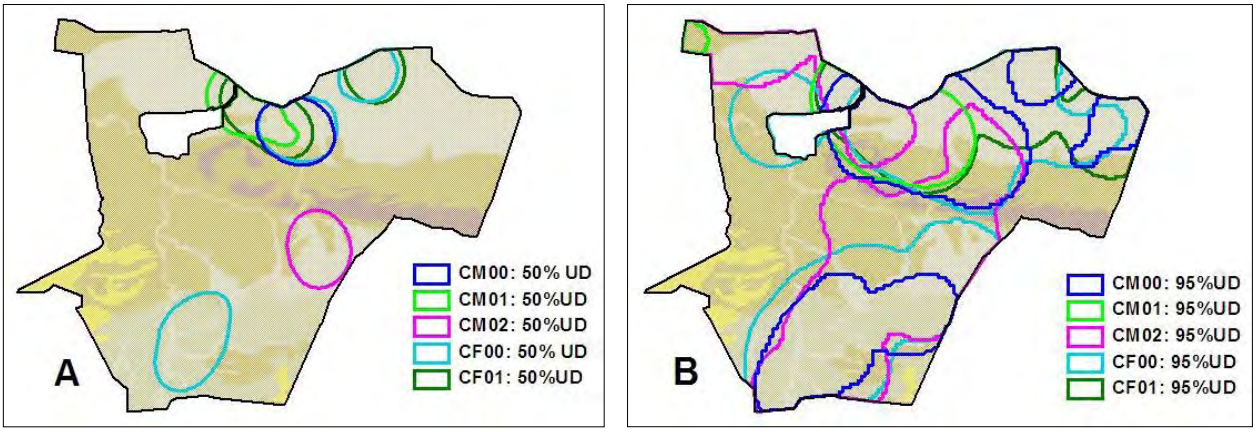


Figure 4.5: Core areas (A) and home ranges (B) of single male cheetahs CM00, CM01, CM02 and female cheetahs CF00 and CF01, showing overlap.

Habitat selection and use

The availability of the six different vegetation types, based on both the total area of the vegetation types and on the number of random points that fell in each vegetation types was calculated (Table 4. 4; Figure 4.6).

Table 4.4: Summary of availability of the six vegetation types based on the Sanbona vegetation map and 2000 random points.

Vegetation Type	Area (km²)	Area (%)	Random 2000 (%)
Solid Fynbos	19.1	5	6
Mosaic Renosterveld	14.9	4	3
Solid Renosterveld	53.0	14	13
River and Floodplain	7.9	2	3
Succulent Karoo	137.0	36	35
Mosaic Thicket	150.6	39	41
Totals	382.5	100	100

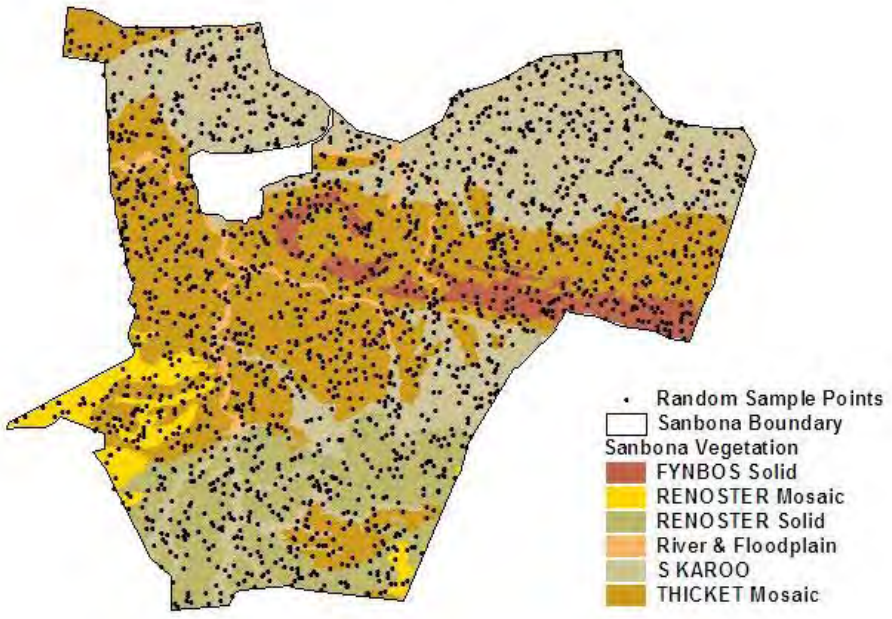


Figure 4.6: Distribution of 2000 random sample points across the study area.

Habitat use by male cheetahs

The only vegetation type completely avoided by all cheetahs was Mosaic Renosterveld. Adult male cheetahs were recorded once only in Solid Fynbos and Solid Renosterveld and thus showed a strong avoidance of these vegetation types

(Table 4.5). The majority (63%) of sightings were in Succulent Karoo which only represents 35% of the reserve, it was therefore strongly preferred (Table 4.5; Figure 4.7). The most preferred vegetation type (D=0.7) was River and Floodplain, in which 11% of sightings were located. Twenty four percent of sightings were in Thicket Mosaic. However this vegetation type occupied 41% of the reserve and hence it was avoided (D=-0.4).

Habitat use by female cheetahs

Adult females were never recorded in Solid Fynbos, and strongly avoided Thicket Mosaic (D=-0.8; Table 4.5). The only strongly preferred vegetation type (D=0.7) was Succulent Karoo (Figure 4.8 A&B). The female with cubs showed a similar total avoidance of Solid Fynbos, Mosaic Renosterveld and River and Floodplain, and a similar avoidance of Mosaic Thicket as the single females by themselves. The only vegetation types preferred by adult female with mobile cubs were Solid Renosterveld and Succulent Karoo (Table 4.5; Figure 4.8D). Vegetation type selection by a female at a den was quite different from that of single females and females with mobile cubs strongly avoided Succulent Karoo(D=-0.7), but preferred Mosaic Thicket (Table 4.5; Figures 4.8 A,B,C,D).

