THE FEEDING ECOLOGY, HABITAT SELECTION AND HUNTING BEHAVIOUR OF RE-INTRODUCED CHEETAH ON KWANDWE PRIVATE GAME RESERVE, EASTERN CAPE PROVINCE

A thesis submitted in fulfilment of the requirements

for a degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

by

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December 2004

ABSTRACT

The re-introduction of cheetah onto small reserves in the Eastern Cape Province has created the opportunity to study this species in an environment (Valley Bushveld) in which it has not previously been studied and which is quite different from the less wooded habitats in which previous studies have occurred. Thus the aim of this study is to add to the growing number of studies of cheetah in more wooded habitats and to contribute a better understanding of the level of specialization or adaptability in space use, habitat selection, diet and hunting behaviour that the cheetah possesses. The research was conducted on Kwandwe Private Game Reserve from February 2003 to August 2004. Direct observations, scat analysis and continuous observations were used to avoid bias towards large sized prey found when only using direct observations to study diet. The cheetah killed 15 species and four of the five most important prey species (kudu, springbok, grey duiker and bushbuck) were hunted according to their abundance on the reserve, while impala, the fifth most important prey species, was avoided (i.e. preference index less than one) by the cheetah. The cheetah's main prey was medium sized ungulates, although the three male coalition killed larger prey than females and females with cubs. The daily food intake per cheetah per day was calculated to range from 5.3kg/cheetah/day for the coalition to 8kg/cheetah/day for a solitary female. Home range areas ranged from 11.1 km² for female cheetah with cubs in a den to 65.6 km² for single female cheetah and core areas ranged from 6 km² for the three male coalition to 26.5 km² for independent cubs. Habitat selection by cheetah on Kwandwe varied between the social groups depending on their susceptibility to predation by lions, their need for cover and need for water, and was similar to what has been previously reported. The home range of the coalition incorporated the most open vegetation type (karroid shrubland) with surrounding denser vegetation, while females occupied areas of denser vegetation. Activity patterns and hunting behaviour varied between different cheetah social groups with female cheetah being more active during day light hours compared to males which made 38% of their kills after dark. The average chase distances for the various cheetah groups varied considerably, and the chase distance for successful hunts was longer than for unsuccessful for all groups except single female cheetah. The percentage of kills' kleptoparasitised on Kwandwe was very low compared to other studies possibly due to the low density of direct competitors, which in turn lead to longer mean kill retention times.

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ACKNOWLEDGEMENTS

The contributions of the following individuals during the period of my study are gratefully acknowledged:

- My supervisor, Ric Bernard, for his constant patience, guidance and support. His door was never closed and he was always there whenever I needed him, whether it was for advice or for assisting with a cheetah capture. Thank you!
- Carl de Santis and Erika Stewart, of Kwandwe, for their financial assistance and permission to conduct the research.
- Angus Sholto-Douglas for all his support in terms of my research, a vehicle, accommodation, assistance with captures, proof reading my thesis and always ensuring that I never lost my sense of humour.
- To all the Gillis staff for making me feel at home at Krantzdrift and all the laughs (and biltong, of course!) especially, Keith Craig, Hennie Odendaal, Mark Galpin, Mike Webber, Hendrik Odendaal, Debbie Heinen, Tracy Sholto-Douglas, Celeste Were, Cindy Tutton, Sunette Odendaal and Helen Steyn.
- Mickey Green for all the time he dedicated to servicing my vehicle and always finding the time to chat.
- Gus Mills, Luke Hunter and Laurie Marker for their expert advice and help in answering even the most obscure questions.
- Gillian McGregor for assistance with the GIS component.
- Martin Villett for statistical assistance.
- Martin Hill and Dan Parker for proof reading my thesis and always keen to talk it through over a couple of cold ones, although sometimes in spirit.

- To those who sacrificed their time to assist me in the field or laboratory. Thanks to Kurt Koller, Gay Papenhuizen, Andy Hughes, Paul Warner and Dayne Davey.
- All the rangers of Kwandwe for their input and assistance, especially Nick Kyriacos, Andre Macdonald, Wesley Bahlmann, Bryan Olver, Richard Cooper, Kerri Smythe, Bruce Ochse, Tim Vuyk, Anthony Tranter and Natasha de Woronin. Thanks for the friendship and the beers!
- The Kwandwe staff, in particular, Steve Mills, Altus du Toit, Mynie Lochner and Sanette Scholtz.
- To Jackie Rapson, Gareth Moore, Derek Brown, Gareth Whitting-Jones, Lucy Scott and Guy Paulet thanks for all your friendship and the interest you showed in my work.
- And finally, to my family for all the encouragement, love and support, and believing in me.

PREFACE

This thesis is structured as follows:

Chapter 1 is a general introduction that broadly sets the scene. However, it does not serve to introduce the major research chapters. These chapters each have their own introduction and aims.

Chapter 2 provides a detailed description of the study site, study animals and general methodology used throughout the study.

Chapters 3, 4 and 5 presents the major results of the study and each chapter has its own introduction, methods, results and discussion.

- **Chapter 3** examines the diet and prey selection of different cheetah social groups.
- **Chapter 4** addresses the question of space use and habitat selection by cheetah in a small, enclosed reserve.
- **Chapter 5** presents results for cheetah hunting behaviour.

Chapter 6 is a final discussion and some management implications derived from the research.

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Appendix A: Scientific names of all species mentioned in the text.

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CHAPTER 1

GENERAL INTRODUCTION

The cheetah (*Acinonyx jubatus*, Schreber 1775) is one of 36 species worldwide in the Family Felidae and one of 7 species in southern Africa (Skinner & Smithers 1990; Sunquist & Sunquist 2002). Five subspecies of cheetah have been recognized (Caro 1994; Hunter & Hamman 2003) and are listed in the Convention on International Trade of Endangered Species (CITES) Appendix 1 and classified as Vulnerable (sub-Saharan Africa) or Endangered (North Africa to Asia) by the World Conservation Union (IUCN) (Marker *et al.* 2003a; 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. Initially, studies of cheetah biology were undertaken in the Serengeti and as a consequence, the cheetah is known as a highly specialized felid that selects open savannah habitats where it kills medium to small sized prey after a high speed chase (Schaller 1972; Caro & Collins 1986; 1987; Durant *et al.* 1988; Fitzgibbon 1990; Caro 1994; Laurenson 1994; 1995; Laurenson *et al.* 1995; Durant 1998; 2000a; 2000b). However, historically cheetah occurred across most of non-forested Africa, the Middle East and southern Asia (Caro 1994; Sunquist & Sunquist 2002; Hunter & Hamman 2003), suggesting that this species should be able to tolerate and hunt in a relatively wide range of environmental conditions and habitats. Indeed, cheetah currently inhabit a wide range of bush, scrub and woodland habitats in southern Africa (Purchase & du Toit 2000; Broomhall *et al.* 2003; Marker *et al.* 2003a) although far less is known about their ecology in these habitats than on the open plains. Recent studies in woodland savannahs have increased the understanding of cheetah ecology in these areas and have shown that cheetah are more adaptable than was previously thought (Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003).

