THE ECOLOGY AND MANAGEMENT OF THE LARGE CARNIVORE GUILD ON SHAMWARI GAME RESERVE, EASTERN CAPE

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

DOCTOR OF PHILOSOPHY of RHODES UNIVERSITY

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2012

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ABSTRACT

Shamwari Game Reserve was the first enclosed conservation area in the Eastern Cape Province of South Africa to reintroduce free ranging lions, cheetahs, leopards and wild dogs back into their historic range. At that time (2000 – 2001), little information was available on the ecology and behaviour of these predators in the habitats of the Eastern Cape, and management decisions were based on assumptions and unfounded comparisons with extant populations but from quite different habitats. The aim of this study was therefore to obtain a better understanding of the feeding ecology and space use of the predator guild, and the carrying capacity of Shamwari Game Reserve to enable more informed management decisions. In addition, the reserve is a photographic based tourism venture and understanding both the ecological and financial sustainability of the predator guild was important.
The diets of the predators were similar to those reported in other studies; larger predators killed a greater range of prey species than did smaller predators and a small number of prey species made up the majority of the kills. The larger predators had a higher mean kill mass than the smaller species and prey selection was influenced by prey size, prey abundance and prey habitat preference, and risk associated with hunting the species. Diet was flexible and responded to natural and management induced changes in prey abundance. There was a considerable overlap in space use by the lions, cheetahs and leopards with their core areas being centred on and around the Bushmans River. Space use was driven by resource distribution and landscape attributes, and by the presence of other predators of the same or different species. The long term viability of wild dog within the reserve was explored and the results confirmed that there was neither the required space nor the ecological processes and the wild dogs were removed from the reserve.

A carrying capacity of the reserve for the predator guild was determined using the Maximum Sustainable Yield method to assess the potential prey species off take and a resultant density of 3.3 to 6.6 lion female equivalent units per 10 000 ha was established. The natural carrying capacity of the reserve with respect to predators will not sustain the tourism objectives and consequently prey supplementation was necessary to maintain predator density at levels high enough to sustain tourism. Under these conditions the large predator guild is still sustainable financially although careful, responsible management is needed to provide ecological sustainability.

ACKNOWLEDGEMENTS

I would like to thank both the founder of Shamwari Game Reserve, Adrian Gardiner, and the current owners, Dubai World Africa, for supporting this study.

A big thank you to Dr Johan Joubert, Group Wildlife Manager for the Shamwari Group, for recognizing the importance of and encouraging this study.

A special thank you to my supervisor, Prof. Ric Bernard, for not only his professional assistance and guidance but also for his patience.

I would like to acknowledge Andrew Skowno and Candy Roux for their assistance with the GIS.

To all the staff at Shamwari and specifically the rangers and the coordinator, Anja, for assistance with data collection.

Thanks to Charlene Bissett for proof reading this thesis.

Thank you to my mother, Anne, for all her support and encouragement not only during this study but throughout my academic career.

Finally, a very special thank you to my wife, Peta-Lynn, and daughters, Tyla-Anne and Cassidy, for all their support, encouragement, patience, understanding and love over the past few years. It is much appreciated.

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CHAPTER 1: GENERAL INTRODUCTION

Africa supports the Earth's richest assemblage of large mammalian predators, which coexist despite a high degree of dietary overlap (Hayward & Kerley, 2009). Almost 25% of these carnivore species are threatened with extinction and are characterised by loss of habitat, reduction in distribution range and reduction in population sizes (Ginsberg, 2001; Hayward *et al*., 2007a). These declines are particularly evident in the Eastern Cape of South Africa where, in the late 1800s and early 1900s, the expansion of agriculture led to the local extinction of most of the large predators (Skead, 2007). The last record of lions in the Eastern Cape was in 1879, cheetahs in 1918 and wild dogs in 1919, while free-ranging leopards continue to occur in the Province (Skead, 2007; see Appendix I for all scientific names). Nationally, recent conservation efforts have started to slow and in some cases reverse these declines using methods that include translocation and reintroduction (Breitenmoser *et al*., 2001; Hayward *et al*., 2007b). The translocation of large carnivores is common in South Africa and elsewhere (Rowe-Rowe, 1992; Hofmeyr & van Dyk, 1998; Hofmeyr *et al*., 2003, Hayward *et. al*, 2007c) yet post-release monitoring has rarely occurred and, where it has, the results suggest that success rates are low and that the causes of failure are poorly understood (Hunter, 1998; Hayward *et al*., 2007c).

The Eastern Cape is South Africa's poorest province and recently large areas of land that had been used for various agricultural activities have been converted to more economically viable game farming, ecotourism and conservation (Kerley & Boshoff, 1997). In 2000 Shamwari Game Reserve (SGR) became the first game reserve to reintroduce the large carnivore guild back into the Eastern Cape, including lions, cheetahs, leopards and wild dogs. Since 2000, ten other conservation areas in the Eastern Cape have reintroduced large predators (Hayward *et al*., 2007a). The reintroduced populations of predators in the Eastern Cape are "managed wild populations" according to The Government Gazette's (2003) "National Principles, Norms and Standards for the Sustainable use of Large Predators in South Africa". These norms require that the predators are free ranging; live on wild prey populations whose numbers may be supplemented; occur in their natural habitat within the historical distribution range and that the social requirements of the species are met.

If these relatively small game reserves (about 20 000 – 30 000 ha) are to make a contribution to the conservation of large mammalian predators, then it is vital that predator behaviour in enclosed systems is fully understood and that metapopulation management is initiated

(Bissett, 2007; Hayward *et al*., 2009). Furthermore, because these predator species have been locally extinct for almost 100 years, there are no basic data on any aspect of their biology or ecology in the habitats, such as succulent thicket, that are peculiar to the region. Thus, the reintroduction of large mammalian predators to the reserves in the Eastern Cape has created the opportunity to study aspects of their ecology and behaviour in habitats in which they have not previously been studied (Bissett *et al.,* 2012). This information is not only of fundamental interest as it will supplement what is already known from different systems, but is also crucial for the successful management of the reintroduced predators (Hayward *et al*., 2007b).

The management challenges on the reserves are exaggerated because the reserves are often relatively small and are fenced. Legislation requires predator proof fencing and all conservation areas in South Africa that house dangerous animals are enclosed with game-proof fencing. Avoiding human–animal conflict and reducing the impact of introduced predators are the two most common benefits of fences (Hayward & Kerley, 2009) but they present a number of important ecological problems. Fences block migration routes and limit range use which may result in overabundance, inbreeding and isolation; restriction of evolutionary potential; and management; amenity and ethical costs (Boone & Hobbs, 2004; Hayward & Kerley, 2009). Fences influence the prey species in the same way that they do the predators, and the inability of prey species to migrate or seek refuge, places them under pressure from unrelenting predation. Since the space use of prey is the primary factor determining home range size and space use of the predators (Spong, 2002; Hemson, 2003; Hayward *et al*., 2009) the fences both directly and indirectly influence space use by the predators.

It is widely held that relatively small, enclosed conservation areas require more intense management than larger, open systems (van Dyk, 1997; Druce *et al*., 2004) which is characterised by the complexity of the decision making processes (Kettles & Slotow, 2009; Slotow & Hunter, 2009). A lack of knowledge may result in one, and often several, of the following consequences: overpopulation (Vartan, 2001; Hayward *et al*., 2007b); inbreeding depression (Hendrick & Miller, 1992; Newmark, 1996; Vartan, 2001; Packer *et al*., 2005; Trinkel *et al*., 2008); impact on other predators or prey species (Mills & Shenk, 1992; van Dyk & Slotow, 2003, Hayward *et al*., 2007c); break-outs as a result of pressure from other

predators within the protected area (Steele, 1970; Slotow & Hunter, 2009); the intra- and interspecific spread of disease (Hunter, 2001; Packer *et al*., 2005). This further emphasises the need for fundamental biological information to underpin all management interventions. The conservation of mammalian carnivores has traditionally been a species by species effort, with management actions aimed at reversing human caused species declines (Mech, 1995; Bangs & Fritts, 1996; Linnell & Strand, 2000). Recently however there has been a shift from single species to ecosystem conservation with a focus at the guild level (Estes, 1996; Loveridge *et al.,* 2009). A guild may be defined as a group of sympatric taxa using similar resources (Root, 1967; St-Pierre *et al*., 2006). While it may be easier to work at a single species level, even within the small enclosed reserves the predators form part of a large carnivore guild which is characterised by complex interactive effects (Mills 1991; Loveridge *et al*., 2009). Since these effects, such as kleptoparasitism and other aggressive interspecific interactions may influence conservation efforts (Caro & Stoner, 2003), it makes more sense to work at the guild or ecosystem level.

The present study, based on a single conservation area, SGR, addresses a number of questions and has a number of applied and fundamental aims. The biology of the reintroduced predators was studied from shortly after release with the broad aim of understanding the feeding and spatial ecology of members of the large carnivore guild and to provide the information required to support management decisions. A particular focus was on the diet of the predators and explored the factors that influence prey selection at both prey species and prey size levels. Similarly, a focus was on space use and habitat selection exploring the factors affecting range size and its location. These data are then used to establish the carrying capacity of SGR for large predators.

CHAPTER 2: STUDY SITE

Objectives

In order to understand the ecological functioning of SGR, an understanding of the historical and current impacts, both climatic and human induced, is essential. Thus the objective of a description of the study site is to gather information on any factors that may influence vegetation structure and pattern as well as other ecological processes in order to provide a background for better understanding of the general ecology.

Locality

At the time of study SGR comprised 18 746 ha of land falling in both the Alexandria and Albany Districts of the Eastern Cape, South Africa (Figure 2.1). The study area lies between 33°20' S 26° 01' E and 33° 32' S 26° 10' E. The Bushman's River flows through the reserve for 27.6km.

Figure 2.1. Locality map for SGR (shown in green).

Geology and topography

The dominant geological formations in the study area are Bokkeveld Series shales, Witteberg quartzites, Karoo sandstones and Sundays River Formations. The quartzite ridges traverse the central and northern parts of the study site dividing it into distinct geomorphological zones separated from one another by the ridges (Burroughs & Palmer, 1992). The southern part of the study site is dominated by the Sundays River Formation resulting in shallow soils underlain by calcrete. The elevation gradient of the study area is important as it ranges from 196m above sea level in the south to 628m above sea level in the north. This steep elevation gradient generally parallels the rainfall gradient. Four major substrata are found, namely shale, sandstone, quartzite and calcrete. Some deeper alluvial soils are found on the lower lying areas (Burroughs & Palmer, 1992).

Rainfall

Rainfall data come from two sources, firstly from historical data obtained from a neighbouring property, Schietkop 485, for the period 1925 to 1990 (Table 2.1) and secondly in SGR for the period of the study i.e. 2000 to 2007 (Table 2.2). For Schietkop the mean annual rainfall was 422mm, with a maximum of 800mm and a minimum of 180mm.

Rainfall figures for the duration of the study period for SGR have been recorded in the north and in the south (Figure 2.2). The mean annual rainfall for the study period (591.3mm in the south, 604mm in the north) is greater than the long term average of 422mm. Similarly the average monthly rainfall figures (Figure 2.3) are also higher.

Table 2.1. Monthly (mean with 1sd) rainfall for SchietKop on the eastern boundary of SGR for the period 1925 to 1990.

month	mean (mm)	standard deviation
January	28.1	36.6
February	30.4	32.1
March	39.0	42.8
April	47.2	34.4
May	39.2	37.5
June	29.7	30.0
July	26.1	31.7
August	35.0	26.7
September	49.7	45.0
October	33.4	30.2
November	34.6	41.6
December	26.3	25.9

Table 2.2. Monthly rainfall (mean with 1SD) for the duration of the study period for the south and north of SGR.

	south		north	
month	mean (mm)	standard deviation	mean (mm)	standard deviation
January	46.8	31.7	53.5	36.9
February	38.1	24.4	41.3	22.9
March	58.8	43.2	75.5	40.5
April	61.6	42.2	54.8	25.9
May	49.8	52.8	36.5	43.6
June	18.7	13.1	22.3	15.5
July	29.8	22.5	31.3	23.9
August	68.1	85.0	72.8	81.1
September	51.8	41.1	57.3	44.7
October	41.3	24.5	46.6	20.4
November	49.6	45.0	73.3	89.0
December	47.1	37.7	61.9	47.4

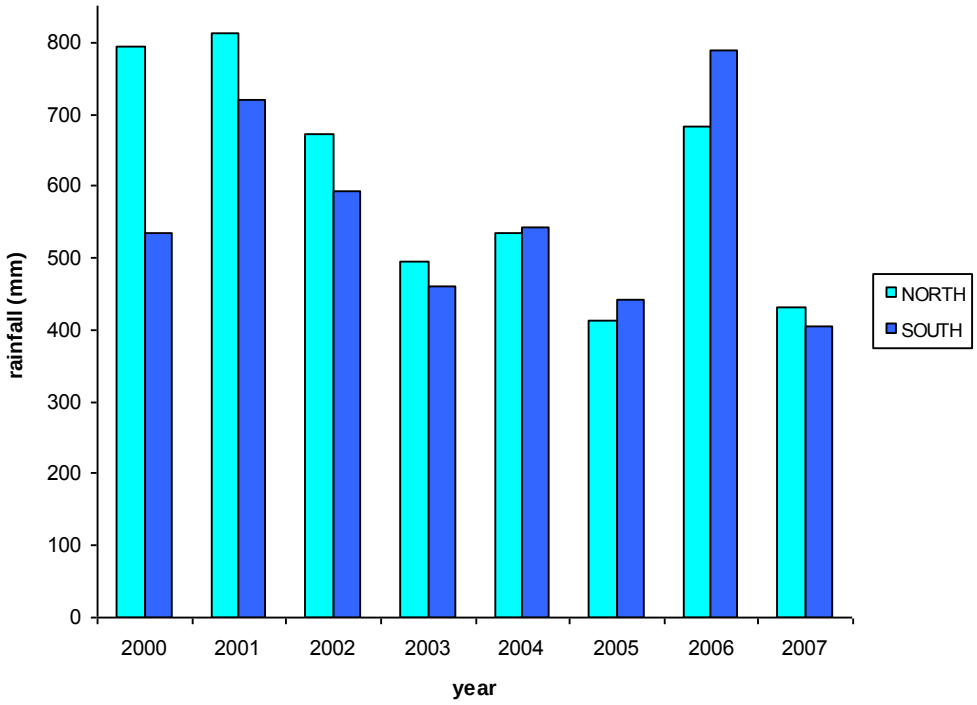


Figure 2.2. Annual total rainfall figures in the north and south of SGR for the study period (2000 – 2007).

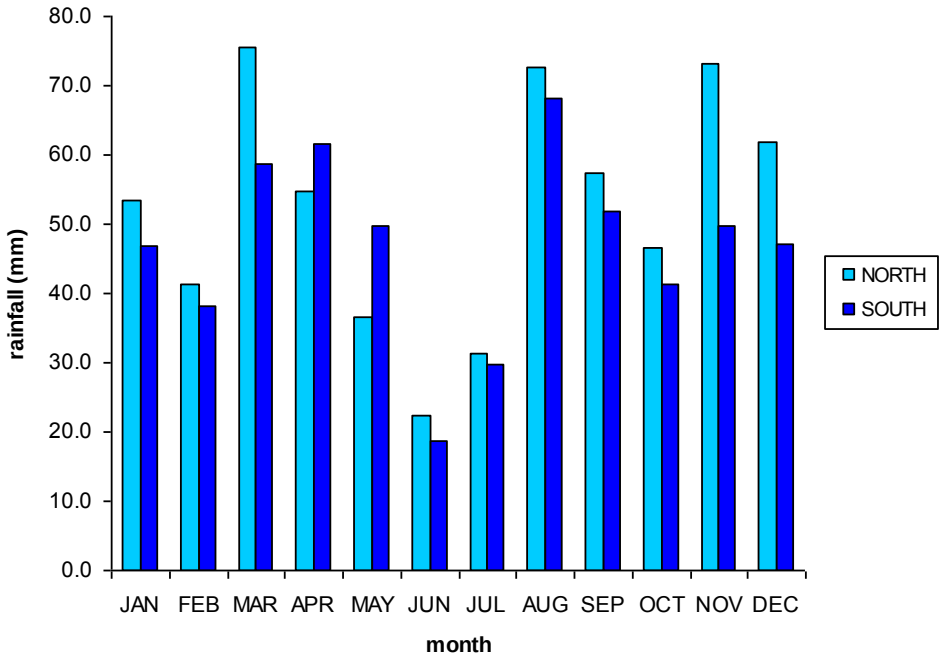


Figure 2.3. Mean monthly rainfall in the north and south of SGR (2000 – 2007).

Size and Zoning

SGR is split into four zones based on management intensity (Figure 2.4). The wilderness area (2 651 ha) is managed in compliance with the international wilderness ethic. All internal structures have been removed and only two groups of eight trailers may be on the wilderness area at any time under the guidance of a trail guide. Motorized transport is prohibited (Joubert & O'Brien, 2001). The bulk of the reserve (10 824 ha) is managed as a natural area with roads for game drives while the rural high impact areas (1 811 ha) are those areas around lodges, workshop and staff accommodation and as such are subject to higher vehicle traffic and impacts such as waste management and water utilization. The breeding centres (2 497.5 ha) are areas physically separated from the main reserve, here animals are bred in the absence of predators and the areas are managed according to agro-economic principles. The reserve, high impact areas and the wilderness area are available to predators totaling 15 286.5 ha in extent.

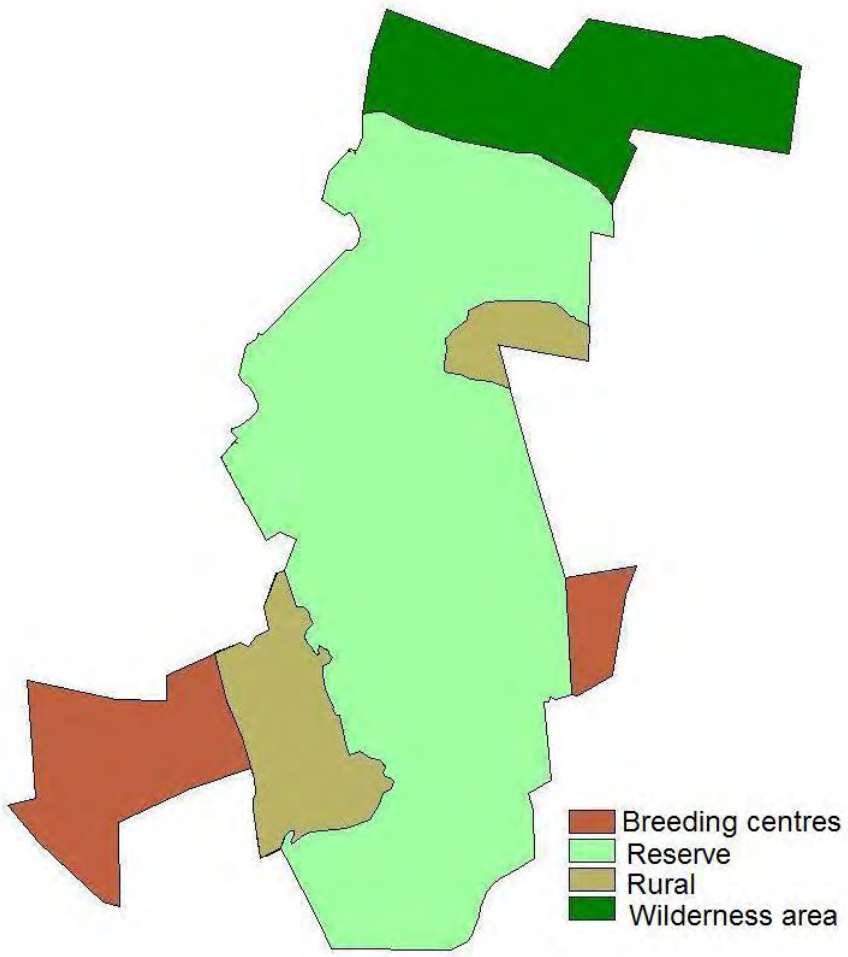


Figure 2.4. The zoning of SGR, showing the different management zones.

Land use history

On arrival of the 1820 settlers in the Grahamstown area they found the soils of the Zuurveld unsuitable for intensive agriculture (Lubke *et al*., 1988). Farming with Merino sheep became widespread together with extensive cattle farming while cultivation was restricted to the alluvial soils close to permanent water. The Xhosa stock invasion of December 1834, which resulted in the Sixth Frontier War, refers to the herds of cattle. After the Sixth Frontier War farmers changed from wheat to more suitable crops like rye, barley and maize and later pineapples and chicory. Lubke *et al*. (1988) add that sheep and cattle were the 'mainstay' for the area.

At present farming is still much the same in the area with sheep and cattle (primarily dairy) being the primary produce while crops include wheat, oats, chicory and pineapples. Pastures planted for livestock are common. Cropping in SGR prior to 1990 was prevalent in the southern sector along the Bushman's River where most of the vegetation on the alluvial soils was cleared, often to the water's edge. Sheep, goats and cattle were the main livestock in SGR, with social hunts for bushbuck and kudu being regular annual events (pers. comm. with local farmers).

Farm acquisitions

The first farm, Excelsior, to be bought for the formation of SGR was purchased in 1990. During the drought of the early 1990s, further farms were purchased and to date 53 title deeds have been purchased from 17 land owners (Figure 2.5).

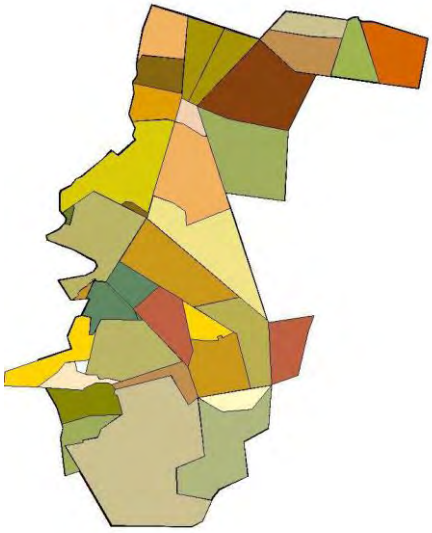


Figure 2.5. The cadastral boundaries of the 17 farms purchased in the formation of SGR.

Regional context

SGR forms part of the Maputaland-Pondoland-Albany Global Biodiversity Hot Spot of the Eastern Cape (Figure 2.6) due to its high levels of endemism and diversity (CEPF, 2010).

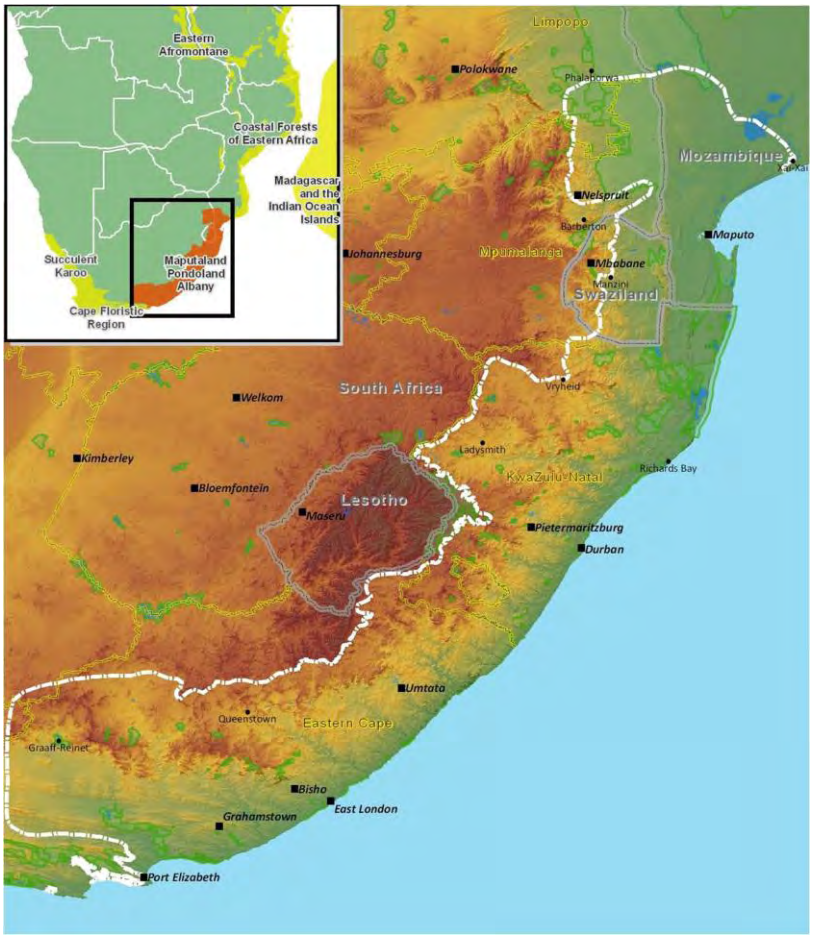


Figure 2.6. The location of the Maputaland-Pondoland-Albany Global Biodiversity Hotspot in Southern Africa (CEPF, 2010).

The Eastern Cape is a transition region where a great complexity of floras and vegetation types converge. The reason for this phenomenon is the transitional nature of the climate, geomorphology and geology of this region (Lubke & van Wijk, 1988). This diversity of vegetation results in a diverse fauna (Table 2.3).

Table 2.3. Regional species list showing the diversity of the Eastern Cape compared to other provinces (Low & Rebello, 1996).

	biome	plant	mammal	bird	amphibian	reptile
Eastern Cape	7	6 163	156	384	51	57
Free State	3	2 984	93	334	129	47
Gauteng	2	3 303	125	326	25	53
KwaZulu-Natal	4	6 141	177	462	68	86
Mpumalanga	3	4 782	160	464	48	82
North West	2	3 025	138	384	27	59
Northern Cape	6	5 067	139	302	29	53
Northern Province	3	4 236	239	479	44	89
Western Cape	6	8 925	153	305	39	52

Vegetation Classification

SGR comprises five biomes (Table 2.4, Figure 2.7), according to Low & Rebelo's (1996) classification. These biomes are represented by 12 vegetation units (Table 2.5, Figure 2.8) with a further two units were identified for disturbed lands (Table 2.5). All vegetation data are from O'Brien, (2004).

Forest biome

Afromontane forest (68 ha)

Afromontane Forest occurs in patches, particularly in deep kloofs or in steep gullies within the Subtropical Thicket. Afromontane Forest is structurally dominated by tall trees that can be 30-40 m high with distinct strata of emergent trees to canopy trees. Shrub and herb layers are present (Low & Rebelo, 1996). Indicator species used to identify the Afromontane element in SGR are: *Podocarpus falcatus, Schotia latifolia, Harpephyllum caffrum* and *Hippobromus pauciflorus*.

Thicket biome

For practical purposes the Succulent and Woody Subtropical Thickets are mapped together although they are recognized as separate vegetation units. Subtropical Thicket is an important component of the reserve and is situated predominantly on the sloping ground on shale and sandstone derived substrata. Aspect and slope of Subtropical Thicket appear to determine the abundance of succulents, which is the basis for the division into Succulent and Woody components. The Bontveld and Bushclump Savanna vegetation units are classified under the Thicket biome.

Subtropical thicket (6 548 ha)

Succulent subtropical thicket

Succulent Subtropical Thicket generally occurs on slopes subject to direct radiation from the sun, therefore dominate north facing, steep slopes. Characteristic is the high percentage of succulents, as the major diagnostic feature, in particular *Portulacaria afra,* which is an indicator species as well as the dominant species. Other indicator species are *Crassula muscosa* and *C. perforata*. Other characteristic tree species of Succulent Subtropical Thicket are *Schotia afra, Carissa bispinosa, Pappea capensis, Euclea undulata, Sideroxylon inerme* and *Aloe* spp.

Woody subtropical thicket

Woody Subtropical Thicket generally occurs on the south facing more gentle slopes where direct radiation from the sun is reduced. The absence of succulents *Portulacaria afra* and *Crassula* spp. differentiate the Woody Subtropical Thicket from the Succulent Subtropical Thicket. Species characteristic to Woody Subtropical Thicket are *Euphorbia triangularis, Olea europaea, Ptaeroxylon obliquum, Cassine aethiopica, Scutia myrtina* and *Plumbago auriculata*.

Bontveld (1234 ha)

Bontveld is situated on flat to moderately sloping calcrete in the southern part of the reserve. The vegetation consists of bushclumps where the interspersed vegetation is grass in a complex of shrubs of karroid affinity. The differentiating feature between Bontveld and Bushclump Savanna is the depth of the topsoil with 10cm being the cut off point for Bontveld as soils on calcrete are very shallow. The reason for this division is the potentially different

management strategies due to different soil depth. The bushclumps are composed of a number of species such as *Zanthoxylum capense, Canthium inerme, Scutia myrtina, Rhus undulata, Rhus perota, Aloe ferox* and *Grewia occidentalis.* The clumps include climbers such as *Rhoicissus tridentata* and *Secamone alpinii*. The dominant perennial grasses are *Themeda triandra, Eragrostis curvula, Brachiaria serrata, Digitaria eriantha, Sporobolus africanus* and *S. fimbriatus*.

Bushclump savanna (555 ha)
Bushclump Savanna has the same basic structure as Bontveld except that it occurs on deep soils and does not have calcrete as a substratum. Bushclump Savanna also has the same vegetation makeup except the frequency of *Olea europea* and *Cussonia spicata* is higher in Bushclump Savanna.

Savanna biome

Riverine bush (385 ha)
Riverine Bush is limited to the banks of the Bushman's River as well as some of the larger temporary water courses throughout the reserve. It is vulnerable to degradation due to the large herbivores that frequent the water ways. The indicator species are *Combretum caffrum, Acacia caffra* and *Rhus macowanii.* Other *Rhus* spp*., Acacia karroo* and *Plumbago auriculata* are also common along the water courses. Riverine Bush has been classed as Savanna as the species composition has Primary *Acacia* Thicket affinities and, bar the steep river banks, the grass matrix is such that fire will have an effect on the structural component.

Primary Acacia thicket (873 ha)
Primary *Acacia* Thickets are generally found on the low-lying flat land, normally associated with water courses. Often these areas have been cleared for cultivation for which the alluvial soils are ideally suited. Primary *Acacia* Thicket is characterized by a combination of two indicator species which are also the dominant woody species, namely *Rhus longispina* and *Acacia karroo*. The defining difference between Primary and Secondary *Acacia* Thicket is the proportion of the above two indicator species. Primary *Acacia* Thicket is dominated by *Rhus longispina* with *Acacia karroo* scattered in between. Other characteristic species are *Azima tetracantha, Euclea undulata, Maytenus heterophylla* and *Cadaba aphylla.*

Secondary Acacia thicket (322 ha)

Secondary *Acacia* Thicket occurs where Primary *Acacia* Thicket has been disturbed, be it by physical clearing or by mismanagement and over grazing. *Acacia karroo* totally dominates this vegetation unit and depending on the reason of degradation, *Rhus longispina, Cadaba aphylla* and *Azima tetracantha* may be found in low numbers.

Fynbos biome

Grassy fynbos (99 ha)

The Grassy Fynbos component of SGR is situated on the quartzite ridges in the northern parts of the reserve. Both elevation (550-650 m above sea level) and rainfall (530 mm per annum) are at their highest for the reserve. These communities are rich in species diversity with a complex mixture of grasses, woody shrubs and small-leaved Fynbos elements. Indicator Fynbos species include *Leucadendron salignum, Phylica axillaris* var. *microphylla, Aspalathus chortophila, Passerina vulgaris, Relhania genistifolia* and *Metalasia muricata*. The grass component includes *Pentachistis pallida, Heteropogon contortus* and *Themeda triandra*.

Calcrete fynbos (11 ha)

The Calcrete Fynbos component in SGR is limited to only eleven hectares. Size wise this is insignificant, however due to the vulnerability of the indicator species, *Syncarpha recurvata*, it warrants special conservation status and is thus included as a vegetation unit. Calcrete Fynbos occurs on a calcrete substratum and has a much lower elevation and annual rainfall than Grassy Fynbos.

Grassland biome

Montane grassland (2 594 ha)

Montane grassland occurs on top of the quartzite ridges above the fringe of Subtropical Thicket at altitudes greater than 400 meters above sea level yet lower than the Grassy Fynbos, with a sandstone substratum. In the absence of bushclumps, Montane Grassland results with *Themeda triandra, Heteropogon contortus, Eragrostis curvula***,** *Brachiaria serriata* and

Sporobolus fimbriaus being dominant. These areas are vulnerable to invasion by woody species such as *Elytropappus rhinocerotis, Pteronia incana, Rhus undulata* and *Selago corymbosa* when mismanaged.

Lowland grassland (572 ha)
Lowland Grassland is found only in the south of the study area at low altitudes of between 220 and 230 meters above sea level. This area is grassland with three dominant grass species (*Themeda triandra, Eragrostis curvula* and *Digitaria eriantha*) with very little woody growth and little to no variation in topography.

Disturbed lands
Any vegetation that has been transformed by man's activities to the point where it no longer conforms to the recognized biomes of southern Africa has been classified under disturbed lands. A distinction has been made within the disturbed lands between cleared and cultivated lands as future management programs might vary due to factors such as leaching of soils of cultivated lands, past uses of fertilizers and different land uses.

Cleared lands (213 ha)
Cleared lands refer to areas where the vegetation has either been mechanically cleared to create grazing for livestock or has been severely over utilized (generally by goats) so that it no longer resembles its original state. Cleared land as a result of over utilization is often found around old homesteads as well as near water points. "Cut lines" or cleared paths within Subtropical Thicket are regarded as cleared lands but due to their intricate network are not included in the map. Lands that have been mechanically cleared are generally cleared Primary *Acacia* Thicket or Woody Subtropical Thicket. The species composition of the successional stages vary according to the original vegetation unit. If left to rehabilitate for long enough, cleared Primary *Acacia* Thicket will ultimately result in Secondary *Acacia* Thicket. Rehabilitation of Subtropical Thicket takes a lot longer but new vegetation growth in cut lines include *Azima tetracantha* and *Panicum maximum.*

Cultivated lands (1811 ha)
Cultivated lands are old lands that were used for cultivating crops and are in various stages of rehabilitation. These lands are found throughout the study area but concentrated along the

Bushman's River. In the early stages of succession they are dominated by ephemeral weedy species such as *Conyza scabrida, Galenia pubescens* and *Sasola kali;* succulents *Drosanthemum floribundum* and *Mesembryanthemum aitonis* and grasses such as *Cynodon incompletus* and *Tragus racsmosus*. In later stages of succession, species representing sub-climax grassland include *Cynodon dactylon, Sporobolus africanus* and *Eragrostis plana.* Some cultivated lands have been seeded with a mixture of *Panicum maximum, Cenchrus ciliaris* and *Digitaria eriantha* by SGR's conservation department.

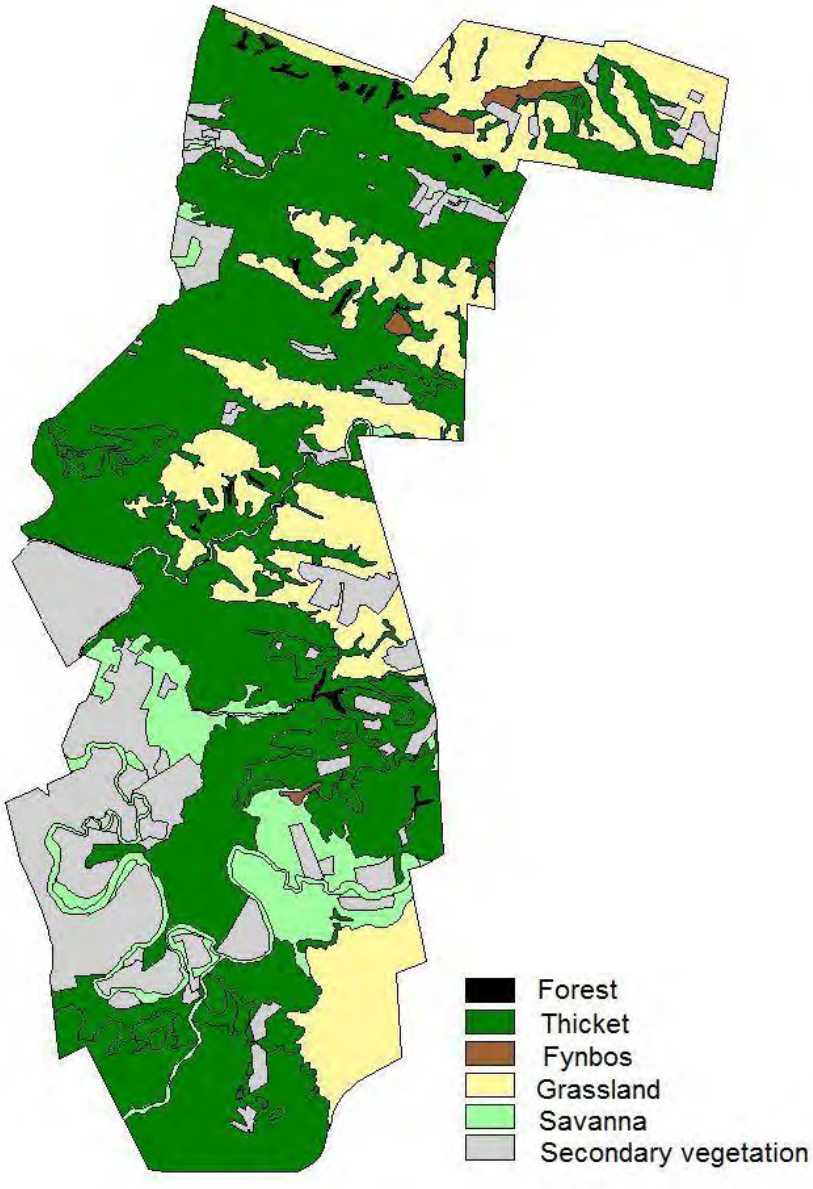


Figure 2.7. Biomes of SGR.

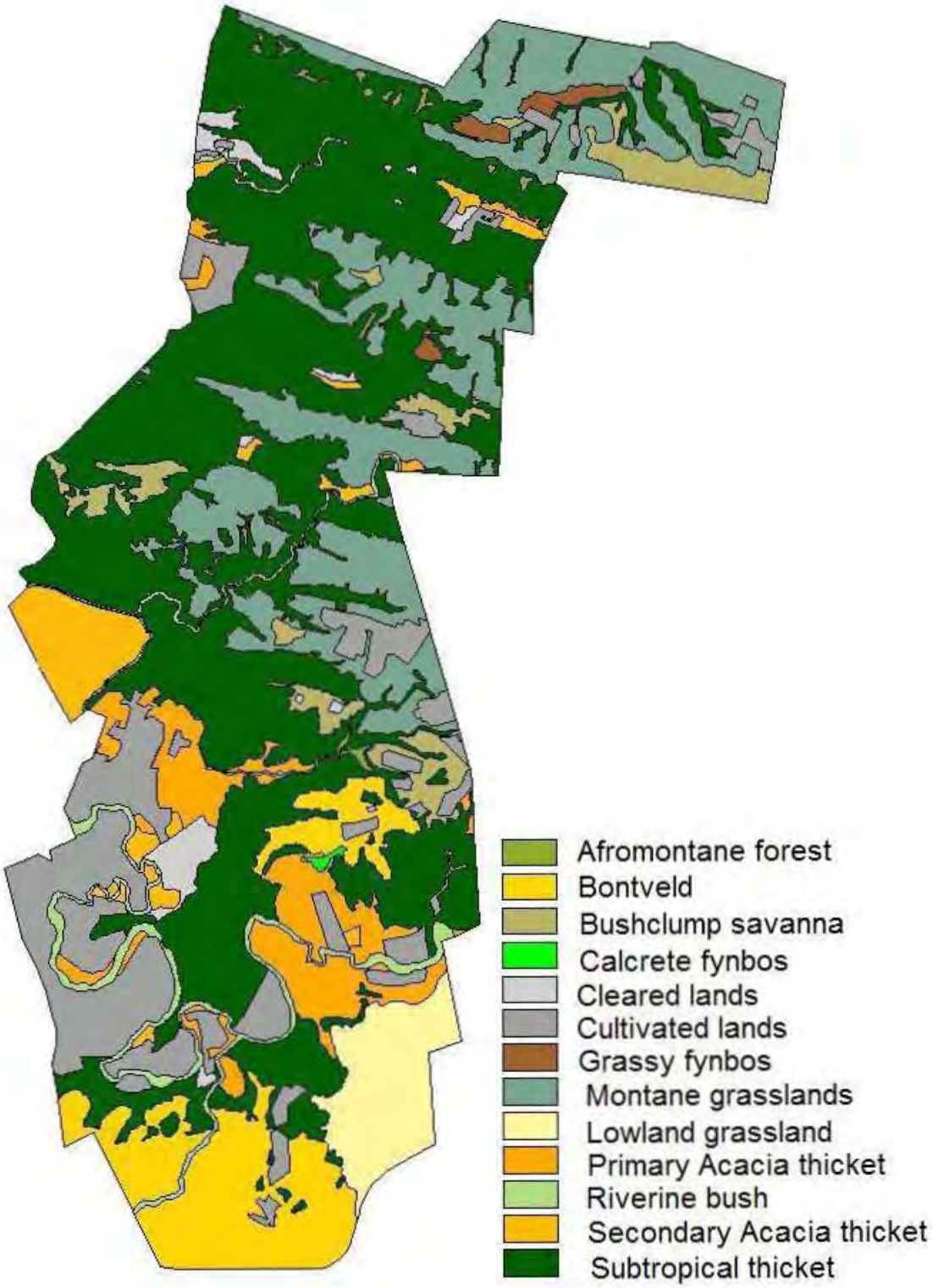


Figure 2.8. Vegetation units of SGR.

Table 2.4. Area in hectares and as a percentage for each biome and for disturbed lands represented in SGR.

biomes and disturbed lands	area (ha)	%
Forest Biome	68.23	0.4
Thicket Biome	8 362.53	54.7
Savanna Biome	1 233.28	8.1
Fynbos Biome	110.05	0.7
Grassland Biome	3 165.88	20.7
disturbed lands	2 346.70	15.4

Table 2.5. Area (ha) and as a percentage for each vegetation type in SGR

biomes and disturbed lands	vegetation type	area (ha)	%
Forest Biome	Afromontane Forest	68.23	0.4
Thicket Biome	Subtropical Thicket (Succulent and Woody)	6 547.61	42.8
	Bontveld	1 234.33	8.1
	Bushclump Savanna	555.45	3.6
Savanna Biome	Riverine Bush	384.81	2.5
	Primary *Acacia* Thicket	873.44	5.7
	Secondary *Acacia* Thicket	322.33	2.1
Fynbos Biome	Grassy Fynbos	98.80	0.7
	Calcrete Fynbos	11.26	0.07
Grassland Biome	Montane Grassland	2 593.92	17.0
	Lowland Grassland	571.96	3.7
disturbed lands	cleared lands	212.99	1.4
	cultivated lands	1 811.37	11.9

Animals of Shamwari Game Reserve

Historical incidence of animals in the region

Historically the Eastern Cape was rich in wildlife prior to the arrival of the 1820 Settlers and onset of agriculture. The following exerts from Skead (2007) are evidence that the large predators of this study where indigenous to the area:

Lion: "In 1775, Sparrman met lions near the Bushmans River at a place that must have been on the Quaggasvlakte". This is in the Upper Alexandria District. The south western sector of SGR falls within the area historically known as Quaggasvlakte.