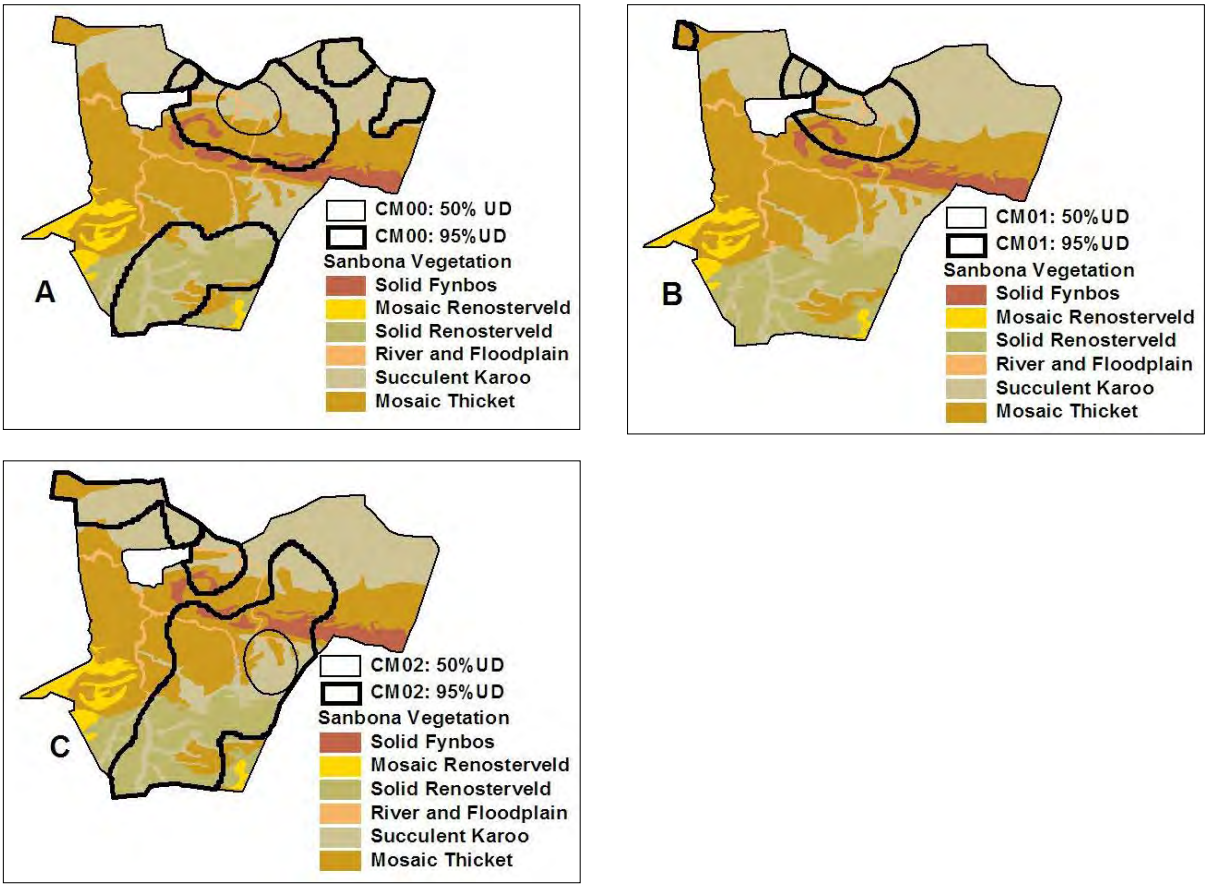


Figure 4.7: Core areas and home ranges of three male cheetahs (CM00, CM01, CM02), showing vegetation use.

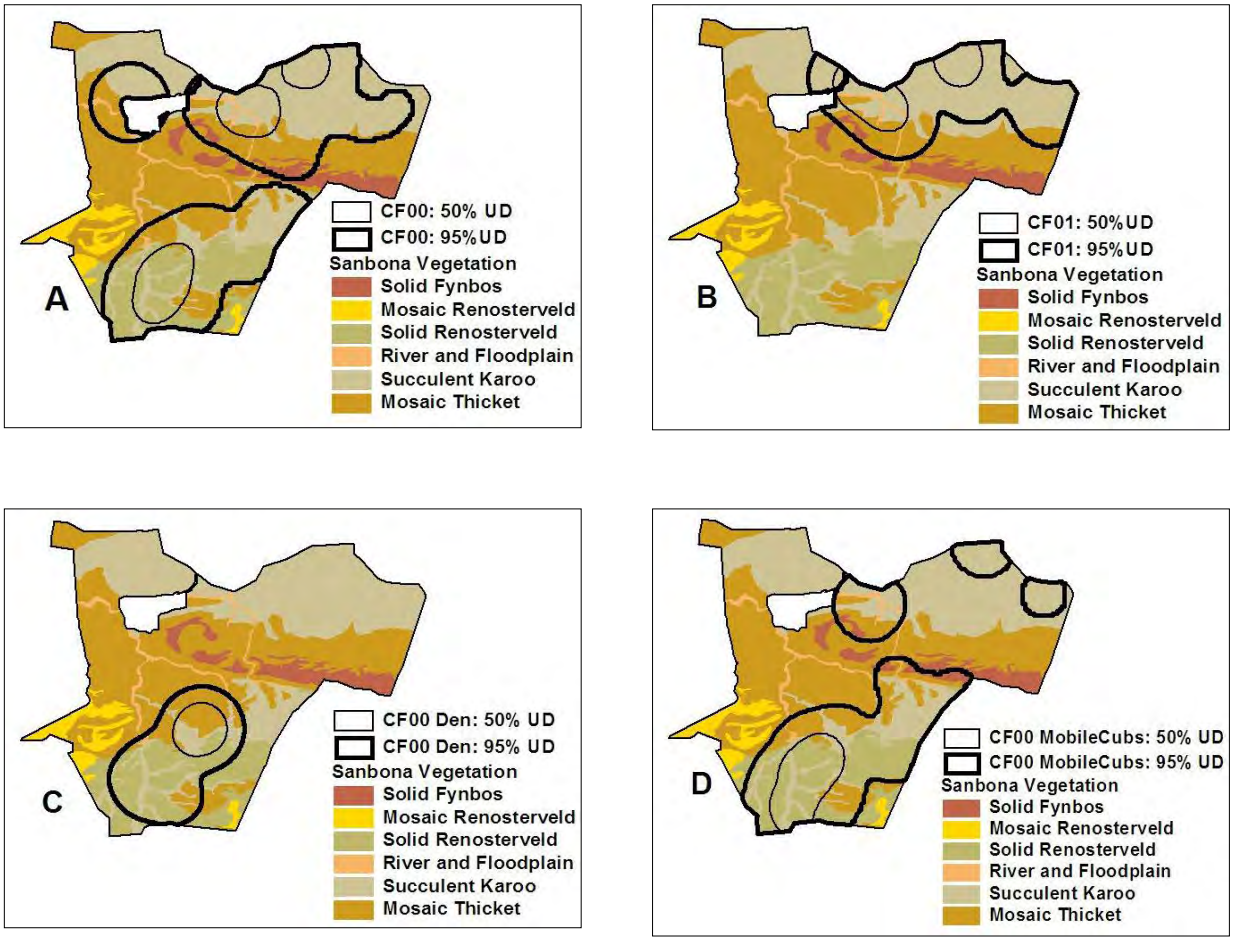


Figure 4.8: Core areas and home ranges of single female cheetahs, CF00 and CF01 (A&B) and CF00 at the den (C) and CF00 with mobile cubs (D), showing vegetation use.

Table 4.5: Habitat use and selection by cheetahs. Data covers number of sightings in each vegetation type with the percentage of all sightings in the home range in brackets and D: Jacobs' Index.

	Cheetahs				
Vegetation Type	**Den**	**Mobile Cubs**	**Females**	**Males**	**Random 2000 (%)**
Fynbos Solid	0 (0%) D= -1.0	0 (0%) D= -1.0	0 (0%) D= -1.0	1 (1%) D= -0.8	121 (6%)
Renosterveld Mosaic	0 (0%) D= -1.0	0 (0%) D= -1.0	0 (0%) D= -1.0	0 (0%) D= -1.0	65 (3%)
Renosterveld Solid	5 (25%) D= 0.4	14 (35%) D= 0.6	20 (13%) D= 0.0	1 (1%) D= -0.9	257 (13%)
River and Floodplain	0 (0%) D= -1.0	0 (0%) D= -1.0	3 (2%) D= -0.1	15 (11%) D= 0.7	50 (3%)
Succulent Karoo	2 (10%) D= -0.7	25 (63%) D= 0.5	119 (78%) D= 0.7	87 (63%) D= 0.5	691 (35%)
Thicket Mosaic	13 (65%) D= 0.5	1 (2%) D= -0.9	11 (7%) D= -0.8	33 (24%) D= -0.4	816 (41%)

Slope

More than 50% of the 2000 random points fell on slopes with a slope value of 1 and 82.9% of all points fell on land with a slope value of 1 or 2 (Table 4.6).

Table 4.6: The percentage availability of land with different slopes on Sanbona based on 2000 random points.

Slope Value	Gradient (Degrees)	Availability
1	0°-9°	60.85%
2	10°-19°	22.05%
3	20°-29°	11.20%
4	30°-39°	4.35%
5	40°-49°	1.30%
6	50°-59°	0.25%
7	>60°	0%

All cheetahs preferred flat areas with a slope value between 1 and 2 (0°-19°) (Table 4.7). There was no significant difference between the slopes used by any of the cheetahs, and the slopes used by all cheetahs except CF01 and CM01 were significantly lower than the average slope for the reserve bases on the 2000 random points ($F_{7, 2\,404} = 11.5$; $P<0.05$).