The conservation of large carnivores in general presents various problems with human and livestock conflicts being a central issue. Real or potential conflicts with human activities restrict large carnivores to reserves and adjacent areas in much of the world (Creel & Creel 2002). Such reserves must be ecologically intact in order to accommodate large carnivores which have very low population densities relative to smaller species or those occupying lower trophic levels (Blackburn & Gaston 1994). Furthermore, some large carnivores (for example African wild dogs) range more widely than others (Woodroffe & Ginsberg 1998; Creel & Creel 2002) while others such as the leopard are difficult to confine. The confinement of large carnivores to smaller reserves poses many additional problems including the prevention of inbreeding, the lack of refuges for both predators and prey and the high densities that can arise from the limited available space. (A small reserve is a system where sustainability depends on active management strategies and in this study, small reserves referred to are no bigger than 300km^2.)

The cheetah is threatened throughout its range by habitat loss, declining prey numbers and direct persecution, and its survival presents a challenge to conservationists (Caro 1994; Sunquist & Sunquist 2002). In Africa cheetah ranged through all suitable habitats except desert and tropical forest, from the Mediterranean to the Cape of Good Hope (Guggisberg 1975, Sunquist & Sunquist 2002). Today, the cheetah has almost disappeared from Asia and is extinct in India. In Africa, the cheetah’s distribution has been fragmented and greatly reduced although they inhabit a broad section of central, eastern and southern Africa, principally Kenya, Tanzania and Namibia (Skinner & Smithers 1990; Caro 1994; Sunquist & Sunquist 2002). In 1900, it was estimated that 100 000 cheetah lived in 44 countries throughout Africa and Asia. Today it is estimated that at most 12 000 to 15 000 cheetah remain in 26 African countries, with approximately 200 in Iran (Myers 1975; Marker *et al.* 2003a). Much of this decline can be attributed to increasing human populations, the conversion of land to agriculture and livestock farming which has increased the conflict between cheetah and farmers, and a decline in the abundance of prey species (Woodroffe & Ginsberg 1998; Marker & Schumann 1998; Marker *et al.* 2003a). The largest population of cheetah in the wild is now found in Namibia, primarily only on commercial farm lands and is estimated at 2000 to 3000 animals (Marker *et al.* 2003a). In Namibia conservation organizations such as the Cheetah Conservation Fund and AfriCat are working with local government ministries, farm associations, conservation groups and tribal councils to try and eliminate the loss of cheetah due to human exploitation, through the development of conservation management plans which are beneficial to both the cheetah and farmers (Marker & Schumann 1998; Hunter & Hamman 2003; Marker *et al.* 2003a). In addition, cheetah are recognized as having very little genetic diversity and this contributes to the likelihood of local extinction (Caro 1994; Caro 2000).

Cheetah do not breed well in captivity and captive populations were not self-sustaining (Marker & O’Brien 1989). However, captive management and breeding success has improved since 1986 although most of the breeding has occurred at only a few institutions, such as De Wildt Breeding Center in South Africa, Whipsnade Zoological Park in England (Caro 1994) and four institutions in North America (Marker & O’Brien 1989). The increased success in captive breeding programmes may lead to increased cheetah sustainability within captive populations (zoos) but the re-introduction of captive bred animals into the wild is more complicated. There are various reasons for this, including the fact that cheetah learn and perfect hunting techniques from their mothers in the wild, and that captive bred cheetah have no experience of interaction with superior predators such as lions (Caro 1994; Sunquist & Sunquist 2002).

Re-introduction programmes of large felids in South Africa and Zimbabwe have yielded some encouraging results (Pettifer 1981b; Hofmeyr & van Dyk 1998; Hunter 1998; Purchase & du Toit 2000). In all these cases, re-introductions have been of wild animals (i.e. not captive bred); suggesting that the re-introduction of large felids into newly established conservation areas may be a viable method for re-establishing resident felids. This supports Caro's (1994) observation that greater efforts should be put on the conservation of cheetah re-introduced to small reserves.

In South Africa, the development of ecotourism has lead to the re-evaluation of historical patterns of land use by governments, tribal communities and the private sector, and this has brought about 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 approximately 12 privately owned game reserves opening in the province in the last 15 years. As part of this process, mammalian species that had been locally extirpated by hunters have been re-introduced. Large predators such as lions and cheetah were eradicated from their natural ranges in the Eastern Cape Province in the latter half of the nineteenth century as a result of conflict with humans and the last record for a cheetah within this area was 35km north of Grahamstown in 1888 (Skead 1987). The majority of these newly developed reserves within the East Cape Province have re-established, or are in the process of re-establishing large predators such as lions and cheetah to their reserves. Importantly, cheetah were extirpated from the Eastern Cape Province before scientific research started and hence there have been no studies of cheetah in this area. The absence of research would not be relevant if the vegetation of the Eastern Cape Province was similar to that of the Serengeti. However, the vegetation of the region, while quite variable, is characterized by several vegetation types including Valley Bushveld that are much thicker than the more open savannahs in which cheetah are usually found and have previously been studied.

Whether or not the re-introduction of a carnivore is successful will depend on various factors including the availability of food, water, habitat in which the species can hunt, and refuge. These needs may be reflected in the space use or habitat selection by the individuals of the introduced individuals. An area occupied by an animal, whether it is defended or not, should contain all the necessities of life including not only sufficient food, water and shelter but provision must also be made for establishing the normal social relationships of the species (Ewer 1973). This would include access to conspecifics for reproduction and, where appropriate for the species, care of young (Ewer 1973). For these reasons, it is necessary to take food requirements, social organization and breeding behaviour into account when considering space use and habitat selection of carnivores (Ewer 1973). These ideas ignore the importance of inter-specific interactions between members of a guild of large carnivores in shaping habitat choice and thus are in line with the theory of Ideal Free Distribution (IFD; Fretwell & Lucas 1970). This theory suggests that an individual's options will be determined both by the suitability of the habitat and densities of conspecifics in that habitat. If several habitats are available but differ in their basic suitability and an individual within a single species is free to settle wherever his or her expected fitness is highest, the IFD will apply (Cressman *et al.* 2004). However, the risk of predation by for example, superior members of a guild of large carnivores, may also affect individuals by limiting their use of high-quality habitat and the IFD theory has been modified to accommodate this. In the modified theory, known as the Ideal-Despotic Distribution (IDD), each individual is free to choose its territory, regardless of repulsion attempts by other individuals. 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 but in most cases the results have suggested that the IDD and not the IFD is applicable (Kohlmann & Risenhoover 1997; Beckmann & Berger 2002; Zimmerman *et al.* 2003). The IDD may therefore apply to the sub-ordinate predator such as cheetah as the space used by the sub-ordinate predator is strongly influenced by the space use of the superior predator, such as lions (Beckmann & Berger 2002). If the IDD applies to space use by cheetah, then it is predicted that as reserve size decreases, or the density of predators' increases, the opportunity to avoid superior predators will decrease and the influence of superior predators will be exaggerated.