Wild Dog: "Mr JM Mullins (pers. comm. 26 May 1969) knew that his grandfather-in-law, the late Mr Walter Fowlds, who farmed on the Quaggasvlakte, saw in the 1890s five wild dogs just west of Routenbach's Drift on the Bushmans River between Sandflats and Sydbury". Routenbach's Drift is on the present day SGR.

Cheetah: "Cheetahs…became extinct in the Albany District about the year 1888, when two were killed at 'Bowden'. This is a farm about 35km north of Grahamstown.

Leopard: "Backhouse (1844) tells of how the skin of a leopard killed at Salem was sold in Grahamstown…."

In Table 2.6 the list of indigenous large mammal species is given for the Upper Alexandria and Lower Albany Districts of the Eastern Cape from Skead (2007). SGR is represented by both these districts.

Table 2.6. Large mammal species indigenous to the Upper Alexandria and Lower Albany Districts. (See Appendix 1 for scientific names of all animals in this study).

herbivores	carnivores
elephant	wild dog
black rhinoceros	spotted hyena
hippopotamus	brown hyena
red hartebeest	leopard
eland	lion
kudu	serval
Cape buffalo	cheetah
true quagga	caracal
Cape mountain zebra	black backed jackal
springbok	
true reedbuck	
mountain reedbuck	
grey rhebok	
oribi	
klipspringer	
grey duiker	
steenbok	
blue duiker	
bushbuck	
bushpig	
warthog	
Cape grysbok	

SGR's large mammal species numbers

The first animals were introduced into SGR in 1992 but it was not until the end of 2000 that the first of the large predators were introduced. Table 2.7 is a list of all game numbers in SGR for the study period (2000 to 2007; see Chapter 3 for game count methods).

Table 2.7. Animal numbers for SGR for the period 2000 to 2007. (NC = not counted; A = absent)

species	2000	2001	2002	2003	2004	2005	2006	2007
baboon	NC	NC	NC	115	122	42	86	86
blesbok	347	305	294	243	175	149	185	168
buffalo	30	32	15	15	5	0	1	0
bushbuck	750	750	950	950	930	212	224	224
bushpig	200	200	250	250	250	83	83	83
cheetah	A	2	1	7	4	7	4	3
duiker (grey)	900	900	850	850	850	67	31	31
eland	115	105	85	93	69	88	56	14
elephant	43	49	53	49	53	59	64	49
gemsbok	55	61	45	54	59	43	57	62
giraffe	15	18	16	18	25	24	26	30
grysbok	75	75	75	75	50	0	0	0
hippopotamus	14	16	18	21	15	17	22	23
hyena (brown)	A	A	11	14	15	15	18	19
impala	465	694	791	852	656	520	627	578
kudu	750	800	850	900	900	334	415	305
leopard	NC	2	1	4	3	2	2	2
lion	A	6	12	15	20	17	14	14
ostrich	A	A	13	21	12	4	1	5
red hartebeest	140	132	102	131	112	136	129	126
reedbuck (mountain)	275	300	350	350	325	60	52	18
rhinoceros (black)	11	13	14	16	18	23	15	19
rhinoceros (white)	14	14	16	19	19	20	25	25
springbok	295	257	166	153	132	75	121	109
warthog	25	65	56	184	231	251	481	416
waterbuck	60	65	52	62	61	46	38	59
wild dog	A	A	A	12	11	13	10	3
wildebeest (black)	165	92	104	72	55	177	83	159
zebra (plains)	60	84	92	98	113	160	167	164
total	4804	5033	5281	5643	5290	2644	3037	2794

The study animals

Cheetahs: In September 2000 cheetahs were the first predators to be released into SGR. Originally a coalition of two males were introduced. The first female was only introduced two years later (Table 2.8). By mid 2003 nine cheetahs had been introduced into SGR all of which were part of the National Cheetah Management Program (NCMP). The NCMP capture wild cheetah off stock farms in the northern parts of South Africa and redistribute them to game reserves across the country. The cheetahs captured by the NCMP lacked experience with lions and this is supported by the fact that by 2004 four of the initial nine cheetahs introduced into SGR had been killed by lions (Table 2.8).

Table 2.8. The age, sex and date of cheetahs introduced into SGR through the NCMP.

cheetah	release date	fate
adult male	9/2000	
adult male	9/2000	killed by lions 7/2002
adult female	8/2002	killed by lions 1/2003
sub adult female	8/2002	
adult male	2/2003	
adult male	2/2003	killed by lions 12/2003
adult female	3/2003	killed by lions 3/2004
juvenile female	3/2003	
juvenile male	3/2003	

Lions: Two prides of lions were introduced into SGR in November 2000 after a month in a holding boma. One pride of three lions comprising one male and two females was released in the north of the reserve and the other pride of the same composition in the south. The lions came from Pilansberg and Madikwe Game Reserve in the North West Province of South Africa. For genetic purposes the northern pride consisted of two females from Madikwe Game Reserve and a male from Pilansberg Game Reserve. The southern pride consisted of two females from Pilansberg Game Reserve with the male from Madikwe Game Reserve. All lions were captured from different prides and bonded together. The historical origin of the lions was Etosha National Park, Namibia.

The lion population in SGR was managed during the study period and the population kept between 10 and 15 individuals. In 2007, the dominant males on the reserve were removed and an unrelated male of Etosha origin was introduced tin increase genetic diversity.

Leopards: A male and a female leopard was introduced into SGR in 2001 from a rehabilitation centre in Mpumalanga. The male died of a snake bite in that year while the female was shot on a neighbouring stock farm in 2002. In 2003, three female leopards were introduced from Mpumalanga and a male from the NCMP. The male was killed by lions in 2003 while two of the females died in 2004, one from a porcupine quill in her intestines and another female was shot on a neighbouring stock farm. A further male was introduced in 2004. Naturally occurring vagrant leopards are sighted on the rare occasions.

Wild dogs: Wild dogs were introduced into SGR in May 2003. The introductory pack consisted of two male and three females. For genetic purposes the males came from Shambala Game Reserve in the Northern Province and the females from Karongwe Game Reserve in the Limpopo Province. The wild dogs were removed from SGR at the beginning of 2007 due to repeated escapes and the burden on the prey populations.

Stocking rates

SGR management works towards a maximum stocking rate of one large stock unit (lsu) per nine hectares as per recommendation from local Extension Officers in Alexandria and Humansdorp (Joubert & O'Brien, 2005). Although more accurate browse and graze units have not been established, the herbivore impact is determined via a vegetation monitoring program established in 2003. The feedback from the monitoring helps determine carrying capacities and management is adaptive (O'Brien, 2004).

With the total size of the study site being 15 286 ha and working to a carrying capacity of nine hectares per large stock unit the total carrying capacity for SGR is 1 698.5 lsu. Thus with a total of 1 181 lsu's at present in the reserve SGR is currently under stocked at 13.97 ha/lsu. The present herbivore biomass is 32.21 kg/ha or 492.4 tons for the reserve.

CHAPTER 3. GENERAL METHODS

Certain components of the methods of data collection were uniform for all aspects of this study. These components are included in this chapter while the chapter specific methods for each of the three research chapters are dealt with in the appropriate chapters.

Radio telemetry

All predators released into SGR were fitted with either a radio collar or internal abdominal radio transmitter to allow repeated and relatively easy location and the collection of baseline data on feeding and spatial ecology. A Telonics (Mesa, USA) TR-4 receiver in combination with a Telonics (Mesa, USA) RA-14K antenna was used to track the predators. Radio collars were African Wildlife Tracking (AWT, RSA) transmitters with a VHF range of 148-152 MHz fitted with D-Cell batteries and the abdominal implants were AWT transmitters with a VHF frequency range of 148 – 152 MHz with C-Cell batteries. Once the life of the batteries on these collars and implants had expired, the collars were removed from all species except the leopards whose elusive behaviour and ability to breech the perimeter fencing of the reserve made the presence of a radio collar important. A cellular (GPS/GSM) collar was fitted to a single adult male leopard to determine more precisely his movements and home ranges when not on the reserve. Battery life was about 18 to 24 months. All procedures that required the capture and sedation of an animal were performed by a qualified veterinarian.

Collection of baseline data for feeding biology

Efforts were made to locate all the large predators at least once a day and records came from three sources; the field guides, a set of continuous observations, and a wildlife monitor whose job it was to locate all key animals on a regular basis. Each method is described in more detail below.

Field guide observations

The SGR is an eco tourism reserve with photographic safaris being the primary objective. Game drives typically lasted about four hours and on average eleven (range 3 – 22) game drive vehicles traversed the reserve daily in the early morning and late afternoon. An experienced field guide conducted each game drive and maintained radio contact with other field guides and the base station where a stand-by guide recorded all sightings, locations and

kills. Although the focus of each drive was determined by the interests of the guests, sightings of the large predators were a high priority and thus the field guides were an important source of records. A number of previous studies have successfully used carefully collected data from field guides (Radloff & du Toit, 2004; Bissett, 2007). Field guides were given regular training to ensure the collection of a standardized data set and particular emphasis was placed on ensuring that all field guides were able to consistently assign kills to the correct age class. The information recorded for each kill was as used by Rapson (2004) and Bissett (2007) in similar studies on nearby reserves, and included the date and location, identification of the predator, vegetation type and the species, age and sex of the prey species killed. Age categories were defined as follows: a juvenile was a small dependant calf; a sub adult was a young, independent animal but not fully grown and not sexually mature; and an adult was a full grown, sexually mature animal. It is accepted that data collected from game drives will be biased to kills of larger prey species because the predators will spend more time at the kill and thus be more easily located on such kills (Owen-Smith & Mills 2008a). One of the few ways to balance this bias is to follow a selected animal or group and record all kills made over a period of time. Such periods of continuous observation were undertaken and are described in Chapter 4.

Wildlife monitor

The SGR had a wildlife monitor whose daily function was to monitor all key species on the reserve, including predators. Radio telemetry was used when available and other predators were located in cooperation with the field guides. The wildlife monitor was responsible for collecting, consolidating and recording all predator sightings and kills.

Wilderness area

The presence of a wilderness area in the most northern part of SGR resulted in difficulties in monitoring as no motorized transportation was permitted in this area (2651 ha). When any of the study animals could not be located in the north (specifically the northern pride of lions and the wild dogs) the wildlife monitor would walk into the wilderness area to get a rough location via radio telemetry. Fewer kills were thus recorded in the wilderness area.

Prey abundance

Game Count Methods in SGR

Road game counts were conducted in the first half of the study (2001-2004) and helicopter-based game counts were used from 2005 to 2007.

Road Counts:

The reserve was divided into four sections with clear boundaries. Four vehicles with two observers on each vehicle were used to ensure the whole reserve was counted in its entirety on that day. Plains game such as zebra, springbok, blesbok and black wildebeest were counted *in situ* on the open plains while for the forest ungulates in the dense vegetation 'beaters' were used to chase animals out of the thickets (specifically kudu and bushbuck) and counters were positioned on roads and old cutlines to count the animals that were being chased out of the thickets. A representative sample of the various vegetation types where counted in this manner and the results extrapolated for each vegetation type. Each of the above methods was repeated three times per section.

For the plains game, the total recorded counts per species for each of the four reserve sectors were combined to give the absolute count for each repetition. The average of the three repetitions per species was taken as the final game count figure. For the forest ungulates, as well as the other browser species, the average of the three 'beats' per species, per vegetation type and area size were taken and extrapolated into the total area per vegetation type. Counts were conducted once a year during the spring months. Counts were conducted in early mornings from 6:00 to 9:00 and again from 16:00 to 18:00.

Helicopter Counts:

The total count was done from a four seater helicopter (Robinsons 44) with the pilot, a data capturer and two observers (where possible the same pilot, data capturer and observers were used throughout the study). Counts were done from a height of 30-50 m above the ground and the flying speed was approximately 60 km/hr, increasing to 90 km/hr in the more open areas. A predefined flight path was flown east to west with transects 300 m apart and therefore animals within 150 m wide strips were counted on either side of the helicopter. The count was conducted over two consecutive days (weather dependent). Counts were done in

October so that an assessment of the survival rate of the previous breeding season could be made. Counting started early in the morning and when necessary continued into the afternoon i.e. 6:00-15:30. Observer fatigue was minimized by taking breaks every two hours. All observations were relayed to the data capture and recorded on a GeoXM Trimble (California, USA) GPS with Cybertracker (RSA) software.

There are numerous direct and indirect methods of assessing the abundance of large mammals (Eberhardt, 1978). Each has its own biases and each is appropriate in particular circumstances and to answer particular questions. For example, aerial counts are known to underestimate the true number and the extent of the underestimation varies with species and habitat (Eltringham, 1979). Decisions as to which method to use are then made based on the information required (e.g. absolute number or change in population size), the vegetation type (open grass land or thicket); the species being counted (highly detectable and diurnal or nocturnal) and available resources (Bowland & Perrin, 1994; Mayle, Peace & Gill, 1999). In the case of SGR, the species ranged from easily counted plains game to less detectable thicket dwelling species such as bushbuck. The information required was a reliable estimate of numbers so that trends in population size could be established. The change in game count method in the middle of the study was unfortunate but was a management decision that could not be changed.

CHAPTER 4: FEEDING ECOLOGY

Introduction

The feeding ecology of individual large mammalian carnivore species has been the focus of attention for many years and numerous papers report the diet of a particular species at a particular site (for example, lions, Pienaar 1969; Power, 2003; cheetahs, Mitchell *et al*., 1965; Purchase & du Toit, 2000; leopards, Bothma & le Riche, 1986; Stander *et al*., 1997; and wild dogs, Creel & Creel, 2002; Radloff & du Toit, 2004). Information from these studies has been collated and synthesized in a number of comparative studies (Carbone *et al*., 1999; Hofmeyr *et al.,* 2003; Sinclair *et al*., 2003; Hayward & Kerley, 2005; Hayward, *et al*., 2006a). While these studies are valuable in that they draw together all the published information for one species, by doing this they tend to mask the temporal and spatial variability that is characteristic of large mammalian predators. A smaller number of studies have taken an ecosystem function approach and have studied the feeding ecology of members of the carnivore guild at one site over time (Schaller, 1972; Mills, 1984; Radloff & du Toit, 2004; Owen-Smith & Mills, 2008a,b). These studies build on the information from the earlier autecological work and make the first contributions to understanding how these ecosystems and food webs are structured.

Large mammalian predator-prey systems in the African savannah are complex (Mills, 1991; Mills & Schenk, 1992). They comprise multiple predator and prey species of varying sizes, and body size of both predator and prey is accepted as an important structuring force in these systems (Woodward *et al*., 2005; Owen-Smith & Mills, 2008b; Hayward & Kerley, 2009). At its simplest level, predator size affects maximum prey size, and larger predator species capture larger prey than smaller predators (Gittleman, 1985; Vezina, 1985; Carbone *et al*., 1999; Radloff & du Toit, 2004; Owen-Smith & Mills, 2008b). Most predators, irrespective of body size will kill similarly small prey items, and as a result, larger predators typically have access to a greater diversity of prey (Gittleman, 1985; Cohen *et al*., 1993; Radloff & du Toit, 2004; Owen-Smith & Mills, 2008b). This predator body size effect is refined by aspects of the behaviour of the predator, and group hunting results in a relatively small species such as the wild dog being able to capture larger than expected prey items (Creel & Creel, 2002). In lions and cheetahs, larger prides and male coalitions capture larger prey items than do smaller

groups (Schaller, 1972; Stander, 1992; Caro 1994; Funston *et al*., 2001). Within the mammalian carnivores, there are two functional feeding groups based on predator body size (Radloff & du Toit, 2004). Predator species with a body mass below 21.5 kg tend to kill prey weighing less than 45% of their mass while those predators that weigh more than 21.5 kg tend to kill larger prey, equal to or greater than their mass (Carbone *et al*., 2007). In general, the smaller predators feed on invertebrates and small vertebrates (reptiles, birds and small mammals) and switch between insectivory, omnivory and carnivory, while the larger predators kill mostly large mammals but also feed on smaller vertebrates (Carbone *et al*., 2007). In the present study, all the predators weigh more than 21.5 kg and thus focused exclusively on members of one of the functional groups.

The diet of predators in a multiple predator, multiple prey system is shaped by a range of biotic and abiotic factors. As mentioned above, the body size of predator and prey is an important biotic component that also affects the structure of the food web (Owen-Smith & Mills, 2008b). Prey size is not just a species level characteristic but varies with the age and sex of the prey and the predator. For example, in the Kruger National Park, lions select adult blue wildebeest and juvenile zebra (Mills & Shenk, 1992) while in Etosha, lions select juvenile springbok (Stander, 1992). Cheetahs select adult female Thompson's Gazelle in the Serengeti (Kruuk & Turner, 1967), male springbok in the Kalahari (Mills, 1984) and male impala in the Kruger National Park (Mills *et al*., 2004). The selective killing of animals of a particular age or sex is likely to be due to differences in their accessibility to predators. Thus, young and old animals may be more vulnerable than intermediate aged animals and differences in behaviour, group size or armament of one sex over the other will result in one sex being more vulnerable than the other.

Prey abundance is an important factor that shapes diet and many studies have reported that a particular predator kills the most abundant appropriately sized prey species in the area (Skinner & Chimimba, 2005 for review; Radloff & du Toit, 2004). Prey abundance does not directly equate to availability because abundance is influenced by aspects of the species' behaviour such as time of activity and habitat selection. For example, leopards may consume more bushbuck and grey duiker than the more abundant springbok and steenbok (Hayward *et al*., 2006b), but the selection of bushbuck reflects a match in habitat use by predator and prey and not prey abundance per se.

Vulnerability, mentioned above in relation to age and sex, is an important factor that shapes diet and vulnerability varies between and within prey species. A medium sized prey species such as the warthog, which burrows and is armoured with tusks, will be less vulnerable than a similar sized antelope such as the duiker, and this is seen in the diet of cheetahs which avoid warthogs and select springbok (Hayward *et al*., 2007d). Within a species, vulnerability will vary with age and also body condition and, in drought years, some species will become more vulnerable than others. In the Kruger National Park, buffalo are more susceptible to drought than wildebeest and zebra, and lions switch to killing buffalo in drought years (Owen-Smith & Mills, 2008a). The behaviour of the predator (solitary or group hunting) and prey (group size and habitat choice) will also influence diet. In the Kalahari, springbok form large mixed age and sex groups while territorial males are isolated (Jackson *et al.,* 1993). It is likely that the selection of the males by cheetahs (Mills, 1984) is a function of their relatively higher vulnerability.

The presence of other large predators in the area will affect diet in a number of ways. Larger predators may displace smaller guild members from preferred habitats with a particular set of possible prey items, to less preferred habitats with a different set of possible prey (Mills & Gorman, 1997). In this way, interference competition may affect diet. Smaller predator species are also susceptible to kleptoparasitism and this is likely to shape diet (Hayward, *et al*., 2006c). Cheetahs lose as much as 12% of their kills to lions and spotted hyaenas (Kruuk, 1972; Schaller, 1972) and in Namibia, where there are few or no kleptoparasites, cheetahs kill larger prey than where kleptoparasites are present (McVittie, 1979). It is argued that if the likelihood of losing prey to a kleptoparasite is high, then smaller prey will be selected (Hayward *et al*., 2006c).

Finally, large predators may exert exploitative competitive forces by preying on smaller prey species that are killed by the smaller predators (Owen-Smith & Mills, 2008b). Since many of the factors that shape diet will vary in time and space so too does carnivore diet and there are many examples of this in the literature. Where some prey species migrate and others do not such as in Chobe and the Serengeti, diet changes on a predictable, seasonal basis (Schaller, 1972; Viljoen, 1993, 1997). Where prey vulnerability changes with change in climate, as in the Kruger National Park, so diet changes (Owen-Smith & Mills, 2008a). Where the species composition of available prey species differs, so does diet and while cheetahs on Phinda kill

mostly nyala, in the Kruger National Park it is impala and reedbuck (Pienaar, 1969; Hunter, 1998).

The Optimal Foraging Theory (OFT; MacArthur & Pianka, 1966) provides a theoretical framework which can be used to understand feeding ecology. OFT predicts that the diet of generalist predators will vary with the relative abundance of one or more alternative prey species (Pyke *et al*., 1977). These changes in food abundance may track seasonal climatic changes as is seen in some small carnivores (Carss *et al*., 1998; Begg *et al*., 2003) but also in the Serengeti where some prey species of lions migrate on a seasonal basis (Schaller, 1972). Or the changes in food abundance may be part of a longer cycle such as the rodent cycles in the northern hemisphere (Hanski *et al*., 2001). It is relatively easy to test the predictions of OFT and examine the impact of predation on population dynamics of invertebrates and small vertebrates, it is far less easy to do the same with large mammalian predators. Experimental manipulation of food availability is very difficult in large mammalian systems and thus, data are collected through long term observations (Estes, 1994; Radloff & du Toit, 2004; Miller *et al.,* 2006; Owen-Smith & Mills, 2008a,b). The reintroduction of large mammalian predators to SGR initiated a series of natural experiments and created the opportunity to study the feeding ecology of members of the large carnivore guild.

The translocation of large carnivores and establishment of new game reserves is a common conservation practice (Rowe-Rowe, 1992; Hofmeyr & van Dyk, 1998; Hofmeyr *et al*., 2003, Hayward *et. al*, 2007c) the success of which requires a sound understanding of feeding ecology, trophic linkages and carrying capacities for predators. The potential for large carnivores to influence the population dynamics of prey species is exaggerated on small enclosed game reserves (Fryxell *et al*., 1988) as there may be limited refuges from predation or the chance to disperse from high concentrations of predators, and no chance of natural supplementation of numbers by immigration. Therefore it is particularly important to understand the predator/prey dynamics and the factors affecting predator diet on such reserves. In the absence of such knowledge, small, enclosed reserves are typically managed intensively with large scale introductions and removals of both predator and prey in an attempt to balance an unnatural closed system. These interventions represent a form of adaptive management and can prove to be very costly and disruptive. With a proper

understanding of predator-prey dynamics, it may be possible to manage less intensely and allow some more natural processes such as prey switching to occur.

The general aims of this aspect of the study were twofold, to contribute to the basic understanding of the factors that affect the diet in the members of the large carnivore guild on a closed reserve and to use these data to improve management of large carnivores on small enclosed reserves, particularly the re-introduction of such species.

A particular focus was on the relationship between body size (predator and prey) and diet, and the data from the study would allow me to test the hypothesis that larger predators have more diverse prey, have a greater mean prey size and preferentially kill larger prey species than smaller predators. The occurrence of group living predators and solitary species allowed me to test the effect of group size on diet, and the hypothesis that members of groups will have a greater mean kill mass than solitary predators.

Natural changes in prey abundance at inter and intra-specific levels, and management controlled reintroductions of prey species would provide an opportunity to test the OFT and whether or not prey switching occurs.

Methods

Collection of base line data for feeding biology

Efforts were made to locate and observe the behaviour and diet of all the large predators at least once a day and records came from three sources; the field guides, a set of continuous observations, and a wildlife monitor whose job it was to locate all key animals on a regular basis. The methods of field guides and wildlife monitor are fully explained in Chapter 3 while the continuous observation method is described in more detail below.

Continuous observations

Continuous observations were conducted (24 hours per day for 14 days) in summer and again in winter for select individuals of each predator species. The southern pride of lions, a female cheetah with three cubs and a female leopard were selected to represent the carnivore guild. Continuous observations were not carried out on the wild dogs because in the summer they

were denning in the wilderness area and it was not possible to follow them on foot. They had been removed from the SGR by winter. To enable continuous monitoring, a radio collar was fitted to the adult females of each species. The continuous observations were carried out by the researcher and a team of field guides in eight-hour shifts. The researcher was permanently available should the location of the predator be temporarily lost. Monitoring was done at the furthest distance possible that still allowed for an unhindered view of the target while reducing the likelihood of affecting the natural hunting behaviour of the predator. This distance varied according to thickness of the vegetation. Spot lights were used rarely and only to maintain contact with the predator when not actively hunting. Where necessary, and specifically for the leopard, kills that were made in the thicket, were located after the predator had left the area by walking in to the kill. Data collected for each kill were the same as collected by the field guide (Chapter 2).

The numbers of kills for each predator were not directly comparable since data were collected over different periods. Monitoring of the lions occurred throughout the study while that of the leopards commenced in 2003, monitoring of the wild dogs and cheetahs commenced in 2004 and the wild dogs were removed from the reserve for management reasons at the end of 2006.

General description of the diet of the members of the large carnivore guild

The general description of the diet of the members of the large carnivore guild of SGR is a summary of the kills recorded during the study period for each large predator species. The two lion prides were analyzed independently but the records for the other species did not allow any further sub-division by sex, group size or female reproductive status, and data for leopards and cheetahs have been pooled for each species. For each predator, a prey list was developed which showed the number of each prey species killed and the total corrected mass of the prey sizes killed. Body mass of prey species was derived from Meissner (1982), Bothma (2002), Skinner & Chimimba (2005) and Radloff & du Toit (2004) and was corrected for age. The mass of sub adults was calculated as the mass of an adult male or female multiplied by a factor of 0.7 while the factor for juveniles was 0.3 (Radloff & du Toit, 2004). Where the age and, or sex of the prey were unknown the mass was recorded as ¾ of that of an adult female (Owen-Smith, 1988). The use of corrected mass gives a more accurate measure of kill size and corrected mass was used in all analyses of prey size.

Daily food consumption

Data from the continuous observations were used to calculate daily mean food consumption. The corrected mass of each prey item was calculated as described above and further corrected to take into account the proportion of the carcass that was edible. Correction factors were derived from Blumenschine & Caro (1986), Viljoen (1977) and Carbone *et al*. (2005) and I generated a value for each prey item referred to as the edible biomass. To accommodate differences in the number of predators and their sex and age, standard (female equivalent unit) FEQ were used (Bertram, 1973). An adult female lion was 1.0 FEQ; adult male lion 1.5 FEQ; sub adult lion of either sex (two to three years of age) 1.0 FEQ; large cubs (one to two years) 0.75 FEQ; small cubs 0.3 FEQ. The adult female cheetah and leopard were 1 FEQ each, and the same ratios were applied to other age categories.

Analyses of the predator-prey body mass relationships

Average body masses per predator were from the Eastern Cape for cheetahs (Bissett, 2007), the Kruger National Park for lions (Smuts *et al*., 1980) and wild dogs (Gorman *et al*., 1998) and from the Sabi Sands for leopards (Radloff & du Toit, 2004). The sources for prey mass are given above.

Analyses of prey diversity in the diet

Using the total predation lists for each predator, two measures of prey diversity were calculated. Prey richness was simply the total number of prey species killed while the 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.

Analyses of prey preference

Prey preferences were calculated using the total predation list for each predator and the mean abundance of each prey species. The total predation list was used rather than an annual list because it is very likely that in the early years after re-introduction factors such as prey and predator naivety may have affect predation. In calculating prey abundance, only those species that were killed by the predator were included. The prey preference values were determined using Jacobs' Index:

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

For each prey species, r is the proportion of all kills made by a predator and p is the proportional abundance of that prey species (Jacobs, 1974).

Jacobs' Index may range from +1 which indicates maximum preference to -1 which indicates maximum avoidance. Jacob's Index was selected from a range of preference indices because it has been used in a number of studies on the diet of large mammalian carnivores and because it minimizes the problems associated with many other preference indices (Chesson, 1978; Strauss, 1979; Hayward & Kerley, 2005). The accuracy of all preference indices depends on the accuracy of the kill list and the accuracy of the abundance data. Although the continuous observations should minimize missed kills, the records from the field rangers will always be incomplete, and missed kills will result in an error in the preference index. Similarly, it is quite unlikely that game counts will record all individuals of each species and undercounting will result in an over estimation of the preference index. For this reason it is important not to over interpret the Jacobs' Indices, and values below -0.3 were interpreted as avoidance; values between -0.3 and 0.3 as indicating that the prey was utilized according to its abundance, and values greater than 0.3 as indicating a preference for a particular prey species (Bissett, 2007). To allow an analysis of the effect of prey size on prey preference at a species level (see Radloff & Du Toit, 2004), prey species were categorized as either large (>65 kg), medium sized (30-65 kg) or small (<30 kg; after Hunter, 1998).

Statistical Analyses

The mean prey mass from the total predation list was compared to that from the continuous observations using Student's t-tests.

The proportions of each prey species in the total predation list and from the continuous observations were compared using χ^2tests.

The relationships between predator size and prey size and between predator size and prey species richness were examined using linear regression analyses.

The effect of prey size category (small, medium and large) on Jacobs' Index was examined separately for each predator using ANOVA.

The effect of predator species on the mean size of kudu killed was explored using ANOVA.

Where required, ANOVAs were followed by appropriate post hoc tests.

Linear regressions were used to examine the changes in numbers of warthog and kudu kills with time and a Pearson's Correlation analysis was used to examine the changes in mean prey mass with time.

χ^2 analyses were used to compare the proportions of prey species in the kill lists before and after introduction of black wildebeest.

An ANOVA was used to examine the effect of adult prey size category on the percentage of juveniles of the species killed by cheetahs.

A Student's t-test was used to compare the mean prey mass of cheetahs during the lambing season with the mean prey mass for the whole study.

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).

Results

General description of the diet of members of the large carnivore guild

Between 2001 and 2007, 1349 kills of 22 prey species were recorded for members of the large carnivore guild. This included 880 kills by lions (65% of all kills), 82 kills by leopards (6.1% of all kills), 185 kills by cheetahs (13.7% of all kills) and 202 kills by wild dogs (15% of all kills; Tables 4.1 – 4.6).

Lions:

Lions killed 22 different prey species of which four constituted 65.4% of all recorded kills and 72.2% of the total prey mass (Table 4.1). The average corrected prey mass for all recorded kills was 119.9 ±109.7 kg (range 4 – 960 kg) (Table 4.7). The diets of the two prides were similar. Both killed 19 species, and the mean corrected prey mass was 118.9 kg ± 90.8 kg (weight range of 766 kg) for the Northern Pride and 121.0 kg ±127.3 kg (weight range of 953.8 kg) for the Southern Pride. The prides preyed on 16 prey species in common with three species that were unique to one or other pride (Tables 4. 2 & 4.3). The five species that made the greatest contribution to the corrected mass of prey killed (kudu, eland, black wildebeest, warthog and zebra) were the same for the two prides (Tables 4.2 & 4.3).

Table 4.1. The prey consumed by both prides (all lions) in SGR for the period 2001 to 2007. Mass of kills is the total corrected mass for that prey species. n is the total number of kills per prey species killed between 2001 and 2007 while n% is n as a percentage of the total kills for all prey species. Mass (kg) is the total mass per prey species killed between 2001 and 2007 and mass % is mass (kg) as a percentage of the total mass killed for all prey species.

species	n	n%	mass (kg)	mass %
kudu	204	23.2	37156.0	34.9
eland	33	3.8	14266.0	13.4
black wildebeest	132	15.0	13721.0	12.9
warthog	206	23.4	11759.1	11.0
plains zebra	31	3.5	6600.5	6.2
gemsbok	22	2.5	3693.0	3.5
red hartebeest	34	3.9	3636.0	3.4
giraffe	6	0.7	3558.0	3.3
waterbuck	19	2.2	2759.2	2.6
bushbuck	60	6.8	2737.8	2.6
blesbok	40	4.5	2546.6	2.4
ostrich	17	1.9	1890.0	1.8
impala	26	3.0	1079.3	1.0
bushpig	11	1.3	423.0	0.4
grey duiker	17	1.9	319.8	0.3
springbok	10	1.1	314.3	0.3
porcupine	7	0.8	67.8	0.1
aardvark	1	0.1	45.5	0.0
baboon	1	0.1	15.0	0.0
mountain reedbuck	1	0.1	8.1	0.0
scrub hare	1	0.1	4.0	0.0
monitor lizard	1	0.1	4.0	0.0
total	880	100.0	106604.0	100.0

Table 4.2. The prey consumed by the Northern lion Pride in SGR. Mass of kills is the total corrected mass for that prey species. n is the total number of kills per prey species killed between 2001 and 2007 while n% is n as a percentage of the total kills for all prey species. Mass (kg) is the total mass per prey species killed between 2001 and 2007 and mass % is mass (kg) as a percentage of the total mass killed for all prey species.

species	n	n%	mass (kg)	mass %
kudu	73	17.6	14056.0	27.4
eland	24	5.8	10836.0	21.1
warthog	134	32.3	7315.3	14.3
black wildebeest	64	15.4	6617.8	12.9
plains zebra	14	3.4	2742.5	5.3
giraffe	4	1.0	2500.0	4.9
gemsbok	11	2.7	1855.5	3.6
red hartebeest	15	3.6	1575.0	3.1
bushbuck	28	6.7	1389.0	2.7
blesbok	16	3.9	1036.0	2.0
impala	16	3.9	678.0	1.3
waterbuck	2	0.5	319.3	0.6
grey duiker	7	1.7	115.7	0.2
bushpig	2	0.5	1080.0	0.2
ostrich	1	0.2	90.0	0.2
aardvark	1	0.2	45.4	0.1
springbok	1	0.2	23.3	0.0
baboon	1	0.2	15.0	0.0
mountain reedbuck	1	0.2	8.1	0.0
total	415	100.0	51325.9	100.0

Table 4.3. The prey consumed by the Southern lion Pride in SGR. Mass of kills is the total corrected mass for that prey species. n is the total number of kills per prey species killed between 2001 and 2007 while n% is n as a percentage of the total kills for all prey species. Mass (kg) is the total mass per prey species killed between 2001 and 2007 and mass % is mass (kg) as a percentage of the total mass killed for all prey species.

species	n	n%	mass (kg)	mass %
kudu	131	28.2	23100.0	41.8
black wildebeest	67	14.4	7103.3	12.8
warthog	72	15.5	4443.8	8.0
plains zebra	17	3.7	3858.0	7.0
eland	8	1.7	3430.0	6.2
waterbuck	17	3.7	2440.0	4.4
red hartebeest	19	4.1	2061.0	3.7
gemsbok	11	2.4	1837.5	3.3
ostrich	16	3.4	1800.0	3.3
blesbok	24	5.2	1510.6	2.7
bushbuck	32	6.9	1348.8	2.4
giraffe	2	0.4	1058.0.	1.9
impala	10	2.2	401.0	0.7
bushpig	9	1.9	315.0	0.6
springbok	9	1.9	291.0	0.5
grey duiker	12	2.6	204.5	0.4
porcupine	7	1.5	67.8	0.1
scrub hare	1	0.2	4.0	0.0
monitor lizard	1	0.2	4.0	0.0
total	465	100.0	55278.6	100.0

Leopards:

A total of 15 prey species were consumed by leopards (Table 4.4). More than one third of all kills were of bushbuck and these comprised 30% of the corrected mass of all kills. No other species made up more than 10% of prey but kudu and gemsbok together represented 27.9% of the corrected mass of all kills (Table 4.4). The mean corrected mass of the prey was 45.5 ± 41.2 kg and the prey mass range was 224 kg (Table 4.7).

Table 4.4. The prey consumed by the leopards in SGR. Mass of kills is the total corrected mass for that prey species. n is the total number of kills per prey species killed between 2001 and 2007 while n% is n as a percentage of the total kills for all prey species. Mass (kg) is the total mass per prey species killed between 2001 and 2007 and mass % is mass (kg) as a percentage of the total mass killed for all prey species.

species	n	n%	mass (kg)	mass %
bushbuck	31	37.8	1201.2	30.5
kudu	8	9.8	660.0	16.7
gemsbok	4	4.9	442.5	11.2
eland	2	2.4	366.0	9.3
blesbok	5	6.1	301.5	7.6
warthog	4	4.9	242.5	6.1
plains zebra	1	1.2	202.5	5.1
impala	5	6.1	185.3	4.7
grey duiker	7	8.5	128.5	3.3
waterbuck	1	1.2	94.3	2.4
vervet monkey	7	8.5	56.0	1.4
bushpig	1	1.2	27.0	0.7
porcupine	2	2.4	23.4	0.6
scrub hare	2	2.4	8.0	0.2
guinea fowl	2	2.4	6.0	0.2
total	82	100.0	3944.7	100.0

Cheetahs:

Cheetahs killed 14 prey species, four of which accounted for 64.8% of the total kills and 70% of the corrected mass of all kills (Table 4.5). Duiker were killed relatively frequently but because of their small size, the contribution to the corrected mass of the kills was low (Table 4.5). The mean corrected mass of the prey was 43.10 ± 26.6 kg with a prey mass range of 178 kg (Table 4.7).

Table 4.5. The prey consumed by the cheetahs in SGR. Mass of kills is the total corrected mass for that prey species. n is the total number of kills per prey species killed between 2001 and 2007 while n% is n as a percentage of the total kills for all prey species. Mass (kg) is the total mass per prey species killed between 2001 and 2007 and mass % is mass (kg) as a percentage of the total mass killed for all prey species.

species	n	n%	mass (kg)	mass %
impala	54	29.2	1992.8	24.9
blesbok	28	15.1	1470.7	18.4
kudu	22	11.9	1392.0	17.4
bushbuck	16	8.6	741.0	9.3
red hartebeest	8	4.3	696.0	8.7
grey duiker	22	11.9	371.7	4.6
black wildebeest	8	4.3	357.1	4.5
springbok	12	6.5	327.1	4.1
eland	1	0.5	183.0	2.3
plains zebra	2	1.1	174.0	2.2
warthog	3	1.6	154.8	1.9
gemsbok	1	0.5	67.5	0.8
mountain reedbuck	3	1.6	50.1	0.6
scrub hare	5	2.7	17.5	0.2
total	185	100.0	7995.3	100.0

Wild dogs

Wild dogs killed 10 prey species of which four accounted for 88.6% of the total kills and 91.5% of the corrected mass of all kills (Table 4.6). The mean corrected prey mass was 73.5 ± 59.0 kg with a prey mass range of 231.7 kg (Table 4.7).

Table 4.6. The kill record for the wild dogs in SGR. Mass of kills is the total corrected mass for that prey species. n is the total number of kills per prey species killed between 2001 and 2007 while n% is n as a percentage of the total kills for all prey species. Mass (kg) is the total mass per prey species killed between 2001 and 2007 and mass % is mass (kg) as a percentage of the total mass killed for all prey species.

species	n	n%	mass (kg)	mass (%)
kudu	61	30.2	8856.0	59.8
impala	52	25.7	2513.3	17.0
bushbuck	37	18.3	1654.8	11.2
duiker	29	14.4	522.3	3.5
warthog	10	5.0	504.3	3.4
waterbuck	2	1.0	320.0	2.2
red hartebeest	3	1.5	231.0	1.6
blesbok	3	1.5	125.4	0.8
springbok	4	2.0	65.1	0.4
mountain reedbuck	1	0.5	27.0	0.2
total	202	100.0	14819.2	100.

The relationships between predator size and prey size, and between predator size and prey diversity.

The mean corrected mass of prey consumed differed significantly between the predator species (ANOVA; $F_{3,1354} = 51.7$; $P<0.001$). Lions killed significantly heavier prey than all other predators, whilst wild dogs killed significantly larger prey than cheetahs (Tukey post hoc test; $P<0.05$ for both). There was no significant difference in the mean prey weight of leopards and cheetahs. With the exception of the wild dogs, the mean kill size for the predator species was similar to the mass of an adult female of the species. For the wild dogs,

it was 2.9 times the mass of an adult (Table 4.7). The maximum prey mass was far greater than the adult body mass for all predators, with lions killing prey up to 7.7 times their own body mass, leopards 6.1 times, cheetahs 4.3 times and wild dogs 9.5 times (Table 4.7). There was a significant relationship between predator body mass and maximum prey mass (linear regression; r^2 0.95; $F_{1,2} = 38.1$; $P<0.05$; Figure 4.1) but not for mean or minimum prey mass (Mean prey mass, r^2 0.86; $F_{1,2} = 12.8$; $P>0.05$; minimum prey mass, r^2 -0.32; $F_{1,2} = 0.26$; $P>0.05$).

The number of prey species (species richness) killed decreased with decreasing predator size ($r^2 = 0.9$; $F_{1,2} = 18.9$; $P=0.05$; Table 4.8) with the largest predators, lions killing 22 different prey species and wild dog the smallest predator, only killed 10 prey species. Species diversity in the kill lists was lowest for the wild dogs and highest for the lions and cheetahs (Table 4.8) but there was no significant relationship between predator mass and species diversity in the predation lists ($r^2 =0.34$; $F_{1,2} = 1.05$; $P>0.05$).

Table 4.7. Summary of the recorded kills made by the large predator guild in SGR. Mass of the female predator is from Radloff & du Toit (2004). n is the number of kills recorded for each predator. Mass is the mean corrected mass ± 1sd; figures in parentheses are the extremes of the corrected prey mass range.

	female	prey			predator: kill mass ratio	
predator	mass (kg)	n	mass (kg)	range (kg)	mean prey mass	max prey mass
lion	124.0	880	119.9±109.7	956.0 (960–4)	1:1.0	1:7.7
wild dog	25.2	202	73.5±59.0	231.7 (240–7.3)	1:2.9	1:9.5
leopard	37.3	82	45.5±41.2	224.0 (228–3)	1:1.2	1:6.1
cheetah	43.0	185	43.0±26.6	178.0 (183–4)	1:1.0	1:4.3

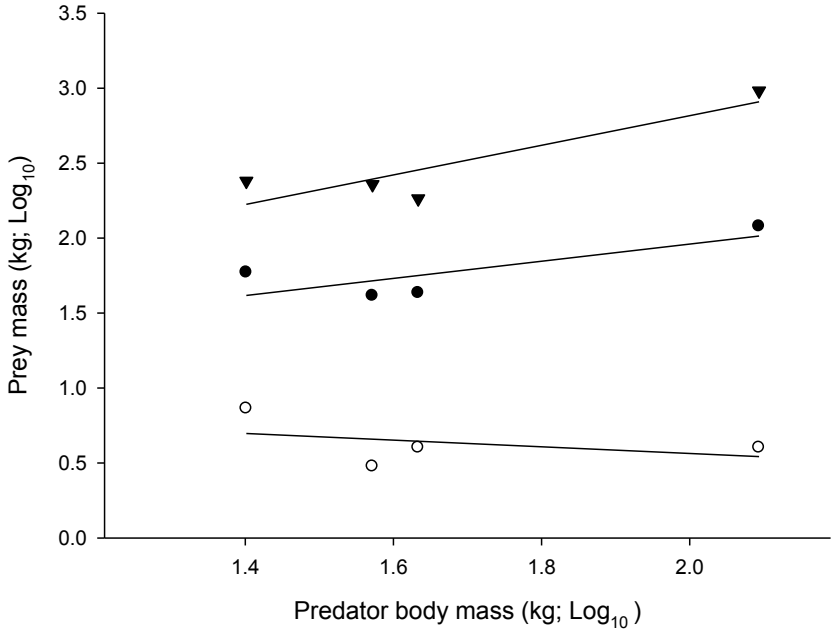


Figure 4.1. Predator – prey body mass relationships. Maximum (solid triangles), mean (solid circles) and minimum (open circles) prey mass is plotted against predator body mass (kg; Log_{10} transformed).

Table 4.8. Summary of the species richness and species diversity in the kill lists of the large predators in SGR.

predator	species richness	species diversity (D)	species diversity (1/D)
lion	22	0.14	6.7
leopard	15	0.17	5.8
cheetah	14	0.15	6.9
wild dog	10	0.21	4.7

Comparison of kill records from continuous observations and from field guides

Lions: During the 28 days of continuous monitoring, the Southern pride of lions made 12 kills of eight different species (Table 4.9). The total corrected prey mass was 1295.7 kg and the mean corrected mass of the kills was 108.0 ± 93.5 kg with a range of 259 kg. There was no significant difference in mean corrected prey mass from the continuous observations and from the total kill list (Student's t-test; $t = 0.4$, d.f. = 475, $p>0.05$). The two observation methods generated different rankings and proportions for the prey species ($\chi^2 = 134.8$; df 21; $P<0.05$; Table 4.9). Kudu and eland, which comprised 23% of all kills in the total kill list, comprised a smaller percentage in the continuous observations, while porcupine and scrub hare represented larger percentages (Table 4.9). Black wildebeest and warthog were ranked highly by both observation methods.