Table 4.7: The average slope value the cheetahs frequented.

Cheetah	Average Slope	SD
Male 00	1.3	0.58
Male 01	1.3	0.69
Male 02	1.1	0.33
Female 00	1.3	0.65
Female 01	1.1	0.35
Female 00 at Den	1	0
Female 00 with mobile cubs	1.1	0.26

Lions

Home range and core area sizes

The mean core area of the four prides was 19.6 ± 8.1km^2 and the mean home range size was 146.4 ± 44.6km^2 (Table 4.8). Core areas covered 5% of the reserve and home range 38% of the reserve (Table 4.8). The home ranges of prides 2 and 4 were almost twice the size of those of prides 1 and 3 (Table 4.8). The core area of the solitary male was smaller than those of the prides while the home range was greater than those of prides 1 and 3 (Table 4.8).

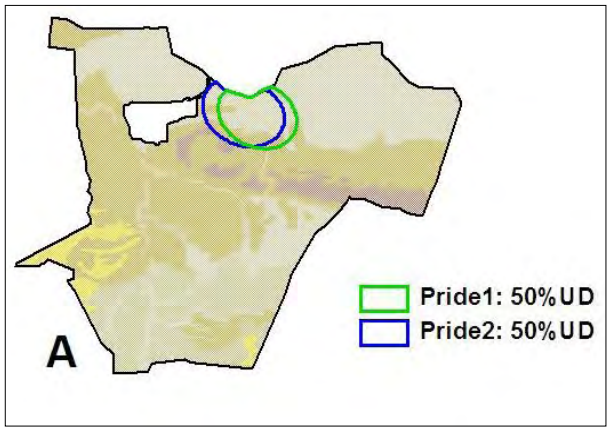
Table 4.8: Space use by lions on Sanbona, showing the sizes of the core areas and home ranges and the percentage of the study area utilised by each group.

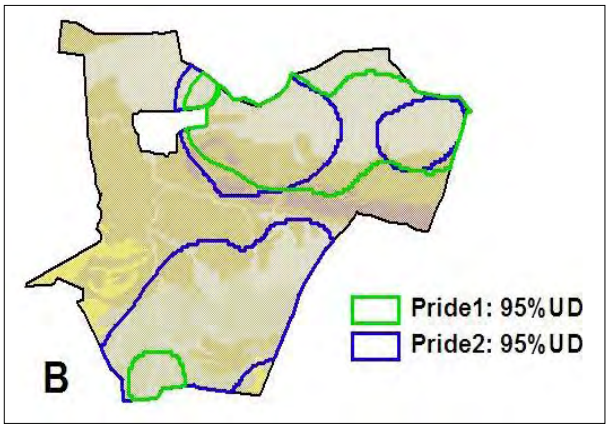
	Area (km²)		% of Reserve	
Lions	**50%UD**	**95%UD**	**50% UD**	**95% UD**
Pride 1	16.5	108.9	4.3	28.5
Pride 2	16.9	182.2	4.4	47.6
Pride 3	13.5	106.8	3.5	27.9
Pride 4	31.6	187.7	8.3	49.1
Average ±1sd	19.6 ±8.1	146.4 ±44.6	5.1 ±2.2	38.3 ±11.7
Solitary male LM39	10.9	146.6	2.8	38.3

Home range and core area location

Core areas: 2003-2005. Two prides (1&2) were present during this period. The core area of the original pride (pride 1) was located in the north of the reserve and overlapped extensively with the core area of pride 2 (Figure 4.9A)

2005-2007. Two prides (3&4) and the solitary male (LM39) were present during this period. As a result of the conflict, prides 1 and 2 broke up in January 2005 after which pride 3 formed, consisting of individuals of prides 1 and 2. The original male of pride 1 became the solitary LM39. Pride 4 was introduced in February 2005 and was removed in July 2006. Between March 2005 and December 2007 pride 3 was the established pride on the reserve (see Chapter2). The core area of pride 3 was located north of the Warmwaterberg while that of LM39 was located in the far south of the study area (Figure 4.9C). Pride 4 had two core areas, one in the south that overlapped with the core area of LM39 and one in the north that overlapped with the core area of pride 3 (Figure 4.9C).





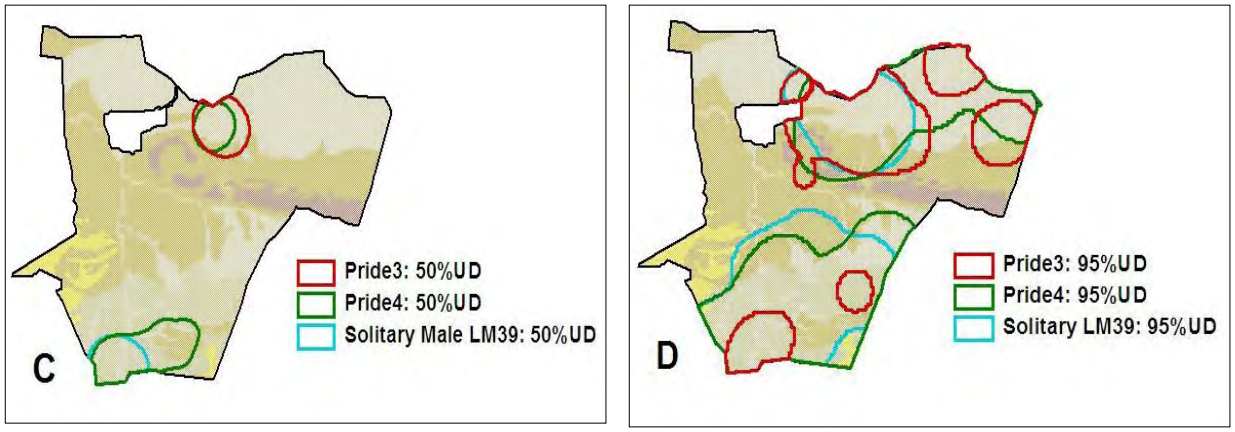


Figure 4.9: Core areas and home ranges of the lions on Sanbona.

Home ranges: 2003-2005. The home range of pride 1 was located mostly north of the Warmwaterberg with a very small section in the far south of the reserve. Pride 2 ranged widely through the reserve and had home ranges both north and south of the Warmwaterberg (Figure 4.9B). Home ranges of pride 1 and 2 overlapped extensively.

2005-2007. Although the core area of pride 3 was located in the north of the reserve, the pride ranged widely through the reserve and the home range was located both north and south of the Warmwaterberg. The home ranges of prides 3 and 4 were also in the north of the study area, but south of the Warmwaterberg. The home range of pride 4 occupied a greater area than that of pride 3 (Figure 4.9D). Although the core area of the solitary male (LM39) was in the far south of the study area, he ranged widely and home ranges were located both in the south and the north (Figure 4.9C&D). The home ranges of prides 3, 4 and LM39 overlapped both in the north and south of the study area (Figure4.9D).

Habitat selection and use

The only vegetation type completely avoided by all of the lion prides was Solid Fynbos (Table 4.9). Mosaic Renosterveld was strongly avoided (D=-0.9) and was only used by pride 4 (Table 4.9; Figure 4.10D). Thicket Mosaic, which made up 41% of the study area, was avoided by all prides (Table 4.9; Figure 4.10). River and Floodplain, which made up only 3% of the study area, was strongly preferred (D=0.8), and Succulent Karoo, which made up 35% of the study area, was preferred (D=0.5; Table 4.9). Solid Renosterveld was used differently by different prides; prides 1 and 3 avoided it (D=-0.6 and D= -0.4) (Figure 4.10A&C), while prides 2 and 4 selected it (D=0.3 for both) (Figure 4.10B&D; Table 4.9). The pattern of vegetation used by LM39 was similar to that used by the prides, and LM39 preferred Solid Renosterveld (Table 4.9; Figure 4.10E).