The re-introduction of cheetah onto small reserves in the Eastern Cape Province has created the opportunity to study this species in an environment (Valley Bushveld) in which it has not previously been studied and which is quite different from the less wooded habitats in which previous studies have occurred. The cheetah has been characterized as a species that is highly specialized and it has been suggested that this level of specialization has made it susceptible to extinction (Hunter 1998). If this is the case, then it is unlikely that cheetah will be able to adapt to the much denser Valley Bushveld and it could be hypothesized that cheetah introduced to areas with large amounts of Valley Bushveld will select the available open habitats or the introduction will be unsuccessful. Thus, a central aim of this study was to add to the growing number of studies of cheetah in more wooded habitats and to contribute to a better understanding of the level of specialization or adaptability (in space use, diet and hunting behaviour) that the cheetah possesses. Furthermore, because of the small size of the reserves and the fact that they support guilds of large carnivores, there is the opportunity to study the effects of the presence of superior predators on the space use of the cheetah. And finally, the data will be used as the basis for some recommendations for the management of cheetah in small reserves.

CHAPTER 2

STUDY AREA AND STUDY ANIMALS

LOCATION

Kwandwe Private Game Reserve (from here on referred to as Kwandwe) lies in the Great Fish River Valley about 35km north of Grahamstown, in the Eastern Cape Province of South Africa. Kwandwe is approximately rectangular in shape with the long axis running in a northeast to southwest direction and has an area of about 160km^2. The R67 arterial road crosses the Great Fish River at Fort Brown (Figure 2.1) and forms the eastern boundary of the reserve. Two minor public roads enter the reserve from the south and west joining at Krantzdrift (Figure 2.1). A single public road then passes eastwards towards Fort Brown. The perennial Great Fish River flows through the reserve for approximately 25km and all the watercourses drain towards the Great Fish River (Figure 2.2). The most important watercourse is the Botha's River that feeds two large man-made dams, which together with several smaller dams and numerous seasonal pans provide important sources of water for the animals (Figure 2.2). Surrounding land comprises 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 utilized for ostrich and small stock farming. As is prescribed for reserves in South Africa that are reintroducing dangerous species, the entire perimeter of Kwandwe (58km) is fenced with electrified game fencing.

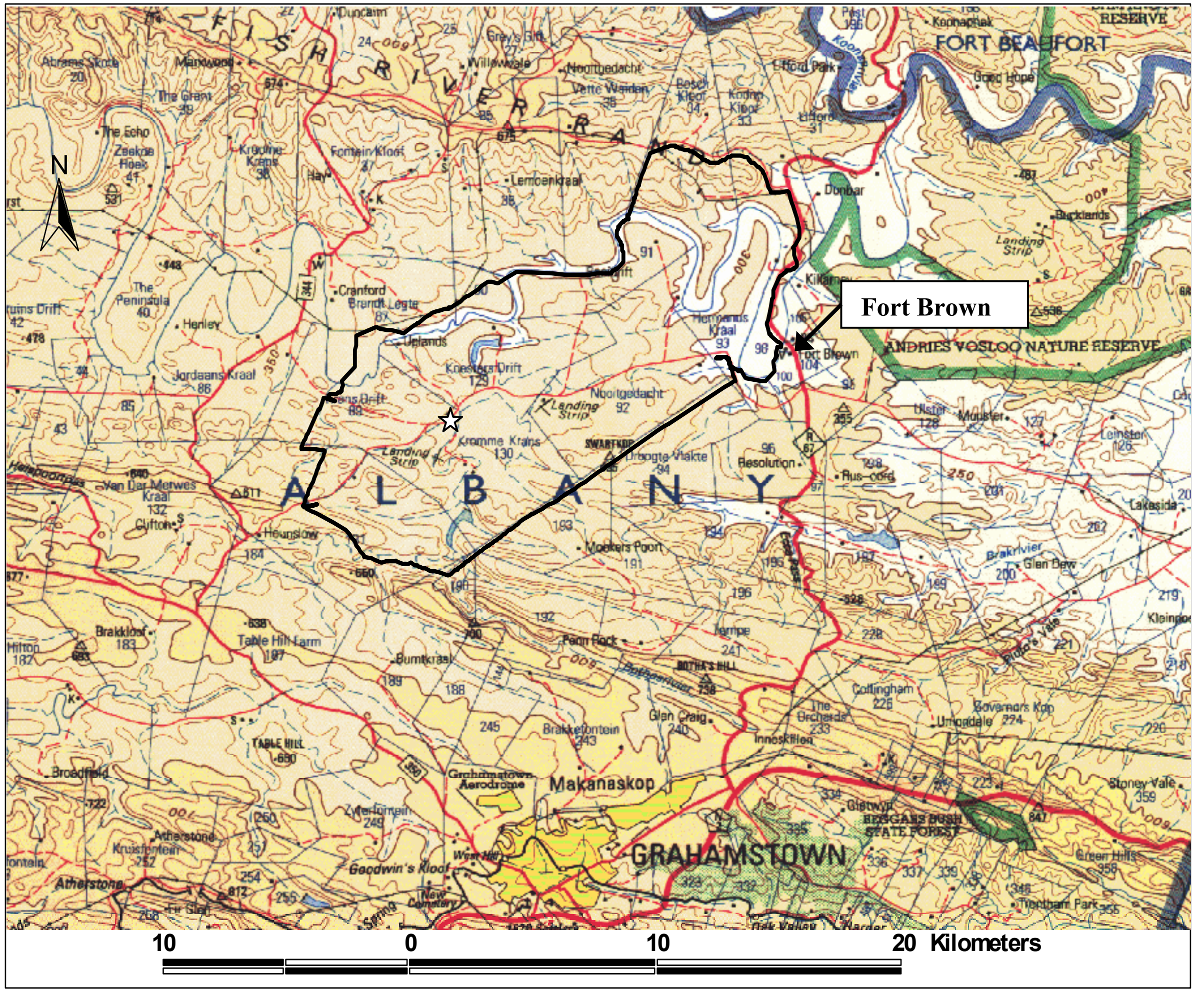


Figure 2.1: Kwandwe Private Game Reserve in relation to Fort Brown and the Great Fish River. (☆Weather station).

