

**THE FEEDING AND SPATIAL ECOLOGIES OF THE
LARGE CARNIVORE GUILD ON KWANDWE PRIVATE
GAME RESERVE**

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ABSTRACT

The reintroduction of lions, cheetahs and African wild dogs to Kwandwe Private Game Reserve in the Eastern Cape Province of South Africa created the opportunity to study the biology and behaviour of these large carnivores in an enclosed system. The research focused on space utilisation and feeding ecology of the predators, using standard observational methods. Changes in the structure of the carnivore guild, and changes in the prey base that occurred during the study were used as natural experiments to examine factors affecting space use and diet. In general, the diets of the predators were similar to previous studies and prey abundance was more important than prey species size in determining prey selection. Changes in the abundance of certain prey species was matched by a dietary switch in lions from kudu to warthog and an increase in the proportion of springbok kills by the cheetahs. There was no significant difference in the proportions of prey species detected by *ad hoc* or continuous observations.

Core areas occupied by the predators were significantly smaller than home ranges except when females were denning. Home ranges overlapped both within and between species, but there was very little overlap of core areas. An increase in the number of lion prides in the area during the study resulted in an increase in overlap of home ranges of lions and cheetahs, but did not result in a change in home range size. Space use by female cheetahs with cubs increased as the cubs grew older. The use of thicket vegetation by cheetahs decreased with an increase in the number of lion prides.

Minimum Daily Energy Expenditure, energy intake and net benefit were calculated for the predators using data from continuous observations. All predators exhibited a

large net benefit and the net benefit for single female cheetahs was greater than for the members of the coalition. Net benefit for the alpha pair of African wild dogs was lower than that of the pack.

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PREFACE

This thesis is structured as follows:

Chapter 1 is a brief introduction that broadly sets the scene and rationale for the study. It does not serve to introduce the research chapters which contain their own introduction, statement of aims and discussion.

Chapter 2 provides a detailed description of the study site and study animals, as well as the general methodology that is common to the subsequent research chapters. It includes a comparison of two game census methods; aerial game counts and road game counts.

Chapter 3 is a research chapter that presents a general description of the diet of lions, cheetahs and African wild dogs on Kwandwe. In addition, factors affecting the diet and prey selection are examined.

Chapter 4 is a research chapter that presents a general description of space use by lions, cheetahs and African wild dogs on Kwandwe. In addition, the effect of an increase in the number of lion prides on space use by the large carnivores is examined.

Chapter 5 is a research chapter that examines the foraging efficiency of lions, cheetahs and African wild dogs on Kwandwe, with particular emphasis on the energetic costs of travel and rest, as well as energy gains from kills.

Chapter 6 highlights the most salient findings from the research chapters, presents the conclusions that may be drawn from these findings and provides recommendations for future management.

CHAPTER 1

GENERAL INTRODUCTION AND RESEARCH RATIONALE

Worldwide, all species of large mammalian carnivores are threatened to various extents by habitat loss, declining prey numbers and direct persecution. Consequently, their continued survival presents a challenge to conservationists (Caro 1994; Nowell & Jackson 1996; Creel & Creel 2002; Sunquist & Sunquist 2002; Sillero-Zubiri *et al.* 2004). In Africa, large carnivores, such as lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*), were once common throughout much of the continent but have undergone extensive range contractions due to the increase in human populations (Schaller 1972; Caro 1994; Creel & Creel 2002; Sunquist & Sunquist 2002; Sillero-Zubiri *et al.* 2004).

The cheetah and lion are two of the 36 species in the Family Felidae occurring worldwide, with seven of these being found in southern Africa (Sunquist & Sunquist 2002; Skinner & Chimimba 2005). Five subspecies of cheetahs have been identified (Caro 1994; Hunter & Hamman 2003) and are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix I and classified as Vulnerable (sub-Saharan Africa) or Endangered (North Africa to Asia) by the World Conservation Union (IUCN) Red Data List (Marker *et al.* 2003; Friedmann & Daly 2004). The subspecies that occurs throughout southern Africa is *Acinonyx jubatus jubatus* (Hunter & Hamman 2003; Friedmann & Daly 2004) and is classified as Vulnerable by the IUCN Red Data List. The lion is listed in CITES Appendix II and is classified as Vulnerable by the IUCN Red Data List (Friedmann & Daly 2004). The African wild dog is one of the 36 species in the Family Canidae occurring worldwide, with 13 of these occurring in Africa (Sillero-

Zubiri *et al.* 2004). The African wild dog is not listed by CITES but is classified as Endangered in the IUCN Red Data List (Friedmann & Daly 2004).

Where large predators still range freely, their conservation must be a priority (e.g. cheetahs in Namibia Marker *et al.* (2003) and African wild dogs and cheetahs in South Africa Lindsey *et al.* (2004); Marnewick & Cilliers (2006)). However, under these conditions, the conservation of large carnivores presents numerous problems, not least among which is the conflict between the predators and humans and their livestock (Mills 1991; Mills *et al.* 2001). Actual or potential conflicts with human activities have restricted large carnivores to reserves and adjacent areas in much of the world (Creel & Creel 2002) and for example, in South Africa there are no free-ranging lions and very few free-ranging African wild dogs and cheetahs (Lindsey *et al.* 2004; Marnewick & Cilliers 2006). If relatively small game reserves are to make a contribution to the conservation of these animals, it is vital that the behaviour of large carnivores in enclosed systems is fully understood. Consequently, increasing the current knowledge store on large carnivore ecology in enclosed reserves is the focus of the current research.

The confinement of large carnivores to small reserves may remove the immediate problem of predator-human conflict but it poses other challenges. For example, large carnivores have low population densities and much greater space requirements compared to smaller species or those occupying lower trophic levels (Blackburn & Gaston 1994; Woodroffe & Ginsberg 1998; Creel & Creel 2002) and this can result in a lack of genetic diversity and the likelihood of inbreeding within a single reserve. The aforementioned is perhaps the most serious problem facing the smaller reserves

and it is being addressed through metapopulation management systems as in the case of the African wild dog (Mills *et al.* 1998).

In South Africa, the development of ecotourism has led to the re-assessment of historical patterns of land use by governments, communities and the private sector, and there has been a shift in land use from agriculture and livestock farming to conservation and game ranching. In the Eastern Cape Province there has been a rapid development of ecotourism ventures with at least 13 privately owned game reserves being established in the province in the last 17 years (Langholz & Kerley 2006) and one of these reserves has been the focus of this study. Large predators, including lions, cheetahs and African wild dogs, which were eradicated from their natural ranges in the Eastern Cape Province in the latter half of the nineteenth century (Skead 2007), have been reintroduced to most of the newly developed reserves in the region. These reintroductions have created both a need for information that can be used to guide the management of the systems, and an opportunity to address more fundamental questions in carnivore biology (see Radloff & du Toit 2004 for an example). From a management perspective, it is important to understand how the predators utilise the different vegetation types and how this utilisation is affected by changes in the structure of the carnivore guild. It is also important to understand the diets of the large carnivores so that their combined effect on the herbivores can be modelled. Together, this information will enable game reserve managers to estimate stocking rates for large predators in enclosed systems. At a fundamental level, the large carnivores were extirpated from the Eastern Cape Province before predator research in Africa started and consequently, their behaviour in the thicket vegetation, which is typical of the region, has only recently been studied (Bissett & Bernard 2007;

Hayward *et al.* 2007; Rapson & Bernard 2007). These studies are important as they broaden our understanding of the behaviour of species such as the cheetah, which had been based on studies in more open, savanna-like systems (Durant *et al.* 1988; Caro 1994; Durant 2000a, 2000b). In addition, the reintroduction of large carnivores has created a number of “natural experiments” that have allowed the factors that affect space use, diet and prey selection by members of a large carnivore guild to be studied and these have been a focus of this study.

Therefore, the broad aims of this research have been to study the functioning of a large carnivore guild in a relatively small, enclosed system. This has been done to provide information that can be used to guide the management of the system and also to contribute at a fundamental level to the understanding of the ecology of large carnivores. The first focus area has been on the feeding ecology (diet and prey selection) of the different predators and the roles of predator and prey size, and prey abundance in shaping prey selection. The second area of focus has been how space is used by different members of the carnivore guild and how space use changes as the structure (numbers of species and individuals) of the guild changes. The basic approach has been to use observational methods, often focussing on following known animals for prolonged periods, and treating a range of management interventions and natural changes as natural experiments.

CHAPTER 2

GENERAL DESCRIPTION OF THE STUDY AREA AND STUDY ANIMALS

LOCATION

Kwandwe Private Game Reserve (from here on referred to as Kwandwe) lies in the Great Fish River Valley approximately 35km north of Grahamstown, in the Eastern Cape Province of South Africa (Figure 2.1). At the start of the current study in 2003 Kwandwe was approximately rectangular in shape with the long axis running in a northeast to southwest direction and occupied an area of approximately 160km². In December 2005 additional land was bought and the area of the reserve increased to about 210km². The perennial Great Fish River flows through the reserve for approximately 25km and all the watercourses drain towards the Great Fish River. The most important watercourse is the Botha's River that feeds three large man-made dams, which together with several smaller dams and numerous seasonal pans, provide important sources of water for the fauna (Figure 2.2). Surrounding land comprised privately owned farmland and state owned land. Kwandwe itself is privately owned and was established as a conservation area in 1999. Prior to this, the land was utilised for ostrich and small stock farming. As is prescribed for reserves in South Africa that are reintroducing dangerous species, the entire perimeter of Kwandwe is enclosed by electrified game fencing.

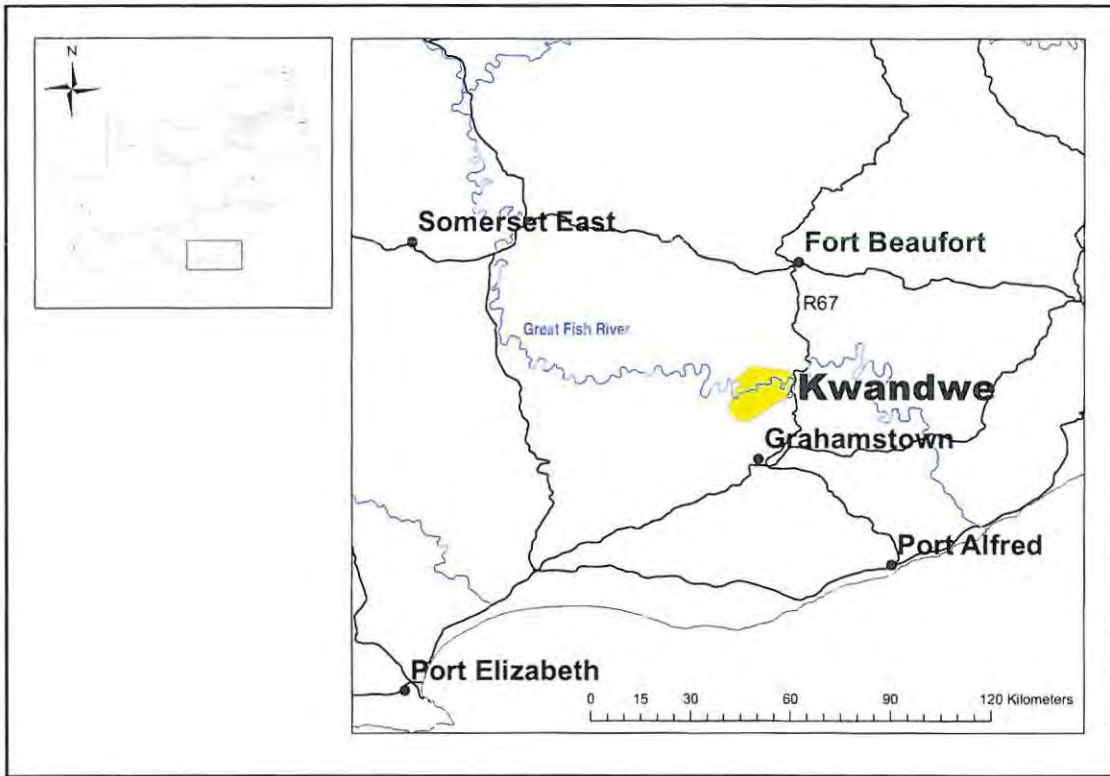


Figure 2.1: Kwandwe Private Game Reserve in relation to Grahamstown and the Great Fish River. (ArcGIS 9; map units: decimal degrees; not projected).

TOPOGRAPHY AND GEOLOGY

The underlying geology of the area consists of predominantly grey/red mudstone and sandstone of the Middleton formation, with sandstone dominating (Johnson & Keyser 1976). The river valleys contain nutrient rich mudstones which are highly erodible while more resistant sandstone occurs on the ridges. Low & Rebelo (1996) describe the geology and soil of the Eastern Cape Province as sandy clays and lithosols of the Cape Supergroup, Dwyka and Ecca Formations, to deep solonetic soils derived from Beaufort Group dolerites. The topography of Kwandwe is fairly complex with a series of east-west orientated sandstone ridges in the south, and wide plains with gentle topography in the centre of the reserve and steep rising ground north of the Great Fish River continuing up to the top of the Fish River Rand along the northern boundary of the reserve. The river itself is deeply incised with steep banks, thus making access to long stretches on the river difficult (Figure 2.2).

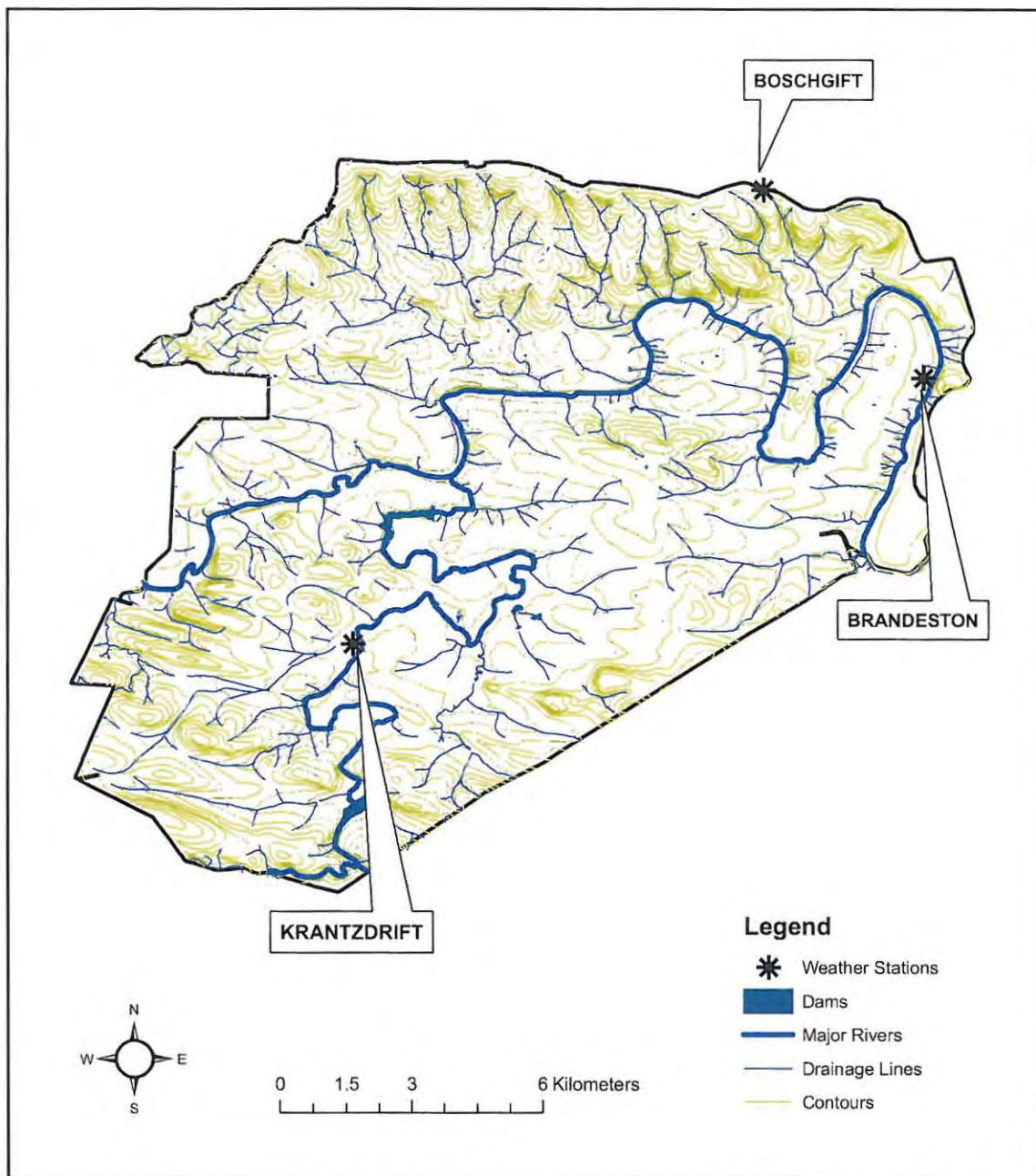


Figure 2.2: The topography and drainage patterns of Kwandwe Private Game Reserve (ArcGIS 9; map units: decimal degrees; not projected). The rainfall data were collected at three sites (Krantzdrift; Brandeston and Boschgift) and the temperature data were collected at the weather station at Krantzdrift. Boschgift is located on the Fish River Rand.

CLIMATE

The Great Fish River Valley has a complex climate because of its topographical complexity. The elevation ranges from 170m above sea level at the Great Fish River to over 600m above sea level on the dividing ridges. This range in elevation has a marked effect on climate and rainfall patterns within the area. Lower elevation areas experience higher mean annual temperatures as well as lower mean annual rainfall, resulting in a hot semi-arid environment. Higher elevation areas have lower mean annual temperatures and higher mean annual rainfall, thus resulting in a cooler wetter environment. Aspect and slope result in further variations in the climate as southern slopes experience cooler more moist conditions, while north facing slopes are characteristically warmer and drier (Stone *et al.* 1998; pers. obs.). Temperatures and rainfall data were recorded from a weather station on the reserve (Krantzdrift, Figure 2.2). However, as mentioned previously, rainfall is highly variable and was thus measured at an additional two sites on the reserve (Figure 2.2). Peaks of rainfall occur from September to November and January to April (Figure 2.3). Mean annual rainfall for the area is 425mm, but ranges between 364mm in the lower lying areas (Krantzdrift in Figure 2.3) and 526mm on the higher ground North of the Great Fish River (Boschgift in Figure 2.3). Kwandwe has a warm temperate climate (Figure 2.4) with maximum daily temperatures often exceeding 35°C in the summer months (December; January and February) and minimum night-time temperatures below 5°C in the winter months (June; July and August).

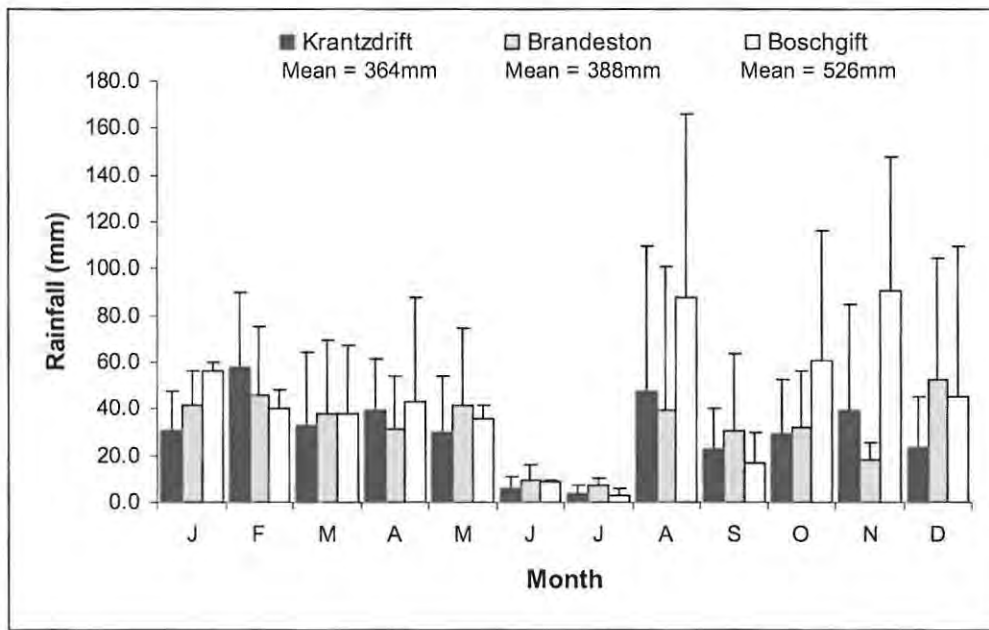


Figure 2.3: The mean monthly rainfall for Kwandwe at each weather station during the study period (2003 – 2007). Data are means \pm 1SD.

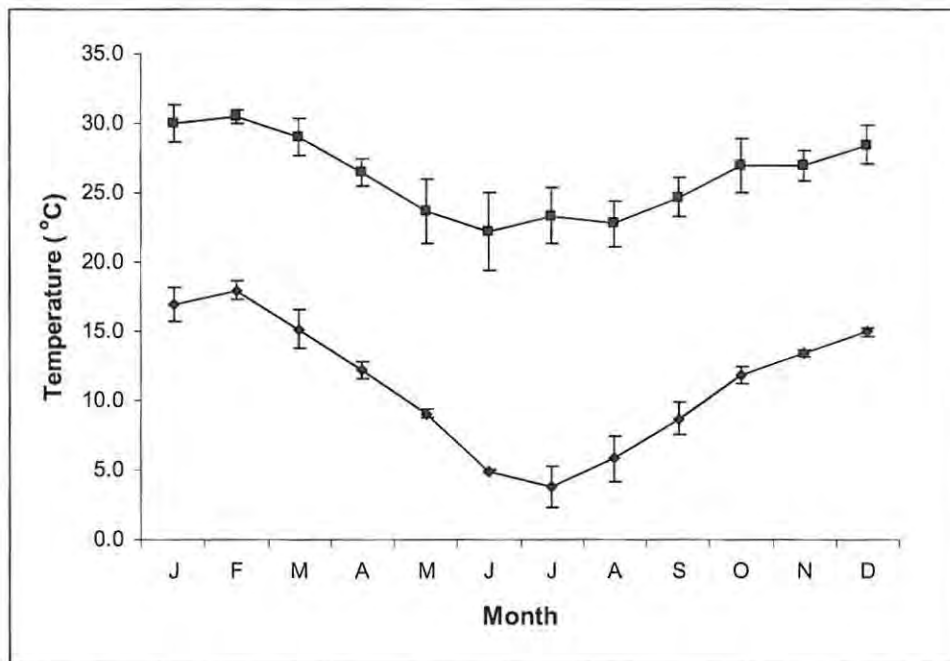


Figure 2.4: The mean monthly maximum and minimum temperatures for Kwandwe during the study period 2003 – 2007. Data are means \pm 1SD.

VEGETATION

Numerous independent studies have been conducted in the Thicket Biome of the Eastern Cape Province, resulting in the vegetation of this area being interpreted in many ways. The vegetation of the lower Great Fish River Valley, which includes most of Kwandwe, is classified by Low & Rebelo (1996) as Valley Thicket (in the higher rainfall areas) and Xeric Succulent Thicket (in the lower rainfall areas). The western edge of the reserve is on the cline from thicket to the more open vegetation described as Eastern Mixed Nama Karoo which is more typical of the middle and upper Great Fish River Valley (Low & Rebelo 1996). Succulent thicket is better known by the terminology used by Acocks (1988) who called it Valley Bushveld. The vegetation of the lower Great Fish River Valley falls into the category, Fish River Scrub. Acocks (1988) described the Fish River Scrub in its undamaged state as an extremely dense, semi-succulent, thorny scrub, about 2m high. Overgrazing of large areas has opened up this vegetation, resulting in the invasion of *Opuntia* species and *Euphorbia bothae* (Acocks 1988).

A preliminary vegetation map for Kwandwe was prepared by the resident ecologist (Mark Galpin) and this was refined in 2003 (Figure 2.5). An aerial photograph (1:50 000) and numerous site visits were used for visual assessment of the vegetation composition and structure. A geographical positioning system (GPS) was used to more accurately define the vegetation blocks. In 2006 the vegetation map was refined once again, and a new vegetation type (Dry forest) was added to the original ten. Dry forest includes a combination of Afro-montane forest and Valley Thicket species. These vegetation types are described below.

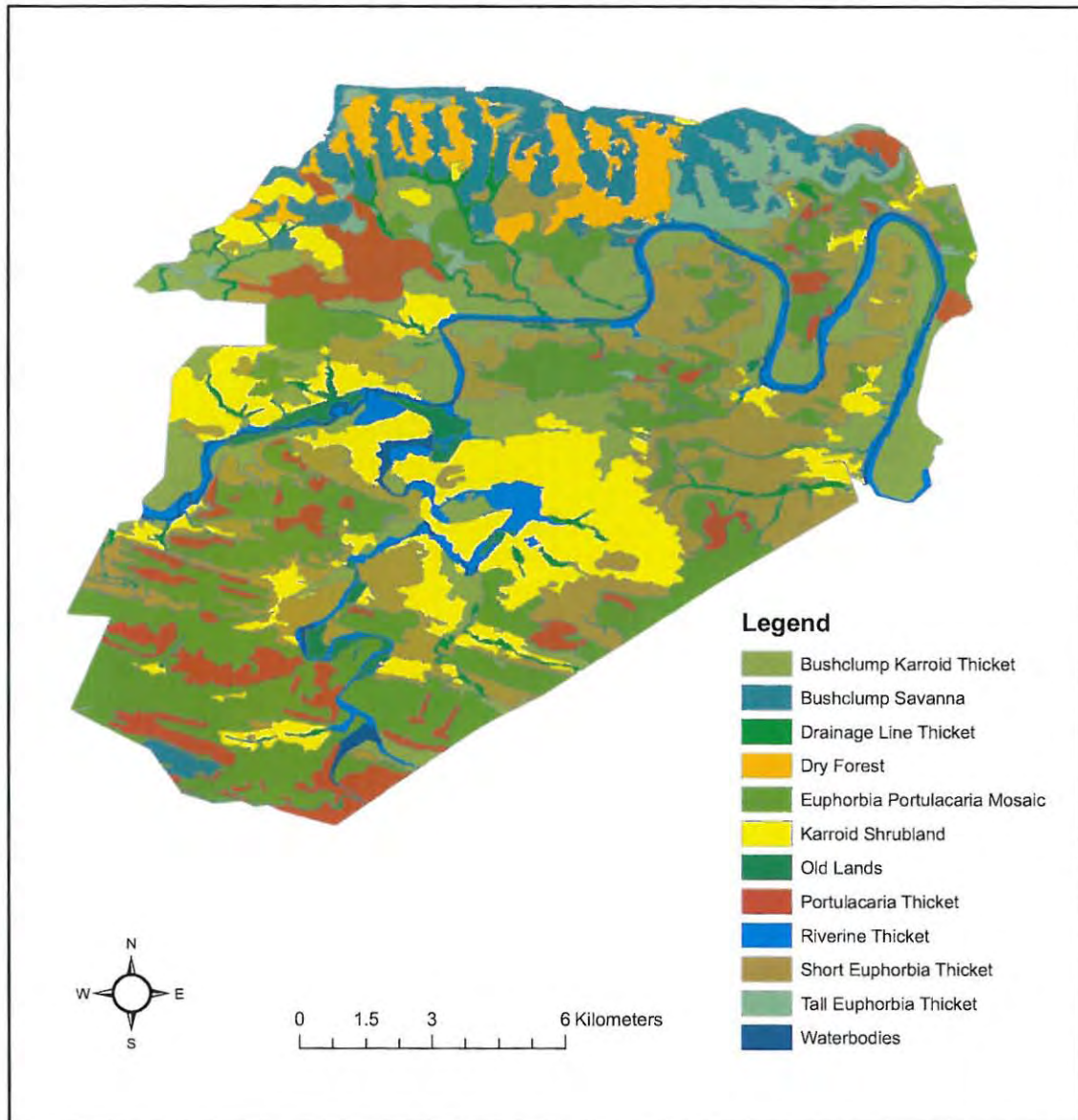


Figure 2.5: Distribution of the vegetation types on Kwandwe Private Game Reserve (ArcGIS 9; map units: decimal degrees; not projected; surface area of the large water bodies was 168.50ha.).

1. Bushclump Karroid Thicket.

This vegetation type is found on the sandy/clay colluvial slopes bordering the alluvial plains of the Great Fish and Botha's Rivers. The soils are characterized by a red colour. Characteristic tree species include: *Rhus refracta*, *Rhus longispina*, *Euclea undulata* and *Maytenus polyacantha*. Characteristic grass species include: *Setaria neglecta* and *Digitaria eriantha*. The landscape is characterized by clumps of the above mentioned tree species interspersed with patches of the above mentioned grass species and *Pentzia incana* as the dominant karroid shrub. This type of vegetation occupied 2501.1ha.

2. *Portulacaria* Thicket.

This vegetation type consists of dense stands of *Portulacaria afra* interspersed with *Pappea capensis* and is found predominantly in the northern and western sections of the reserve on steep slopes. The under storey is entirely bare in the west with no herbaceous layer. However, in the north there is often a herbaceous layer with some grass cover dominated by: *Themeda triandra*; *Digitaria eriantha* and *Panicum maximum*. This type of vegetation occupied 1423.6ha.

3. *Euphorbia Portulacaria* Mosaic.

This vegetation type is the transition between Short *Euphorbia* thicket and *Portulacaria* thicket, and has a greater diversity and density of woody species than the Short *Euphorbia* thicket. It is characterized by clumps of woody species dominated by *Portulacaria afra*, *Pappea capensis*, *Maytenus capitata*, *Ozoroa mucromata*, *Euclea undulata* and *Schotia afra*. These patches are, in turn, interspersed with more open patches characterized by *Euphorbia bothae* and *Rhigozum obovatum* as the woody

species and *Themeda triandra* and *Digitaria eriantha* as the dominant grass species. *Sporobolus fimbriatus* and *Panicum maximum* are the dominating grass species found mainly in the bushclumps of the woody vegetation. This type of vegetation occupied 4274.9ha.

4. Short *Euphorbia* Thicket.

Stands of *Euphorbia bothae* dominate this vegetation type and these may be replaced by *Euphorbia corulescens* in some areas, with sparse patches of *Portulacaria afra*. In some areas especially in the north, the woody component is more dominant than the short *Euphorbia*. Other woody species include *Pappea capensis*, *Rhigozum obovatum*, *Euclea undulata* and *Maytenus capitata*. Grass species include *Themeda triandra*, *Digitaria eriantha* and *Aristida* spp and *Panicum maximum* which is mainly found within the bushclumps. This vegetation type grows on shallow soils overlying Ecca shale. This type of vegetation occupied 3291.1ha.

5. Tall *Euphorbia* Thicket.

Tall *Euphorbia* thicket is dominated by a continuous stand of *Euphorbia tetragona* and/or *Euphorbia triangularis* growing on steep slopes ascending towards the top of the Fish River Rand in the northern section of the property. The under storey is dominated by the grasses *Panicum deustem* and *Panicum maximum*. Other tree species characterizing this vegetation type include: *Maytenus undata*, *Elaeodendron zeyheri* (*Cassine crocea*) and *Cussonia spicata*. This type of vegetation occupied 552.3ha.

6. Bushclump Savanna Thicket.

Bushclump savanna thicket dominates the flatter landscape on the top of the Fish River Rand in the north and a small area in the south western section of the property. It differs climatically from bushclump karroid thicket in that it occurs at higher altitude and thus it is found in a cooler wetter environment. Characteristic tree species include: *Cussonia spicata*, *Scutia myrtina*, *Fluggea verucossa*, *Psydrax ovata*, *Olea europea* and *Pteroxylon obliquum*. The landscape is characterized by clumps of the above mentioned species interspersed with patches of grassland. Characteristic grass species include: *Digitaria eriantha*, *Setaria neglecta* and *Eustachys paspaloides*. *Chrysocoma ciliata* is the dominant karroid shrub as opposed to *Pentzia incana* in Bushclump karroid thicket. This type of vegetation occupied 1291.8ha.

7. Old Cultivated Areas (Old Lands).

These areas comprise previously cultivated fields situated on the alluvial sections of the Great Fish and Botha's Rivers. Grass species include *Pennisetum clandestinum* (Kikuyu), *Cenchrus ciliaris* (Blue buffalo grass) and *Cynodon dactylon*, with each land being dominated by a single stand of one of the above species. These areas lack trees or shrubs. This type of vegetation occupied 268.5ha.

8. Karroid Shrubland.

Karroid shrubland dominates the flatter, low lying areas in the middle of the reserve and a few higher lying areas in the north western section. It is characterized by large open areas dotted throughout with trees and bushes. The dominant tree species include *Pappea capensis* and *Rhus refracta*. The dominant characteristic of this vegetation type is the karroid herbaceous layer, made up exclusively of *Pentzia incana*. Grass

cover is generally sparse and characteristic species include: *Digitaria eriantha*, *Cynodon dactylon* and *Aristida congesta* subspecies *barbicollis*. This type of vegetation occupied 2720.1ha.

9. Drainage Line Thicket.

This vegetation type consists of dense stands of *Rhus refracta* growing in drainage lines. The under storey comprises the woody species, *Plumbago auriculata* and the grass species *Panicum maximum*, which grows on the edge of the thicket. This type of vegetation occupied 425.6ha.

10. Riverine Thicket.

Riverine thicket comprises two distinct zones, the alluvial *Acacia* zone, made up of *Acacia karroo* on the alluvial soils bordering the Great Fish and Botha's Rivers water courses, and the second zone which constitutes the vegetation growing on the steep banks of the Great Fish River and its tributaries. Characteristic species include *Rhus lancea*, *Acacia karroo* and *Combretum caffrum*. The herbaceous layer is dominated almost exclusively by *Panicum maximum*. This type of vegetation occupied 818.7ha.

11. Dry Forest

This vegetation type is the transition between Afro-montane Forest and Valley Thicket and is found in the steep valleys in the northern section of the property. Trees are generally between 5-10m tall and there is a distinct shrub and herbaceous layer. Tree species include: *Harpephyllum caffrum*, *Cassine aethiopica*, *Cussonia spicata*, *Schotia latifolia*, *Clanadendron copense* and *Olea europea*. Shrubs and climbers are common and include: *Maytenus heterophylla*, *Scutia myrtina*, *Carissa bispinosa* and

Rhoicissus tridentate. The under storey is dominated by the grasses *Panicum deustum* and *Panicum maximum*. This type of vegetation occupied 749.5ha.

Vegetation density and visibility

The vegetation density and visibility for each vegetation type was assessed using a modified point centered quarter method (Phillips 1959) and a checker board respectively. In each vegetation type ten 100m long transects were completed. Crosses were marked at 20m intervals along each transect on the ground and in each quarter the distance to the nearest plant that was more than 50cm tall was measured. A height of 50cm was chosen as providing sufficient cover for a hunting predator. Objects at a distance of more than 10m from the point were not counted so as to ensure that the same object was not counted twice. To calculate the density of objects with a height greater than 50cm, the mean of the four distances at each point of the transect was used to calculate the area of the circle that had been sampled at that point. These areas were summed to produce the total area for each transect and the number of objects was then expressed relative to the area. In the same quarters, the percentage of the checker board that was visible at a distance of 10m from the point and with a viewing height of 70cm was recorded. A height of 70cm was chosen to represent the head height of a predator. The checker board was 90cm wide and 60cm high with 10x10cm squares. The mean percentage of the checker board that was visible was calculated for each transect and these figures were used to calculate a mean for the vegetation type (Table 2.1).

Table 2.1: Visibility index and density of the vegetation types on Kwandwe. Data are means \pm 1SD. Visibility Index = % of checkerboard; Density = objects/m².

Vegetation Type	Visibility Index	Density
Bushclump karroid thicket	84.43 \pm 9.42	0.10 \pm 0.14
<i>Portulacaria</i> thicket	36.84 \pm 12.18	1.45 \pm 0.88
<i>Euphorbia Portulacaria</i> mosaic	53.24 \pm 17.11	0.66 \pm 0.6
Short <i>Euphorbia</i> thicket	48.41 \pm 12.37	0.95 \pm 0.54
Tall <i>Euphorbia</i> thicket	61.19 \pm 9.2	0.43 \pm 0.21
Bushclump savanna thicket	69.22 \pm 11.03	0.50 \pm 0.34
Old lands	99.3 \pm 0.82	0.00
Karroid shrubland	98.24 \pm 2.59	0.01 \pm 0.01
Drainage line thicket	55.18 \pm 3.94	0.53 \pm 0.69
Riverine thicket	64.94 \pm 19.76	0.31 \pm 0.21
Dry forest	61.21 \pm 9.1	0.43 \pm 0.21

Simplified Vegetation Map

For certain analyses the vegetation map was simplified by combining some of the vegetation types to form an open, savanna-like habitat and a grouping of denser, thicket vegetations (Figure 2.6). Habitat types with a visibility index (see Table 2.1) greater than 69 were combined to form the open habitat (Karroid Shrubland; Bushclump Karroid Thicket; Bushclump Savanna and Old lands). These habitats covered 37% of the reserve. The denser, thicket habitat is made up of Tall *Euphorbia* Thicket; Short *Euphorbia* Thicket; *Portulacaria/Euphorbia* Mosaic; *Portulacaria* Thicket; Dry Forest; Drainage line Thicket and Riverine Thicket, and covered 63% of the reserve.

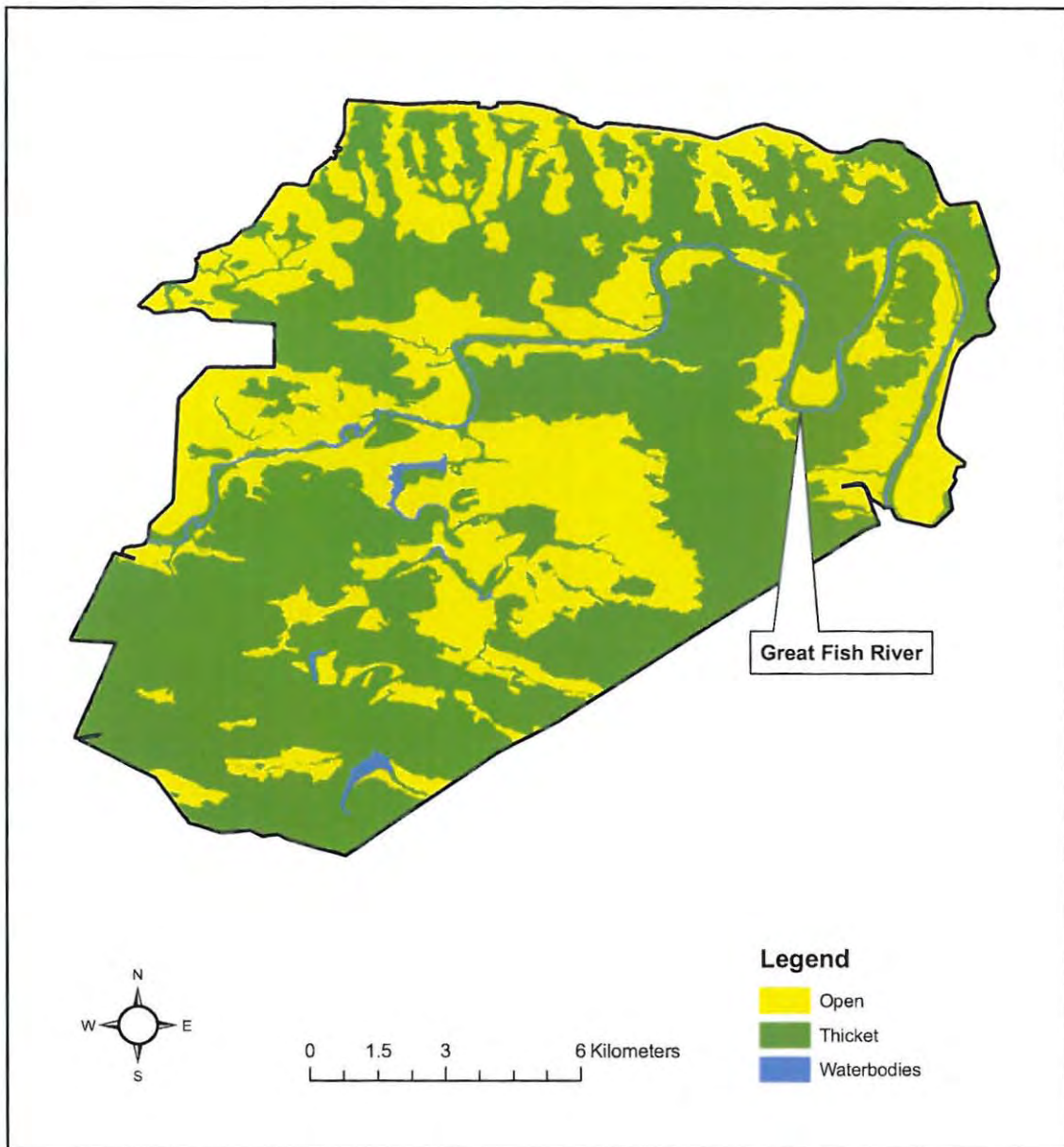


Figure 2.6: Map of Kwandwe Private Game Reserve showing the open and thicket vegetation and their distribution on the reserve (ArcGIS 9; map units: decimal degrees; not projected).