Table 4.9. Comparison of the kill lists for lions from the two observation methods, the total predation list and the continuous observations.

	total predation list		continuous observation	
prey species	no. kills	kills %	no. kills	kills %
warthog	206	23.4	2	16.7
kudu	204	23.2	1	8.3
black wildebeest	132	15.0	2	16.7
bushbuck	60	6.8	0	0.0
blesbok	40	4.5	0	0.0
red hartebeest	34	3.9	1	8.3
eland	33	3.8	0	0.0
plains zebra	31	3.5	1	8.3
impala	26	3.0	0	0.0
gemsbok	22	2.5	2	16.7
waterbuck	19	2.2	0	0.0
ostrich	17	1.9	0	0.0
grey duiker	17	1.9	0	0.0
bushpig	11	1.3	0	0.0
springbok	10	1.1	0	0.0
porcupine	7	0.8	2	16.7
giraffe	6	0.7	0	0.0
aardvark	1	0.1	0	0.0
baboon	1	0.1	0	0.0
mountain reedbuck	1	0.1	0	0.0
scrub hare	1	0.1	1	8.3
monitor lizard	1	0.1	0	0.0
total	880	100.0	12	100.0

Leopards: A single female leopard was selected for the continuous observations. For the winter observations, she was solitary however for the summer observations a young cub was present. During the four weeks of continuous follows, eight kills were recorded of five prey species (Table 4.10). The total corrected mass was 239.4 kg with a mean corrected prey mass of 29.9 ± 24.7 kg and a range of 72.6 kg. There was no significant difference in mean corrected prey mass from the continuous observations and the total kill list (Student's t-test; t = 1.1, d.f. = 88, p >0.05). There was no significant difference in the proportions of the species killed in the total kill list and as recorded in the continuous observations (χ^2 =11.9; df, 15; P>0.05). Bushbuck and kudu were the most important prey species in both kill lists and three species (vervet monkey, scrub hare and guinea fowl) made up a greater percentage of the kills in the continuous observations than in the total kill list (Table 4.10).

Table 4.10. Comparison of the kill lists for leopards from the two observation methods, the total predation list and the continuous observations.

	total predation list		continuous observations	
prey species	no. kills	kills (%)	no. kills	kills (%)
bushbuck	31	37.8	3	37.5
kudu	8	9.8	2	25.0
grey duiker	7	8.5	0	0.0
vervet monkey	7	8.5	1	12.5
blesbok	5	6.1	0	0.0
impala	5	6.1	0	0.0
gemsbok	4	4.9	0	0.0
warthog	4	4.9	0	0.0
eland	2	2.4	0	0.0
porcupine	2	2.4	0	0.0
scrub hare	2	2.4	1	12.5
guinea fowl	2	2.4	1	12.5
plains zebra	1	1.2	0	0.0
waterbuck	1	1.2	0	0.0
bushpig	1	1.2	0	0.0
total	82	100.0	8	100.0

Cheetahs: A single female cheetah with two sub adult cubs was selected for the continuous follow. During this period 17 kills were recorded comprising six different prey species (Table 4.11). The mean corrected mass for kills was 22.9 ± 26.2 kg with a range of 79 kg and this was significantly lower than that from the total kill list (Student's t-test; t = 3.1, d.f. = 200, p < 0.01). There was no significant difference in the proportions of species killed using the two methods (χ^2 16.6; df 14; P>0.05). Of the four top prey species recorded in the continuous observations, three were shared with the top four from the total kill list (Table 4.11). Impala lambs made up 53% of the total kills but only accounted for 12% of the 377 kg total corrected mass of prey killed.

Table 4.11. Comparison of the kill lists for cheetahs from the two observation methods, the total predation list and the continuous observations.

	total predation list		continuous observation	
prey species	no. kills	kills (%)	no. kills	kills (%)
impala	54	29.2	9	52.9
blesbok	28	15.1	2	11.8
kudu	22	11.9	0	0.0
grey duiker	22	11.9	2	11.8
bushbuck	16	8.6	0	0.0
springbok	12	6.5	0	0.0
red hartebeest	8	4.3	1	5.9
black wildebeest	8	4.3	0	0.0
scrub hare	5	2.7	2	11.8
warthog	3	1.6	1	5.9
mountain reedbuck	3	1.6	0	0.0
plains zebra	2	1.1	0	0.0
eland	1	0.5	0	0.0
gemsbok	1	0.5	0	0.0
total	185	100.0	17	100.0

Daily food consumption by members of the large carnivore guild

Using data from the continuous observations reported above, the daily consumption was calculated for each of the large predators. The southern lion pride, which consisted of an adult female, sub adult female, two sub adult males and two cubs (4.6 FEQs) made 12 kills during the 28 days with a total edible biomass of 790.4 kg and a daily intake of 6.1 kg/FEQ/day. The female leopard (solitary in winter and with a cub in summer; 1.15 FEQs) made eight kills with a total edible biomass of 146.0 kg and a daily intake of 4.5 kg/FEQ/day. The female cheetah and cubs (2.1 FEQs) made 17 kills with a total edible biomass of 230.0 kg and a daily intake of 3.9 kg/FEQ/day.

Prey preference of the members of the large carnivore guild

Lions preferred ostrich, black wildebeest and warthog and avoided baboon, bushbuck, impala and springbok (Table 4.12). There was a significant effect of prey size (size of adult) on Jacobs' Index, which was significantly lower for small prey species than medium and large sized species (ANOVA; $F_{2,4} = 8.3$; $P<0.05$; Table 4.13). There was no significant difference in Jacobs' Index for medium and large prey species (Tukeys post hoc test; $P>0.05$). Of the five important prey species (those that comprised the greatest proportion of kill mass; Table 4.1), kudu, eland and zebra were neither preferred nor avoided, while wildebeest and warthog were preferred/avoided/utilized according to abundance (Table 4.12).

Table 4.12. The prey preferences (Jacobs' Index) for lions. The prey abundance and numbers of kills are means for 2005-2007 from the total kill list.

		prey abundance		kills/year		
species	prey size	number	proportion	number	proportion	Jacobs' Index
ostrich	M	3	0.00	1.0	0.01	0.77 †
black wildebeest	L	139	0.05	26.3	0.20	0.55 †
warthog	M	382	0.15	45.7	0.34	0.30 †
eland	L	52	0.02	4.5	0.03	0.25 *
gemsbok	L	54	0.02	4.7	0.03	0.25 *
waterbuck	L	47	0.02	3.0	0.02	0.10 *
giraffe	L	26	0.01	1.3	0.01	-0.01 *
plains zebra	L	163	0.06	8.0	0.06	-0.03 *
grey duiker	S	43	0.02	2.0	0.01	-0.05 *
kudu	L	351	0.13	15.3	0.11	-0.11 *
red hartebeest	M	130	0.05	5.3	0.04	-0.12 *
bushpig	M	83	0.03	3.0	0.02	-0.17 *
blesbok	M	167	0.06	5.3	0.04	-0.24 *
springbok	S	101	0.04	1.5	0.01	-0.55 ¤
baboon	S	71	0.03	1.0	0.01	-0.58 ¤
bushbuck	S	220	0.08	2.0	0.01	-0.70 ¤
impala	S	575	0.22	4.0	0.03	-0.77 ¤
total		2613	1.00	134.0	1.00	

† = preferred * = eaten in accordance with abundance ¤ = avoided

Table 4.13. Summary of the Jacobs' Indices for small (S), medium (M) and large (L) sized prey species for each predator and the predator guild. Data are means ± 1sd.

	prey size category			
predator	S	M	L	ANOVA
lions	-0.5± 0.28	0.09±0.40	0.14± 0.22	P<0.05
leopards	-0.15± 0.88	-0.99± 0.46	0.11± 0.21	P>0.05
cheetahs	-0.21± 0.37	-0.30± 0.54	-0.36± 0.3	P>0.05
wild dogs	-0.12± 0.6	-0.45± 0.45	-0.12± 0.4	P>0.05
guild	-0.26± 0.53	-0.11± 0.24	-0.04± 0.23	P>0.05

Leopards preferred bushbuck, duiker and gemsbok and avoided bushpig, warthog and impala (Table 4.14). Bushbuck not only had the highest preference index but also made up the greatest proportion (37.8%) of all recorded kills (Table 4.4). There was no significant effect of adult prey species body mass on Jacobs' Index (ANOVA; $F_{2,7} = 0.30$; P>0.05; Table 4.13).

Table 4.14. The prey preferences (Jacobs' Index) for leopards. The prey abundance and numbers of kills are means for 2005-2007 from the total kill list.

		prey abundance		kills/year		Jacobs'
species	prey size	number	proportion	number	proportion	Index
bushbuck	M	220	0.11	6.7	0.40	0.48 †
grey duiker	S	43	0.02	1.0	0.06	0.47 †
gemsbok	L	54	0.03	1.0	0.06	0.37 †
eland	L	52	0.03	0.7	0.04	0.20 *
blesbok	M	167	0.08	1.7	0.10	0.07 *
kudu	L	351	0.18	3.3	0.20	-0.01 *
waterbuck	L	47	0.02	0.3	0.02	-0.09 *
bushpig	M	83	0.04	0.3	0.02	-0.36 ¤
warthog	M	382	0.19	1.0	0.06	-0.55 ¤
impala	S	575	0.29	0.7	0.04	-0.78 ¤
total		1976	1.00	16.7	1.00	

† = preferred * = eaten in accordance with abundance ¤ = avoided

Cheetahs preferred duiker and blesbok and avoided eland, gemsbok, bushbuck, zebra and warthog (Table 4.15). The avoided species were of either large or medium body size however, there was no significant effect of prey body mass on Jacobs' Index (ANOVA; $F_{2,10}$ = 2.5; P>0.05; Table 4.13). The four most frequently killed species (see Table 4.5) were either preferred (blesbok), used according to their abundance (impala and kudu) or avoided (bushbuck).

Table 4.15. The prey preference (Jacobs' Index) for cheetahs. The prey abundance and numbers of kills are means for 2005-2007 from the total kill list.

	prey	prey abundance		kills/year		Jacobs'
species	size	number	proportion	number	proportion	Index
grey duiker	S	43	0.02	5.3	0.11	0.71 †
blesbok	M	167	0.07	7.3	0.15	0.35 †
springbok	S	101	0.04	3.7	0.07	0.27 *
impala	S	575	0.24	17.0	0.34	0.02 *
kudu	L	351	0.14	7.3	0.15	-0.03 *
Black wildebeest	L	139	0.06	2.7	0.05	-0.04 *
Red Hartebeest	M	130	0.05	2.3	0.05	-0.07 *
mountain reedbuck	S	43	0.02	0.7	0.01	-0.14 *
eland	L	52	0.02	0.3	0.01	-0.53 ¤
gemsbok	L	54	0.02	0.3	0.01	-0.53 ¤
bushbuck	M	220	0.09	1.0	0.02	-0.64 ¤
plains zebra	L	163	0.07	0.7	0.01	-0.67 ¤
warthog	M	382	0.16	0.7	0.01	-0.85 ¤
total		2424	1.00	49.3	1.00	

† = preferred * = eaten in accordance with abundance ¤ = avoided

The wild dogs preferred duiker and avoided waterbuck, springbok, mountain reedbuck, red hartebeest, warthog and blesbok (Table 4.16). Of the four most frequently killed species (Table 4.6), the first three (kudu, impala, bushbuck) were killed in accordance to their abundance, while duiker were preferentially selected (Table 4.15). There was no effect of body mass of the prey on Jacobs' Index (ANOVA; $F_{2,7}$ = 0.48; P>0.05; Table 4.13).

Table 4.16. The prey preferences (Jacobs' Index) for wild dogs. The prey abundance and numbers of kills are means for 2005-2007 from the total kill list.

	prey	prey abundance		kills/year		Jacobs'
species	size	number	proportion	number	proportion	Index
grey duiker	S	43	0.02	10.3	0.15	0.75 †
bushbuck	M	220	0.11	12.3	0.18	0.22 *
kudu	L	351	0.13	21.0	0.31	0.18 *
impala	S	575	0.28	17.3	0.25	-0.19 *
waterbuck	L	47	0.02	0.7	0.01	-0.41 ¤
springbok	S	101	0.05	1.3	0.02	-0.43 ¤
mountain reedbuck	S	43	0.02	0.3	0.00	-0.62 ¤
red hartebeest	M	130	0.06	1.0	0.01	-0.63 ¤
warthog	M	382	0.19	3.3	0.05	-0.60 ¤
blesbok	M	167	0.08	0.7	0.01	-0.79 ¤
total		2062	1.00	68.3	1.00	

† = preferred * = eaten in accordance with abundance ¤ = avoided

When the data for the large predator guild were combined, duiker and black wildebeest were preferred while zebra, impala, giraffe, bushpig, mountain reedbuck and baboon were avoided as prey species (Table 4.17). Of the five species that were killed most frequently, kudu, warthog and bushbuck were killed according to their abundance, impala were avoided and black wildebeest preferred (Table 4.17). The most preferred species (grey duiker) made up less than 10% of all kills and only 3% of all available prey species. There was no significant effect of prey size on Jacobs' Index (ANOVA; $F_{2,15} = 0.63$; >0.05; Table 4.13).

Table 4.17. The prey preferences (Jacobs' Index) for the entire large predator guild. The prey abundance and numbers of kills are means for 2005-2007 from the total kill list.

	prey	prey abundance		kills/year		Jacobs'
species	size	number	proportion	number	proportion	Index
grey duiker	S	43	0.02	17.3	0.07	0.61 †
black wildebeest	L	139	0.05	29.0	0.11	0.35 †
kudu	L	351	0.13	47.0	0.18	0.11 *
warthog	M	382	0.14	50.7	0.20	0.10 *
gemsbok	L	54	0.02	6.0	0.02	0.07 *
bushbuck	M	220	0.08	22.7	0.09	0.02 *
ostrich	M	3	0.00	0.3	0.00	0.01 *
blesbok	M	167	0.06	15.0	0.06	-0.05 *
waterbuck	L	47	0.02	4.0	0.02	-0.07 *
eland	L	52	0.02	4.0	0.02	-0.12 *
red hartebeest	M	130	0.05	8.7	0.03	-0.19 *
springbok	S	101	0.04	6.0	0.02	-0.25 *
plains zebra	L	163	0.06	8.7	0.03	-0.30 ¤
impala	S	575	0.22	33.0	0.13	-0.31 ¤
giraffe	L	26	0.01	1.3	0.01	-0.32 ¤
bushpig	M	83	0.03	2.3	0.01	-0.55 ¤
mountain reedbuck	S	43	0.02	1.0	0.00	-0.62 ¤
baboon	S	71	0.03	1.0	0.00	-0.75 ¤
total		2656	1.00	258	1.00	

† = preferred * = eaten in accordance with abundance ¤ = avoided

Predation by the large carnivore guild on kudu

Kudu was an important prey species for all the large carnivores and comprised between 10 and 30% of recorded kills for the different carnivores species (Table 4.19). For the carnivore guild as a whole, 22% of all recorded kills were kudu and 36% of the total corrected mass killed was kudu (Table 4.18). Although kudu were not selected (JI between -0.3 and 0.3) by the individual predators it is likely that the combined predation pressure will influence the population dynamics of the kudu. Based on the data for 2005-2007, 47 kudu were killed each

year from a population of 220. It is the case that kills will have been undercounted and it is likely that the same applies to the abundance but nevertheless, this represents a 20% loss to predation each year.

Table 4.18. The percentage kudus killed relative to all kills and the total corrected mass of kudu kills as a percentage of the total corrected mass of all kills for each of the large predators and for the combined large predator guild.

	lion	wild dog	leopard	cheetah	all predators
% of all kills	23%	30%	10%	12%	21%
% of mass (kg)	35%	60%	17%	17%	36%

Wild dogs and lions killed mostly adult kudu (77.3% and 80% respectively) while leopards killed only sub adult and juvenile kudu and cheetahs only killed juveniles (Table 4.19). This was reflected in a significant effect of predator on mean size of kudu killed (ANOVA; $F_{3,293} = 39.0$; $P<0.001$) and mean kudu kill mass for lions was significantly greater than that of all others (Tukey post hoc test; $P<0.05$ for all). The wild dogs killed significantly larger kudu than cheetahs and leopards ($P<0.05$ for both) and there was no significant difference in size of kudu killed by cheetahs and leopards ($P>0.05$).

Table 4.19. The percentage kudu kills by age class as well as the corrected mass (kg) for kudu killed by each large predator species. The mass of male (M) and female (F) kudu is from (Bissett, 2007).

predator	adult kudu M: 240 kg F: 160 kg	sub adult kudu M: 168 kg F: 112 kg	juvenile kudu M: 72 kg F: 48 kg	corrected mass ± 1sd
lion	80.0	9.8	10.2	182.1±61.2
wild dog	77.3	4.6	18.1	145.2±52.7
leopard	0.0	37.5	62.5	82.5±27.4
cheetah	0.0	0.0	100.0	63.3±21.7

The effect of changes in kudu and warthog numbers on the diet of lions.

This analysis was complicated by the change in game census method which prevented any analysis that required abundance data being based on the full data set. Thus while data on aspects of diet could be compared across the full study, data on prey abundance could only be compared from 2005 to 2007. The abundance of the two species killed most frequently by lions (kudu and warthog; Table 4.1) changed substantially during the second half of the study period (Table 4.20).

Table 4.20. Annual changes in the abundance of warthogs and kudu, the number of warthogs and kudu killed by lions and the mean prey mass. Abundance data are for years during which helicopter based counts were done. The total abundance is the total abundance of all the prey species consumed by lions on the study site; the relative abundance of warthog is the number of warthogs divided by the number of kudu. Data for kills are numbers with percentages in brackets. The total kill is the sum of all kills made by lions in each year.

species	2001	2002	2003	2004	2005	2006	2007
abundance							
kudu	/	/	/	/	334	415	305
warthog	/	/	/	/	251	481	416
total abundance	/	/	/	/	2429	2776	2551
relative abundance of warthog	/	/	/	/	0.75	1.15	1.36
kills							
kudu	36(30)	45(31)	31(33)	46(34)	17(15)	13(13)	16(9)
warthog	4(3)	22(15)	18(19)	28(21)	32(29)	41(39)	65(37)
total	129	147	94	134	112	104	177
ratio of warthog to kudu kills	0.1:1	0.5:1	0.6:1	0.6:1	1.9:1	3.2:1	4.1:1
mean prey mass (kg)	133	132	141	141	124	118	95

The number of kudu declined by 8% from 2005 to 2007, while the number of warthogs increased by 66% (Table 4.20). The total abundance of all prey species of lions in SGR increased slightly from 2005 to 2007 (Table 4.20). Kudu comprised 28% of all lion kills recorded in SGR at the beginning of the study and, from 2001 to 2007, there was a significant decrease in kudu kills (linear regression; $r^2 = 0.58$, $F_{1,5} = 6.9$, $P < 0.05$; Table 4.20; Figure 4.2). Over the same period, there was a significant increase in warthog kills ($r^2 = 0.88$, $F_{1,5} = 37.11$; $P < 0.05$; Table 4.20).

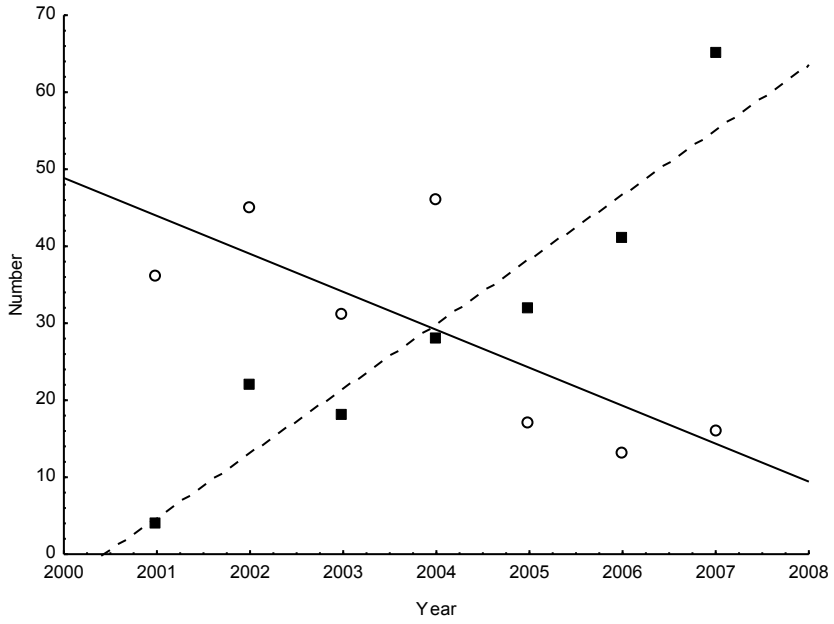


Figure 4.2. Regression of the number of kudu (open circles) and warthogs (closed squares) killed by lions between 2001 and 2007.

The dietary switch from kudu to warthog was reflected in a change in the mean prey mass (Table 4.20), which decreased significantly through the study (Pearson correlation, r^2=-0.76; P<0.05). Note that these analyses were not affected by the change in game census method and thus included data from throughout the study. There was no effect of rainfall on the relative occurrence of kudu or warthog kills (linear regression; kudu, $r^2 = 0.002$; $F_{1,3} = 0.0078$; P>0.05; warthog, $r^2 = 0.14$; $F_{1,3} = 0.48$; P>0.05).

Since there were only three years for which helicopter game count data were available, statistical analyses of relationships between abundance of warthogs and the occurrence of

warthog and kudu kills were not possible, but trends were clear. As the relative abundance of warthogs (warthog numbers relative to kudu numbers) increased, so the proportion of warthog kills increased and the proportion of kudu kills decreased (Figure 4.3). As the relative abundance of warthogs increased, there was little change in the Jacobs' Index for warthogs which was positive at all times, while Jacobs' Index for kudu declined from 0.05 to -0.15 (Figure 4.4).

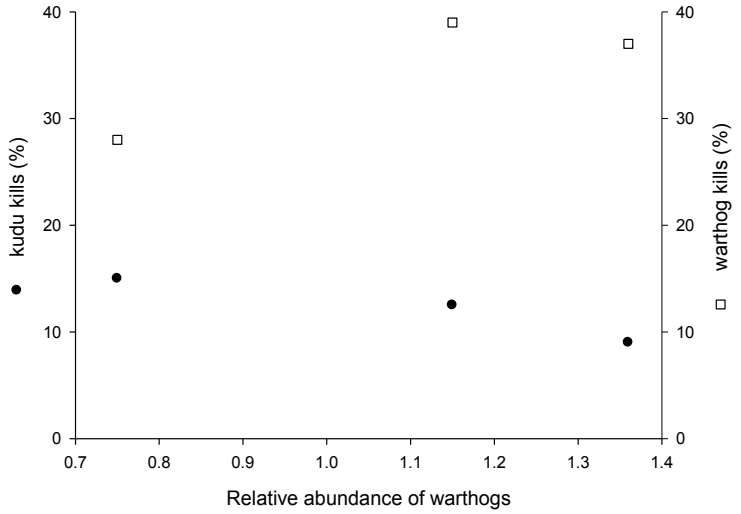


Figure 4.3 The relationship between the relative abundance of warthogs and warthog kills as a percentage of all kills (open squares) and kudu kills as a percentage of all kills (closed circles). Data for 2005-2007 only.

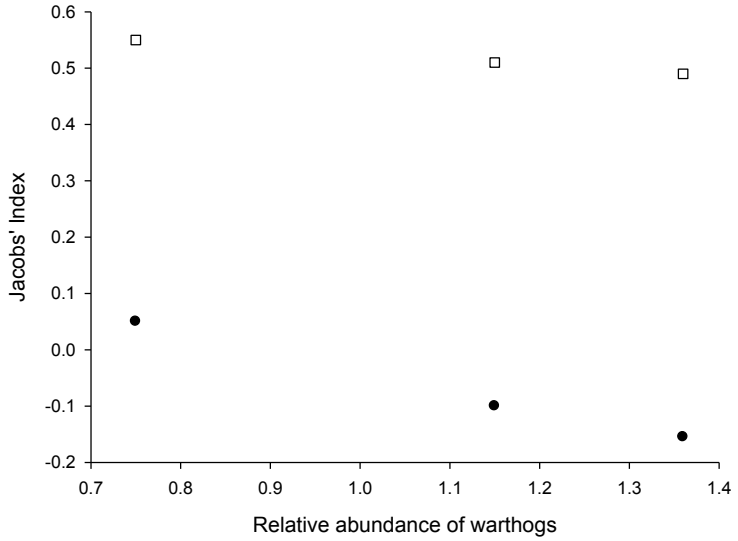


Figure 4.4. The relationship between the relative abundance of warthogs and Jacob's index of warthog (open squares) and kudu (closed circles).

Effects of black wildebeest introduction on lion diet

In 2005 and 2007, additional black wildebeest (of varying age and sex classes) were introduced to SGR resulting in a substantial increase in the abundance of this species. This created the opportunity to test the effect of an abrupt change in abundance of a preferred prey species (Jacobs' Index = 0.55; Table 4.13) on prey selection by lions. The effects of the introductions were tested by comparing the kills of the six most important prey species (Table 4.1) for four months prior to the introduction (= pre-release) and four months post introduction (= post-release). In 2005, 123 black wildebeest were introduced, resulting in a 50% increase in their abundance. During the pre-release phase, 48 lion kills were recorded which comprised 14 different prey species. The three most commonly killed species (kudu, warthog and eland) comprised 64% of the kills and black wildebeest made up only 2% of the kills (Table 4.21). In the post-release phase, 50 kills were recorded, which comprised 12 prey species. Kudu, warthog and eland comprised 26% of all kills while black wildebeest comprised 52% of kills (Table 4.21). The only other prey species that was killed more often after release of the black wildebeest was the zebra (Table 4.21). The proportions of the prey species in the diet were significantly different in the two periods (χ^2= 52.3; df = 4; $p < 0.001$).

Table 4.21. The effects of the introduction of black wildebeest in 2005 on lion diet. n is the total number of kills. For each prey species, kills are given as a percentage of all recorded kills. Total (%) is the number of kills for the six species as a percentage of all kills of all prey species. Change is the difference between post-release and pre-release expressed as a percentage of pre-release.

	kills (%)		
prey species	pre-release	post-release	change
n	48	50	
warthog	31	22	-29%
kudu	27	4	-85%
eland	6	0	-100%
giraffe	2	0	-100%
black wildebeest	2	52	+2500%
plains zebra	2	8	+300%
total (%)	70	86	

In 2007 a further 159 black wildebeest (of varying age and sex classes) were introduced and during the pre-release period 72 kills were recorded of 14 prey species. Kudu and warthog were the two most commonly killed species while black wildebeest made up 13% of the kills (Table 4.22). In the post-release phase, 81 kills were recorded of 12 prey species. Kills of black wildebeest increased to 38% while kills of kudu and warthog declined (Table 4.22). The proportions of the prey species in the diet were significantly different in the two periods (χ^2= 16.2. df = 3, p <0.005). In both years, the decline in warthog kills in the post-release phase was less than that of kudu.

Table 4.22. The effects of the introduction of black wildebeest into SGR in 2007 on lion diet. n is the total number of kills. For each species, kills are given as a percentage of all recorded kills. Total (%) is the number of kills for the six species as a percentage of all kills of all prey species. Change is the difference between post-release and pre-release expressed as a percentage of pre-release.

	kills (%)		
prey species	pre-release	post-release	change
n	72	81	
warthog	40	30	-25%
kudu	12	5	-58%
black wildebeest	13	38	+192%
plains zebra	6	7	+31%
impala	7	4	-36%
red hartebeest	6	7	+31%
total (%)	84	92	

The effect of lambing periods on the diet of cheetah

Field observations suggested that cheetahs selected neonates of a number of prey species, and of all kills for which it was possible to accurately assign an age to the carcass, 50% were of new born lambs or juveniles. This percentage varied between the prey species and it was high for eland, gemsbok, zebra, kudu and black wildebeest and low for bushbuck and duiker (Table 4.23).

There was a significant effect of adult size on the prey species on the percentage of juveniles killed (ANOVA on arcsine transformed percentages; $F_{2,10} = 40.4$; $P<0.05$) and the percentage of juveniles killed of large prey species was significantly greater than that of medium sized and small species (Figure 4.5). There was no significant difference in the percentage of juveniles killed of medium sized and small species (Tukey post hoc test; $P>0.05$).

Table 4.23. The kill record for the cheetahs in SGR showing the number of juveniles of each species killed (excluding scrub hares).

prey species	adult size	no. kills	no. juveniles killed	juvenile kills as % of all kills of the species
eland	L	1	1	100.0%
plains zebra	L	2	2	100.0%
gemsbok	L	1	1	100.0%
kudu	L	22	20	90.9%
black wildebeest	L	8	7	87.5%
impala	S	54	30	55.6%
blesbok	M	28	13	46.4%
red hartebeest	M	8	3	37.5%
springbok	S	12	4	33.3%
warthog	S	3	1	33.3%
mountain reedbuck	S	3	1	33.3%
grey duiker	S	22	5	22.7%
bushbuck	M	16	2	12.5%
total		180	90	50.0%

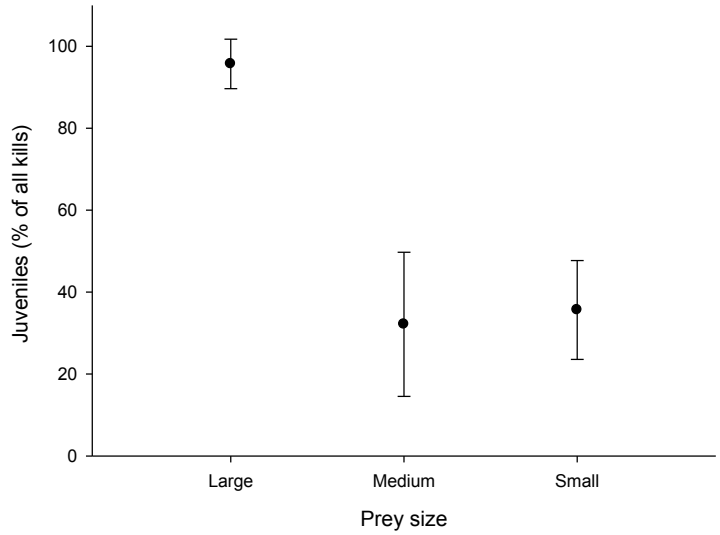


Figure 4.5. Relationship between prey size (size class of adult of the species) and the number of juveniles of that species killed by cheetahs as a percentage of all kills of that species. Data are means ± 1sd.

During a single lambing season (December 2006 to the end of February 2007), when six of the main prey species (impala, springbok, blesbok, black wildebeest, red hartebeest and gemsbok) gave birth, the cheetahs made 27 kills (13 of which were newborn impala) of four prey species with a mean kill mass of 16.1 ± 14.6 kg (Table 4.24). The relatively small number of recorded cheetah kills precluded a comparison with a similar three month period outside the lambing season. However a comparison with the cheetah kill data for the entire study period, suggested that cheetahs killed fewer species and the mean prey mass was significantly lighter (Student's t-test; $t = 4.6$; $df=210$; $p<0.005$; Table 4.24).

Table 4.24. Kill analysis of cheetahs during the lambing season of 2006/2007 compared to the entire study period. Figures in parentheses are the extremes of the prey mass.

	kills				
period	no.	total mass (kg)	mean mass ± 1sd	range (kg)	no. prey spp.
12/2006-02/2007	27	433.3	16.1±14.6	5-45	4
2004-2007	185	7994.9	43.0±26.6	4-183	14

Discussion

General feeding ecology

The recorded kills for lions, leopards, cheetahs and wild dogs in SGR illustrate two trends that have been described previously. Firstly, the number of different species killed by predators increases with increasing body size of the predator and that larger predators have access to a greater range of prey species (Gittleman, 1985; Cohen *et al*., 1993; Sinclair *et al*., 2003). In Mala Mala and Kwandwe, lions kill more prey species than do either cheetahs or wild dogs (Radloff & du Toit, 2004; Bissett, 2007) and in Mala Mala, there was a weak positive relationship between predator body mass and prey richness. In SGR, the pattern was the same and the relationship between predator size and species richness in the kill list was just significant. This will be discussed further later.

A second often reported trend is for a small number of prey species to make up the majority of kills (Funston *et al.,* 1998; Power, 2002; Radloff & du Toit, 2004; Bissett, 2007; Owen-Smith & Mills, 2008b). For example, on Phinda, three species (blue wildebeest, warthog and kudu) from a prey list of 28 species, comprise 86% of prey biomass for lions (Hunter, 1998). In Kwandwe, three species (kudu, springbok and duiker) from a prey list of 18 species, comprise 63% of all kills made by cheetahs (Bissett, 2007). In the Kruger National Park, leopards have been recorded to kill 31 species with impala comprising 78% of all kills (Pienaar, 1969). In Northern Zimbabwe, impala and kudu comprise 64% of the kills made by wild dogs, from a kill list of nine species (Childes, 1988). As a result of this concentration on a relatively small number of species from a long kill list, species diversity (which incorporates both richness and evenness) in the kill list is typically low. In the present and previous studies, no significant relationship has been reported between predator size and species diversity in the kill list although the trend is for larger predators species to have greater diversity in the kill lists (Radloff & du Toit, 2004; Bissett, 2007; present study). The combination of relatively long kill lists with a small number of species comprising the majority of kills probably reflects a balance between the opportunistic nature of most large predators (Schaller,1972; Hayward & Kerley, 2005) and a preference for killing certain species. This preference would result from the interaction of a number of factors including relative abundance, size of the prey species, habitat type, learnt behaviour and competition from other larger predators (Mills & Gorman, 1997; Carbone *et al*., 1999; Creel, 2002; Pole *et al*., 2004; Balme *et al*., 2007). Since these factors vary across landscapes and reserves it is

likely that the most regularly killed species will differ between sites and at the same site over time, and there are many examples of this. Blue wildebeest comprise the majority of lion kills in the KNP, but the species comprises only 4% of kills in Chobe, Botswana (Viljoen, 1993, 1997; Hunter, 1998). In Phinda, nyala comprise the majority of kills made by cheetahs while in the Kruger National Park, it is impala and reedbuck, and in Kwandwe, kudu are killed most often (Pienaar, 1969; Hunter, 1998; Bissett, 2007). This is less apparent for the wild dogs, and across a range of studies, impala comprise the majority of the recorded kills (northern Zimbabwe, Childes, 1988; Kruger National Park, Mills & Gorman, 1996; Moremi, Botswana McNutt, 1996; present study). By contrast, in Kwandwe, where impala comprise 6% and kudu 31% of available prey, kudu comprise 61% and impala 5% of all recorded kills (Bissett, 2007). Clearly multiple interacting factors affect diet and since these vary in time and space it should be expected that so too will prey selection. Prey preference is not a fixed species specific characteristic.

Lions typically kill the most abundant medium to large sized ungulate (50 – 500 kg; Skinner & Chimimba 2005) and in their meta-analysis of 32 studies, Hayward & Kerley (2005) report a mean mass for preferred prey of 200 kg and for significantly preferred prey of 290 kg. Mean prey mass will vary geographically and with variation in the abundance of prey species (as previously discussed), hence in Etosha, where the lions kill springbok, juveniles of larger ungulate species and springhares with a mean prey mass less than 50 kg (Stander, 1992). The mean corrected prey mass for lions in the present study (119.9 kg) was slightly less than that reported in Kwandwe (142 kg; Bissett, 2007) and Mala Mala (126 kg for female lions; Radloff & du Toit, 2004) and much less than reported by Hayward & Kerley (2005). Most of the studies incorporated in Hayward & Kerley (2005) used 0.75 times adult female body mass rather than a corrected mass that accounts for selection of young or females of the species, and the mean masses are for preferred species and not for all kills. Since the preferred prey species of lions tend to be large, the inclusion of all prey species in the calculation of mean prey mass in the present study is bound to produce a lower mass. It is suggested that future studies that aim to establish preferred prey size should be based on the actual size of the prey rather than an estimate based on a certain proportion of the mass of an adult female, and should include all prey and not just preferred prey species.

The preferred range of prey mass for leopards is 10 to 45 kg with a mean mass of preferred species of 25 kg (Hayward *et al*., 2006b) and the mean kill mass in Mala Mala is 25 kg; (Radloff & du Toit, 2004). The mean corrected mass of kills made by leopards in the present study (45.5 kg) was greater than that from Mala Mala and this is discussed later.

The importance of prey abundance in shaping prey selection is supported by some but not all previous studies and the results from the present study are ambivalent. Of the three preferred species, the top two (ostrich and black wildebeest) comprised just 5% of the available prey. While impala which represented 22% of all available prey was the most strongly avoided. Cheetahs typically kill the most abundant small to medium sized ungulate species up to 60 kg (Skinner & Chimimba, 2005) while Hayward *et al.,* (2006c) report a prey mass range of 23-56 kg with a mean preferred prey mass of 27 kg. In most reserves, prey size is small, but this is not always the case and in Phinda, maximum prey size is 120 kg (Hunter, 1998) and in Kwandwe the maximum for an adult female is 240 kg (Bissett, 2007). The mean corrected prey mass for cheetahs (43 kg) in the SGR was slightly less than that recorded in Kwandwe (46 kg; Bissett, 2007) and greater than that recorded in Mala Mala (female cheetah 25 kg; male cheetah 39 kg; Radloff & du Toit, 2004). Although it is within the range reported by Hayward *et al*. (2006c), it is greater than the mean prey mass. This is not surprising since cheetahs select small prey and this will result in a low mass for selected species. In the present study the mean mass is for all kills, including some larger items and this will have increased the mean prey mass.

For the wild dogs, the mean prey mass in the SGR (73.5 kg) was much heavier than that reported for Mala Mala (Radloff & du Toit, 2004), lower than that reported for Kwandwe (112 kg; Bissett, 2007) and falls between the two preferred mass ranges (16-32 kg and 120-140 kg) reported in the meta-analysis of Hayward *et al.* (2006a). In SGR, kudu (mean kill mass 145 kg) were killed most often and fall into the upper mass range while impala were the next most often killed prey species. This combination of kudu and impala is likely to have reduced the mean prey mass of wild dogs in accordance to the two ranges reported by Hayward *et al.* (2006a).

For leopards, cheetahs and wild dogs, the maximum prey mass in Mala Mala is substantially less than in the present study and this will reflect differences in diet. In SGR, the most

frequently killed species by leopards were bushbuck and kudu with impala and duiker making up a small proportion of kills. By contrast, in Mala Mala, impala is the most common prey species followed by warthog for male leopards and duiker for female leopards (Radloff & du Toit, 2004). Similarly, in SGR, impala, blesbok and kudu made up the majority of kills of cheetahs while in Mala Mala, impala, steenbok and duiker comprise the majority of kills (Radloff & du Toit, 2004). In SGR, kudu impala and bushbuck comprised the majority of kills made by the wild dogs while in Mala Mala, it is impala and duiker (Radloff & du Toit, 2004). Thus differences in mean prey mass reflect differences in diet, which in turn reflect differences in the suite of factors that affect prey capture. These will include not just the abundance of prey species but also the habitat, the presence of other large predators and the threat of kleptoparastism.

As has been described in previous studies, the mean corrected prey mass of the predators in SGR differed significantly and larger predators had higher mean prey masses. All predators killed small prey species but maximum corrected prey mass ranged from 960 kg for lions to 178 kg for the cheetahs. Consequently, and as described previously (Gittleman, 1985; Cohen *et al*., 1993; Radloff & du Toit, 2004; Bissett, 2007), there was a significant relationship between predator size and maximum prey size but not between predator size and mean or minimum prey size. Thus the relationship between predator size and mean prey size is driven by increasing maximum prey size. A simple comparison of predator-prey body mass ratios between predators that are solitary and those that hunt in packs is misleading since the pack hunting behaviour of African wild dogs and the group hunting of coalitions of cheetahs and prides of lions allow these predators to kill larger prey than if they hunted alone (Creel & Creel, 2002). This was the case for the predators at SGR (present study) and Kwandwe (Bissett, 2007) where the smaller wild dogs had a greater predator-prey body mass ratio than the lions. The average number of wild dogs in SGR for the study was 11.5 which would represent a predator of about 290 kg and a predator-prey ratio of 1:0.25 which is very similar to the ratio of 1:0.13 in the Kruger National Park (Radloff & du Toit, 2004).
The observations reported above are often interpreted as indicating that larger predators have access to (can capture and kill) a greater range of prey species than do smaller predators (Gittleman, 1985; Cohen *et al*., 1993; Radloff & du Toit, 2004). While this is undoubtedly the case, it is also the case that by selecting smaller members of larger prey species (juveniles

and sub adults), smaller carnivores can broaden their prey base. This point is further discussed later.

Comparison of continuous observations with records from the field rangers

Continuous observations were undertaken in an attempt to overcome the bias that results from the less structured observations of field rangers missing kills of particularly smaller prey species (Mills, 1984, 1996; Radloff & du Toit, 2004; Owen-Smith & Mills, 2008b). In the present study, continuous observations revealed significantly different proportions of prey species for the lions only. Kills of four important prey species in the total kill list (kudu, warthog, bushbuck and blesbok, all medium or large size) were recorded less often in the continuous observations, while two small species (porcupine and scrub hare) were killed more often in the continuous observations. The method of determining prey consumption did not have a significant effect on the result. By contrast, the mean corrected prey mass for cheetahs was significantly lower when using the continuous observation method suggesting this method is better at detecting smaller prey items. However, the summer period of continuous observations coincided with the lambing season for impala, and impala lambs made up a high proportion of observed kills. Thus the lower mean prey mass in the continuous observations was more likely to have been the result of a change in diet rather than the different methods used.

Continuous observations are labour intensive and the question of whether or not they are worthwhile needs to be addressed. In a parallel study in Kwandwe, there was no significant difference in proportions of prey species recorded in the full kill list or by continuous observations for lions, cheetahs and wild dogs (Bissett, 2007). Radloff & du Toit (2004) have argued that where the observation effort is high, as on ecotourism reserves, the bias between prey species lists compiled using the two methods may not be significant. In the Kruger National Park and adjacent Mala Mala game reserve, the prey proportions for lions were similar in studies based on records from field rangers (Owen-Smith & Mills, 2008a), continuous follows (Mills & Biggs, 1993; Funston *et al*., 2001) and from ecotourism game drives (Radloff & du Toit, 2004). If continuous observations are to be carried out then periods of two weeks are probably too short. In the present study, the continuous observations failed to record kills of prey species that had been recorded by the field rangers and thus do not give a complete picture of the diet of large predators. However, increasing the length of

continuous observations will make them more labour intensive and both continuous observations and the less structured observations from field rangers have inherent problems.

Daily food consumption

Daily food consumption will vary between and within predator species, depending on factors including body size of the predator, reproductive condition, level of activity (distance travelled) and seasonal changes in prey abundance and group size (Caro, 1994; Creel & Creel, 2002). In the present study the mass of kills was corrected both for sex and age of the animal killed and for the percentage of the carcass deemed edible. Daily food consumption was also based on data from the continuous observations rather than the full kill list on the assumption that the continuous observations were a better reflection of diet. Estimates of daily intake vary between studies and while these variations may represent real differences in intake, at least some of the variation will result from the different methods used to collect the data and in its analysis.