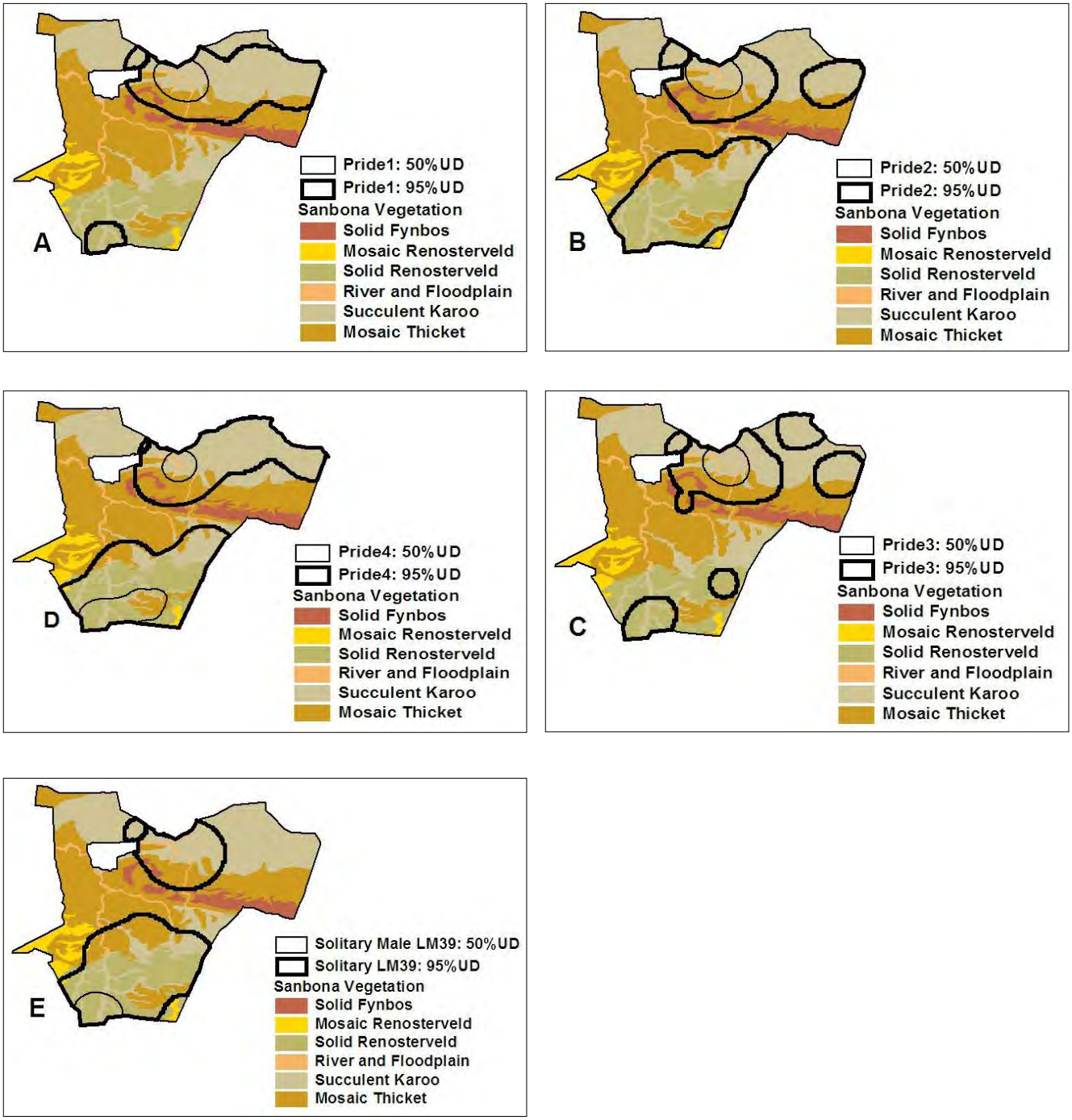


Figure 4.10: Core areas and home ranges of the lions, showing vegetation use.

Table 4.9: Habitat use and selection by lions. Data refers number of sightings in each vegetation type with the percentage of all sightings in the home range in brackets and D: Jacobs' Index.

	Prides						
Vegetation Type	**1**	**2**	**3**	**4**	**Pride mean D**	**Solitary LM39**	**Random 2000 (%)**
Fynbos Solid	0 (0%) D=-1.0	0 (0%) D=-1.0	0 (0%) D=-1.0	0 (0%) D=-1.0	-1.0	0 (0%) D=-1.0	121 (6%)
Renosterveld Mosaic	0 (0%) D=-1.0	0 (0%) D=-1.0	0 (0%) D=-1.0	3 (2%) D=-0.2	-0.9	0 (0%) D=-1.0	65 (3%)
Renosterveld Solid	21 (3%) D=-0.6	52 (23%) D=0.3	38 (6%) D=-0.4	28 (20%) D=0.3	-0.2	70 (32%) D=0.5	257 (13%)
River and Floodplain	149 (24%) D=0.9	35 (15%) D=0.8	90 (15%) D=0.8	5 (4%) D=0.2	0.8	10 (5%) D=0.3	50 (3%)
Succulent Karoo	365 (59%) D=0.5	109 (48%) D=0.3	375 (64%) D=0.5	85 (62%) D=0.5	0.5	120 (55%) D=0.4	691 (35%)
Thicket Mosaic	83 (13%)D=-0.6	30 (13%) D=-0.6	86 (15%) D=-0.6	16 (12%) D=-0.7	-0.6	18 (8%) D=-0.8	816 (41%)

Slope

All lions preferred flat areas with a slope value of approximately 1 (0°-9°) (Table 4.10). There was no significant difference between the slopes used by the four prides and the solitary lion LM39 respectively. All were significantly lower than the average slope for the 2000 random points ($F_{5, 3782}$ =92.8; P<0.05).

Table 4.10: The average slope the lions frequented.

Lions	Average Slope	SD
Pride 1	1.07	0.38
Pride 2	1.12	0.52
Pride 3	1.14	0.51
Pride 4	1.06	0.33
Mean Slope	1.10	0.45
Solitary male	1.16	0.53
Random 2000	1.64	0.96

Distance to water for lions and cheetahs

The mean distance to the nearest water body for lions was 1109.4 ± 853m and that for cheetahs was 1227.5 ± 850m. Both were significantly closer than the 2000 random points (1973.3±1246.9m; F=328.8; df = 2 P<0.05; Figure 4.11).

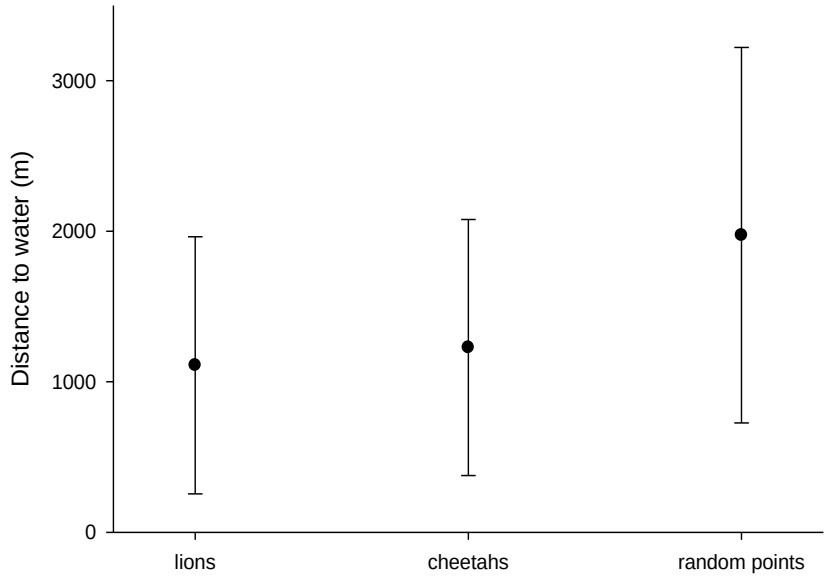


Figure 4.11: Distance of lions, cheetahs, and the 2000 random points to water. Data are means ±1sd.