MAMMALIAN FAUNA

Most of the indigenous large mammalian fauna had been extirpated from the area when Kwandwe assumed control in 1999 but some small and medium-sized ungulates were present. Species that were present included greater kudu (kudu), bushbuck, common duiker, steenbok, cape grysbok, grey rhebuck, mountain reedbuck, bushpig and common warthog (warthog). Between 1999 and 2001 over 2000 head of ungulates were introduced onto Kwandwe. During this period 18 white rhino, six black rhino, 22 giraffe and 23 elephants were also reintroduced. Historical records state that cheetahs, lions and African wild dogs occurred in the Eastern Cape Province and were last recorded in the area in the late 1800's (Skead 2007). Initial carnivore reintroductions (2001-2002) included four lions, nine cheetahs, two leopards, six brown hyenas and 10 servals. An additional two cheetahs were reintroduced in 2003 and six African wild dogs were introduced in 2004.

The common and scientific names of all animal species referred to in the text are listed in Appendix A.

GAME CENSUS

Aerial game counts using a helicopter were done once a year, except for 2006, to obtain information on wild animal numbers. Road strip counts were done seasonally from August 2005 till August 2007 for comparison with the aerial game counts.

Aerial Game Counts

A Jet Ranger III, ZS-HSV helicopter was used with a recorder sitting next to the pilot and two counters, one counting the animals on either side of the helicopter. The pilot drew the attention of the observers to any animals that may be ahead of the helicopter and the recorder recorded all the information, helped the pilot to maintain direction and counted any animals in the blind spot in front of the helicopter. The pilot used GPS flight instruments to fly fixed strips. The transects flown were 250m apart and therefore animals within 125m wide strips were counted on either side of the helicopter. The localities of the animals were recorded using GPS equipment. The flying height was between 30-50m above the ground and the flying speed was approximately 60km/hr, increasing to 90km/hr in the more open areas. The results of the aerial annual game counts are shown in Table 2.2. In 2006, there was no aerial game count and an average of the 2005 and 2007 was used.

Road Game Counts

Herbivores were sampled based on a road strip sampling technique (Lancia *et al.* 1996; Bothma 2002; Ogutu *et al.* 2006). Three separate transect routes totalling 98.3km were driven (Figure 2.7). The roads driven were selected to cover the reserve and to pass through representatives of all vegetation types. Road game counts were undertaken four times a year in spring (November), summer (February), autumn

(May) and winter (August) over a two year period (August 2005 –August 2007). For each season, each route was driven twice over a period of six to eight days. All counts were made in the early morning between 05h30 – 10h00 in the summer and 07h00 – 12h00 in the winter months. The counts were made in a Toyota Hilux 4-wheel drive vehicle with an elevated seat on the back of the vehicle. Vehicle speed was maintained at 15-20km/hr and counts were conducted by the same two observers on the back of the vehicle, counting opposite sides. Once an ungulate was located the following data were recorded: the distance of the animal or herd from the road, GPS co-ordinates, and the direction of the herd from the vehicle, the species, age, sex and total number. The perpendicular distance was measured using a Nikon Laser 800 rangefinder, with 8x magnification. The programme DISTANCE 4.1 (Thomas *et al.* 2003) was used to calculate the overall density of ungulates. DISTANCE 4.1 requires a minimum of 60 individual observations per sample in order to adequately estimate relative density. In order to satisfy this requirement, all individual observations of different ungulate species in each season were combined for the purpose of the analysis. Several models of the probability density function (half-normal Cosine; half-normal Hermite polynomial; hazard-rate Cosine; hazard-rate Simple polynomial; uniform Cosine; uniform Simple polynomial) were applied to the data and the best fit detection models were selected using Akaike Information Criteria. A density of ungulates per hectare was obtained from which the relative density of individual species was calculated using the species specific contribution (frequency of occurrence) to the total group. Although road counts were driven eight times over the two years, all data were pooled to generate a larger data set. The two count methods have been compared using mean values for the 2005 and 2007 aerial game counts and the results from the driven game count.

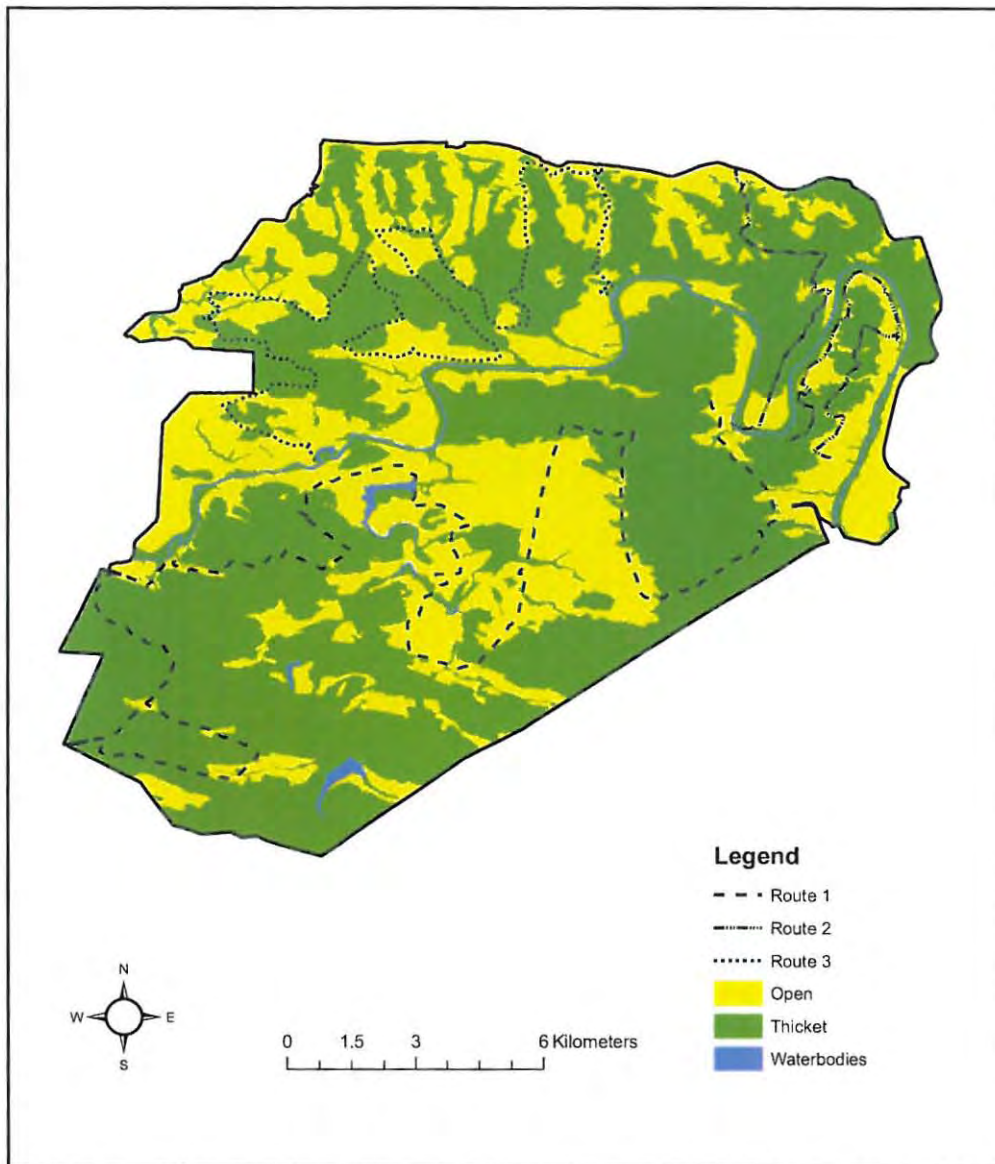


Figure 2.7: Map of Kwandwe Private Game Reserve showing the routes used during the road strip counts overlaid on the simplified vegetation map (ArcGIS 9; map units: decimal degrees; not projected).

Table 2.2: Results from the aerial game census for 2003; 2004; 2005 and 2007.

Species	Total			
	2003	2004	2005	2007
Kudu	1602	1422	1239	1388
Warthog	559	731	835	1447
Springbok	510	403	250	138
Impala	434	306	246	221
Common duiker	337	237	104	152
Red hartebeest	318	183	164	171
Blue wildebeest	252	173	7	1
Black wildebeest	0	0	17	279
Bushbuck	204	166	90	209
Zebra	175	172	184	279
Gemsbok	131	166	184	112
Waterbuck	109	99	128	105
Eland	96	81	77	81
Steenbok	69	50	53	47
Ostrich	77	91	44	36
Blesbok	58	29	6	6
Giraffe	32	36	43	33
Buffalo	37	41	49	60
Mountain reedbuck	29	31	12	19
Bushpig	6	12	1	8
Black backed jackal	41	74	80	34

Comparison of aerial and road count methods

The total number of individuals of each species was significantly different between the aerial and road counts ($\chi^2 = 547.56$, $df = 18$, $P < 0.001$; Table 2.3). However, the percentage contribution of each species to the total number of animals estimated using each method showed no significant difference between the two methods ($\chi^2 = 13.98$; $df = 18$; $P > 0.05$). Species such as common duiker, eland and waterbuck had very similar whole numbers in the aerial counts and the road counts (Table 2.3), whereas

zebra, gemsbok, ostrich, red hartebeest, springbok and steenbok were over counted in the road counts compared to the aerial counts.

Table 2.3: Number of each prey species estimated using two different game census techniques. Numbers in parentheses are percentages of the total number of animals counted with each method.

Species	Method	
	Aerial (%)	Road (%)
Black wildebeest	98 (2.3)	69 (1.8)
Blesbok	6 (0.1)	2 (0.04)
Blue wildebeest	4 (0.1)	2 (0.04)
Buffalo	55 (1.3)	15 (0.4)
Zebra	232 (5.5)	368 (9.6)
Bushbuck	150 (3.6)	25 (0.6)
Common duiker	128 (3.1)	137 (3.6)
Eland	79 (1.9)	83 (2.2)
Gemsbok	148 (3.5)	252 (6.6)
Impala	234 (5.6)	158 (4.1)
Kudu	1314 (31.4)	1039 (27.1)
Mountain reedbuck	16 (0.4)	9 (0.2)
Nyala	7 (0.2)	2 (0.04)
Ostrich	40 (1.0)	129 (3.4)
Red hartebeest	168 (4.0)	237 (6.2)
Springbok	194 (4.6)	267 (7.0)
Steenbok	50 (1.2)	259 (6.8)
Warthog	1141 (27.3)	678 (17.7)
Waterbuck	117 (2.8)	106 (2.8)
TOTAL	4177	3837

By contrast, species such as buffalo, bushbuck, impala, warthog and kudu were under counted in the road counts compared to the aerial counts (Table 2.3). Blesbok, blue wildebeest, mountain reedbuck and nyala numbers were very low on the reserve and

were therefore under represented in the road counts, as the road counts covered a smaller proportion of the reserve than did the aerial counts.

There are many variables that can affect the outcome of a game count, for example: terrain, weather and vegetation. Species that prefer open habitats such as ostrich, zebra and springbok tend to be over represented in road counts as they are more visible further away from the vehicle increasing the number of observations, which can ultimately increase estimates of density when using the DISTANCE program. However, species that prefer dense areas such as bushbuck, buffalo and kudu tend to be under counted as they are more difficult to see further away from the vehicle. During aerial counts, these species would be flushed from the thicker habitats by the helicopter. These problems can be overcome, to a certain extent, by increasing the coverage of the reserve during a road count, utilizing variable cutoff distances for different vegetation types (e.g. lower cutoffs for thicket habitats) and restricting counts to days that experience the same weather (e.g. all conducted on clear, dry days).

Although absolute numbers are important for reserve management, so too are the proportions of the different species, and changes in their abundance. Because road counts were only conducted for two years, it was not possible to establish whether they would detect changes in population size, but road counts generated proportions that were very similar to those from aerial counts. Aerial counts cost approximately R3600/hr flying and the counts on Kwandwe were conducted over three to four days covering 1000ha/hr, giving a total cost of R75 000 per year. The costs of road counts (fuel and proportion of maintenance costs) were R1000 per year and substantially less than the costs of aerial counts.

STUDY ANIMALS

Each animal was assigned a unique alpha-numeric identification number which followed the form of species/sex/number e.g. CF1, would refer to cheetah female one; LM1, would refer to lion male one; WDM1, would refer to African wild dog male one etc. Where sex was unknown, the letter U was used. Sequential numbering was used so that each individual could be identified by a unique number. If animals died or were sold their specific number was not assigned to another animal. Cubs and pups born on the reserve were also numbered sequentially. Where necessary in this thesis cheetahs, lions and African wild dogs will be referred to by their specific alpha-numeric identification.

CHEETAHS

Between August 2001 and August 2003 eleven cheetahs were reintroduced onto Kwandwe (Table 2.4).

Table 2.4: Details of the cheetahs released on Kwandwe and their relatedness. (* NCMP = National Cheetah Management Program).

Release	Origin	Group		Relatedness	Date released
		Composition	ID		
1	Phinda Private Game Reserve	4 adult males (coalition)	CM1-4	CM2-4 brothers CM1 unrelated	August 2001
2	Phinda Private Game Reserve	2 females (adult + juvenile)	CF5,6	Mother + Cub(12mths old)	October 2001
3	Northern Province (*NCMP)	3 (adult female + juvenile female & 1 juvenile male)	CF7,8 CM9	Mother + Cubs(13mths old)	February 2002
4	Karongwe Game Reserve	1 sub-adult female	CF18	Unrelated	August 2003
5	Northern Province (*NCMP)	1 adult female	CF19	Unrelated	August 2003

At the beginning of the current study in February 2003 the composition of cheetah groups had changed considerably from that in Table 2.4. The coalition was reduced to three males (CM1-3) as CM4 was killed by lions within the year of release, therefore at the beginning of the current study the coalition consisted of two brothers (CM2, 3) and one unrelated male (CM1). Of the 2nd release, CF5 left her sub-adult cub (CF6) shortly after release and in 2002 they each had a litter of cubs. As a result of this, at the beginning of the current study CF5 had three seven month old male cubs (CM12-14) and CF6 had two 11 month old female cubs (CF10, 11; Figure 2.8). Of the 3rd release CF7 left her sub-adult cubs (CF8 & CM9) shortly after release and CF8 was not seen again and was presumed to be dead. CF7 had a litter of two cubs in September 2002 of which one died of unknown causes shortly after they were seen for the first time at two months of age. As a result of this, at the beginning of the current study CF7 had one female cub (CF16), five months old (Figure 2.8). CF19 was killed by the coalition two weeks after her release. CM9 was killed by the coalition in October 2003 at about the time CM9 would have reached sexual maturity and would therefore have been in competition with the dominant coalition. CF5 was killed by a pride of lions in May 2003, her three male cubs survived on their own but two of them (CM12, 13), were killed by a male lion inhabiting the same area as the cheetahs, approximately two months after the death of their mother (CF5). The 3rd cub (CM14) survived and later joined up with CF18 on her release. CF6 left her sub-adult cubs in July 2003 and the two females (CF10, 11) remained together until they came into oestrus in January 2004. Cheetah deaths and their causes are summarized in Table 2.5. Due to cheetah births and deaths the composition of the cheetah population changed continuously throughout the study (see Table 2.5; Figure 2.8).

The following cheetahs were not included in the diagram representing the family tree (Figure 2.8) as they did not contribute a substantial amount of data to the study: CF7, CF8, CM9, CU15, CF16, CF18, CF19 and CF31.

Table 2.5: Causes of mortality of cheetahs on Kwandwe.

CHEETAH ID	CAUSE OF DEATH	DATE OF DEATH
CM4	Lions	10 November 2001
CF5	Lions	2 May 2003
CU15	Unknown	November 2002
CF16	Cheetahs (CM1-3)	5 June 2003
CM12	Lions	8 July 2003
CM13	Lions	12 July 2003
CF19	Cheetahs (CM1-3)	31 August 2003
CM9	Cheetahs (CM1-3)	7 October 2003
CF18	Lions	18 May 2004
CU30	Unknown	19 June 2004
CU26	Lions	27 August 2004
CU27	Lions	27 August 2004
CF11	Lions	20 December 2004
CF10	Lions	8 April 2005
CU32	Unknown	15 September 2005
CU33	Unknown	29 October 2005
CM21	Cheetahs (CM1-3)	1 March 2006
CF22	Cheetahs (CM1-3)	22 March 2006
CM36	Lions	5 May 2006

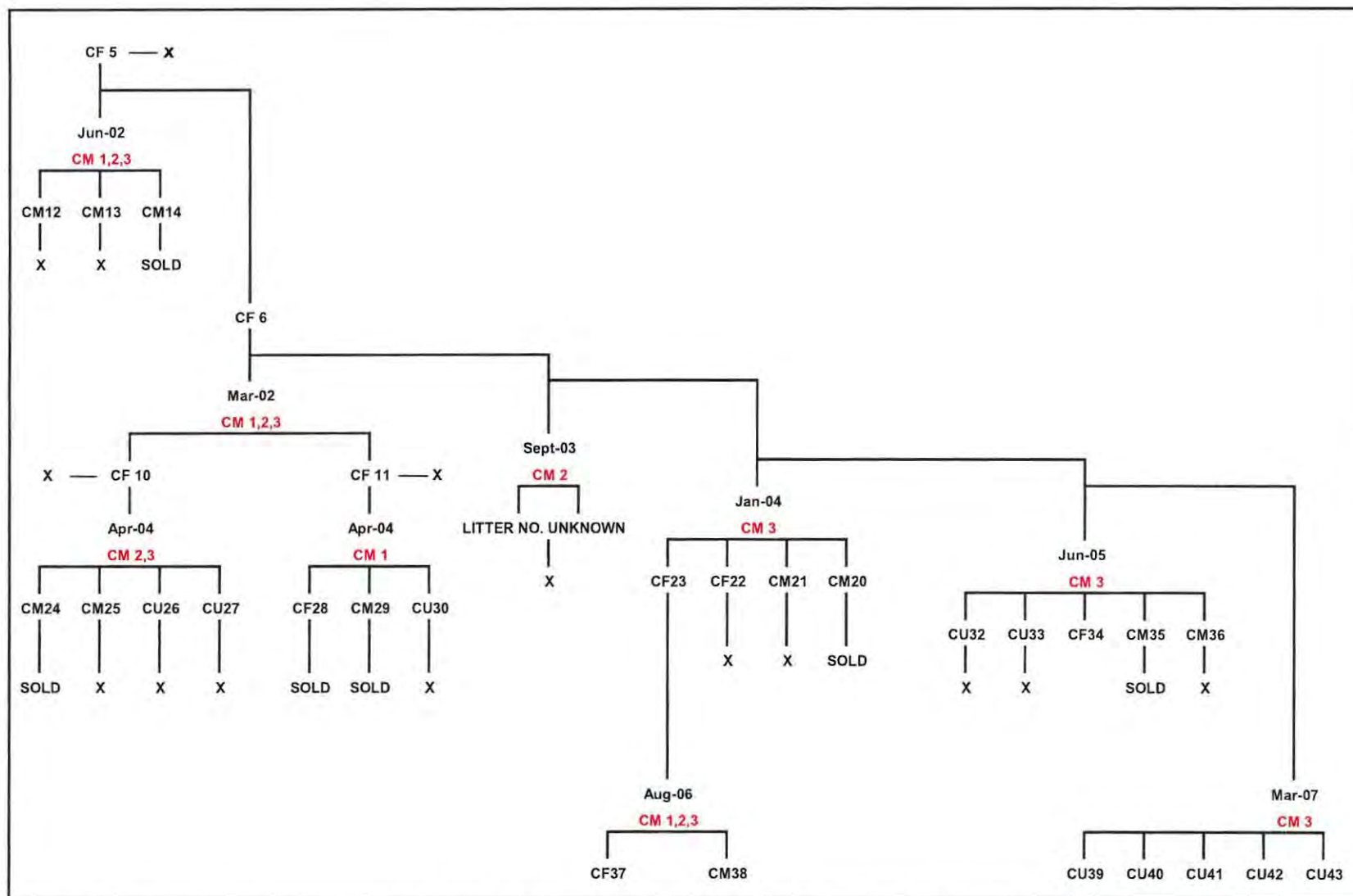


Figure 2.8: Relatedness of cheetahs on Kwandwe. (X cheetahs that have died during the study period; cheetah males that sired cubs)

LIONS

Two adult female (LF 7 & LF8) and two adult male lions (LM1 & LM2) were reintroduced onto Kwandwe in October 2001 (Table 2.6). The females formed a pride and LM1 was the dominant pride male throughout the study. LM2 was solitary and although he sired one litter of cubs, he did not often come into contact with the other lions. The two lionesses had their first litter of cubs in about May 2002 with LF7 having a litter of two male cubs (LM5 & LM6) and LF8 having a litter of three cubs (LM3; LM4 & LF9). Active lion management occurred throughout the study and all male cubs born on the reserve were removed when they were approximately two years old. LF9 joined her siblings once they left the pride in October 2003 and she was not accepted back into the pride when her male siblings were removed from the reserve. She had her first litter of cubs in May 2005 and will be referred to as the Boschgift pride throughout the study (Figures 2.9 & 2.10). The original pride (LF7 & LF8) will be referred to as the Southern pride. A third pride of lions formed in December 2005 which comprised three lionesses (LF15, LF16 & LF17) and they will be referred to as the Nomadic pride throughout the study (Figures 2.9 & 2.10). At first the Nomadic pride did not establish a territory and their home range covered most of the reserve, but after approximately six months, they settled on the western side of the reserve. Therefore, although they are referred to as the Nomadic pride they were not nomadic throughout the entire study period. The pride lionesses from the Boschgift pride and the Nomadic pride are the offspring of the pride lionesses of the Southern pride and they were evicted from the Southern pride at around two years of age (Figure 2.9 & 2.10). The composition of the three lion prides is represented in Table 2.7.

Table 2.6: Details of the lions released on Kwandwe and their relatedness.

Release	Origin	Group Composition	ID	Relatedness	Date released
1	Madikwe	Adult male	LM1	Unrelated	October 2001
2	Pilanesberg	Adult male	LM2	Unrelated	October 2001
3	Pilanesberg	Adult female	LF7	Unrelated	October 2001
4	Madikwe	Adult female	LF8	Unrelated	October 2001

Table 2.7: Composition of the different lion prides on Kwandwe at the beginning of 2007.

Pride Name	Adult Females	Sub-adult Females	Sub-adult males	Cubs
Southern Pride	1 (LF8)	-	-	3 (LM23,LF24,LF25)
Boschgift Pride	1 (LF9)	2 (LF18,LF19)	1 (LM20)	-
Nomadic Pride	3 (LF15,LF16,LF17)	-	-	-

LM1 was the dominant male for all three prides and LM2 was solitary, occasionally joining up with the Boschgift pride.

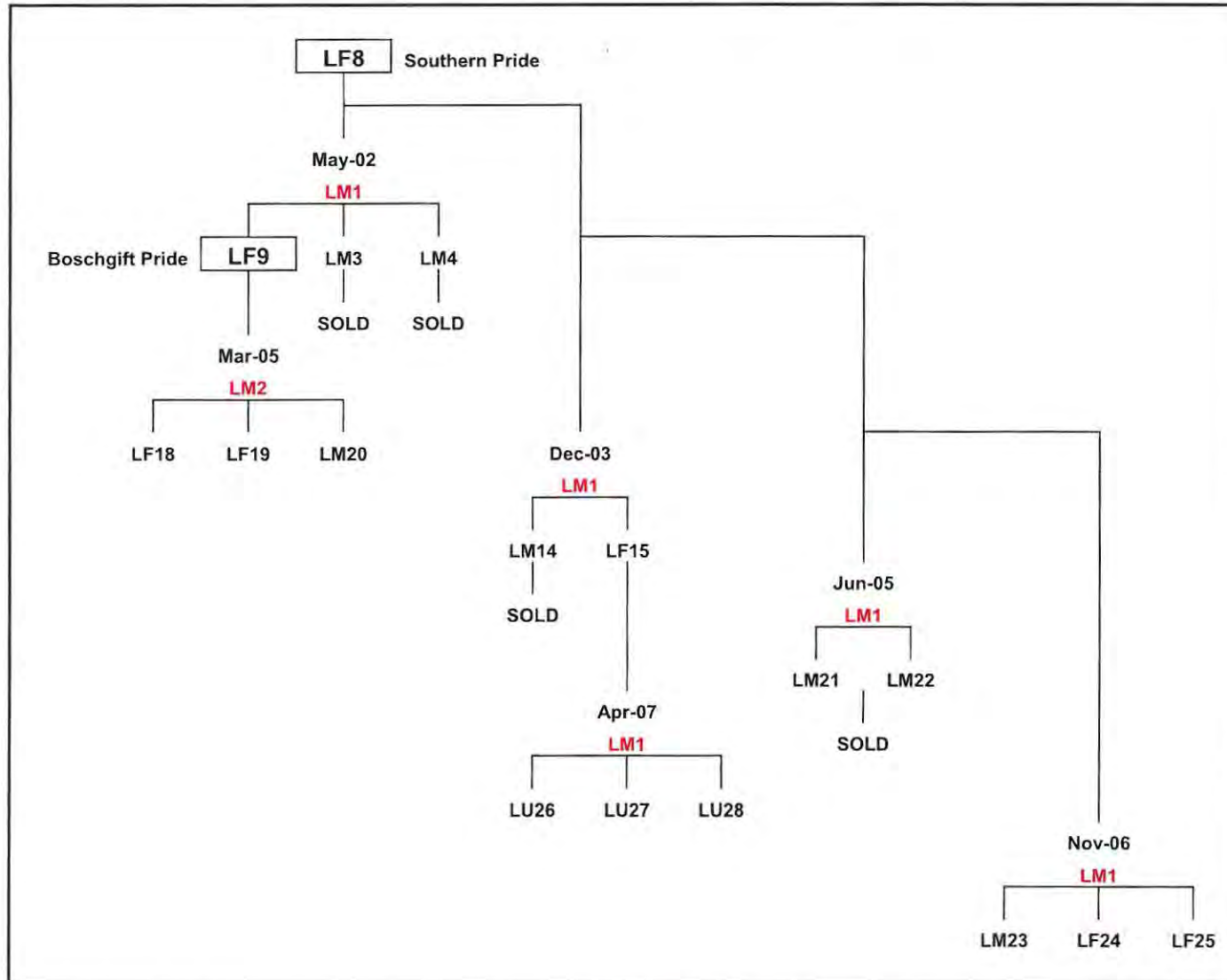


Figure 2.9: Relatedness of the lions on Kwandwe. (lion males that sired cubs)

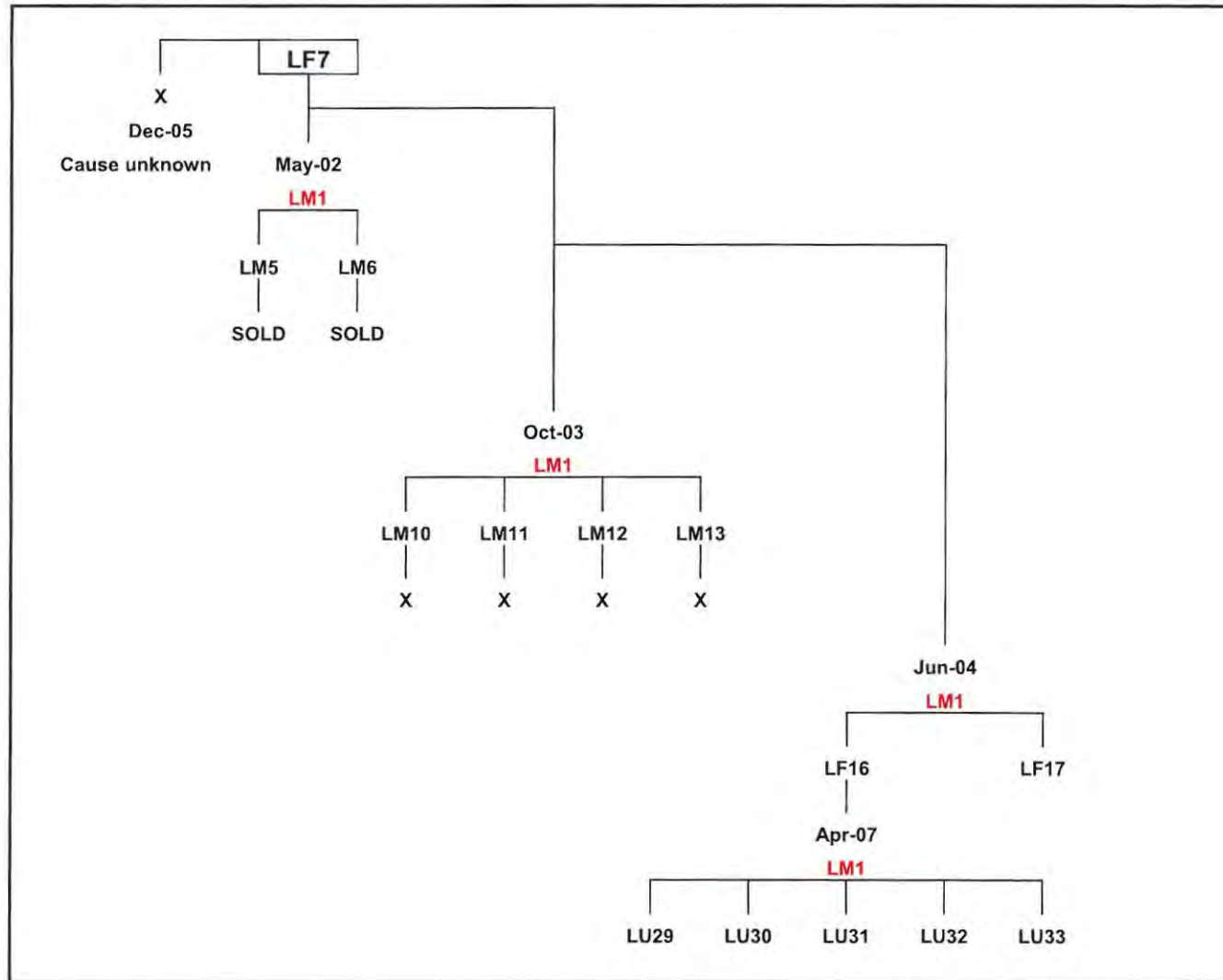


Figure 2.10: Relatedness of the lions on Kwandwe. (X lions that have died during the study period; lion males that sired cubs)

AFRICAN WILD DOGS

A pack of six African wild dogs was released onto Kwandwe in June 2004. The pack was made up of an alpha pair (adult male and adult female) and their four yearling female pups from their 2nd litter which were born on Karongwe in 2003 before their reintroduction onto Kwandwe (Table 2.8).

Table 2.8: Details of the African wild dogs released onto Kwandwe.

Release	Origin	Group Composition	ID	Relatedness	Date released
1	Karongwe	Alpha pair	WDM1 & WDF2	Alpha pair +	June 2004
		4 Sub-adult females	WDF3-6	offspring	
2	Shamwari	4 Sub-adult females	WDF16-19	Siblings	November 2006

At the end of May 2005 the alpha pair had their first litter on Kwandwe. The pups were first introduced to the rest of the pack by the alpha female when they were about three weeks old. The litter was made up of nine pups of which one (unknown sex) was found dead when it was approximately two months old. The remaining eight pups comprised two females and six males. In December 2005 two adult females (WDF3 & WDF5) were sold and in February 2006 two male pups (WDM14 & WDM15) were sold. In April 2006 one of the pups (WDM10) was found dead in a dam and in June 2006 two pups (WDF8 & WDM11) went missing from the pack. The remaining pack made up of the alpha male and female; two adult females and three pups (one female and two males) contracted the Canine Distemper Virus in July 2006 and all the animals died except for the alpha pair. The alpha pair were captured and placed in a boma at the beginning of November 2006 where they were bonded with a new pack of four adult females. The new pack was released at the end of November 2006. The current study therefore included the original pack of African wild dogs which was

studied from their release on the 22 June 2004 to July 2006, and the surviving alpha pair which were studied from July 2006 to 31 October 2006. Due to the time that the African wild dogs spent in the boma as well as the time that new predators generally take to settle into a new area, it was decided not to include the new pack in the current study.

GENERAL METHODOLOGY

The general methodology used throughout the study is detailed in this section and specific techniques are described in detail in the relevant chapters. The field work for the study was done over a 51 month period from February 2003 to May 2007. All cheetahs, lions and African wild dogs on Kwandwe were either fitted with a radio-collar or had a radio transmitter implanted. Radio-collared cheetahs, lions and African wild dogs were located as often as possible throughout the study period, but rarely more than once a day, using a Telonics TR-4 receiver and a two-element antenna. All location points were recorded using a GARMIN 72 GPS and activity of the animal at first sighting, together with vegetation type and time of day, were recorded for each sighting. When it was impossible to visually locate an animal, its position was plotted by triangulation (Kenward 2001). All radio tracking and observations were conducted from a Toyota Hilux 4-wheel drive vehicle or on foot.

CHAPTER 3

FEEDING ECOLOGY AND PATTERNS OF PREDATION BY LIONS, CHEETAHS AND AFRICAN WILD DOGS ON KWANDWE

INTRODUCTION

Factors effecting diet and prey selection

Our understanding of diet and prey selection of mammalian carnivores is based on the results of numerous studies. Many of these have been autecological in nature, describing the diet of one species at one site. For example African wild dogs in Hluhluwe-Imfolozi Park, South Africa (Krüger *et al.* 1999); lions in the Greater Makalali Conservancy, South Africa (Druce *et al.* 2004) and cheetahs in Kruger National Park (Kruger), South Africa (Mills *et al.* 2004). Other studies have used previously published data for one species or a range of species from multiple locations to examine the factors that shape prey selection (for example, Carbone *et al.* 1999; Sinclair *et al.* 2003; Hayward & Kerley 2005). These studies suffer, to a greater or lesser extent, from the various methodological difficulties frequently associated with meta-analytical research (Gates 2002 and see Radloff & du Toit 2004) including the quality of the data used and the way in which it was collected. Only a small number of studies (Schaller 1972; Mills 1984; Radloff & du Toit 2004) have simultaneously examined the diet of members of a carnivore guild at a single site and collected sufficiently detailed data to allow an examination of the relationship between predator and prey size.

The earlier studies of the relationships between predator and prey body sizes have shown that an increase in predator size is associated with increases in mean prey size (Gittleman 1985; Vézina 1985; Carbone *et al.* 1999), as well as an increase in prey

diversity (Gittleman 1985; Cohen *et al.* 1993; Sinclair *et al.* 2003). These very simple relationships have been refined and the energetic requirements imposed by carnivore feeding are now understood to be different for small-bodied carnivore species, which feed mostly on prey smaller than themselves, and large-bodied species, which prefer prey around their own size (Carbone *et al.* 2007). This transition in prey selection occurs at a predator mass of 21.5kg, with those species below this threshold taking prey less than 45% of predator mass and those above 21.5kg taking prey greater than 45% of the predator mass (Carbone *et al.* 1999). This suggests that studies comparing carnivores with body masses on both sides of the body mass threshold could be studying two different functional groups (Radloff & du Toit 2004), thus possibly masking predator-prey relationships.

Perhaps not surprisingly, the results from several studies have contradicted the fundamental relationship between predator size and prey size, as well as the relationship between predator size and prey diversity. For example, in the mammalian carnivore guild in India, analyses of scats and kill records suggested that the largest predator (tiger) kills the largest prey, but pack hunting dholes, which are about a third of the body mass of the leopard, commonly kill larger prey than the solitary leopard (Karanth & Sunquist 1995). Similarly, in North America, coexisting mountain lions and coyotes both prey upon young and adult mule deer despite a substantial difference in predator body size (Pierce *et al.* 2000).

In the most robust analysis of predator-prey relationships within a large carnivore guild, Radloff & du Toit (2004) found that most predators take similar prey in spite of large differences in carnivore body size. However, there is a significant relationship between predator size and mean prey size but it is driven by a positive relationship between predator size and maximum prey size while there is no relationship between

predator size and the minimum prey size. Radloff & du Toit (2004) conclude that in African savannas, larger predators have wider predatory options than smaller predators and that if the larger members of the guild are removed then other members of the guild might be expected to increase their prey size range.

The fact that studies of predator-prey relationships have produced contradictory results is not surprising given that prey selection is shaped by numerous interacting factors. These include prey abundance, prey and predator body size, prey vulnerability (which may be a combination of prey age, condition, group size and habitat) and the presence of competing predators (Mills & Gorman 1997; Krüger *et al.* 1999; Creel & Creel 2002; Pole *et al.* 2004; Radloff & du Toit 2004; Hayward & Kerley 2005). Radloff & du Toit (2004) propose that the complexity of these interacting factors and the opportunistic nature of the large carnivores will confound the analysis of prey diversity in all terms other than body mass. However, simultaneous, long term studies of members of a large carnivore guild at one site, as conducted by Mills (1984) and Radloff & du Toit (2004), result in at least some of the variables being held constant and offers the best opportunity to improve the understanding of how prey selection is determined. For these reasons, further studies that mirror the work of Radloff & du Toit (2004) are essential.

General feeding ecology of lions, cheetahs and African wild dogs

The feeding ecology of lions, cheetahs and African wild dogs has received extensive attention in the scientific literature with most studies focussing on diet, feeding behaviour and hunting patterns of individual species (see for example Eloff 1973; Rudnai 1974; Green *et al.* 1984; Durant *et al.* 1988; Packer & Ruttan 1988; Fitzgibbon 1990; Packer *et al.* 1990; Viljoen 1993; Caro 1994; Mills & Gorman 1997;

Funston *et al.* 1998; Hofmeyr & van Dyk 1998; Krüger *et al.* 1999; Purchase & du Toit 2000; Creel & Creel 2002; Pole *et al.* 2004; Radloff & du Toit 2004; Hayward & Kerley 2005; Bissett & Bernard 2007). This type of information is important in understanding the general behaviour and ecology of large carnivores, as well as the impact that they may have on their prey populations (Caro 1994; Mills 1996; Sinclair *et al.* 2003).

Results from previous studies have suggested that both abundance and size of prey are important factors in prey selection by lions. In many studies, the most important components of their diet are the most abundant species at the time of the study, with prey species weighing between 50kg and 300kg providing most of the diet (Schaller 1972; Mills 1990; Stander 1992; Stander 1997). A large proportion of the diet comprises three to five species of the most locally abundant medium/large ungulates such as blue wildebeest, zebra, kudu and buffalo (Kruuk & Turner 1967; Schaller 1972; Mills & Shenk 1992; Viljoen 1993; Scheel 1993). In Chobe National Park (Chobe), Botswana, warthog (27.6%), buffalo (26.7%), zebra (14.7%), impala (11.2%) and tsessebe (8.6%) constitute 88.8% of all lion kills. Zebra and buffalo are the most abundant medium/large prey species in Chobe and these species are the principle prey species of the lions (Viljoen 1993; 1997). Although warthog make up a large percentage of the overall diet of the lions in Chobe it is only the case in the dry season when larger species such as zebra and buffalo migrate out of the area (Viljoen 1993; 1997). In Kruger, impala (28%), buffalo (18%), zebra (18%) and blue wildebeest (16%) make up 80% of the overall diet of female lions, and zebra and blue wildebeest are the most abundant medium sized prey in the area and make up 34% of the diet of female lions (Funston *et al.* 1998). However, in areas of low prey density

such as Etosha National Park (Etosha), Namibia, smaller prey species are killed (Stander 1992).