Daily consumption rates for lions in South Africa vary from 4.3 kg/FEQ/day (Power, 2003) to 5.8 kg/FEQ/day in the KNP (Owen-Smith & Mills 2008a), 9.5 kg/FEQ/day in Kwandwe (Bissett, 2007) and up to 14 kg/FEQ/day in Etosha in the wet season (Stander, 1992). The results for SGR (10.1 kg/FEQ/day) fall within this range.

Some of the highest daily intake rates have been reported from newly established game reserves where the antelope were naive to the threat of predators (Rapson, 2004; Bissett, 2007). The daily intake for cheetahs (3.9 kg) was similar to that reported by Frame (1999; 2.8 kg/FEQ/day) and lower than that reported for Kwandwe where members of a coalition consumed 5.3 kg/FEQ/day, and single females with cubs, 4.7 kg/FEQ/day; Bissett, 2007). Daily intake of leopards varies considerably from 1.6 – 4.9 kg/FEQ/day (Bothma & Le Riche, 1986; Bailey, 1993; Stander, 1997; Hayward *et al*., 2006b) and the results from the SGR fell at the top end of this range.

There are fewer reports of daily consumption by wild dogs which varies from about 1.7 kg/dog/day to 6.0 kg/dog/day (Fuller & Kat, 1990; Mills & Biggs, 1993; Creel & Creel, 1995; Lindsey *et al*., 2004; Bissett, 2007).

The magnitude of the variation in daily intake rates of large predators does not match the variation in the size of the predators; lions are three to four times the size of leopards and cheetahs but the daily intake rate is only about 50% greater. However, while body size is an important determinant of daily energy requirements other factors such as time spent active each day, distance travelled and speed of locomotion will also play important roles.

Prey preferences

Prey selection by large predators is shaped by factors specific to predators including size, habitat use and behaviour of the predator, factors specific to prey including size, abundance, habitat use, behaviour and vulnerability, and the presence of other predators and the risk of kleptoparasitism (Mills & Gorman, 1997; Creel & Creel, 2002; Radloff & du Toit, 2004; Hayward & Kerley, 2005). Since these will vary in time and place, it is to be expected that predator diet will also vary and this is supported by numerous studies mentioned elsewhere. By contrast, it has been suggested that prey preference is an evolutionary adaptation (see Hayward *et al*., 2011) implying that variation from the norm is suboptimal rather than reflecting dietary flexibility. In this discussion it is assumed that diet is flexible, as supported by the very different diets reported for predators, and as supported by the OFT.

The predation list that is used to calculate prey preference, is the end point of a complex set of processes and events, including the decision 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 (Owen-Smith & Mills, 2008a). While it is often assumed that the record of kills represents prey preference, this need not be the case. For example, if the majority of chases for a highly preferred species were unsuccessful while those for a less preferred prey species were more often successful, then it would be possible for the highly preferred species to occur less often in the kill lists than the less preferred species. The resolution of this problem requires observations of predators while they hunt, which is both difficult and very time consuming. Equally problematic is the way in which abundance of a prey species is estimated and the inclusion of a species that is not consumed (perhaps a megaherbivore) in the total abundance for the area will reduce the relative abundance of a prey species and may result in an artificially elevated preference index. Furthermore, the use of simple abundance as a measure of prey availability is problematic as a variety of aspects of

a species' biology including behaviour and habitat selection, may influence its availability to predators (Owen-Smith & Mills, 2008a).

Thus, while prey preferences will give an indication of the frequency of kills relative to proportional abundance (Owen-Smith & Mills, 2008a), they do not necessarily give a true indication of preference. Observing true prey selection i.e. species for which hunts are initiated as compared to those that are ignored, is problematic even when continuous observations are undertaken. Many of the large predators hunt at night and others in dense vegetation making observations difficult.

Lions are reported to prefer large prey within the mass range of 190-550 kg (Hayward & Kerley, 2005) and this is partially supported by data from the present study. In SGR, lions preferred (Jacobs' Index ≥0.3) ostrich, black wildebeest, warthog, eland and gemsbok, with kills of these species comprising 61% of all kills but only 24% in terms of abundance. Black wildebeest, eland and gemsbok are large, thus supporting Hayward & Kerley (2005) but warthog and ostrich are medium sized. The high preference index for ostrich has been reported in Kwandwe (Bissett, 2007) and there are possibly two reasons for this. Firstly, SGR and Kwandwe are relatively new reserves that were stocked with ostriches that had not experienced large predators, and secondly, on both reserves the numbers of ostrich were low (10-40). It is suggested that the naivety of the ostriches may have made them more susceptible to predation and that kills of a rare species would have resulted in a high Jacobs' Index. The preference for warthogs has been reported in several studies (Viljoen, 1993; Hunter, 1998; Bissett, 2007; Hayward *et al*., 2007 for subadult lions) but in the meta-analysis of Hayward & Kerley (2005), it is reported as being killed in accordance with its relative abundance. The preferred species included two of the most frequently killed species (black wildebeest and warthog) but excluded frequently killed species such as kudu and zebra which were killed in proportion to their abundance. This supports the often stated view that predators prefer the most abundant species within a particular size range (Hayward & Kerley, 2005, 2009). When this is the case, the relative occurrence of kills and the relative abundance will be high and this will generate a JI close to zero. All of the potential prey species that were avoided by lions were small and these included impala which was the most abundant prey species on the reserve. These results are similar to those reported for the Kruger National Park where impala are less likely to be killed by lions relative to their

abundance than large prey species, such as blue wildebeest are the most likely (Owen-Smith & Mills, 2008b). The pattern is also very similar in Kwandwe, where impala are strongly avoided (Jacobs' Index -0.77) and black wildebeest preferred (JI 0.36; Bissett, 2007). Thus the diet of lions in SGR supports the widely reported preference of lions for medium and large sized prey.

In SGR, leopards preferred three prey species, one small (duiker), one medium sized (bushbuck) and one large (gemsbok) and there was no relationship between prey size and Jacobs' Index. Although kudu were not preferred, they were the second most regularly killed species. Hayward *et al*. (2006a) suggest that leopards prefer species in the mass range of 10 to 40 kg, which occur in small herds, in dense habitat and which pose a small injury risk to the predator. This description is appropriate for duiker and bushbuck but it is less so for gemsbok and kudu. Adult gemsbok and kudu are above the mass range, able to defend themselves with large horns and gemsbok do not typically occur in thick vegetation. These problems were negated by the fact that the leopards in SGR selected juvenile or sub adult animals of these two species (all gemsbok and 62% of kudu were juveniles) which would have been within the preferred mass range and much less able to defend themselves. Bushbuck were strongly preferred in SGR and this is supported by the meta-analysis of Hayward *et al.* (2006b). The very strong avoidance of impala by leopards in SGR is interesting since impala are the most important (in terms of numbers killed) prey species in Mala Mala and is a preferred prey species (Hayward *et al*., 2006b). Although impala is in the mass range suggested by Hayward *et al*. (2006b), it lives in large herds and tends not to occupy dense vegetation and thus could be expected to have a low preference index as reported in the present study.

Cheetahs prefer prey in the mass range of 23 to 56 kg and there are two main reasons for this. Firstly, to minimize the risk of injury during the hunt, and secondly, because smaller prey can be consumed quickly before kleptoparasites arrive (Hayward *et al*., 2006c). In SGR, cheetahs avoided large and medium sized prey and selected small and medium sized species. The species killed most frequently (impala) was also the most abundant species on the reserve, supporting the observation that cheetahs select the most abundant small to medium sized prey (Hayward *et al*., 2006c). In SGR, of 13 prey species only two (kudu, JI = -0.03; bushbuck, JI = -0.64) were forest ungulates, the remainder being species that occupy savannah woodland

and grassland. This reflects the tendency for cheetahs to hunt in open habitats and to avoid heavily wooded or thicket vegetation (Hayward *et al*., 2011). Grey duiker were strongly preferred with a Jacob's Index value of 0.71 whereas in Kwandwe they were preferred by single cheetah females and independent cubs but completely avoided by the coalition (Bissett & Bernard 2007; Bissett, 2007). Warthog, despite their abundance, use of open areas and their appropriate weight were avoided by the cheetahs in SGR and Kwandwe. There are several possible reasons for this including the risk of injury from the tusks of the warthog.

The wild dogs at SGR killed the most abundant prey species with the exception of grey duiker which was the most frequently killed species but only represented 0.02% of the prey population. As a result of killing the abundant prey species (bushbuck, kudu, impala) they were neither selected nor avoided (JI between -0.3 and 0.3). Similar results have been reported for Kwandwe (Bissett, 2007) and at Shambala Private Game Reserve, South Africa (Rhodes & Rhodes, 2004). Kudu is a frequently killed species and depending on abundance, may or may not be preferred (Pole *et al*., 2004; Rhodes & Rhodes, 2004; Bissett, 2007). Experience from previous wild dog re-introductions suggests that perimeter fencing may be a complicating factor where wild dogs learn to utilize perimeter fencing during hunting, resulting in a higher hunting success rate with large prey species, specifically kudu, than is typical (Hofmeyr, 1997; van Dyk & Slotow, 2003; Bissett, 2007; pers. obs.). The three most preferred prey species, grey duiker, bushbuck and kudu are all forest ungulates and this reflects the preference for Thicket vegetation as a hunting habitat for wild dogs in SGR. The wild dogs avoided a range of small and medium sized grassland species such as blesbok, springbok and red hartebeest.

The pooling of data for all members of the predator guild, as has been done in this study, is used to indicate the cumulative predation pressure on the prey species. Grey duiker was the most preferred prey species for the large carnivore guild. The high JI for grey duiker was a result of a relatively small population size and a relatively high number of recorded kills. Although the absolute number of duiker killed per year was relatively low (sixth on the list) this is likely to be enough to threaten the duiker population. Even if duiker were undercounted in the game count, which is likely to be the case, it is also likely that kills were under recorded and thus the threat remains. Other species which were killed regularly, such as kudu and warthog, occurred in larger numbers than duiker and it is less likely that the

populations will be threatened by predation pressure. Black wildebeest was the only other prey species with a preferred Jacob's Index value of 0.35. Kills of black wildebeest represented about 25% of the population and it is quite likely that predation will cause a population decline. Impala comprised 22% of the prey population in SGR but only represented 13% of the kills. This is interesting since in other reserves where impala numbers are high, impala form an important part of the diet of the large predator guild (Radloff & du Toit, 2004). Impala are avoided by lions in four previous studies on small, enclosed reserves (Hunter, 1998; Power, 2002; Bissett, 2007; Lehmann *et al*., 2008) yet in Mala Mala, which is part of the greater Kruger National Park, impala form 40% of lion diet (Radloff & du Toit, 2004). It appears that impala are more frequently preyed upon in larger reserves (Bryden, 1978; Mills & Biggs, 1993; Funston *et al*., 2001) and the fact that they are under selected on small, enclosed reserves could be ascribed to the extreme alertness and vigilance of the species (Mooring, 1999). Hunter and Skinner (1998) observed a 200% increase in vigilance of impala following reintroduction of lions at Phinda while Begon *et al.* (1996) found that impala successfully utilize 'enemy-free space'.

Two examples of intraspecific prey selection.

The previous discussion has focused on prey selection at a species level which is a relatively coarse grain analysis since in at least some instances, selection is made at the within species level. Selection by age and or sex has been previously reported for a number of large predators. In Etosha, lions select juvenile springbok over adults but show no preference for age or sex of zebra or blue wildebeest (Stander,1992). By contrast, in the Kruger National Park, lions select adult blue wildebeest and zebra (Mills, 1984).

1. *Predation on kudu by the large predator guild*

Within species selection is illustrated by data on predation on kudu by the large carnivore guild in SGR. Kudu was an important (killed frequently) prey species for all the predators and kudu comprised between 10 and 30% of all recorded kills. Adult kudu are large (adult males up to 250 kg, adult females up to 210 kg, Skinner & Chimimba, 2005) and it is therefore not surprising that they are killed by lions. However, kudu do not fall into the preferred prey range for the other large predators (Hayward *et al*., 2006a,b,c) yet the species is frequently killed by them. The pack hunting behaviour of the wild dogs allows them to kill larger prey than expected based on the body size of an individual wild dog (Creel & Creel,

1995; 2002) and in SGR, 77% of the kudu killed by the wild dogs were adults. By contrast, the leopards and cheetahs selected sub adult and juvenile animals and this was reflected in the mean corrected mass of kudu killed. The mean corrected mass of kudu killed by the cheetahs was 63 kg, which is similar to the mass of an adult blesbok, a species preferentially killed by the cheetahs, and similar to the maximum mass of an adult male impala, the species most frequently killed by the cheetahs (Hayward *et al*., 2006c). The mean kudu kill mass for the leopards were greater than that of the cheetahs which probably reflects the more robust body and greater strength of the leopard (Skinner & Chimimba, 2005). The reported loss of 20% of the kudu each year in the present study is likely to be an overestimate. While it is the case that some kills will have been missed, it is also the case that as much as 50% of kudu may be missed during helicopter counts (Bothma *et al*., 1990).

2. Prey selection by cheetahs

The pattern of prey selection by cheetahs for juvenile kudu discussed above was repeated for other prey species of the cheetah, and in SGR, there was a significant effect of adult size on the proportion of juveniles killed. Although the sample sizes were small, 100% of the recorded kills of eland, zebra and gemsbok were of juveniles.

Within species selection occurs for various reasons most of which will be linked to vulnerability of the prey and driven by the OFT. Factors such as age, group size, sexual dimorphism or habitat use that make one age class or sex more vulnerable to predation than the other may drive within species selection by a predator. In the examples discussed above, it is likely that predator size, group size (number of animals in the pride, coalition or pack) and prey size (i.e. optimal foraging) were the driving factors.

These two examples illustrate how, for the cheetah, selection for a particular age class within a species gave the predator access to a prey species that would normally be regarded as being outside its prey size range. This is relevant in the context of the often reported relationship between predator size and prey diversity, typically expressed as the dietary range of large carnivores being broader than that of small carnivores (Gittleman, 1985). There is no doubt that as a general rule, this applies and it is supported by results from the present study where lions kill a greater range of species than do the cheetahs. However, it is possible for the

smaller predators to broaden their prey base by selecting from within a specific age class of a larger prey species.

Finally, while a great deal of emphasis is placed on prey selection at a species level, the examples above illustrate the importance of size and the importance of considering selection at and within species level.

The effect of prey abundance on predator diet; three examples

1. Effects of a natural change in kudu and warthog numbers on the diet of lions

Predators will switch to an alternative food source when the abundance of their preferred prey declines (Murdoch, 1969; Bissett, *et al*., 2012) and it is thought that this may promote the persistence of predator-prey systems (van Baalen *et al*., 2001). Prey switching may also occur when the abundance of a secondary prey species increases, as is predicted by the Optimal Foraging Theory (OFT; Krivan, 1996).

In SGR, the abundance of two important prey species for lions changed through the study. Kudu numbers decreased while warthog numbers increased and this was reflected in a shift in the proportion of kills of the two species. Kills of warthogs increased from 3% in 2001 to 37% in 2007 and kudu kills declined from 28% to 9% over the same period. One of the requirements for prey switching is that the relative proportion of kills of a prey species changes (Murdoch, 1969; Garrott *et al*., 2007) and this will be reflected in a change in Jacobs' Index. This was seen in SGR as kudu were preferred when the species was relatively abundant early in the study and avoided when less common. The data suggest that the change in diet was primarily in response to the increase in warthog numbers which was much greater than the decline in kudu numbers.

Similar changes in the diet of lions have been reported previously and in the Chobe National Park, Botswana, large prey (buffalo and zebra) comprise the majority of the diet but, in the dry season, when they migrate out of the area, warthogs become an important prey species (Viljoen, 1993; 1997). Similarly, in the Kruger National Park, selection for alternative prey, including warthogs, is affected by changing relative abundance and vulnerability of the three principal prey species (wildebeest, zebra and buffalo; Owen-Smith & Mills, 2008a). The

latter example clearly illustrates how changes in diet are not simply driven by changes in prey numbers and that a full understanding of the ways in which climate changes, such as drought influence susceptibility to predation is essential.

Both examples differ from the present study in that in Chobe and Kruger National Parks, the change in diet is due to a decline in the numbers of the preferred larger prey or increase in vulnerability of a secondary prey species, whilst in the present study it was principally due to an increase in the abundance of a preferred but secondary prey species. Furthermore, in the Kruger National Park, the relative selection of warthogs peaked during a two-year drought (Owen-Smith and Mills, 2008a) while in the present study, annual rainfall was not an important predictor of the relative occurrence of warthogs in the diet.

The reasons for the dietary switch in SGR are likely to lie in a combination of factors including the small pride size, which will increase the risk associated with killing large prey species (Packer, Scheel & Pusey, 1990; Funston, Mills & Biggs, 2001), the relative vulnerability of warthogs and kudu, the energetic returns from the two prey species and their relative abundance. I suggest that as the abundance of warthogs increased (and the relative abundance of kudu decreased), the encounter rate and or search time for warthogs decreased and the lions killed more warthogs. Over time, the lions became more efficient at catching and killing warthogs and relatively more warthogs and fewer kudu were killed. These results contradict those of some other studies which have suggested that lions prefer large prey regardless of abundance (Hunter, 1998). However, if lions are opportunistic predators (Schaller, 1972) then it should be expected that their diet will be influenced by prey abundance as well as other factors.

True prey switching is likely to promote the persistence of predator-prey systems (van Baalen *et al.,* 2001) as predator pressure on a declining prey species will decrease through density dependence, providing the opportunity for that species to recover. This will be particularly important on relatively small fenced conservation areas where opportunities to escape predation are few (i.e. predator refuges) and population renewal through immigration is not possible. It is also important in SGR where, as discussed earlier, the predation pressure on kudu from the large carnivore guild was considerable. Thus, an understanding of the factors that influence prey selection is important for the management of enclosed conservation areas.

The other members of the large predator guild did not respond to the increase in abundance of warthogs and although each predator species killed a few warthogs, they were amongst the most strongly avoided (most negative Jacobs' Index) of all possible prey. There are a number of possible explanations for this. While lions are equipped to dig warthogs from their burrows, the more gracile cheetahs cannot do this, an idea that is supported by Hayward *et al*. (2012). In addition, warthogs occur in family groups and are armed with tusks which can inflict damage to the predator. Of the other predators, warthogs formed the largest proportion of recorded kills for the wild dogs (5%) and this may be related to the pack hunting of this predator.

2. The response of cheetahs to the lambing season of important prey species.

The lambing season is characterized by an abundance of small and vulnerable prey items and it might be expected that a predator species that tends to select smaller prey items would show a dietary switch at this time. One of the important predictions of OFT is that as a preferred prey species becomes scarce, so new prey types should be added (Stephens & Krebs, 1986), also that any predator will take a prey item if it is easily captured with minimal injury risk. The converse of this is that as a preferred prey species becomes increasingly available so prey diversity in the kill list is expected to decrease. In SGR, the cheetahs killed fewer species during the lambing season, than the non-lambing season, as predicted by OFT and 48% of recorded kills were of impala lambs. Some other studies of the diet of cheetah have reported a preference for sub adult and juvenile animals (Eaton, 1970; Schaller, 1972; Pettifer, 1981; Hunter, 1998; Mills *et al*., 2004) while a few other studies have failed to detect any selection for young animals (Kruuk & Turner, 1967).

3. The effect of black wildebeest introductions on lion diet

SGR, and other small fenced game reserves with large predators, often manage decreases in the numbers of a preferred prey species by supplementing the populations from outside. When this takes place it results in a sudden increase of a preferred prey species. This not only increases the relative abundance of the prey species, but the animals are often from reserves where there are no predators and they are thus naive to the threat of predation. The OFT predicts that animals will act to maximize their rate of energy intake (Stephens & Krebs, 1986) and it is predicted that a predator when faced with an increased population of a

preferred species will increase the proportion of that species killed. In SGR, the introductions of black wildebeest, which was a favoured prey species of lions, resulted in a significant change to the prey profile. The number of species killed declined and the number of black wildebeest killed increased. These are the same trends reported for cheetahs during the lambing season. It might be expected that predation on black wildebeest will be reduced over time as the black wildebeest become more vigilant to the presence of lions, and numbers decline, but the value of this management intervention should be questioned. Alternative approaches might be to allow a natural process such as diet switching to occur and for the black wildebeest population to recover naturally. Alternatively, it might be possible to increase the numbers of a secondary prey species and in this way initiate a diet switch and thus reduce predation pressure on the black wildebeest. Although these reintroductions are clearly artificial, a natural equivalent might be the annual changes in the numbers of wildebeest in the Serengeti that take place with the migration. Wildebeest and zebra are preferred prey species and predation is a major contributor to mortality. However, when the migratory populations of wildebeest and zebra move away, the lions switch to killing more buffalo and other non-migratory species (Scheel, 1993; Sinclair *et al*., 2003).

Conclusions

In this study I investigated the variable effects of features of the predator including body size and strength, social system and habitat preference; features of the available prey, such as species composition, body size and armament, abundance and habitat use; and other factors, including the presence of other predators of the same and other species, and climate and concluded that the diets of large mammalian predators are set by a range of interacting biotic and abiotic factors. In SGR, predator size influenced maximum prey size and only the lions killed adult eland. The effect of body size was modulated by social structure and pack hunting in the wild dogs enabled them to kill prey that was much larger than predicted based on the size of an adult wild dog. Only lions and the wild dogs killed adult kudu. The preference of both leopards and bushbuck for heavily wooded habitats and the medium size of the bushbuck resulted in bushbuck being the principal prey species of the leopards. Similarly, the habitat use of the impala would be a principal reason for it being strongly avoided by leopards. The importance of the size and abundance of prey species is illustrated by the lions and cheetahs. Kudu were relatively abundant and large, and were the principal prey species of lions. Impala were the most abundant and medium sized, and the principal

prey of the cheetahs. Warthog were only killed in large numbers by lions and this was probably due to the armament of the warthogs acting as a deterrent for them against other predators, and the ability of lions to excavate their burrows. Diet is not a fixed, species level attribute but varies in time as is illustrated by the examples of diet switching.

Finally, while it is convenient to view diet in terms of the species killed it may be that size and vulnerability are more important. Some prey species such as steenbok are small and in such cases, size could be seen as a species level characteristic, but in other species, where the adult is large, younger animals are not. Prey selection is thus best interpreted at a size level rather than at a species level. Size and vulnerability of an animal will often, but not always be linked and the degree of vulnerability will depend on the predator. A large animal may be vulnerable to a large predator but not to a much smaller predator. A small animal (or species) may be equally vulnerable to all predators (Sinclair *et al*., 2003). Species level differences in susceptibility to climate change (drought; Owen-Smith & Mills, 2008a) results in changes in vulnerability which adjusts prey selection. Prey selection is neither fixed in time or space and is rather continuously shaped and reshaped by the interaction of the factors described and discussed in this chapter.

CHAPTER 5: SPATIAL UTILIZATION

Introduction

An important question in ecology is how species and individuals distribute themselves in space and particularly within a heterogeneous environment (Hammond *et al*., 2007). While the concept of the Ideal Free Distribution (IDF; Fretwell & Lucas, 1970) develops a theoretical framework to understand how a single species may respond (an individual will settle wherever expected fitness is highest; Cressman *et al*., 2004) it has little applicability in natural systems. African savannah ecosystems are characterised by a heterogeneous environment, multiple possible prey species and a large carnivore guild. Interference competition is a characteristic of such systems (Mills & Gorman 1997; Durant, 2000a) and direct and indirect interactions among carnivores, including kleptoparasitism, outright killing and harassment, are likely to influence distribution patterns (Linnell & Strand, 2000; Carbone & Gittleman, 2002; Berger & Gese, 2007).

To accommodate interference competition, the IFD has been modified and, according to the Ideal-Despotic Distribution (IDD), in which an individual's options for settling are constrained by the territorial behaviour of already established individuals (Kohlmann & Risenhoover, 1997). The applicability of the IFD has been tested in several models which have suggested that the IDD, and not the IFD, is the most suitable application (Kohlmann & Risenhoover, 1997; Beckmann & Berger, 2002; Zimmerman *et al*., 2003). Consequently, in thinking about distribution patterns, it is important not to overlook inter and intra-guild interactions.

In a predator-prey system, the distribution of predator and prey will be shaped by many interacting abiotic and biotic factors (see Celesia *et al*., 2009). This distribution will affect encounter rates of predator and prey which consequently may have effects at the population and community levels (Hammond *et al*., 2007). Thus understanding patterns of distribution is crucial for a full understanding of population ecology. In experimental systems, predators generally, but not always, prefer areas with high prey densities and prey tend to avoid areas with high predation risks (Stephens & Krebs, 1986; Sih, 1998). However, the applicability of this to natural systems in which both predators and prey can move is questionable, and little is known about the nature of interactions in systems where movement is possible (Hammond

et al., 2007). While one might expect spatial patterns to be fluid, with prey shifting space use in response to predation, and this being tracked by the predators, this is not always the case. In certain circumstances, models predict that space use will settle down and predator space use will match that of the prey (Sih, 1998). There is also a confounding predator body size effect, and in a study of a mammalian carnivore guild in Europe, smaller predators (least weasel and ermine stoat) were less flexible in space use than larger predator species (red fox) and it is suggested that larger species can range further and have a better ability to track changes in prey distribution (Šálek *et al*., 2010).

Since the distribution of prey is often an important factor in the distribution patterns of predators, it is important to consider factors that may affect distribution of the prey species. The distribution patterns of large herbivores are driven primarily by abiotic factors such as distance to water and slope, and biotic factors including features of the forage (quality, quantity, patch size) (Bailey *et al.*, 1996). The distribution of prey may also be influenced by the presence of predators and recently, attention has been drawn to the role of fear in shaping the distribution and behaviour of prey. While there are many ways in which prey can respond to the presence of a predator, or perceived predation pressure (fear) one response is to move from the area (change distribution pattern) (Brown *et al*., 2001; St-Pierre *et al*., 2006). In a multi-predator system, the predation pressure may be higher than if a single predator is present and this may increase the likelihood of prey species moving. But, it also makes it harder for each predator to capture prey, because of increased levels of vigilance (Kotler, 1992) and it may be expected that predators might select to hunt elsewhere.

While it might be expected that the distribution of prey would be a major factor in determining the distribution of predators (prey abundance hypothesis; Hopcraft *et al*., 2005) this is not always the case. Different carnivores species hunt in different ways (Murray *et al*., 1995) and prey capture will be easier in one habitat than in another (landscape hypothesis; Stephens & Krebs, 1986). In the same way that the presence of predators can affect the distribution and behaviour of prey, so the presence of "larger" or more powerful predators can affect the smaller species. The distribution patterns of wild dogs, cheetahs and San Joaquin foxes are influenced more by the distribution of larger guild members (lions, spotted hyaenas and coyotes) than by the distribution of their preferred prey (Mills & Gorman, 1997; Warrick & Cypher, 1998; Durant, 2000b).

Patterns of space use within a species may differ between the sexes. While the spacing patterns of females are generally dictated by the food supply, proximity of water and availability of den sites for rearing young (Caro, 1994; Mizuntani & Jewell, 1998; Sunquist & Sunquist, 2002), the spacing patterns of male felids are thought to be driven primarily by female distribution (Stander *et al*., 1997; Sunquist & Sunquist, 2002).

In a heterogeneous environment, with multiple prey species and multiple large predator species, it is likely that the control of space use will be complex. This complexity is likely to be exaggerated in the present study site where access to water was limited, patches of high quality vegetation were available close to water on the old disturbed lands, and the reserve was fenced making large scale movements impossible.

In studies of space use the interest is not only on where the home range is located (distribution patterns) but also on the amount of space used (home range and core area sizes). Understanding variation in home range size, and identifying the factors that underlie this variation, are important to understanding the distribution and abundance of animals, and ultimately their population regulation (Wang & Grimm, 2007), habitat selection (Rhodes *et al*.,2005), community structure (Fagan *et al*., 2007), and for management and conservation of ecosystems (Woodroffe & Ginsberg, 2000).

At a physiological level, range size is driven by body size of the predator (Gittleman & Harvey, 1982). Metabolic needs increase with body weight $^{0.75}$ and larger predators will need more energy and are likely to require more space. However larger ranges will require more energy for their defence and it is argued that the home range of a carnivore is generally as large as is necessary to meet the energetic requirements of the animals, but as small as possible to reduce the energetic costs of defending the space (Lehmann *et al*., 2008) and to limit resource loss to competitors (Jetz *et al.,* 2004).

The simple body size effect on space use will be modified by aspects of social structure (group size) and predator density, and abundance, size and distribution patterns of prey. Predators that prey on plains game which often form large groups may need less space than a predator that hunts in forests where prey are more often solitary. The Resource Dispersion Hypothesis (Macdonald, 1983) predicts that range size will be controlled by the patchiness of

food while predator group size will be determined by patch size and quality. Since the patchiness of food is likely to vary between study sites, it is likely that range sizes will also vary. Indeed this is the case and there is substantial variation within species which typically reflects particular features of the study site (Gittleman & Harvey, 1982; Nilsen & Linnell, 2006; Hayward *et al.*, 2009). However, if a consistent, albeit complex, set of interacting factors affect range size then it might be expected that patterns of range size (e.g. larger predator species requiring larger ranges than smaller; group living species or sexes using more space than solitary species) will be repeated across different study sites.

Social systems and space use

Lions: Lion pride size and composition are independent of lion density; lion density and home range size are inversely related; and lion density is positively related to rainfall, soil nutrients and annual mean temperature, with some interactive effects between rainfall and soil nutrients, because of the effect of these variables on herbivore density (Coe *et a*l., 1976; Celesia *et al*., 2009).

African lions are large social carnivores (Schaller, 1972), exhibiting pronounced group territorial behaviour. Prides of females, generally related (Gilbert *et al.*, 1991; Spong & Creel, 2001), defend a permanent home range that can persist for generations (McComb *et al*., 1994), whereas males defend access to pride females (Schaller, 1972; Grinnell *et al*., 1995). Prides that fail to defend their home range cannot move elsewhere and perish, and solitary females have very low reproductive success (Pusey & Packer, 1987). Maintaining a home range is thus of great importance, evidenced by the fact that fatalities are relatively common during intergroup encounters (McComb *et al*., 1994). When new prides form they frequently settle adjacent to their natal range, often including parts of their natal range (Pusey & Packer, 1987). As a result pride neighbours are often closely related (Gilbert *et al*., 1991; Spong & Creel, 2001).

Lion density varies regionally, with lower densities in the harsher desert ecosystems such as the Kalahari and Kunene (Mills *et al*., 1978; Funston, 2001; Eloff, 2002; Stander, 2005; Celesia *et al*., 2009) and higher densities in tropical moist savannah such as the Serengeti and Ngorongoro (Makacha & Schaller, 1969; Schaller, 1972; Bertram, 1978; Hanby *et al*.,1995). Lion density and home range size are inversely related; home ranges >140 000 ha are observed in Kalahari-Kunene and <30 000 ha in Serengeti- Ngorongoro (Schaller, 1972;

Bertram, 1978; Mills *et al*., 1978; Smuts, 1978; Van Orsdol *et al*., 1985; Hanby *et al*., 1995; Dricuru, 1999; Funston, 2001; Ogutu & Dublin, 2004). In the arid areas of Namibia (Etosha) lion pride home ranges are as high as 207 500 ha (Stander, 1991) while in other areas the home ranges are smaller: 63 000 ha in Waza National Park (Bauer & de Iongh, 2005); 21 700 ha in Chobe National Park (Viljoen, 1993); 20 000 ha in the Serengeti (Hanby *et al*., 1995); 10 000 to 15 000 ha in Kruger National Park (Whyte, 1985) and as low as 5 200 ha in the Selous Game Reserve (Spong, 2002) which corresponds with the home range size of the reintroduced lions into Phinda (Hunter, 1998). Lion pride home ranges can also vary according to seasons and the associated prey availability. For example, in the Savuti lion home range size increases from 13 600 ha in the wet season to 21 700 ha in the dry season (Viljoen, 1993).

Lions are ambush predators relying on good cover to catch prey (Sunquist & Sunquist, 2002; Hopcroft *et al*., 2005; Roxburgh, 2008). Therefore the structure of the vegetation type influences the hunting success of lions. Lions utilised areas with more thicket vegetation than open vegetation (Funston, 1999). This has been reported previously and vegetation cover is an important variable in hunting success of lions, with the highest success rate occurring in long grass and dense scrub (Schaller, 1972; van Orsdol, 1984; Funston *et al.,* 2001; Spong, 2002). By contrast, in Phinda, lions show greater than expected selection of grasslands and less than expected selection of dense vegetation types, although prides with riparian forest in their ranges show greater than expected use of this habitat type (Hunter 1998). In the Selous Game Reserve, lions prefer the riverine habitat which is expected as areas adjacent to lakes and waterholes are classified as riverine habitat and create good ambush opportunities for a stalking predator like the lion (Spong 2002). Habitat selection of lions may be determined by the availability and abundance of prey, the availability of cover for stalking and lying up, the availability and spacing of suitable den sites, and the availability of water (Schaller 1972; Hanby *et al.,* 1995; Spong, 2002) while Hopcroft *et al*. (2005) suggest that lions select habitats where prey animals are easier to catch, rather than where prey densities are high.

Cheetahs: Like lions, cheetahs display a far greater degree of sociality than most other felids Schaller, 1972; Caro & Collins, 1986; Hunter, 1998). Cheetahs have a very variable social organization that is unique among the felids. Females are solitary or accompanied by dependent young, males are either solitary or live in stable coalitions of two to four males,

and independent adolescents of both sexes stay together for approximately six months (Caro, 1994; Bissett, 2004; Bissett & Bernard, 2007). Most coalitions consist of brothers, but unrelated males may also form part of a coalition (Caro, 1994). Among cheetahs, females appear to be non-territorial and range over wide areas sometimes occupying home ranges as large as 150 000 ha (Caro, 1994; Marker *et al*., 2003). Male cheetahs mate with many females and in the Kruger National Park extensive overlap of male home ranges with female home ranges has been reported (Broomhall *et al*., 2003). Considerable variation in cheetah home range has been observed. In the Serengeti, Thompson's gazelles make up 90% of the cheetah's diet and female cheetahs and non-territorial males travel widely following the gazelle herds and have been reported to have home range sizes of between 77 700 ha and 83 300 ha respectively (Schaller, 1972; Caro & Collins, 1986; Durant *et al*., 1988; Sunquist & Sunquist, 2002). By contrast, the majority of male cheetahs that live in coalitions, are more sedentary than females. In the Kruger National Park and Phinda, where prey are non migratory, male and female cheetahs have smaller overlapping ranges which are similar in size (Hunter, 1998; Broomhall *et al*., 2003, Bissett, 2007). In Zimbabwe's Matusadona National Park female home ranges vary from 1 100 to 2 300 ha (Purchase & du Toit, 2000). In Botswana single males have home ranges ranging from 49 400 to 66 300 ha, while coalitions average 84 900 ha and females 24 100 to 30 600 ha. Relative to those studied elsewhere, Namibian cheetahs have very large home ranges, averaging 105 600 ha annually and 164 200 ha over a lifetime. Ranges are significantly smaller during the wet season, and are inversely related to rainfall. Cheetahs show intensive utilisation of core areas, which comprise a mean of 13.9% of their total home range area (Marker, 2002).

There is a perception that cheetahs have a preference for open plains habitat (Dorst & Dandelot, 1970). However, cheetahs also occur across a wide range of woodland savannas (Skinner & Smithers, 1990; Mills & Hes, 1997). More recent studies of cheetahs in woodland savannas have increased our knowledge of cheetah ecology in these areas (Zank, 1995; Hunter, 1998; Purchase & du Toit, 2000; Broomhall *et al*., 2003; Bissett & Bernard, 2007). Conflicting findings do however still occur such as Hayward *et al.* (2006c) finding that cheetahs do not capture larger prey in more densely vegetated sites, leading to the conclusion that the prey they kill is limited by morphological factors rather than kleptoparasitism avoidance. This contrasts with Bissett's (2007) results which show that cheetah catch adult male kudu in thick bush. Marker (2002) found evidence of habitat preference between sexes,

with female cheetahs preferentially occupying areas of sparse bush and single males appearing to select for thicker bush.

Leopards: Leopards are the most widely distributed wild cats, and occupy a broad variety of habitats, from rainforests to deserts and from the fringes of urban areas to remote mountain ranges (Kitchener, 1991; Nowell & Jackson, 1996). In Africa leopards inhabit over 40 countries ranging from Senegal to South Africa (Nowell & Jackson, 1996), with the most cited sub-Saharan population estimated at 714 000 (Martin & de Meulenaar, 1988) although Nowell & Jackson (1996) believes this to be an over estimation. Leopards are almost entirely solitary, with the territories of females being overlapped by larger territories of similarly solitary males (Bertram, 1999). Leopards show a remarkable degree of variation in range size between different geographical regions (Mizutani & Jewell, 1998; Norton & Henley, 1987; Bothma *et al*., 1997), and this has often been explained in terms of resource availability (McManus, 2009). A comparison of mean home ranges from various studies show that leopards' home ranges in India vary between 2 510 ha and 3 130 ha (Karanth & Sunquist, 2000). In Kenya, home range size of males and females is 3 280 ha and 1 400 ha respectively (Mizutani & Jewell, 1998). In the Kruger National Park, South Africa, home ranges vary from 560 ha to 9 610 ha (Bailey, 1993). In Namibia mean ranges of 21 600 ha and 12 780 ha are utilized by male and female leopards respectively (Mizutani & Jewell, 1998). Previous studies in the Cape Province show range size varying from 38 800 ha to 48 700 ha (Norton & Lawson, 1985) while the greatest mean range size from all studies is for the Kalahari Desert were male leopards use 152 900 ha and females 60 700 ha (Bothma & Bothma, unpublished). Marker & Dickman's (2005) study conversely showed there was no difference in home range size between male and female leopards, either overall, or between wet and dry seasons on Namibian farmlands.

Whether or not home ranges overlap, and the extent to of the overlap, varies in different areas (Stander *et al*., 1997; Mizutani & Jewell, 1998; Marker & Dickman, 2005; McManus, 2009). In Namibia, Marker & Dickman (2005) found that leopards have a mean annual range overlap of 26 ± 15% with conspecifics. Male leopards overlap with each other slightly more 24 ± 13% than females do (22 ± 12%). There is significant variation in the degree of inter- and intrasexual home range overlap, with females overlapping significantly more with males

(40.4 ± 12.2%) than with other females, and intersexual overlap accounting for a greater percentage of female than male ranges.

Leopards do not use available habitat at random (McManus, 2009) and in Phinda leopards hunt in habitats where it is easier to catch prey rather than where prey is more common (Balme *et al*., 2007). Leopards are widely perceived to favour the densest habitats for hunting (Hes, 1991; Bailey, 1993; Sunquist & Sunquist, 2002). The probability of a kill occurring is greater in habitat types with intermediate cover levels, even though areas with the densest vegetation also have the highest abundance of available prey (Balme *et al.,*2007).

Wild dogs: African wild dogs are highly social, cooperative breeding predators that live in packs in which the alpha pair typically monopolizes the breeding while non-reproductive members care for the offspring (Frame *et al*., 1979; McCreery & Robbins, 2001; Creel & Creel, 2002). Across all ecosystems wild dogs occur at low densities relative to competing carnivores (Creel & Creel, 2002) and are affected by substantial edge effects in all but the largest reserves, as a result of the ranging behaviour (Woodroffe & Ginsberg, 1998). It has been suggested that long term viability of wild dog populations and the ecological processes that characterize them may require protected areas as large as 1 000 000 ha (Woodroffe & Ginsberg, 1998). In South Africa, the decision was taken to establish a meta-population through the introduction of wild dogs into geographically isolated reserves, linked through management, to complement the single viable population occurring in the Kruger National Park.

The average of mean multiyear home range of wild dog packs from various studies in southern and eastern Africa is 53 700 ha with an average minimum of 25 820 ha and average maximum of 91 880 ha. Home ranges in the Selous Game Reserve average 43 300 ha (ranging from 15 600 ha to 84 600 ha), with core areas averaging 6 400 ha (ranging from 1 000 ha to 12 400 ha) (Creel & Creel, 2002). In the Kruger National Park, the average home range size for African wild dogs is 53 700 ha (range 35 700 – 93 000 ha). The home range of a denning wild dog pack is reduced and more likely to be in the 5 000-20 000 ha range (CAP 2004).

Packs spend more time near the centre of their range than at the edges, with a core area as small as 14% on average of the total home range. If the average home range size for African wild dogs is 53 700 ha, the average core area will be about 7 500 ha (Andre, 2006). African wild dogs actively defend the core area of their home range and scent-mark it and actively avoid meetings with other packs. Overlap between core areas is rare and the maximum observed is 12% (Creel & Creel, 2002). However, intrusion in the periphery is tolerated with extensive overlaps from 30-35% in Kruger National Park (Reich, 1981); 10-50% (up to 80%) in the Masai Mara (Fuller *et al*., 1990) and 57% being the average area used by a second pack within the home range of a first one in Selous Game Reserve (Creel & Creel, 2002). Overlap can exist between home ranges of more than two packs and within the home range of one pack in Selous Game Reserve, 26% is used by 3 packs, 10% by 4 packs, 5% by 5 packs and even 0.2% by 6 packs (Creel & Creel, 2002). The trend observed is that overlap between areas intensively used is rare while much more common between areas of infrequent use or between areas of infrequent and intensive use (Creel & Creel, 2002). All the authors that have studied the subject agree that such a correspondence in space use is balanced by a strong temporal avoidance making the encounter between two neighbouring packs as rare as possible (Fuller *et al*., 1990, Mills & Gorman, 1997; Creel & Creel, 2002).

In this chapter I have used observations of members of a large carnivore guild at one site across seven years to achieve three main goals. The first goal is site specific and is a better understanding of the space use and distribution patterns of members of a large predator guild that had been reintroduced to SGR. This section deals with the species individually and does not consider interspecific interactions. Such information is important for the management of the system but will also add to the species specific data and allow comparisons to be made with previously published information. Secondly, although this study included no experimental components, some of the natural and management induced changes could be regarded as quasi experimental and allowed an examination of some of the factors that may affect space use. Finally, the spatial distribution of the guild is considered with a focus on intra-guild interactions. Here, I predict that the space use by the lions will closely match that of the prey in line with the prey abundance hypothesis. That space use by cheetahs and wild dogs will be influenced by the presence of lions as a result of both intra-guild competitive interactions and differences in hunting methods. Space use by the leopards will be different from that of the other guild members as a result of differences in diet and hunting behaviour.

Materials and Methods

Data collection and study duration

The data for this chapter were collected by the Shamwari field guides and the monitor using the methods described in Chapter 3. The sightings and kill locations were recorded as grid references and location descriptions which were allocated geographic coordinates and transferred into Arcview 3.2.

Although the study period was from January 2001 to December 2007 this was extended to July 2008 for the study of the space use of the lions so as to include any changes in space use associated with the introduction of a new adult male lion. For all the other members of the large predator guild the study period ended in December 2007.