A comparison of space use by lions and cheetahs

Home range and core area sizes

In a two-way ANOVA with predator species, social group and female reproductive status (lion, cheetah adult male, adult female, adult female with cubs at a den, and adult females with mobile cubs) and space type (home range or core area) as the independent variables, there was no significant effect of species or social group on the area of the space used ($F_{4,12}$ = 2.58; P>0.05). There was no significant interaction between social group and space type (F4,12 = 2.63; P>0.05). Not surprisingly, home ranges (95% UDs) were significantly greater than core areas (50% UDs; $F_{1,12}$ = 79.37; P<0.05). There were

no significant differences between core areas (Tukey post hoc tests; P>0.05 for all pairs) or between home ranges (Tukey post hoc tests; P>0.05 for all pairs).

Home range and core area location

It is clear, from Figures 4.4, 4.5 and 4.9, that the lions and cheetahs had core areas and home ranges in similar sections of Sanbona. This was a result of the clustering of carnivores around the dams and small water bodies and resulted in core areas overlapping considerably. Lion prides 1 and 2 and cheetahs CM00 and CF01, for example, had core areas around Bellair Dam, northwest within the study area (Figure 4.12). The core areas of the two prides and two cheetahs overlapped with a common area of overlap of 1026ha which represented between 60% and 72% of the individual core areas (Table 4.11).

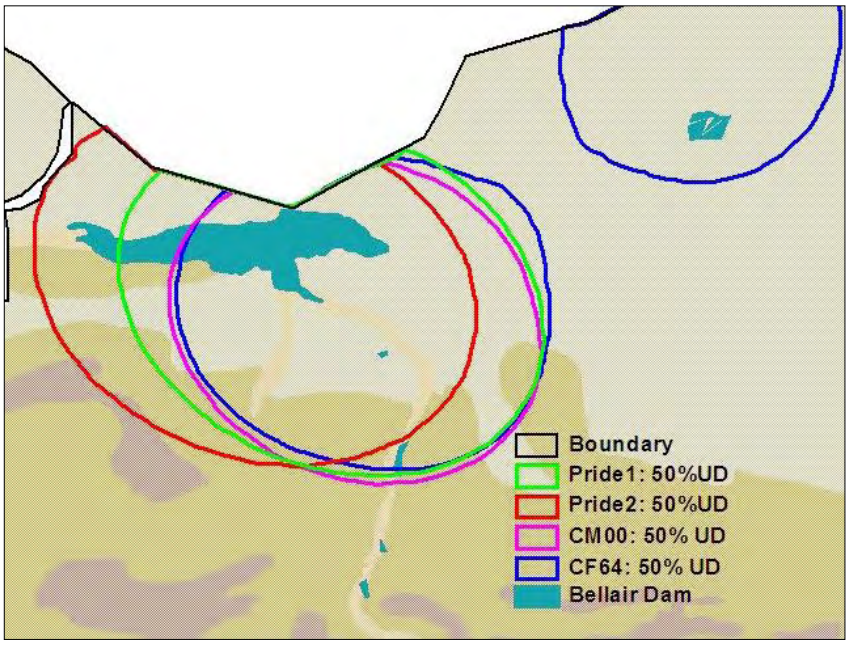


Figure 4.12: The Bellair Dam, in the north western section of the study area, with the core areas of CM00, CF00 and lion prides 1 and 2, showing the considerable overlap.

Table 4.11: Core area sizes and percentage overlap of lions and cheetahs around Bellair Dam.

	Area (ha)	% Overlap
Pride 1	1646	62
Pride 2	1691	61
Cheetah CM00	1417	72
Cheetah CF00	1427	72
Common area of overlap	1026	

Habitat selection and use

The members of the large predator guild on Sanbona avoided Solid Fynbos and Mosaic Renosterveld and, except the female cheetah with cubs at a den, Mosaic Thicket (Table 4.12). Together, these vegetation types covered 50% of the reserve. Succulent Karoo, which covered 35% of the reserve, was selected by all predators except the female cheetah with cubs at the den. River and Floodplain was selected by adult male cheetahs as well as the lions and was avoided by adult female cheetahs, whether with cubs, at a den, or mobile.

Table 4.12: Selection of habitats by cheetahs and lions on Sanbona. Data are from tables 4.5 & 4.9 and show values for Jacobs' Index. To simplify interpretation, selection (D≥0.3) is indicated in green and avoidance (D≤-0.3) in red.

Predators	Vegetation types					
	Solid Fynbos	Mosaic Renosterveld	Solid Renosterveld	River & Floodplain	Succulent Karoo	Mosaic Thicket
Area	6%	3%	13%	3%	35%	41%
Cheetahs						
Adult male	-0.8	-1.0	-0.9	0.7	0.5	-0.4
Adult female	-1.0	-1.0	0.0	-0.1	0.7	-0.8
Female with cubs at den	-1.0	-1.0	0.4	-1.0	-0.7	0.5
Female with mobile cubs	-1.0	-1.0	0.6	-1.0	0.5	-0.9
Lions						
Prides	-1.0	-1.0	-0.2	0.8	0.5	-0.6
Solitary male	-1.0	-1.0	0.5	0.3	0.4	-0.8

Discussion

Although cheetahs have been re-introduced to a number of reserves in southern Africa, the majority of these reserves are characterised by relatively high stocking rates. Phinda, in KwaZulu-Natal, for example has about 30 prey animals perkm^2 (Hunter 1998), Kwandwe in the Eastern Cape Province has about 20 prey animals perkm^2 (Bissett 2007) and Matusadona in Zimbabwe has 200-300 impala perkm^2 (Purchase & du Toit 2000). By contrast, Sanbona is stocked at about two to three prey animals perkm², which is similar to that reported for the density of springbok in the arid Kalahari Gemsbok National Park : 2-17/km^2 (Mills 1984; 1998) and lower than that reported in Namibia: 13 greater kudu/km^2 (McVittie 1979; Marker *et al*. 2003). In view of the widely reported link between prey density and home range size (Macdonald 1983; Spong 2002), it was

predicted that the home ranges of cheetahs (and for the same reasons the home ranges of lions) at Sanbona would be larger than those reported for many of the other reserves. This was indeed the case and the home range of male cheetahs on Sanbona (94km^2) was larger than that on Kwandwe (35km^2); female cheetahs at Sanbona 163km^2 and Kwandwe 90km^2 (Bissett 2007). The home range of female cheetahs on Sanbona was larger than those in the Kruger National Park: 126-135km^2 (Broomhall *et al*. 2003) and Matusadona: 29km^2 (Purchase & du Toit 2000), but smaller than those in very large or open systems such as the Kalahari Gemsbok National Park: 329km^2 (Mills 1998), the Serengeti: 800km^2 (Caro 1994) and Namibia: 1500km^2 (Marker *et al*. 2003). While it may be convenient to see the variation in home range size simply in terms of prey density, many other factors affect space use at the different sites. Such factors are the availability of other resources such as water and denning sites and the migratory pattern and distribution of prey as seen in the Serengeti (Schaller 1972; Caro & Collins 1986), or the nomadic springbok of the Kalahari Gemsbok National Park (Mills 1984; 1998), as well as the presence of other species of large carnivore (Carbone & Gittleman 2002). The restrictive boundaries of fenced and relatively small reserves will also influence the size of the space used (Hunter 1998; Broomhall *et al*. 2003).