The selective killing of animals of a specific age class or sex by lions has been widely reported. Mills and Shenk (1992) found that lions select adult blue wildebeest and juvenile zebra in Kruger, while in Etosha, lions show no preference for age and sex of blue wildebeest or zebra, but juvenile springbok are preferred to adults (Stander 1992). In the Kalahari Gemsbok National Park (Kalahari), South Africa, adult blue wildebeest and gemsbok form the bulk of lion kills, while juvenile gemsbok and springbok kills are relatively common (Mills 1984). The reasons for such a pattern of selection are complex, and would include factors described earlier such as body size, group size, vulnerability and other aspects of behaviour that vary between the sexes and age classes of the prey species.

Lions tend to be opportunistic predators (Schaller 1972; Hayward & Kerley 2005) and the diversity of prey species in their prey profiles varies substantially in different areas with a range of between six and 37 different prey species recorded (Smuts 1978; Stander 1992; 1997; Hunter 1998; Radloff & du Toit 2004). Prey selection by lions not only varies in space between different study sites, but also in time and several studies have shown that prey preferences track seasonal or longer term changes in prey availability (Schaller 1972; Dunham 1992; Scheel & Packer 1993; Viljoen 1993).

Hayward & Kerley (2005) analysed data from 32 studies and concluded that lions prefer species with a weight range of 190-550kg with a most preferred weight of 350kg. Avoided species within the preferred weight range such as eland, have features that reduce predation (large herd size and increased vigilance of eland; Hayward & Kerley 2005). In addition, Hayward & Kerley (2005) showed that there is no

relationship between prey availability and lion prey preference but there is a significant relationship between prey size and Jacobs' Index.

Existing studies on cheetahs suggest that these carnivores feed predominantly upon the most abundant medium sized antelope (30-65kg), although they are able to kill both larger and smaller prey (Mills 1996). For example, in the Serengeti National Park (Serengeti), Tanzania, Thomson's gazelles are the most abundant ungulate and the cheetahs' most important prey species (Caro 1994), in Kruger, impala are the most abundant ungulate and they form a far greater proportion of the diet of the cheetahs than any other species (Mills *et al.* 2004); in Phinda Resource Reserve (Phinda), South Africa, nyala are the most abundant species and the most common prey species in the diet (Hunter 1998) and in the Kalahari, springbok are the most important prey species as well as the most abundant medium sized ungulate (Mills 1984). Cheetahs have an unusual felid social system in which adult females are solitary, unless they are with their cubs, and males may form coalitions or remain alone (Caro 1994). Male cheetahs in coalitions can hunt larger prey than lone males or single females (Radloff & du Toit 2004; Bissett & Bernard 2007) and hunting larger prey is one adaptation that male cheetahs use to meet the increased energetic demands of group living (Schaller 1972; Caro 1994). By contrast, solitary female cheetahs and females with cubs generally hunt smaller prey than male cheetahs (Caro 1994; Hunter 1998; Mills *et al.* 2004; Radloff & du Toit 2004). In different studies cheetahs have shown preferences for prey species of different age and sex. For example, Schaller (1972) found that 55% of Thomson's gazelles killed by cheetahs in the Serengeti are sub-adult, whereas Kruuk and Turner (1967) found a preference for adult females in the same species in the Serengeti. In contrast to this, cheetahs select adult male

Thomson's gazelles in the Serengeti (Fitzgibbon 1990), male springbok in the Kalahari (Mills 1984) and male impala in Kruger (Mills *et al.* 2004). In Nairobi National Park, Kenya (Eaton 1970) and Suikerbosrand Nature Reserve, South Africa (Pettifer 1981) cheetahs select adult females and juveniles of prey species, while in Phinda and Kruger cheetahs select juveniles rather than adults and particularly juveniles from large prey species (Hunter 1998; Mills *et al.* 2004). Finally, it has been suggested that kleptoparasitism may affect prey size of cheetahs. For example in Namibia, in areas where potential kleptoparasites are rare or absent, cheetahs kill larger prey compared to their counterparts existing within an intact large carnivore guild in East Africa (McVittie 1979). This variation in prey selection by cheetahs highlights the need to analyse the different social groups separately and independently analyse different areas and situations. Furthermore, the preceding discussion underscores the need to gather information on the age and sex of species preyed upon by predators.

African wild dogs are social pack living carnivores (Fanshawe *et al.* 1991) and are typically communal hunters which allow them to kill larger prey than an individual dog could (Creel & Creel 1995; 2002). African wild dogs mostly hunt medium sized antelope with prey ranging in weight from 15 - 200kg (Creel & Creel 2002; Radloff & du Toit 2004; Sillero-Zubiri *et al.* 2004). In most areas their principle prey species are impala, kudu, Thomson's gazelle and blue wildebeest (Sillero-Zubiri *et al.* 2004). For example, in Kruger and in the Savé Valley Conservancy in Zimbabwe, impala and kudu are the principal prey species (Mills & Gorman 1997; Pole *et al.* 2004), whereas, impala and blue wildebeest are their preferred prey species in the Selous Game Reserve, Tanzania (Creel & Creel 2002).

Pole *et al.* (2004) found that African wild dogs in the Savé Valley Conservancy select more kudu juveniles and adult impala and that the prey base is dependent on the time of year. In the Serengeti African wild dogs most commonly kill adult and juvenile Thomson's gazelles and juvenile blue wildebeest (Carbone *et al.* 2005), while in Hluhluwe-Imfolozi Park adult nyala and juvenile impala are preyed upon more frequently than other age classes, and female prey are taken more frequently than male (Krüger *et al.* 1999).

In Africa large mammal predator-prey systems are complex due to the large number of species of both predator and prey (Mills & Shenk 1992). In large, open ecosystems predation generally has little effect on largely migratory prey populations, such as in the Serengeti (Kruuk & Turner 1967; Schaller 1972; Berry 1981). However, resident populations of herbivores and those within enclosed reserves may be more heavily influenced by predation (Fryxell *et al.* 1988) and populations of smaller ungulate species, which are preyed on by a wide variety of carnivores (species and individuals), may be controlled by predation (Sinclair *et al.* 2003). From a management perspective, the re-development of large carnivore guilds on small enclosed reserves could have a negative impact on resident populations of the smaller prey species and therefore understanding the feeding ecology and predation patterns of these carnivores is important. Small, enclosed reserves are tightly managed and are characterised by introductions and removals of both predators and prey. These management interventions create research opportunities that can rarely be recreated in an open system and provide an opportunity to begin to tease apart the factors that affect prey selection.

The broad aim of this chapter is to present a general description of the diets of lions, African wild dogs and cheetahs on Kwandwe. Differences in prey selection between the predator species and between the social groups of the cheetahs are examined and the factors that affect prey selection are explored. Finally, the effects of changes in prey availability through the duration of the study are used as natural experiments to study the effects of prey size and abundance on prey selection.

METHODS

Data Collection

The majority of the cheetahs, lions and African wild dogs on Kwandwe were either fitted with a radio collar or an implanted radio transmitter (as detailed in Chapter 2). In this study data were collected on feeding ecology by three means; the opportunistic (*ad hoc*) observations of kills; kills recorded during continuous observations of various carnivore social groups, and kills recorded by field guides on their daily game drives.

Ad hoc observations and kills recorded by field guides

All cheetahs, lions and African wild dogs were located as often as possible throughout the study period. However, during periods of continuous observations (described below) it was not possible to locate animals other than those under continuous observations and at this time in particular, the field guides on the reserve proved to be important sources of information with regard to the position and kills of various carnivores. Kwandwe is an ecotourism reserve and there are usually approximately five game-viewing vehicles out on the reserve on any one day, taking guests on dawn and dusk game drives. An experienced field guide conducts each game drive, accompanied by a tracker, and constant radio contact is maintained with other field guides. Field guides follow a road network and coordinate their movements to maximize encounters with 'charismatic' species, with large carnivores being particularly sought after. Radio contact with field guides was maintained throughout the study and in this way the loss of information was minimized (see Radloff & du Toit 2004 for use of this type of data). The date, species, sex and, where possible, the age (juvenile, sub-adult, adult) of prey were recorded for all kills found. Age

categories were defined as follows: juvenile was a small and dependent animal; sub-adult was a young, independent animal not fully grown and not reproductively active and adult was a full grown, reproductive animal. The field guides recorded all their sightings and detailed records of kills on an excel spreadsheet which was emailed to me every evening after the day's game drives. These *ad hoc* observations are likely to artificially increase the contribution of large kills to the diet, because the predators are more likely to spend more time on larger kills and thus disproportionately increasing the chances of large kills being found relative to smaller ones. In order to counteract this suspected problem, two-week continuous observations were undertaken in the hope that smaller kills would be recorded while following the various study animals.

Continuous observations

Most study animals or social groups were the subject of periods of continuous observations (Table 3.1). Continuous observations were made from a vehicle and I remained with the focus animal or group for 24 hours a day for 14 days. I only left the focus animal or group in the heat of the day when they had settled down in the shade, and was never away for more than three hours. I usually followed the predators at a distance of about 100-200m in the open vegetation types and 40-50m in more dense areas, so as to minimize interference with the hunting behaviour. For the study animals which hunted at night, I used a spotlight, with a red filter that I switched off when the animal had encountered prey and waited until a kill had been attempted before relocating them. If I lost sight of the study animals in thick bush and they remained stationary in the bush it often meant that they had made a kill. I located the kill using triangulation and attempted to walk into the site once the study animal had left the area. In this way I often located fresh kill remains. The date, species, sex and

age of the prey were recorded for all kills found. The vegetation type in which the kill was made and the location and/or GPS readings for the carcass were recorded. The area was searched for drag marks in an attempt to ascertain precisely where the kill had been made.

Table 3.1: Time period of two-week continuous observations on the different social groups of large carnivores on Kwandwe.

Social Group	2004	2005	2006	2007
Cheetahs				
Coalition	19/01-4/02; 1-15/05	2-15/06; 1-15/12	30/05-12/06; 1-16/09	-
Females with mobile cubs	-	24/04-8/05; 11-25/11	5-19/07; 16-29/11	-
Single females	28/02-13/03	-	1-15/04	-
Independent cubs	-	28/09-13/10	-	2-15/02
Lions				
Southern Pride	-	5-19/04; 11-24/09	19/04-3/05	-
Nomadic Pride	-	-	18-30/06; 25/10-7/11	-
Boschgift Pride	-	-	7-21/10	-
African Wild Dogs				
Pack	-	13-27/05; 21/10-3/11	11-26/05; 20/09-4/10	-

Data Analysis

Lions exhibit marked sexual size dimorphism and the males and females tend to segregate when hunting, so the sexes were treated separately in most analyses. Kills attributed to female lions were all kills where a female was present, including those made by single females, females accompanied by their offspring and occasionally by adult males. Kills made by male lions were all those where no females were present. African wild dogs hunt in mixed packs and the sexes are of similar size. Consequently, these animals were not divided into male and female groups. Cheetahs have a complex social system and were divided into the following social groups:

coalition of three adult males, female cheetahs with cubs, single female cheetahs and independent cheetah cubs. Kills made by the different social groups were analysed separately. Few previous studies have undertaken diet analysis at a social group or sex level and to allow comparison with published work, an initial general diet analysis at the species level is presented. The general diet analysis included animals killed by a single male cheetah. However, due to the small sample size, animals killed by this individual were excluded from the social group analysis.

Species recorded as having been killed but rarely consumed (e.g. other predators, such as bat eared fox) were not considered as prey and were omitted from the kill lists.

Analysis of predator-prey body mass relationships

Body mass values for the predators were drawn from published records from sites as close as possible to the study area. No data from the area were available for lions and African wild dogs. Consequently, data from the Kruger was used for these species (lions; Smuts *et al.* 1980 and African wild dogs; Gorman *et al.* 1998). The mass used for male cheetahs is for the males on Kwandwe as these animals were weighed when they were tranquilised for radio collaring. These males are substantially larger than published data from Namibia. In published data, female cheetahs are ~10kg lighter than the males in the same area, while sub-adults are ~10kg lighter than female cheetahs (Labuschagne 1979). Therefore, the female cheetahs on Kwandwe were assumed to be ~10kg lighter than the males, while the independent cheetah cubs were assumed to be ~10kg lighter than the female cheetahs.

Values of adult male and female body mass for prey species were taken from Meissner (1982); Bothma (2002) and Skinner & Chimimba (2005). Sub-adult mass of each sex was approximated by multiplying adult male or female mass by 0.7; values

for juveniles were approximated by multiplying mean adult mass by 0.3, as suggested by Radloff & du Toit (2004).

The typical or corrected mass for each prey species was calculated separately for each predator species or social group using the proportions of males and females, sub-adults and juveniles of that particular species killed by the predator. So, for example, the corrected mass for kudu varies between the predator groups because the different predators killed different proportions of adult kudu.

The mean prey mass for each predator was calculated using the corrected mass of every kill rather than using a simple species body mass. For kills where age and sex were unknown, the unit mass for that species was used (3/4 adult female body mass; Owen-Smith 1988).

The total edible biomass for all individuals of each species killed by the predators was estimated from the categories suggested by Blumenschine & Caro (1986) for cheetahs, Viljoen (1997) for lions and Carbone *et al.* (2005) for African wild dogs and took into account the age and sex of the kills.

Analysis of prey diversity in the diet

Species diversity is a measure of the number of species (species richness) in the community and the evenness with which the individuals are distributed across the species (Krebs 1999). Therefore, richness represents the number of different prey species killed by a particular predator, while evenness represents the numerical dominance of preferred or common prey species compared to all other prey.

Simpson's Index (Magurran 2004) was used to compare evenness across prey profiles as it is relatively unaffected by the rare species in the sample and is not sensitive to

species richness (Magurran 2004). The index ranges from $E_{1/D} = 0$ (no evenness) to $E_{1/D} = 1$ (complete evenness).

Analysis of prey preference at a species level

To determine whether the predators selected certain species preferentially, a preference index was calculated for prey species. Calculations were not made for species such as aardvark, bushpig and scrub hare as adequate game count records were not available for these species. The preference ratings were determined using Jacobs' Index:

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

where r is the proportion of the total kills at a site made by a species and p is the proportional availability of the prey species (Jacobs 1974). The resulting values range from +1 to -1, where +1 indicates maximum preference and -1 indicates maximum avoidance (Jacobs 1974). Prey abundance was based on data from game counts (2003-2007) and was expressed as the number of a particular species as a proportion of the total number of all species preyed upon by a particular carnivore species or social group. Game count data were not corrected for visibility of different species as a similar correction factor could not be applied to the kill lists. Jacobs' Index has been used to allow comparison with previously published data (Hayward & Kerley 2005; Hayward *et al.* 2006a, 2006b).

Analysis of prey preference at a body mass level

For some analyses, prey availability and prey killed by the various predators was divided into different body mass categories. This was done separately for each



carnivore species or social group and only prey species that were recorded in the kill lists for that carnivore were used for analyses. For prey availability, species numbers came from game census data from 2003 to 2007 and the population structure was assumed to be 70% adult; 18% sub-adult and 12% juvenile within each species. These percentages are estimates based on data for species where age categories could be recognised during game censuses. Although it is known that sex ratios are skewed towards females in some species, the allocation of animals to body mass classes was not refined to include this. For kills, a corrected mass (corrected for age and sex) was allocated to every kill and these kills then allocated to the different body mass categories.

Comparison of ad hoc and continuous observations

While continuous observations were collected over 14 day periods, it was not possible to use the same duration for *ad hoc* kills, as the number of kills would have been far lower. Similarly, a comparison of kills over 14 days, or several 14 day periods, with all kills made by the carnivores during the study would be unbalanced. To resolve these problems, the following approach was adopted. Firstly, kills made during the continuous observations were excluded from the *ad hoc* observation kill records. Secondly, a time period for the *ad hoc* observations was chosen that included the period or periods covered by the continuous observations. For the cheetahs, *ad hoc* observations were for the full year in which the continuous observations were conducted. For the lions and African wild dogs, *ad hoc* observations were from the first month of the first period of continuous observation to the last month of the final period of continuous observations in a year. For example, for African wild dogs in 2005, kills recorded from May to November were used for the *ad hoc* analysis, Table

3.1. Independent cheetah cubs were excluded from the analyses due to a very small number of kills observed during *ad hoc* observations.

Statistical analyses

The proportions of adult, sub-adult and juvenile kudu killed by the various cheetah social groups were compared by means of a chi-square test. The mean mass of kudu killed by various cheetah social groups was compared using a one-way ANOVA followed by post-hoc tests. One-way ANOVAs were used to compare the corrected mass of each prey species killed by the different carnivore groups. Mean prey size of the different predators was compared with a one-way ANOVA. Multiple regression analyses were used to determine the relationship between predator size and maximum, minimum and mean prey mass, and between predator size and the richness and evenness of prey profiles.

Linear regression analyses were used to determine the relationship between prey abundance or prey corrected body mass and proportion of kills for each predator.

Chi-square tests were used to compare the proportions of prey species in the prey profiles generated by the two observation methods.

Multiple regression analyses were used to determine the relationship between prey abundance and numbers killed or Jacobs' Index for various prey species and predators.

A one-way ANOVA was used to compare mean prey mass of lions from the start to end of the study. All statistical analyses were done using Statistica (Statsoft, version 7.0) and SigmaStat (Jandel Scientific).

RESULTS

General description of diet

A total of 869 kills, comprising 23 species, were recorded over a period of four years and four months for lions, cheetahs and African wild dogs on Kwandwe. 91.4% of all kills recorded were mammals, 4.3% were birds and 4.3% were reptiles. Lions preyed upon 21 species, and five of these (warthog, 34.9% of all kills; kudu, 26.1%; eland 7.9%, red hartebeest, 4.8% and gemsbok, 4.8%) constituted 78.4% of all animals killed and 84.5% (28 721.7kg) of the total edible biomass (Table 3.2). The cheetahs killed 19 species, of which five species (kudu, 38.1%; springbok, 15.3%; common duiker, 9.8%; bushbuck, 6.8% and impala, 6.5%) constituted 76.5% of the animals killed and 71.1% (11 461kg) of the total edible biomass (Table 3.2). By contrast, three of the 12 species preyed on by African wild dogs made up 73% of the animals killed by the African wild dogs (kudu, 61.5%; warthog, 6.8% and red hartebeest, 6.1%) and 91.6% (9831.1kg) of the total edible biomass (Table 3.2). Analysis of both the number of animals killed and their edible biomass is necessary since a small number of large kills may make a similar contribution to the predator's energetic and nutrient requirements as a large number of smaller kills. This is evident in the cheetahs where zebra constituted 2.7% of all kills and 3.6% of edible biomass while common duiker constituted 9.8% of kills and only 3.1% of edible biomass (Table 3.2).

Table 3.2: Complete list, body mass and total edible biomass of all prey species killed by cheetahs, lions and African wild dogs.

Prey species	Mass of individuals (kg)				Cheetahs				Lions				African wild dogs			
	J	SA	AM	AF	Kills		Total edible biomass		Kills		Total edible biomass		Kills		Total edible biomass	
					No.	%	kg	%	No.	%	kg	%	No.	%	kg	%
Aardvark	13	30.3	45.4	41	0	0.0	0	0.0	4	1.1	136.5	0.4	0	0.0	0	0.0
Black wildebeest	37.5	87.5	135	115	5	1.4	359	2.2	12	3.4	1096.9	3.2	5	3.4	172.3	1.6
Blesbok	22.2	51.8	81	67	11	3.0	552.6	3.4	0	0.0	0	0.0	0	0.0	0	0.0
Blue wildebeest	56.3	131.3	215	160	1	0.3	24.2	0.2	6	1.7	721	2.1	0	0.0	0	0.0
Zebra	87	203	310	270	10	2.7	586.9	3.6	11	3.1	1546.7	4.6	0	0.0	0	0.0
Bushbuck	14.4	33.6	60	36	25	6.8	792.8	4.9	1	0.3	23	0.1	8	5.4	228.2	2.1
Bushpig	28.2	65.8	84	104	0	0.0	0	0.0	3	0.8	194.3	0.6	0	0.0	0	0.0
Common duiker	5.5	12.1	17	21	36	9.8	504.8	3.1	4	1.1	40.8	0.1	8	5.4	101	0.9
Eland	183	427	760	460	3	0.8	531.3	3.3	28	7.9	7535.5	22.2	0	0.0	0	0.0
Gemsbok	67.5	157.5	240	210	7	1.9	416.3	2.6	17	4.8	2369.5	7.0	1	0.7	43.9	0.4
Giraffe	259.5	605.5	960	770	0	0.0	0	0.0	1	0.3	174.5	0.5	0	0.0	0	0.0
Impala	15.8	36.8	60	45	24	6.5	696.2	4.3	3	0.8	126	0.4	8	5.4	258.9	2.4
Kudu	60	140	240	160	140	38.1	8104.4	50.3	92	26.1	12058.6	35.5	91	61.5	9217	84.7
Mountain reedbuck	8.1	18.9	30	24	2	0.5	48.6	0.3	1	0.3	6.5	0.0	0	0.0	0	0.0
Ostrich	36	84	120	120	5	1.4	210	1.3	8	2.3	675	2.0	0	0.0	0	0.0
Porcupine	3.7	8.5	12.6	11.7	0	0.0	0	0.0	4	1.1	32.1	0.1	0	0.0	0	0.0
Red hartebeest	40.5	94.5	150	120	15	4.1	916.9	5.7	17	4.8	1436	4.2	9	6.1	482.6	4.4
Scrub hare	2.2	2.5	4	3.2	4	1.1	13	0.1	0	0.0	11.5	0.0	1	0.7	2.2	0.0
Springbok	10.1	23.5	36	31	56	15.3	1362.8	8.5	4	1.1	66.2	0.2	5	3.4	80	0.7
Steenbok	3.4	7.8	11.3	11	6	1.6	46.9	0.3	1	0.3	9	0.0	1	0.7	9.8	0.1
Warthog	21.8	50.1	80	65	2	0.5	39.2	0.2	123	34.8	5322.1	15.7	10	6.8	287.5	2.6
Waterbuck	94.4	134.8	225	160	10	2.7	908.1	5.6	4	1.1	422.9	1.2	0	0.0	0	0.0
Unknown					5	1.4			6	1.7			1	0.7		
TOTAL					367	100	16114	100	350	100	33993.1	100	148	100	10883.4	100

- One leopard tortoise killed by the lions was excluded from the table due to unknown body mass and a sample size of one.

J = juvenile; SA = sub-adult; AM = adult male; AF = adult female.

The diets of the various cheetah social groups varied considerably and have been analysed separately (Table 3.3). The coalition killed 15 species of which five (kudu, 32.4%; springbok, 13.0%; red hartebeest, 10.2%; blesbok 10.2% and zebra, 8.3%) constituted 74.1% of all animals killed and 73.5% (5384.7kg) of the total edible biomass (Table 3.3) Female cheetahs with cubs preyed on 14 species, four of which (kudu, 37.8%; springbok, 20.7%; impala, 10.8% and common duiker, 8.1%) made up 77.4% of all animals killed and 79.5% (3116kg) of the total edible biomass (Table 3.3). Single female cheetahs killed 10 species of which three (kudu, 49.0%; common duiker, 15.6% and springbok, 13.5%) constituted 78.1% of all animals killed and 80.7% (2843.2kg) of the total edible biomass (Table 3.3). Independent cheetah cubs preyed on eight species of which three (kudu, 29.2%; common duiker, 20.8% and bushbuck, 20.8%) made up 70.8% of all animals killed and 77.9% (1342kg) of the total edible biomass (Table 3.3). The coalition tended to kill larger prey species than the other cheetah social groups. The coalition was also the only cheetah social group to kill species such as black wildebeest, blue wildebeest and blesbok (Table 3.3).

Table 3.3: Complete list, body mass and total edible biomass of all prey species killed by the various cheetah social groups.

Prey species	Coalition				Female cheetah with cubs				Single female cheetahs				Independent cheetah cubs			
	Kills		Total edible biomass		Kills		Total edible biomass		Kills		Total edible biomass		Kills		Total edible biomass	
	No.	%	Kg	%	No.	%	kg	%	No.	%	kg	%	No.	%	kg	%
Black wildebeest	5	4.6	359.0	4.9	0	0	0	0	0	0	0	0	0	0	0	0
Blesbok	11	10.2	552.6	7.5	0	0	0	0	0	0	0	0	0	0	0	0
Blue wildebeest	1	0.9	24.2	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Zebra	9	8.3	528.6	7.2	0	0	0	0	0	0	0	0	1	2.1	58.3	3.4
Bushbuck	1	0.9	38.7	0.5	6	5.4	219.6	5.6	8	8.3	277.6	7.9	10	20.8	359.8	20.9
Common duiker	0	0.0	0.0	0.0	9	8.1	120.6	3.1	15	15.6	218.6	6.2	10	20.8	165.6	9.6
Eland	2	1.9	408.7	5.6	1	0.9	122.6	3.1	0	0	0	0	0	0	0	0
Gemsbok	5	4.6	315.1	4.3	1	0.9	50.6	1.3	2	2.1	163.2	4.6	0	0	0	0
Impala	2	1.9	90.0	1.2	12	10.8	408.6	10.4	5	5.2	121.3	3.4	5	10.4	99.9	5.8
Kudu	35	32.4	3121.2	42.6	42	37.8	1996.6	51.1	47	49.0	2305.0	65.4	14	29.2	816.6	47.4
Mountain reedbuck	0	0	0.0	0	2	1.8	48.6	1.2	0	0.0	0.0	0.0	0	0	0	0
Ostrich	3	2.8	145.2	2.0	1	0.9	32.4	0.8	1	1.0	32.4	0.9	0	0	0	0
Red hartebeest	11	10.2	825.8	11.3	3	2.7	91.1	2.3	0	0	0	0	0	0	0	0
Scrub hare	0	0.0	0.0	0.0	2	1.8	7.1	0.2	2	2.1	7.2	0.2	0	0	0	0
Springbok	14	13.0	356.5	4.9	23	20.7	590.2	15.1	13	13.5	319.6	9.1	6	12.5	96.5	5.6
Steenbok	1	0.9	10.1	0.1	3	2.7	23.4	0.6	2	2.1	13.5	0.4	0	0	0	0
Warthog	1	0.9	19.6	0.3	0	0	0	0	0	0	0	0	1	2.1	19.6	1.1
Waterbuck	5	4.6	535.3	7.3	3	2.7	199.3	5.1	1	1.0	66.3	1.9	1	2.1	107.2	6.2
Unknown	2	1.9			3	2.7			0	0			0	0		
TOTAL	108	100	7330.6	100	111	100	3910.7	100	96	100	3524.7	100.0	48	100	1723.5	100.0

Kudu was the most common prey species of all cheetah social groups, but the sex and age of kudu killed by the cheetahs varied between the social groups (Table 3.4). Overall, more juveniles and adults were killed than sub-adults (Table 3.4) and this pattern was evident across all the cheetah groups. Most of the kudu kills made by the coalition were adult females (66%), whereas the most common age class of kudu killed by the female cheetahs with cubs, single female cheetahs and independent cheetah cubs was juvenile (78-96%; Table 3.4). The proportion of kills of adult and juvenile kudu varied significantly across the cheetah social groups ($\chi^2 = 43.9$, $df = 3$, $P < 0.0001$). As a consequence of the selection of different sex and age classes, the mean mass of kudu killed by the coalition was significantly larger ($F = 33.8$, $df = 3$, $P < 0.001$) than the mean mass of kudu killed by the other social groups of cheetahs (Table 3.4).

Table 3.4: A comparison of kudu kills made by the various cheetah social groups. Data are numbers of kills in each sex and age class. Total is the total number of kudu kills with kudu kills as a percentage of all kills in parentheses. Mean kill mass is the corrected kudu mass for each social group

Social group	Age and sex of kudu killed by different cheetah social groups												Mean kill mass (kg)	
	Adult (A)				Sub-adult (SA)				Juvenile (J)					Total (% of all kills)
	M	F	U	% A	M	F	U	% SA	M	F	U	% J		
Coalition	0	23	0	65.7	1	1	0	5.7	3	1	6	28.6	35 (32.4)	131.0
Females with cubs	0	1	1	4.8	0	0	0	0	1	0	39	95.2	42 (37.8)	63.5
Single females	1	1	0	4.9	0	1	0	2.1	1	3	41	93	47 (49.0)	63.7
Independent cubs	0	3	0	21.4	0	0	0	0	0	0	11	78.6	14 (29.2)	81.4

M = male; F = female; U = unknown.

The corrected mass for all prey species varied between the different carnivore species and social groups (Table 3.5) and for example, the mean size of kudu killed by the different predators on Kwandwe varied significantly ($F = 67.32$, $df = 6$, $P < 0.0001$; Figure 3.1). A post-hoc test suggested that female cheetahs with cubs, single females and independent cubs killed similarly small kudu ($P > 0.05$ for all) that were significantly smaller than those killed by all other predators ($P < 0.05$ for all comparisons). Male and female lions killed significantly larger kudu than all other predators, with the exception of African wild dogs. The differences between the size of kudu killed by male lions and African wild dogs only just failed to reach statistical significance at the 5% level ($P = 0.06$). The coalition and African wild dogs killed similar sized kudu ($P > 0.05$) which were significantly larger than those killed by the other cheetahs ($P < 0.05$ for all comparisons).

Lions killed larger eland, kudu, wildebeest and gemsbok, than other carnivores did. For example, lions killed significantly larger black wildebeest, gemsbok and zebra than African wild dogs or cheetahs did ($F = 10.37$, $df = 2$, $P < 0.001$ for black wildebeest; $F = 6.18$, $df = 2$, $P < 0.001$ for gemsbok; $F = 17.37$, $df = 1$, $P < 0.0001$ for zebra; Table 3.5). By contrast, for smaller prey species such as steenbok, springbok, impala and bushbuck, the various carnivores all killed prey of a similar size (Table 3.5). In some of the smaller prey species, there was variation in mean kill size, but this was not significant ($F = 0.19$, $df = 3$, $P > 0.05$ for bushbuck; $F = 1.49$, $df = 3$, $P > 0.05$ for springbok; Table 3.5).

The mean prey mass for warthog varied significantly among the predator groups with African wild dogs killing significantly smaller warthog than female lions ($F = 4.77$, $df = 1$, $P < 0.05$; Table 3.5). Cheetahs were only recorded killing juvenile warthog upon two occasions, once by the coalition and once by the independent cubs (Table 3.5).

Table 3.5: Typical, corrected body mass (kg) of the ungulate prey of the predators on Kwandwe. Mean adult mass (kg) of predators is given in parentheses.

Prey species	Predator type (and body mass)						
	Lion male (188)	Lion female (126)	Cheetah male (64.7)	Cheetah SF (54.7)	Cheetah FC (54.7)	Cheetah IC (44.7)	African wild Dog (25.2)
Black wildebeest*	135.0	120.7	105.5				53.0
Blesbok			72.5				
Blue wildebeest		168.3	56.3				
Zebra*		209.1	87.7			87.0	
Bushbuck		14.4	48.0	41.2	44.0	46.3	46.4
Bushpig		83.6					
Common duiker		12.8		16.2	16.0	18.4	19.5
Eland	560.0	388.4	282.5		183.0		
Gemsbok*	182.1	199.5	86.7	67.5	67.5		63.0
Giraffe		259.5					
Impala*		55.0	60.0	29.6	44.9	23.9	49.8
Kudu*	200.0	194.5	131.0	63.7	63.5	81.4	153.4
Mountain reedbuck		8.1			27.0		
Red hartebeest*		114.6	109.6		40.5		82.5
Springbok		23.1	28.2	27.3	27.4	17.4	23.1
Steenbok		11.0	11.2	7.3	8.6		11.0
Warthog*	70.0	56.3	21.8			21.8	42.7
Waterbuck		147.4	117.2	78.4	94.5	160.0	

Statistical comparisons were only made for prey species where the number of kills by a predator was greater than one and * = prey species for which the mean prey mass varied significantly between predator groups. SF = single female cheetahs; FC = female cheetahs with cubs; IC = independent cheetah cubs.

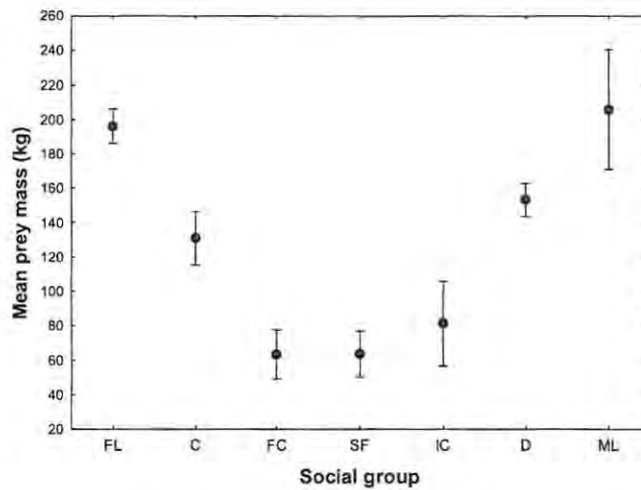


Figure 3.1: Mean mass of kudu kills made by the various predators. (FL = female lion; ML = male lion; C = coalition; FC = female cheetahs with cubs; SF = single female cheetahs; IC = independent cheetah cubs; D = African wild dogs).

Prey size in relation to predator size

Mean prey size varied significantly between the various carnivore groups ($F = 34.9$, $df = 6$, $P < 0.001$; Table 3.6). Male lions were the heaviest of the seven predator groups and killed the heaviest prey (max. mass = 213.8kg). They also utilised the second largest range of body masses (12.2 - 760kg; Table 3.6). Female lions were the second heaviest of the predator groups, had the second highest mean prey mass and the greatest range of prey body masses (3.7 - 760kg; Table 3.6). African wild dogs, although individually weighing less than all cheetah social groups, killed heavier prey (mean prey mass = 112.31kg) than all the cheetah social groups, but utilised the same range of body masses as the single female cheetahs (3.4 - 240kg; Table 3.6). The mean kill mass of the coalition was just less than 100kg and they utilised a greater range of body masses than the African wild dogs and the other cheetah social groups (9.3 - 427kg; Table 3.6). Female cheetahs with cubs, single female cheetahs and independent cheetah cubs killed prey with an average mass less than 50kg, with single

female cheetahs utilising a greater range of body masses (3.4 - 240kg; Table 3.6). Interestingly, the largest predators did not achieve the highest prey-predator body mass ratios (Table 3.6). Pack hunting African wild dogs killed prey that were four and a half times heavier than the average African wild dog, although this ratio changed to 0.7:1 when a pack size of six adults was included in the analysis. The coalition killed prey one and a half times larger than an individual male cheetah while the lions killed prey that was of similar size to an individual lion. The female cheetahs killed prey which were slightly smaller than an individual female cheetah, whereas independent cheetah cubs killed prey which were slightly larger than an independent cheetah cub (Table 3.6). Post-hoc tests revealed that the mean kill size of male lions was significantly greater than that of all other predators except the female lions ($P < 0.05$).

Table 3.6: Descriptive statistics for the corrected body mass data (kg) of prey killed by each predator type or social group

Predator type	n	Mean prey		95% confidence Interval of mean	Range of prey mass		Prey : predator body mass ratio
		body mass	SE		Minimum	Maximum	
Male lions	22	213.76	35.44	140.06 - 287.46	12.2	760	1.1 : 1
Female lions	322	141.98	6.49	129.22 - 154.75	3.7	760	1.1 : 1
African wild dogs	147	112.31	5.71	101.10 - 123.61	3.6	240	4.5 : 1
Coalition	106	97.47	5.76	86.05 - 108.89	9.3	427	1.5 : 1
Female cheetahs with cubs	108	46.51	2.70	41.15 - 51.87	3.4	183	0.9 : 1
Single female cheetahs	96	45.14	3.23	38.29 - 51.56	3.4	240	0.8 : 1
Independent cheetah cubs	42	47.55	6.56	34.29 - 60.81	9.3	160	1.1 : 1

n = number of kills per predator type or social group.

There was a significant relationship between predator body mass and maximum prey mass ($r^2 = 0.64$, $F_{1,5} = 11.44$, $P < 0.05$) but not with either mean ($r^2 = 0.07$, $F_{1,5} = 1.46$, $P > 0.05$) or minimum ($r^2 = 0.01$, $F_{1,5} = 1.03$, $P > 0.05$) prey body mass (Figure 3.2).

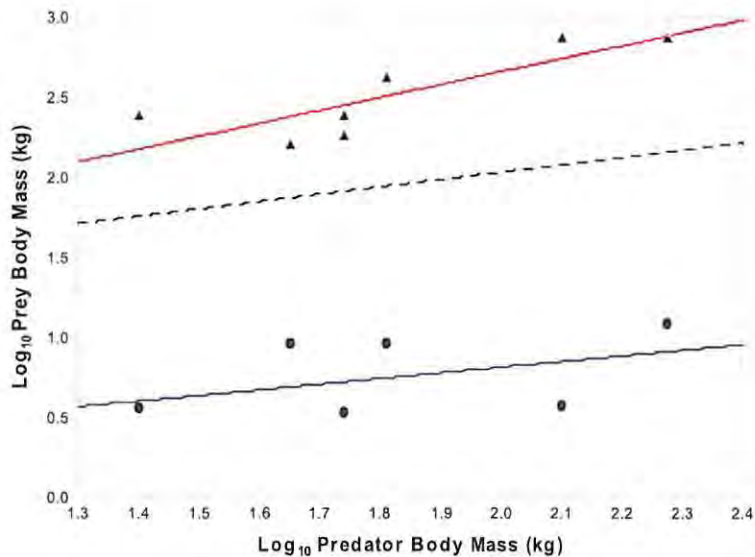


Figure 3.2: Predator-prey body mass relationships. Maximum (triangles), mean (squares) and minimum (circles) prey body mass (Log_{10} transformed) is plotted against predator body mass (Log_{10} transformed). Regressions: $Y_{\text{mean}} = 1.12 + 0.46 * x$; $Y_{\text{min}} = 0.10 + 0.36 * x$; $Y_{\text{max}} = 1.04 + 0.81 * x$. Y_{mean} , Y_{min} and Y_{max} are mean (dashed line), maximum (red line) and minimum (blue line) values.

Prey diversity in relation to predator size

Female lions killed the greatest number of prey species while male lions killed the fewest (Table 3.7). Independent cheetah cubs selected the most evenly among prey species ($E_{1/D} = 0.68$), while female lions had the most uneven prey profiles ($E_{1/D} = 0.22$; Table 3.7). There was no relationship between predator body size and prey richness ($r^2 = -0.2$, $F_{1,5} = 0.01$, $P > 0.05$) and a non significant, inverse relationship between prey evenness and predator body mass ($r^2 = -0.09$, $F_{1,5} = 0.49$, $P > 0.05$). Prey species richness for male lions was one third of that for female lions and if the data pair for male lions is omitted from the analysis, there is a significant positive relationship between predator body size and prey richness ($r^2 = 0.79$, $F_{1,4} = 14.8$, $P < 0.05$).

Table 3.7: Prey richness and evenness of the prey profile of each predator species or cheetah social group. Evenness is indicated by Simpson's Index $E_{1/D}$.