Home range and core area determination (95% UD and 50% UD)

The home range sizes of all the predator groups were determined using the ArcView extension package, Animal Movement Extension (Hooge & Eichenlaub, 1997). Home range and core area sizes were estimated using a non-parametric method; the fixed kernel utilization distribution (UD) method (Worton, 1989; Powell, 2000). The Kernel UD method was chosen for this study as it more accurately reflects habitat use making it more suitable for studies of habitat selection as opposed to other non-parametric methods such as the minimum convex polygon (MCP; Harris *et al.,* 1990; White & Garrott, 1990; Börger *et al.,* 2006). The UD method is a probability density estimation, which calculates the home range of an animal in terms of the relative amount of time that an animal spends in different areas of the range (Worton, 1989; 1995; Seaman & Powell, 1996). Therefore, the density of points at any location in the reserve is an estimate of the amount of time that a particular animal spent there (Bissett, 2007). In addition, while the MCP method generates a single polygon at each level (50% and 95%), the UD method generates more than one polygon where appropriate (Katajisto & Moilanen, 2006). The UD method is an accurate way to meaningfully calculate home range size (Worton, 1995; Seaman & Powell, 1996; Nilsen *et al.,* 2007; Keating & Cherry, 2009), is increasingly preferred to more traditional methods (Worton, 1995) and has previously been used for analysis of home range patterns in large carnivores (Seaman & Powell, 1996; Bothma *et al*., 1997; Loveridge *et al*., 2009; Thaker *et al*., 2011). The key variable in the UD method is the smoothing factor (H) and in this study, an H value of 1000

was used as it avoided over or under smoothing resulting in too wide or too narrow kernels. The 50% and 95% probabilities were selected as they are generally considered the most robust estimators of an animal's core area and total range size excluding outliers (Mizutani & Jewell 1998; Simcharoen *et al.,* 2007; Loveridge *et al.,* 2009). The 95% and 50% UDs were calculated directly in the Animal Movement Extension. Where necessary, the UDs were clipped to exclude regions outside the reserve boundaries and the remaining areas were recalculated.

Space use was calculated separately using all sightings and a subset of sightings which were sightings of kills only, in order to establish if specific parts of the range were used for hunting more than for other activities.

There is considerable debate around the need to reduce the number of fixes used per day so as to avoid autocorrelation (Börger *et al*., 2006). Indeed, it is argued that by reducing the number of fixes to one per day, biologically valuable information on for example fine scale habitat use, is lost. In this study, the number of fixes per day was rarely more than one and where it was, this was often multiple sightings of animals at a kill site. Since such sightings would be autocorrelated (a second sighting not being independent of the first) a single sighting has been used per day.

Space use per FEQ (lions)

Because the composition of lion prides changed with time, and it can be expected that space use will change with pride size, it was necessary to standardize space use per FEQ. The regular location of large predators on the reserve meant that the number and age of all animals was known. These animals were converted to FEQs as described in Chapter 4 and an average for each year calculated as the mean of the number of FEQs present each month.

Inter-and intra-specific overlap of space use

The overlap of home range and core areas of the different individuals and species was calculated using ArcView 3.2. The 95% UDs and 50% UDs of the neighbouring groups of predators were overlaid, and if their ranges overlapped, the size of the area shared by the neighbouring animals was calculated using the Geoprocessing Tools in ArcView 3.2 (Bissett, 2007). The percentage area overlap was then determined using the following equation

(Millspaugh *et al*., 2004):

$$\% \text{ overlap} = \frac{A_{1,2}}{(A_1+A_2)-A_{1,2}}$$

Where $A_{1,2}$ is the area of overlap, A_1 is the area of animal 1's range and A_2 is the area of animal 2's range.

Habitat use

This analysis was done at a species level using pooled data for all observations of each species and separately, using the subset of kill records. The vegetation of SGR has been described in Chapter 2. The proportion of sightings and kills for each species in each vegetation type was determined using Geoprocessing Tools in Arcview 3.2. To determine the preference or avoidance of specific vegetation types the corresponding proportions of sightings were divided by the proportional availability of the vegetation types in SGR to give a Space Use Index for sightings and a Kill Index for kills per vegetation type (see Kauhala & Auttila, 2010 for similar methodology for second order selection). The relative use of a habitat type for hunting and killing compared to general use (all sightings) was assessed by dividing the Kill Index by the Space Use Index per vegetation type producing what is termed the Kill Conversion Index (a measure of the extent to which time spent in a vegetation type was converted into kills). The possible values for the indices range from 0 to 99.9. A value of one indicates that the vegetation type was used according to its availability, a value of less than one, that it was used less than expected and a value of greater than one, that it was used more than expected. In order to be conservative in the interpretation of these indices, values of 0 to 0.7 were interpreted as avoidance; values of 0.8 to 1.3 were interpreted as use that was in accordance with the relative availability; and values greater than 1.4 as preference.

Where data have allowed, the relationships between a number of factors such as prey distribution and presence of conspecifics, and space use of the predator have been investigated. These analyses differ for the different predators.

Data analysis and statistics

The relationships between the number of lion FEQs and their 95% UDs were examined using linear regression.

ANOVAs, followed by Tukey post hoc tests, were used to examine the effect of range type (95% and 50% UDs), pride and where possible sex, on space used by the predators.

The mean space used by each lion pride per FEQs was compared using a Student's t-test.

Correlation analyses were used to establish if space use per FEQ changed with time.

The effects of changes in the 95% UDs of one pride on space use by the other was examined using linear regressions.

The relationship between predator body size and range size was examined using a linear regression analysis.

Data were tested for normality and non parametric tests were used where appropriate. All statistical tests are described in the results and not listed here. All statistical analyses were done using Statistica (version 9; StatSoft inc. Tulsa, OK, USA).

Results

Lions

Although the number of lion FEQs changed through the study, there was no significant relationship between the number of FEQs in either the northern or southern prides and the sizes of the 95% UD (linear regressions; northern pride, $R^2 = 0.32$; $F_{1,6} = 4.4$; $P>0.05$; southern pride $R^2 = -0.06$; $F_{1,6} = 0.6$; $P>0.05$) or the 50% UD (northern pride $R^2 = -0.12$; $F_{1,6} = 0.2$; $P>0.05$; southern pride, $R^2 = -0.14$; $F_{1,6} = 0.09$; $P>0.05$) (Figure 5.1).

In a two way ANOVA, with range type (95% and 50% UDs) and pride as independent variables, there was a significant effect of range type ($F_1 = 254.0$; $P<0.05$) and pride ($F_1 = 12.7$; $P<0.05$) on the size of the space used, and a significant interaction between the two factors ($F_1 = 6.2$; $P<0.05$). As expected, the 50% UDs of the two prides were significantly smaller than the 95% UDs (Table 5.1). There was no significant difference between the 50% UDs of the two prides, but the 95% UD of the northern pride was significantly larger than that of the southern pride ($P<0.05$; Tukey post hoc test).

When space use was calculated based on location of kills rather than location of all lion sightings, the same pattern occurred and both the 95% and 50% UDs of the northern pride were larger than those of the southern pride (Table 5.1).

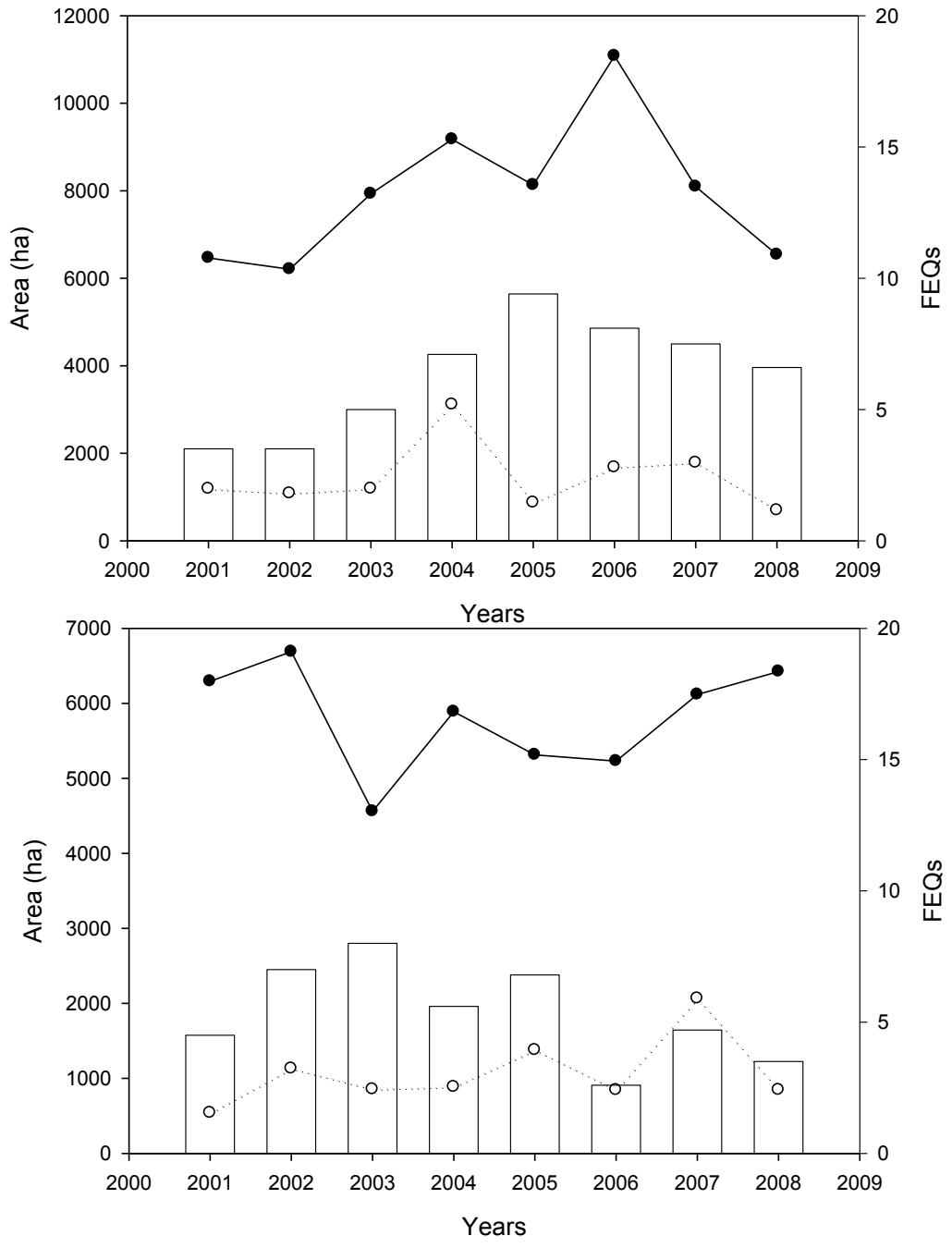


Figure 5.1. Annual changes in the FEQs (bar chart) and in the size of the 95% UD (solid symbols and solid line) and 50% UD (open symbols and dotted line) of the northern pride (top graph) and southern pride (lower graph).

Table 5.1. The space use in hectares for the 50% and 95% UDs of the northern and southern lion prides. In the bottom row, space use is calculated from the location of kills made between 2005 and 2008.

	area (ha)							
	northern pride				southern pride			
period	fixes	FEQ	95% UD	50% UD	fixes	FEQ	95% UD	50% UD
2001	159	3.5	6465	1187	189	4.5	6293	541
2002	154	3.5	6206	1082	143	7.0	6688	1131
2003	164	5.0	7932	1191	182	8.0	4560	855
2004	206	7.1	9173	3116	262	5.6	5888	887
2005	199	9.4	8131	871	234	6.8	5313	1378
2006	277	8.1	11082	1678	290	2.6	5230	845
2007	221	7.5	8092	1782	265	4.7	6118	2066
2008	116	6.6	6538	697	126	3.5	6424	847
2005 - 2008 space use based on kills	813		11 038	2041	915		5624	968
2005 - 2008	188		9705	1935	123		5458	730

For the first four years after introduction, the 95% UD of the northern pride utilized 24.3% of the reserve and the 50% UD occupied 3.4% of the reserve (Table 5.2). For the same period the 95% UD of the southern pride was 20.9% and the 50% UD occupied 4.9% of the reserve. For the second half of the study, the percentage utilization of the reserve by the northern pride increased three fold to 72.2% while the 50% UD increased nearly fourfold to 13.3% of the reserve. The increase in space used by the southern pride during this period was smaller with increases of 1.8 and 1.3 times for the 95% and 50% UDs respectively (Table 5.2). As a result of the differential increase in space use between the prides, in the last four years of the study, the relative size of the space used by the southern pride (southern pride space use/ northern pride space use *100) was about 50% at the 95% UD level and 38% at the 50% UD level (Table 5.2). The analysis of range use based on location of kills gave very similar results to those from the second half of the study (Table 5.2).

Table 5.2. Space use by the northern and southern prides as a percentage of all space available on the reserve. In the bottom row of data, space use is based on locations of kills. Relative size of the southern pride is southern pride space use (ha)/ northern pride space use (ha) * 100.

	northern pride			southern pride			relative size of southern pride	
	fixes	95%	50%	fixes	95%	50%	95%	50%
2001 - 2004	683	24.3	3.4	776	20.9	4.9	86.0	141.1
2005 - 2008	813	72.2	13.4	915	36.8	6.3	51.0	37.8
kills								
2005 - 2008	188	63.5	12.7	123	35.7	4.8	56.2	37.8

The mean space use per FEQ for the two prides was similar (Table 5.3) and there was no significant difference between the mean area per FEQ at the 95% UD or 50% UD levels for the two prides (95% UD; Student's t-test; $t = 0.5$; $df = 14$; $P>0.05$; 50% UD; $t = 0.46$; $df = 14$; $P>0.05$).

Table 5.3. Space use per FEQ for the northern and southern lions.

	area (ha) per FEQ			
	northern Pride		southern Pride	
year	95%	50%	95%	50%
2001	1847.1	339.1	1398.4	120.2
2002	1773.1	309.1	955.4	161.6
2003	1586.4	238.2	570.0	106.9
2004	1292.0	438.9	1051.4	158.4
2005	865.0	92.7	781.3	202.6
2006	1368.1	207.2	2011.5	325.0
2007	1078.9	237.6	1301.7	439.6
2008	990.6	105.6	1835.4	242.0
mean	1350.2	246.0	1238.2	219.5
sd	363.2	116.3	500.6	113.4

Through time, the area per FEQ for the northern pride (95% UD) decreased significantly (correlation coefficient -0.80; $P<0.05$) but the area per FEQ at the 50% UD level did not change significantly (correlation coefficient -0.71; $P>0.05$). The results for the southern pride were the reverse and there was no significant change through time at the 95% UD level (correlation coefficient 0.43; $P>0.05$) but at the 50% UD level, area per FEQ increased significantly (correlation coefficient 0.81; $P<0.05$).

For both prides, the 50% UD was about one fifth (0.18) that of the 95% UD (Table 5.4) and there was no significant relationship between 95% UD and 50% UD for either pride (linear regressions; northern pride $R^2=0.18$; $F_{1,6}$ 2.8; $P>0.05$; southern pride R^2-0.16; $F_{1,6}$ 0.04; $P>0.05$).

Table 5.4. The size of the 50% UD relative to that of the 95% UD (50% UD/95% UD) for the two lion prides.

year	northern pride	southern pride
2001	0.18	0.09
2002	0.17	0.17
2003	0.15	0.19
2004	0.34	0.15
2005	0.11	0.26
2006	0.15	0.16
2007	0.22	0.34
2008	0.11	0.13
mean ± 1sd	0.18 ± 0.08	0.19 ± 0.08

Since it is possible that changes in the 95% UD of one pride might have affected the space used by the other pride, the relationship between 95% UDs and 50% UDs of both prides was investigated (Figures 5.2 & 5.3). Although the 95% UD of the southern pride decreased in size as the 95% UD of the northern pride increased (Figure 5.2), the relationship was not significant (Spearman rank order correlation, $R = 0.38$; $P>0.05$). The lack of significance is likely to result from the very small 95% UD of the southern pride in 2003 (Figure 5.3). However, this value cannot be considered an outlier as it may have been a response to the

increase in 95% UD of the northern pride at this time (Figure 5.3). In Figure 5.3 it can be seen that there were periods when an increase or decrease in the 95% UD of the northern pride was matched by an opposite response from the southern pride (2002-2003; 2006-2008) but this was not consistent. There was no significant relationship between changes in the 50% UD of the northern pride and that of the southern pride (linear regression; $R^2 = -0.16$; $F_{1,6} = 0.02$; $P>0.05$).

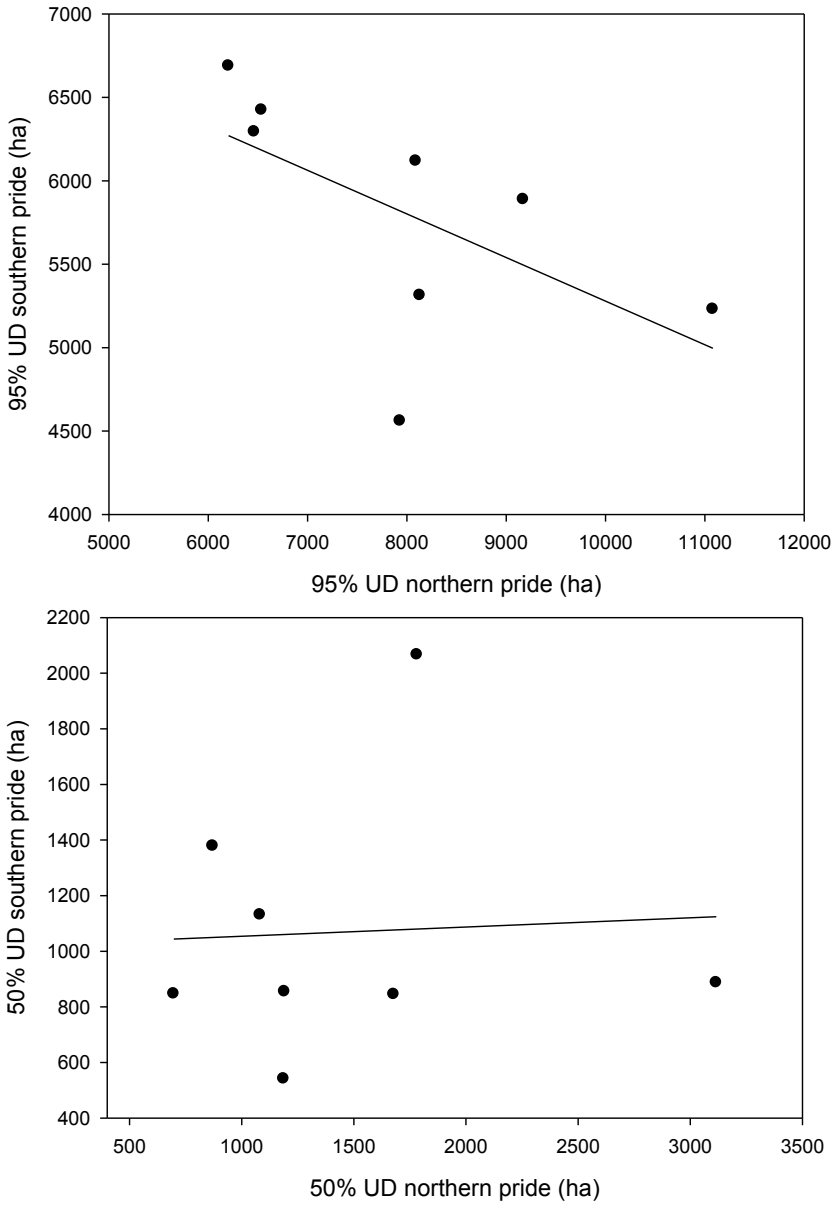


Figure 5.2. The relationship between 95% UDs and 50% UDs of the two lion prides.

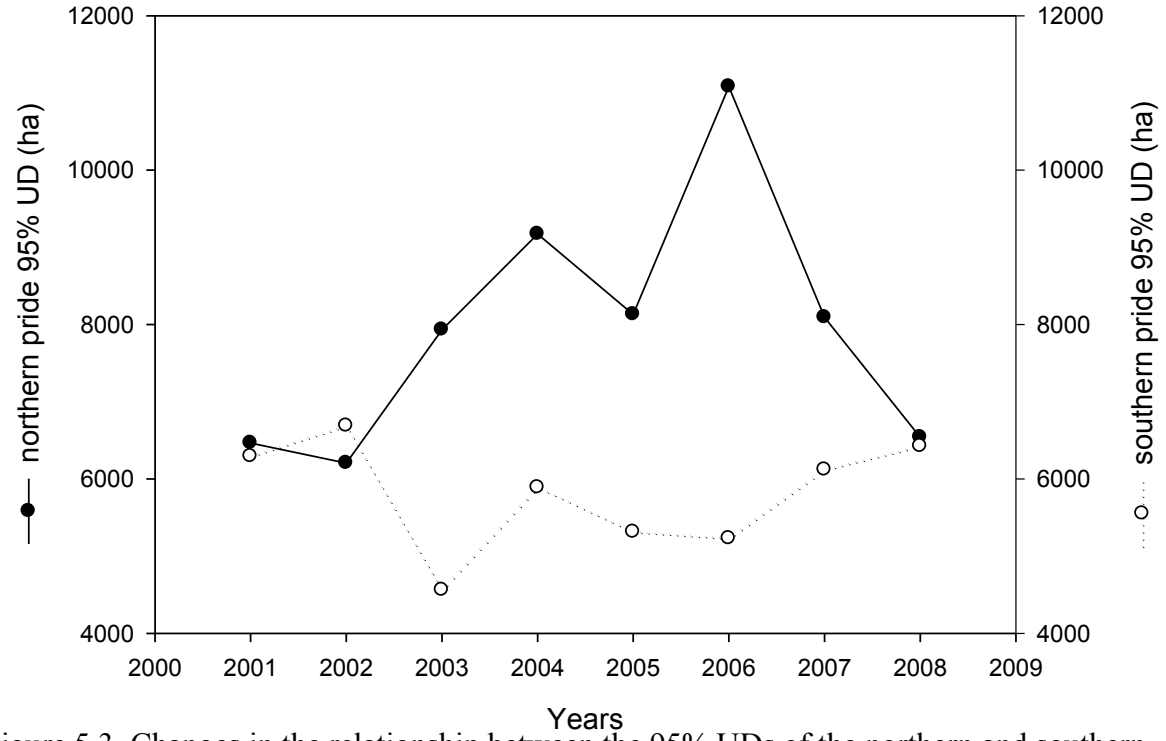


Figure 5.3. Changes in the relationship between the 95% UDs of the northern and southern prides over time.

A comparison of space use based on sightings with that based specifically on the location of kills.

The data sets for all sightings and those for kills were not independent (the kill data set was a subset of the all sightings data set) and it is likely that where the kills comprised a large proportion of the total sightings, the patterns of space use will inevitably be similar and should be interpreted with care. However, where the kills comprised a small proportion of the total observations then differences in space use are more likely to represent real differences between space used for hunting and killing and space used for other activities. No particular threshold has been set for this proportion and decisions have been made based on the percentage (see below).

Southern pride

Kills comprised 13% of all sightings and are unlikely to have played a substantial role in shaping the space use for all sightings. The kills made by the southern pride were concentrated on the open areas along the Bushmans River (Figure 5.4a), and the locations of

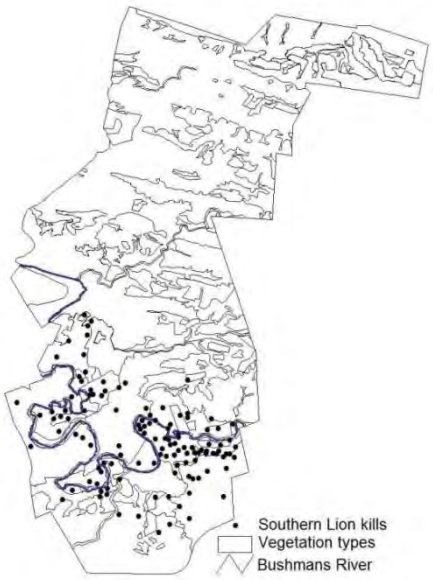
the 95% and 50% UDs based on kills (Figure 5.4b) were very similar to those based on sightings (Figure 5.4c). The overlap between space use and kills was high for both the 95% and 50% UDs (Table 5.5).

Table 5.5. The overlap of space use and kill distribution for the northern and southern prides of lions

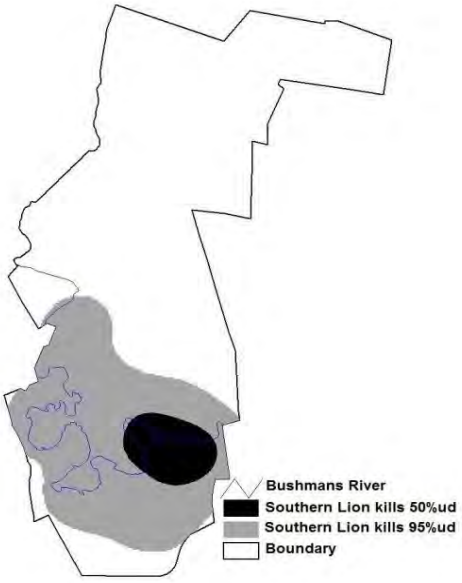
pride	overlap of kill and sighting UDs	
	95% UDs	50% UDs
southern	86.2%	74.3%
northern	74.9%	21.5%

Northern pride

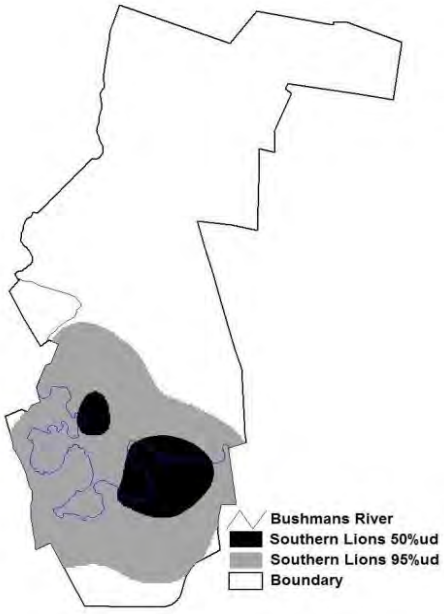
For the northern pride, kills comprised 23% of all sightings and it is more likely that the distribution of kills would have shaped the overall space use based on all sightings. The kills made by the northern pride were more dispersed than those of the southern pride with several smaller pockets of higher density kills, specifically on the more open areas in the north east and north west of the reserve (Figure 5.5a). The 95% UD based on kills (Figure 5.5b) closely resembled the 95% UD based on all sightings (Figure 5.5c) and there was substantial overlap (Table 5.5). The 50% UD based on kills differed from the 50% UD (all sightings) and the overlap was less (Table 5.5).



a) Map of the reserve showing the GPS locations of known kills.



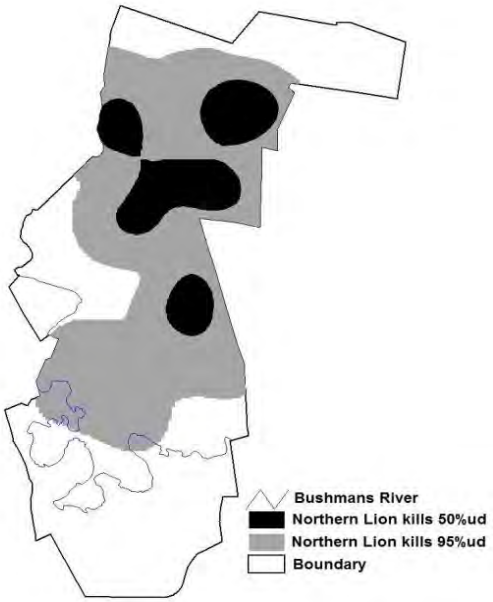
b) Map of the reserve showing the 50% and 95% UD of known kills.



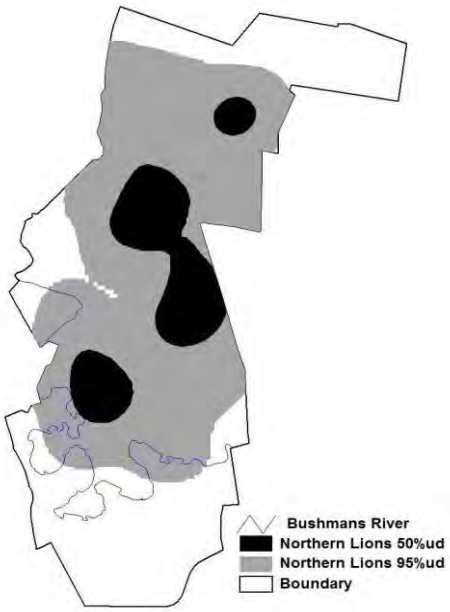
c) Map of the reserve showing 50% and 95% UD of sightings and their position relative to the Bushmans River, reserve boundary and vegetation types.

Figure 5.4. Space use of the southern pride for the duration of the study period based on the actual positions of all kills (a & b) and the sightings (c).

a) Map of the reserve showing the GPS locations of known kills and their position relative to the Bushmans River, reserve boundary and vegetation types.



b) Map of the reserve showing the 50% and 95% UD of known kills and their position relative to the Bushmans River and reserve boundary.



b) Map of the reserve showing 50% and 95% UD of sightings and their position relative to the Bushmans River, reserve boundary and vegetation types.

Figure 5.5. Space use of the northern pride for the duration of the study period based on the actual positions of all kills (a & b) and the sightings (c).

Habitat Selection (Pride level analysis)

Southern pride

The 95% UD (based on sightings) of the southern pride included eight vegetation types of which three (Subtropical Thicket, Primary *Acacia* Thicket and cultivated lands) comprised 75% of the space used (Table 5.6). Of these, the proportions of Primary *Acacia* Thicket and cultivated lands in the 95% UD were greater than their availability in the reserve while for Subtropical Thicket, it was substantially less (Table 5.6). The southern pride preferred the Riverine Bush, Primary *Acacia* Thicket, Secondary *Acacia* Thicket, Lowland Grassland, cleared lands and cultivated lands (Table 5.6). The strongest preferences were for Primary *Acacia* Thicket and cleared lands with preference indices of 6.1 and 4.5 respectively although cleared lands made up a small proportion of the space used by the southern pride (Table 5.6). The proportional use of all other vegetation types was less than the proportional availability in SGR and they were avoided. Of particular significance was the avoidance of Subtropical Thicket which comprised 43% of the reserve but only 20% of the space used by the lions (Table 5.6).

Kills were observed in all of the vegetation types represented within the 95% UD of the southern pride and 59% of kills were recorded in two vegetation types (Primary *Acacia* Thicket and cultivated lands) and 86% of kills in four vegetation types (Table 5.6). Subtropical Thicket, Bontveld and Riverine Bush were avoided for hunting (kill index <0.8). The records of kills in the different vegetation types followed a similar pattern to that of the general space use except for Riverine Bush which comprised more than 4% of the space used but in which less than 2% of kills were recorded (Table 5.6). The kill conversion index (which compares the kill index and the space use index) was greater than one for only Lowland Grassland (1.7) and cultivated lands (1.2) (Table 5.6).

Table 5.6. Habitat use and habitat in which kills of the southern pride were recorded. The available column is the availability of each vegetation type in the reserve as a percentage. Space use and kills is the percentage of all sightings and kills in each vegetation type within the 95% UD. Disturbed lands is included as a biome.

		space			space use	kills	kill conversion
biome	vegetation type	available	use	kills	index	index	index
Forest	Afromontane Forest	0.5	0.0	0.0	0.0	0.0	0.0
Thicket	Subtropical Thicket	42.8	20.1	15.7	0.5	0.4	0.8
	Bontveld	8.1	4.0	4.1	0.5	0.5	1.0
	Bushclump Savanna	3.6	0.0	0.0	0.0	0.0	0.0
Savanna	Riverine Bush	2.5	4.7	1.7	1.9	0.7	0.4
	1^{o} *Acacia* Thicket	5.7	34.8	33.9	6.1	5.9	1.0
	2^{o} *Acacia* Thicket	2.1	3.1	2.5	1.5	1.2	0.8
Fynbos	Grassy Fynbos	0.7	0.0	0.0	0.0	0.0	0.0
	Calcrete Fynbos	0.0	0.0	0.0	0.0	0.0	0.0
Grassland	Montane Grassland	17	0.0	0.0	0.0	0.0	0.0
	Lowland Grassland	3.7	6.7	11.6	1.8	3.1	1.7
disturbed	cleared lands	1.4	6.3	5.8	4.5	4.1	0.9
lands	cultivated ands	11.9	20.3	24.8	1.7	2.1	1.2
		100.0	100.0	100.0			

Northern pride

The 95% UD (based on sightings) of the northern pride incorporated nine vegetation types of which four (Subtropical Thicket, Primary *Acacia* Thicket, Montane Grassland, cultivated lands) comprised 80% of the space used (Table 5.7). Of these, the proportions of sightings in Primary *Acacia* Thicket, Montane Grassland, cultivated lands in the 95% UD were greater than the availability on the reserve, while for Subtropical Thicket, it was less (Table 5.7). The northern pride preferred the Primary and Secondary *Acacia* Thickets as well as the cleared and cultivated lands. The cleared lands were the most preferred and were utilized 4.4 times more than their representation on the reserve (Table 5.7). Despite spending more time

(29.2%) in the Subtropical Thicket than any other vegetation type, this vegetation type was avoided as it was the most abundant vegetation in SGR. Bontveld and Riverine Bush were also avoided while the rest were utilized in accordance with their abundance on the reserve. Kills were recorded in all the vegetation types that occurred in the 95% UD of the northern pride and 76% of kills were recorded in four vegetation types (Table 5.7). Secondary *Acacia* Thicket, cleared and cultivated lands and Bushclump Savanna were preferred vegetation types for killing and Subtropical Thicket, Bontveld and Riverine Bush were avoided (Table 5.7). The kill conversion index was greater than one for Bushclump Savanna with a kill conversion rate of 1.5 and cultivated lands (1.3) (Table 5.7).

Table 5.7. Habitat use and location of kills of the northern pride. The available column is the availability of each vegetation type in the reserve as a percentage. Space use and kills is the percentage of all sightings and kills in each vegetation type within the 95% UD. Disturbed lands is included as a biome.

		space					kill
biome	vegetation type	available	use	kills	space use index	kills index	conversion index
Forest	Afromontane Forest	0.5	0.0	0.0	0.0	0.0	0.0
Thicket	Subtropical Thicket	42.8	29.2	29.3	0.7	0.7	1.0
	Bontveld	8.1	2.1	0.5	0.3	0.1	0.2
	Bushclump Savanna	3.6	4.2	6.4	1.2	1.8	1.5
Savanna	Riverine Bush	2.5	1.4	0.5	0.6	0.2	0.4
	1^{o} *Acacia* Thicket	5.7	10.8	6.9	1.9	1.2	0.6
	2^{o} *Acacia* Thicket	2.1	5.7	5.3	2.7	2.5	0.9
Fynbos	Grassy Fynbos	0.7	0.0	0.0	0.0	0.0	0.0
	Calcrete Fynbos	0	0.0	0.0	0.0	0.0	0.0
Grassland	Montane Grassland	17	21.0	22.9	1.2	1.3	1.1
	Lowland Grassland	3.7	0.0	0.0	0.0	0.0	0.0
disturbed	cleared lands	1.4	6.1	3.7	4.4	2.6	0.6
lands	cultivated lands	11.9	19.3	24.5	1.6	2.1	1.3
		100	100	100			

Factors affecting space use

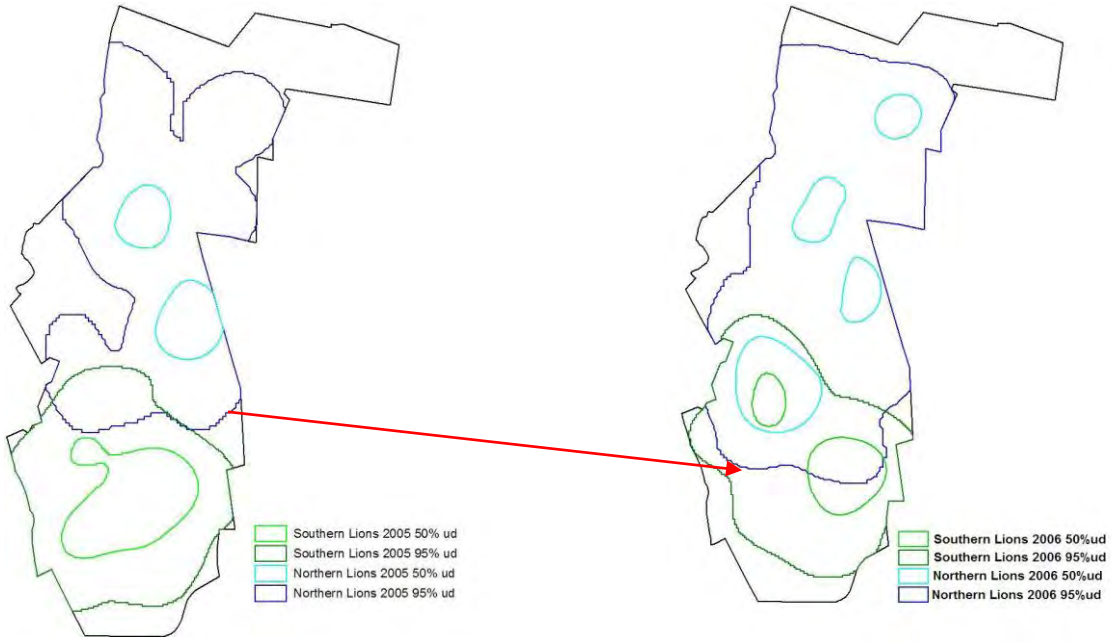
In the following sections, the influences of a number of factors that might affect space use are explored.

The influence of the presence of adult male lions on space use by the prides.

During the study, the number of adult males in each pride varied as a result of natural processes and management interventions. Associated with these changes in the presence of adult males were changes in space use, and two examples are described below.

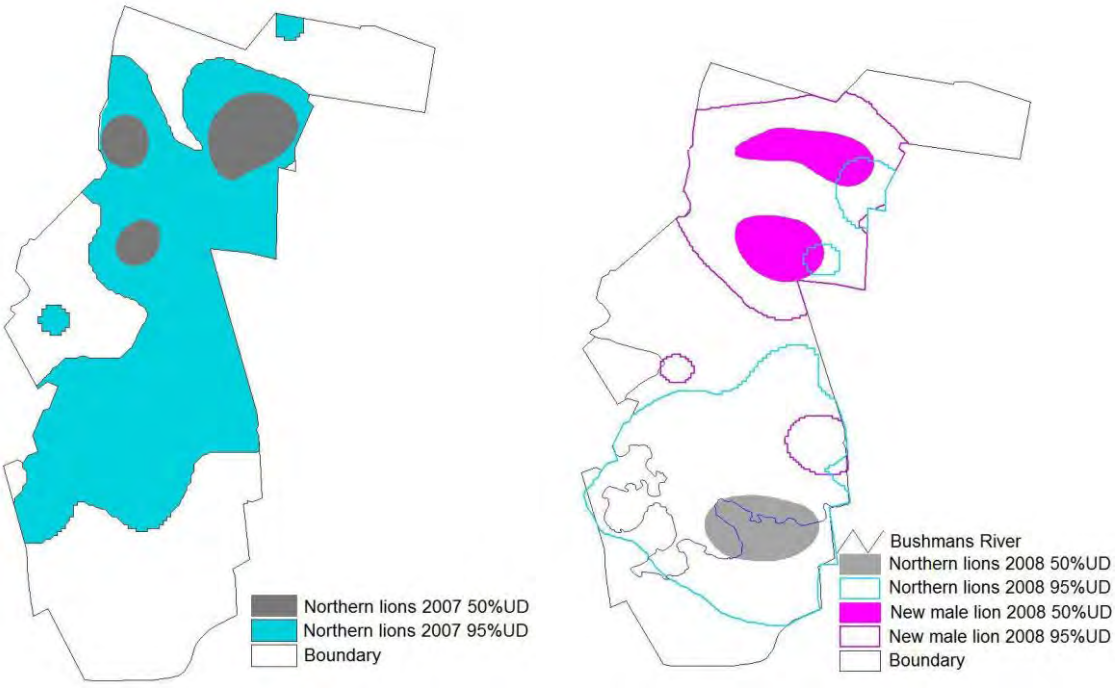
In 2005, both the northern and southern prides had single adult pride males. At this stage the northern pride had a home range of 8131 ha and a core area of 871 ha and the southern pride 5313 ha and 1378 ha respectively (Figure 5.6a; Table 5.1). In 2006, the adult male lion in the southern pride was killed by the adult male lion from the northern pride and, associated with this, the northern pride's home range extended to the south and increased to 11082 ha and the core area to 1678 ha (Figure 5.6b; Table 5.1). Although the southern pride's home range remained stable, the core area shrank to 845 ha. In 2005, there was no overlap of the 50% UDs of the two prides, but in 2006, one section of the 50% UD of the northern pride overlapped completely with one section of the 50% UD of the southern pride (Figure 5.6b).

In 2008 both adult male lions were removed from the reserve and exchanged for a genetically unrelated adult male lion to enhance the genetic diversity of the lions in SGR. On release the introduced male lion occupied the northern part of the reserve while the northern pride, at that time without a pride male, moved south (Figure 5.7b). This southward displacement of the northern pride is evident in comparison to the northern pride's space use for 2007, the year preceding the release of the new male (Figure 5.7a). The 95% UD of the northern pride overlapped substantially with that of the southern pride however the core areas of both prides remained separate. This space use pattern remained for several months until a female in the northern pride came into oestrus and the northern pride moved back north late in 2008.



a) Space use by lion prides 2005. B) Space use by lion prides in 2006

Figure 5.6. Changes in space use by the two lion prides between 2005 (a) and 2006 (b). Note the southwards extension of the 95% UD of the northern pride in 2006.

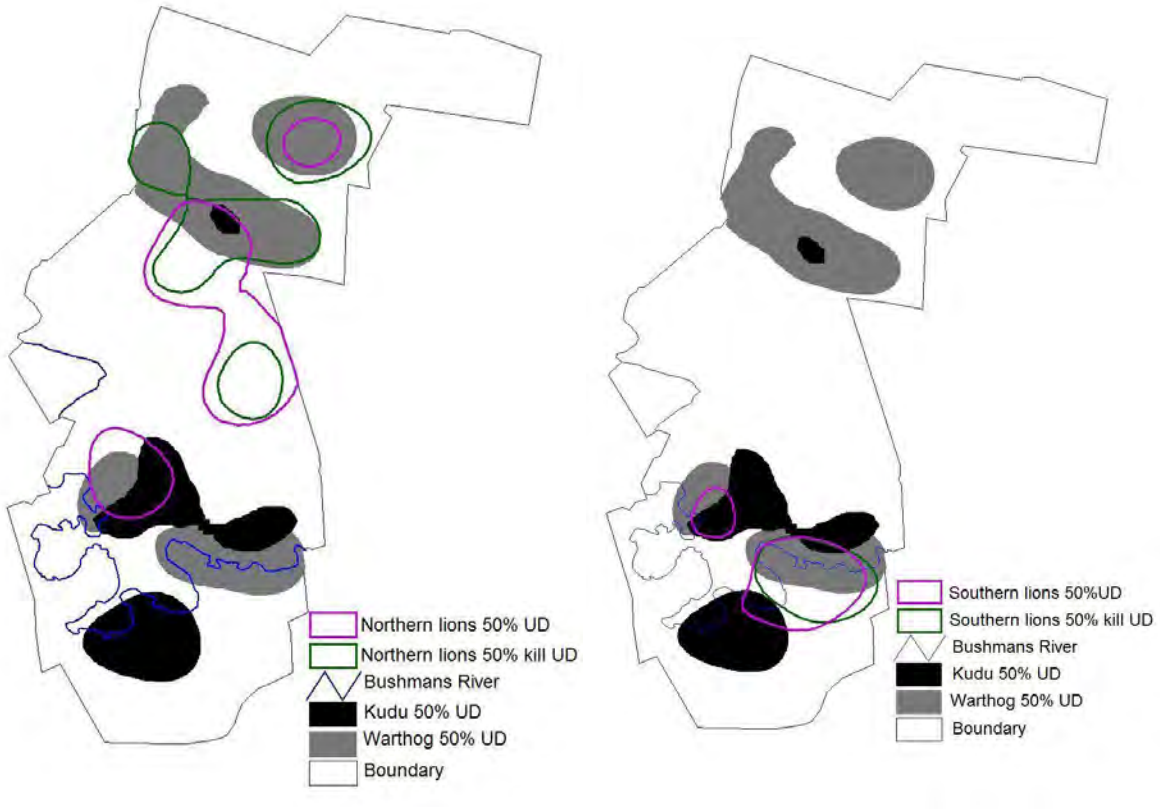


a) Northern pride 2007 b) Northern pride and new male 2008

Figure 5.7. A comparison of space used by the northern pride in 2007 with space used in 2008 after introduction of a new adult male.