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, with wide plains with gentle topography in the centre of the reserve and steep rising ground north of the Great Fish River up to the top of the Fish River Rand. The river itself is deeply incised with steep banks, thus making access to long stretches on the river difficult (Figure 2.2).

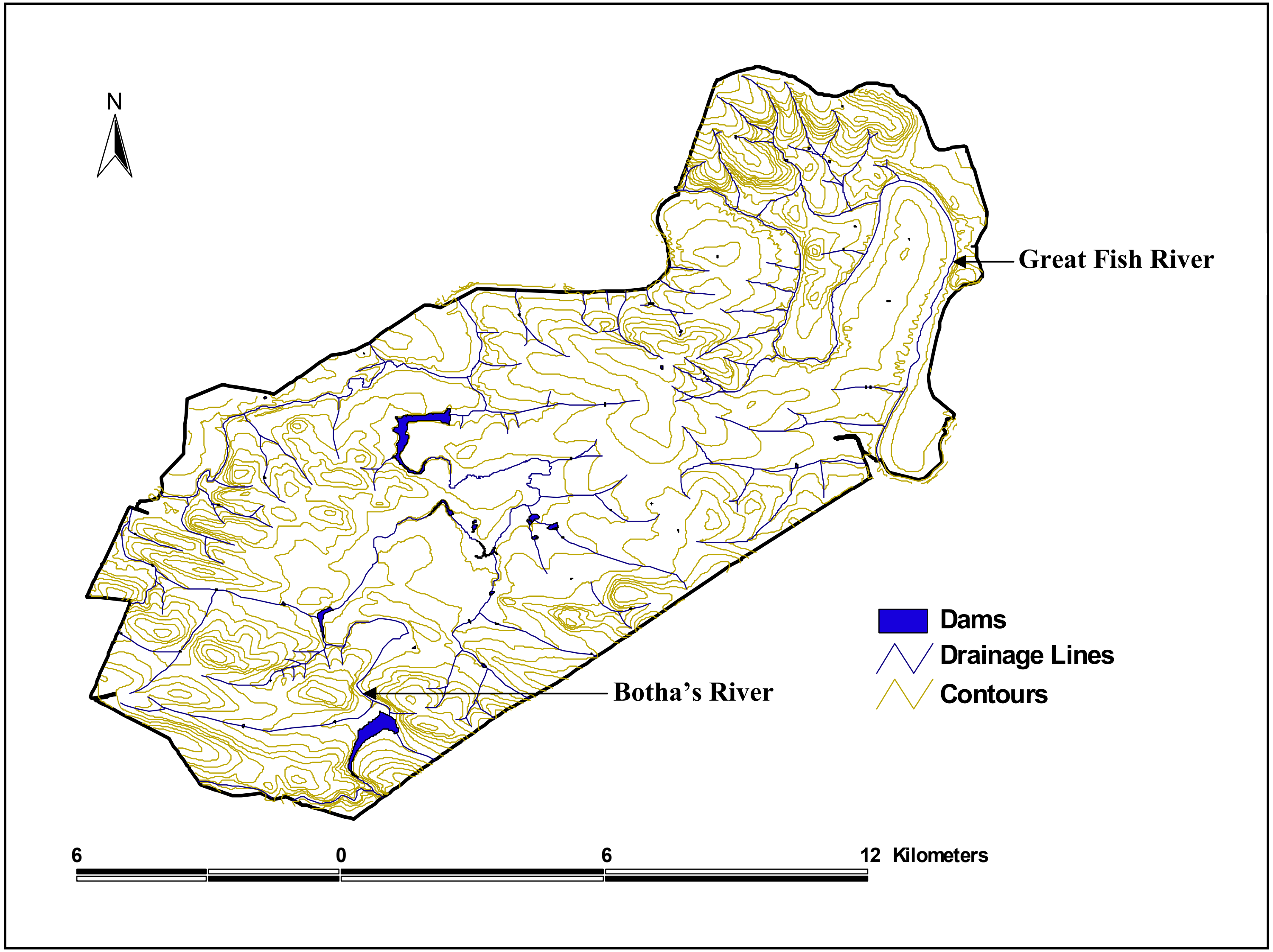


Figure 2.2: The topography and drainage patterns of Kwandwe Private Game Reserve.

CLIMATE

The Great Fish River Valley has a complex climatic environment 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 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 figures, 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; Kwandwe Environmental Management Plan 2001; pers. obs.). Mean annual rainfall for the area is 435mm, ranging from under 400mm in the Great Fish River Valley to over 600mm north of the Great Fish River, on the relatively higher ground of the Fish River Rand (Low & Rebelo 1996).

Kwandwe has a warm temperate climate 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). Temperature and rainfall data were taken from a weather station on the reserve (see Figure 2.1). Rainfall is highly variable but peaks of rainfall occur from September to November and January to April (Figure 2.4).

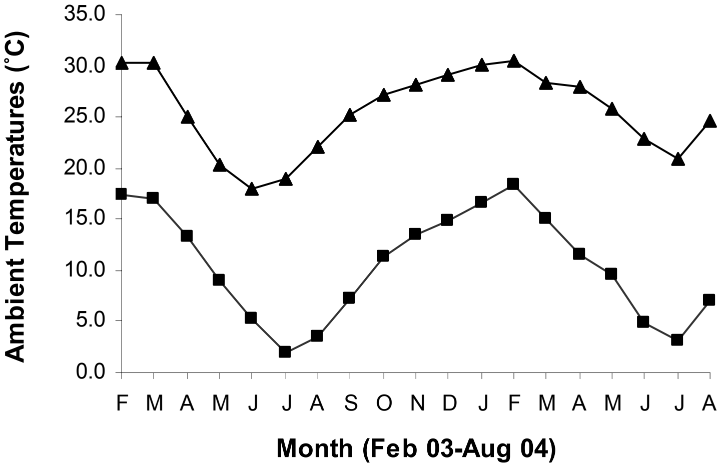


Figure 2.3: Mean daily maximum and minimum temperatures for each month of the study.