Predator type	Prey richness	Evenness (E)
Male lions	7	0.26
Female Lions	21	0.22
African wild dogs	11	0.23
Coalition	15	0.43
Female cheetah with cubs	13	0.36
Single female cheetahs	10	0.35
Independent cheetah cubs	8	0.68

Predator kills in relation to prey abundance: analysis at a prey species level and calculation of predator-prey preferences

Because of the inherent biases in all preference indices, a conservative approach has been adopted to interpreting Jacobs' Index. In this analysis, values below -0.3 have been interpreted as avoidance, values between -0.3 and 0.3 as indicating that the prey was utilised according to its abundance on the reserve and values greater than 0.3 as indicating a preference for a particular species. These ranges were chosen to accommodate inherent errors in the kill list and game counts which then result in errors in the prey preference indices. Kudu, which was the most common prey species (32% of all prey animals), was preyed upon according to its relative abundance by most predator species and cheetah social groups except for African wild dogs which selected for kudu (Tables 3.8 – 3.13). Lions selected for black wildebeest, eland and warthog and avoided species such as bushbuck, common duiker, giraffe, impala, springbok, steenbok and waterbuck (Table 3.8). Blue wildebeest, zebra, gemsbok, kudu, mountain reedbuck, ostrich and red hartebeest were preyed upon in accordance to their abundance on the reserve (Table 3.8). There was a significant positive relationship between the proportional abundance of prey species and their proportion

in the prey profile ($r^2 = 0.78$, $F_{1,14} = 49.4$, $P < 0.05$) but not between corrected mass of the prey species and their proportion in the prey profile ($r^2 = 0.013$, $F_{1,14} = 0.18$, $P > 0.05$).

African wild dogs selected for kudu and avoided gemsbok, springbok, steenbok and warthog (Table 3.9). There was a significant positive relationship between the proportional abundance of prey species and their proportion in the prey profile ($r^2 = 0.70$, $F_{1,8} = 20.3$, $P < 0.05$) and between corrected mass of the prey species and their proportion in the prey profile ($r^2 = 0.74$, $F_{1,8} = 22.7$, $P < 0.05$).

The coalition selected black wildebeest, blesbok, red hartebeest and waterbuck, and avoided blue wildebeest, bushbuck, impala and warthog (Table 3.10). The very high selection index ($JI = 0.92$) for blesbok may be an overestimate as a result of the very small number of blesbok on the reserve during the study. When the population of a prey species is very small then a single predation incident will produce a very high preference rating. In this case, a number of blesbok were killed and this, in conjunction with the small population size, generated the high Jacobs' Index. There was a significant but weak positive relationship between the proportional abundance of prey species and their proportion in the prey profile ($r^2 = 0.47$, $F_{1,13} = 11.4$, $P < 0.05$) but not between corrected mass of the prey species and their proportion in the prey profile ($r^2 = 0.02$, $F_{1,13} = 0.31$, $P > 0.05$).

Table 3.8: Preference indices for all species preyed upon by lions on Kwandwe during the study period. Abundance is the mean abundance across all years and is shown as the proportion of each species derived from annual game counts. Kills is the proportion of each species killed by the lions. Prey species are ranked by decreasing Jacobs' Index.

Species	Abundance	Kills	Jacob's Index
Eland	0.02	0.08	0.65*
Black wildebeest	0.02	0.04	0.36*
Warthog	0.22	0.37	0.35*
Ostrich	0.01	0.02	0.29
Gemsbok	0.03	0.05	0.21
Red hartebeest	0.05	0.05	0.05
Blue wildebeest	0.02	0.02	-0.06
Kudu	0.32	0.27	-0.11
Zebra	0.05	0.03	-0.19
Mountain reedbuck	0.005	0.003	-0.24
Waterbuck	0.03	0.01	-0.37 [†]
Giraffe	0.01	0.00	-0.48 [†]
Common duiker	0.04	0.01	-0.58 [†]
Steenbok	0.01	0.00	-0.61 [†]
Springbok	0.07	0.01	-0.72 [†]
Impala	0.07	0.01	-0.77 [†]
Bushbuck	0.04	0.00	-0.86 [†]

* preference; [†] avoidance

Table 3.9: Preference indices for all species preyed upon by African wild dogs on Kwandwe during the study period. Abundance is the mean abundance across all years and is shown as the proportion of each species derived from annual game counts. Kills is the proportion of each species killed by the African wild dogs.

Species	Abundance	Kills	Jacob's Index
Kudu	0.37	0.62	0.47*
Black wildebeest	0.02	0.03	0.28
Bushbuck	0.04	0.06	0.13
Red hartebeest	0.05	0.06	0.08
Common duiker	0.05	0.06	0.04
Impala	0.08	0.06	-0.17
Steenbok	0.01	0.01	-0.35 [†]
Springbok	0.08	0.03	-0.41 [†]
Warthog	0.25	0.07	-0.64 [†]
Gemsbok	0.04	0.01	-0.71 [†]

* preference; [†] avoidance

Table 3.10: Preference indices for all species preyed upon by the coalition on Kwandwe during the study period. Abundance is the mean abundance across all years and is shown as the proportion of each species derived from annual game counts. Kills is the proportion of each species killed by the coalition.

Species	Abundance	Kills	Jacob's Index
Blesbok	0.01	0.10	0.92*
Black wildebeest	0.02	0.05	0.46*
Red hartebeest	0.05	0.10	0.39*
Ostrich	0.01	0.03	0.35*
Springbok	0.07	0.13	0.33*
Waterbuck	0.03	0.05	0.28
Zebra	0.05	0.09	0.28
Gemsbok	0.04	0.04	0.03
Kudu	0.34	0.33	-0.01
Eland	0.02	0.02	-0.02
Steenbok	0.01	0.01	-0.16
Blue wildebeest	0.02	0.01	-0.38 [†]
Impala	0.07	0.02	-0.59 [†]
Bushbuck	0.04	0.01	-0.62 [†]
Warthog	0.23	0.01	-0.94 [†]

* preference; [†] avoidance

Female cheetahs with cubs selected mountain reedbuck and springbok and avoided eland, gemsbok, ostrich and red hartebeest (Table 3.11), whereas bushbuck, common duiker, impala, kudu, steenbok and waterbuck were preyed upon according to their abundance on the reserve (Table 3.11). There was a significant positive relationship between the proportional abundance of prey species and their proportion in the prey profile ($r^2 = 0.85$, $F_{1,10} = 57.1$, $P < 0.05$) but not between corrected mass of the prey species and their proportion in the prey profile ($r^2 = 0.03$, $F_{1,10} = 0.27$, $P > 0.05$).

Common duiker was preferred by single female cheetahs, whereas gemsbok, impala, ostrich and waterbuck were avoided and bushbuck, kudu, springbok and steenbok were preyed upon according to their abundance on the reserve (Table 3.12). There was a significant positive relationship between the proportional abundance of prey species and their proportion in the prey profile ($r^2 = 0.92$, $F_{1,7} = 82.1$, $P < 0.05$) but not between corrected mass of the prey species and their proportion in the prey profile ($r^2 = 0.03$, $F_{1,7} = 0.17$, $P > 0.05$).

Independent cheetah cubs selected for bushbuck and common duiker and avoided zebra and warthog (Table 3.13). There was no significant relationship between the proportional abundance of prey species and their proportion in the prey profile ($r^2 = 0.13$, $F_{1,6} = 0.9$, $P > 0.05$) or between corrected mass of the prey species and their proportion in the prey profile ($r^2 = 0.09$, $F_{1,6} = 0.6$, $P > 0.05$).

Table 3.11: Preference indices for all species preyed upon by female cheetahs with cubs on Kwandwe during the study period. Abundance is the mean abundance across all years and is shown as the proportion of each species derived from annual game counts. Kills is the proportion of each species killed by female cheetahs with cubs.

Species	Abundance	Kills	Jacob's Index
Mountain reedbuck	0.01	0.02	0.47*
Springbok	0.10	0.22	0.44*
Steenbok	0.02	0.03	0.23
Common duiker	0.06	0.09	0.16
Impala	0.10	0.11	0.10
Bushbuck	0.05	0.06	0.03
Waterbuck	0.04	0.03	-0.14
Kudu	0.46	0.39	-0.15
Ostrich	0.02	0.01	-0.34 [†]
Red hartebeest	0.07	0.03	-0.42 [†]
Eland	0.03	0.01	-0.49 [†]
Gemsbok	0.05	0.01	-0.69 [†]

* preference; [†] avoidance

Table 3.12: Preference indices for all species preyed upon by single female cheetahs on Kwandwe during the study period. Abundance is the mean abundance across all years and is shown as the proportion of each species derived from annual game counts. Kills is the proportion of each species killed by single female cheetahs.

Species	Abundance	Kills	Jacob's Index
Common duiker	0.07	0.16	0.43*
Bushbuck	0.06	0.09	0.18
Springbok	0.11	0.14	0.13
Steenbok	0.02	0.02	0.03
Kudu	0.51	0.50	-0.03
Ostrich	0.02	0.01	-0.34 [†]
Impala	0.11	0.05	-0.36 [†]
Gemsbok	0.05	0.02	-0.45 [†]
Waterbuck	0.04	0.01	-0.60 [†]

* preference; [†] avoidance

Table 3.13: Preference indices for all species preyed upon by independent cheetah cubs on Kwandwe during the study period. Abundance is the mean abundance across all years and is shown as the proportion of each species derived from annual game counts. Kills is the proportion of each species killed by independent cheetah cubs.

Species	Abundance	Kills	Jacob's Index
Common duiker	0.05	0.24	0.69*
Bushbuck	0.05	0.17	0.61*
Springbok	0.08	0.14	0.30
Impala	0.08	0.10	0.10
Waterbuck	0.03	0.02	-0.14
Kudu	0.39	0.29	-0.22
Zebra	0.06	0.02	-0.43 [†]
Warthog	0.26	0.02	-0.87 [†]

* preference; [†] avoidance

In summary, the lions, African wild dogs and coalition selected larger prey species such as black wildebeest, eland, kudu, blesbok and red hartebeest, while female cheetahs with cubs, single female cheetahs and independent cheetah cubs selected smaller prey species. For example, smaller species such as common duiker were avoided by the lions but selected by single female cheetahs and independent cheetah cubs, while springbok were avoided by lions and African wild dogs but selected by female cheetahs with cubs. Black wildebeest, a preferred species of lions and the coalition, were not killed by the female cheetahs with cubs, single female cheetahs and independent cheetah cubs. Despite the apparent importance of prey size, there was only a significant relationship between corrected prey mass and the proportion of kills for the African wild dogs while the relationship between kills and prey abundance was significant for all predators except the independent cheetah cubs.

Predator kills in relation to prey abundance: analysis at a prey mass level

More than 75% of available prey on Kwandwe fell into three prey mass categories weighing less than 250kg (Figure 3.3). As a consequence of this, all predators on Kwandwe killed very few animals that weighed more than 250kg (Figure 3.4). Most kills by lions fell into body mass categories of 50-99kg and 200-249kg, while African wild dogs selected animals that had a body mass between 150-199kg (Figure 3.4). The majority of the coalition's prey fell into body mass categories of 50-99kg and 150-199kg, while female cheetahs with cubs, single female cheetahs and independent cheetah cubs selected relatively small prey with body masses between 0-49kg (Figure 3.4).

The two predominant mass categories for lions represent their two most important prey species, with warthog in the 50-99kg category and kudu in the 200-249kg category. 61.4% of kills by the African wild dogs were kudu (Table 3.2) and because they killed smaller (sub-adult or adult females) kudu than the lions, they fell into the modal prey mass category (150-199kg). By contrast, the modal mass category (50-99kg) for the coalition did not represent the most important single prey species (kudu) but rather a group of species including blesbok, kudu (juvenile), zebra (juvenile), gemsbok (juvenile) and impala. Adult kudu, which constituted 21.3% of all kills, were in the 150-199kg category, which was the second largest mass category. For female cheetahs with cubs, single female cheetahs and independent cheetah cubs, kills of smaller species such as common duiker, springbok and bushbuck fell in the modal mass category (0-49kg). Most of the kudu killed by the female cheetahs with cubs, single female cheetahs and independent cheetah cubs were juvenile and fell in the 50-99kg category.

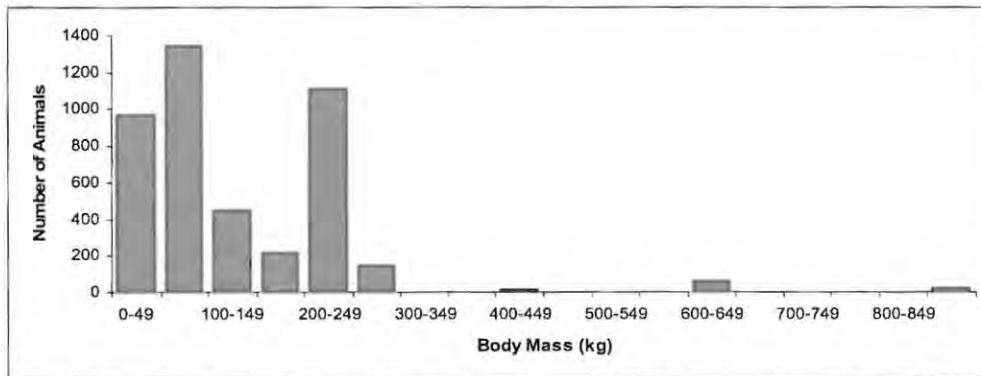


Figure 3.3: Availability of prey of different body masses (pooled data for 2003-2007).

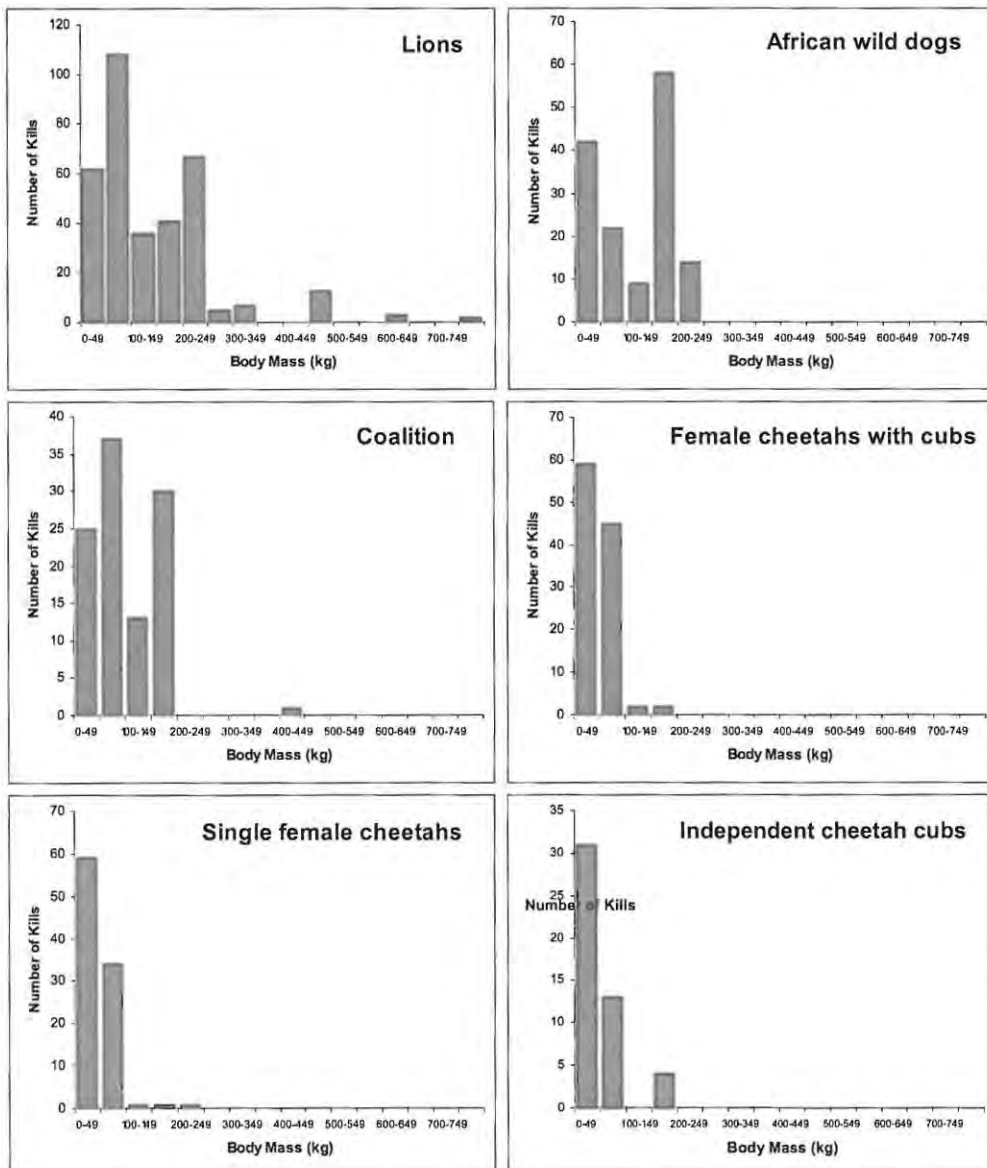


Figure 3.4: Prey mass categories and kills per mass category made by the various predator species and cheetah social groups. (pooled data for Jan 2003 to Apr 2007).

Comparison between *ad hoc* and continuous observation kill lists

During six periods of continuous observations on the lions, 45 kills of nine different species were observed (Table 3.14). By contrast, *ad hoc* observations recorded 58 kills of 10 species (Table 3.14). Eland kills comprised a relatively high percentage of the prey profile during the *ad hoc* observations but eland kills were not recorded during the continuous observations (Table 3.14). Two small species (bushbuck and common duiker) were only recorded in the continuous observations (Table 3.14). However, there was no significant difference in the proportion of each species recorded by the two observation methods for lions ($\chi^2 = 40.5$, $df = 30$, $P > 0.05$).

In the four sets of continuous observations of African wild dogs, 38 kills of nine different species were recorded, while *ad hoc* observations recorded 47 kills of seven species (Table 3.15). Seven of nine species were recorded in both the *ad hoc* and continuous observations (Table 3.15). One small species (steenbok) and one large species (black wildebeest) were only recorded in the continuous observations (Table 3.15). There was no significant difference in the proportion of each prey species detected by the two methods of observation ($\chi^2 = 20.0$, $df = 16$, $P > 0.05$).

Table 3.14: Comparison of kills located during two week continuous observations and *ad hoc* observations for lions on Kwandwe in 2005 & 2006.

Prey species	<i>Ad hoc</i> kills		Continuous observation kills	
	No.	%	No.	%
Warthog	29	51.8	17	40.5
Kudu	13	23.2	9	21.4
Eland	4	7.1	0	0.0
Red hartebeest	3	5.3	2	4.8
Black wildebeest	1	1.8	3	7.1
Gemsbok	1	1.8	2	4.8
Zebra	2	3.6	2	4.8
Bushpig	1	1.8	0	0.0
Springbok	1	1.8	3	7.1
Leopard tortoise	1	1.8	0	0.0
Common duiker	0	0.0	3	7.1
Bushbuck	0	0.0	1	2.4
TOTAL	56	100	42	100

Table 3.15: Comparison of kills located during two week continuous observations and *ad hoc* observations for African wild dogs on Kwandwe in 2005 & 2006.

Prey species	<i>Ad hoc</i> kills		Continuous observation kills	
	No.	%	No.	%
Kudu	36	76.6	18	51.3
Warthog	2	4.3	3	8.6
Common duiker	3	6.4	3	8.6
Bushbuck	1	2.1	1	2.9
Red hartebeest	2	4.3	4	11.4
Black wildebeest	0	0.0	2	5.7
Impala	2	4.3	2	5.7
Springbok	1	2.1	1	2.9
Steenbok	0	0.0	1	2.9
TOTAL	47	100	35	100

For the coalition, both observation methods recorded kills of 12 species (Table 3.16). Nine species were shared between methods with three unique to each method (Table 3.16). Eland, warthog and steenbok were not recorded during the six sets of continuous observations, while blue wildebeest, ostrich and bushbuck were not recorded during *ad hoc* observations (Table 3.16). The difference in the proportion of each prey species detected by the two methods of observation was just significant ($\chi^2 = 43.97$, $df = 30$, $P = 0.05$).

Table 3.16: Percentage occurrence of kills located during two week continuous observations and *ad hoc* observations for the coalition on Kwandwe in 2004 - 2006.

Prey species	<i>Ad hoc</i> kills		Continuous observation kills	
	No.	%	No.	%
Kudu	13	30.9	9	25.0
Blesbok	5	11.9	2	5.6
Springbok	5	11.9	7	19.3
Red hartebeest	4	9.5	5	13.8
Black wildebeest	4	9.5	1	2.8
Zebra	4	9.5	2	5.6
Gemsbok	2	4.8	3	8.3
Warthog	1	2.4	0	0.0
Eland	1	2.4	0	0.0
Waterbuck	1	2.4	2	5.6
Steenbok	1	2.4	0	0.0
Impala	1	2.4	1	2.8
Blue wildebeest	0	0.0	1	2.8
Ostrich	0	0.0	1	2.8
Bushbuck	0	0.0	2	5.6
TOTAL	42	100.0	36	100.0

For female cheetahs with cubs, both observation methods detected nine prey species, six were shared and three were unique to each method. Gemsbok, eland and ostrich were not recorded during the four sets of continuous observations, while steenbok, mountain reedbuck and scrub hare were not recorded during *ad hoc* observations

(Table 3.17). Overall there was no significant difference in the proportion of each species recorded by the two observation methods for female cheetahs with cubs ($\chi^2 = 37.4$, $df = 25$, $P = 0.053$).

Table 3.17: Percentage occurrence of kills located during two week continuous observations and *ad hoc* observations for female cheetahs with cubs on Kwandwe in 2005 & 2006.

Prey species	<i>Ad hoc</i> kills		Continuous observation kills	
	No.	%	No.	%
Kudu	8	25.8	8	29.7
Springbok	12	38.7	2	7.4
Gemsbok	1	3.2	0	0.0
Eland	1	3.2	0	0.0
Waterbuck	2	6.5	1	3.7
Steenbok	0	0.0	1	3.7
Impala	3	9.7	3	11.1
Ostrich	1	3.2	0	0.0
Mountain reedbuck	0	0.0	2	7.4
Common duiker	1	3.2	3	11.1
Bushbuck	2	6.5	6	22.2
Scrub hare	0	0.0	1	3.7
TOTAL	31	100.0	27	100.0

For single female cheetahs, *ad hoc* observations recorded kills of six species compared to only three in two sets of continuous observations. Springbok, waterbuck, impala and bushbuck were not recorded during continuous observations, while gemsbok were not recorded during *ad hoc* observations (Table 3.18). There was no significant difference in the proportion of each prey species detected by the two methods of observation ($\chi^2 = 14.0$, $df = 10$, $P > 0.05$).

Table 3.18: Percentage occurrence of kills located during two week continuous observations and *ad hoc* observations for single female cheetahs on Kwandwe in 2004 & 2006.

Prey species	<i>Ad hoc</i> kills		Continuous observation kills	
	No.	%	No.	%
Kudu	26	63.4	10	83.3
Springbok	2	4.9	0	0.0
Gemsbok	0	0.0	1	8.3
Waterbuck	1	2.4	0	0.0
Impala	1	2.4	0	0.0
Common duiker	8	19.5	1	8.3
Bushbuck	3	7.3	0	0.0
TOTAL	41	100.0	12	100.0

One of the reasons for undertaking the continuous observations was to increase the likelihood of getting an accurate record of the prey profiles of the different carnivores and, in particular, of recording kills of small species. For the lions, continuous observations recorded kills of two small species (common duiker and bushbuck) that were not recorded in *ad hoc* observations and the percentage of springbok kills was higher in continuous observations (6.7%) than *ad hoc* observations (1.7%). In the African wild dogs, the continuous observations recorded one kill of a small species (steenbok) that was not recorded in the *ad hoc* observations but also recorded kills of the large black wildebeest. Similar results were achieved for the coalition where continuous observations detected kills of one small species (bushbuck) and one large species (blue wildebeest) that were not recorded during *ad hoc* observations. However, *ad hoc* observations detected one kill of steenbok while the continuous observations did not. Continuous observations on female cheetahs with cubs detected kills of three small species (scrub hare, mountain reedbuck and steenbok) and kills of bushbuck constituted a higher percentage of all kills in continuous observations

(21.4%) than in *ad hoc* observations (5.9%). Observations on single female cheetahs yielded different results and the continuous observations did not record kills of three small species (springbok, impala and bushbuck) that were recorded during *ad hoc* observations. In spite of these differences, chi-square tests showed that only the prey profiles of the coalition differed significantly.

Annual changes in the abundance of prey species

The abundance of prey species changed substantially during the study period with the major change being in the numbers of kudu and warthog (Figure 3.5). Kudu numbers decreased from 2003 to 2005 and then levelled off from 2005 to 2007 while over the same period, warthog numbers increased twofold (Figure 3.5). There were relatively low numbers of larger species such as red hartebeest, wildebeest, zebra, gemsbok and eland on the reserve compared to kudu and warthog (Figure 3.5) and these numbers remained more or less constant throughout the study. During 2003 and 2004 there were 213 blue wildebeest on the reserve. However, this species was not indigenous to the Great Fish River valley and they were removed and replaced with the indigenous black wildebeest. In 2005 blue wildebeest numbers were very low (seven) and in 2006 and 2007 there were 73 black wildebeest and three blue wildebeest on the reserve (Figure 3.5). There was a decline in smaller prey species such as springbok and impala from the beginning of the study to the end (Figure 3.6). Springbok declined from 510 in 2003 to 138 in 2007; while impala declined from 434 in 2003 to 221 in 2007 (see Table 2.2 in Chapter 2). Bushbuck and common duiker numbers declined from 2003 to 2005, followed by a slight increase from 2005 to 2007 (Figure 3.6). Steenbok numbers remained more or less constant throughout the study (Figure 3.6).

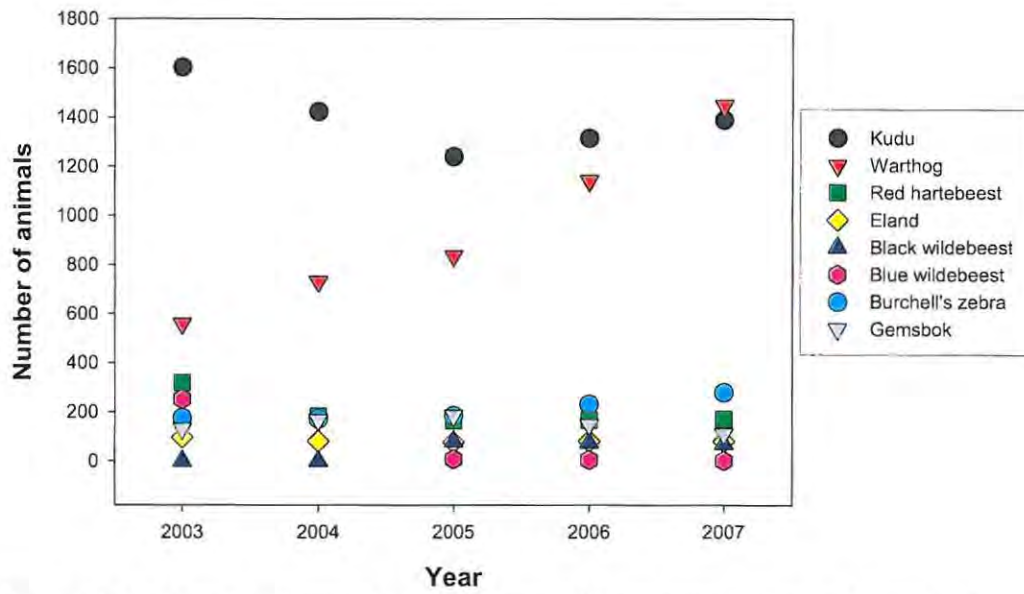


Figure 3.5: Annual changes in the abundance of large prey species on Kwandwe.

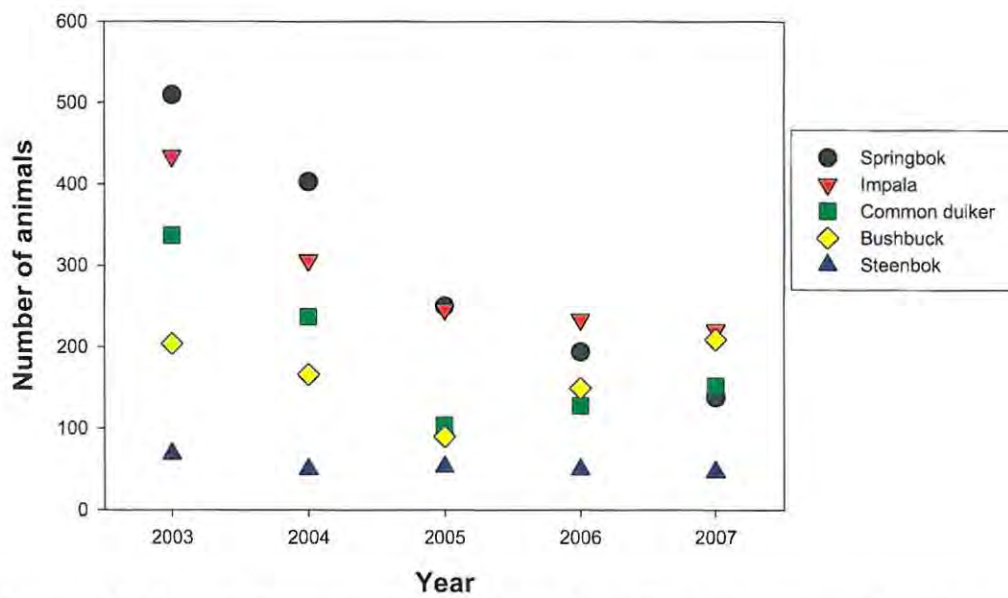


Figure 3.6: Annual changes in the abundance of small prey species on Kwandwe.

Annual changes in prey availability by weight class

The changes in the abundance of the prey species resulted in changes in the number of animals in each mass category and to illustrate this, prey availability data from 2003 and 2004 (period 1) and from 2005 and 2006 (period 2) were combined. In period 1, 95% of available prey weighed less than 250kg and in period 2, 94% of available prey weighed less than 250kg (Figure 3.7). There was a substantial decline in small prey animals weighing between 0-49kg from period 1 to period 2 which was due to the decrease in numbers of small prey species. There was a slight increase in the numbers of animals in mass category two, which was probably due to the increased numbers of warthog, and a small decrease in the number of animals in mass category five which was probably due to the decline in the numbers of kudu (Figure 3.7).

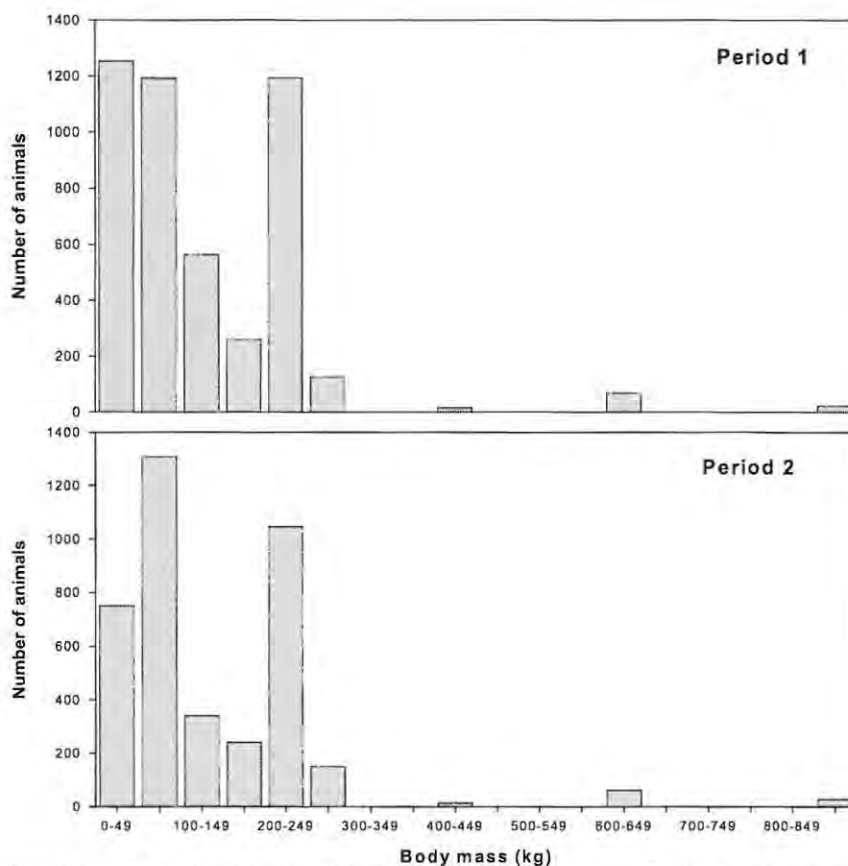


Figure 3.7: Changes in the availability of prey of different mass categories from period 1 to period 2.

These changes in the prey base have created the opportunity to examine the effects of changes in prey size and abundance on the diet of the carnivores and this is addressed in the following sections. Specific questions have been asked to examine the effects of the change in prey base on predators of different size, the assumption being that changes in the abundance of smaller prey species may have a more marked effect on the smaller predators than the larger and vice versa.

The effect of changes in the prey base on the diet of the lions

Although kudu abundance declined through the study, their proportional abundance was constant. In spite of this, there was a decrease in kudu kills by lions from period 1 to period 2 and Jacobs' Index changed from a slight preference in period 1 to a slight avoidance in period 2 (Table 3.19). There was no significant relationship between kudu abundance and kudu kills ($r^2 = -0.02$, $F_{1,3} = 0.92$, $P > 0.05$). There was a substantial increase in warthog abundance and warthog kills from period 1 to period 2 (Table 3.19) and a significant positive relationship between warthog abundance and warthog kills ($r^2 = 0.91$, $F_{1,3} = 41.44$, $P < 0.001$; Figure 3.8). The Jacobs' Index for warthog increased from period 1 (0.21) to period 2 (0.42) and there was a significant positive relationship between warthog abundance and Jacobs' Index for warthog ($r^2 = 0.87$, $F_{1,3} = 27.21$, $P < 0.01$; Figure 3.9). Interestingly there was a switch in the diet of lions from kudu (44% of kills) to warthog (42% of kills) from period 1 to period 2 (Table 3.19) and as warthog abundance increased there was a significant decrease in kudu kills ($r^2 = 0.86$, $F_{1,3} = 26.56$, $P < 0.001$; Figure 3.10).

Blue wildebeest, which fall into one of the preferred weight ranges of lions (Figure 3.4), were killed according to their abundance on the reserve in period 1 and were not killed in period 2. In period 2, the lions showed a strong selection for black wildebeest

(Table 3.19). The strong avoidance for blue wildebeest in period 2 probably simply reflects the fact that there were very few (approximately five) on Kwandwe at this time.

The lions strongly avoided small species weighing less than 60kg (Table 3.19) and there was no effect of the reduction in their numbers.

Table 3.19: Prey preference and proportion of kills made by the lions in Period 1 (2003 & 2004) and Period 2 (2005 & 2006).

Species	Prey abundance		Kills		Jacobs' Index	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
Kudu	0.32	0.32	0.44	0.21	0.24	-0.29
Warthog	0.14	0.25	0.20	0.42	0.21	0.38*
Red hartebeest	0.05	0.04	0.07	0.05	0.11	0.06
Blue wildebeest	0.05	0.001	0.07	0.00	0.19	-1.00 [†]
Black wildebeest	-	0.02	-	0.05	-	0.47*
Zebra	0.04	0.05	0.02	0.03	-0.34 [†]	-0.23
Gemsbok	0.03	0.05	0.06	0.05	0.29	0.00
Eland	0.02	0.02	0.07	0.10	0.62*	0.70*
Waterbuck	0.02	0.03	0.02	0.01	-0.09	-0.72 [†]
Ostrich	0.02	0.01	0.05	0.01	0.46*	-0.01
Bushbuck	0.04	0.03	0.00	0.01	-1.00 [†]	-0.71 [†]
Common duiker	0.06	0.03	0.00	0.02	-1.00 [†]	-0.17
Impala	0.08	0.06	0.02	0.01	-0.64 [†]	-0.85 [†]
Mountain reedbuck	0.01	0.003	0.00	0.01	-1.00 [†]	0.20
Springbok	0.10	0.06	0.00	0.02	-1.00 [†]	-0.47 [†]
Steenbok	0.01	0.01	0.00	0.01	-1.00 [†]	-0.43 [†]

* preference; [†] avoidance

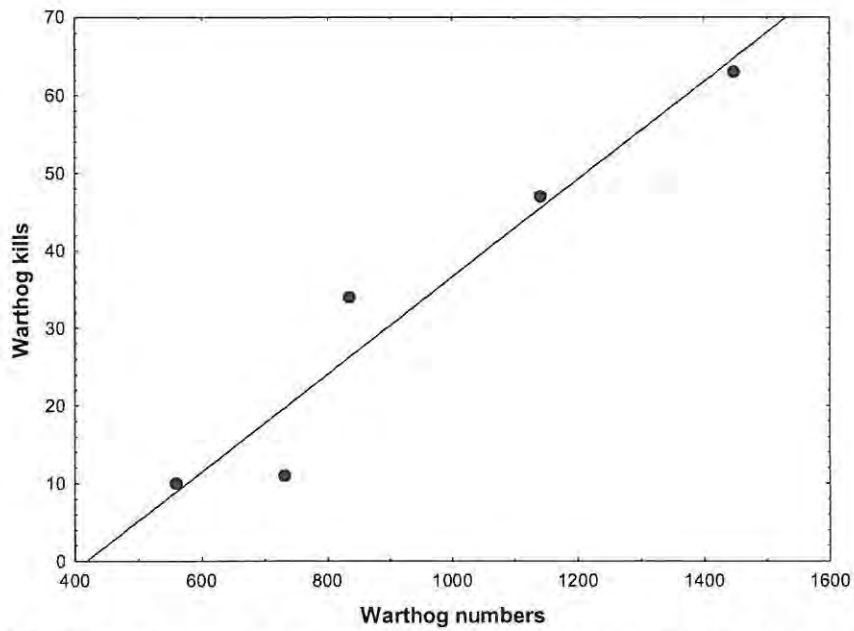


Figure 3.8: The relationship between warthog abundance and warthog kills. Total warthog numbers are plotted against total lion warthog kills. Regression: $y = -26.29 + 0.06 * x$ ($r^2 = 0.91$, $F_{1,3} = 41.44$, $P < 0.001$).

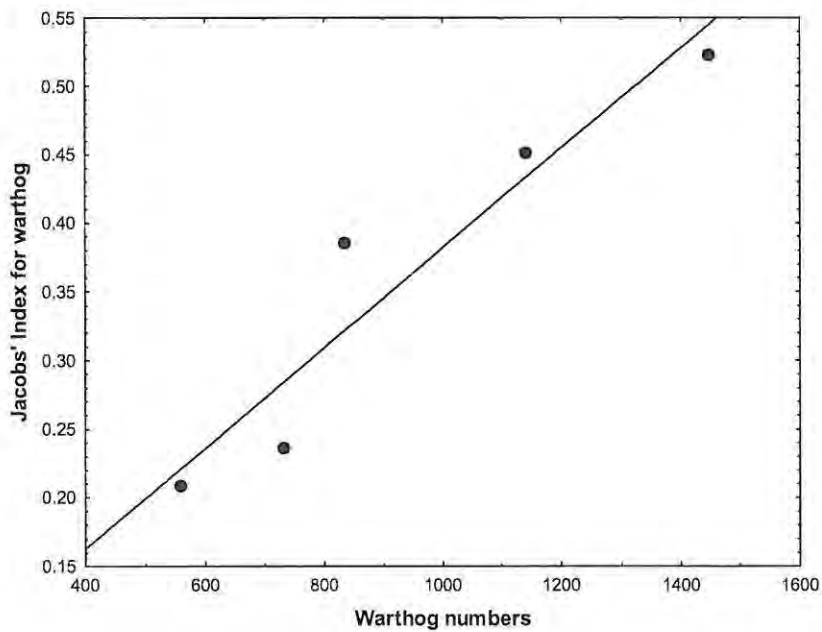


Figure 3.9: Relationship between warthog abundance and Jacobs' Index for warthog. Total warthog numbers are plotted against Jacobs' Index for warthog. Regression: $y = 0.017 + 0.0004 * x$ ($r^2 = 0.87$, $F_{1,3} = 27.21$, $P < 0.01$).