The relationship between the distribution of kudu and warthog, and space use of lions

As shown in Chapter 4, kudu and warthog were important components of the diet of the lions in SGR. The 50% UD of kudu was in the south of the reserve, with a small patch in the north, while the 50% UD of the warthog was in four sections, two in the south and two in the north (Figure 5.8). Throughout the study, there was considerable overlap of the 50% UDs of the northern lions (Figure 5.8a) and southern lions (Figure 5.8b) with the 50% UD of warthog and less overlap with the 50% UD of kudu (Table 5.8).



a) Northern pride b) Southern pride

Figure 5.8. The relationship between space use of warthogs and kudu, and the 50% UD space use of lions.

Table 5.8. Summary of the extent of the overlap of space used by the lions and two of their important prey species, warthog and kudu.

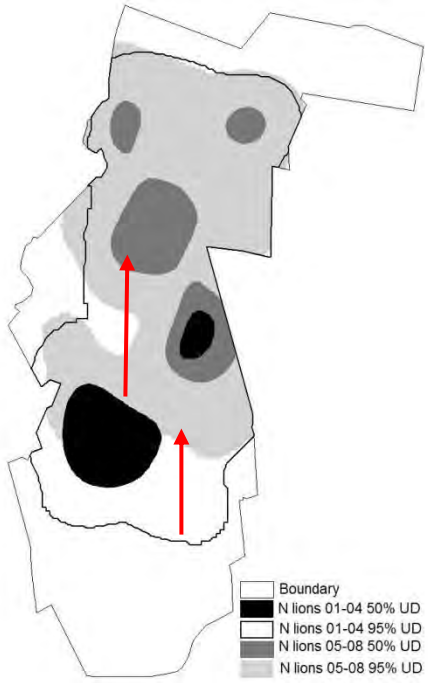
	northern pride		southern pride	
	50% UD	50% UD (kills)	50% UD	50% UD(kills)
warthog 50% UD	24.7%	23.2%	28.0%	25.3%
kudu 50% UD	14.0%	2.7%	19.5%	3.0%

As reported in Chapter 4, the diet of the lions changed from one dominated by kudu in the first half of the study (2001-2004), to a diet dominated by warthog in the second half of the study (2005-2008). Since the distribution of kudu was predominantly in the south and warthogs equally in the north and the south, it might be expected that the diet shift would be matched by a shift in space use of the two prides. For the northern pride, there was a slight northwards shift in the 95% and 50% UDs for sightings between the first half of the study and the second half (Figure 5.9a). The 50% UD was larger in the second half of the study than in the first (Table 5.9). The northward shift in space use was less apparent for UDs based on kills (Figure 5.9b).

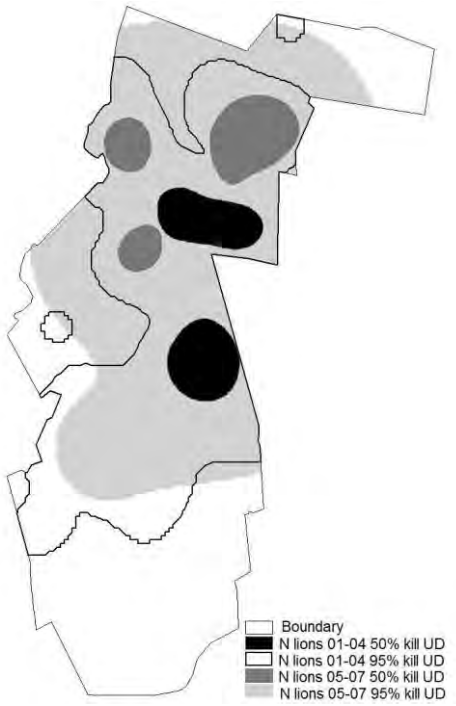
For the southern pride there was very little change in space use, or size of the space used, based on sightings or kills from the first to the second half of the study (Figure 5.9 c,d; Table 5.9).

Table 5.9. The space use in hectares for sightings and kills of both the northern and southern prides of lions in SGR for the first and second half of the study period.

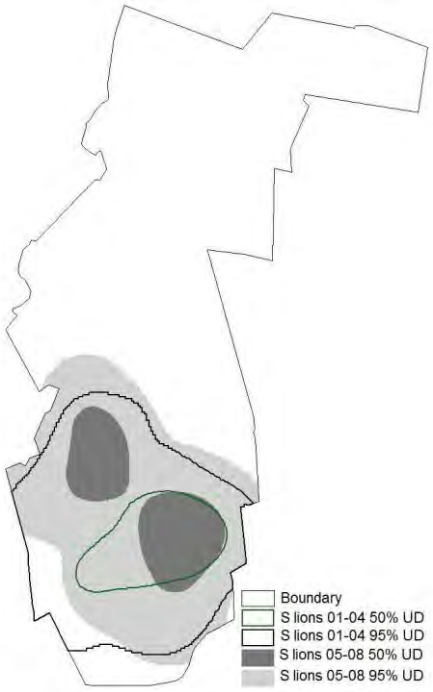
	sightings (ha)		%	kills (ha)		%
	2001 - 2004	2005 - 2008	change	2001 - 2004	2001 - 2007	change
southern pride						
50% UD	1125	1223	8.7	687	743	8.2
95% UD	5175	5550	7.2	4829	5576	15.5
northern pride						
50% UD	950	1540	62.1	993	991	-0.2
95% UD	10422	9008	-13.6	9822	13306	35.5



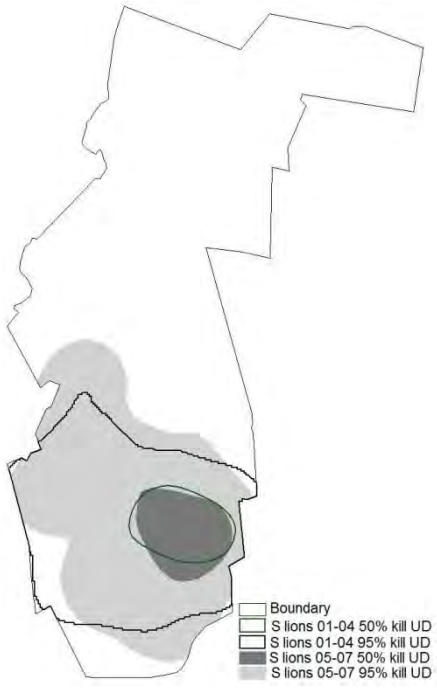
a) northern pride, all sightings



b) northern pride, kills



c) southern pride, all sightings



d) southern pride, kills

Figure 5.9. The change in space use based on all sightings and on kills from the first half (2001 – 2004) to the second half (2005 – 2007) of the study for the northern pride (a & b) and the southern pride (c & d).

For both prides, the percentage overlap of space use with that for kudu was lower in the second half of the study than the first (Table 5.10). However, overlap with space used by warthog did not increase in the second half of the study for the northern pride but did for the southern pride (Table 5.10). In the first half of the study the overlap of lion 50% UDs (all sightings) was similar for both kudu and warthog (20 – 30%) and in the second half of the study, overlap was in all cases higher with space used by warthogs than with kudu (Table 5.10).

Table 5.10. Summary showing the extent of overlap between the space used by lions and by kudu and warthog.

years	overlap with	northern pride		southern pride	
		50% UD (sightings)	50% UD (kills)	50% UD (sightings)	50% UD (kills)
2001-2004	warthog 50% UD	21.9%	23.1%	26.5%	28.9%
2005-2008	warthog 50% UD	10.4%	18.6%	41.3%	25.3%
2001-2004	kudu 50% UD	32.8%	3.6%	24.6%	2.2%
2005-2008	kudu 50% UD	2.8%	0%	13.3%	0.6%

Leopards

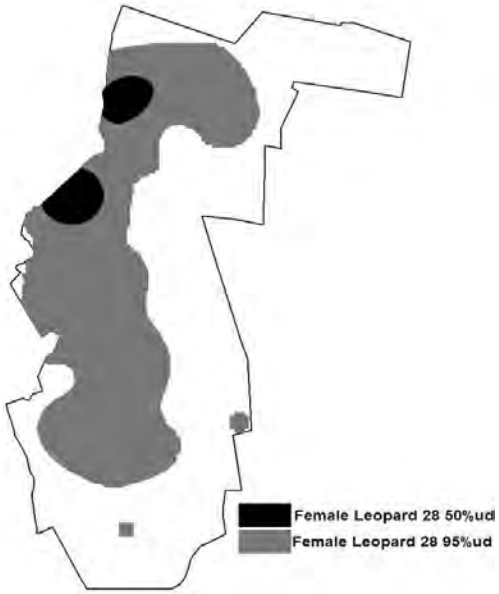
Two of the female leopards (#98 and #38) had home ranges that were predominantly in the south of the reserve, while the third female (28) utilised most of the western length of the reserve (Figure 5.10). The space used by females 98 and 38 was similar in size (Table 5.11) and the proportional size of the 50% UD was the same (0.16; Table 5.11). The third female (Figure 5.10a), had a much larger 95% UD but similar sized 50% UD and the proportional size of the 50% UD was half that of the other females (Table 5.11). The home range of the male leopard extended beyond the western boundary of the reserve and covered most of the reserve with four separate core areas (Figure 5.10d). The average size of the 95% UD of the female leopards was 5713 (± 1664) ha which covered 37.4% of the reserve (Table 5.9). The average size of the female core areas was 725 (± 83) ha which covered 4.7% of the reserve. The 95% UD of the male leopard was larger than the reserve (104.4%) because it extended beyond the reserve boundaries although there were small sections of the reserve that fell outside the 95% UD (Figure 5.10). When all sightings of leopards were combined, the 95%

UD for the species covered 83.3% of the reserve and the 50% UD represented 4.6% of the reserve.

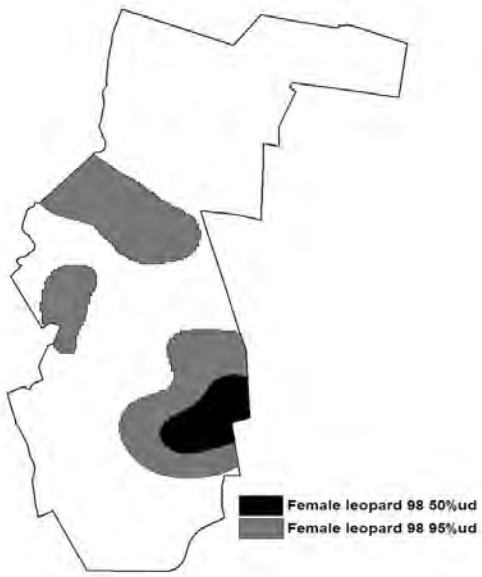
The sightings of kills comprised a small proportion of all sightings (0.02%) and it is thus unlikely that the positions of kills had much influence on the overall space use. However, it is also unlikely that the observed distribution of kills, which was predominantly in the south of the reserve (Figure 5. 11) reflects their real distribution due to the locations of missed kills. The 95% UD based on kills was approximately half that based on general space use while the 50% UD based on kills was almost double (Table 5.11).

Table 5.11. The sizes of the 95% and 50% UDs for the leopards in SGR.

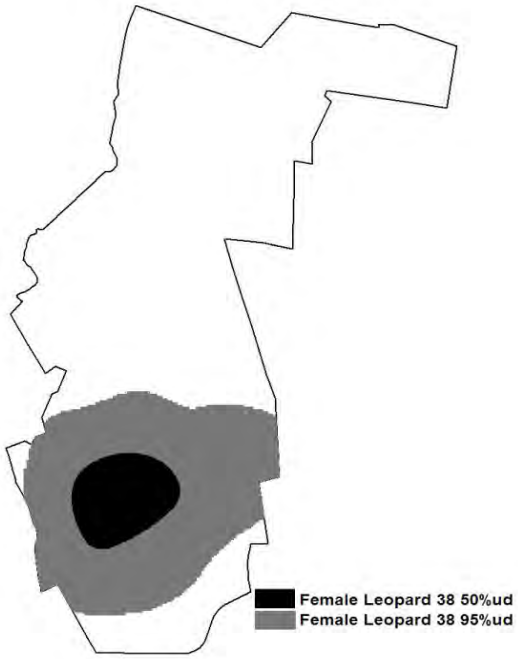
		area (ha)			percentage of reserve	
period	fixes	95% UD	50% UD	50%/95%	95% UD	50% UD
female leopard 28	133	7618	644	0.08	49.9%	4.2%
female leopard 98	101	4538	723	0.16	29.7%	4.7%
female leopard 38	717	4985	809	0.16	32.6%	5.3%
mean female		5713.7	725.3	0.13	37.4%	4.7%
male leopard unclipped	1177	15946	2113	0.13	104.4%	13.8%
all leopards	2128	12723	699	0.05	83.3%	4.6%
leopard kills	46	6414	1534	0.24	42.0%	10.0%



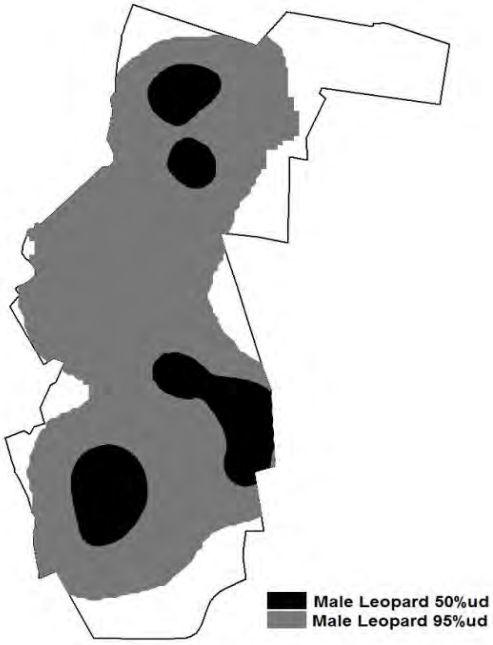
a) Female leopard #28



b) Female leopard #98



c) Female leopard #38



d) Male leopard (clipped to show reserve space use)

Figure 5.10. Map of SGR showing the 50% and 95% UDs of leopards based on sightings.

Leopard space use overlap

The 95% UD of the male leopard overlapped completely with those of the three females while at the core area level, there was some overlap with the core area of each female (Figure 5.11; Table 5.12). The core areas of the female leopards did not overlap (Table 5.12; Figure 5.11).

Table 5.12. Overlap of home ranges (above the diagonal) and core areas (below the diagonal) of the leopards.

leopards	female 28	female 98	female 38	male
female 28	/	12.4%	29.2%	100%
female 98	0.0%	/	31.1%	100%
female 38	0.0%	0.0%	/	100%
male	3.5%	20.0%	23.3%	/

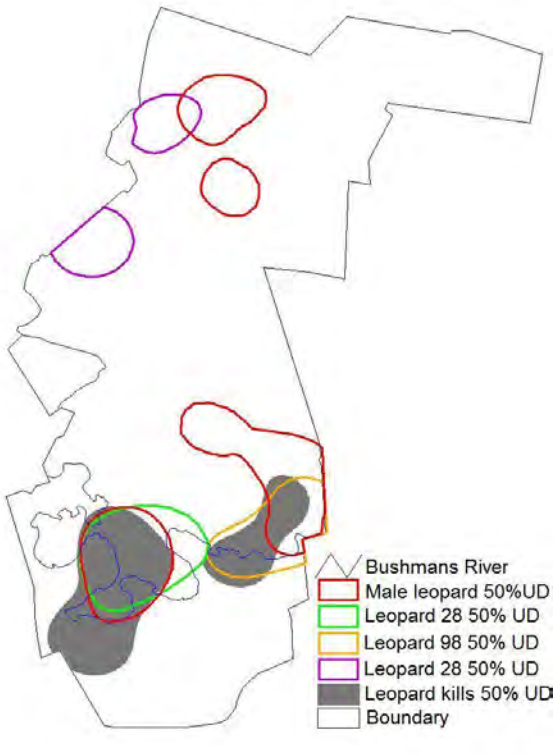
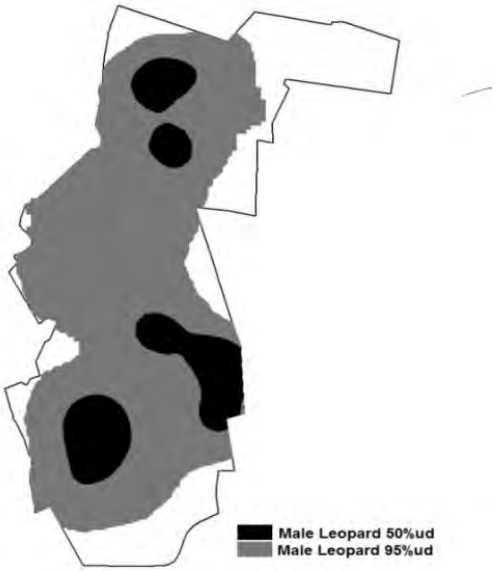


Figure 5.11. The 50% UDs for all leopards in SGR as well as the 50% UD based on recorded kills of all leopards.

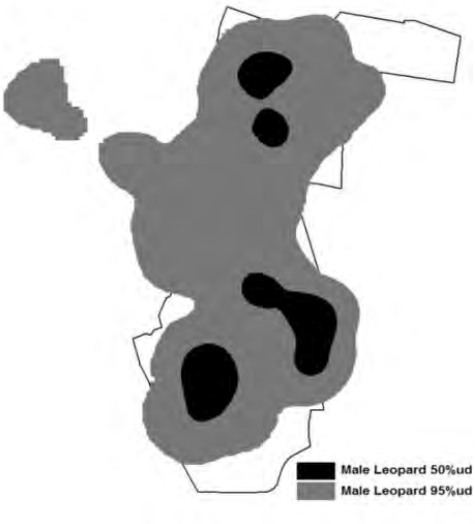
Change in space used by the male leopard with time.

The male leopard was introduced into SGR at 10 months of age in 2004. For the first 17 months only the southern sector of the reserve was used (Figure 5.12a) with a 95% UD of 5205 ha and a 50% UD of 1260 ha. Thereafter, the range expanded to include most of the reserve and areas outside the western boundary of the reserve (Figure 5.12b & c).

a) Male leopard space use for the first 17 months



b) Male leopard clipped space use after first 17 months



c) Male leopard unclipped space use after first 17 months.

Figure 5.12. The changes in space use by the male leopard in SGR.

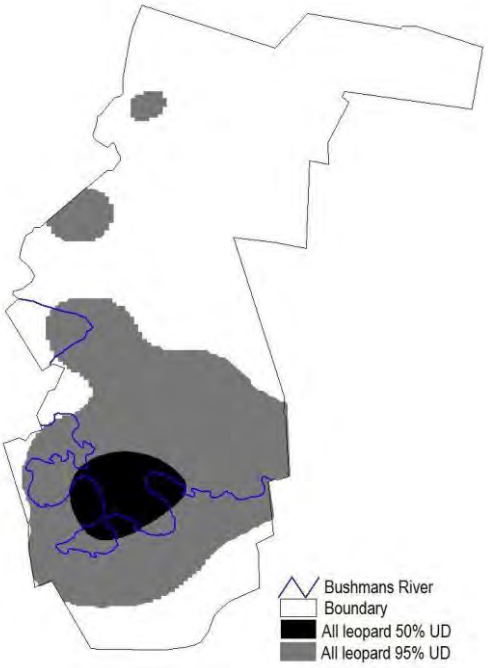
A comparison of leopard space use based on sightings with that based specifically on the location of kills.

Although the data sets for all sightings and those for kills were not independent, the number of kills recorded was very low (46) in relation to the total number of sightings (2128) and it is unlikely that the location of kills had a substantial effect on the overall space use.

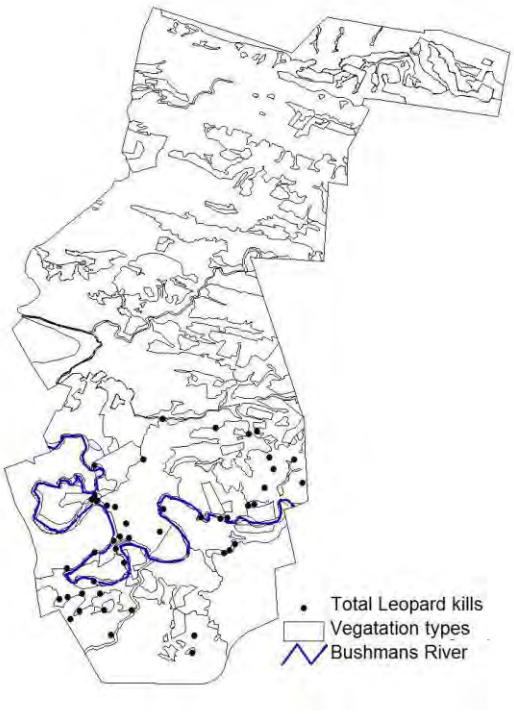
When the sightings for all leopards were combined, most of the reserve was used (Figure 5.13). The 95% UD was 12723 ha (83.3% of the reserve) with a 50% UD of 699 ha (4.6% of the reserve; Table 5.11). The recorded kills made by all the leopards were concentrated in the south of the reserve, along the Bushmans River and primarily in the Subtropical Thicket vegetation (Figure 5.13b). The 95% UD based on the location of kills was 6414 ha and the 50% UD was 1534 ha (Figure 5.13; Table 5.11). The 50% UD based on all sightings and the 50% UD based on kills overlapped in the vicinity of the Bushman's River (44.7% overlap). The extent of the overlap differed between the different individual leopards (Table 5.13). As expected, it was lowest for female 28 whose 50% UD was in the North of the reserve and higher for the other females and male (Table 5.13).

Table 5.13. The overlap of space use and kill distribution for all leopards

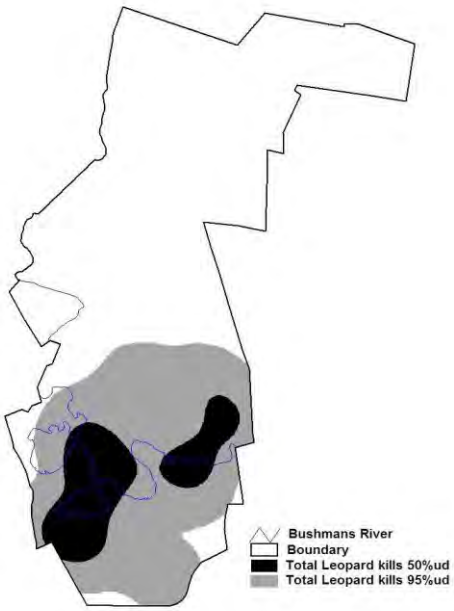
leopard	overlap of kill and sighting UDs		number of kills
	95% UDs	50% UDs	recorded
all leopards	72.4%	44.7%	46
female 28	27.9%	0%	12
female 38	75.8%	47.3%	23
female 98	33.7%	33.5%	8
male	42.5%	33.6%	3



a) Map of the reserve showing the 50% and 95% UD of known kills and their position relative to the Bushmans River, reserve boundary and vegetation types.



b) Map of the reserve showing the GPS locations of known kills and their position relative to the Bushmans River, reserve boundary and vegetation types.



c) Map of the reserve showing 50% and 95% UD of sightings and their position relative to the Bushmans River, reserve boundary and vegetation types.

Figure 5.13. The location of 50% and 95% UDs for all leopard sightings (a), the actual positions of all kills (b) and for all kills (c)

Habitat Selection of leopard (species level analysis)

The 95% UDs of the leopards incorporated 11 of the 13 vegetation types (Table 5.14). More than 50% of all observations were in Subtropical Thicket and 18% were in Riverine Bush. In relation to the availability of the vegetation types, the leopards used Afromontane Forest, Riverine Bush, Primary and Secondary *Acacia* Thickets preferentially (Table 5.14). The strongest preference was for Riverine Bush which was used 7.3 times that of its relative abundance. Subtropical Thicket was not preferred (42.8% available). Bontveld, Bushclump Savanna and the disturbed lands were avoided with the Fynbos elements and Montane Grassland not being utilized at all. The remainder of the vegetation types were utilized in accordance with their relative abundance (Table 5.14).

Leopard kills were recorded in eight of the 11 vegetation types with half of the kills being recorded in Subtropical Thicket and more than 10% of the kills in each of Riverine Bush and Primary *Acacia* Thicket (Table 5.14). Leopards killed more frequently in Bontveld, Riverine Bush and Primary *Acacia* Thicket than expected based on the relative abundance of these vegetation types. Kills in Secondary *Acacia* Thicket and Subtropical Thicket were made in accordance with their relative abundance while the remainder of the vegetation types were avoided for hunting. The conversion rate for the number of kills in a vegetation type relative to the amount of time spent in that area was greatest for Bontveld, Bushclump Savanna and Lowland Grasslands with the latter two having a kill conversion index of 7.3 (Table 5.14).

Table 5.14. Habitat use and location of kills of the leopards. The available column is the availability of each vegetation type in the reserve as a percentage. Space use% and kill% is the percentage that each vegetation type comprised within the 95% UDs based on all sightings or kills. Disturbed lands is included as a Biome.

		space			space use	kill	kill conversion
biome	vegetation type	available	use	kills	index	index	index
Forest	Afromontane Forest	0.5	0.7	0.0	1.4	0.0	0.0
Thicket	Subtropical Thicket	42.8	55.5	50.0	1.3	1.2	0.9
	Bontveld	8.1	3.4	13	0.4	1.6	3.8
	Bushclump Savanna	3.6	0.3	2.2	0.1	0.6	7.3
Savanna	Riverine Bush	2.5	18.2	13.0	7.3	5.2	0.7
	1^{o} *Acacia* Thicket	5.7	11.0	10.9	1.9	1.9	1.0
	2^{o} *Acacia* Thicket	2.1	3.6	2.2	1.7	1.0	0.6
Fynbos	Grassy Fynbos	0.7	0.0	0.0	0.0	0.0	0.0
	Calcrete Fynbos	0.0	0.0	0.0	0.0	0.0	0.0
Grassland	Montane Grassland	17.0	0.2	0.0	0.0	0.0	0.0
	Lowland Grassland	3.7	0.3	2.2	0.1	0.6	7.3
disturbed	cleared lands	1.4	0.5	0	0.4	0.0	0.0
lands	cultivated lands	11.9	6.3	6.5	0.5	0.5	1.0
		100.0	100.0	100.0			

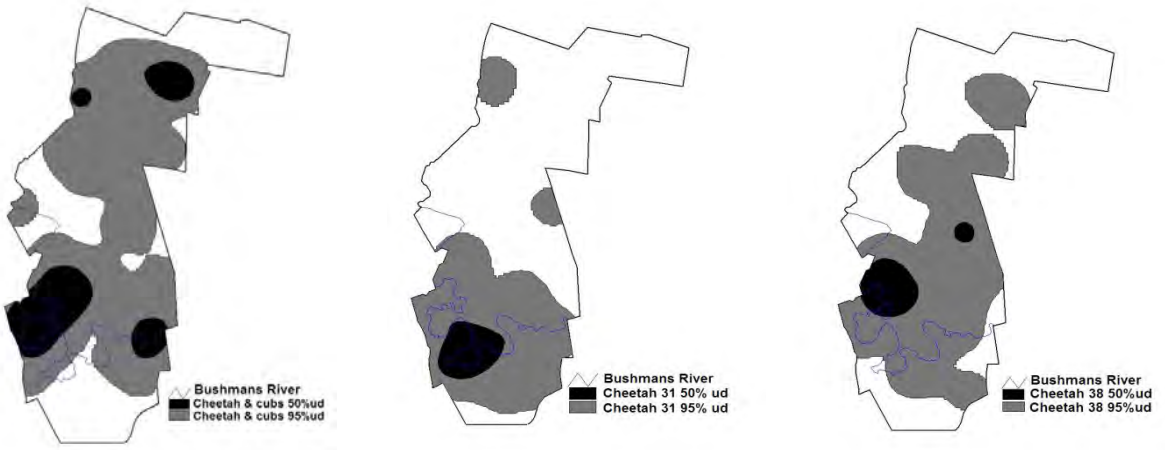
Cheetahs

Data on space use were available for three solitary adult females (31, 38 & 58), for adult female 22 with cubs and for a single adult male. These animals were not all on the reserve for the entire study period and this is mentioned in the results, where relevant. The sample sizes are small and data are interpreted with caution.

The home ranges of the adult female cheetahs varied in size and the 95% UD of female 38 was almost twice that of female 58 (Table 5.15). By contrast, the core areas were less variable. The adult female with cubs ranged further than any of the single adult females and had the largest 95% and 50% UDs (Table 5.15). The ranges of females 31 and 58 were in the south of the reserve while that of 38 was in the south and central regions of the reserve (Figures 5.14b,c&d). Female 22 with cubs ranged widely through the reserve with multiple core areas in the north and south (Figure 5.14a). Compared to the adult female cheetahs, the male had a smaller 95% UD and larger core area (Table 5.15) and used space in the south east of the reserve (Figure 5.14e).

Table 5.15. The sizes of the 95% and 50% UDs for the cheetahs in SGR.

		area ha			percentage of reserve	
cheetah ID	fixes	95% UD	50% UD	50%/95%	95% UD	50% UD
female 38	91	9473	801	0.08	62.0%	5.2%
female 58	74	4883	981	0.20	32.0%	6.4%
female 31	85	7360	791	0.11	48.2%	5.2%
all females	250	7238.7	857.7	0.12	47.4%	5.6%
female 22 & cubs	87	12576	2029	0.16	82.3%	13.3%
male	94	6850	1504	0.22	44.8%	9.8%
all cheetahs	431	13210	1985	0.15	86.5%	13.0%
cheetah kills	160	12915	870	0.07	84.5%	5.7%

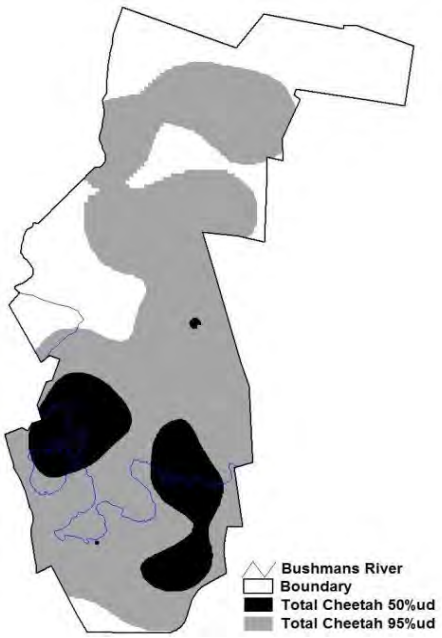


a) Female cheetah 22 & cubs b) Female cheetah 31 c) Female cheetah 38

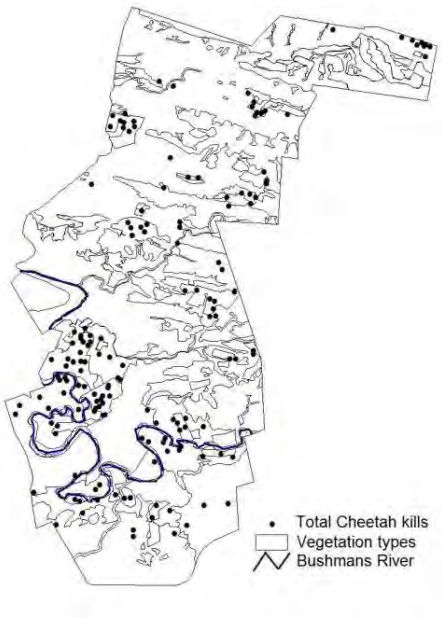
d) Female cheetah 58 e) Male cheetah

Figure 5.14. The locations of 50% and 95% UDs of the cheetahs in SGR.

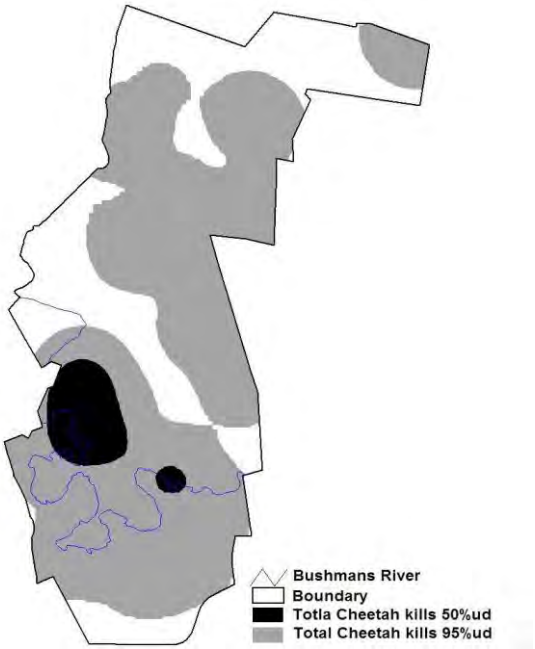
At the species level (data for all the cheetahs pooled), the 95% UD of the cheetahs was 13210 ha of the 15286 ha available (Table 5.15) while the core area represented 1985 ha in the southern part of SGR. The kills recorded for the cheetahs were concentrated in the south and were generally located in the open and sparsely wooded areas (Figure 5.15b). The 95% UD based on location of recorded kills was 12915 ha and the 50% UD was 870 ha (Table 5.15) and was situated on the old lands along the Bushmans River (Figure 5.15c). Based on the pooled data, the overlap between 50% UDs based on all observations and just on kills was 44.2%. At an individual level, the extent of the overlap at both 50% UD and 95% UD levels varied widely between the cheetahs (Table 5.16).



a) Map of the reserve showing the 50% and 95% UD of known kills and their position relative to the Bushmans River, reserve boundary and vegetation types.



b) Map of the reserve showing the GPS locations of known kills and their position relative to the Bushmans River, reserve boundary and vegetation types.



c) Map of the reserve showing 50% and 95% UD of sightings and their position relative to the Bushmans River, reserve boundary and vegetation types.

Figure 5.15. The location of 50% and 95% UDs for all cheetah sightings (a), the actual positions of all kills (b) and for all kills (c)

Table 5.16. The overlap of space use and kill distribution for all cheetahs in SGR

cheetah	overlap of kill and sighting UDs		number of kills recorded
	95% UDs	50% UDs	
all cheetahs	32.9	44.2%	160
female 38	23.7%	77.2%	51
female 58	47.3%	9.3%	28
female 31	49.5%	0%	25
female 22 with cubs	36.3%	40.9%	37
male	39.2%	0%	19

Overlap of space used by the cheetahs

The 95% UD of the male cheetah overlapped substantially with the 95% UDs of all the females (Table 5.16) but there was little or no overlap at the 50% UD level. Female space use overlapped at both the 50% and 95% UD levels (Table 5.17). Females 31 and 58, which were on the reserve at the same time, had the highest degree of overlap for both the 50 and 95% UDs with 66.7% and 67.1% respectively. Both these females had a low overlap if any with the other female cheetah for both the 50 and 95% UDs.

Table 5.17. Overlap of home ranges (above the diagonal) and core areas (below the diagonal) of the cheetahs.

	female 38	female 58	female 31	female 22 with cubs	male
female 38	/	45.8%	50.2%	58.0%	53.6%
female 58	10.0%	/	67.1%	32.4%	55.0%
female 31	0%	66.7%	/	39.9%	56.6%
female 22 with cubs	40.8%	16.5%	5.0%	/	40.8%
male	0%	0%	0%	9.2%	/

Cheetah Habitat selection (species level analysis)

The cheetahs were recorded in 10 of the 13 vegetation types with almost 40% of records in the cultivated lands (Table 5.18). More than 10% of records were in each of three other vegetation types (Subtropical Thicket, Bontveld and Primary *Acacia* Thicket). Of these, the cheetahs selected cultivated and cleared lands and Primary *Acacia* Thicket, avoided Subtropical Thicket because of its high availability, and used Bontveld according to its availability (Table 5.18). Observations in Lowland Grassland and cleared lands comprised less than 10% of all sightings but these vegetation types were selected (Table 5.18). Other avoided vegetation types included Bushclump Savanna, Riverine Bush, Secondary *Acacia* Thicket and Montane Grassland.

Kills were recorded in all vegetation types in which observations were made with 40% of kills in the cultivated lands (Table 5.18). Fifteen percent of kills were recorded in Primary *Acacia* Thicket, a selected vegetation type, but also in Montane Grassland which was avoided (Table 5.18). The highest kill conversion index was for Bushclump Savanna in which only one percent of observations were made but in which five percent of kills occurred (Table 5.18).

Table 5.18. Habitat use and location of kills of the cheetahs. The available column is the availability of each vegetation type in the reserve as a percentage. Space use and kill is the percentage that each vegetation type comprised within the 95% UDs based on all sightings or kills. Disturbed lands is included as a Biome.

		space			space use	kill	kill conversion
biome	vegetation type	available	used	kills	index	index	index
Forest	Afromontane Forest	0.5	0.0	0.0	0.0	0.0	0.0
Thicket	Subtropical Thicket	42.8	11.1	7.5	0.3	0.2	0.7
	Bontveld	8.1	10.1	3.1	1.2	0.4	0.3
	Bushclump Savanna	3.6	1.0	5.0	0.3	1.4	5.0
Savanna	Riverine Bush	2.5	1.0	0.6	0.4	0.2	0.6
	1^{o} *Acacia* Thicket	5.7	15.0	15.0	2.6	2.6	1.0
	2^{o} *Acacia* Thicket	2.1	1.0	2.5	0.5	1.2	2.5
Fynbos	Grassy Fynbos	0.7	0.0	0.0	0.0	0.0	0.0
	Calcrete Fynbos	0.0	0.0	0.0	0.0	0.0	0.0
Grassland	Montane Grassland	17.0	5.2	15.0	0.3	0.9	2.9
	Lowland Grassland	3.7	9.1	1.9	2.5	0.5	0.2
disturbed	cleared lands	1.4	6.8	8.8	4.9	6.3	1.3
lands	cultivated lands	11.9	39.7	40.6	3.3	3.4	1.0
		100.0	100.0	100.0			

Factors affecting space use of cheetahs in SGR

The relationship between space use by cheetahs and space use by important prey species.

The main prey species of the cheetahs were springbok, blesbok and black wildebeest (Chapter 4) and there was considerable overlap between the 50% UD based on kills and the 50% UDs of these prey species (Figure 5.16). The 50% UDs of the prey species occurred in two separate areas in the south of the reserve, one on old cultivated lands adjacent to the Bushmans River and the other in the south eastern corner of the reserve (Figure 5.16). The 50% UD based on all kills was located on the old cultivated lands adjacent to the Bushmans

River where overlap with the 50% UDs of prey species was very high, but very few kills were recorded in the south eastern corner. At the 50% UD level, overlap was 58.8% with the blesbok; 44.9% with the black wildebeest and a 46.0% with the springbok 50% UD.

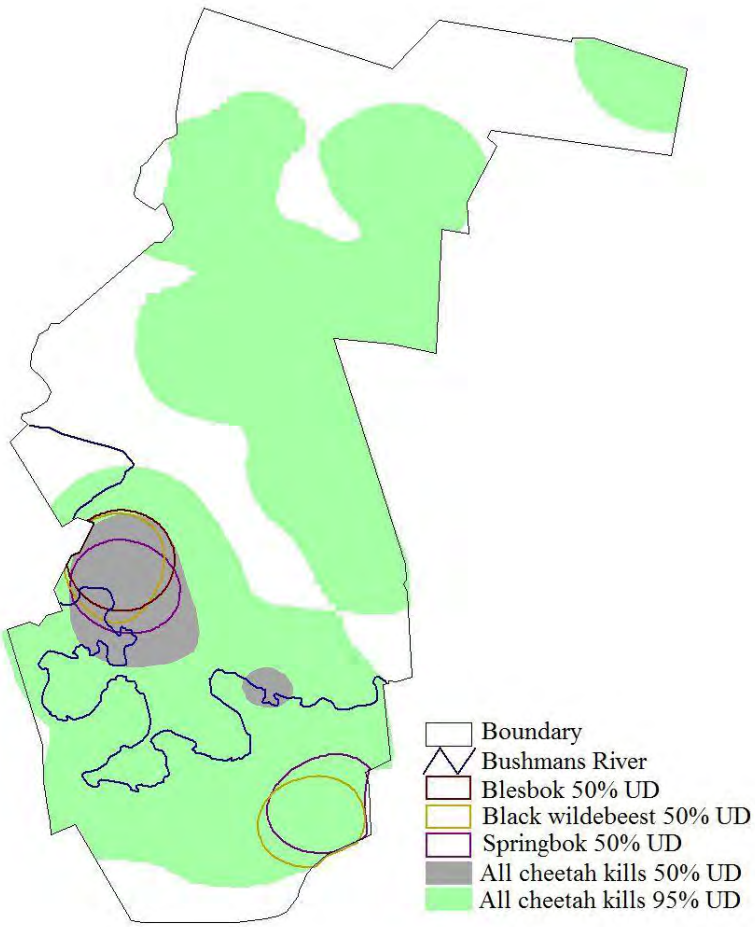


Figure 5.16. The location of 95% and 50% UDs based on all kills in relation to the core distribution of the main prey species.

The weakness of this analysis, where kills from all cheetahs were pooled, is that the pooled data do not reflect the particular space use of the male cheetah. Of a total of 160 recorded kills by cheetahs, only 19 were made by the male. The 50% UD of the male cheetah (see Figure 5.14e) was located in the south eastern corner of the reserve and overlapped the 50% UD of prey species in this area.

Changes in cheetah space use during the lambing season

In order to establish if space use changed in response to short term aggregations of easily caught prey, the space use of Cheetah 38 during the lambing season (December 2006 to February 2007) for the important prey species was compared to her total space use for the duration of the study, for which a similar number of GPS fixes were available. While it would have been ideal to make the comparison with a similar three month period outside the lambing season, the number of GPS fixes would have been too low. During the lambing season, the 95% UD was 2011 ha compared to 9473 ha for the remainder of the study period and was located in close proximity to the core areas of the prey species (Figure 5.17). In the lambing season, the 50% UD of female 38 overlapped the 50% UDs of the prey species by 46.0% (springbok), 71.8% (blesbok) and 50.6% (black wildebeest). This analysis is weakened by the very small sample size (one female and one event) but it does provide some baseline data that can be used justify future studies.