The space used by the lion prides on Sanbona (100-187km^2) was greater than that of lions in Phinda: 53km^2 (Hunter 1998), the Kruger National Park: 100-150km^2 (Whyte 1985), Nairobi National Park: 25km^2 (Rudnai 1974), but smaller than in Chobe National Park ,Botswana: 217km^2 (Viljoen 1993), the Serengeti: 200km^2 (Hanby *et al*. 1995), Waza National Park: 630km^2 (Bauer & de longh 2005) and Etosha National Park, Namibia:

2075km^2 (Stander 1991), and similar to that on Kwandwe:120km^2 (Bissett 2007). These differences will reflect differences in prey abundance and pride size (Spong 2002) and the migratory habits of prey, as in Chobe (Viljoen 1993).

Home range size may differ between the sexes of a species as has been reported for cheetahs where males often have smaller ranges than females (Ewer 1973; Caro & Collins 1986; Sandell 1986; Durant *et al*. 1988). Males establish a range that is centred on a predictably abundant source of prey and the presence of suitable cover, and large enough to meet their requirements (Caro 1994; Caro & Collins 1986; Mills 1998; Spong 2002; Delahay *et al*. 2006). The ranges of female cheetahs include suitable thick cover and slope for concealment of a den, but also extend to overlap with at least part of a male range and as such they tend to be larger than male ranges (Caro 1994; Mills 1998). Sanbona did not follow this pattern and males had a larger home range than females, a pattern also reported Kwandwe (Bissett 2007). If the larger range of female cheetahs is to ensure that suitable denning sites are included then this may partly explain why female ranges on Sanbona and Kwandwe (Bissett 2007) were smaller than those of males. Both reserves are characterised by an abundance of hills and gulleys, providing numerous possible denning sites and thus reducing the need for an extended female range.

Overlap of core areas and home ranges of male and female cheetahs on Sanbona was considerable and, at the core area level, greater than reported in many previous studies (Sandell 1986; Caro 1994; Broomhall *et al*. 2003; Bissett 2007). Typically, the core areas of male and female cheetahs have little overlap while home ranges do overlap. A

possible reason for the overlap of core areas on Sanbona was the limited availability of permanent water bodies which serve as a focus for both predators and their prey. This will be discussed further. It should be emphasised that the core areas and home ranges in this study were based on less than one GPS fix per day and should not be interpreted as indicating that animals were necessarily sharing the same space at the same time. It is quite possible that there was a temporal sharing of common space at the core area level. The core areas of the female cheetah with cubs at a den and with mobile cubs did not overlap with any of the core areas of male cheetahs or the lion prides. This avoidance of male cheetahs and lion prides is best understood in light of the widely reported killing of cheetahs (particularly cubs) by lions and male cheetahs (Caro 1994; Laurenson 1994; Carbone & Gittleman 2002).

Habitat selection by lions is influenced by accessibility and density of suitable prey species, the availability of cover for hunting and resting, the availability of water and the availability of suitable den sites (Schaller, 1972; Hanby *et al*. 1995; Spong 2002). Cheetahs have been characterised as preferring open grassland habitats, using their speed to catch prey (Schaller 1972, Caro & Collins 1986, Durant *et al.* 1988, Fitzgibbon 1990, Caro 1994, Laurenson 1994; 1995, Laurenson *et al.* 1995, Nowell & Jackson 1996, Durant 1998, Durant 2000a; 2000b) and selecting marshes, patches of thick vegetation, along seasonal drainage lines and kopjes for den sites (Laurenson 1993). More recent studies have indicated that cheetahs may prefer more dense and wooded vegetation types. In the Kruger National Park, cheetah males prefer open areas, while females prefer denser woodlands (Broomhall *et al*. 2003). Purchase & du Toit (2000) found that

cheetahs prefer the open lake shore of Matusadona for hunting and the thicker adjacent woodland vegetation for resting and moving through the area. Hunter (1998) found that cheetah on Phinda prefer open grassy patches within the denser woodland to hunt. In Kwandwe, male cheetahs prefer the flatter open areas, while females prefer the denser woody areas and undulating hills (Bissett 2004). Thus, it is clear that cheetahs are more adaptable than was thought.

The patterns of vegetation selection and avoidance shown by lions and cheetahs on Sanbona were similar and are discussed together. Solid Fynbos and Mosaic Renosterveld were strongly avoided by lions and cheetahs. These vegetation types occurred on the top and steep sides of mountains and represented a very small part of the study area (9% in total). They were also not associated with standing water. It is likely that this avoidance was not primarily driven by the vegetation itself, but the slope on which it occurred. Mosaic Thicket was avoided by all predators except the female cheetah with cubs at a den. On Sanbona, there was a transition from Solid Fynbos and Mosaic Renosterveld into Mosaic Thicket which was typically associated with steep slopes and the absence of standing water. The female cheetah with cubs selected a site for her den which represented a transition between Solid Renosterveld and Mosaic Thicket, with the combination of slope and dense vegetation for necessary cover. A preference for denser vegetation and sometimes steeper slopes for den sites has been reported previously and is thought to reduce the likelihood of aggressive encounters with more dominant predators (Caro 1994; Mizutani & Jewell 1998; Sunquist & Sunquist 2002; Broomhall *et al*. 2003; Bissett 2007). The female with mobile cubs moved out of the

thickets into slightly less dense Solid Renosterveld. This vegetation type provided sufficient cover, with increased visibility and prey abundance in the adjacent River and Floodplain and Succulent Karoo.

Succulent Karoo was selected by all predators except the female cheetah with cubs at a den. It covered the greatest proportion of the study area, it occurred on mostly flat or gently sloping ground and was associated with standing water and some stream lines. It was the most complex of the Biomes and offered both cover and open areas. Single females strongly preferred Succulent Karoo. This vegetation type was predominantly open with scattered bush clumps providing shade and cover along the bases of hills and ridges. In the Succulent Karoo, cheetahs generally preferred flat areas, with cheetah males hunting greater kudu and duiker in the wooded river lines. Female cheetahs preferred the open plains to hunt, while resting on flat areas of steeper and higher ridges which provided lookout and cover.

Solid Renosterveld was avoided by male cheetahs and selected by some female cheetahs and the solitary male lion. Solid Renosterveld occurred on flat land and rolling hills and was associated with some standing water suitable for the predators. The avoidance by male cheetahs was probably because they established their range around Bellair Dam in the north of the reserve, and Solid Renosterveld only occurred in the south. It is likely that intraspecific interactions played a role in shaping habitat choice of the lone male lion. The lion prides were established in the north of the reserve, leaving the south of the reserve, mostly covered with Solid Renosterveld, an enemy free space.

Finally, River and Floodplain was strongly selected by male cheetahs, the lion prides and less so by the lone male lion and avoided by female cheetahs with cubs. This biome comprised a very small proportion of the reserve and a relatively small number of sightings would have produced a strong selection. However, it is likely that the high and low values for Jacobs' Index reflect real selection and avoidance. This vegetation type, because of the moisture and at times standing water, served as a focus for prey species and predators. It provided the cover necessary for hunting lions and some open areas for hunting cheetahs. Vegetation cover is an important variable in the hunting success of lions. Success is greater in dense scrub and long grass (Schaller 1972; van Orsdol 1984; Funston *et al*. 2001). Lions, for example, showed a similar preference for riverine habitats in the Selous Game Reserve where small water bodies and the dense vegetation provided hunting opportunities (Spong 2002). The increased presence of lions and male cheetahs in this vegetation type is probably why it was avoided by female cheetahs with cubs at a den and mobile cubs. As mentioned earlier, there are reported incidences of lions and male cheetahs killing cheetah cubs.