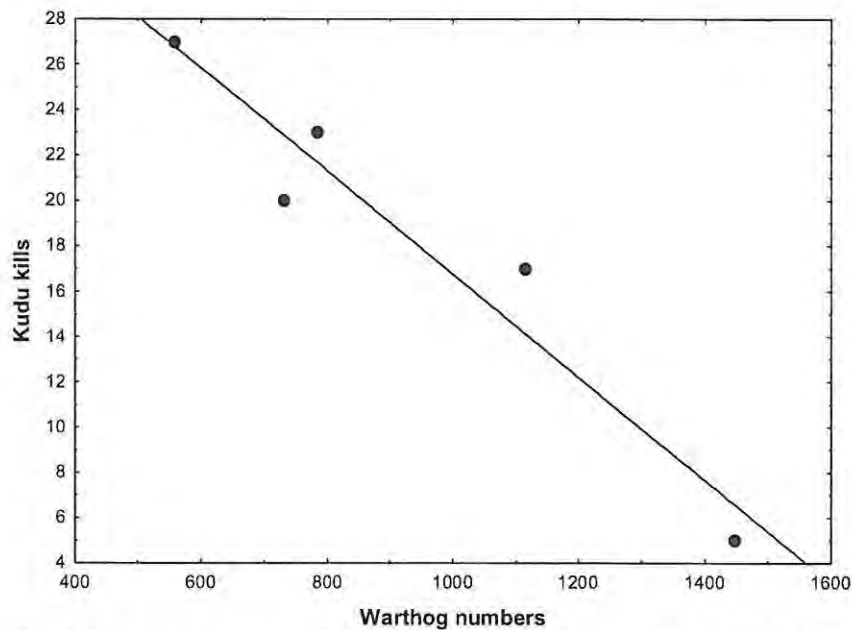


Figure 3.10: Relationship between warthog abundance and kudu kills. Total warthog numbers are plotted against total kudu killed by lions. Regression: $y = 39.47 - 0.02 \cdot x$ ($r^2 = 0.86$, $F_{1,3} = 26.56$, $P < 0.001$).

The mean prey mass for lions decreased during the study period, with a significant decrease from 2003 to 2006 and 2007 (ANOVA on ranks; $H = 20.78$, $df = 4$, $P < 0.001$; Figure 3.11). There was also a significant decrease in mean prey mass for the lions from period 1 to period 2 ($t = 2.14$, $df = 307$, $P < 0.05$; Table 3.20).

Table 3.20: Mean prey mass for lions in period 1 and period 2. N is the total number of lion kills during period 1 & 2.

	Period 1	Period 2
Mean mass (kg)	166.5	135.3
Sd	118.9	126.9
Min	3.7	5.5
Max	460	760
N	113	196

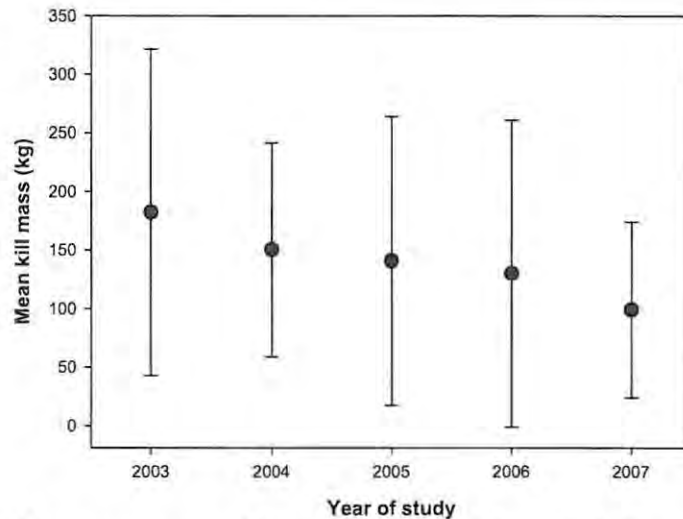


Figure 3.11: Mean prey mass of lions during the study period. Data are means \pm 1SD.

The effect of changes in the prey base on the diet of the coalition

There was no significant relationship between kudu kills made by the coalition and kudu abundance ($r^2 = 0.10$, $F_{1,3} = 1.44$, $P > 0.05$), although there was a slight decrease in kudu kills made by the coalition from period 1 to period 2 and kudu were hunted according to their abundance during both periods (Table 3.21). Despite the increase in warthog abundance from period 1 to period 2 there was no change in the occurrence of warthog kills made by the coalition during this time and warthog were strongly avoided during both periods (Table 3.21). Blesbok was a strongly preferred prey species in period 1 (although the low abundance of blesbok on the reserve could have elevated the preference) and with the drop in blesbok numbers there was a significant drop in kills ($r^2 = 0.90$, $F_{1,3} = 36.11$, $P < 0.001$; Figure 3.12; Table 3.21). Interestingly there was an inverse relationship between springbok abundance which decreased and springbok kills which increased from period 1 to period 2, but it was not significant ($r^2 = -0.17$, $F_{1,3} = 0.41$, $P > 0.05$; Table 3.21). Jacobs' Index for springbok switched

from avoidance in period 1 to preference in period 2 (Table 3.21). The increase in springbok kills also coincided with a decrease in kills and abundance of kudu and blesbok, however there was no significant relationship between these factors. In period 1 the coalition avoided blue wildebeest whereas in period 2 when the blue wildebeest were replaced by black wildebeest, the coalition selected black wildebeest (Table 3.21). Overall, the coalition avoided the smaller prey species and the preferred prey species had a mean body mass of between 60 – 160kg (Table 3.21). Adult warthog fell into the preferred weight range but were strongly avoided by the coalition (Table 3.21).

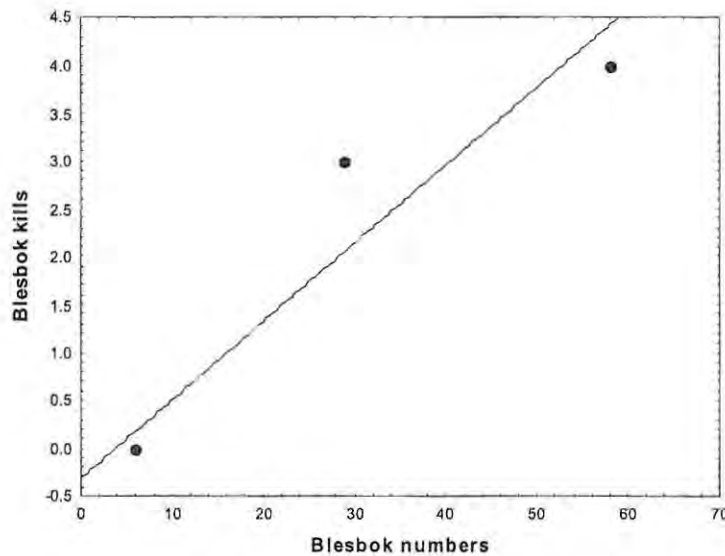


Figure 3.12: Relationship between blesbok numbers and blesbok kills. Total blesbok numbers are plotted against total blesbok kills for the coalition. Regression: $y = -0.31 + 0.08 * x$ ($r^2 = 0.90$, $F_{1,3} = 36.11$, $P < 0.001$).

Table 3.21: Prey preference and proportion of kills made by the coalition in different years. Prey abundance is the mean of 2003 & 2004, period 1; mean of 2005 & 2006, period 2.

Species	Prey abundance		Kills		Jacobs' Index	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
Kudu	0.33	0.33	0.37	0.28	0.10	-0.11
Warthog	0.14	0.25	0.00	0.02	-1.00 [†]	-0.89 [†]
Blesbok	0.01	0.002	0.20	0.00	0.93*	-1.00 [†]
Red hartebeest	0.05	0.04	0.11	0.10	0.37*	0.43*
Eland	0.02	0.02	0.02	0.02	-0.01	0.00
Ostrich	0.02	0.01	0.04	0.02	0.35*	0.30
Springbok	0.10	0.06	0.06	0.20	-0.30	0.61*
Blue wildebeest	0.05	0.001	0.02	0.00	-0.43 [†]	-1.00 [†]
Black wildebeest	-	0.02	-	0.10	-	0.69*
Zebra	0.04	0.05	0.09	0.08	0.45*	0.21
Gemsbok	0.03	0.04	0.04	0.06	0.08	0.18
Waterbuck	0.02	0.03	0.04	0.06	0.25	0.33*
Impala	0.08	0.06	0.02	0.02	-0.64 [†]	-0.53 [†]
Bushbuck	0.04	0.03	0.00	0.02	-1.00 [†]	-0.22
Steenbok	0.01	0.01	0.00	0.02	-1.00 [†]	0.21
Common duiker	0.06	0.03	0.00	0.00	-1.00 [†]	-1.00 [†]
Mountain reedbuck	0.01	0.004	0.00	0.00	-1.00 [†]	-1.00 [†]

* preference; [†] avoidance

The effect of changes in the prey base on the diet of the female cheetahs with cubs

There was no significant relationship between kudu abundance and kudu kills made by female cheetahs with cubs ($r^2 = 0.13$, $F_{1,3} = 1.62$, $P > 0.05$), but there was an almost 50% decrease in kudu kills from period 1 to period 2 and kudu were selected for in period 1 but killed according to their abundance on the reserve in period 2 (Table 3.22). The female cheetahs with cubs did not respond to the decrease in springbok numbers ($r^2 = -0.33$, $F_{1,3} = 0.02$, $P > 0.05$) and in fact there was a slight increase in springbok kills from period 1 to period 2 and springbok were strongly selected during both periods (Table 3.22). The decline in important prey species of the

female cheetahs with cubs for example springbok, impala and common duiker was matched by the inclusion of kills of seven species in period 2 that were not killed in period 1. Both impala and common duiker were preyed upon according to their abundance on the reserve in both periods (Table 3.22). Overall female cheetahs with cubs strongly avoided large prey species and did not kill warthog.

Table 3.22: Prey preference and proportion of kills made by the female cheetah with cubs in different years. Prey abundance is the mean of 2003 & 2004, period 1; mean of 2005 & 2006, period 2.

Species	Prey abundance		Kills		Jacobs' Index	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
Kudu	0.33	0.33	0.54	0.28	0.42*	-0.12
Springbok	0.10	0.06	0.20	0.24	0.38*	0.68*
Impala	0.08	0.06	0.13	0.10	0.27	0.28
Common duiker	0.06	0.03	0.09	0.07	0.18	0.41*
Steenbok	0.01	0.01	0.04	0.02	0.56*	0.13
Bushbuck	0.04	0.03	0.00	0.10	-1.00 [†]	0.57*
Mountain reedbuck	0.01	0.004	0.00	0.03	-1.00 [†]	0.82*
Warthog	0.14	0.25	0.00	0.00	-1.00 [†]	-1.00 [†]
Blesbok	0.01	0.002	0.00	0.00	-1.00 [†]	-1.00 [†]
Red hartebeest	0.05	0.04	0.00	0.05	-1.00 [†]	0.10
Eland	0.02	0.02	0.00	0.02	-1.00 [†]	-0.08
Ostrich	0.02	0.01	0.00	0.02	-1.00 [†]	0.23
Blue wildebeest	0.05	0.001	0.00	0.00	-1.00 [†]	-1.00 [†]
Black wildebeest	-	0.02	-	0.00	-	-1.00 [†]
Zebra	0.04	0.05	0.00	0.00	-1.00 [†]	-1.00 [†]
Gemsbok	0.03	0.04	0.00	0.02	-1.00 [†]	-0.43 [†]
Waterbuck	0.02	0.03	0.00	0.05	-1.00 [†]	0.25

* preference; [†] avoidance

DISCUSSION

Comparison of *ad hoc* and continuous observations

It has been argued that *ad hoc* observations of predators may result in an over-emphasis on kills of large prey and underestimate the smaller, more quickly consumed animals (species and individuals) (Mills 1984, Radloff & du Toit 2004). To counter this, it has been suggested that the best way to collect data on diet is through continuous periods of observations as used in this study (Mills 1996). In this study, the two methods produced variable results with each method detecting small and large species that were not detected by the other method. While it remains intuitively likely that *ad hoc* observations will underestimate kills of small species, it has been argued that where observation effort is high, as on ecotourism reserves, the undercount may not be significant (Radloff & du Toit 2004). This is supported by the results from the present study which suggest that observation effort on Kwandwe is high enough to give accurate prey profiles.

Diet and prey selection by members of the large carnivore guild on Kwandwe

The prey profiles of lions, African wild dogs and cheetahs on Kwandwe are very similar to those reported elsewhere and are thus not discussed in great detail here. For all predator species and social groups, the number of species in the prey profile and the number of important species (those that together constituted >75% of all kills) decreased with decreasing predator size. Similar results have been reported in the Kruger where four species make up 80% of the diet of lions (Funston *et al.* 1998), three species make up 69.2% of the cheetahs' diet (Mills *et al.* 2004) and two species make up 78.6% of the diet of African wild dogs (Mills & Gorman 1997). In Mala Mala Private Game Reserve (Mala Mala), South Africa, five species make up 79.9%

of the lions' diet, three species make up 87.8% of the diet of cheetahs, and two species make up 83.4% of the diet of African wild dogs (Radloff & du Toit 2004). See Hunter (1998) and Pole *et al.* (2004) for similar results from Phinda Private Game Reserve and Savé Valley Conservancy. The trend of increasing dietary breadth with increasing predator size is further emphasized in this study in the analysis of species richness in the prey profiles of the predators and in the analysis of prey size in relation to predator size. Male lions were the exception to the trend, killing the fewest species, and when they were excluded from the analysis, there was a significant positive relationship between predator size and species richness in the prey profile. This trend has been reported previously but the relationship was not significant (Radloff & du Toit 2004). The body size of the predators on Kwandwe ranged from 25kg (African wild dogs) to 188kg (male lions) and it is not surprising that this was reflected in differences in the prey profile. In general, the larger predators (lions and coalition of cheetahs) killed larger individuals from the larger prey species, while all predators killed similar sized animals of the smaller species. The mean prey mass for all prey species varied significantly between the predators and there was a significant positive relationship between predator size and maximum prey size but not between predator size and the mean or minimum prey size. Because all predators on Kwandwe killed small prey (≤ 12 kg), the prey size range was entirely dependent upon maximum prey size. Consequently, the prey size range was greatest for lions. These results are very similar to those recorded in other multi-carnivore systems (e.g. Radloff & du Toit 2004) and highlight the fact that the larger predators have wider predatory options than the smaller species (Gittleman 1985; Cohen *et al.* 1993; Radloff & du Toit 2004). Few previous studies of the prey profiles of cheetahs have separately investigated the different social groups found in this species. Consequently, findings in this regard

from the current study will be discussed in detail. The prey profiles of the different cheetah social groups varied with regard to the species killed as well as with regard to the sex, age and mass of the kills. Most of the diet comprised medium sized prey (30-65kg), which is consistent with previous studies (Mills 1984; Caro 1994; Mills *et al.* 2004; Bissett & Bernard 2007). The coalition of three males killed significantly larger prey than the other cheetahs and this was particularly clear for kudu. There appears to be some controversy in the existing literature with regard to the extent that coalitions of cheetahs hunt cooperatively (Kruuk & Turner 1967; Eaton 1970; Caro 1994) however, on Kwandwe, the coalition accompanied one another on hunts and actively co-operated in the hunts. On a number of occasions, the cheetahs drove prey toward concealed coalition partners (pers. obs.). It is probable that the co-operative hunting enabled them to kill larger prey than the solitary females and this corresponds to what has been reported in some previous studies (Caro 1994; Hunter 1998; Mills 1998; Mills *et al.* 2004). Cheetah coalitions will require more food per unit time than solitary cheetahs (Caro 1994) and this need could be met by making more frequent kills or by killing larger prey. It has been suggested that large carnivores will resist changing kill frequency due to the risk associated with each hunting event, and that changes in group size are associated with change in the size of prey (Caro 1994) as was found on Kwandwe. It is also possible that the selection of larger prey by the coalition is related to susceptibility to kleptoparasitism. It has been suggested that cheetahs kill small prey to reduce consumption time and reduce the likelihood of kleptoparasitism (Hayward *et al.* 2006a). This is supported by data from Namibia, which show that cheetahs kill larger prey than their counterparts existing within an intact large carnivore guild in East Africa (McVittie 1979). It is possible that a coalition of three male cheetahs will be better able to defend a kill against competitors

and thus be in a better position to feed from a larger kill. It is also the case that three adult male cheetahs may consume a large kill as rapidly as a single female consumes a smaller kill.

In the current study female cheetahs with cubs, single female cheetahs and independent cheetah cubs preyed mostly on animals weighing less than 50kg (mean prey mass was < 48kg for all) and killed significantly smaller kudu than the coalition. Likely reasons for this reduced prey size could be that female cheetahs are solitary and smaller than male cheetahs, and are thus less able to defend their prey and themselves against larger members of the predator guild. However, it is also likely that habitat selection by female cheetahs and behaviour of the most abundant prey species (kudu) played a role in prey selection. Juvenile kudu are hidden for the first two to three months of their lives, after which they follow their mothers and rejoin the family herds (Owen-Smith 1994). Female cheetahs inhabit dense thicket vegetation (see Chapter 4) and while doing this will flush the kudu calves from their hiding places and then kill them. Furthermore, once the calves join the herds, they are slower and less experienced than the adults, and are thus easier targets for predators. Prey selection by female cheetahs may therefore be the result of multiple interacting factors, including prey abundance (kudu is the most abundant species), size (by selecting young animals), behaviour of the prey species and habitat selection of the female cheetahs.

It has been predicted that predator-prey body mass ratios will be largest for the largest predators (Vézina 1985) and that carnivores weighing more than 21.5kg will kill prey with a body mass greater than 45% of their own mass (Carbone *et al.* 1999). These predictions are supported by findings from Mala Mala where the predator-prey body

mass ratio is highest (2.1) for the largest predator type (male lion) and the ratio decreases with decreasing predator body size (Radloff & du Toit 2004). However, on Kwandwe, the trend was slightly different and the coalition of cheetahs and the pack of African wild dogs had higher ratios than the lions. There are probably two reasons for this. Firstly, 94% of available prey weighed less than 250kg and this effectively set an upper limit on the prey killed by lions. Secondly, the low levels of kleptoparasitism on Kwandwe resulted in the coalition and African wild dogs killing larger animals than reported in many other studies (Radloff & du Toit 2004). The role of kleptoparasitism in shaping the prey profile of cheetahs was discussed earlier and it is likely that the same reasoning may, in part explain, the very high mean kill mass for the African wild dogs (Caro 1994; Carbone *et al.* 1999; Bissett & Bernard 2007). African wild dogs are able to kill adult zebras (Creel & Creel 2002) and adult kudu bulls (present study), and the low levels of kleptoparasitism (there are no spotted hyenas on Kwandwe) allows time for the African wild dogs to feed from a large carcass. In the Selous, African wild dogs are susceptible to kleptoparasitism by spotted hyenas and a small loss in food to kleptoparasites has a large impact on the African wild dogs because of the high energy costs of hunting (Creel & Creel 1996; Gorman *et al.* 1998).

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 (Creel & Creel 2002) and the co-operative hunting of the coalition allow these predators to kill larger prey than if they hunted alone. If aggregated predator mass rather than individual mass is used for group hunters such as African wild dogs and the coalition of male cheetahs (Cohen *et al.* 1993), the predator-prey

body mass ratios are reduced to 0.7:1 for African wild dogs and 0.5:1 for male cheetahs and the pattern predicted by Vézina (1985) and Carbone *et al.* (1999) is supported. The influence of sociality and pack hunting is further illustrated by the mean prey mass of kudu for African wild dogs which was greater than that of the larger male cheetahs. The relatively high predator-prey body mass ratio (1.1:1) of independent cheetah cubs could be attributed to the fact that independent cheetah cubs are inexperienced hunters and have been reported to hunt larger animals than adults (Caro 1994).

Prey preference

Although indices of prey preference are widely used, there are problems associated with interpreting preference (Chesson 1978). True preference for a prey species is difficult to demonstrate unless direct observations of the selection are made when predators are presented with a choice of prey species (Stander 1992). This was rarely possible on Kwandwe due to dense vegetation, which made it difficult to follow hunting predators. Norbury & Sanson (1992) suggested that many researchers overstate the accuracy of their preference ratings and that the validity of methods used to measure diet selection is often overlooked. Due to the biases in preference indices (Chesson 1978) and the inherent errors in the prey profiles (missed kills) and game censuses (uncounted animals), prey preferences of predators on Kwandwe have been analysed with caution.

On Kwandwe the lions, African wild dogs and the coalition selected (i.e. high Jacobs' Index) larger prey species (adult body size) and avoided smaller species, while female cheetahs with cubs, single female cheetahs and independent cheetah cubs selected smaller prey species and avoided larger species. However, despite the apparent

importance of prey species size, only the African wild dogs showed a significant positive relationship between corrected prey mass and number of kills. The reason for this apparent contradiction is that the species characterisation as large or small in the preference analyses was based on adult size. By contrast, the regression analyses used corrected prey mass which reflected the predators' abilities to control prey mass within a species by selecting animals of different age and sex. With the exception of the independent cheetah cubs, there was a significant positive relationship between the abundance of a prey species and the number of that species that were killed. These results suggest an important role for prey abundance in prey selection and a lesser role for species size. These results are substantially different from those of Hayward & Kerley (2005) who reported that there was no relationship between prey availability and lion prey preference but maintained that prey body mass significantly contributed to the prediction of prey preference. It is likely that problems associated with meta-analysis, particularly the use of different observation methods across studies and the temporal separation of availability and kill data in many studies may explain the variations in the available results. Hayward & Kerley (2005) used adult prey body mass and not a corrected mass in their analyses and this probably explains the significant effect for prey body size in their study.

The importance of prey abundance in shaping prey selection is supported by some, but not all previous studies. The majority of the diet of cheetahs comprises the most abundant medium sized prey species in an area (Mills 1984; Caro 1994; Hunter 1998). In the Selous Game Reserve, as well as in the present study, prey abundance affects prey selection by African wild dogs although this is modulated by pack size (Creel & Creel 2002). In the Selous, blue wildebeest is the most abundant prey species, yet small packs of African wild dogs (less than nine individuals) are specialist hunters of

impala (the second most abundant species) and show a strong avoidance of blue wildebeest. By contrast, large packs are less selective and prey upon most prey types including blue wildebeest according to their abundance (Creel & Creel 2002). On Kwandwe, African wild dogs selected the most abundant prey species (kudu) and similarly in Shambala Private Reserve, South Africa (Rhodes & Rhodes 2004) and Savé Valley Conservancy (Pole *et al.* 2004) kudu are killed in greater numbers relative to their abundance.

Amongst lions, the tendency appears to be to kill the most abundant medium to large prey species (Mills & Shenk 1992; Viljoen 1993; Scheel 1993). However, this is not always the case as in areas with low prey density such as Etosha, smaller prey species are killed by lions (Stander 1992), whereas, in Chobe, warthog make up a large percentage of the overall diet of the lions during the dry season when larger species have migrated out of the area (Viljoen 1993; 1997).

The importance of abundance, size and vulnerability of the prey, together with the size of the predator is well illustrated by the selection or avoidance of warthog. Warthog were the second most abundant prey species on Kwandwe and the species was avoided by all cheetah social groups, as well as by African wild dogs, despite being within the preferred mass range (Hayward *et al.* 2006a; 2006b). Warthog have been killed by cheetahs in other areas (Mills *et al.* 2004; Radloff & du Toit 2004), but never in large numbers and this is possibly due to warthog's ability to actively defend themselves against the attack of cheetahs (pers. obs.). Furthermore, it may be impossible for cheetahs to dig them out of their burrows. By contrast, warthog, despite their medium size, were strongly selected by lions and this is discussed in more detail in the next section. This example highlights the importance of prey

vulnerability (or the opposite) and aspects of species behaviour, in addition to size and abundance in determining prey selection.

Finally, it has been suggested that the use of boundary fences as an aid in hunting by African wild dogs allows them to capture large prey such as adult kudu (van Dyk & Slotow 2003). The African wild dogs on Kwandwe also used the boundary fence to capture prey, especially kudu, but adult kudu were also killed away from the boundary, which suggests that the fence is not essential for the capture of large prey by African wild dogs.

The changes in prey availability on Kwandwe allowed the direct comparison of the way in which members of the same large carnivore guild responded to fluctuations in the abundance of prey of different sizes. Because lions, cheetahs and African wild dogs generally kill the most abundant medium sized prey for cheetahs and medium to large sized prey for lions and African wild dogs it was expected that changes in the prey base would affect the different predators in different ways.

The decline in numbers of kudu and increase in numbers of warthog, the two most frequently killed species by lions on Kwandwe, provided the rare opportunity to study the effects of change in abundance on prey selection by lions. The results showed that as kudu numbers declined and warthog numbers increased, the lions switched from killing kudu to killing warthog. The relationships between kudu abundance and kudu kills and the Jacobs' Index for kudu were not significant. However, those between warthog numbers and warthog kills and preference were significant. The prey switching was driven more by the increase in abundance of warthog than the decline in numbers of kudu. This contradicts the results of Hunter (1998) who showed that lions prefer large species regardless of the abundance. Predators will switch to an

alternative food source when the abundance of their preferred prey declines (Murdoch 1969) and it is thought that this will promote the persistence of predator-prey systems (van Baalen *et al.* 2001). The results from the present study suggest that prey switching may also occur when the numbers of a secondary prey species increase as is predicted by the Optimal Foraging Theory (Křivan 1996). The prey switching apparent amongst lions on Kwandwe suggests a stronger effect of abundance of prey as compared to the influence of prey size, as warthog are very much smaller than what is often regarded as the preferred prey size of lions (Scheel & Packer 1993; Viljoen 1997; Hayward & Kerley 2005).

Although blue wildebeest are as much as 100kg heavier than black wildebeest, both fall within the preferred weight range of lions (Radloff & du Toit 2004; Hayward & Kerley 2005) and blue wildebeest is a preferred species of lions (Hayward & Kerley 2005). It is therefore not surprising that the removal of blue wildebeest and the subsequent introduction of black wildebeest did not affect prey selection by the lions. Similarly, it is not surprising that the lions did not respond to the decline in numbers of smaller prey species since these are typically not an important part of the diet of lions (Schaller 1972; Mills 1990; Stander 1992).

The coalition of male cheetahs did not kill warthog and there was no effect of the increase in warthog numbers on their prey selection. There was evidence of prey switching and as the numbers of blesbok, a highly preferred species for the coalition, declined so did the number of kills. Kills of two species increased, these being springbok, which occurred despite declining springbok abundance, and black wildebeest. A number of studies have reported springbok as a preferred species of cheetahs (Mills 1984; Mills 1998; Marker *et al.* 2003). The coalition did not kill blue wildebeest but showed a strong preference for black wildebeest. It is likely that this

reflects a body size effect, as the black wildebeest may be as much as 100kg lighter than the blue wildebeest. Significantly, it is not likely to be a prey abundance effect, since the blue wildebeest were three times as abundant as black wildebeest. Clearly, a number of factors affect prey selection by the coalition. These include co-operative hunting, prey size, prey behaviour and armaments (tusks). However, for the coalition, these factors do not appear to be as important as prey abundance in prey selection.

Female cheetahs with cubs selected smaller species and smaller individuals within larger species than did the coalition and would thus have been expected to have been affected by the decline in abundance of the smaller prey species. Like the coalition, the females with cubs killed increasing numbers of springbok despite their abundance declining throughout the study. The reduction in abundance of the smaller prey species was matched by the inclusion of seven species that were not killed in the first part of the study. This form of diet switching has been reported before and Charnov's (1976) model of optimal diet predicts the inclusion of alternative prey species as the abundance of the most profitable prey declines.

In conclusion, prey selection by large predators is shaped by many varied and interacting factors. These include size, habitat use and behaviour of the predator, size, abundance, habitat use, behaviour and vulnerability of the prey, and the presence of other predators and the risk of kleptoparasitism. Results from this study can be used to illustrate how each of these factors might function individually and how the factors may interact. Predator size and prey size probably explain why lions are the only predator to kill adult blue wildebeest, and the habitat use of female cheetahs explains why they kill young kudu. The pack hunting behaviour of the African wild dogs may explain their very high predator-prey body mass ratio. Prey abundance is a significant

predictor of the proportion of kills of a particular prey species for all predators and this was seen clearly in the prey switching of lions from kudu to warthog as warthog numbers increased. The behaviour of kudu calves makes them prone to predation by female cheetahs and the behaviour and armaments of warthog makes them resistant to female cheetahs. Finally, the threat of kleptoparasitism and the need to consume kills quickly may cause female cheetahs to kill small animals. The way that some of these factors may interact to affect prey selection can be illustrated with a single example. About half of all kills made by female cheetahs were kudu and of these, 93% were juveniles. Kudu were the most abundant prey species on Kwandwe but adults may be too large to be killed by a single female cheetah; the risk of injury outweighs the potential benefit from such a large kill. In addition, the threat of kleptoparasitism could mean that the cheetahs would not be able to feed from the kill for long enough to benefit from the size of the prey. Female cheetahs occupy the thicket habitats, and it is here that they kill the majority of juvenile kudu. Selection for juvenile kudu by female cheetahs is thus the result of the interaction of predator size and habitat selection, prey size and behaviour as well as the threat posed by larger members of the predator guild. A final important point illustrated by this example relates to the basic question of the relative importance of prey size and abundance. The results from this study suggest that, although species size is important, abundance is of greater importance. The reason for this is that, within limits, the predators can influence prey size within a species by selecting a particular sex or age to kill.

The results suggest that prey selection and preferences are not fixed, but change as the structure of the large carnivore guild and the abundance of prey change. This supports the observation that predation should be analysed separately for each situation as the influence of predation may vary spatially, as well as temporally within a certain area

(Smuts 1978) or that “everything changes with circumstance” (D.W. Macdonald pers. comm.).

CHAPTER 4

SPATIAL ECOLOGY OF LIONS, CHEETAHS AND AFRICAN WILD DOGS ON KWANDWE

INTRODUCTION

Factors affecting space use and habitat selection

Home range size in mammals is influenced by a number of interacting factors including food availability, group size, body mass and population density (Clutton-Brock & Harvey 1978; Macdonald 1983; Reiss 1988; Oli *et al.* 2002; Spong 2002; Jetz *et al.* 2004; Grassman *et al.* 2005; Marker & Dickman 2005; Benson *et al.* 2006).

A key determinant of home range size is food availability (Macdonald 1983; Spong 2002) and there is often an inverse relationship between home range size and food availability (Sandell 1986; Mills & Knowlton 1991). Carnivores tend to acquire a home range that is large enough to provide for the requirements for their particular species and/or sex (Caro 1994; Spong 2002; Delahay *et al.* 2006). However, the maintenance of a larger home range comes at an additional energetic cost and increases the risk of losing resources to neighbours due to the reduced likelihood of detecting intruders (Jetz *et al.* 2004).

Home range size increases with increasing body mass simply because of the greater energy required by the larger species (McNab 1963; Litvaitis *et al.* 1986). For similar reasons, there is usually a positive correlation between home range size and group size (Spong 2002), and in several primate species, home range size correlates positively with group size (Zucker *et al.* 1996; Di Bitetti 2001). It is suggested that larger lion prides will maintain larger home ranges containing more resources and that larger prides may more successfully defend areas high in resources (Spong 2002).

Population density is inversely correlated with home range size but it is often difficult to separate the effects of population density from those of food availability, as the two are often linked (Forsyth & Smith 1973; Maza *et al.* 1973; Marker & Dickman 2005).

Amongst large carnivores, the availability of cover and access to a sufficient supply of water are important determinants of range use, but the spacing patterns of females are generally dictated by the food supply and availability of den sites for rearing young (Caro 1994; Mizuntani & Jewell 1998; Sunquist & Sunquist 2002). In most species, females rear young on their own and their reproductive success is greatly influenced by access to food (Sunquist & Sunquist 2002). The distribution and density of female felids is therefore generally determined by the abundance of suitable prey and their spatial and temporal distribution. By contrast, spacing patterns of male felids are thought to be driven primarily by female distribution (Sunquist & Sunquist 2002).

The preceding discussion excludes inter- and intra-specific interactions and as such is in line with the concept of the Ideal Free Distribution (IFD; Fretwell & Lucas 1970). This theory suggests that if several habitats are available, but differ in their basic suitability, an individual within a single species will settle wherever expected fitness is highest (Cressman *et al.* 2004). However, interference competition, which is the consequence of direct interactions among carnivores, such as kleptoparasitism, outright killing and harassment, could result in spatial or temporal avoidance, reduction in the density of the subordinate species or even competitive exclusion from certain habitats or regions (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), an individual's

options for settling are constrained by the territorial behaviour of already established individuals. The applicability of the IFD has been tested on several animal models. However, the majority of these studies have suggested that the IDD, and not the IFD, is most applicable (Kohlmann & Risenhoover 1997; Beckmann & Berger 2002; Zimmerman *et al.* 2003).

Social systems and space use by lions, cheetahs and African wild dogs

Lions and cheetahs display a far greater degree of sociality than most other felids (Schaller 1972; Hunter 1998; Caro & Collins 1986) and African wild dogs are among the most social of all canids (Frame *et al.* 1979; McCreery & Robbins 2001). 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). Male cheetahs mate with as many females as possible and in the Kruger extensive overlap of male home ranges with female home ranges has been reported (Broomhall *et al.* 2003). Recent evidence suggests that female cheetahs also mate with numerous males and multiple paternity within a single litter has been reported (Gotelli *et al.* 2007). This is unlike the coalitions formed by male lions, which remain attached to and mate with the females in a single pride (Estes 1991; Caro 1994; Sunkist & Sunkist 2002). Amongst cheetahs, females appear to be non-territorial and range over wide areas sometimes occupying home ranges as large as 1500km² (Caro 1994; Marker *et al.* 2003), whereas among lions, the prides, which consist mainly of adult females and their offspring, are territorial and will

actively protect their territory from intruders (Heinsohn & Packer 1995; Heinsohn 1997). In arid areas, such as the Etosha in Namibia, lion pride home ranges may be as large as 2075km² (Stander 1991). Male cheetah social organization resembles that of male lions in that coalitions of males establish exclusive territories and defend them against other males in occasionally fatal clashes (Caro & Collins 1986; Caro 1994; Hunter & Skinner 1995; Hunter 1998; pers. obs).

Considerable variation in cheetah range size has been observed in different parts of their geographical range due to previously mentioned factors. In the Serengeti, Thomson's gazelles make up 90 percent 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 833km² and 777km² respectively (Schaller 1972; Caro & Collins 1986; Durant *et al.* 1988; Caro 1994; Sunquist & Sunquist 2002). By contrast, the majority of male cheetahs that live in coalitions, are more sedentary than females and, unlike most other felids, have territories that are smaller than those of the females. The main determinants of territory location in the Serengeti are a combination of adequate cover and adequate densities of Thomson's gazelles (Caro 1994). In Kruger 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).

Lions live in fission-fusion groups called prides which allow them to forage as a group and to defend their young and their territories more effectively (Schaller 1972; Gittleman 1989; Packer *et al.* 1990; Funston *et al.* 2001). Prides are formed by related adult females together with their offspring and attendant males. Prides may occupy the same home range for generations and generally exclude unrelated females (van

Orsdol *et al.* 1985; Hanby *et al.* 1995; Hunter 1998) although overlap between home ranges may occur. Large pride territories may overlap with the territories of neighboring prides, but where territories are small there is little overlap (Sunquist & Sunquist 2002). In the Serengeti, home ranges often overlap but members of adjacent prides usually remain several kilometers apart (Hanby *et al.* 1995). Members of a pride do not necessarily all move together within the home range but may regularly split up and forage in smaller sub-groups often associated through reproductive status (Schaller 1972; van Orsdol *et al.* 1985; Packer *et al.* 1990). Prides occupy home ranges that vary greatly in size depending on local conditions, the availability of food, water and the availability and distribution of suitable den sites for rearing cubs (Sunquist & Sunquist 1989; Packer *et al.* 1990; Hanby *et al.* 1995). In an area inhabited by more than one pride, males, or coalitions of males, generally associate with the female groups and attempt to defend them from other males. Consequently, male home ranges tend to be larger than those of the females (Grinnell *et al.* 1995; Hunter 1998; Spong 2002).

African wild dogs are highly social, cooperative breeding predators and live in packs in which the alpha pair typically monopolizes breeding while non-reproductive members help care for the offspring (Frame *et al.* 1979; McCreery & Robbins 2001; Creel & Creel 2002). African wild dogs occupy very large home ranges which vary from 150km² to 1110km² in the Kruger (Fuller *et al.* 1992), while in East Africa packs may roam areas of 600-2500km² (Frame *et al.* 1979; Fuller & Kat 1990; Fuller *et al.* 1992; Creel & Creel 1995). Home range size is greatly reduced during denning when the pack needs to feed pups at the den, and in the Kruger the mean home range size during the denning period is only 80km² (Gorman *et al.* 1992).

Rationale and aims

Habitat selection and space use (territory size) in large mammalian carnivores, as in other mammals, is the result of numerous interacting factors some of which have been discussed in the preceding section. In large mammals it is difficult to assess the relative importance of these factors because it is rarely possible to manipulate one factor (such as food abundance or predator density) while others are held constant, and there is a reliance on opportunistic observations (Benson *et al.* 2006). The reintroduction of large carnivores to small, enclosed reserves presents an opportunity to study the effects of factors such as changes to the large carnivore guild, or changes in prey abundance, on space use and habitat selection of large carnivores. Thus, the broad aim of this chapter is to present a general description of space use by lions, cheetahs and African wild dogs on Kwandwe. This is followed by an examination of the effects of an increase in the number of lion prides on space use by the large carnivores (particularly lions and the cheetah coalition), and an examination of the extent to which space is shared by members of the guild of large carnivores. If the IDD applies to space use by cheetahs and African wild dogs, then it is hypothesized that as the density of predators (number of lion prides) increases, the opportunity to avoid superior predators would decrease and the influence of superior predators would be exaggerated.

METHODS

Data collection

Ad hoc observations

Where possible, all cheetahs, lions and African wild dogs were located by radio-telemetry on a daily basis and their positions were recorded using a GPS. The field guides on the reserve helped with data collection and recorded all their sightings of the various predators on morning and evening game drives. These data were also included in the analysis. When it was impossible to visually locate an animal, its position was plotted by triangulation (Kenward 2001). To avoid autocorrelation among sequential locations and to ensure that data points were independent of each other, only one fix was used per day for each animal (Gehrt & Fritzell 1998; Boydston *et al.* 2003; Broomhall *et al.* 2003; but see De Solla *et al.* 1999). This particular methodology was based on the assumption that one day allowed enough time for each predator group to cross its home range and was thus sufficient for statistical independence of observations (Mizutani & Jewell 1998). The importance of a standardised sampling regime as used in this study is emphasised by Börger *et al.* (2006) as it is more likely to generate comparable measures of home range size.

Comparison of ad hoc and continuous observations

Two week continuous observations were conducted on various social groups of cheetahs, lions and African wild dogs (see Chapter 3 for detailed methods) and GPS fixes were recorded every time the animal or group of animals moved. The data on space use gained from the two week continuous observations were compared to the data from *ad hoc* monitoring for the two monthly periods that included the period of continuous observations. For every data set, the computer package BiotasTM 1.0.3

Beta was used to determine whether the number of fixes was sufficient for home range size estimations to reach an asymptote.

Home range characterization

Home range and core area size

The home range sizes of all the predator groups were determined using an ArcView extension package, Animal Movement Extension (Hooge & Eichenlaub 1997). Location points from triangulation and direct observations recorded between February 2003 and April 2007 were used for home range analyses. Home range and core area sizes were estimated using one non-parametric method; the fixed kernel utilization distribution (UD) method (Worton 1989; Powell 2000). 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. Kernel UDs more accurately reflect habitat use and are therefore more appropriate for studies of habitat selection than other non-parametric methods like the minimum convex polygon (MCP; Harris *et al.* 1990; White & Garrott 1990; Börger *et al.* 2006). 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); 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).

The key variable in the UD method is the smoothing factor (H). In this study, H was calculated using the least squares cross validation available in the Animal Movement Extension. This value was then tested on a number of data sets and modified slightly to reduce the extent to which the polygons overlapped the reserve boundary. While an H value of 1000 worked well with the very large data sets, it was too sensitive for the two monthly data sets. Consequently, H was set at 1400. No comparisons were made between areas calculated using different H values.

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). 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.