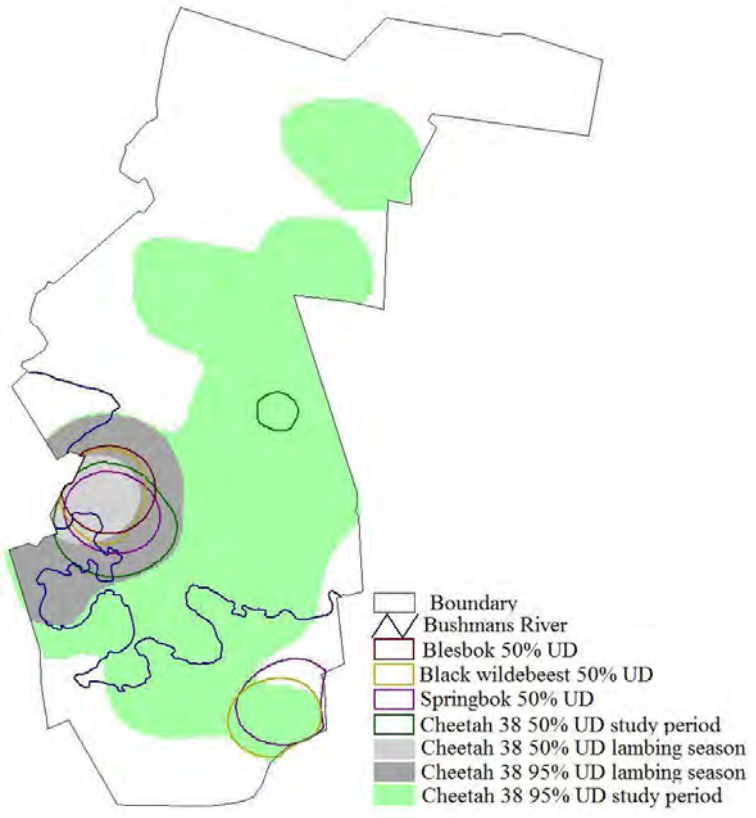


Figure 5.17. The space use difference for female cheetah 38 for the 2006/7 springbok lambing season and for the full duration of the study period. The small, localised 95% UD for the cheetah in the lambing season is clearly shown in dark grey

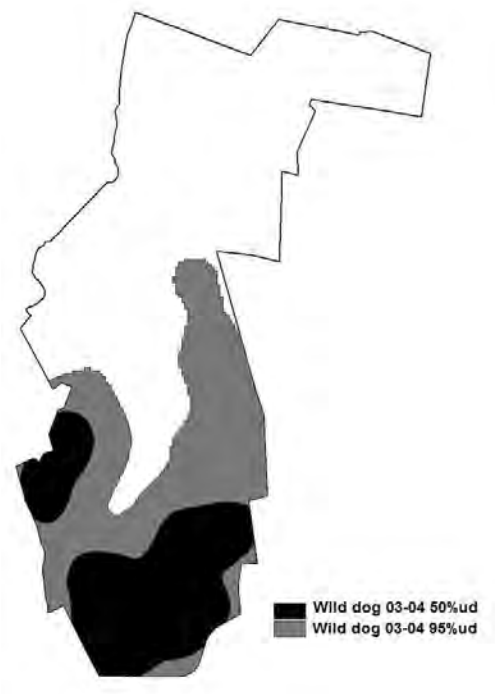
Wild dogs

The wild dogs had two distinct patterns of land use which were separated in time. For the first two years after their release, they remained in the southern sector of the reserve (Figure 5.18a) with a 95% UD of 9406 ha and a 50% UD of 3150 ha (Table 5.19). The space use changed completely for the next two years being almost exclusively in the north (Figure 5.18b) with a smaller 95% UD and 50% UD (Table 5.19).

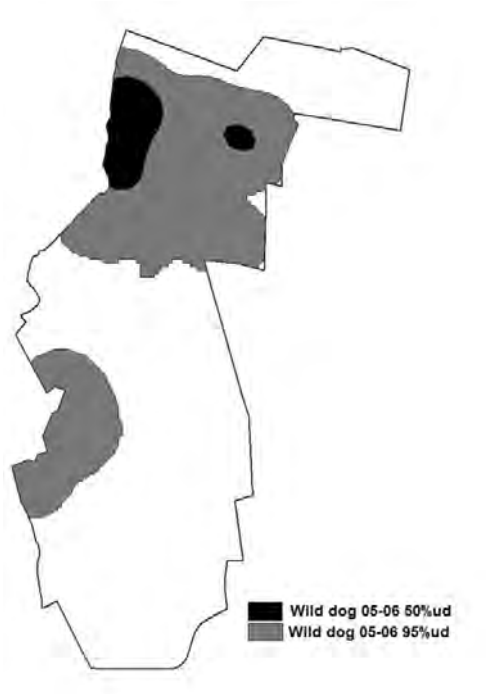
Table 5.19. The sizes of the 95% and 50% UDs for the wild dogs in SGR. .

		area ha			percentage of the reserve	
period	fixes	95% UD	50% UD	50%/95%	95% UD	50% UD
2003 - 2004	183	9406	3150	0.33	61.6%	20.6%
2005 - 2006	227	6834	778	0.11	44.7%	5.1%
wild dog kills	94	7193	1353	0.19	47.1%	8.9%

The space use based on location of kills was similar to that based on general observations, showing two areas in which kills were concentrated (Figure 5.14c,d). In the south of the reserve, kills were located in Primary *Acacia* Thicket, adjacent to areas of disturbed lands and in the north of the reserve, kills were concentrated in the disturbed lands in a thicket dominated area (Figure 5.16 d).

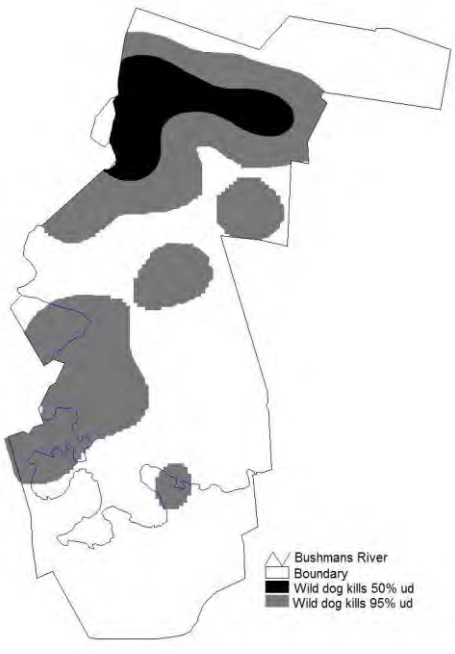


a) Wild dogs space use 2003 to 2004



b) Wild dogs space use 2005 to 2006

c) Wild dogs' kill distribution



d) Wild dogs 95% and 50% kill UD 2003 to 2006

Figure 5.18. The location of 50% and 95% UDs of the wild dogs in SGR, based on all observations between 2003 – 2004 (a) and 2005 – 2006 (b) showing the actual location of all recorded kills (c) and on kills (d).

Habitat selection of the wild dogs (Species level analysis)

The wild dogs were recorded in 10 of the 13 vegetation types with more than half the records in Subtropical Thicket and cultivated lands (Table 5.20). Observations in Bontveld and Primary *Acacia* Thicket each comprised 10% of the total, and records in all other vegetation types were less than 10% (Table 5.20). The wild dogs preferred the cleared and cultivated lands as well as Primary and Secondary *Acacia* Thickets and Lowland Grassland (Table 5.20). Bontveld and Riverine Bush were utilized in accordance with their relative abundance while the remainder of the vegetation types were avoided.

Kills were recorded in eight of the ten utilized vegetation types with no kills in either Bontveld or Lowland Grassland and more than half the recorded kills in Subtropical Thicket or cultivated lands (Table 5.20). The highest Kill Index was for cleared lands (6.1) where 8.5% of all kills were recorded while this vegetation type comprised just 1.4% of the reserve. The second highest was for Secondary *Acacia* Thicket (4.6) where 9.6% of kills were recorded. The highest Kill Conversion Index was for Secondary *Acacia* Thicket while Subtropical Thicket, Montane Grasslands and cleared lands had positive kill conversion indices.

Table 5.20. Habitat use and location of kills of the wild dogs. The available column is the availability of each vegetation type in the reserve as a percentage. Space use and kill is the percentage that each vegetation type comprised within the 95% UDs based on all sightings or kills. Disturbed lands is included as a Biome.

		space			space use	kills	kill conversion
biome	vegetation type	available	use	kills	index	index	index
Forest	Afromontane Forest	0.5	0.0	0.0	0.0	0.0	0.0
Thicket	Subtropical Thicket	42.8	24.1	34.0	0.6	0.8	1.4
	Bontveld	8.1	10.5	0.0	1.3	0.0	0.0
	Bushclump Savanna	3.6	2.2	2.1	0.6	0.6	1.0
Savanna	Riverine Bush	2.5	3.2	2.1	1.3	0.8	0.7
	1^{o} *Acacia* Thicket	5.7	10.0	11.7	1.8	2.1	1.2
	2^{o} *Acacia* Thicket	2.1	4.4	9.6	2.1	4.6	2.2
Fynbos	Grassy Fynbos	0.7	0.0	0.0	0.0	0.0	0.0
	Calcrete Fynbos	0	0.0	0.0	0.0	0.0	0.0
Grassland	Montane Grassland	17	2.2	3.2	0.1	0.2	1.5
	Lowland Grassland	3.7	5.9	0.0	1.6	0.0	0.0
disturbed	cleared lands	1.4	5.9	8.5	4.2	6.1	1.4
lands	cultivated lands	11.9	31.5	28.7	2.6	2.4	0.9
		100.0	100.0	100.0			

A comparison of space use by members of the large carnivore guild.

Location of space used

Members of the large carnivore guild used the majority of the reserve with some areas being used by several species and other areas by at least one species. The 95% UDs for the southern lions, the leopards and the cheetahs were located at least partially in the southern section of the reserve (Figure 5.19b-d) and in the first half of the study, the wild dogs also used the southern section. Although the cheetahs used the southern section, their range extended to the north of the reserve which was also occupied by the northern lion pride and the wild dogs

(Figure 5.19a, e). The large predator guild used most of the reserve (Figure 5.19f) with only a small area on the west of the reserve that was not utilized and the area to the north east which was part of the declared wilderness area where very little monitoring was conducted.
The 50% UDs for the predator guild were concentrated along the Bushmans River (Figure 5.20). The 50% UDs for the southern lions, the leopards and the cheetahs were restricted to the south (Figure 5.20) and even the northern lion pride had a section of the core area along the Bushmans River. Only the 50% UD of the wild dogs (2005-2006) was limited to the north (Figure 5.20).

a) Northern lions

b) Southern lions

c) Leopards

d) Cheetahs

e) Wild dogs (2005/2006)

f) All predators

Figure 5.19. The 95% UDs for the different members of the large predator guild in SGR for the duration of the study period.

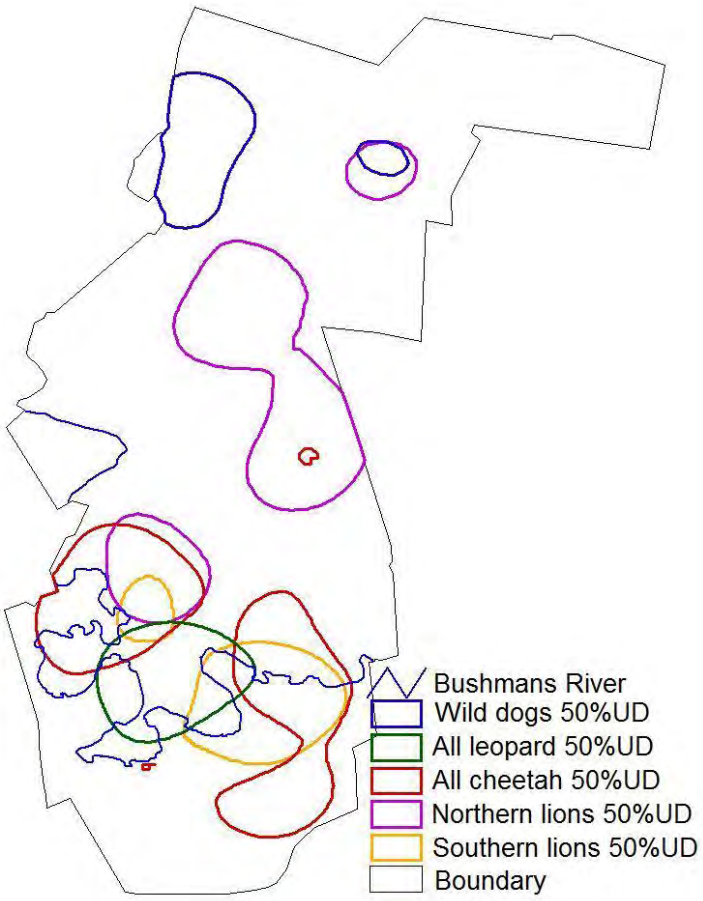


Figure 5.20. The locations of the 50% UDs of the large carnivore guild in SGR.

Size of space used

The leopards and cheetahs (species level analysis) had the greatest 95% UDs of all the predators utilizing just more than 80% of the reserve, and the southern lions had the smallest 95% UD (36.8% of SGR; Table 5.21). At a core area level, the cheetahs, northern lions and wild dogs had similar 50% UDs while that of the leopards was the smallest (Table 5.21).

Table 5.21. The sizes of the 95% and 50 % UDs (ha) based on all sightings through the study and the percentage of the reserve that these areas covered is included.

	southern lions	northern lions	all cheetahs	all leopards	wild dogs
95% UD	5624	11038	13210	12723	8120
50% UD	968	2041	1985	699	1964
95% UD % of reserve	36.8%	72.2%	86.5%	83.3%	51.2%
50% UD % of reserve	6.3%	13.4%	13.0%	4.6%	12.4%
Relative size of 50% UD	0.19	0.18	0.15	0.05	0.24

Table 5.22. Mean (± 1sd) range size (ha) for the members of the large predator guild. Body size is an approximation and species are arranged in order of decreasing size.

species	body size (kg)	(n)	95% UD	50% UD
Lion prides	150	2	8331± 3828.3	1504.5±758.7
Lion FEQ	120	2	1294±79.2	232.5±19.1
Cheetahs (male)	50	1	6850	1504
Cheetahs (female)	40	3	7238.7±2297.4	857.7±106.9
Leopards (male)	30	1	15946	2113
Wild dogs	25	2	8120±1818.7	1964±1677.3
Leopards (female)	20	3	5713.6±1664.3	725.3±85.2

In a two way factorial ANOVA, with range type (95% or 50% UD) and predator (species and sex) as predictor variables and range size as the dependent variable (data as in Table 5.22), there was a significant effect of range type (as expected, 50% UDs were significantly smaller than the 95% UD of the same species or sex; F_1 82.7; $P<0.05$), and of species/ sex (F_5 3.46; $P<0.05$). In a Tukey HSD test, the only significant differences were between the 95% UD of the male leopard, which had the largest range, and the 95% UD of the female leopards and the 95% UD of the female cheetahs ($P<0.05$ for both; Figure 5.21).

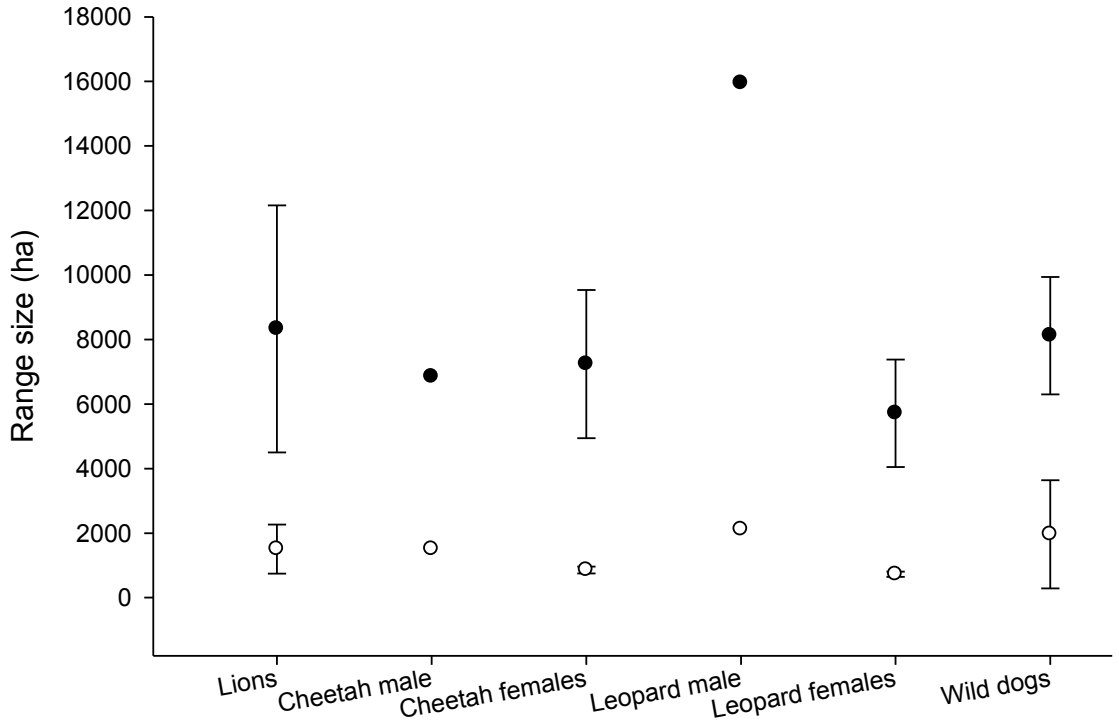


Figure 5.21. Home range sizes (ha; closed circles) and core area sizes (open circles) for the members of the large predator guild. Data are means ± 1sd.

The relationship between predator body size and range size was examined using linear regressions and the data in Table 5.22. Analyses were run both including and excluding space use per lion FEQ. At both the 95% UD and 50% UD levels, there was no significant relationship (95% UD with lion FEQ, $r^2 =$ -0.01; $F_{1,12} = 0.8$; P>0.05; without lion FEQ, $r^2 =$ -0.09; $F_{1,10} =$ 0.06; P>0.05; 50% UD, with lion FEQ, $r^2 =$ -0.06; $F_{1,12}$ 0.19; P>0.05; without lion FEQ, $r^2 =$ -0.08, $F_{1,10} =$ 0.20, P>0.05).

Overlap of space used by members of the large carnivore guild

In the preceding sections it has been reported that all the large predators, with the exception of the northern lion pride and the wild dogs (2005-2006), had core areas located around the Bushmans River and its associated disturbed lands in the south of the reserve. As a consequence of this, there was considerable overlap between the core areas of members of the large carnivore guild (Figure 5.22; Table 5.23). The southern lions overlapped substantially with the cheetahs (38%) and to a lesser extent with the wild dogs and leopards

for the duration of the study period (Table 5.23). The leopards showed the least overlap with other members of the large carnivore guild, with very low levels of overlap with cheetahs and wild dogs (<10%). The north of the reserve was less intensely utilized and levels of space use overlap were much lower (Figure 5.22; Table 5.23). When space use was based on the location of kills, the results were slightly different although overlap between the species remained (Table 5.23).

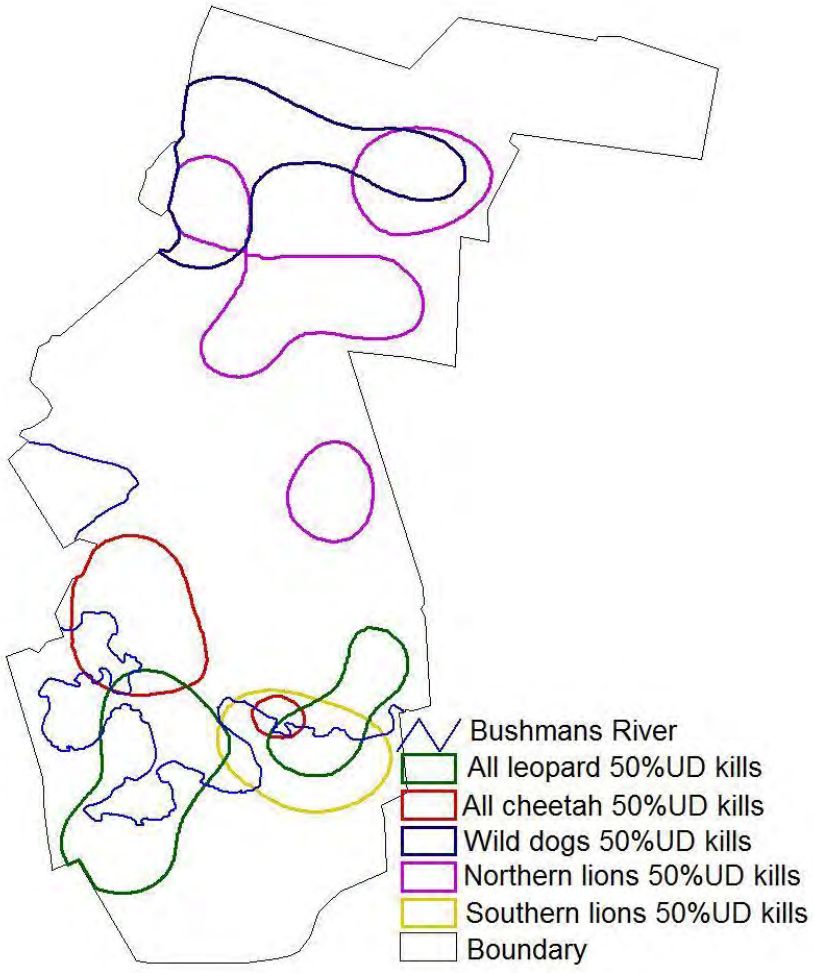


Figure 5.22. The locations of the 50% UDs of the large carnivore guild in SGR based on kills.

Table 5.23. The percentage overlap of the 50% UDs and 50% kill UDs for all members of the large carnivore guild in SGR. Values above the diagonal are for UDs based on kills.

	southern lions	northern lions	cheetahs	leopards	wild dogs
southern lions	//	0.0%	9.4%	22.0%	0.0%
northern lions	6.4%	//	0.0%	0.0%	31.8%
cheetahs	38.0%	18.6%	//	7.1%	0.0%
leopards	23.2%	0.0%	8.9%	//	0.0%
wild dogs 03-04	26.5%	1.1%	26.8%	2.4%	//

The relationship between the space used by all predators and space use of the prey.
When data for all predators were pooled, the 50% UD (all sightings) was located in the south of the reserve while the 50% UD (based on kills only) occurred in two sections, one in the north and the other in the south of the reserve (Figure 5.23). The 50% UD of all prey species was similarly split with areas of concentrated use in the north and south. The 50% UD (all sightings) of the large carnivore guild overlapped by 28.8% with that of the prey species, while the 50% UD based on kills overlapped by 59.5% with that of the prey species.

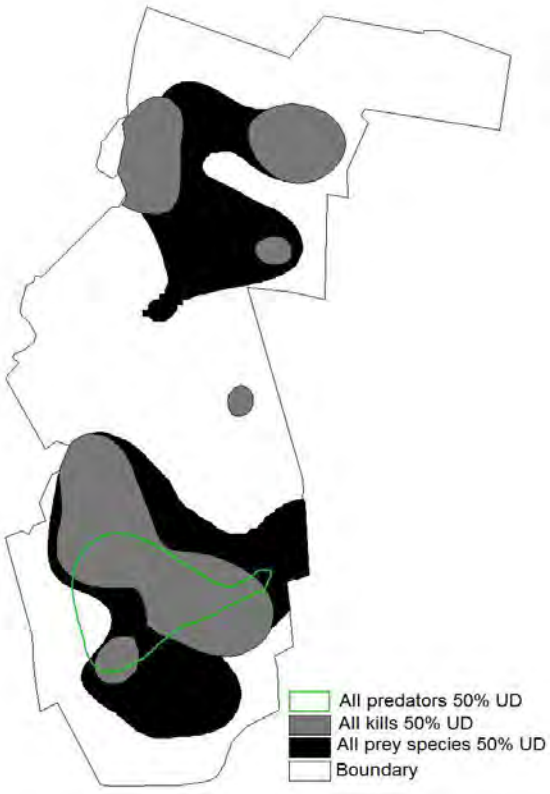


Figure 5.23. The locations of the 50% UDs of the predator guild based on all sightings, on kills and the 50% UD of all prey.

Habitat selection by the large carnivore guild.

This analysis excludes the far North of the SGR which is a wilderness area in which survey effort was reduced. Primary and Secondary *Acacia* Thicket were preferred by all the predators, excluding the cheetahs, for either space use or kills and in most cases both (Table 5.24). The cleared and cultivated lands were preferred by all the predators except the leopards (Table 5.24). The highest preference for any vegetation type by any predator for all sightings was Riverine Bush by leopards with a space use index of 7.3, while for kills it was the preference of cleared lands by the cheetahs with a kill index of 6.3 (Table 5.24). The four strongly preferred vegetation types (Table 5.25) comprised 21.1% of the reserve. Afromontane Forest, Grassy Fynbos and Calcrete Fynbos were not used except by the leopards and comprised just more than 1% of the reserve. Other vegetation types tended to be avoided, including Bontveld, Subtropical Thicket and Montane Grassland (Table 5.24). The most common vegetation type (Subtropical Thicket), which comprised about 43% of the reserve, was avoided by most predators, and used according to its abundance by the leopards

(Tables 5.24, 5.25). However, in this case, the avoidance does not indicate that the vegetation type was not used but is rather an effect of the very high proportional availability of Subtropical Thicket. It is interesting to note that the most preferred or important vegetation types were not natural. Cleared and cultivated lands had been used for grazing or for crops and were in the process of rehabilitation. Primary *Acacia* Thicket results from the invasion of *Acacia karroo* into cleared areas.

Table 5.24. Summary of habitat selection by members of the large carnivore guild in SGR. SUI = Space Use Index; KI = Kill Index. Bold face is used to highlight avoidance (index ≤0.7) and yellow to indicate selection (index >1.3).

	avail	northern		southern							
	able	lions		lions		cheetahs		leopards		wild dogs	
vegetation type	%	SUI	KI	SUI	KI	SUI	KI	SUI	KI	SUI	KI
Afromontane Forest	**0.5**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	1.4	**0.0**	**0.0**	**0.0**
Subtropical Thicket	42.8	0.7	0.7	**0.5**	**0.4**	**0.3**	**0.2**	1.3	1.2	**0.6**	0.8
Bontveld	8.1	**0.3**	**0.1**	**0.5**	**0.5**	1.2	**0.4**	**0.4**	1.6	1.3	**0.0**
Bushclump Savanna	3.6	1.2	1.8	**0.0**	**0.0**	**0.3**	1.4	0.1	**0.6**	**0.6**	**0.6**
Riverine Bush	2.5	**0.6**	**0.2**	1.9	0.7	**0.4**	**0.2**	7.3	5.2	1.3	0.8
1° *Acacia* Thicket	5.7	1.9	1.2	6.1	5.9	2.6	2.6	1.9	1.9	1.8	2.1
2° *Acacia* Thicket	2.1	2.7	2.5	1.5	1.2	**0.5**	1.2	1.7	1.0	2.1	4.6
Grassy Fynbos	0.7	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Calcrete Fynbos	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Montane Grassland	17.0	1.2	1.3	**0.0**	**0.0**	**0.3**	0.9	**0.0**	**0.0**	**0.1**	**0.2**
Lowland Grassland	3.7	**0.0**	**0.0**	1.8	3.1	2.5	**0.5**	**0.1**	**0.6**	1.6	**0.0**
cleared lands	1.4	4.4	2.6	4.5	4.1	4.9	6.3	**0.4**	**0.0**	4.2	6.1
cultivated lands	11.9	1.6	2.1	1.7	2.1	3.3	3.4	**0.5**	**0.5**	2.6	2.4
	100										

Table 5.25. A measure of the importance of the vegetation types in SGR. Data are means for the space use index and kill index and in the final column, the sum of the two means. Vegetation types are ranked in order of increasing importance.

		indices		
vegetation type	available %	mean space use	mean Kill	sum of space use and kill
Grassy Fynbos	0.7	0.0	0.0	0.0
Calcrete Fynbos	0	0.0	0.0	0.0
Afromontane Forest	0.5	0.2	0.0	0.2
Montane Grassland	17	0.3	0.4	0.7
Bontveld	8.1	0.6	0.4	1.1
Bushclump Savanna	3.6	0.4	0.7	1.1
Subtropical Thicket	42.8	0.6	0.6	1.1
Lowland Grassland	3.7	1.0	0.7	1.7
Riverine Bush	2.5	1.9	1.2	3.1
2^{o} *Acacia* Thicket	2.1	1.4	1.8	3.2
cultivated lands	11.9	1.6	1.8	3.4
1^{o} *Acacia* Thicket	5.7	2.4	2.3	4.7
cleared lands	1.4	3.1	3.2	6.3

Discussion

SGR is a medium sized conservation area (15286 ha) and is larger than the reported ranges of the resident members of the large predator guild under conditions of adequate prey abundance and where space is either naturally or artificially constrained (lions, 5300-15000 ha; Hunter, 1998; Bissett, 2007; Vorster, 2011; cheetahs, 2900 – 16200 ha; Purchase & du Toit, 2000; Bissett, 2007; Vorster, 2011; leopards, 1000 -17900 ha; Myers, 1986; Mizutani & Jewel, 1998; Marker & Dickman, 2005; wild dogs, 15600 ha; Creel & Creel, 2002).

However, the reserve is smaller than many of the recorded range sizes for the same predators under conditions of low prey abundance and where migration of prey occurs (lions, 21700 ha; Viljoen, 1993; cheetahs, 80000 ha, Caro, 1994; leopards, up to 80000 ha, Martins & Martins

2006; wild dogs most often greater than 20000 ha and up to 200000 ha, Frame *et al*., 1979). Like other medium sized conservation areas in Southern Africa, SGR is a fenced and managed system. The fencing limits movement of the predators (with the exception of some leopards) and their prey, and as such the very large ranges reported for predators such as cheetahs in the Serengeti (83 300 ha) where female cheetahs and non-territorial males follow the migration of their main prey species (Schaller, 1972; Caro, 1994; Caro & Collins, 1986; Durant *et al*., 1988; Sunquist & Sunquist, 2002) will not be seen. In addition to being constrained by fencing, the predators populations are often managed to control numbers and genetic diversity, while the populations of prey species may be supplemented as necessary. For these reasons, it is perhaps unlikely that space use concepts such as expansionism and contractionism (Kruuk & Macdonald, 1985) will be relevant in small managed populations of large predators. In such populations of predators, management interventions to control group size, and the presence of fences tends to favour contractionism (Kruuk & Macdonald, 1985). Nevertheless, the existing ideas of how space use is determined provide a framework in which the results from the present study may be understood.

If it is accepted that space use (both location and size) is the outcome of complex interacting biotic and abiotic factors, then it is likely that space use will vary from one site to another, and the extent of that variation will depend on how similar the systems are. There is therefore little to be gained by simply comparing space use in SGR with that elsewhere in Africa and this discussion focuses on the factors that may be influencing space use. Where appropriate, comparable data from elsewhere in Africa, are provided with emphasis on data from systems that are similar to SGR.

The role of resource distribution

The relationship between the distribution of a predator and that of its prey is complex (Celesia *et al*., 2009). Intuitively, one might expect predator distribution to closely reflect that of the prey and this often is the case (Hopcraft *et al*., 2005). However, factors other than prey abundance and distribution, such as catchability of prey and presence of other predators, may result in reduced coincidence of predator and prey distribution (Mills & Gorman, 1997; Durant, 2000a; Orrock *et. al.*, 2010). In SGR, the distribution of prey (mostly small to large ungulates) for the large predator guild was patchy with ungulates concentrating in the vicinity of water and disturbed lands. SGR was developed by consolidating a number of farms that

had been used for small livestock rearing and crop production. Crop production was restricted to areas close to water (Bushmans River in the south and earth dams and boreholes in the North) and involved clearing of natural vegetation, ploughing, irrigation and growing of crops such as wheat, oats, chicory and vegetables. Rehabilitation of these areas is slow and they remain mostly free of trees and covered by natural grasses and some small bushes. Where trees have become established, it is typically a monoculture of *Acacia karroo*, the vegetation type known as Secondary *Acacia* Thicket. The original vegetation that was cleared is likely to have been Subtropical Thicket and this is the vegetation type that typically now abuts either the Secondary *Acacia* Thicket or the disturbed lands. In its natural form, Subtropical Thicket (which comprises 42.8% of SGR) offers little grazing but abundant food for browsers such as kudu and bushbuck, and it is the disturbed lands that provide resource rich patches for grazers. Plains game species, which are mostly grazers, are more easily viewed by tourists than the browsers that occur in thicket, and to meet the needs of tourists, large numbers of grazers were introduced to SGR (see Chapter 2). Combining these factors, SGR is characterised by resource rich patches for grazers which are artificial, located close to water and bordered by Subtropical Thicket. According to Bailey *et al*. (1996), the distribution patterns of large herbivores are influenced by proximity to water and food quality and quantity, and the distribution of browsers and mixed feeders (for example kudu, bushbuck, impala) are positively associated with river courses in Kruger National Park (Redfern *et al*. 2003; Smit *et al*., 2007). Thus the riparian vegetation associated with the Bushmans River and the adjacent disturbed lands have served as a preferred habitat for many of the ungulates in SGR.

The presence of disturbed lands (13.3% of the reserve) is significant for two reasons. Firstly, as described above, they provide grazing for many of the ungulates on the reserve (impala, zebra, blesbok, wildebeest, and red hartebeest and warthog). Secondly, it is likely that the boundary between the more open disturbed lands and the thicket vegetation is important for both the prey species, providing cover for species such as kudu and bushbuck, and for the predators, providing cover for hunting. The boundary between the disturbed lands and the natural vegetation was often distinct and transition zones, ecotones or edges between habitat types have been recognised as of fundamental importance in ecology and have been the focus of study for decades (Ries *et al*., 2004). Habitat edges may be sites of increased intensity of interactions; they typically separate two or more different habitat types, and are often areas of

high productivity and elevated biodiversity (Lidicker, 1999). While habitat edges may bring together species that are typical of the different habitats, there are also species that are more common in the region of the edge (Lidicker, 1999; Dijak, 2000), benefiting from features in the two habitats; the edge providing maximum access to both resources (Ries *et al*., 2004). Although studies of mammalian predators at habitat edges are few in number, it has been suggested that generalist predators may benefit from habitat fragmentation, particularly associated with agriculture (Matthiae & Stearns, 1981). This is because generalists are able to feed on a range of prey species, use a range of habitats and therefore use habitat edges (Saunders *et al*., 1991). Within the vertebrates, these studies have focussed on birds and on nest predation in transition zones and to a lesser extent on small mammals (rodents and insectivores) and small predators (Reis *et al.,* 2004 for review). While there are examples of both positive and negative effects at habitat edges, studies have produced contradictory results. In some instances there is evidence of increased nest predation at or near edges (Donovan *et al*., 1995; Heske *et al*., 1999 for further examples) but in other studies this effect is not observed (Heske *et al*., 1999). In the context of the present study, it is likely that the edges and the two habitat types that they linked, brought together concentrations of browsers and grazers in the vicinity of water. This then served as a strong attraction for lions, cheetahs and wild dogs.

On similar medium sized conservation areas in South Africa, the use of disturbed lands by both prey and predators is varied. In Kwandwe, where disturbed lands comprise only 1% of the total area, there is little evidence of lions, cheetahs or wild dogs focussing space use on such areas (Bissett, 2007). This is possibly because there is more permanent water and associated riparian vegetation and less disturbed lands in Kwandwe than in SGR. By contrast, in Sanbona, a conservation area in the far more arid Western Cape of South Africa, space use by predators (lions and cheetahs) and prey species is focussed around a single large, man-made dam (Vorster, 2011).

While it is to be expected that concentrations of prey, such as reported in this study for SGR, will serve as a focus for members of the large predator guild (Hopcraft *et al*., 2005) it is also the case that intra-guild interactions may result in some members of the guild avoiding such areas (Mills & Gorman, 1997; Durant, 2000a, 2000b). In SGR, there was considerable overlap in space used by the lions, cheetahs and leopards, with their core areas being centred

on and around the Bushmans River. This suggests that the benefits of being in the vicinity of resource rich patches outweighed the costs. While the costs of intra-guild interactions may be high (kleptoparasitism and death), these interactions can be reduced through other mechanisms including changing the time of feeding. For example, it has been suggested that cheetahs avoid periods of lion activity by hunting at dawn and dusk (Estes, 1991; Sunquist & Sunquist, 2002). It is possible that the movement of the wild dogs from the south of the reserve to the north was a response to the presence of lions in the south, although once in the north, their range overlapped with that of the northern lion pride. It is also the case that the space use analyses presented here are at a coarse scale, being based on a single GPS fix per day, and it is possible that fine scale habitat preferences would reduce space use overlap and assumed intra-guild interactions.

It might be expected that the prey species would respond to the predation pressure around the Bushmans River by moving away (Šálek *et al*., 2010). While this study did not monitor changes in space use by the prey species, the limited number of patches that were suitable for grazers makes this unlikely and introduces a constraint that will be typical of many small, fenced conservation areas.

The dietary switch of the lions from killing mostly kudu in the first half of the study, to killing mostly warthog in the second, was matched by changes in space use by the lions (the overlap of space use between the lions and the kudu was greater in the first half of the study than in the second half), providing further evidence for an important role for prey distribution on predator space use. It could be argued that some other factor drove a change in space use which then resulted in a change in diet and while this remains possible, it seems unlikely. As indicated in Chapter 4, the change in diet was probably driven by a decrease in the abundance of kudu and an increase in abundance of warthogs and the change in diet resulted in a small change in space use.

The lambing season represents a period during which resource distribution for predators is even more patchy than normal in SGR. The response of the cheetahs at this time (greatly reduced core area and home range, focussed on the core area of the prey species) provides further support for the importance of resource distribution in space use.

The role of habitat preference and hunting behaviour in space use

There are both inter- and intra-specific differences in habitat preferences and hunting behaviour and these will influence space use in the large predator guild. The high speed chases of cheetahs (Sunquist & Sunquist, 2002; Hunter & Hamman, 2003), the pack hunting of wild dogs (Creel & Creel, 1995), the stalk and ambush of lions (Schaller, 1972; Packer *et al.,* 1990) and the solitary stalk and ambush of leopards (Balme *et al*., 2007) are each best suited to different habitats (Balme *et al*., 2007) and may result in differences in space use in a heterogeneous environment. Within these species level characteristics, there is some flexibility and cheetahs can hunt in thicket vegetation using an ambush and short chase strategy (Bissett & Bernard, 2007). Leopards have an adaptable hunting strategy that enables them to catch a wide variety of prey species of different sizes, but which always requires cover to conceal the approach (Balme *et al*., 2007). Similarly, there are reported cases of differences in hunting strategies of different sexes. Male cheetah select more open habitat than females where they use a more typical high speed chase to catch prey while females select denser habitats and use an ambush, slow stalk and short chase strategy (Broomhall *et al*., 2003; Bissett & Bernard, 2007). In the cheetahs, these differences are likely to reflect the interplay of group size and predation pressure whereby solitary female cheetahs select vegetation types with greater cover to avoid larger predator species, while the group living male cheetahs select more open vegetation types.

The previous two sections of the discussion have dealt with resource distribution, and habitat preference and hunting strategy separately but they are clearly linked and interact to shape space use. Landscape attributes and prey abundance were the two proximate factors that shaped habitat use in carnivores (Stephens & Krebs, 1986; Balme *et al*., 2007) and the results for SGR support this. Landscape attributes (= habitat features) were probably the primary driver of habitat use by leopards, while prey abundance is likely to have had a greater influence for the lions, cheetahs and wild dogs. The leopards were the only species to select Riverine Bush, with its dense cover and avoid the far more open disturbed lands. Balme *et al*. (2007) suggest that although leopards are often perceived as generalists, they display a strong preference for areas with intermediate cover and it may be this specialization that prevented them from using the disturbed lands in SGR. For the other predator species it is not possible to comment on the relative importance of prey abundance as compared to habitat features. However, it is clear that the concentrations of prey on the disturbed lands and adjoining areas,

and the landscape features, possibly including the edges between Subtropical Thicket and disturbed lands, served to concentrate the space use of the lions, cheetahs and wild dogs.

Factors affecting range size

Like habitat selection, what is measured as range size is the end result of the interaction of a variety of biotic and abiotic factors including body size, resource richness and patchiness and intra-guild interactions (Gittleman & Harvey, 1982; Macdonald, 1983; Litvaitis *et al*., 1986; Jetz *et al*., 2004; Hayward *et al*., 2009). As such, and as indicated earlier, it must be expected that ranges will differ from one site to another and at a single site, over time.

Lion home range size in Africa ranges from 2 200 ha in Lake Manyara (Ndhlovu & Balakrishnan, 1991) to 282 300 ha in dune savannah of the southern Kalahari (Funston, 2001). Leopard space use varies substantially, specifically in relation to aridity and resource availability. In the arid and resource poor Kalahari, home ranges of leopards are as high as 112 400 ha (Eloff, 1973; Hemson, 2003) while in the more mesic and resource rich Matopos (Zimbabwe) and Londolozi (South Africa) ranges are smaller (1 000-2 500 ha; Smith, 1977; Hemson, 2003). Similarly, cheetah home ranges vary enormously from 2 900 ha in Matusadona National Park (Purchase & du Toit, 2000) to 32 000 ha in the Kalahari Gemsbok Park (Mills, 1998) and from 80 000 ha in the Serengeti (Caro, 1994) to 150 000 ha in Namibia (Marker *et al*., 2003). Wild dogs have large home ranges ranging from 150 000 to 200 000 ha in the Serengeti (Frame *et al*., 1979). In areas with more sedentary prey such as the Kruger National Park, ranges are smaller (35 700 to 93 900 ha; Fuller *et al.,* 1990; Mills & Gorman, 1997) and the smallest ranges are reported on the fenced, medium sized conservation areas such as Kwandwe (15 200 ha; Bissett, 2007) and the present study (13 600 ha). Woodroffe & Ginsberg (1998) have suggested that the long term viability of wild dog populations and the ecological processes that characterize them may require protected areas as large as 1 000 000 ha. This appears true and both SGR and Kwandwe have subsequently removed their wild dogs.

Range sizes in SGR were not greatly different from those reported for medium sized conservation areas in the region. The home range of lions in Kwandwe ranges from 6 900 to 13 000 ha (Bissett, 2007) and in the Addo Elephant National Park (AENP) lion home range is 11 400 ha (Hayward *et al*., 2009). The AENP is close to SGR and similar in vegetation, climate and size (AENP is 13400 ha). These home ranges are similar to those reported for

lions in SGR (5 600 to 11 000 ha). The home range of single female cheetahs in Kwandwe (8 600 ha; Bissett, 2007) was similar to that reported for SGR (4 900 to 9 400 ha) as was the range of females with cubs (10 900 ha, Kwandwe, Bissett, 2007; 12 600 ha, SGR). Wild dog home ranges varied very slightly between Kwandwe (15 800 ha; Bissett, 2007) and SGR (13 600 ha). The home ranges for male leopards varied substantially between SGR (15 900 ha) and AENP 3 800 ha (Hayward *et al*., 2009) respectively. Leopards in the Kruger National Park and adjacent Londolozi Game Reserve had home ranges of 2 500 ha (Hemson, 2003) and 2 800 ha (Le Roux & Skinner, 1989) suggesting that the range size on the AENP may be a better indication of range size in the Eastern Cape. The range size for SGR was for a single male and ranges recorded for three females (4 500 to 7 600 ha) were more similar to the smaller ranges reported elsewhere. Notwithstanding this, large ranges have been reported for leopards in the Baviaanskloof of the Eastern Cape Province of South Africa (McManus, 2009). The Baviaanskloof is a mountainous conservation area with surrounding farm lands but which has not been stocked with ungulates. Prey density, while not assessed, is likely to be very much lower than in SGR, Kwandwe and the AENP. The home ranges of male leopards in the Baviaanskloof range from about 8 500 to 49 700 ha ($\bar{x}$ = 24 430 ± 22 180 ha; n=3) while that of female leopards is smaller ($\bar{x}$ = 115.6 ± 1 300 ha; n = 3; ranges measured using satellite collars; McManus, 2009). The similarity in space use patterns between the lions, cheetahs and wild dogs on similar reserves within the Eastern Cape may be attributed to the similarities in habitat (vegetation and topography), climate, prey densities and size. However, these range sizes are not dissimilar to those of Phinda (a reserve of 7 500 ha; Hunter, 1998) and Makalali (9 800 ha; Druce *et al*., 2004), which have different habitats but are of similar size. It is perhaps the case that in an open system, habitat and prey density and distribution are important, but that in a closed system, the size of that system plays an important role in setting range size.