In the results referred to earlier, the Bellair Dam was used as an example of how permanent standing water in an arid landscape can serve as a focus for predators. As a result of this, core areas of lion pride 1 and 2, and of a male and female cheetah overlapped by as much as 72%. It might be expected that this would have resulted in increased aggressive interactions between the lions, and between the lions and the cheetahs. This was indeed the case and the initial efforts to maintain two lion prides on Sanbona were discontinued. A cub from pride 1 was killed by members of pride 2 and

cubs from pride 4 were killed by lions from pride 3 (Table 2.8). Two adult female cheetahs and two mobile cubs were killed by lions and six other cheetahs died of unknown causes. As mentioned earlier, spatial overlap based on a relatively small number of GPS points, as in the present study, does not necessarily mean that animals used the same space at the same time. The area around Bellair Dam would be an excellent study site for a much more detailed and refined study of space use by lions and cheetahs, ideally using GPS collars and recording multiple fixes per day for all the predators over the same period of time. This would allow a more refined scale analysis of space use and habitat selection and the effect of time.

In conclusion,, the size of the space used by lions and cheetahs and the location of that space (habitat selection) on Sanbona are likely to have been affected by a number of interacting factors.

Firstly, it is likely that the abundance and distribution of water (limited and not evenly distributed) had a strong effect on both the size and location of core areas and ranges. The bodies of water would have attracted prey species, provided water for the predators and cover for hunting.

Secondly, the density of prey species was low and this would have played an important role in the size of the areas used.

Thirdly, the topography of Sanbona with the Warmwaterberg dividing the reserve into a northern and southern section and resulting in about half of the reserve being too mountainous for the predators. Predators thus occurred either to the north or to the south of the Warmwaterberg.

Fourthly, it is likely that inter and intraspecific interactions affected habitat selection by the solitary male lion and the female cheetahs.

Finally, group size of both the prides of lions and the male cheetahs were small and it is very likely that this had influenced range size.

Chapter 5

General Conclusion and Management Recommendations

The re-introduction of large mammalian predators to relatively small (<300km^2) fenced conservation areas has taken place for various reasons including tourism, the conservation of single species and in an attempt to recreate a more natural ecosystem (Stanley Price 1991; Breitenmoser *et al*. 2001; Langholz & Kerley 2006).

Even in relatively large fenced reserves such as Sanbona (540km^2) these systems are artificial (Beier 1993). The fences prevent natural dispersal and immigration of predators and disrupt natural patterns of movement of prey species. The areas are often too small to include suitable refuges for prey species, and predator stocking rates are often abnormally high to ensure a good viewing experience for guests. Yet, populations within these fenced reserves are too small to be genetically viable and inbreeding occurs (Soule 1987; Bjorklund 2003). As a consequence of these and other limitations, small fenced reserves have to be closely managed. Management interventions should be based on research, however this is often not the case and relevant data are not available (Radloff & du Toit 2004). The principal goal of this project was to provide some baseline data on the feeding and spatial ecologies of lions and cheetahs that could be used to inform future management interventions.

In terms of diet, the two methods (*ad hoc* observations and faecal analysis) generated different results and it is important that both be implemented for continued research. Three species can be used to illustrate this point. Based on *ad hoc* observations, it could

be predicted that eland would comprise 16% -17% of all kills by lions while faecal analysis would suggest a much lower percentage. If the data from *ad hoc* observations were used in a modeling exercise to guide management on either the number of lions that could be sustained on Sanbona, or the number of eland that had to be stocked, then the results would be very different from those generated using faecal analysis. Similarly, with duiker, *ad hoc* observations would give a far lower predicted impact by lions than would faecal analysis. Finally no kills of plains zebra were observed while hairs of zebra occurred in 12% of scats. Plains zebra numbers decreased from 51 animals in 2005, to 41 animals in 2007, this being in spite of births of foals each year. Since there were no records of cheetahs killing zebras, the most likely cause of this loss was lion predation and it was surprising that this was not detected by *ad hoc* observations. Theoretically *ad hoc* observations will result in an underrepresentation of smaller prey species (Mills 1996) and this appears to be the case in the present study. It is not possible to say with certainty which of the two methods most closely reflected the diet of the lions on Sanbona. What can be concluded from these results is that species such as greater kudu, eland, ostrich, gemsbok and black wildebeest will be killed by lions on Sanbona and lions may cause population declines. The best way to cope with the lack of certainty around the diet of lions on this and other reserves is to adopt an adaptive management approach (Holling 1978; Walker 1986). Observations and theory are combined to inform and direct management interventions. The results of such interventions are carefully monitored and the intervention refined if the outcome is unexpected. The results from the present study suggest which prey species are likely to

be negatively affected by lions and these species should receive particular attention during the annual census.

While it is of interest to consider the diets of lions and cheetahs separately, at the reserve level their affect on prey is combined. The impact of the predator guild on prey species will differ depending on the abundance of the prey species and this is illustrated by springbok and black wildebeest. Both lions and cheetahs preferred black wildebeest and it is likely that the combined predation pressure will result in population decline. The abundance of black wildebeest on Sanbona was very low further exacerbating this problem. By contrast, springbok was the third most frequently killed species by lions and cheetahs but the abundance of this species resulted in it being avoided by lions (negative Jacobs' Index) and used according to the level of abundance by cheetahs. Nevertheless, a combined predation pressure that focused on juveniles or a single adult sex could bring about population decline.

Although not part of this study, an important next step is to calculate the carrying capacity of Sanbona for lions and cheetahs. In the absence of site specific data for daily food consumption, it will be necessary to use data from other sites that are similar to Sanbona. This information, combined with the density of prey species, the maximum sustainable yield for the prey species, and the requirements set by tourism will be used to decide on a stocking rate for predators (Coe *et al*. 1976; Power 2003).

Sanbona is a relatively large reserve, but a large proportion was not used by predators. Both lions and cheetahs avoided areas with a slope steeper than 19˚ and selected areas that were about one kilometer from water. They avoided vegetation types associated

with steep slopes and high mountains, an area equaling about 50% of the reserve. Thus the size of the utilized portions of Sanbona was about 191km^2 and this has to be taken into account in all planning exercises. Within this area, space was not used uniformly and the permanent water bodies and stream lines served as a focus for the predators. This resulted in overlap of core areas, aggressive inter and intraspecific interactions and injury and death of predators. Clearly, the limited availability of water will play a major role in setting the carrying capacity for predators, as mentioned in chapter 4. A decision has already been taken to reduce the number of prides of lions to one. However, another option is to drop the fence between Sanbona South (the study area) and Sanbona North which would increase the size by 105km², of which 13.3km² (13%) is river and floodplain, and 91.7km² (87%) is Succulent Karoo. This would result in a 42% increase in preferred habitat and might allow the introduction of a second pride of lions.

Ongoing research on Sanbona will ensure that the reserve does not only function as an ecotourism destination. Such research will provide support for adaptive management, and monitor the outcome of management interventions and allow the reserve to play a greater role in both species and ecosystem conservation.