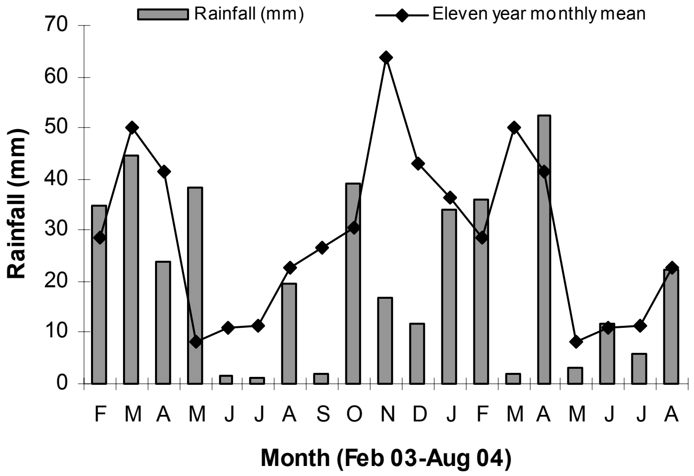


Figure 2.4: Total monthly rainfall for the study period, February 2003 to August 2004. Mean monthly rainfall for 11 years (1994 to 2004; data from Coniston, a neighboring farm in the Great Fish River Valley) is included to allow comparison.

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. He stated that overgrazing of large areas has opened up this vegetation, resulting in the invasion of *Opuntia* species and *Euphorbia bothae*.

A preliminary vegetation map for Kwandwe was prepared by the resident ecologist (Mark Galpin) and this was refined in 2003 by Mark Galpin and myself (Figure 2.5). We used a 1:50 000 aerial photograph and numerous site visits for visual assessment of the vegetation composition and structure. A GPS was used to more accurately define the vegetation blocks. Ten vegetation types were identified and these are described below.

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

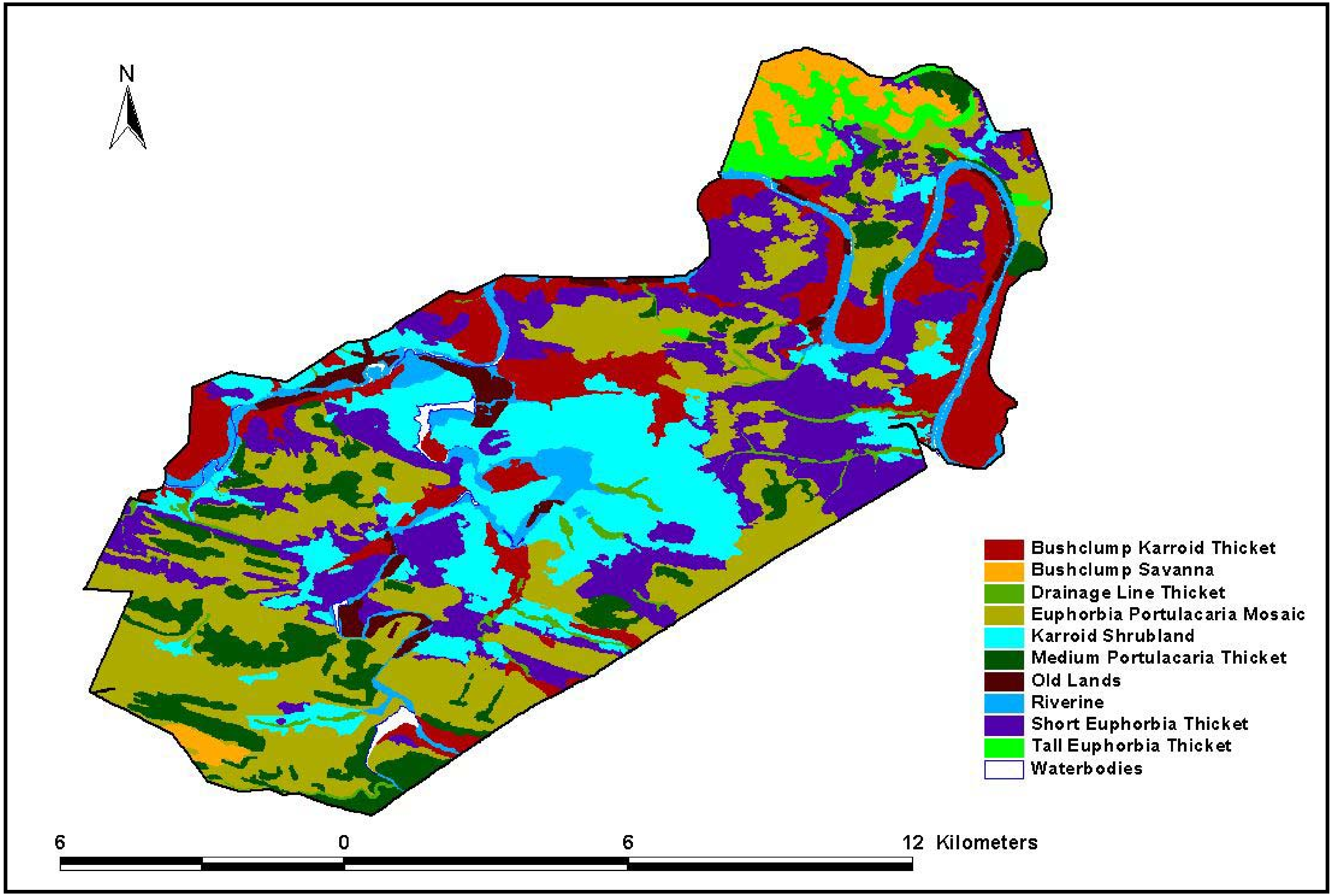


Figure 2.5: Distribution of the vegetation types of Kwandwe Private Game Reserve.

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 (Figure 2.6; the area of this vegetation type is 1738.4ha).

2. Medium *Portulacaria* Thicket.

This vegetation type consists of dense stands of *Portulacaria afra* interspersed with *Pappea capensis* and is found predominantly in the western section of the reserve on steep slopes. The under storey is entirely bare with no herbaceous layer (Figure 2.7a, b; the area of this vegetation type is 1174.8ha).

3. *Euphorbia Portulacaria* Mosaic.

This vegetation type is the transition between Short *Euphorbia* thicket and Medium *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* 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 (Figure 2.8; the area of this vegetation type is 3776.9ha).

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*. Other woody species include *Pappea capensis*, *Rhigozum obovatum* and *Maytenus capitata*. Grass species

Figure 2.6: A view looking east of bushclump karroid thicket showing bushclumps with *Rhus* species as the dominant species in this example.

Figure 2.7a: A view of medium *Portulacaria* thicket showing the domination of *Portulacaria afra* and an entirely bare under storey.