Body size

While it is logical that there should be a fundamental role for body size in determining range size, this was not detected in SGR where there was no significant difference between the ranges of the different size predator species. Analyses of data for Kwandwe (in Bissett, 2007) and Sanbona (in Vorster, 2011) reveal a similar lack of significant effect for body size. This is unlikely to indicate that body size has no role but rather that other factors such as hunting strategy, other aspects of social behaviour, and resource patchiness, which also

influence range size, mask the effect of body size. The prediction that body size will affect range size is not being met on at least some small reserves. The reason for this is unknown and is a topic for future research.

Group size

There is usually a positive correlation between home range size and group size (Loveridge *et al*., 2009) both within and between species. It is suggested that larger lion prides will maintain larger home ranges containing more resources and that larger prides may more successfully defend areas of high quality resources (Spong, 2002). This is not supported by results from the present study or from Kwandwe (Bissett, 2007). In both studies, there was no significant difference between the range sizes of the predator species with lion prides and pack of wild dogs using similar ranges to single adult female cheetahs for example. It is possible that the group sizes in SGR and Kwandwe were not large enough to detect a group size effect.

Inter and intra-specific interactions

Aggressive interactions both between members of the large carnivore guild and between members of the same species have been reported (Linnell & Strand, 2000) and it is very likely that these interactions will influence space use and range size. Although the present study was not designed to collect information on such interactions, it is possible to comment on the role of intra-guild interactions. For example, the introduction of an adult male lion to SGR was associated with a movement of the northern pride away from the area it had occupied, and, there was a trend for the range size of the northern pride to decrease as that of the southern pride increased. It is well documented that lions will steal prey from cheetahs (Caro & Collins, 1987; Caro, 1994; Durant, 1998) and that they kill cubs and adults (Caro, 1994; Laurenson, 1994) and it is thus likely that the location and density of lions will influence space use by cheetahs (Carbone & Gittleman, 2002). One could predict that in an enclosed system these effects will be exaggerated and that the range size of cheetahs would decrease as that of lions increased, and that the amount of overlap in space use would be small. This was not observed in SGR, and there was substantial overlap of the core areas of cheetahs and lions. However, in Kwandwe only the space use by the coalition of male cheetahs overlapped with that of the lions (Bissett, 2007) while the female cheetahs in Kwandwe avoided other large predators, including the coalition of male cheetah, and selected

areas that had no overlap at home range level with the lions, wild dogs and the coalition (Bissett, 2007). As mentioned earlier, the resolution of the spatial analyses was coarse and would not have detected fine scale habitat selection and thus avoidance of lions by cheetahs. It is also the case that different patterns of activity could have reduced the chance of aggressive interaction.

In conclusion, in SGR, space use by lions, cheetahs and wild dogs appeared to be strongly driven by resource distribution. This was evident along the Bushmans River in the South of the reserve where the 50% UDs of the southern lions, the cheetahs, the wild dogs (first two years of study), two leopards and to a lesser extent the northern lions were concentrated with varying degrees of overlap between these competing predators. This area was characterised by access to water, open vegetation types that had once been agricultural lands, and a denser vegetation (Subtropical Thicket). It is suggested that these features created suitable conditions for a range of ungulates (browsers and grazers) and suitable combination of landscape features and resources for lions, cheetahs and wild dogs. Of the four members of the large carnivore guild, the leopard showed a different pattern of habitat selection avoiding the cleared agricultural lands. In this case, the specific hunting requirements of the leopard (intermediate cover), restricted their access to the open old lands and the ungulates that accumulated on them.

While it is likely that space use will have been influenced by intra-guild interactions, with the exception of the effects of the introduction of an adult male lion, these were not detected.

CHAPTER 6: THE ESTIMATION OF THE CARRYING CAPACITY OF SGR FOR LARGE PREDATORS AND THEIR TRUE IMPACT.

Introduction

It is widely accepted that an understanding of the landscape and other requirements of predators is important to their conservation (Van Schalkwyk, 1994; Jacoby, 1997; Hunter, 1998; Fuller & Sievert, 2001; Hayward *et al*., 2007a;). This is particularly the case on small enclosed reserves, where small resident populations of prey, when subjected to predation, lack suitable refuge from predators, and where migration is inhibited by fencing, prey can undergo significant declines (Caughley & Sinclair, 1994; Fryxell *et al*., 1988; Power, 2002). It is equally important to understand the carrying capacity of the conservation areas for both prey and predators and this necessitates a sound understanding of the biology and ecology of predators and prey.

The carrying capacity of reserves can be estimated in a number of different ways. Hayward *et al*. (2007b) derived relationships between preferred prey species (species and weight range) of Africa's large predator guild, and their population densities, to derive predictions of carrying capacity in eight South African conservation areas. Here the predicted population density of each large African predator was related to the biomass of significantly preferred prey and the biomass of prey in the preferred weight range. Predicted predator density in SGR, based on biomass, was 12 lions, nine leopards and six cheetahs (Hayward *et. al*., 2007b). Their predictions when based on biomass of prey in the preferred weight range were 18 lions, seven cheetahs, nine leopards and six wild dogs.

Power (2003) on the other hand employed and evaluated two methods for determining the sustainability of lions in an enclosed single-predator system. The first method involved the large herbivore biomass (LHB) and the second, the maximum sustainable yield (MSY) of the prey. For both methods (LHB & MSY) the following was incorporated to calculate the number of lions that can be sustained per annum: herbivore biomass (kg) available for consumption, the daily food intake of lionesses (kg/day); carcass utilization percentage; and the edible portion of the carcasses.

The estimation of carrying capacity requires a sound understanding of the diet of the predators in that reserve and of daily food intake. No kill records are ever 100% accurate with most studies acknowledging that smaller kills are regularly missed (Power, 2003; Lehmann *et al*., 2008). Small kills are quickly consumed and lions and wild dogs can finish small to medium kills in a matter of minutes (Skinner & Chimimba, 2005). Mills (1996) recognizes that the highest likelihood of a lion kill is between sunset and sunrise, a period of time with little to no monitoring activity on photographic reserves. Thus, it is necessary to develop a correction factor that can be used to adjust the number of kills recorded, to more accurately reflect the diet.

SGR is a tourism based reserve and the predators are an essential component of what attracts tourists. The objective of this chapter is to determine at what predator density the tourism product can be satisfied while not having a detrimental effect on the ecology of the reserve.

In this chapter, I use data from the two previous chapters on diet and space use to estimate the carrying capacity for each of the large predators on a sustainable basis which includes the annual supplementation of the prey base. An indication of the carrying capacity of SGR for predators is calculated by combining the biomass estimated by the MSY method and the biomass provided by the introduced prey, and dividing by the biomass required per FEQ per year. I also include some recommendations that may be used to guide future management practices.

Materials and Methods

Kill Correction Factors

In order to determine the shortfall in the predator kill records and hence establish a correction factor per predator, the daily biomass killed per FEQ as established during the two by two week follows was used as the expected value. The expected kill rate was then compared with the observed total biomass killed (all records for the years 2004 to 2007) to determine a correction factor by the following equation:

$$KCF = \frac{pFEQ \times tFEQ \times 365}{rBM}$$

Where KCF is the Kill Correction Factor per predator species
pFEQ is the expected kill rate (biomass killed/day/FEQ in kg recorded during the continuous follows).
tFEQ is the average number of FEQs per predator species per day.
rBM is the total kill biomass recorded per predator species per year in kg.
tFEQ was calculated as the average of the number of FEQs on the same day of each month of the year.

Predator Carrying Capacity

In order to establish the carrying capacity for the large predator guild, a standard feeding unit, the lion feeding unit (LFU) was established. To do this, the total daily biomass killed per predator species was expressed as a proportion of that killed by lions (= LFU equivalent, see Chapter 4). The reciprocal of the LFU equivalent gives an indication of the number of the smaller predator species that are equivalent to one lion.

The reciprocal of the LFU alone cannot be used to guide decisions around the carrying capacity for the individual members of the large predator guild, because different members of the guild cannot all kill the same prey. Smaller predators cannot kill the larger prey killed by lions, and the lower maximum kill size will set a lower limit on maximum carrying capacity for that predator. To accommodate this, the maximum prey biomass available to each of the large predators was determined by summing all the available biomass that fell below the maximum kill weight per predator (Chapter 4). The maximum kill of the lions was 960 kg and the entire prey biomass in SGR under 960 kg of 255477 kg was available to the lions. For each other predator, the available biomass was expressed as a proportion of 255477 kg.

Estimating the carrying capacity of SGR for the large predator guild will be addressed in two components, firstly the available prey off take from the existing prey population and secondly the additional predator FEQs that can be sustained by the annual prey replacements released onto the reserve. By combining these two methods a clearer indication of the predator carrying capacity suitable for the objectives of tourism can be achieved.

Existing Prey Population

To determine the available prey off take from the existing prey population at SGR, the Maximum Sustainable Yield (MSY) of all the prey species was used. The MSY method was preferred over the LHB method as it has been used for cheetahs (Purchase & du Toit, 2000; Lindsey *et al*., 2011), for lions on a small enclosed reserve (Power, 2003), and for wild dogs (Lindsey *et al*., 2004). Furthermore, the LHB method was found to be not useful in determining the sustainability of lions on a reserve (Power, 2003).

The MSY was determined by Caughley's (1977) equation as follows:

$$MSY = (r_m \,.\, K/4)$$

where r_m is the maximum potential growth rate of the population in a given environment and K is the long term equilibrium of a given game population under given habitat conditions (Bothma, 1996). The intrinsic growth rate r_m is calculated as follows:

$$r_m = 1.5W^{-0.36}$$

where W is the mean adult live body mass (Bothma 1996; Lindsey *et al*., 2004).

Lindsey *et al.* (2004) used the MSY method to determine the viability of small, enclosed reserves for the use as meta-population sites for wild dogs. For K, Lindsey *et al*. (2004) used the population size at a steady density. For this study the average population for the study period per prey species was used for K and a conservative approach was adopted using K/4 as opposed to K/2 (Caughley & Sinclair, 1994; Bothma, 1996; Power, 2003).

Once the MSY was determined for each of the known prey species the combined available weight was calculated to establish the prey biomass available for the predators per year on a sustainable basis (Power, 2003).

Annual Prey Replacements

SGR has an annual budget to supplement the prey population to maintain predator densities needed to achieve the tourism objectives. In order to determine how to optimize these introductions for the predators, two aspects will be taken into account. Firstly, ranking the prey species to be introduced in terms of lowest cost per kilogram. The cost per animal is taken from SGR's audit and determined by averaging 17 auction prices throughout South

Africa in 2008. Secondly, ranking the various potential prey species for introduction according to preference by the predators as determined by the Jacob's Index (Chapter 4).

The South African Rand/USD exchange rate of 0.148:1 as of 31/12/2007 is used in this study.

Results: Predictions and Management Recommendations

Predator Kill Correction Factors

The daily kill rate (kg/FEQ/day) for each predator varied from 6.3 - 10.1 (kg/FEQ/day; Table 6.1).

Table 6.1. The daily kill rate of the large predators as determined using data from the two by two week follows. * From Bissett (2007). FEQ is the adult female equivalent per predator species, n is the total number of kills made per predator during the four weeks of continuous observation and total biomass is the total mass on n in kilograms.

	kills			expected daily kill rate
	n	total biomass (kg)	FEQs	(kg/FEQ/day
lion	12	1295.66	4.6	10.06
leopard	8	239.4	1.15	7.43
cheetah	17	377	2.13	6.32
wild dog				9.99*

Lions: The difference between observed biomass killed and expected biomass killed for the Northern pride of lions varied from a factor of 3 to 4.3 (Table 6.2). Daily consumption rates were 2.3 – 3.4 kg/day/FEQ with an average of 2.8 kg/day instead of the expected 10.1 kg/day/FEQ. The proposed correction factor for the Northern lions was 3.7.

Table 6.2. The difference between the number of kills recorded and their total biomass, and the expected biomass off take based on the number of FEQs, for the Northern pride of lions. All weights are kg. Correction factor is the factor by which the recorded kills per predator species must be multiplied to provide an approximation of actual kills determined by predicted kill biomass.

year	no. kills	biomass killed	no. FEQs	kg/day/FEQ	predicted kill biomass	correction factor
2004	49	6941.0	5.6	3.4	20562.6	3.0
2005	65	9771.5	9.4	2.9	34332.3	3.5
2006	61	7666.2	8.1	2.6	29742.4	3.9
2007	80	6884.3	8.1	2.3	29742.4	4.3
average	63.8	7815.7	7.8	2.8	28594.9	3.7

The difference between observed biomass killed and expected biomass killed for the Southern pride of lions varied from a factor of 1.3 - 5.3 (Table 6.3). Daily consumption rates were 1.9 – 7.6 kg/day/FEQ with an average of 4.0 kg/day/FEQ.

Table 6.3. The difference between the number of kills recorded and their total biomass, and the expected biomass off take based on the number of FEQs, for the Southern pride of lions. All weights are kg. Correction factor is the factor by which the recorded kills per predator species must be multiplied to provide an approximation of actual kills determined by predicted kill biomass.

year	no. kills	biomass killed	no. FEQs	kg/FEQ/day	predicted kill biomass	correction factor
2004	83	10201.7	7.1	3.9	26070.5	2.6
2005	46	4707.9	6.8	1.9	24785.3	5.3
2006	41	4660.0	2.6	4.9	9546.9	2.1
2007	100	9748.9	3.5	7.6	12851.7	1.3
average	67.5	7329.6	5.0	4.0	18313.6	2.5

When data from the two lion prides were combined, the correction factor was 3.1 (Table 6.4).

Table 6.4. The difference between the number of kills recorded and their total biomass, and the expected biomass off take based on the number of FEQs, for all lions. Data are averages. All weights are kg. Correction factor is the factor by which the recorded kills per predator species must be multiplied to provide an approximation of actual kills determined by predicted kill biomass.

year	no. kills	biomass killed	no. FEQs	kg/day/FEQ	predicted kill biomass	correction factor
total n+s*	65.6	7572.7	6.4	3.4	23454.3	3.1

*total n + s is the northern and southern lions combined for the duration of the study period.

Wild dogs: The difference between observed biomass killed and expected biomass killed for the wild dogs varied from a factor of 4.3 to 4.5 (Table 6.5). Daily consumption rates were 2.2 – 2.3 kg/day/FEQ at an average of 2.3 kg/day instead of the predicted 9.9 kg/day/FEQ (Bissett, 2007). The proposed correction factor for wild dogs was 4.3.

Table 6.5. The difference between the kills recorded and biomass off take expected for the wild dogs with corrections factors. All weights are in kg. Correction factor is the factor by which the recorded kills per predator species must be multiplied to provide an approximation of actual kills determined by predicted kill biomass.

year	no. kills	biomass killed	no. FEQs	kg/day/FEQ	predicted kill biomass	correction factor
2004	75	4544.3	5.4	2.3	19512.9	4.3
2005	70	4612.3	5.6	2.2	20163.3	4.5
2006	59	5899.8	7.0	2.3	25294.5	4.3
average	68	5018.8	6.00	2.3	21656.9	4.3

Cheetahs: The difference between observed biomass killed and expected biomass killed for the cheetahs varied from 3.3 to 7.2 times (Table 6.6). Daily consumption rates were 0.9 – 1.9 kg/day/FEQ at an average of 1.3 kg/day instead of the predicted 6.3 kg/day/FEQ). The proposed correction factor for the cheetahs was 5.1.

Table 6.6. The difference between the kills recorded and biomass off take expected for the cheetah with corrections factors. All weights are in kg. Correction factor is the factor by which the recorded kills per predator species must be multiplied to provide an approximation of actual kills determined by predicted kill biomass.

year	no. kills	biomass killed	no. FEQs	kg/day/FEQ	predicted kill biomass	correction factor
2004	33.0	1294.8	4.0	0.9	9319.5	7.2
2005	55.0	2843.9	6.2	1.3	14302.2	5.0
2006	29.0	1157.7	3.3	1.0	7612.4	6.6
2007	58.0	2305.0	3.3	1.9	7612.4	3.3
average	43.8	1900.3	4.2	1.3	9711.6	5.1

Leopards: The difference between observed biomass killed and expected biomass killed ratio for the leopards varied from 7.3 to 9.5 times (Table 6.7). Daily consumption rates were 0.8 – 1.0 kg/day/FEQ at an average of 0.9 kg/day instead of the predicted 7.4 kg/day/FEQ based on the continuous follows. The proposed correction factor for the leopards was 8.5.

Table 6.7. The difference between the kills recorded and biomass off take expected for the leopard with corrections factors. All weights are in kg. Correction factor is the factor by which the recorded kills per predator species must be multiplied to provide an approximation of actual kills determined by predicted kill biomass.

year	no. kills	biomass killed	no. FEQs	kg/day/FEQ	predicted kill biomass	correction factor
2004	26	855.4	3.0	0.78	8135.9	9.5
2005	19	1010.6	3.5	0.79	9491.8	9.4
2006	16	926.9	2.5	1.02	6779.9	7.3
2007	22	1099.8	3.3	0.93	8813.8	8.0
average	20.8	973.2	3.1	0.88	8305.4	8.6

The correction factors are not only necessary to calculate carrying capacity for the predators but also to calculate the financial impact of the large predator guild of SGR. The recorded kills for the large predator guild in 2005, when the wild dogs were present on the reserve, had a financial value of R584 426 (USD 86 491.9) yet when the average correction factors for the study period per predator were applied the value increased 4.2 times to R2 434 968.2 (USD 360 362.3; See Appendix 2). In making this correction, it was assumed that the recorded shortfall in biomass killed was composed of the same ratio of prey species as those of the recorded kills.

Management Recommendations

In order for wildlife managers at SGR to be able to utilize the correction factors annually to determine the full effect of the predators on the prey base the standard method of predator monitoring (Chapter 2) must be maintained.

Predator Carrying Capacity

For a predator species (cheetah for example), the reciprocal of the LFU equivalent (which is a measure of how many cheetahs are equivalent to a lion) and the proportion of biomass available (cheetahs have access to about half the biomass that lions do) can be combined to indicate a maximum stocking rate relative to lions. In table 6.8, the reciprocal of the LFU equivalent is multiplied by the proportional biomass availability to generate a maximum

stocking rate relative to lions. The final values are close and it is suggested that lions and the other predators can be stocked at the same rate.

Table 6.8. The maximum relative predator stocking rates for predators in SGR. The final column gives the stocking rate per predator species relative to one adult lioness (LFU). All weights are in kg.

predator	max kill weight	biomass available	ratio of total prey available	LFU equiv.	1/LFU equiv.	relative stocking rate
lion	960	255477.0	1.0	1.0	1.0	1.0
wild dogs	240	194207.2	0.8	1.0	1.0	0.8
leopard	228	162963.4	0.6	0.7	1.4	0.9
cheetah	183	147576.1	0.6	0.6	1.6	0.9

In Chapter 4 it was established that one LFU required 3671.9 kg of prey annually. The maximum sustainable yield (Caughley's 1977) estimated that 18 509.3 kg would be available of which kudu (3 396.0 kg), impala (2 734.2 kg), warthog (2419.3 kg) and zebra (2 317.1 kg) represented more than half (Table 6.9). This calculation uses K/4 which is very conservative and if K/2 is used the MSY is doubled to about 37000 kg.

The total MSY for the prey base divided by the LFU annual biomass requirements to give a carrying capacity of five or ten LFUs (Table 6.9). The MSY for SGR equates to between seven and fourteen percent of the total prey biomass.

Table 6.9. Maximum sustainable yield for the prey base in SGR including Jacobs Index values from Chapter 4. Where r is the intrinsic growth rate per prey species and the available mass is the resultant available offtake in kilograms according to MSY per prey species.

prey species	mass	number	r	MSY	avail. mass	Jacob's Index
kudu	200.0	305	0.2	17.0	3396.0	0.4
impala	52.5	578	0.4	52.1	2734.2	-0.9
warthog	72.5	416	0.3	33.4	2419.3	0.3
plains zebra	290.0	164	0.2	8.0	2317.1	0.3
black wildebeest	125.0	159	0.3	10.5	1310.0	0.6
red hartebeest	135.0	126	0.3	8.1	1090.8	0.1
bushbuck	48.0	224	0.4	20.8	1000.3	0.3
blesbok	74.0	168	0.3	13.4	990.1	0.3
giraffe	865.0	30	0.1	1.0	856.4	0.0
waterbuck	192.5	59	0.2	3.3	641.0	0.0
gemsbok	225.0	62	0.2	2.3	519.8	0.4
springbok	33.5	109	0.4	11.6	386.9	0.1
bushpig	48.0	83	0.4	7.7	370.6	-0.3
eland	610.0	14	0.1	0.5	305.0	0.4
grey duiker	19.0	31	0.5	4.0	76.6	0.8
mountain reedbuck	27.0	18	0.5	2.1	55.6	-0.2
ostrich	120.0	5	0.3	0.3	39.6	0.7
total					18509.3	

The carrying capacity of five LSUs (10 LFUs if K/2 is used) does not meet the requirements for the tourism objectives of SGR where regular sightings of the large predators are an expectation. The assumed minimum number of predators required to sustain tourism in SGR (*Pers. Comm.* Joe Cloete (General Manager, SGR); Dr. Johan Joubert (Wildlife Director, SGR); *Pers. Obs*) represents about 16.5 LFUs (Table 6.10). This would require an annual biomass of 60 586 kg which is more than double the MSY when calculated with K/2 and

almost four times that when calculated using K/4. Thus supplementation of the prey base with between 23500 and 42 000 kg of prey is required

Table 6.10. The minimum number of predators required to sustain tourism represented in lion feeding units (LFUs) in SGR and the annual biomass required annually to sustain each predator species.

predator	min. no.	LFUs	biomass required (kg)
lion	9 to 12	10.0	36 719
leopard	4	3.7	13 586
cheetah	4	2.8	10 281
total		16.5	60 586

Management Recommendations

Several factors influence which prey species are used for supplementation. Firstly, they should be preferred prey species in terms of the Jacobs Index. Secondly, they must be available for purchase at a reasonable price (Table 6.11). Zebra is one of the more economical prey species to supplement but has a Jacobs' Index of +0.02 but it was not killed by cheetahs and rarely killed by leopards and therefore not suitable for prey supplementation. By spending R120 000 on each of the six most preferred prey species, for a total of R720 000, an addition 43 839.91 kg of prey biomass can be supplemented (Table 6.11). This supplemented biomass combined with the MSY biomass of 18 509.27 kg gives a total of 62 349.18 kg prey biomass which is sufficient to maintain the 16.5 LFUs required for the tourism objective. Prey supplementation is expensive and in many ways an experiment. It is therefore essential that the results are closely monitored to see if it has the desired effect. Prey supplementation can also be used to trigger prey switching and reduce predation pressure on a favoured prey species possibly allowing that population to recover.

Table 6.11. The additional prey biomass created by supplementing the preferred prey species into SGR. The Jacob's Index is an average for all predators. All mass is in kg.

prey species	unit cost R*	mass	cost/kg R*	no. animals per R120 000*	added mass	Jacob's Index
eland	5162	525.8	9.82	23.3	12 223.6	0.4
ostrich	1476	103.4	14.27	81.3	8 409.8	0.7
kudu	2943	172.4	17.07	40.8	7 029.6	0.4
blesbok	1139	63.0	18.09	105.4	6634.2	0.3
plains zebra	5551	250.0	22.21	21.6		0.0
gemsbok	4876	194.0	25.14	24.6	4773.2	0.4
black wildebeest	2680	106.5	25.16	44.8	4769.6	0.6
red hartebeest	3860	116.4	33.17	31.1		0.1
springbok (heartwater)	8617	28.9	298.37	13.9		0.1
total				215.5	43 839.9	

* South African Rand/USD exchange rate of 0.148:1 as of 31/12/2007

The 16.5 LFUs can be shared between the predators in many ways. In the earlier section, it was suggested that the ratio between lions, cheetahs and leopards should not exceed 1:1:1 as the smaller predators will place too much predation pressure on the smaller prey species. The reserve management has recommended a greater number of lions and fewer cheetahs and leopards and this is acceptable since the lions utilize the entire range of the prey below 960 kg.

Despite Hayward *et. al.* (2007b)'s carrying capacity predictions for SGR being for individuals and that for this study in FEQs (Table 6.12) and the fact that prey replacements were not taken into account, comparison shows that the proposed stocking rates for predators by Hayward *et. al*. (2007b) are greater than those predicted in this study, specifically when comparison is made to the existing prey base and its MSY off take of this study (Table 6.12).

Table 6.12. A comparison between the predator carrying capacities for SGR by Hayward *et. al*. (2007b) with this study.

	Hayward *et. al*., 2007b individuals		this study FEQs	
predator	preferred prey species	preferred weight range	MSY	MSY + replacements
lions	12	18	1.8	5.9
leopards	9	9	1.6	5.1
cheetahs	6	7	1.7	5.45

Predator Space Use

Predictions, observations and results

In the previous section, carrying capacity has been based on dietary requirements only. While there is no doubt that this is very important, so too are aspects of space requirements and behaviour. For example, the extent to which members of the same and different species will tolerate overlap of ranges or core areas will influence carrying capacity. So too will landscape requirements and the extent to which those landscape features are available on the conservation area.

Most members of the predator guild in SGR concentrated their core areas (50% UD) in the southern part of the reserve along the Bushmans River where there was considerable overlap of space used. This is likely to result in negative competitive interactions between the predators as was observed (*Pers. Obs*.) with leopards, cheetahs and wild dogs being killed by lions, and cheetahs killed by leopards. If predator density is allowed to increase, it is predicted that such negative competitive intra-guild interactions will increase.

The adult male leopard's home range (95% UD) extended far beyond the borders of SGR. This was also evident for a female leopard with multiple breeches of the perimeter fence onto neighbouring farms (*Pers. Obs*.). It is predicted that if the leopard density is allowed to exceed its recommended capacity (Table 6.12) and if the prey density is allowed to decline through no further prey introductions leopards will continue to leave the reserve, specifically

juvenile leopards looking for their own territory. The social carrying capacity must be taken into account and if leopard ranges tend not to overlap and if new young males have to find new ranges, then this may be more important in determining carrying capacity than food. The wild dogs were ultimately removed from the reserve not only due to their impact on the prey base but primarily due to repeated escapes from the reserve onto neighbouring farms. When the lion total was at its highest (22 individuals) there were two breakouts in two days. The prediction is that as the density of predators increases the effects will not only be on the prey base but their space use will also be affected to the point of intra-guild conflict resulting in mortality and predator breakouts.

Management Recommendations

In order to minimize inter-predator conflict and to reduce the risk of predator breakout from the reserve it is recommended that the predator densities are kept close to the densities in Table 6.12 which excludes wild dogs.

It is recommended that prey species density is kept constant by annual prey supplementation as described in this chapter. Finally it is recommended that a vegetation management program be implemented to provide for better grazing in the northern parts of the reserve to enable a better prey distribution throughout the reserve and reduce the predator pressure around the Bushmans River in the south.

Discussion

Correction Factors

Mills (1996) suggested that the best way to collect data on predator feeding ecology is through periods of continuous observation to counter the over emphasis of large kills and underestimation of the smaller, more quickly consumed animals, a problem identified by Mills (1984), Radloff & du Toit (2004) and Power (2003). However, it has also been suggested that where observation effort is high, as on many of the private conservation areas, the undercount of small prey is not substantial (Radloff & du Toit, 2004; Bissett, 2007). This was not supported at SGR where there was a high observation effort yet the recorded kills accounted for between 12% for leopards and 48% for the southern lions of the expected kills. On Karongwe Game Reserve, Lehmann *et al*. (2008) estimated that 1539 kills were made by

lions over a six year period but only 43% of these were located. This figure is similar to that recorded for the southern pride (48%) over the four year study period, however it was much higher than the northern pride.

The correction factors will be site specific and will be affected by three variables which themselves influence the likelihood of a kill being recorded. Firstly the density of the vegetation will influence whether or not a kill is recorded. In SGR, the southern sector had more open Bontveld, Primary *Acacia* Thicket and Bushclump Savanna as well as the old cleared and cultivated lands along the Bushmans River (O'Brien, 2004) while the northern sector was dominated by Thicket. Secondly the intensity of the monitoring will also affect the detection of kills. In SGR, more guest lodges were situated in the southern sector resulting in more activity and hence a greater probability of *ad hoc* sightings of kills. Also the Wildlife Department of SGR was based in the south and the southern sector was monitored more intensely than the north. Finally, the hunting behaviour of the species will influence the likelihood of kills being detected. The kills of species that hunt at night in thick vegetation and those of smaller predators that kill smaller prey are more likely to be missed than those that kill large prey at dawn and dusk.

Predator Carrying Capacity Predictions

Predator ratio

The proposed predator ratio of one leopard, to one cheetah to one lion is a guide to the maximum numbers of cheetahs and leopards relative to the number of lions. It is suggested that an increased number of leopards and cheetahs will result in non-sustainable predation on the smaller prey (species and age classes). For example, the cheetahs preyed heavily on new born antelope and it is possible that too many cheetahs could result in few young animals reaching maturity to replenish the adults that were preyed upon by other predators.

Maximum Sustainable Yield

The final value for MSY depends on the estimated value for K and whether K is divided by 2 or 4 in the equation. K is the carrying capacity for a species and in this study it is assumed that the average numbers for each prey species represented equilibrium where births balanced deaths. The conservative approach is to use K/4 particularly in variable climates (Caughley & Sinclair, 1994). However, at K/2 the effects of density dependent factors on growth should be

minimal and this is also often used in calculating MSY (Caughley & Sinclair, 1994). According to Mills & Biggs (1993) the MSY can be of value in determining the capacity to sustain lions in larger reserves and National Parks that anticipate lion reintroduction and apportionment with other carnivores must be accounted for. Mills (1991) furthermore warns that multi-predator communities in African savanna can be exceedingly complex and the determination of MSY should acknowledge such complexities. It is for this reason that the FEQ for the different large predators in SGR were standardized into LFUs.

The estimated MSY for SGR gave an annual biomass yield of between 18500 kg and 37000 kg which amounted to between 7 and 14% of the available biomass on the reserve. On Karongwe Game Reserve, lions kill between 3.3 and 7.1% of the available biomass annually with an LFU requirement of 6.9 – 12.1 kg/day/LFU (Lehmann *et al*., 2008). The results for SGR were similar with 10.1 kg/day/LFU.

Carrying Capacity

From the MSY calculations, SGR can sustain between five and ten LFUs. This equates to a density of between 3.3 and 6.6 LFUs/10 000 ha. Power (2003) recommends a stocking density of 6 – 7 LFUs/10 000 ha in a savanna area with an average annual rainfall between 500 and 700 mm. SGR has a lower annual rainfall of 422 mm and since rainfall is believed to be the ultimate driver of savanna ecosystems (Chapter 2) it is not surprising that the predicted predator density is lower. Predator densities for a number of natural populations vary between about 7 – 10 LFUs/10 000 ha (Schaller, 1972; Rodgers, 1974; Creel & Creel, 1997) while the highest natural population densities of 38 – 40 lions/10 000 ha are attained in East Africa (Makacha & Schaller, 1969; Schaller, 1972). The simple comparison of predator stocking densities between different areas is of little value as the areas will be characterized by different vegetation, soils and annual rainfall as well as different prey species. SGR naturally has less than half the predator stocking densities than the savanna areas further north as it has a much lower annual rainfall, is located in the thicket biome and hence a lower large herbivore biomass (LHB) standing crop available for predation.

Prey Supplementation

In keeping with the Government Gazette (2003) definition of SGR's predators as Managed Wild Populations, their prey may be supplemented when necessary. The reason for this is that

the predator density required to meet the tourism needs (a subjective estimate based on experience of SGR management team), exceeds that of the density allowed through predation of the existing prey as estimated by the MSY. There are various aspects to consider when introducing prey species to supplement the predators including what prey species are available for purchase; the cost of desired species, and the prey preference of the predators and the size of the prey species (Power, 2003). In SGR, supplementation is with the six most preferred prey species which also have the lowest cost per kilogram. The warthogs in SGR however do not need to be supplemented as despite being the preferred prey species for lions their numbers continued to increase each year.

One problem with prey reintroductions is that the available prey species come from game ranches without predators. These animals are naive to the threat of predation and some of the results presented in Chapter 4 illustrate that such prey experience very high initial predation pressure. It is well known that some predators will kill more than required to meet daily energy requirements (Balme *et al*., 2007) and will not consume all the available biomass from a carcass. When this is the case, the reserve will not gain the full benefits from the reintroduced animals. There will however be a knock on effect to aerial and terrestrial scavengers.

Sustainability

SGR subscribes to the concept that the reserve needs to be financially, socially and ecologically sustainable in the long term (Taylor *et al*., 2009). From a social point of view eco-tourism as a land use has substantially more benefits than traditional extensive agriculture. SGR is a founder member of Indalo, an association for the private game reserves of the Eastern Cape which is chaired by the NGO Wilderness Foundation. Indalo commissions a socio-economic report for the 12 members biennially, the findings of which show positive benefits to the area (Langholz & Kerley, 2006: Appendix 3).

Financially SGR must function as a successful business in order to be sustainable. The value of the predators can be assessed by comparing their costs to the reserve income. In 2005 the predators killed R2 434 968 (after correction factors were applied) worth of prey. When the cost of prey reintroduction was added, the total cost was R3 154 968. In 2005, tourism brought in R61.08 million (audited figures for 2005 from head office) and while all of this

cannot be attributed to the large predators, they are a very important part of the tourism experience as surveyed by Lindsey *et al*. (2007) where leopard, lion and cheetah were the three most sought after species by tourists visiting game reserves in South Africa. In 2005, the cost of the predators in SGR was about 5% of the total tourism income. Without the large predators SGR would not be able to compete in the market (*pers. Comm.* Joe Cloete, Shamwari Group General Manager).

For ecological sustainability, it is essential that predator numbers are kept to the minimum needed to sustain tourism. Calculations of MSY suggest that without prey supplementation, SGR cannot support sufficient predators to meet the tourism needs. Without supplementation it is likely that populations of non-replaceable prey species such as bushbuck, duiker and grysbok will become locally extinct, not to mention the smaller non prey species that are killed by large predators such as bat eared foxes. Expansion of the SGR to include what could become prey refugia is an attractive option but the multiple demands for land in the Eastern Cape Province make this not possible.

While the calculation of MSY gives a basis for stocking of large predators, a form of adaptive management should be implemented to monitor the effects of the predators on the populations of prey and to monitor the effects of prey supplementation. Careful observations will generate the required data on which future management decisions can be based.

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APPENDICES

Appendix 1.

Common and scientific names of mammalian species referred to in the study

Class Mammalia

Order Lagomorpha

Scrub Hare	*Lepus saxatilis* (Cuvier 1823)

Order Tubulidentata

Aardvark	*Orycteropus afer* (Pallas 1766)

Order Primates

Chacma baboon	*Papio hamadryas* (Linnaeus 1758)
Vervet monkey	*Chlorocebus pygerythrus* (Linnaeus 1758)

Order Carnivora

Bat-eared fox	*Otocyon megalotis* (Desmarest 1822)
African wild dog	*Lycaon pictus* (Temminck 1820)
Black-backed jackal	*Canis mesomelas* (von Schreber 1775)
Coyote	*Canis latrans* (Say 1823)
Cheetah	*Acinonyx jubatus* (von Schreber 1775)
Caracal	*Caracal caracal* (von Schreber 1776)
Serval	*Leptailurus serval* (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)
Juaquin fox	*Vulpes macrotis macrotis* (Merriam 1902)
Red fox	*Vulpes vulpes* (Linnaeus 1758)
Least weasel	*Mustela nivalis* (Linnaeus 1776)
Ermine stoat	*Mustela ermine* (Linnaeus 1758)

Order Proboscidea

African savannah elephant	*Loxodonta africana* (Blumenbach 1797)

Order Perissodactyla

Black rhino	*Diceros bicornis* (Linnaeus 1758)
White rhino	*Ceratotherium simum* (Burchell 1817)
Mountain zebra	*Equua zebra* (Linnaeus 1758)

Order Artiodactyla

Warthog	*Phacochoerus africanus* (Gmelin 1788)
Bushpig	*Potamochoerus larvatus* (F.Cuvier 1822)
Giraffe	*Giraffa camelopardalis* (Linnaeus 1758)
Bushbuck	*Tragelaphus scriptus* (Pallas 1766)
Kudu	*Tragelaphus strepsiceros* (Pallas 1766)
Eland	*Tragelaphus oryx* (Pallas 1766)
Nyala	*Tragelaphus angasii* (Gray 1849)
Buffalo	*Syncerus caffer* (Sparrman 1779)
Waterbuck	*Kobus ellipsiprymmus* (Ogilby 1833)
Gemsbok	*Oryx gazella* (Linnaeus 1758)
Mountain reedbuck	*Redunca fulvorufula* (Afzelius 1815)
Southern reedbuck	*Redunca arundinum* (Boddaert 1785)
Grey rhebuck	*Pelea capreolus* (Forster 1790)
Red hartebeest	*Acelaphus buselaphus* (Pallas 1766)
Blesbok	*Damaliscus pygargus phillipsi* (Pallas 1767)
Blue wildebeest	*Connochaetes taurinus* (Burchell 1823)
Black wildebeest	*Connochaetes gnou* (Zimmerman 1780)
Grey duiker	*Sylvicapra grimmia* (Linnaeus 1758)
Impala	*Aepyceros melampus* (Lichtenstein 1812)
Springbok	*Anitdorcus marsupialis* (Zimmerman 1780)
Steenbok	*Raphicerus campestris* (Thunberg 1811)
Cape grysbok	*Raphicerus melanotis* (Thunberg 1811)

Thomson's gazelle *Gazella thomsoni* (Günther 1884)

Order Rodentia

Cape porcupine *Hystrix africaeaustralis* (Peters 1852)

Class Aves

Order Struthioniformes

Ostrich *Struthio camelus* (Linnaeus 1758)

Order Galliformes

Helmeted guineafowl *Numida meleagris* (Linnaeus 1758)

Class Sauropsida

Order Testudines

Leopard tortoise *Geochelone pardalis* (Bell 1828)

Order Squamata

Monitor lizard *Varanus albigularis* (Daudin 1802)

Appendix 2.

The kill list and prey values (South African Rand) for 2005 for the lions, leopards, cheetahs and wild dogs with the average annual Correction Factor of each predator for the study period applied.

Lions 2005

prey	no. kills	unit price	kill value	annual correction
baboon	2	0	0	0
black wildebeest	23	2680	61640	191084
blesbok	2	1139	2278	7062
bushbuck	5	2943	14715	45617
bushpig	4	350	1400	4340
grey duiker	2	1178	2356	7304
eland	5	5162	25810	80011
gemsbok	3	4876	14628	45347
giraffe	1	17317	17317	53683
impala	1	880	880	2728
kudu	21	2918	61278	189962
red hartebeest	6	3860	23160	71796
springbok	1	8617	8617	26713
warthog	26	418	10868	33691
waterbuck	4	5470	21880	67828
plains zebra	5	5551	27755	86041
total	111		294582	913204

Leopards 2005

prey	no. kills	unit price	kill value	annual correction
blesbok	1	1139	1139	9682
bushbuck	9	2943	26487	225140
bushpig	1	350	350	2975
grey duiker	1	1178	1178	10013
eland	1	5162	5162	43877
impala	2	880	1760	14960
kudu	1	2918	2918	24803
vervet monkey	1	0	0	0
warthog	1	418	418	3553
waterbuck	1	5470	5470	46495
total	19		44882	381497

Cheetahs 2005

prey	no. kills	unit price	kill value	annual correction
black wildebeest	2	2680	5360	27336
Blesbok	8	1139	9112	46471
bushbuck	1	2943	2943	15009
grey duiker	7	1178	8246	42055
impala	18	880	15840	80784
kudu	4	2918	11672	59527
mountain reedbuck	4	2918	11672	59527
red hartebeest	3	3860	11580	59058
scrub hare	2	0	0	0
springbok	3	8617	25851	131840
warthog	2	418	836	4264
plains zebra	1	5551	5551	28310
total	55		108663	554181

Wild dogs 2005

prey	no. kills	unit price	kill value	annual correction
black wildebeest	1	2680	2680	11524
blesbok	3	1139	3417	14693
bushbuck	13	2943	38259	164514
grey duiker	6	1178	7068	30392
impala	24	880	21120	90816
kudu	17	2918	49606	213306
red hartebeest	1	3860	3860	16598
springbok	1	8617	8617	37053
warthog	4	418	1672	7190
total	70		136299	586086

Appendix 3.

The executive summary for the socio economic report done for Indalo by Langholz and Kerley (2006).

- The socio-economic profile of ten ecotourism-based private game reserves (PGRs) was established, using a self-completed questionnaire, in order to assess their contribution to conservation and development in the Eastern Cape region.
- This is a follow-up to a similar study for which data were collected during winter 2003 and published in 2004. The objectives of the current study were to: 1) validate findings from the 2004 study, using a larger sample size; 2) collect new information beyond what the previous study produced; and 3) identify changes among private game reserves (PGRs) that may have occurred since the original study.
- The PGRs varied widely in data provision, property size, and duration of operation, which limited the analyses possible. The findings are, however, of considerable value and are summarised here. Especially helpful is the fact that all seven PGRs from the 2004 study also participated in the 2006 study, plus three new respondents.
- In changing from farming to game-based ecotourism, the total number of employees increased by a factor of 4.5. This number reflects data from 10 reserves, and differs somewhat from the factor of 3.5 reported in 2004.
- Each of the 10 reserves is estimated to support an average of 107 full-time employees per reserve (median of 78), as well as an additional 375 people per reserve who are family members or other dependents of the full-time employees (median of 353). Thus, the

1,060 full-time employees across all ten PGRs support an estimated 3,745 dependents.

- Conversion from agriculture to ecotourism resulted in the average wage bill per PGR spiking from R121,145 to R3.87 million – a 32-fold increase. This number is based on a larger sample size than the 2004 study, which documented a 20-fold increase post-conversion (R160,367 to R3.2 million per annum*).*
- Average annual salary per full-time employee increased 4.8 fold, from R6,157 to R29,930. This post-conversion salary increase generally corroborates annual salary figures from the 2004 report (5.7 fold increase, from R5,498 p.a. to R31,263).
- Private game reserves are moving upscale. Accommodations are increasingly luxurious and the average price charged per person has risen 37% compared to the 2004 study.
- The total cost of establishing a PGR has risen R10 million compared to 2004, to a new median of R42 million.
- Gross revenues, and revenues per hectare, have shown steady increases over the past four years and are projected to continue rising. A lack of data on operating costs, however, precludes any analysis of reserves' profitability.
- The ten PGRs in the study were protecting a total of 116,608 hectares (average of 11,661; median 6,993), representing six of South Africa's eight biomes and an immense diversity of plants and animals.
- Respondents are engaged in a wide variety of social development projects in and around their reserves.

• This survey has shown that PGRs provide a highly desirable land-use option in relation to
traditional land uses in this area. A number of recommendations are presented, including
the need to assess the full economic impacts of the industry, regularly updating these
socio-economic surveys, auditing the contribution of the PGRs to biodiversity conservation, assessing the costs of extra-limital wildlife species and making these findings available to stakeholders and policymakers.