Social systems within the various predator species vary and therefore the social groups were analysed separately. The predators were divided into the following social groups for analysis: cheetah groups were: a coalition of three males (n=1), female cheetahs with cubs (n=7), single female cheetahs (n=4), female cheetahs with cubs in a den (n=6) and independent cheetah cubs (n=2). The lion social groups were: prides (n=3), adult males (n=2), sub-adult lions (n=2) and lionesses with cubs in a den (n=4). There was only one pack of African wild dogs and they were divided into the original pack (which consisted of an alpha pair and four adult females; n=1); the pack with pups in a den (n=1); the pack with mobile pups (n=1) and the alpha pair (n=1). The space use of the female cheetahs and the lionesses with cubs in a den was calculated over a two month period, i.e. from when the female gave birth until she moved her cubs out of the area. The space use of the African wild dogs with pups in a den was

calculated over a three month period, from when the alpha female gave birth until the pups started joining the pack and moved away from the den site.

Inter- and intra-specific overlap of space use

The overlap of home range and core areas of the different 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 groups of animals was calculated, using the Geoprocessing Tools in ArcView 3.2. In order to establish whether space use and overlap changed with the reproductive condition of female cheetahs, the data for female cheetahs were divided into two-monthly intervals dependent upon the various stages of reproduction (Table 4.1). To enable comparisons with the other large carnivores on the reserve all the data for the various study animals were similarly divided into two monthly intervals.

Table 4.1: Classification of the various reproductive stages of female cheetahs.

Stages of Reproduction	Description of Reproductive Stages
A	Pregnant (female on her own)
B	Cubs in den (0-2 months old)
C	Cubs 2-4 months old
D	Cubs 4-6 months old
E	Cubs 6-8 months old
F	Cubs 8-10 months old
G	Cubs 10-12 months old
H	Cubs 12-14 months old
I	Cubs 14-16 months old

Habitat use

The vegetation found on Kwandwe has been fully described in Chapter 2. However, for the purpose of the analysis in this chapter, vegetation types have been combined to form an open, savanna-like habitat and a grouping of denser, thicket vegetations (Figure 4.1). Habitat types with a visibility index (see Chapter 2) greater than 69 were combined to form the open habitat which comprised Karriod Shrubland, Bushclump Karriod Thicket, Bushclump Savanna and Old lands. This area covered 37% of the reserve. The denser, thicket habitat was consisted of Tall *Euphorbia* Thicket, Short *Euphorbia* Thicket, *Portulacaria/Euphorbia* Mosaic, *Portulacaria* Thicket, Dry Forest, Drainage line Thicket and Riverine Thicket. The thicket habitat covered 63% of the reserve.

The simplified vegetation map of Kwandwe was used to determine the proportion of open and thicket vegetation in the home ranges and core areas of the various social groups of predators using Geoprocessing Tools in ArcView 3.2.

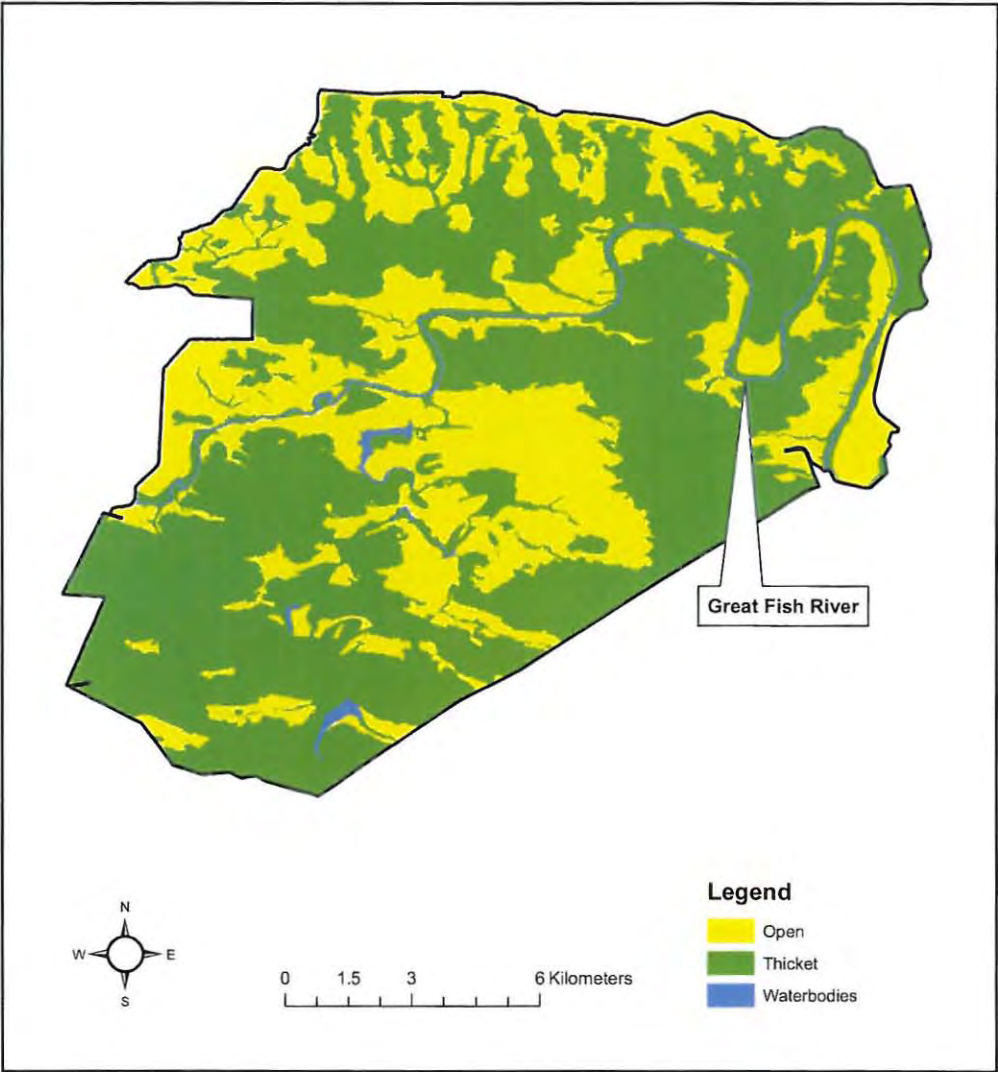


Figure 4.1: Map of Kwandwe Private Game Reserve depicting the open and thicket vegetation and their distribution on the reserve (ArcGIS 9; map units: decimal degrees; not projected).

Statistical analyses

The effects of various independent categorical variables on the size of the space used, area of overlap, and on the proportion of thicket and open vegetations in the core areas and home ranges were tested with two-way and three-way ANOVAs, followed by post-hoc tests, or the non-parametric equivalent. The categorical variables are described in the results and, in most cases, include space type (core area and home range). Core areas are almost always much smaller than home ranges and it is only biologically significant when this is not the case. Therefore, in the results, a significant effect of space type has not been reported but the lack of a significant difference has. Paired t-tests have been used to compare data from *ad hoc* and continuous observations. Percentages were transformed (Arcsine) prior to statistical analyses. All statistical analyses were done using Statistica (Statsoft, version 7.0) and SigmaStat (Jandel Scientific).

RESULTS

Comparison of ad hoc and continuous observations

Estimates of home range size had reached an asymptote for eight out of the 23 sets of continuous observations and there was no obvious relationship between the number of fixes and whether or not an asymptote was reached. The minimum sample size at which an asymptote was reached was 15 fixes and the maximum sample size at which an asymptote was not reached was 180 fixes. For the coalition, lions and African wild dogs there were sufficient data sets to allow a comparison of home ranges estimated from data sets that had reached an asymptote with those from data sets that had not reached an asymptote. There was no effect of whether or not an asymptote had been reached on size of home range or core area ($P > 0.05$ for both) and, in view of this result, all data sets have been used.

At both core area and home range levels, the continuous observations generally produced smaller areas than the *ad hoc* observations. The exception was the coalition for which the continuous observations generated larger areas (Table 4.2). At the core area level, the only significant difference between continuous and *ad hoc* observations was for the coalition (paired t-test; $t = 2.8$; $df = 5$; $P < 0.05$; Table 4.2).

At the home range level, continuous observations gave a significantly greater area than *ad hoc* observations for the coalition ($t = 2.9$; $df = 5$; $P < 0.05$) while for single female cheetahs and the Nomadic pride, the continuous observations gave a significantly smaller home range than the *ad hoc* observations (Table 4.2).

Table 4.2: Comparison of two methods of observation showing the mean ($\pm 1SD$; except where $n=1$) size of the home ranges and core areas for the various large carnivore social groups on Kwandwe. Results of statistical tests between the observations are also provided.

Social Group	Core Area (ha)			Home Range (ha)		
	Cont. Obs.	<i>Ad hoc</i> Obs	Statistics	Cont. Obs.	<i>Ad hoc</i> Obs	Statistics
Coalition	1335 \pm 332	966 \pm 66	$t=2.8$, $df=5$, $P<0.05$	7029 \pm 1752	5316 \pm 875	$t=2.9$, $df=5$, $P<0.05$
Female cheetahs with mobile cubs	1737 \pm 1047	2143 \pm 1422	$t=-0.9$; $df=3$; $P>0.05$	4760 \pm 2298	8245 \pm 3080	$t=-2.9$, $df=3$, $P>0.05$
Independent cheetah cubs	1579	1954		6857	10940	
Single female cheetahs	869 \pm 122	1600 \pm 1063	$t=-0.8$, $df=$, $P>0.05$	4238 \pm 753	8612 \pm 1115	$t=-17.1$, $df=1$, $P<0.05$
Southern pride	2058 \pm 381	2038 \pm 823	$t=0.06$, $df=2$, $P>0.05$	6300 \pm 315	6899 \pm 996	$t=-1.0$, $df=2$, $P>0.05$
Nomadic pride	2584 \pm 717	3423 \pm 3501	$t=-0.2$, $df=1$, $P>0.05$	8333 \pm 2168	12953 \pm 2167	$t=-4199$, $df=1$, $P<0.005$
Boschgift pride	3539	2023		10647	12728	
African wild dogs	1372 \pm 474	1713 \pm 1440	$t=-0.5$, $df=3$, $P>0.05$	8687 \pm 5589	8199 \pm 5085	$t=0.2$, $df=3$, $P>0.05$

Space use and habitat selection by large carnivores

General description of space use and habitat selection

This is based on pooled data for the period February 2003 to April 2007 and represents a general description of the amount of space used and the proportions of open and thicket habitats in the core areas and home ranges of the large carnivores. In each section results are firstly described and then compared statistically.

CHEETAHS

Size of Home Range and Core Area

Single female cheetahs, female cheetahs with cubs and independent cheetah cubs had similar sized 95%UDs with means ranging from 86.4km² for single females to 89.6km² for females with mobile cubs (Table 4.3). Female cheetahs with cubs in a den had the smallest 95%UD (mean = 13km²), followed by the coalition with a 95%UD (35.4km²; Table 4.3). Core areas were similarly small for all social groups (Table 4.3). A two-way ANOVA with social group and space type as categorical variables and area (km²) as the dependent variable, showed a significant effect of social group ($F = 7.2$; $df = 4$; $P < 0.001$) and space type ($F = 35.7$; $df = 1$; $P < 0.0001$), and a significant interaction between space type and social group ($F = 4.7$; $df = 4$; $P < 0.005$). Post-hoc tests showed that there was no significant difference between the size of the home range and core area of females at dens and the coalition ($P > 0.05$). There was no significant difference between the core areas of the different social groups ($P > 0.05$), and the home range of the females at dens was significantly smaller than home range of females with mobile cubs, single females and independent cubs ($P < 0.05$; Table 4.3; Figure 4.2).

Table 4.3: Home range and core area sizes of the various cheetah social groups on Kwandwe. Data are means \pm 1SD except where $n = 1$.

Social Group	Sample Size	Area (km ²)	
		50%	95%
Coalition of male cheetah	1253(n=1)	5.6	35.4
Female cheetahs with mobile cubs	1122(n=7)	14.6 \pm 11.7	86.4 \pm 30.6
Female cheetahs with cubs (den)	232(n=6)	3.9 \pm 0.2	13.0 \pm 2.7
Single female cheetahs	353(n=4)	11.0 \pm 4.1	89.6 \pm 29.0
Independent cheetah cubs	201(n=2)	6.6 \pm 4.5	88.8 \pm 77.1

Sample size is the total number GPS fixes; n = the number of replicates for that social group.

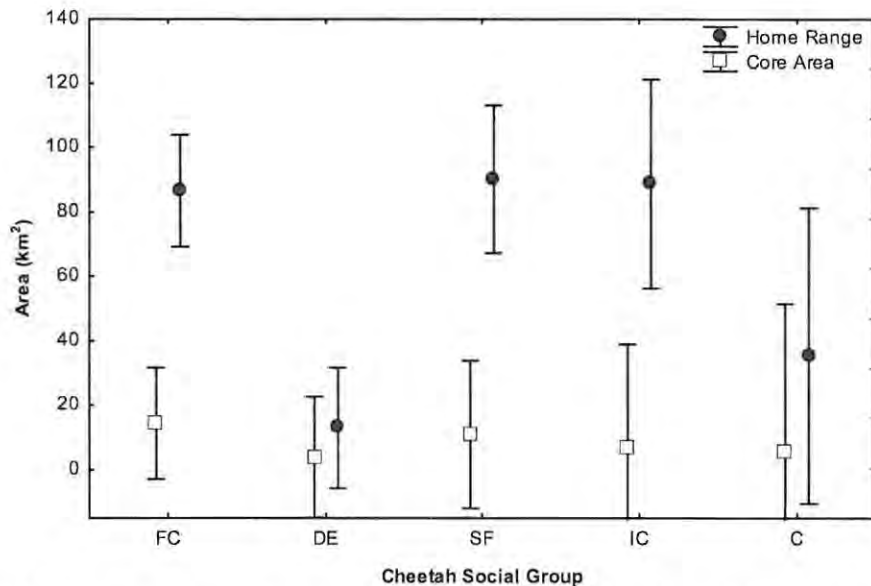


Figure 4.2: Home range and core areas for the various cheetah social groups. Data are means with error bars denoting 95% confidence intervals. (FC = female cheetahs with mobile cubs; DE = female cheetahs with cubs in a den; SF = single female cheetah; IC = independent cheetah cubs; C = coalition).

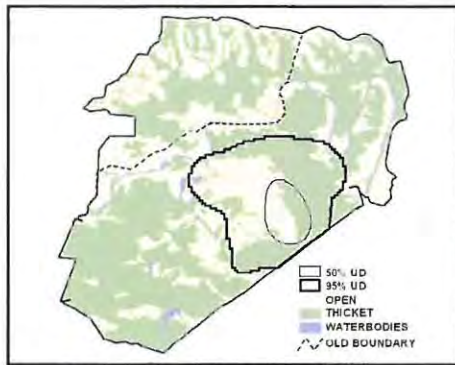
Description of home range and core area

Single female cheetahs and female cheetahs with cubs in a den had a much higher percentage of thicket vegetation in their home ranges and core areas compared to the other social groups (Table 4.4; Figures 4.4 & 4.5). The coalition had an almost equal amount of open and thicket vegetation in their home range and core area (Table 4.4; Figure 4.3), whereas female cheetahs with mobile cubs had 64% thicket vegetation within their home range and core area (Figure 4.6). The independent cheetah cubs had more thicket vegetation in their home range than in the core areas (Table 4.4; Figure 4.7). In a two-way ANOVA with social group and space type (home range and core area) as categorical variables and percentage thicket as the dependent variable, the only significant factor was social group ($F = 9.7$; $df = 3$; $P < 0.001$). The space used by females at dens had significantly more thicket than females with mobile cubs, independent cubs and the coalition ($P < 0.05$ for all), while the difference between single females and independent cubs was almost significant ($P = 0.07$).

Table 4.4: Percentages of open and thicket vegetation found within the home range and core area of each cheetah social group. Data are means \pm 1SD except where sample size = 1.

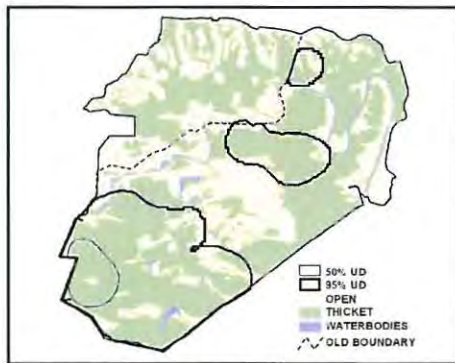
Social Group	Sample Size	50% UD		95% UD	
		Open (%)	Thicket (%)	Open (%)	Thicket (%)
Coalition	1	52.4	47.6	42.2	57.8
Females with mobile cubs	7	36.0 \pm 20.9	64 \pm 20.9	35.5 \pm 5.8	64.5 \pm 5.8
Females with cubs (den)	6	8.7 \pm 5.6	91.3 \pm 5.6	19.9 \pm 11.7	80.1 \pm 11.7
Single females	4	18.5 \pm 16.9	81.5 \pm 16.9	28.8 \pm 9.7	71.2 \pm 9.7
Independent cubs	2	53.4 \pm 3.6	46.6 \pm 3.6	36.3 \pm 2.8	63.7 \pm 2.8

Sample size is the number of replicates for that social group

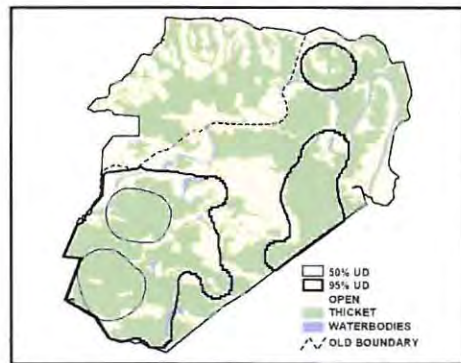


Area: 50%: 5.6km², 95%: 35.4km²
Time Period: 1/2/03-31/12/06

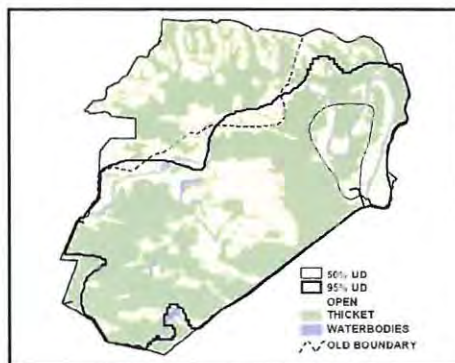
Figure 4.3: Home range and core areas for the coalition.



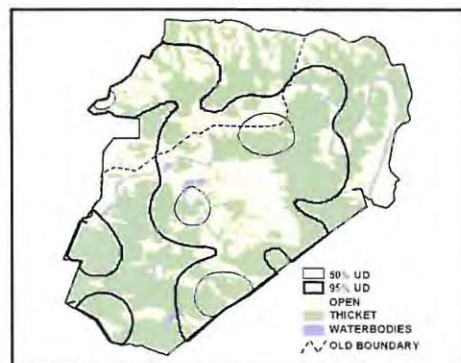
(a) Area: 50%: 6.2km², 95%: 61.5km²
Time Period: 19/1/04-24/4/04



(b) Area: 50%: 15.9km², 95%: 69.9km²
Time Period: 19/1/04-21/4/04

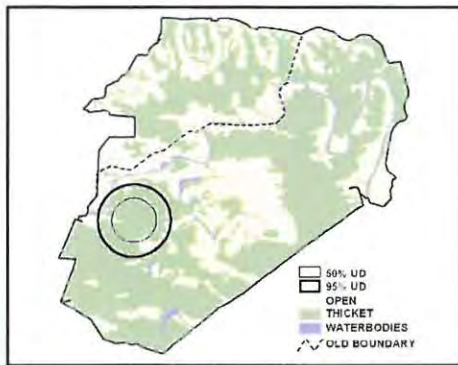


(c) Area: 50%: 9.8km², 95%: 125.9km²
Time Period: 25/7/03-12/1/04

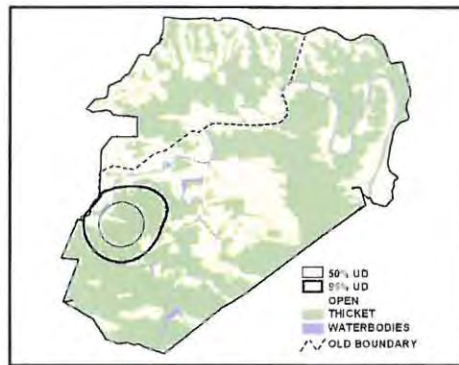


(d) Area: 50%: 12km², 95%: 103.6km²
Time Period: 2/2/06-11/8/06

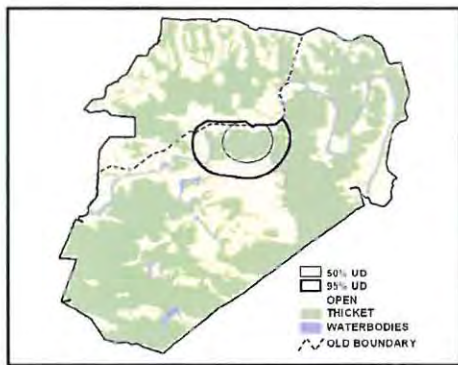
Figure 4.4: Home range and core areas for single female cheetahs. (a = CF11; b = CF10; c = CF6; d = CF23).



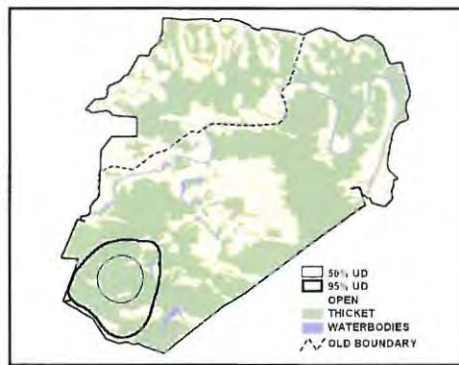
(a) Area: 50%: 3.7km², 95%: 10km²
Time Period: 25/4/04-30/6/04



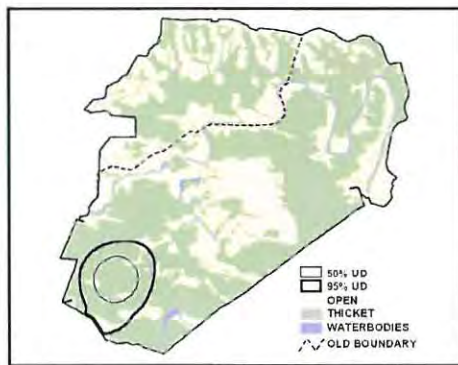
(b) Area: 50%: 3.8km², 95%: 11.7km²
Time Period: 22/4/04-3/7/04



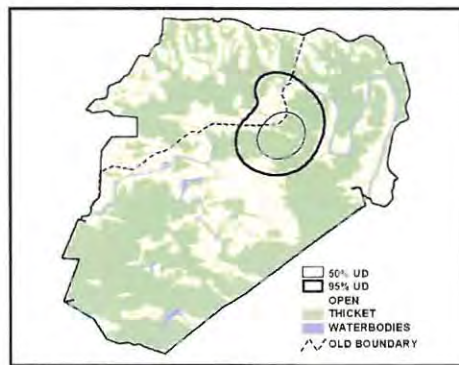
(c) Area: 50%: 3.9km², 95%: 11.2 km²
Time Period: 13/1/04-9/1/04



(d) Area: 50%: 4.1km², 95%: 16.6km²
Time Period: 2/7/05-18/8/05

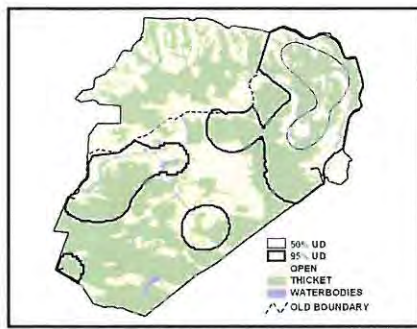


(e) Area: 50%: 3.9km², 95%: 12.5km²
Time Period: 6/3/07-23/4/07

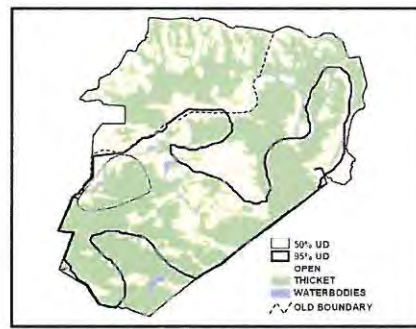


(f) Area: 50%: 4.1km², 95%: 16.2km²
Time Period: 14/8/06-7/10/06

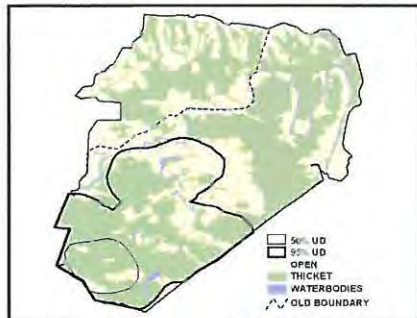
Figure 4.5: Home range and core areas for female cheetahs with cubs in a den. (a = CF11+2; b = CF10+4; c = CF6+4; d = CF6+5 in 2005; e = CF6+5 in 2007; f = CF23+2).



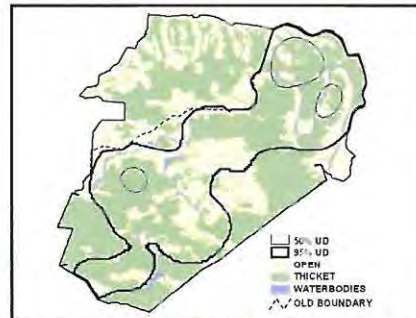
(a) Area: 50%: 11.8km², 95%: 66.6km²
Time Period: 6/2/03-1/5/03



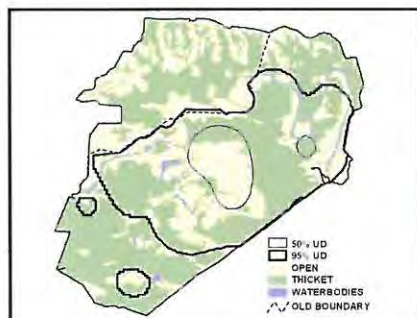
(b) Area: 50%: 8km², 95%: 85.1km²
Time Period: 3/2/03-24/7/03



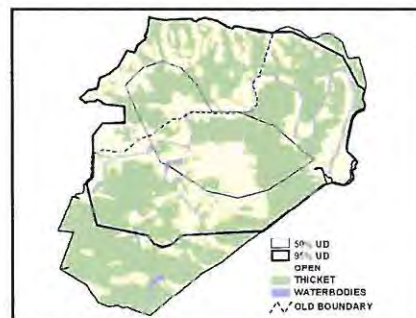
(c) Area: 50%: 9.4km², 95%: 63.3km²
Time Period: 1/7/04-29/12/04



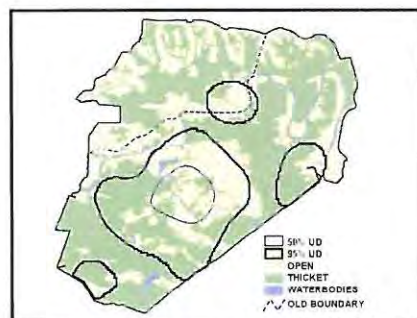
(d) Area: 50%: 9.8km², 95%: 92.3km²
Time Period: 4/7/04-8/4/05



(e) Area: 50%: 12.8km², 95%: 90.3km²
Time Period: 11/3/04-15/5/05



(f) Area: 50%: 40.7km², 95%: 148.6km²
Time Period: 18/8/05-7/1/07



(g) Area: 50%: 8.3km², 95%: 59.8km²
Time Period: 13/10/06-30/4/07

Figure 4.6: Home range and core areas for female cheetahs with mobile cubs. (a = CF5+3; b = CF6+2; c = CF11+2; d = CF10+4; e = CF6+4; f = CF6+5; g = CF23+2).

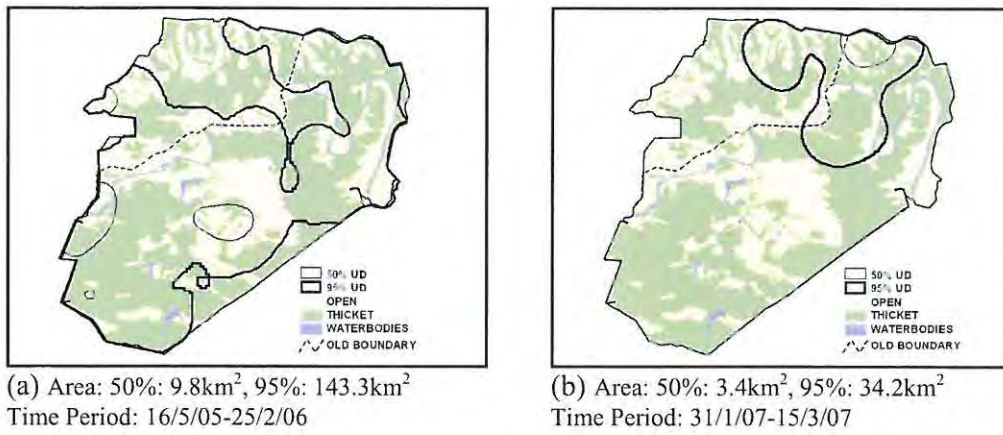


Figure 4.7: Home range and core areas for independent cheetah cubs. (a = CM20, 21; CF22, 23; b = CF34; CM35).

*LIONS**Size of Home Range and Core Area*

The lion prides had the largest 95%UD (120.5km²; Table 4.5), while lionesses with cubs in a den had the smallest 95%UD (14.2km²). The adult male lions had the smallest 95%UD (89.8km²) except for the lionesses with cubs in a den, where the small areas were due to the adult females rarely moving far from the den. There was a significant effect of social group on the size of the space used ($F = 3.5$; $df = 3$; $P < 0.0001$) and a significant interaction between social group and space type ($F = 20.8$; $df = 3$; $P < 0.0001$). There was no significant difference between core area size and size of the home range of females at dens ($P > 0.05$), and the home ranges of adult males, sub-adult lions and the prides were similar and significantly larger than the home range of females at dens ($P < 0.05$ for all).

Table 4.5: Home range and core area sizes of various lion social groups on Kwandwe as calculated by the fixed kernel method. Data are means \pm 1SD.

Social Group	Sample Size	Area (km ²)	
		50%	95%
Females with cubs (den)	98(n=4)	3.9 \pm 0.2	13.6 \pm 1.3
Sub-adult lions	271(n=2)	24.4 \pm 16.6	113.7 \pm 16.4
Adult male lions	810(n=2)	10.4 \pm 2.5	89.8 \pm 20.4
Prides	1403(n=3)	15.4 \pm 6.4	120.5 \pm 22.7

Sample size is the total number GPS fixes; n = the number of replicates for that social group.

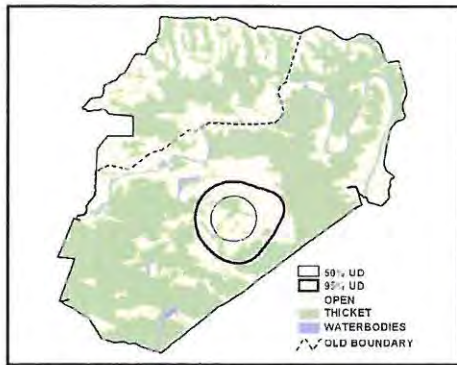
Description of home range and core area

Lionesses with cubs in a den selected areas with slightly more open than thicket vegetation in both home range and core area (Table 4.6; Figure 4.8), whereas sub-adult lions selected areas with more thicket vegetation in their home range and core area (Table 4.6; Figure 4.11). The lion prides selected areas with more thicket vegetation in their home range and core area (Table 4.6; Figure 4.9) whereas the adult male lions selected areas with more thicket in their home range but had similar percentages of open and thicket vegetation in their core area (Table 4.6; Figure 4.10). The proportion of thicket vegetation in core areas and home ranges of the different social groups of lions did not vary significantly ($P > 0.05$ for both factors and the interaction).

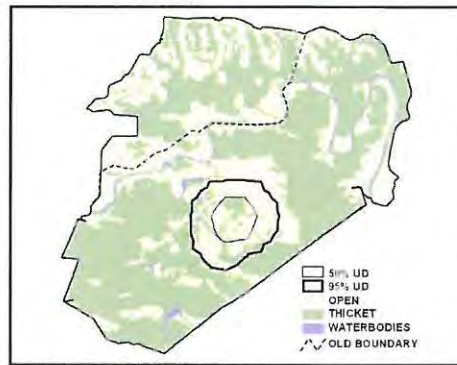
Table 4.6: Percentages of open and thicket vegetation found within the home range and core area of each lion social group. Data are means \pm 1SD.

Social Group	Sample Size	50% UD		95% UD	
		Open (%)	Thicket (%)	Open (%)	Thicket (%)
Females with cubs (den)	4	54.5 \pm 23.0	45.5 \pm 23.0	58.2 \pm 21.9	41.8 \pm 21.9
Sub-adult lions	2	29.6 \pm 0.9	70.4 \pm 0.9	36.1 \pm 6.0	63.9 \pm 6.0
Adult male lions	2	52.9 \pm 48.7	47.1 \pm 48.7	28.4 \pm 6.0	71.5 \pm 6.0
Prides	3	33.7 \pm 16.0	66.3 \pm 16.0	35.7 \pm 3.2	64.3 \pm 3.2

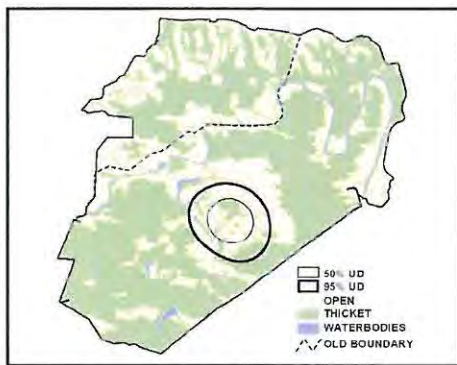
Sample size is the number of replicates for that social group



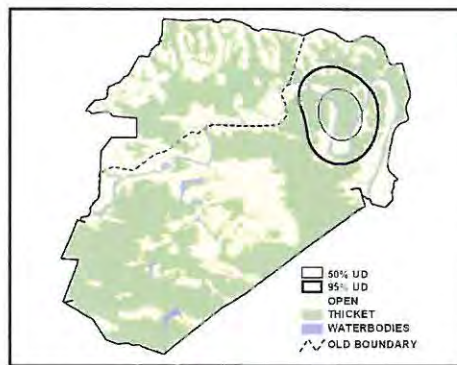
(a) Area: 50%: 3.9km², 95%: 13.1km²
Time Period: 11/10/03-30/11/03



(b) Area: 50%: 3.7km², 95%: 14.7km²
Time Period: 27/6/04-30/7/04

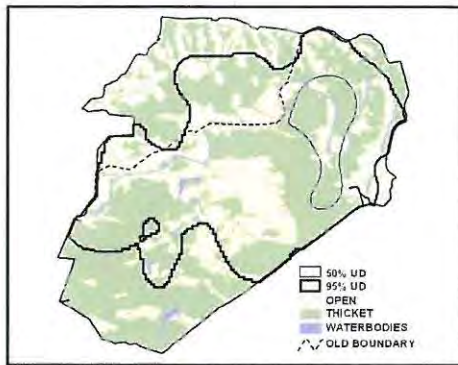


(c) Area: 50%: 3.8km², 95%: 11.9km²
Time Period: 7/1/04-19/2/04

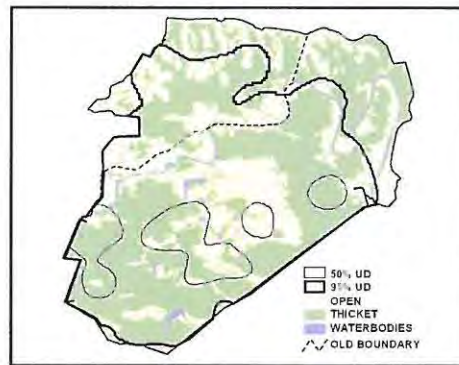


(d) Area: 50%: 4.2km², 95%: 14.6km²
Time Period: 29/3/05-7/6/05

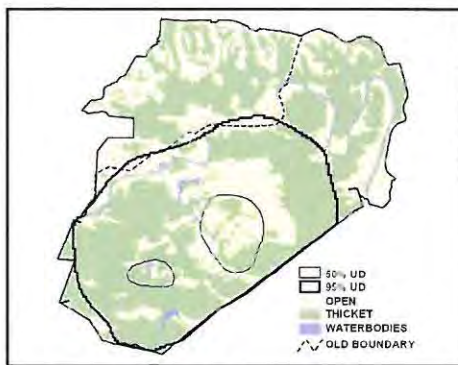
Figure 4.8: Home range and core areas for lionesses with cubs in a den. (a = LF7 in 2003; b = LF7 in 2004; c = LF8; d = LF9).



(a) Area: 50%: 12.1km², 95%: 120.2km²
Time Period: 20/5/04-31/1/07

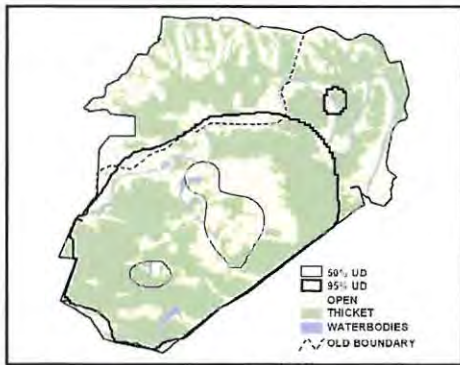


(b) Area: 50%: 22.8km², 95%: 143.3km²
Time Period: 18/8/05 – 31/1/07

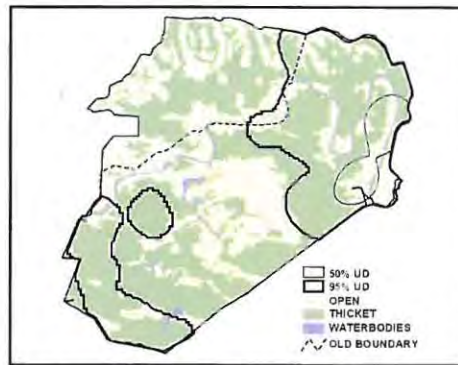


(c) Area: 50%: 11.4km², 95%: 98km²
Time Period: 5/1/03-31/1/07

Figure 4.9: Home range and core areas for the lion prides. (a = Boschgift Pride; b = Nomadic Pride; c = Southern Pride).

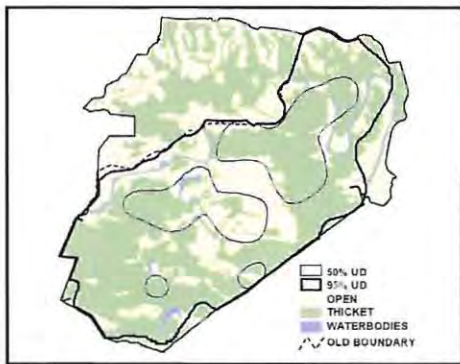


(a) Area: 50%: 12.2km², 95%: 104.3km²
Time Period: 5/1/03-30/12/06

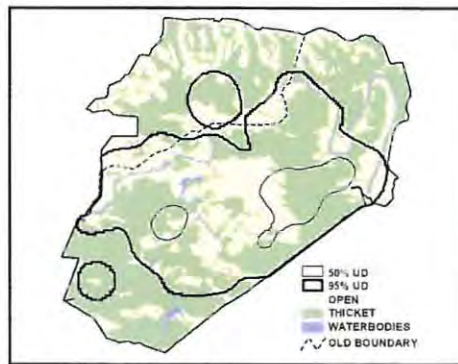


(b) Area: 50%: 8.6km², 95%: 75.4km²
Time Period: 5/1/03-30/12/06

Figure 4.10: Home range and core areas for the adult male lions. (a = Pride Male; b = Nomadic Male).



(a) Area: 50%: 36.1km², 95%: 125.3km²
Time Period: 1/8/03-19/5/04



(b) Area: 50%: 12.6km², 95%: 102.1km²
Time Period: 18/7/06-13/4/07

Figure 4.11: Home range and core areas for the sub-adult lions. (a = Sub-adult lions in 2004; b = Sub-adult lions in 2006).