Figure 2.7b: Medium *Portulacaria* thicket, which is mainly found on the western side of the reserve on steep slopes.

Figure 2.8: A view of *Euphorbia Portulacaria* mosaic showing *Euphorbia bothae* in the foreground and *Portulacaria afra* in the background. Note the grassy under storey.

include *Themeda triandra*, *Digitaria eriantha* and *Aristida* spp. This vegetation type grows on shallow soils overlying Ecca shale (Figure 2.9; the area of this vegetation type is 2933.8ha).

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 north eastern 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* (Figure 2.10; the area of this vegetation type is 390.9ha).

6. Bushclump Savannah Thicket.

Bushclump savannah thicket dominates the flatter landscape on the top of the Fish River Rand and John Dell ridge in the north eastern and south western sections of the property respectively. It differs climatically from bushclump karroid thicket in occurring 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 (Figure 2.11; the area of this vegetation type is 359.9ha).

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*

Figure 2.9: Short *Euphorbia* thicket with *Euphorbia bothae* dominated stands and *Pappea capensis* in the background.

Figure 2.10: Tall *Euphorbia* thicket with *Euphorbia tetragona* and *Euphorbia triangularis* stands growing on steep slopes.

Figure 2.11: Bushclump savannah thicket dominating the flatter landscape on the top of John Dell ridge in the south western section of the property.

Figure 2.12: Old cultivated areas on the alluvial section of the Great Fish River dominated by *Pennisetum clandestinum*.

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 (Figure 2.12; the area of this vegetation type is 266.9ha).

8. Karroid Shrubland.

Karroid shrubland dominates the flatter, low lying areas in the middle of the reserve. 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* (Figure 2.13; the area of this vegetation type is 2202.2ha).

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 (Figure 2.14; the area of this vegetation type is 208.6ha).

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 comprises 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* (Figure 2.15; the area of this vegetation type is 754.6ha).

Figure 2.13: Karriod shrubland with large open areas dominated by *Pentzia incana* and tree species such as Pappea *capensis* and *Rhus refracta*.

Figure 2.14: Drainage line thicket with dense stands of *Rhus refracta* in the background and *Plumbago auriculata* in the front.

Figure 2.15: Riverine thicket with *Acacia karroo* growing on the alluvial soils bordering the Great Fish River.

Vegetation density and visibility

For each vegetation type the density of the vegetation and visibility was assessed using a modified point centered quarter method (Phillips 1959) and a checker board method. In each vegetation type ten 100m long transects were completed. At 20m intervals along each transect a cross was marked 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 cheetah. 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. For each transect, these areas were summed to produce the total area for that transect and then the number of objects was 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 cheetah. 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 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.

Vegetation Type	Visibility Index	Density
Bushclump karroid thicket	84.4 ±9.4	0.1±0.1
Medium *Portulacaria* thicket	36.8±12.2	1.5±0.9
Euphorbia Portulacaria mosaic	53.2±17.1	0.7±0.6
Short *Euphorbia* thicket	48.4±12.4	0.9±0.5
Tall *Euphorbia* thicket	61.2±9.2	0.4±0.2
Bushclump savannah thicket	69.2±11.0	0.5±0.3
Old lands	99.3±0.8	0.0
Karroid shrubland	98.2±2.6	0.01±0.01
Drainage line thicket	55.2±3.9	0.5±0.7
Riverine thicket	64.9±19.8	0.3±0.2

MAMMALIAN FAUNA

Prior to 1999, the study site comprised a number of privately owned farms with a mixture of land uses such as ostrich and small stock farming. The majority of the indigenous large mammal fauna had been extirpated but small and some medium-sized ungulates were present when Kwandwe assumed control of the area in 1999. Species that were present included greater kudu, bushbuck, grey duiker, steenbok, cape grysbok, grey rhebuck, mountain reedbuck, bushpig and 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 re-introduced. Carnivore re-introductions included four lion, nine cheetah, six African wild dogs, two leopards, six brown hyenas and 10 serval. At the start of this study some populations had changed and there were: nine lions, 13 cheetah, two leopards, six brown hyenas and 10 serval. African wild dogs were only re-introduced in year 2 (2004) (common and scientific names of mammalian species found on Kwandwe are given in Appendix A).

Historical records show that cheetah occurred in the Eastern Cape Province and were last recorded 35km north of Grahamstown in 1888 (Skead 1987). Between 2001 and 2003 Kwandwe released 11 cheetah (Table 2.3; and see next section).

Aerial game counts using a helicopter are done once a year to obtain information on wild animal numbers. A Jet Ranger III, ZS-HSV helicopter is used with a recorder sitting next to the pilot and two counters each counting the animals on each side of the helicopter. The pilot draws the attention of the observers to any animals that may be ahead of the helicopter and the recorder records all the information, helps the pilot to maintain direction and counts any animals in the blind spot in front of the helicopter. The counters convey their information to the recorder. The pilot uses GPS flight instruments to fly fixed strips. The transects flown are 250m apart and therefore animals within 125m wide strips are counted on either side of the helicopter. The localities of the animals are recorded using GPS equipment. The flying height is between 30-50m above the ground and the flying speed is approximately 40mph, increasing to 60mph in the more open areas. The results of the annual game counts for my study period are shown in Table 2.2.

Table 2.2: Kwandwe game census for 2003 and 2004.

SPECIES	TOTAL	
	2003	2004
KUDU	1602	1422
WARTHOG	559	731
SPRINGBOK	510	403
IMPALA	434	306
GREY DUIKER	337	237
RED HARTEBEEST	318	183
BLUE WILDEBEEST	252	173
BUSHBUCK	204	166
BURCHELL'S ZEBRA	175	172
GEMSBOK	131	166
WATERBUCK	109	99
ELAND	96	81
STEENBOK	69	50
OSTRICH	77	91
BLESBOK	58	29
GIRAFFE	32	36
BUFFALO	37	41
MOUNTAIN REEDBUCK	29	31
BUSHPIG	6	12
BLACK BACKED JACKAL	41	74
CHEETAH	7	16
LIONS	9	7
WILD DOG	0	6
BROWN HYEANA	0	1
CARACAL	1	1

STUDY ANIMALS

Between August 2001 and August 2003 eleven cheetah were reintroduced onto Kwandwe (Table 2.3). Each animal was assigned a unique alpha-numeric identification number which followed the form of species/sex/number e.g. CF1, will refer to cheetah female one. The numbering is sequential so that each individual could be identified by a unique number alone and if an animal died or was sold that number was not used again. Cubs born on the reserve were numbered sequentially according to this system. Throughout this thesis I will refer to the cheetah according to the alpha-numeric identification system.