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Appendix A

Scientific and common names of mammalian species found on Sanbona Wildlife Reserve

Class Mammalia

Order Macroscelidea

Round-eared elephant-shrew	*Macroscelides proboscideus* (Shaw 1800)

Order Tubulidentata

Aardvark	*Orycteropus afer* (Pallas 1766)

Order Hyracoidea

Rock hyrax	*Procavia capensis* (Pallas 1766)

Order Proboscidea

African savannah elephant	*Loxodonta africana* (Blumenbach 1797)

Order Lagomorpha

Cape hare	*Lepus capensis* (Linnaeus 1758)
Scrub Hare	*Lepus saxatilis* (Cuvier 1823)
Riverine rabbit	*Bunolagus monticularis* (Thomas 1903)
Smith's red rock rabbit	*Pronolagus rupestris* (A. Smith 1834)

Order Rodentia

Cape porcupine	*Hystrix africaeaustralis* (Peters 1852)
African molerat	*Cryptomys hottentotus* (Lesson 1826)
Brants' whistling rat	*Parotomys brantsii* (A. Smith 1834)
Bush vlei rat	*Otomys unisulcatus* (F. Cuvier 1829)

Four-striped grass mouse	*Rhabdomys pumilio* (Sparrmann 1784)
Spectacled dormouse	*Graphiurus ocularis* (A. Smith 1829)
Hairy footed gerbil	*Gerbillurus paeba* (A. Smith 1836)
Cape gerbil	*Tatera afra* (Gray 1830)
Order Primates	
Chacma baboon	*Papio hamadryas* (Linnaeus 1758)
Vervet monkey	*Cercopithecus pygerythrus* (F. Cuvier 1821)
Order Eulipotyphla	
Reddish-grey musk shrew	*Crocidura cyanea* (Duvernoy 1838)
Order Chiroptera	
Egyptian free-tailed bat	*Tadarida aegyptiaca*(E. Geoffroy Saint-Hilaire 1818)
Cape serotine bat	*Neoromicia capensis* (A. Smith 1829)
Egyptian slit-faced bat	*Nycteris thebaica* (E. Geoffroy Saint-Hilaire 1813)
Order Carnivora	
Aardwolf	*Proteles cristatus* (Sparrmann 1783)
Black-backed jackal	*Canis mesomelas* (von Schreber 1775)
Bat-eared fox	*Otocyon megalotis* (Desmarest 1822)
Cape fox	*Vulpes chama* (A. Smith 1833)
Black footed cat	*Felis nigripes* (Burchell 1824)
Spotted genet	*Genetta genetta* (Linnaeus 1758)
South African Large-spotted genet	*Genetta tigrina* (von Schreber 1776)
African wild cat	*Felis silvestris* (von Schreber 1777)

Cheetah	*Acinonyx jubatus* (von Schreber 1775)
Caracal	*Caracal caracal* (von Schreber 1776)
Leopard	*Panthera pardus* (Linnaeus 1758)
African lion	*Panthera leo* (Linnaeus 1758)
Brown hyena	*Parahyaena brunnea* (Thunberg 1820)
Yellow mongoose	*Cynictis penicillata* (G.Guvier 1828)
Large grey mongoose	*Herpestes ichneumon* (Linnaeus 1758)
Cape grey mongoose	*Garella pulverulenta* (Wagner 1839)
Marsh mongoose	*Atilax paludinosis* (G.Guvier 1829)
Honey badger	*Mellivora capensis* (von Schreber 1776)
Cape clawless otter	*Aonyx capensis* (Schinz 1821)
Striped polecat	*Ictonyx striatus*(Perry 1810)
Order Perissodactyla	
Black rhino	*Diceros bicornis* (Linnaeus 1758)
White rhino	*Ceratotherium simum* (Burchell 1817)
Plains zebra	*Equus quagga* (Boddaert 1785)
Cape mountain zebra	*Equus zebra* (Linnaeus 1758
Order Whippomorpha	
Hippopotamus	*Hippopotamus amphibius* (Linnaeus 1758)
Order Ruminantia	
Giraffe	*Giraffa camelopardalis* (Linnaeus 1758)
Greater kudu	*Tragelaphus strepsiceros* (Pallas 1766)

Eland	*Tragelaphus oryx* (Pallas 1766)
Buffalo	*Syncerus caffer* (Sparrman 1779)
Gemsbok	*Oryx gazella* (Linnaeus 1758)
Grey rhebuck	*Pelea capreolus* (Forster 1790)
Red hartebeest	*Alcelaphus buselaphus* (Pallas 1766)
Bontebok	*Damaliscus pygargus pygargus* (Pallas 1767)
Black wildebeest	*Connochaetes gnou* (Zimmerman 1780)
Common duiker	*Sylvicapra grimmia* (Linnaeus 1758)
Klipspringer	*Oreotragus oreotragus* (Zimmermann 1783)
Springbok	*Antidorcus marsupialis* (Zimmerman 1780)
Steenbok	*Raphicerus campestris* (Thunberg 1811)
Cape grysbok	*Raphicerus melanotis* (Thunberg 1811)

Appendix B

Scientific and common names of all species referred to in the study

Class Mammalia

Order Tubulidentata

Aardvark	*Orycteropus afer* (Pallas 1766)

Order Hyracoidea

Rock hyrax	*Procavia capensis* (Pallas 1766)

Order Proboscidea

African savannah elephant	*Loxodonta africana* (Blumenbach 1797)

Order Lagomorpha

Scrub Hare	*Lepus saxatilis* (Cuvier 1823)
Riverine rabbit	*Bunolagus monticularis* (Thomas 1903)

Order Rodentia

Cape porcupine	*Hystrix africaeaustralis* (Peters 1852)

Order Primates

Chacma baboon	*Papio hamadryas* (Linnaeus 1758)
Vervet monkey	*Cercopithecus pygerythrus* (F. Cuvier 1821)

Order Carnivora

African wild dog	*Lycaon pictus* (Temminck 1820)
Black-backed jackal	*Canis mesomelas* (von Schreber 1775)
Black footed cat	*Felis nigripes* (Burchell 1824)
Spotted genet	*Genetta genetta* (Linnaeus 1758)

African wild cat	*Felis silvestris* (von Schreber 1777)
Cheetah	*Acinonyx jubatus* (von Schreber 1775)
Caracal	*Caracal caracal* (von Schreber 1776)
Leopard	*Panthera pardus* (Linnaeus 1758)
African lion	*Panthera leo* (Linnaeus 1758)
Brown hyena	*Parahyaena brunnea* (Thunberg 1820)
Spotted hyena	*Crocuta crocuta* (Erxleben 1777)
Yellow mongoose	*Cynictis penicillata* (G.Guvier 1828)
Honey badger	*Mellivora capensis* (von Schreber 1776)
Dhole	*Cuon alpinus* (Pallas 1811)
Order Perissodactyla	
Black rhino	*Diceros bicornis* (Linnaeus 1758)
White rhino	*Ceratotherium simum* (Burchell 1817)
Plains zebra	*Equus quagga* (Boddaert 1785)
Order Suiformes	
Common warthog	*Phacochoerus africanus* (Gmelin 1788)
Order Whippomorpha	
Hippopotamus	*Hippopotamus amphibius* (Linnaeus 1758)
Order Ruminantia	
Giraffe	*Giraffa camelopardalis* (Linnaeus 1758)
Greater kudu	*Tragelaphus strepsiceros* (Pallas 1766)
Eland	*Tragelaphus oryx* (Pallas 1766)

Nyala	*Tragelaphus angasii* (Gray 1849)
Buffalo	*Syncerus caffer* (Sparrman 1779)
Gemsbok	*Oryx gazella* (Linnaeus 1758)
Grey rhebuck	*Pelea capreolus* (Forster 1790)
Red hartebeest	*Alcelaphus buselaphus* (Pallas 1766)
Bontebok	*Damaliscus pygargus pygargus* (Pallas 1767)
Blue wildebeest	*Connochaetes taurinus* (Burchell 1823)
Black wildebeest	*Connochaetes gnou* (Zimmerman 1780)
Common duiker	*Sylvicapra grimmia* (Linnaeus 1758)
Impala	*Aepyceros melampus* (Lichtenstein 1812)
Klipspringer	*Oreotragus oreotragus* (Zimmermann 1783)
Springbok	*Antidorcus marsupialis* (Zimmerman 1780)
Steenbok	*Raphicerus campestris* (Thunberg 1811)
Cape grysbok	*Raphicerus melanotis* (Thunberg 1811)
Thomson's gazelle	*Gazella thomsoni* (Günther 1884)

Class Aves

Order Struthioniformes

Ostrich	*Struthio camelus* (Linnaeus 1758)

Class Sauropsida

Order Testudines

Leopard tortoise	*Geochelone pardalis* (Bell 1828)