*AFRICAN WILD DOGS**Size of Home Range and Core Area*

The pack of African wild dogs with mobile pups had a much larger home range compared to the other social groups and the home range of the pack with pups in a den was very small (Table 4.7). The core areas of the different social groups were relatively small with the alpha pair having the smallest core area (Table 4.7). These data have not been analysed statistically because of the sample size of one.

Table 4.7: Home range and core area sizes for the various African wild dog social groups on Kwandwe, as calculated by the fixed kernel method. No SD as $n = 1$.

Social Group	Sample Size	Area (km²)	
		50%	95%
African wild dogs (adults)	257(n=1)	6.1	97.1
African wild dogs with pups (den)	109(n=1)	3.1	9.7
African wild dogs with mobile pups	217(n=1)	5.5	158.3
African wild dogs (alpha pair)	35(n=1)	0.7	70.8

Sample size is the total number GPS fixes; n = the number of replicates for that social group.

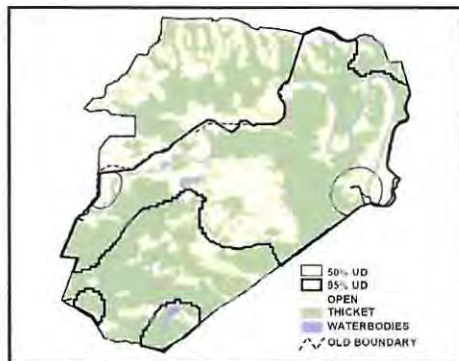
Description of home range and core area

The percentage of open and thicket vegetation in the home ranges was similar for the various social groups, with a greater percentage of thicket vegetation compared to open vegetation (Table 4.8; Figures 4.12 – 4.15). There was an equal amount of open and thicket vegetation in the core areas of all the social groups except for the alpha pair which had a much greater percentage of open vegetation compared to thicket vegetation (Table 4.8; Figures 4.12 – 4.15).

Table 4.8: Percentages of open and thicket vegetation found within the home range and core area of each African wild dog social group. No SD as $n = 1$.

African Wild Dog Pack	Sample Size	50% UD		95% UD	
		Open (%)	Thicket (%)	Open (%)	Thicket (%)
African wild dogs (adults)	1	55.2	44.8	37.9	62.1
African wild dogs with pups (den)	1	54.7	45.3	38.0	62.0
African wild dogs with mobile pups	1	55.2	44.7	37.8	62.2
African wild dogs (alpha pair)	1	80.2	19.8	39.5	60.5

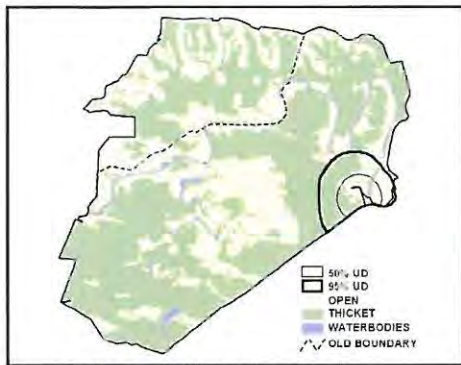
Sample size is the number of replicates for that social group



Area: 50%: 6.1km², 95%: 97.1km²

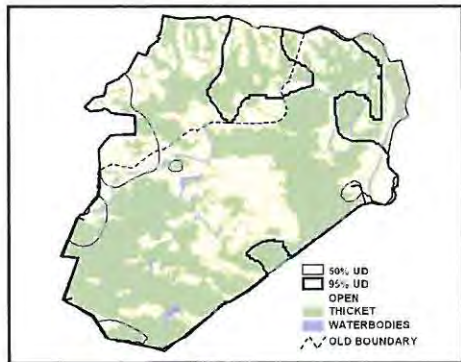
Time Period: 22/06/04–28/5/05

Figure 4.12: Home range and core area for the original pack of African wild dogs comprising only adult animals.



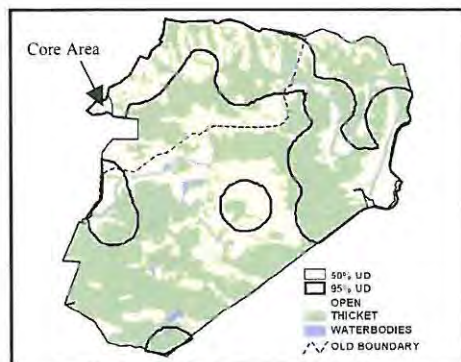
Area: 50%: 3.1km², 95%: 9.7km²
Time Period: 29/5/05-8/9/05

Figure 4.13: Home range and core area for the pack of African wild dogs with pups in a den.



Area: 50%: 5.5km², 95%: 158.3km²
Time Period: 09/09/05-21/07/06

Figure 4.14: Home range and core area for the pack of African wild dogs with mobile pups.



Area: 50%: 0.7km², 95%: 70.8km²
Time Period: 22/07/06-30/10/06

Figure 4.15: Home range and core area of the alpha pair of African wild dogs.

The effect of increasing pride numbers on space use by lions on Kwandwe

Over the duration of the study the number of lion prides increased. The Southern pride was the only pride on Kwandwe for two years (2003-2004), it shared the reserve with the Boschgift pride for one year (2005) and with the Boschgift and Nomadic prides for one year (2006). The increase in pride number has created the opportunity to examine the effect of increasing pride number on space use and overlap of space used by lions.

No significant effect was found of pride number on the space used at either home range or core area level of either the Southern pride ($F = 0.04$; $df = 2$; $P > 0.05$; Figure 4.16) or the Boschgift pride ($F = 0.80$; $df = 1$; $P > 0.05$; Figure 4.17).

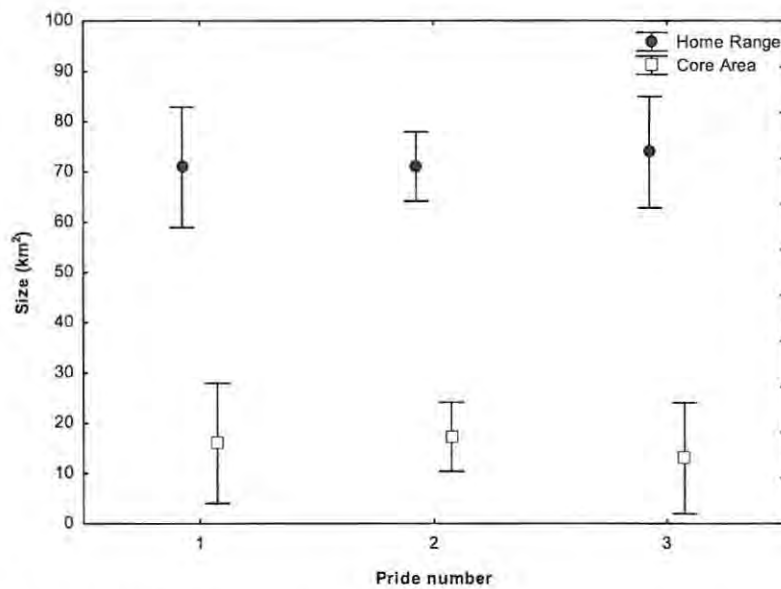


Figure 4.16: Relationship between the size of the home range and core areas of the Southern pride with increase in pride number on Kwandwe over a four year period. Data are means with error bars denoting 95% confidence intervals.

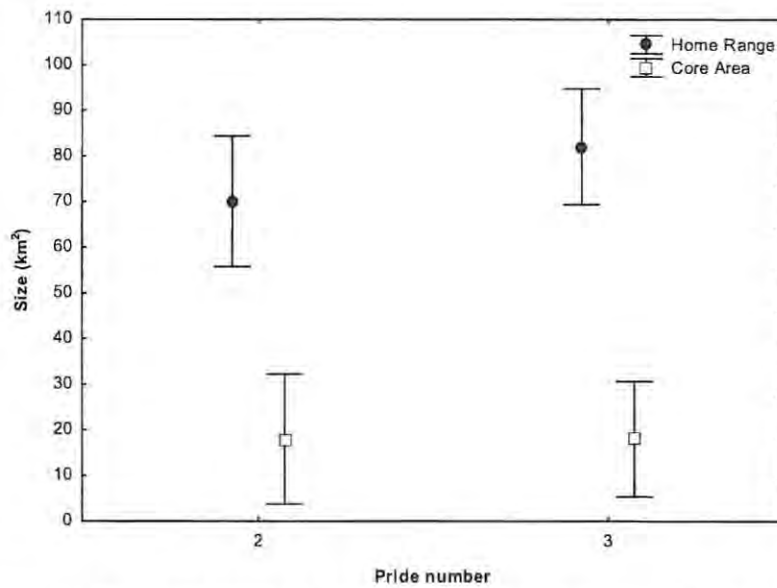


Figure 4.17: Relationship between the size of the home range and core areas of the Boschgift pride with increase in pride number on Kwandwe over a four year period. Data are means with error bars denoting 95% confidence intervals.

A three-way ANOVA with pride (Southern or Boschgift), pride number (two or three) and space type as categorical variables and area of overlap as the dependent variable showed a significant effect of pride number ($F = 14.7$; $df = 1$; $P < 0.001$; Figure 4.18) and a significant interaction between space type and pride number ($F = 11.5$; $df = 1$; $P < 0.001$; Figure 4.18), but no effect of pride. Post-hoc tests revealed that for the Southern pride, there was a significant increase in the extent to which the home range overlapped with that of other lion prides with increase in pride number ($P < 0.05$), but no effect at the core area level. For the Boschgift pride, overlap increased with increase in pride number but the difference was just not significant ($P = 0.05$).

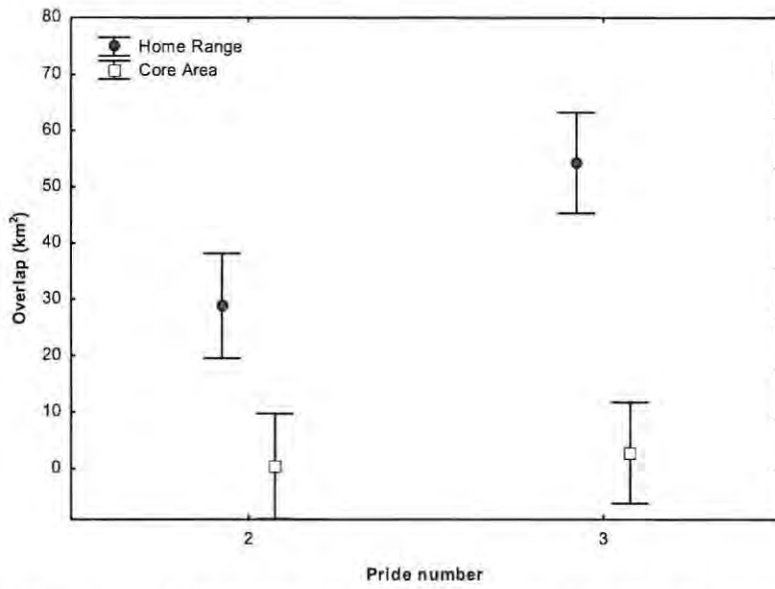


Figure 4.18: The effect of increasing pride number on the overlap of home ranges and core area of lions on Kwandwe. Data are means with error bars denoting 95% confidence intervals.

The effect of increasing pride number on space used by cheetahs and African wild dogs

The effect of increasing pride number on the space use of the coalition.

There was no effect of pride number on the size of the home range or core area of the coalition ($F = 0.46$; $df = 2$; $P > 0.05$). Overlap of the home ranges of the coalition with that of the lions increased with an increase in pride number and there was a significant effect of pride number on overlap ($F = 3.3$; $df = 2$; $P < 0.05$; Figure 4.19). Overlap increased significantly with the increase from 2 to 3 prides ($P < 0.05$). However, there was almost no overlap of the core areas and no significant effect of number of prides ($P > 0.05$).

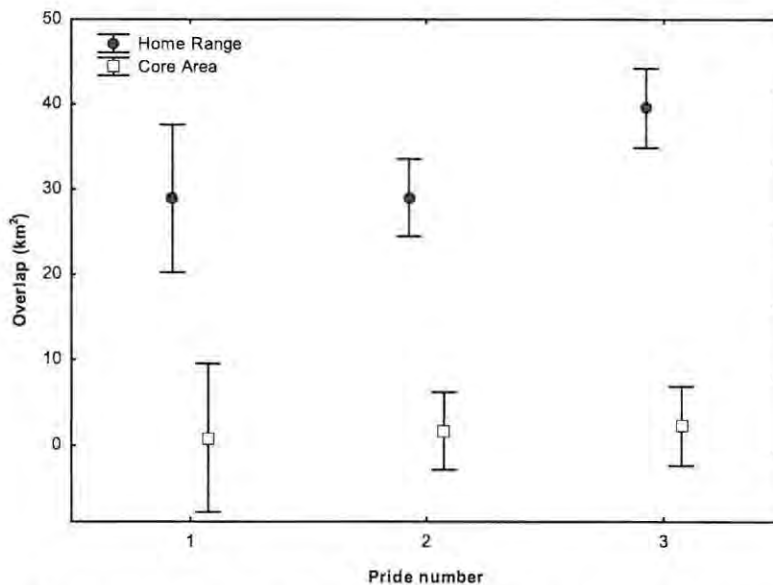


Figure 4.19: Overlap of space used by the coalition with lions with increase in pride number. Data are means with error bars denoting 95% confidence intervals.

The effect of increasing pride number on proportion of thicket vegetation in the home range and core area of the coalition.

A three-way ANOVA (with pride number, vegetation type and space type as categorical variables and proportion of vegetation type as the dependent variable) showed a significant effect of vegetation type ($F = 255.9$; $df = 1$; $P < 0.001$), with significantly more thicket than open vegetation (Figure 4.20). There was a significant interaction between the number of prides and the proportion of thicket vegetation in the space used by the coalition ($F = 12.5$; $df = 2$; $P < 0.001$) and with increasing pride number, the proportion of thicket decreased (Figure 4.20).

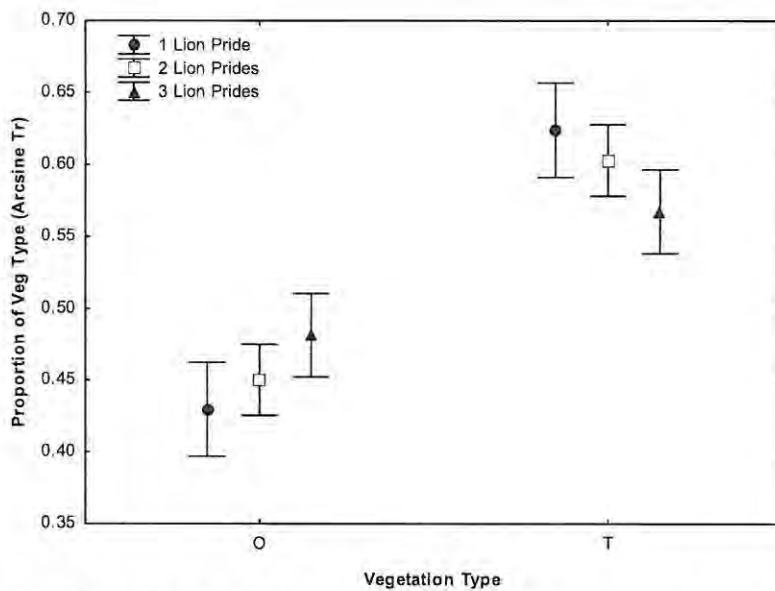


Figure 4.20: The effect of pride number on the proportion of open and thicket vegetation in the space used by the coalition (O = open vegetation; T = thicket vegetation). Data are means with error bars denoting 95% confidence intervals.

Overlap in space use by female cheetahs with cubs, with space used by the coalition, lions and the African wild dogs.

There was a significant difference in the extent to which the space used by female cheetahs overlapped with that of the coalition, lions and African wild dogs ($F = 4.1$; $df = 2$; $P < 0.05$; Figure 4.21). Overlap of female home ranges was significantly greater with lions and African wild dogs than the coalition of cheetah ($P < 0.05$ for both). There was no significant difference in overlap at a core area level where there was almost zero overlap with the other carnivores ($P > 0.05$; Figure 4.21). This suggests that female cheetah select core areas that do not overlap with other species and home ranges that tend to avoid the coalition more than the lions and African wild dogs.

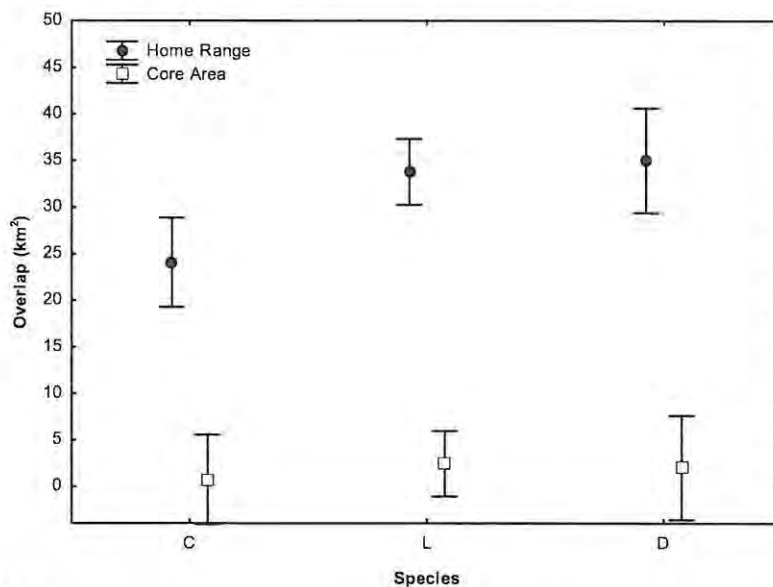


Figure 4.21: Home range and core area overlap of female cheetahs with cubs with lions, African wild dogs and the cheetah coalition (C = coalition; L = lions; D = African wild dogs). Data are means with error bars denoting 95% confidence intervals.

The effect of stage of reproduction in female cheetahs on space use and on intra and inter-species overlap.

The size of the female cheetahs' home range and core area changed with the stage of reproduction ($F = 22.8$; $df = 8$; $P < 0.0001$). At a home range level the space used by female cheetahs was significantly smaller when they were denning than during any other stage of the reproductive cycle ($P < 0.05$; Figure 4.22). The size of the home range was significantly greater when the cubs were between 12-16 months compared to when they were between six to eight months ($P < 0.0001$; Figure 4.22). There was no significant effect of the stage of reproduction on the size of the core area ($P > 0.05$).

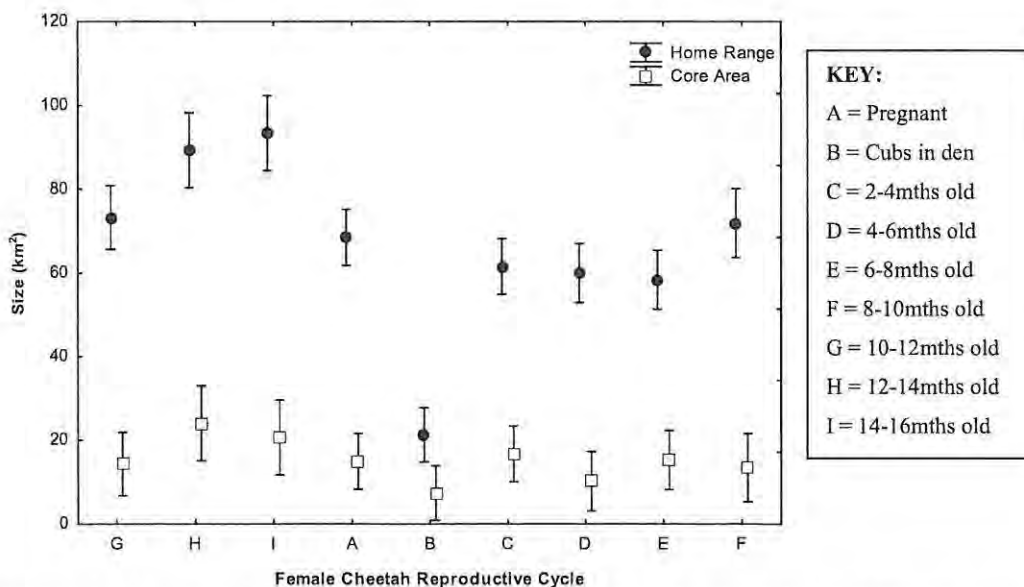


Figure 4.22: Size of home range and core area of female cheetahs at different stages of their reproductive cycle. Data are means with error bars denoting 95% confidence intervals.

A two-way ANOVA was conducted to investigate the effect of other large carnivores (the coalition; lions and African wild dogs) and the stage of the female cheetahs' reproductive cycle on overlap of home ranges. This analysis has been done at a home range level only because the previous analyses had shown that it was more sensitive to the presence of other large carnivores than core areas. There was significantly less overlap with the coalition than lions or African wild dogs ($F = 4.2$; $df = 2$; $P < 0.05$; Figure 4.23) and significantly less overlap when female cheetahs were pregnant or had cubs in a den ($F = 6.5$; $df = 8$; $P < 0.001$; Figure 4.23).

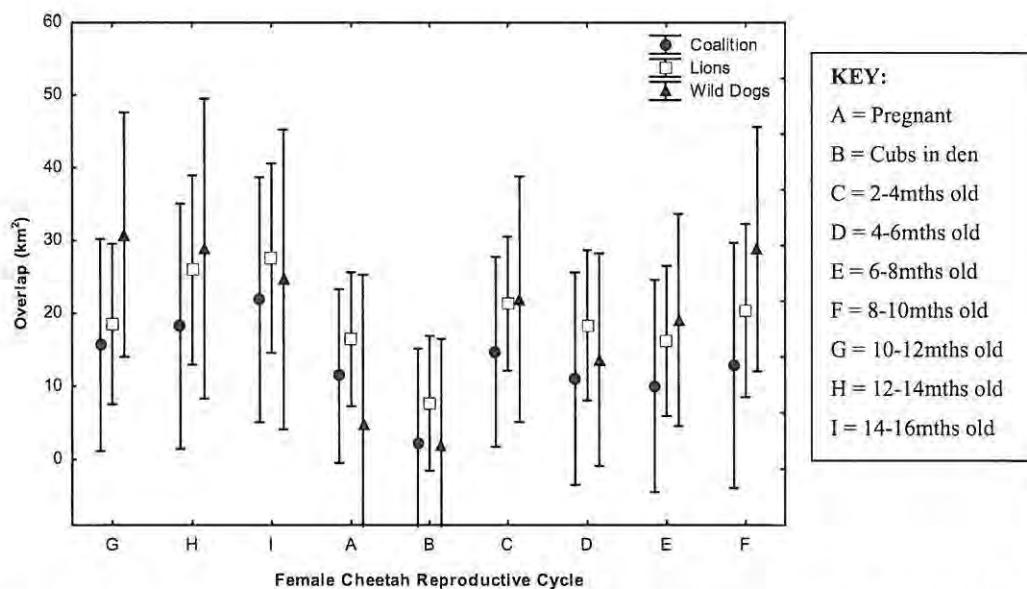


Figure 4.23: Overlap of space use (home range) of female cheetahs, through their reproductive cycle with the coalition, lions and African wild dogs. Data are means with error bars denoting 95% confidence intervals.

In summary at a home range level there was a strongly significant effect of stage of reproduction on the size of the home range and the overlap of the home range with home ranges of the coalition; lions and African wild dogs. The home range size and the overlap were significantly smaller when female cheetahs had cubs in a den. The size of the female cheetahs' home range and percentage of overlap with other predators increased with an increase in the age of the cubs. There was significantly less overlap of female cheetah with the coalition at a home range level compared to overlap with lions and African wild dogs (Figure 4.23).

The effect of increasing prides of lions on the percentage thicket in the home range and core areas of female cheetahs.

To examine the effect of increasing pride number on habitat selection it was necessary to combine reproductive stages to balance the ANOVA. Pregnant female cheetahs and females with cubs in a den (A & B) were combined as were the other stages of reproduction (C-I = females with mobile cubs) to produce two categories which were then used in a three-way ANOVA with pride number and vegetation type. There was a significant effect of the stage of reproduction ($F = 9.2$; $df = 1$; $P < 0.001$) and number of prides ($F = 7.1$; $df = 2$; $P < 0.001$). Female cheetahs with mobile cubs had less thicket vegetation in their home range and core areas than pregnant female cheetahs and females with cubs in a den. There was a significant decrease in thicket vegetation with an increase from two to three prides (Figure 4.24).

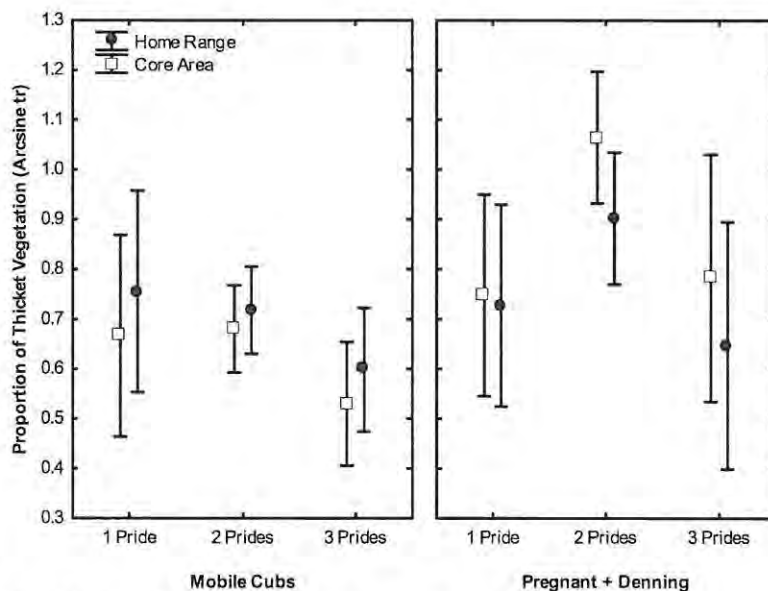


Figure 4.24: Effect of pride number on the proportion of thicket vegetation in the home range and core area of female cheetah with mobile cubs and pregnant female and female with cubs in a den. Data are means with error bars denoting 95% confidence intervals.

DISCUSSION

Comparison of methods

There has been considerable debate in the recent literature about how home ranges should be measured. Much of this debate has centred around whether or not it is necessary to avoid autocorrelation of data points and it is now widely accepted that this is not necessary (Cushman *et al.* 2005). Börger *et al.* (2006) used real data sets to compare the performance of several methods of estimating space use. They concluded that the MCP method is the least efficient; that kernel density estimation methods are the most efficient; that 10 fixes per month (for their data sets) are sufficient to generate a reliable estimate of space use; and that a standardised sampling regime is crucial if comparisons are to be made between space use estimates. In the present study, the sampling regime was standardised, although the original reason for this was to avoid autocorrelation of data, and thus satisfies the requirement of Börger *et al.* (2006). It was assumed that data sets that had reached an asymptote would give a different estimate of space use size to those data sets that had not reached an asymptote but this was not the case. A possible reason for this is that in all cases, the data sets had more than 10 GPS fixes (the minimum suggested by Börger *et al.* (2006) and most were greater than 25 GPS fixes). Most recently, Nilsen *et al.* (2007) have confirmed that kernel density estimators are the preferred method when studying similar species, or making comparisons of space use at an intra-species level.

The two-week continuous observations of the carnivores were done primarily to collect data on diet. However, since GPS fixes were taken every time an animal moved the continuous observations also generated data that could be used in analyses of space use. At a home range level, the only significant difference was for the coalition where the continuous observations yielded a greater area than the *ad hoc*

observations. The coalition were the most territorial of all the large carnivores on Kwandwe and their home range changed little in size or position through the study. Consequently, the *ad hoc* observations continually recorded the coalition in the same location while it seems that the continuous observations detected rare movements away from the favoured area and thus generated greater estimates of space use. At a core area level, a similar trend is apparent. Continuous observations generated a significantly greater estimate for the coalition only and significantly smaller estimates for single female cheetahs and the Nomadic pride. Single female cheetahs and the Nomadic pride used most of the reserve and it is likely that the full extent of the space used was only detected by the longer two months of *ad hoc* observations. It appears therefore that two-week long continuous observations may be valuable for a species or sex that is territorial and maintains a small space but may not be the best method for establishing space use of a non-territorial animal.

General space use and habitat selection

Previous studies of space use by cheetahs have shown that size of the home range varies enormously from 29km² in Matusadona National Park (Purchase & du Toit 2000) to 320km² in Kalahari Gemsbok Park (Mills 1998) and from 800km² in the Serengeti (Caro 1994) to 1500km² in Namibia (Marker *et al.* 2003). This variation in home range size is probably a result of differences in habitat structure and prey availability across different landscapes or vegetation types (Caro 1994; Purchase & du Toit 2000; Broomhall *et al.* 2003) but may also include sex differences in home range size. In the Serengeti, the large home ranges of female cheetahs (averaging 833km²) are attributed to the patchiness and migration of their main prey (Thomson's gazelle) and not directly to prey density. Movements of female cheetahs and non-territorial

male cheetahs in the Serengeti mirror the migration patterns of Thomson's gazelles and thus they have very large home ranges (Schaller 1972; Caro & Collins 1986; Durant *et al.* 1988; Caro 1994; Sunquist & Sunquist 2002). By contrast, the male cheetahs that establish territories do so in areas in which there is a year round high concentration of gazelles and sufficient cover, and have much smaller home ranges (37.4km^2) (Caro & Collins 1986; 1987; Durant *et al.* 1988; Caro 1994). In Namibia the lack of suitable hunting habitat and low prey availability (13.5 kudu per km^2) has led to male and female cheetahs having large home ranges (McVittie 1979; Marker *et al.* 2003). Similarly, in the Kalahari Gemsbok National Park, the nomadic nature of the springbok (2-17 springbok per km^2 , with the higher densities occurring along the drainage lines) is partly responsible for the large home ranges of female cheetahs while the male cheetahs have a smaller territory size (Mills 1984; 1998). The relatively small home range sizes of male (126km^2 – 95% MCP) and female (135km^2) cheetahs in Kruger (Broomhall *et al.* 2003) are possibly a consequence of the nature of the environment where thickets on one side and hills on the other flank a region of open savanna. Whereas the high density of prey (200-300 impala per km^2) and easily accessible cover provided by adjacent woodland in Matusadona National Park result in cheetahs having small home ranges (Purchase & du Toit 2000).

Other factors such as the distribution of suitable habitat for hunting and restrictive boundaries of small reserves may affect cheetahs' home range size (Hunter 1998; Broomhall *et al.* 2003). The relatively small home ranges of the female cheetahs on Kwandwe is attributed to a combination of relatively high prey density (8 kudu per km^2 and 20 prey animals per km^2), the sedentary nature of the prey, restrictive boundaries of the reserve and availability of suitable habitat, and possibly avoidance of dominant predators. The sizes of the home range and core area of the coalition

were smaller than those of the females, which is unusual in felids (Ewer 1973; Sandell 1986; Mizutani & Jewell 1998) but may be typical for cheetahs. In the Serengeti and to a lesser extent in Kruger female cheetahs have large home ranges which overlap the much smaller home ranges of the males presumably to increase mating opportunities (Sandell 1986; Caro 1994; Broomhall *et al.* 2003). In the present study the home range of the coalition overlapped the home ranges of the female groups to some extent, except for females with cubs in a den. However, there was rarely overlap between the core areas of the female cheetahs and the coalition. Thus, while there was extensive overlap in space use at the home range level, the cheetahs avoided each other by maintaining exclusive core areas, which is more typical of asocial felids (Sandell 1986; Caro 1994; Broomhall *et al.* 2003). As reported by Caro (1994) and in the present study, much of the apparent overlap in home ranges is likely to represent sequential and not simultaneous residence. Differences in the range size of male and female cheetahs is not surprising in view of the differences in adult body size, group size and prey (see Chapter 3) and the different requirements of the two sexes (particular denning in females).

The results from Kwandwe are strikingly similar to those from Kruger where female cheetahs use denser woodland habitat while male cheetahs utilise the more open savannas (Broomhall *et al.* 2003). Female cheetahs on Kwandwe selected denser vegetation types found on steeper slopes and at higher elevation while the coalition selected the most open vegetation types on flat ground with adjacent cover. In the Serengeti, vegetation cover plays an important role in home range selection of both sexes (Caro 1994). Resident male cheetahs' territories are located in areas with consistent environmental features and most of the resident male territories are situated

on the plains-woodland border and territories that are not located on this border contained drainage lines and extensive kopje systems (Caro & Collins 1987; Caro 1994). Although female cheetahs' movements mirror the migration of their main prey (Thomson's gazelle), vegetation cover plays an important role especially for females with cubs, and a greater proportion of females' diet comprised gazelles in areas with high vegetation cover (Caro 1994).

Sunquist & Sunquist (2002) suggested that spacing patterns of male felids are shaped by female distribution however results from the present study suggest that this may not be the case for cheetahs at least on Kwandwe. The space used by the coalition on Kwandwe did not vary during the study and was similar to that used by male cheetahs in other studies. The number of females increased during the study and the space they used varied depending on their reproductive condition, and it appears that the location and size of the home ranges of females was determined at least in part by the location of the home range of the coalition.

As with cheetahs, it is likely that multiple factors interact to fix the ranging patterns of lions. Home ranges of lion prides on Kwandwe were smaller than lion pride home ranges in larger open systems with migratory prey, for example: Etosha (2075km², Stander 1991), Chobe (217km², Viljoen 1993) Serengeti (200km², Hanby *et al.* 1995) and Waza National Park (630km², Bauer & de Iongh 2005), but similar in size to home ranges in Kruger (100-150km², Whyte 1985) and Associated Private Game Reserves (84-172km², Turner 2005). However, reintroduced lions in Phinda (53km², Hunter 1998) had much smaller home ranges which were similar in size to home ranges in the Selous Game Reserve (52km², Spong 2002). The range size of lions across various habitats is inversely correlated with lean season prey availability (van Orsdol *et al.* 1985). This is illustrated by the effect of prey abundance in the Savuti

region in Chobe (Viljoen 1993) where lion home range size increases from 136km² in the wet season to 217km² in the dry season coinciding with a decrease in herbivore biomass in the dry season and lions foraging more widely. It is likely that the smaller home range sizes on Kwandwe can be attributed to a combination of small pride sizes, high prey densities, sedentary nature of prey and the restrictive boundaries of the reserve.

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). Lions on Kwandwe utilised areas with more thicket vegetation than open vegetation. 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 not unsurprising as areas adjacent to lakes and waterholes are classified as riverine habitat and these create good ambush opportunities for a stalking predator like the lion (Spong 2002).

In general, ecosystems that hold high densities of lions and spotted hyenas hold few African wild dogs and in some areas no African wild dogs are present (Creel & Creel 1996). Parallel to their low population density, African wild dogs have large home ranges ranging between 1500 – 2000km² in the Serengeti (Frame *et al.* 1979). Home

ranges in the Selous Game Reserve average 433km^2 (ranging from 156km^2 to 846km^2), with core areas averaging 64km^2 (ranging from 10km^2 to 124km^2) (Creel & Creel 2002). In Kruger, the average home range size for African wild dogs is 537km^2 (ranging from 357km^2 to 930km^2) and it is likely that in areas with more sedentary and predictable prey (Kruger) territories will be smaller (Fuller *et al.* 1992; Mills & Gorman 1997). This is supported by the results from Kwandwe where the home range size of the pack of African wild dogs was 158km^2 . The very small home range for Kwandwe is probably partly due to the constraints of the boundary fence and small size of the reserve. African wild dogs are generally known to avoid lions and on Kwandwe the core areas of the pack of African wild dogs were mostly found on the boundary of the reserve possibly because they were selecting areas as far from the lions as possible. The pack of African wild dogs selected areas with similar percentages of open and thicket vegetation, whereas when the alpha pair was alone, they selected areas with substantially more open vegetation in their core area. This switch may have been because the pack was reduced to two individuals and vigilance was easier in open areas compared to thickets.

Intra- and inter-specific effects on home range size and habitat selection

Although it is widely accepted that food availability plays a key role in influencing space use in many species of mammals (Schaller 1972; Tait 1981; Litvaitis *et al.* 1986; Durant *et al.* 1988; Caro 1994; Larter & Gates 1994) other factors may play an important role. Food availability may be expected to have less of an effect on space use in areas where prey is non-migratory and relatively abundant throughout the reserve, which is the case on Kwandwe. Here, a case is presented in which space use was influenced by density and interference competition from other carnivores. The

number of lion prides on Kwandwe increased during the study period, creating an opportunity to study the effect of increasing pride numbers within an enclosed system. There was no effect of increasing pride number on the sizes of the core areas or home ranges of the lions but rather, the amount of overlap at the home range level increased significantly. Core areas showed almost no overlap between the lion prides. This suggests that the space used by the original lion pride on Kwandwe (Southern pride) was the minimum required to provide for all the needs of the pride (Caro 1994; Spong 2002; Delahay *et al.* 2006). Thus reduction in home range size was not possible and rather increased overlap with the home ranges of the other prides was tolerated.

Lion prides, which generally consist of related females, defend permanent home ranges which may persist for many generations (van Orsdol *et al.* 1985; Hanby *et al.* 1995; Hunter 1998; Spong 2002) whereas males defend access to pride females (Schaller 1972; Grinnell *et al.* 1995). Maintaining a home range is thought to be of great importance for lion prides and fatalities are relatively common during inter-group encounters (McComb *et al.* 1994; Spong 2002). The formation of new prides is common and these new prides often settle adjacent to their natal range and include parts of the natal range in their new range and thus overlap at the home range level is often tolerated (Pusey & Packer 1987; Packer *et al.* 1990). In the Selous Game Reserve, outer areas of the home range are used less frequently and although there is large spatial overlap, only 10% of core areas overlap another core area and simultaneous temporal overlap is relatively uncommon (Spong 2002). Although pride encounters occur in the Selous Game Reserve, they are rare and none led to fatalities. In the Serengeti, large spatial overlap also occurs, and some lion prides have no exclusive area within their ranges (Schaller 1972). Similar results were recorded on

Kwandwe where although there was substantial overlap of lion pride home ranges, there was very little overlap at a core area level and very few pride encounters were observed during the study period.

It is well documented that lions will steal prey from cheetahs (Caro & Collins 1987; Caro 1994; Durant 1998; Durant 2000a, 2000b) 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). On Kwandwe, the coalition's home range was situated near that of the Southern pride but, there was no change in the size or location of the home range or core area of the coalition with the increase in pride number. There was however, a significant increase in overlap of the coalition's home range with those of the lion prides as the pride number increased. Nevertheless, the carnivores maintained core areas that showed little or no overlap. Male cheetah coalitions are thought to be less affected by other predators than female cheetahs as coalitions are more likely to detect and therefore avoid other predators than a solitary animal (Caro 1994; Hunter *et al.* 2007). Therefore the coalition on Kwandwe is possibly less affected by interference competition and thus the increase in lion pride numbers had little effect on their space use. The consistent position and size of the space used by the coalition of cheetahs on Kwandwe suggests that their space use may be better explained by the Ideal Free Distribution hypothesis than the Ideal Despotic Distribution hypothesis.

It is likely that female cheetahs, because of their solitary nature, will be more susceptible to larger carnivores and that their space use will be affected by interference competition. On Kwandwe, female cheetahs avoided other large

predators including the coalition, the lions and the African wild dogs. Female cheetahs selected core areas that did not overlap with those of other large carnivores but tolerated overlap of home ranges. Home ranges overlapped substantially with those of the coalition, lions and African wild dogs and interestingly there was significantly more overlap at a home range level with the lions and African wild dogs than the coalition. This result is counterintuitive in light of the recorded threat posed by lions. However, simple overlap of space use does not necessarily result in interaction between the species and it is likely that different activity patterns reduced the likelihood of encounters.

The stage of reproduction of female cheetahs had a significant effect on the size of their home range and the overlap of the home range with home ranges of other predators. The home range and core area sizes were significantly smaller when females were denning, which was to be expected as female cheetahs were confined to a small area as the cubs were not mobile. As cubs became mobile there was a slight increase in home range size, and females with cubs between 12-16 months had the largest home ranges. This appears to be a period of exploration as the area covered by the female with cubs is greater than the home range used by the female before she had cubs. Through all stages of reproduction, there was, once again less overlap with the coalition compared to the lions and African wild dogs. There was almost no home range overlap when female cheetahs had cubs in a den, which suggests that suitable habitat for den sites is important in the space use and habitat selection of female cheetahs.