Table 2.3: Details of the cheetah released on Kwandwe and their relatedness. (* NCMP – National Cheetah Management Program)

Release	Origin	Group Composition	ID	Relatedness	Date released
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 my study in February 2003 the composition of cheetah groups (Figure 2.16) had changed considerably from that in Table 2.3. The coalition was reduced to three males (CM1-3) as CM4 was killed by lions within the same year of release, therefore at the beginning of my study the composition of the coalition was two brothers (CM2, 3) and one unrelated male (CM1). Of the second release, CF5 left her cub (CF6) shortly after release and in 2002 they each had a litter of cubs. As a result of this, at the beginning of my study CF5 had three male cubs of approximately seven months old (CM12-14) and CF6 had two female cubs of approximately 11 months old (CF10, 11; Figure 2.17). Of the third release CF7 left her 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 approximately two months old. As a result of this, at the beginning of my study CF7 had one female cub (CF16) of approximately five months old (Figure 2.17). CF19 was killed by the three male coalition two weeks after her release. CM9 was killed by the coalition in October 2003 at about the time he would have reached sexual maturity and would therefore have been in competition with the coalition. CF5 was killed by the pride of lions in May 2003, her three male cubs survived on their own but unfortunately two of them (CM12, 13), were killed by the single male lion approximately two months after the death of their mother. The third cub (CM14) survived and later joined up with CF18 on her release. CF6 left her 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 2.4.

Table 2.4: Causes of mortality of cheetah on Kwandwe.

Cheetah ID	Cause of Death	Date of Death
CM4	Lion	10 November 2001
CF5	Lion	2 May 2003
CU15	Unknown	November 2002
CF16	Cheetah (CM1-3)	5 June 2003
CM12	Lion	8 July 2003
CM13	Lion	12 July 2003
CM9	Cheetah (CM1-3)	7 October 2003
CF19	Cheetah (CM1-3)	31 August 2003
CF18	Unknown (possibly lion)	18 May 2004
CU30	Unknown	19 June 2004
CU26	Unknown (possible lion)	27 August 2004
CU27	Unknown (possible lion)	27 August 2004

Due to the losses and births of cheetah at Kwandwe in 2003 the cheetah composition was once again very different in my second year of study (2004) (Figure 2.16). CF6 gave birth to a litter of four cubs in January 2004. Her female cubs from her previous litter (CF10, 11) were both mated by the coalition in January 2004 and gave birth to four and three cubs respectively in April 2004. CF11 lost one of her cubs shortly after they were seen for the first time at approximately two months old, and the cause of death was unknown (Table 2.4; Figure 2.17). CF10 lost two of her cubs when they were approximately four months old and the cause of death was unknown (Table 2.4; Figure 2.17). A single lioness was in the same area the night the cubs went missing and it is possible that the lioness killed the two cubs. CF18 was mated in February 2004 and was thought to have had a litter of unknown number of cubs when she was killed in May 2004 (Figure 2.17). Her carcass was eaten by black-backed jackal and the cause of death could not be established.

She was found dead in the territory of a single male lion and it is possible that she was killed by the lion. Her cubs were never found.

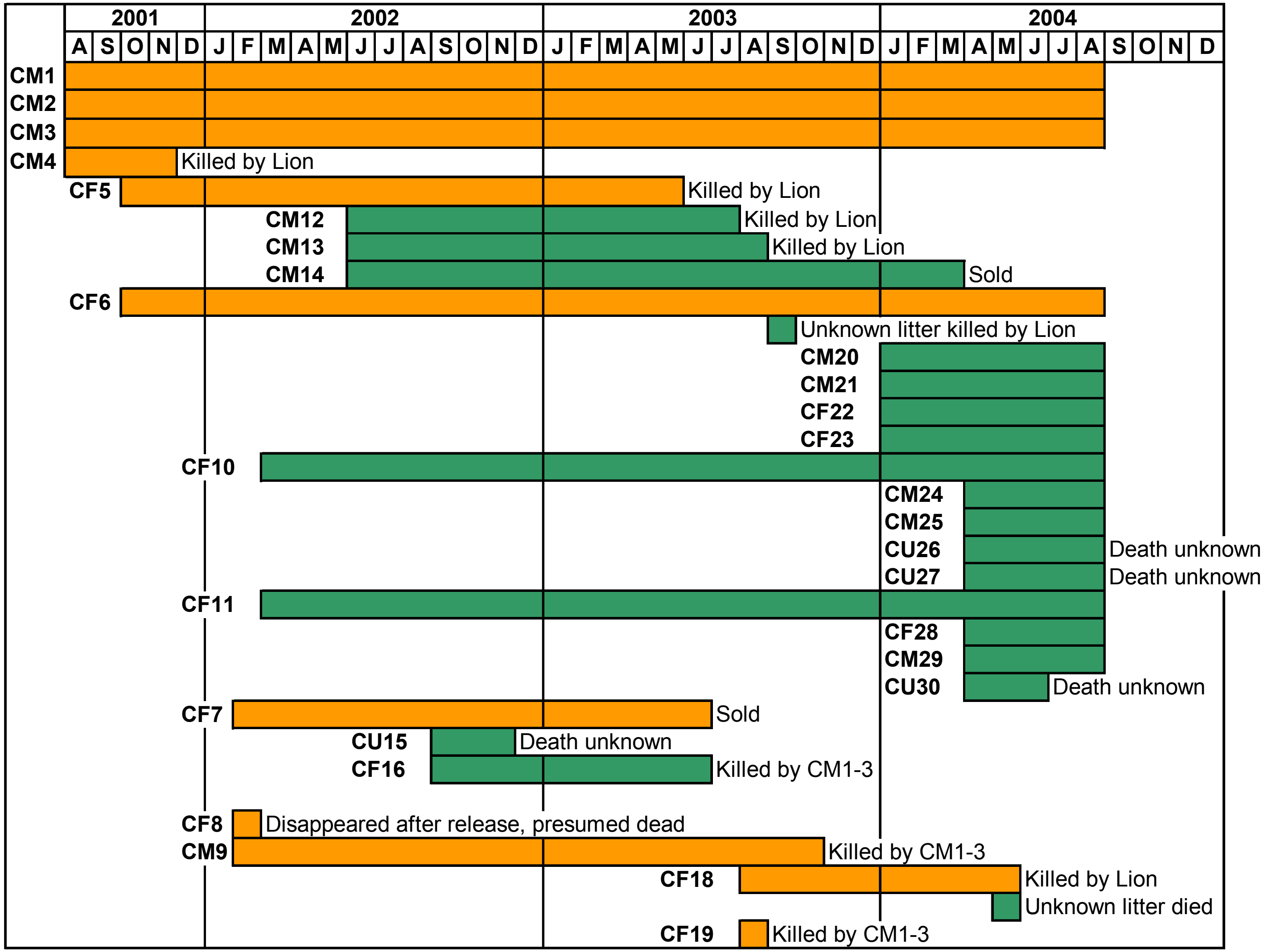


Figure 2.16: Details of the study animals and their fate during the study period (February 2003-August 2004).