Habitat use

Male cheetahs on Kwandwe selected areas with similar amounts of open and thicket vegetation. In more densely vegetated regions male cheetahs tend to select more open areas (Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003). This has been interpreted as indicating that the species prefers open areas for hunting even when the prey density is lower than in adjacent more heavily wooded areas (Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003; Mills *et al.* 2004; Bissett & Bernard 2007). In Kruger male cheetah coalitions were less affected by cover and prey densities and seemed to prefer the more open savanna habitat (Broomhall *et al.* 2003). It was suggested that the open habitats might make it easier for the coalition to detect intruding males and dominant predators such as lions (Broomhall *et al.* 2003). Similar results were found on Kwandwe where the coalition selected areas with more or less equal amounts of open and thicket habitat. However, the percentage of thicket habitat decreased with an increase in lion pride numbers suggesting that the increase in the number of lions had an influence on habitat selection. The changes of the lions' diet to warthog (see Chapter 3) lead to the lions being more active during the daytime which could have influenced the habitat selection of the male cheetahs. Selecting more open areas would enable the cheetahs to be more vigilant.

Female cheetahs tend to select denser vegetation types which provide cover and suitable den sites for rearing young (Caro 1994; Mizuntani & Jewell 1998; Sunquist & Sunquist 2002; Broomhall *et al.* 2003). In Kruger, the main prey of female cheetahs are impala which also prefer the more dense woodland habitats and Broomhall *et al.* (2003) suggest that the habitat selection by female cheetahs is influenced by the distribution of the prey. Mills *et al.* (2004) demonstrated that prey of a suitable size is an important factor in determining habitat selection in Kruger. On Kwandwe, the

relatively high density of prey throughout the reserve probably reduced the importance of this factor (Bissett & Bernard 2007) and habitat selection was possibly determined by a combination of interference competition, cover and suitable den sites. It is well documented that lions will steal prey from cheetahs (Caro 1994; Durant 2000a, 2000b) and that they can kill cubs and adults (Durant 2000a, 2000b).

The reproductive cycle of female cheetah on Kwandwe had an effect on habitat selection. Pregnant females and females with cubs in a den selected areas with denser vegetation types compared to females with mobile cubs. In other words female cheetahs selected habitats which provided greater concealment from dominant predators as has been suggested by Caro (1994); Mizuntani & Jewell (1998); Sunquist & Sunquist (2002); Broomhall *et al.* (2003). Solitary females and females with cubs in a den are more susceptible to predation and kleptoparasitism by lions and hyenas (Caro 1994) and position their home ranges to include more heavily wooded areas than do adult males, who occur in functional groups and are less susceptible to predation. However the percentage of thicket vegetation within female cheetahs' home range decreased with an increase in lion pride numbers. As mentioned above the change in lion diet and therefore hunting behaviour could have lead to the female cheetahs utilizing more open areas as an increase in lion and pride numbers increased the chances of inter-specific interaction.

In conclusion, home range size and habitat selection is influenced by multiple factors. On Kwandwe prey abundance did not seem to play an important role but rather avoidance of superior predators which may be exaggerated in closed systems, may be a more important factor.

CHAPTER 5

FORAGING EFFICIENCY OF LIONS, CHEETAHS AND AFRICAN WILD DOGS ON KWANDWE

INTRODUCTION

Many studies have presented data on daily food intake by large carnivores, a few of these have converted intake in kilograms into a measure of energy intake and even fewer have attempted to compare energy intake with Daily Energy Expenditure (DEE) or any other measure of energy expenditure. Calculations of DEE for large carnivores are simplified by the fact that about 22 hours of each day are spent resting (Schaller 1972; Caro 1994; Gorman *et al.* 1998; Creel & Creel 2002) and values for energy expenditure at rest can be calculated from existing allometric equations (Gorman *et al.* 1998). However, the costs for the few hours of activity are far more difficult to estimate as they include periods of locomotion at different speeds, energy expended overpowering the prey and feeding. Allometric equations that allow for the estimation of energy expenditure for slow speed locomotion of carnivores have been formulated (Taylor *et al.* 1982) and these can be used to calculate a minimum energy expenditure for locomotion as long as the time spent moving and speed are known (Creel & Creel 2002). The use of the doubly-labelled water technique allows the measurement of DEE in the field but does not reveal how that energy expenditure is partitioned between the various functions (resting, hunting etc). In African wild dogs, DEE measured by the doubly-labelled water technique ranged from about 8000kJ/day to 20000kJ/day (average 15300kJ/day; Gorman *et al.* 1998). Energy expended during 21 hours of rest was calculated using an allometric equation and the remainder of the energy (3140kJ/hr) was assumed to have been spent hunting (Gorman *et al.* 1998).

Differences in energy intake can only be understood when compared to DEE and despite the obvious need for measurements of DEE, they have not been formulated for any other large carnivores.

Although DEE has not directly been measured in this study, the 14 day periods of continuous observations allowed the measurement of distance travelled, time taken travelling and speed of movement, and time spent resting. In this chapter, these were converted into energetic costs of travel and rest and used to estimate a minimum value for DEE. This was then compared to energy intake and the net energy gain of the different predators.

METHODS

Data Collection

All data used in this chapter were collected during the continuous observations (see Chapter 3 for detailed methods). GPS fixes and the time were recorded every time the animal or group of animals under observation moved. When study animals were lost in thick bush, their location was determined using triangulation. The following data were recorded for all located kills: date, species, sex and age of the prey and amount of the carcass consumed.

Data Analysis

Distance travelled and time spent travelling

The straight line distance moved between each GPS fix of each study animal was calculated using an ArcView extension package, Animal Movement Extension (Hooge & Eichenlaub 1997). Total time spent moving was the sum of all individual periods of movement.

Daily intake rates

The body mass of male and female prey species were taken from Meissner (1982), Bothma (2002) and Skinner & Chimimba (2005). The body mass of sub-adults of each sex was estimated by multiplying adult male or female mass by 0.7; values for juveniles were estimated by multiplying mean adult mass by 0.3, as suggested by Radloff & du Toit (2004). The edible percentage of carcasses was estimated according to the categories suggested by Viljoen (1997) for lions; Blumenschine & Caro (1986) for cheetahs and Carbone *et al.* (2005) for African wild dogs and took into account the age and sex of the kills. In instances where the group being followed

comprised more than one animal (i.e. a pride of lions), the total number of animals at each kill was expressed in Female Equivalent Units (FEQs). FEQs are units equal to the body weight of an adult female (Bertram 1973). Using published data on the food consumption of lions (Schaller 1972; van Orsdol 1982; Packer *et al.* 1990), FEQs were allocated as follows: adult female lion, 1 FEQ; male lion, 1.5 FEQ; sub-adult lions (two to three years), 1 FEQ; large cubs (one to two years), 0.75 FEQ; small cubs of less than one year old, 0.3 FEQ. Adult male cheetahs were allocated 1.3 FEQ. The body masses of male and female African wild dogs are similar, therefore the FEQs were 1.0 for both males and females. The sub-adults and cubs of cheetahs and sub-adults and pups of African wild dogs were allocated the same FEQs as were the sub-adult lions and lion cubs.

Estimation of energy intake, travel cost and energy expended during rest

Benefits and costs of travel were measured in kilojoules as suggested by Creel & Creel (1995; 2002), rather than kilograms of meat or kilometres run, as this allows comparisons to be made between species (Creel & Creel 1995). The conversion of kilograms of prey consumed to kilojoules of energy obtained was based on the available data for African wild dogs (Creel 1997; Creel & Creel 2002) which was a mean of 6862kJ/kg of meat consumed. Energy intake was adjusted assuming a digestive efficiency of 93% and an energy loss in the urine of 10% (Gorman *et al.* 1998).

Costs of travel (E_t) were calculated using an existing allometric relationship for carnivores (Taylor *et al.* 1982) that has been used in a similar study of African wild dogs (Creel 1997). The allometric equation is:

$$E_t/M = 6.47 M^{0.289} + 10.23 M^{0.310} v$$

where E_t = energy expended for travel (watts), M = body mass (kg) and v = speed (m/s). The body mass per FEQ calculated for each predator was as follows: lions = 126kg; cheetahs = 54.7kg; African wild dogs = 25.2kg (see Chapter 3 for predator weights). Speed varied depending on the activity of the predator. Normal low speed locomotion of the predators was estimated by dividing the mean distance travelled per day by the number of hours of travel time per day (Table 5.1). The energy expenditure in watts was converted to kJ/hr of travel (1 watt/kg = 3.6kJ/hr) and then to an energetic cost of travel per day.

All predators spent approximately 22 hours each day resting and this energy expenditure was estimated using an existing allometric equation ($E_r = 5.5M^{0.75}$; Carbone *et al.* 2007). E_r is the resting energetic cost in watts and M is the body mass in kilograms. E_r in watts was converted to kJ/hr and then to kJ/day for the hours not spent travelling. An estimation of minimum DEE (kJ/FEQ/day) was calculated by adding E_r and E_t and this was compared to the energy intake gained from the kills.

Statistical analyses

Distance travelled, kill rate and daily consumption rates of lions, cheetahs and African wild dogs were compared with one-way ANOVAs followed by post-hoc tests. Energetic costs of travel and gains from feeding are described but have not been compared statistically because of the small sample sizes. All statistical analyses were conducted using Statistica (StatSoft, version 7.0).

RESULTS

The distance travelled by the different predator groups varied significantly during continuous observations ($F = 7.8$, $df = 6$, $P < 0.0001$; Table 5.1). The African wild dog alpha pair travelled significantly further per day than all the other predator groups ($P < 0.05$; Table 5.1; Figure 5.1). The coalition travelled the second greatest distance per day and their movements were concentrated around their core area with regular excursions out of their home range (Figure 5.2). The coalition travelled significantly further per day than the lion prides, female cheetahs with cubs and single female cheetahs ($P < 0.05$ for all; Figure 5.1). The single female cheetahs travelled the shortest distance per day (Table 5.1; Figure 5.1) but there was no significant difference in the distance travelled by single female cheetahs, female cheetahs with cubs, independent cheetah cubs or the pack of African wild dogs.

Table 5.1: Mean daily distance travelled, kill rate and consumption by the various predators during two week continuous observations.

Predator Group	Distance Travelled (km/day)	Kill Rate		Daily Intake Rates	
		(kills/day)	(kg/FEQ/day)	(kg/FEQ/km)	(kg/FEQ/km/day)
Lion Prides	3.9	0.5	9.5	2.7	0.19
Coalition	6.4	0.4	5.3	0.8	0.06
Female cheetahs with cubs	3.1	0.5	4.7	1.9	0.13
Single female cheetahs	2.8	0.4	13.1	4.6	0.33
Independent cheetah cubs	3.6	0.4	5.7	2.6	0.18
African wild dog pack	5.2	0.8	6.0	1.3	0.08
African wild dog alpha pair	10.5	0.2	4.5	0.4	0.03

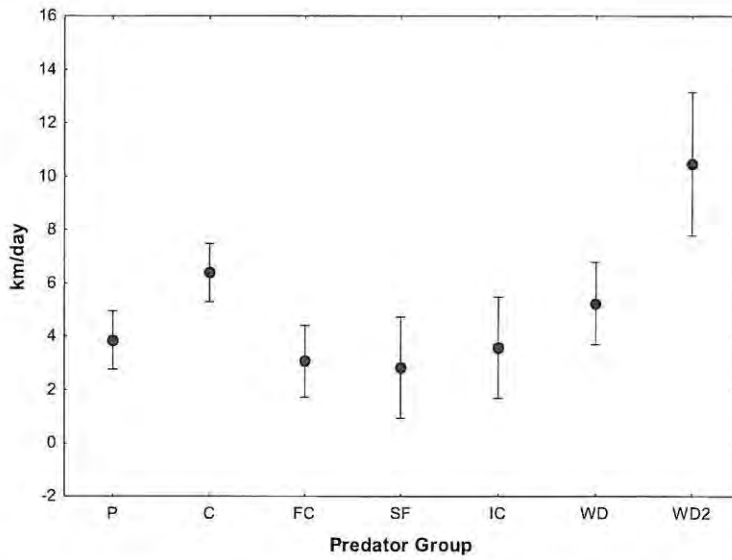


Figure 5.1: Distance travelled (km/day) by each predator group during two week continuous observations. Data are means \pm 1SD. (P = lion prides; C = coalition; FC = female cheetahs with cubs; SF = single female cheetahs; IC = independent cheetah cubs; WD = African wild dog pack; WD2 = African wild dog alpha pair).

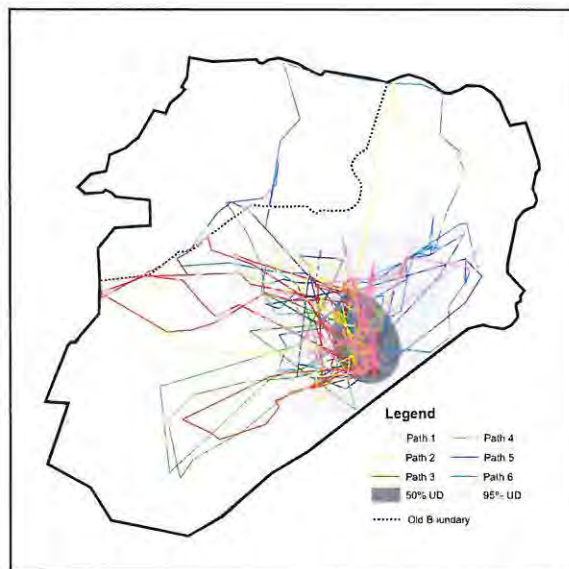


Figure 5.2: Routes travelled by the coalition during six two week continuous observation sessions. Each path represents a separate two week continuous observation session. Home ranges and core areas were calculated from location points for the whole study period.

The African wild dog pack killed more often than any of the other predator groups. However, the frequency of kills (kills/day) did not vary significantly between the predator groups ($F = 2.2$, $df = 6$, $P > 0.05$; Table 5.1). Food consumption (kg/FEQ/day) varied significantly between the predators ($F = 4.4$, $df = 6$, $P < 0.001$) and single female cheetahs consumed significantly more meat per day than the coalition and female cheetahs with cubs ($P < 0.05$ for both; Table 5.1; Figure 5.3). Finally, there was a significant variation in the meat consumption per km travelled (kg/FEQ/km/day) ($F = 3.4$, $df = 6$, $P < 0.05$) with single female cheetahs eating significantly more than the coalition ($P < 0.05$; Table 5.1; Figure 5.4). Although no other pairs were significantly different, the alpha pair of African wild dogs consumed the smallest amount per day per km moved.

In summary, the African wild dog alpha pair travelled the furthest distance, made the fewest kills and consumed the least (kg/day and kg/km/day). The coalition of three male cheetahs travelled significantly further per day than the other cheetahs but made the same number of kills and their intake (kg/FEQ/km/day) was significantly lower than that of single females. Single adult female cheetahs had the highest intake (kg/FEQ/km/day) because their daily movement was the lowest, their kill rate was not significantly different from the other predators and they did not have to share their kills.

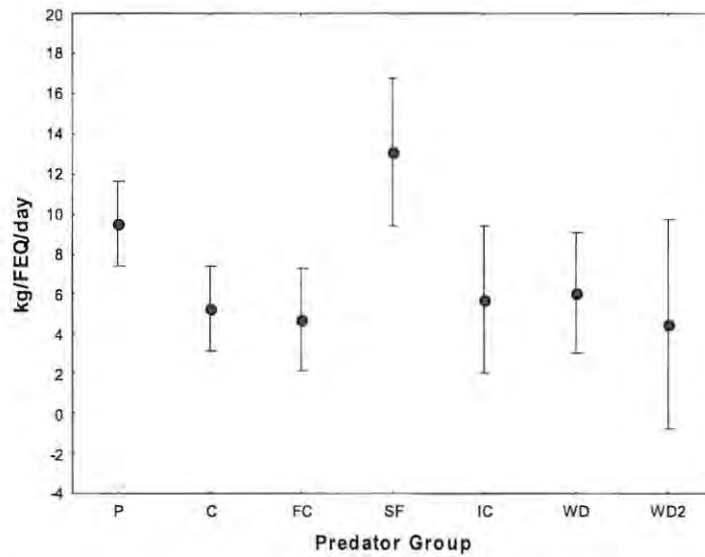


Figure 5.3: Meat consumption (kg/FEQ/day) for the different predators during the two week continuous observations. Data are means \pm 1SD. (P = lion prides; C = coalition; FC = female cheetahs with cubs; SF = single female cheetahs; IC = independent cheetah cubs; WD = African wild dog pack; WD2 = African wild dog alpha pair).

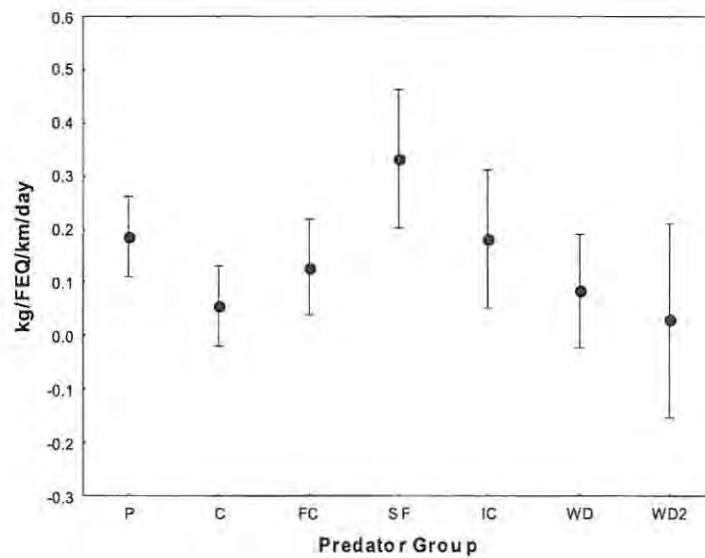


Figure 5.4: Meat consumption per km travelled (kg/FEQ/km/day) by the different predators during the two week continuous observations. Data are means \pm 1SD. (P = lion prides; C = coalition; FC = female cheetahs with cubs; SF = single female cheetahs; IC = independent cheetah cubs; WD = African wild dog pack; WD2 = African wild dog alpha pair).

All predators spent less than 2.2 hours per day travelling, with the coalition spending the most time travelling and single female cheetahs spending the least time travelling (Table 5.2). Travel speed, which was calculated as distance travelled divided by time spent travelling, varied from a maximum of 5km/hr for the African wild dog alpha pair to 1.8km/hr for female cheetahs with cubs (Table 5.2). The travel costs of the single female cheetahs (kJ/FEQ/day) were the lowest and were half that of the coalition (Table 5.2). Travel costs of the lion prides were the highest (Table 5.2). Time spent resting was similar for all predators (approximately 22 hours) and the energetic costs associated with rest (E_r) varied according to the body mass of the predator (Table 5.2). E_r for the lions was approximately twice that of the cheetahs and four times that of the African wild dogs (Table 5.2).

Table 5.2: Summary of energetic cost of travel and rest. Distance travelled is from Table 5.1. Travel speed is distance travelled divided by travel time.

Predator Group	Distance Travelled (km/day)	Travel Time (hr/day)	Travel Speed (km/hr)	Travel Cost (E_t) (kJ/FEQ/day)	Time Resting (hr/day)	Rest Cost (E_r) (kJ/FEQ/day)
Lion Prides	3.9	1.8	2.2	2445.5	22.2	16530.9
Coalition	6.4	2.2	2.9	1914.3	21.8	8681.8
Female cheetahs with cubs	3.1	1.8	1.8	1218.1	22.2	8857.1
Single female cheetahs	2.8	1.2	2.3	927.6	22.8	9080.1
Independent cheetah cubs	3.6	1.7	2.1	1259.1	22.3	8881.0
African wild dog pack	5.2	2.1	2.5	982.8	21.9	4877.1
African wild dog alpha pair	10.5	2.1	5.0	1480.6	21.9	4877.1

Minimum DEE varied threefold between the predators from a minimum of about 6000kJ/FEQ/day for the African wild dog pack to about 18000kJ/FEQ/day for the lions (Table 5.3). The estimated minimum DEE was similar for all cheetah social groups. However, the single females' exhibited the highest energy intake and the highest overall net benefit compared to the other predator groups (Table 5.3). Travel

costs (E_t) for the coalition were double that for the single females, energy intake was less than half and consequently the net benefit for the coalition was less than one third of that for the single female cheetahs (Table 5.3; Figure 5.5). Female cheetahs with cubs had the lowest energy intake (kJ/FEQ/day) of all cheetahs and the lowest net benefit of all the predators (Table 5.3).

Travel costs for the African wild dog alpha pair were nearly twice that for the African wild dog pack and energy intake was lower (Table 5.3). Consequently, the net benefit for the alpha pair was lower than for the African wild dog pack (Figure 5.5).

Travel cost for the lion prides was the highest but this was balanced by the second highest energy intake per day and consequently, lions were calculated to have the second highest net benefit (Table 5.3; Figure 5.5).

Table 5.3: Summary of energetic cost of travel and rest and energy gained through kills for the various predator groups.

Predator Group	Travel Cost (E_t) (kJ/FEQ/day)	Rest Cost (E_r) (kJ/FEQ/day)	DEE (E_t+E_r) (kJ/FEQ/day)	Energy Intake (kJ/FEQ/day)	Net Benefit (kJ/FEQ/day)
Lion Prides	2445.5	16530.9	18976.4	54563.2	35586.8
Coalition	1914.3	8681.8	10596.1	30440.5	19844.4
Female cheetahs with cubs	1218.1	8857.1	10075.2	26994.4	16919.2
Single female cheetahs	927.6	9080.1	10007.7	75239.8	65232.1
Independent cheetah cubs	1259.1	8881.0	10140.1	32737.9	22597.8
African wild dog pack	982.8	4877.1	5859.9	34461.0	28601.1
African wild dog alpha pair	1480.6	4877.1	6357.6	25845.7	19488.1

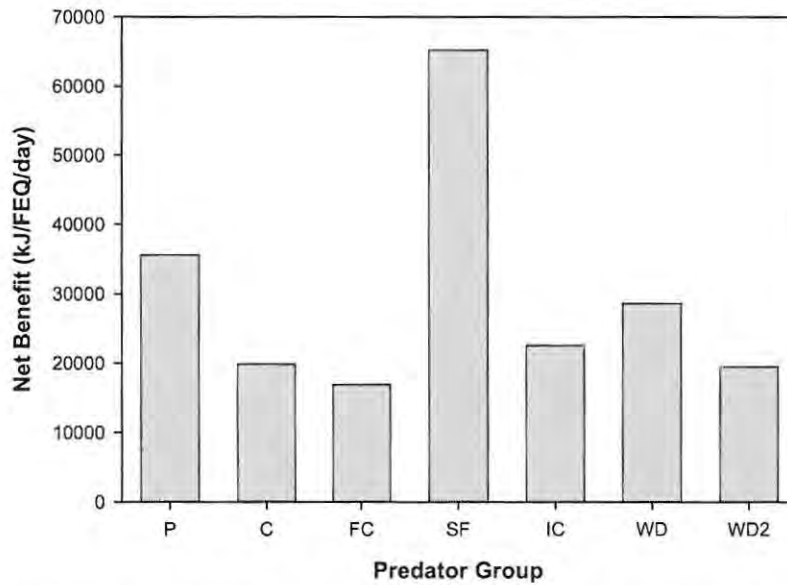


Figure 5.5: Foraging efficiency of various predator groups on Kwandwe. (P = lion prides; C = coalition; FC = female cheetahs with cubs; SF = single female cheetahs; IC = independent cheetah cubs; WD = African wild dog pack; WD2 = African wild dog alpha pair).

DISCUSSION

The estimated total Daily Energy Expenditure (DEE), using the doubly-labelled water method, for six African wild dogs from a pack of 48 animals in the Kruger is 15300kJ/FEQ/day (Gorman *et al.* 1998). The DEE per dog varied from 8043kJ/day to 20281kJ/day and values are likely to be high as the pack included 27 pups aged three to four months (Gorman *et al.* 1998). This measurement of DEE is not directly comparable to the estimate of minimum DEE calculated in the present study, which was obtained by summing the estimated costs of low speed travel and the estimated costs of approximately 22 hours of rest. However, the minimum DEE estimated for African wild dogs at Kwandwe (approximately 6000kJ/day) is the same as the value predicted by allometric equations (Burger & Johnson 1991) for a 25kg moderately active domestic dog and is only 25% lower than the lowest value for African wild dogs (Gorman *et al.* 1998). The lower values at Kwandwe can be explained in terms of the much smaller pack size (average of 7.8 animals) and the high prey density (20 prey animals/km²).

The African wild dogs on Kwandwe were active for just over two hours per day, whereas in Kruger the African wild dogs are active for more than three hours per day. In the Serengeti, the duration of activity depends upon the size of the pack and the prey density. If the pack is large they often kill more than once a day, but these animals are never active for more than four to five hours per day (Schaller 1972). These differences in duration of activity are probably due to the smaller pack size and the higher resident prey density on Kwandwe.

Finally, the way in which the data were collected will influence the time animals are expected to have spent engaged in activity. In the study at the Kruger, the time spent away from the den was recorded (Gorman *et al.* 1998) and it was assumed that this

was the same as the time spent active. Failure to take time spent inactive while away from the den into account would have resulted in an inflated estimate of time spent active.

The alpha pair were the only members of the African wild dog pack that survived an outbreak of canine distemper on Kwandwe, and the loss of the pack members six weeks before the continuous observations were conducted, probably affected their behaviour. However, previous studies have shown that pack size affects the foraging success of African wild dogs and in the Selous Game Reserve daily consumption per dog per kilometre was found to increase with an increase in pack size (Creel & Creel 2002). Similar results were achieved in the present study and the pack of African wild dogs on Kwandwe consumed more per day and per kilometre travelled than the alpha pair alone. Despite the reduction in feeding efficiency, the food intake of the alpha pair (approximately 26000kJ/FEQ/day) was more than the maximum DEE for members of a pack in the Kruger (20281kJ/dog/day; Gorman *et al.* 1998).

In the Serengeti, cheetahs seldom travel more than 3-5km per day and are active for less than four hours per day (Schaller 1972). Results for Kwandwe are similar and the travelling distance of cheetahs ranged from 2.8km/day for single females to 6.4km/day for the coalition, and the length of activity varied from 1.2hr/day for single female cheetahs to 2.2hr/day for the coalition. In the Serengeti, coalitions of three male cheetahs consume 3.6kg/individual/day, which is almost double that consumed by coalitions of two male cheetahs (Caro 1994). The coalition of three male cheetahs on Kwandwe consumed more meat (5.3kg/FEQ/day) than the coalitions of three male cheetahs in the Serengeti and this probably reflects differences in prey abundance and possibly the density of other larger members of the predator guild. Where the

likelihood of kleptoparasitism is low, cheetahs may stay on a kill for longer and eat more from a kill than where the density of larger predators is high and the consequent risk of kleptoparasitism is greater. While it appears from the above discussion that one advantage of increased group size in male cheetahs is an increased food intake, the results from Kwandwe suggest that an alternative explanation may be required. Despite the fact that the mean kill size for female cheetahs was significantly lower than that of the coalition (see Chapter 3), single female cheetahs on Kwandwe consumed much more meat (13.1kg/FEQ/day) than the coalition, and displayed a higher energy intake and net benefit compared to the coalition. The reasons for these differences are that the single females travelled shorter distances, were active for shorter periods per day and did not have to share their kills with other cheetahs. The very high daily consumption is likely to also reflect the high prey density and low levels of kleptoparasitism on Kwandwe (Bissett & Bernard 2007). The benefits that group living hold for male cheetahs cannot purely be explained in terms of energetics, at least not on Kwandwe. It is more likely that group living reduced the likelihood of fatal encounters with larger members of the predator guild and increased the ability of the group to protect kills from kleptoparasitism. This suggestion is supported by unpublished data from Kwandwe, where, over six and-a-half years, five adult females were killed by lions, whereas only one adult male was killed over the same period of time.

The rates of food consumption by lions measured in this study (9.2kg/FEQ/day) are much higher than those estimated for lions by Schaller (1972) in the Serengeti (5kg/day) and Green *et al.* (1984) in Hluhluwe-Imfolozi Game Reserve (6kg/day). In the Savuti region of the Chobe National Park, the average daily meat intake is

5.7kg/FEQ/day, with a higher intake in the wet season (7.8kg/FEQ/day) compared to the dry season (4.6kg/FEQ/day) and an average kill frequency of 0.6 kills per day (Viljoen 1993). The kill frequency in the Savuti region is similar to that recorded in this study (0.5 kills/day) although the daily meat intake in the Savuti is lower. As argued in the previous examples, it is likely that the higher food intake on Kwandwe is a result of the prey density and the small pride sizes.

In areas with low prey density such as Etosha (approximately one prey animal per km²), lions travel 13.2km/day (Stander 1992), whereas in East Africa, where prey density is much higher (approximately 37 prey animals per km²), lions seldom travel distances of more than 5km/day (Schaller 1972; van Orsdol 1984). A similar trend was seen on Kwandwe where the lions' average daily travelling distance was 3.9km. In the Serengeti lions are active for about two hours (Schaller 1972) whereas on Kwandwe the lions were active for just under two hours per day, yet their daily consumption rate was much higher than that reported for the Serengeti lions.

For all the predators, the net energy gained was greater than 10000kJ/day, which is greater than predicted by Carbone *et al.* (2007). It is likely that this is because the estimate of DEE in the present study includes the cost of travel but not of hunting, and is expressed as a minimum value. It is also likely, as discussed previously, that the high prey density may have resulted in reduced energetic costs and elevated intake.

In conclusion, time spent travelling and distance covered by the large carnivores was typically smaller on Kwandwe than in other systems. This is probably due to smaller group sizes and higher prey density. Although, in this study, it has not been possible to measure DEE, the estimated minimum DEE (costs of slow travel and rest) are less than the energy intake for all predators. The alpha pair of African wild dogs had a

lower net benefit than the pack of African wild dogs and single female cheetahs, despite hunting alone and killing smaller prey, had a much higher net benefit than members of a three male coalition. This net benefit was greatly reduced when the female cheetahs had cubs.

CHAPTER 6

GENERAL CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

While it is acknowledged that where large predators remain free-ranging, their conservation must be a priority, it is recognised that in many regions they are now restricted to fenced game reserves. It is thus necessary to strengthen our understanding of the ecology of large predators in relatively small, enclosed game reserves and this has been the primary goal of this research.

General conclusions

The methods used in this study have allowed two methodological comparisons, the first between aerial and road game counts and the second between *ad hoc* observations and continuous observations. Although the two game count methods gave different absolute numbers for each species, the proportional representation of each species was not significantly different. It is likely that with further refinement, the accuracy of the driven game count will improve and it will become a cost effective alternative for aerial game counts.

Although continuous observations were undertaken as part of the study of diet and prey selection, they have contributed data to the study of space use and were essential for the estimation of DEE. The value of continuous observations is discussed further below.

A number of recent meta-analytical studies have reported prey preference indices and preferred prey mass for a range of predators (Hayward & Kerley 2005; Hayward *et al.* 2006a, 2006b). These analyses are based on pooled data from a number of published

studies and report species level characteristics. However, by presenting mean values with a measure of variance, the impression is created that prey selection and preference is fixed at a predator species level and does not vary in space or time. The results from the study at Kwandwe have illustrated the adaptable nature of predator diets and support the contention that predation should be analysed separately for each situation as the influence of predation may vary spatially as well as temporally within a certain area (Smuts 1978). The diet of lions and cheetahs on Kwandwe changed significantly throughout the study as the prey base changed. In lions, the proportion of warthog increased, as did Jacobs' Index for warthog, and mean kill mass decreased during the study. For cheetahs, the Jacobs' Index for springbok increased through the study although the abundance of springbok declined. Thus, prey selection and prey preferences are not fixed in time or space and change with changes in prey abundance and the structure of the large predator guild. This dietary flexibility will play an important role in the conservation of large predators, contributing to their survival in both open and enclosed systems.

Previous studies have suggested that *ad hoc* observations will under represent small prey species in the diet (Mills 1984). However, Radloff & du Toit (2004) have suggested that, where observation effort is high, under counting of small prey species will be minimized. Results from Kwandwe are equivocal and neither fully support nor refute Mills (1984). In some instances, continuous observations detected small kills that were not detected by *ad hoc* observations. However, in other instances, this was not the case and there was no significant difference between the proportions of each prey species detected by the two methods.

For all the predators on Kwandwe, core areas were much smaller than home ranges and while home ranges of the different predators overlapped, the core areas had little or no overlap and may be regarded as exclusive. Only when female predators had cubs at a den was the home range similar in size to the core area. The increase in the number of lion prides on Kwandwe did not result in a reduction in size of the home range of the lions or the coalition but rather in an increase in overlap of space used. The toleration of varying amounts of space overlap within the home ranges of the predators will accommodate the changes in predator numbers that will occur with reproduction and in the absence of dispersal in enclosed systems.

Space use by female cheetahs varied significantly depending on the age of their cubs and space use was greatest when the cubs were oldest and smallest when using a den. The use of thicket vegetation by cheetahs declined as the number of lion prides increased and, although not analysed in this thesis, this may have an impact on the predation on kudu calves by female cheetahs.

The continuous observations typically produced smaller areas than the *ad hoc* observations at both core area and home range levels, the exception being the coalition for which the continuous observations generated larger areas. It is likely that for a territorial predator, *ad hoc* observations will tend repeatedly to locate the animal in the same area and this will result in a small home range. Continuous observations will detect forays out of the home range and generate a larger home range.

Only one previous study has measured Daily Energy Expenditure (DEE) in large carnivores (African wild dogs, Gorman *et al.* 1998) and the estimates of minimum DEEs for lions, African wild dogs and cheetahs at Kwandwe allow a better

understanding of energy gained from kills. On Kwandwe, all predators showed a large net benefit, which reflects the high prey density and suggests that the predators kill more than required. Net energy gain increases with increase in pack size up to an optimal pack size in African wild dogs (Creel 1997; Creel & Creel 2002) and this is supported by data from Kwandwe for the African wild dogs where the net benefit of the alpha pair was lower than that of the pack. However, results for the cheetahs were the opposite and single females killed smaller prey but showed a greater net benefit than the coalition. This is an important result as it casts doubt on the assumption that a key benefit of group living is that it allows larger prey to be killed and yields a relatively greater return to the members of the group. It is perhaps more likely that the key benefit of group living for a small member of the large predator guild lies in improved resilience to other, stronger members of the predator guild.

Management recommendations

The information collected in this study can be used to begin to understand the predator-prey and predator-predator dynamics on enclosed reserves. The carrying capacity of a reserve (especially enclosed systems) for large carnivores can be calculated in several ways based on food requirements (Power 2003), but an understanding of the spatial requirements of the carnivores and the nature of intra- and inter-specific interactions is equally important. Intra- and inter-specific killing is common amongst large carnivores (Palomares & Caro 1999; Durant 2000a, 2000b) and can be expected to be exaggerated in relatively small enclosed reserves, and mortality from inter-specific killing can be high. This is particularly true for cheetahs and African wild dogs, and for these species, there is an inverse relationship between their densities and the densities of lions and spotted hyenas (Laurenson 1994; Creel &

Creel 1996; Palomares & Caro 1999). Subordinate predators will avoid suitable habitats where superior predators are common (Mills & Gorman 1997; Durant 1998), however, this may be difficult if space is limiting or if the density of carnivores is high. On many reserves, as on Kwandwe, prey density is high and space rather than any aspect of diet, is probably the most important issue in the management of a large carnivore guild. Space use by members of the large carnivore guild should therefore be monitored, particularly as the structure of the guild changes. While home ranges were not exclusive on Kwandwe, there was very little overlap at a core area level suggesting that it is essential to ensure there is enough suitable space for core areas of all members of the large carnivore guild.

Although space is of prime importance in the management of a large carnivore guild, it is likely that large predators will affect populations of resident prey in small, enclosed systems. For example, on Phinda the impact of increasing populations of reintroduced lions and cheetahs led to the decline of some herbivore species (Hunter 1998), and this led to a management decision to reduce the numbers of both lions and cheetahs. On Kwandwe, kudu were the preferred prey species for all large predators and it is likely that this will affect the kudu population. However, the switch in the diet of the lions from kudu to warthog indicates that predation pressure on kudu will decline and the population may recover. These observations highlight the importance of ongoing monitoring of the predators and their prey.

The results from this study indicate that road game counts may be an alternative census method to the much more expensive aerial counts, and road counts should be continued and refined. It is likely that the differential visibility in different vegetation

types is responsible for some of the error, and manipulating the truncation distances from the road may yield a better estimate of numbers.

The careful collection of *ad hoc* kill records by field rangers has value (Radloff & du Toit 2004), and should be a part of the monitoring regime of all game reserves. However, continuous observations provided data that were used in the analyses of diet and space use, and were essential in the calculation of DEE. Thus, although continuous observations are time consuming and logistically difficult they have tremendous value and should be incorporated into reserve monitoring programmes where possible.

The conservation of large predators requires equal effort at two different scales. On the one hand, the last remaining free-ranging large predators must be conserved bringing with it a particular set of problems that centre on predator-human interactions. At a smaller spatial scale, if the relatively small, enclosed systems are to play a role in the conservation of predators, then the behaviour and biology of predators in these systems must be understood. My study has built on a previous study on Mala Mala (Radloff & du Toit 2004) and has illustrated how careful observation can contribute to an understanding of the ecology of predators in a small system.

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APPENDIX A

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 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)
Bengal tiger *Panthera tigris tigris* (Linnaeus 1758)
Brown hyena *Parahyaena brunnea* (Thunberg 1820)
Spotted hyena *Crocuta crocuta* (Erxleben 1777)
Dhole *Cuon alpinus* (Pallas 1811)
Mountain lion *Puma concolor* (Linnaeus 1771)
Domestic dog *Canis lupus familiaris* (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)
Plains zebra *Equus quagga* (Boddaert 1785)

Order Artiodactyla

Common warthog *Phacochoerus africanus* (Gmelin 1788)
Bushpig *Potamochoerus larvatus* (F.Cuvier 1822)
Giraffe *Giraffa camelopardalis* (Linnaeus 1758)
Bushbuck *Tragelaphus scriptus* (Pallas 1766)
Greater kudu *Tragelaphus strepsiceros* (Pallas 1766)
Eland *Tragelaphus oryx* (Pallas 1766)
Nyala *Tragelaphus angasii* (Gray 1849)
Buffalo *Syncerus caffer* (Sparman 1779)
Waterbuck *Kobus ellipsiprymnus* (Ogilby 1833)
Gemsbok *Oryx gazella* (Linnaeus 1758)
Mountain reedbuck *Redunca fulvorufula* (Afzelius 1815)
Grey rhebuck *Pelea capreolus* (Forster 1790)
Red hartebeest *Alcelaphus buselaphus* (Pallas 1766)
Blesbok *Damaliscus pygargus phillipsi* (Pallas 1767)
Tsessebe *Damaliscus lunatus* (Burchell 1823)
Blue wildebeest *Connochaetes taurinus* (Burchell 1823)
Black wildebeest *Connochaetes gnou* (Zimmerman 1780)
Common duiker *Sylvicapra grimmia* (Linnaeus 1758)
Impala *Aepyceros melampus* (Lichtenstein 1812)
Springbok *Anitdorcas marsupialis* (Zimmerman 1780)
Steenbok *Raphicerus campestris* (Thunberg 1811)
Cape grysbok *Raphicerus melanotis* (Thunberg 1811)
Mule Deer *Odocoileus hemionus* (Rafinesque 1817)
Thomson's gazelle *Gazella thomsoni* (Günther 1884)

Order Rodentia

Cape porcupine *Hystrix africaeaustralis* (Peters 1852)

Class Aves

Order Struthioniformes

Ostrich

Struthio camelus (Linnaeus 1758)

Class Sauropsida

Order Testudines

Leopard tortoise

Geochelone pardalis (Bell 1828)