(🟧 re-introduced cheetah; 🟩 cheetah born on Kwandwe).

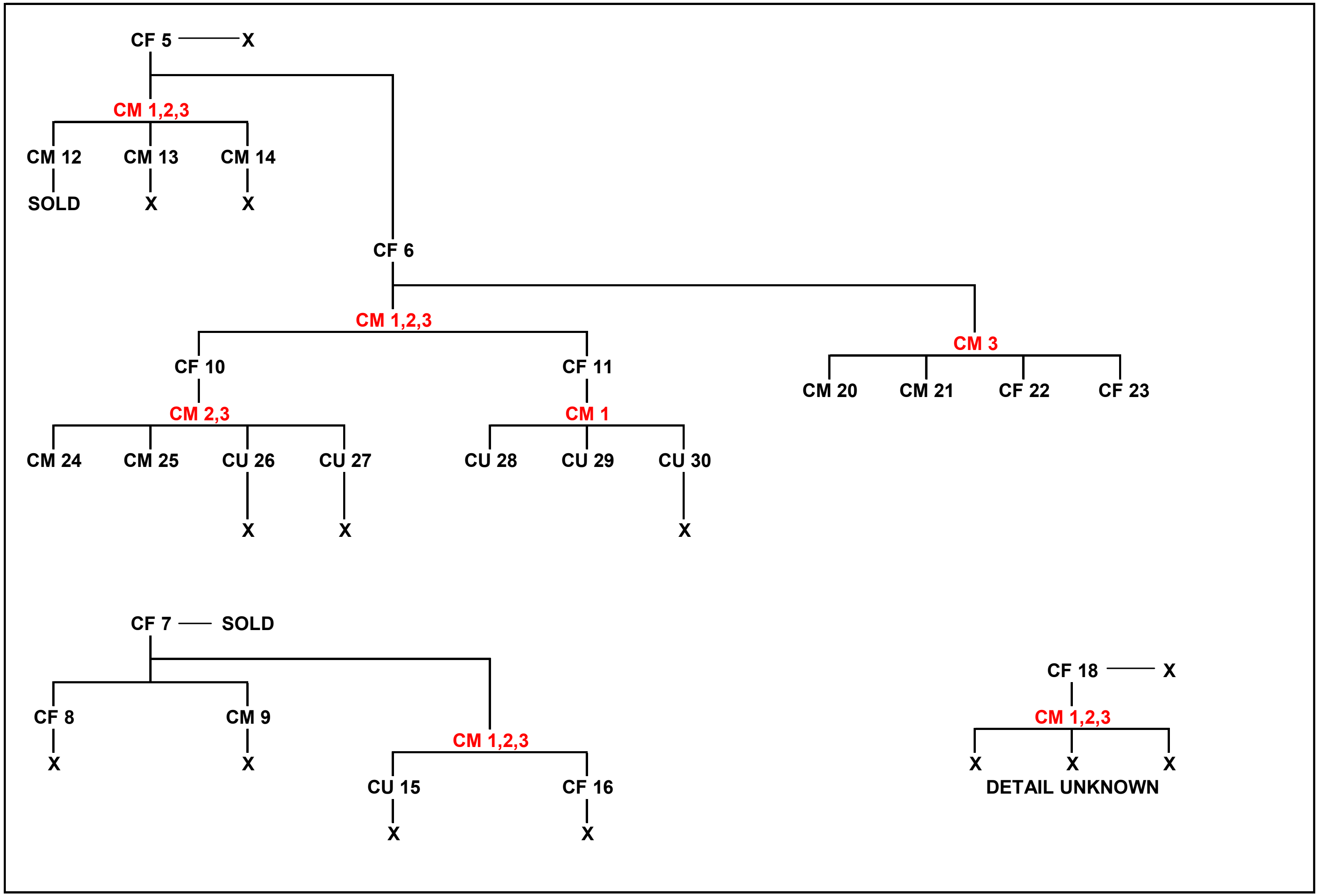


Figure 2.17: Relatedness of cheetah on Kwandwe.

(**X** cheetah that have died during the study period; cheetah males that sired the cubs. Where more than one number is given, it was not certain which male sired the cubs).

GENERAL METHODOLOGY

The general methodology used throughout the study period is detailed in this section and more specific techniques are described in detail in the relevant chapters. The field work for the study was done over a 17 month period from February 2003 to June 2004. All cheetah on Kwandwe were fitted with either a radio-collar or an implanted radio transmitter and an attempt was made to locate all animals once daily. Each day the cheetah were located using a Telonics TR-4 receiver and a two-element antenna. All location points were recorded using a GARMIN 72 global positioning system (GPS) and activity of the animal at first sighting, together with vegetation type and time of day, were recorded each time a cheetah was visually located. 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. Tourist guides assisted in gathering data on some parameters (see Observation of Cheetah).

Observation of Cheetah

Observations were usually made from 20m-50m away but during hunts this distance was far greater to ensure their hunting behaviour was not affected. Although I intended to follow active animals until they became inactive or made a kill, this was rarely possible because the dense vegetation made following the animals difficult.

One of the most effective ways of studying large carnivores is to follow them for long-term continuous sessions (Mills 1992) and I followed certain cheetah groups continuously for up to 18 days throughout the study (see Chapter 3 for details).

As a tourism operation, Kwandwe has guided game drives operating on the reserve in the early morning and late afternoon-early evening on a daily basis, and the large felids are highly sought after by the drives. When the game drives were out, I rarely remained at a sighting and relied on the rangers for information. However, I was in constant radio contact with rangers and in this way I could minimize the loss of information. Where possible the rangers' reports were confirmed by visiting the kill sites and only data that I collected or reports that I was able to confirm by site visits have been included in this thesis. Male and female cheetah have different social systems and for this reason the cheetah on Kwandwe were divided into the following groups for the purpose of analyzing the results: a three male coalition, females with cubs, females with cubs in a den, single females and independent cubs. The number of single females and females with cubs changed throughout the study due to births and deaths (Figure 2.16).

CHAPTER 3

FEEDING ECOLOGY: DIET AND PREY SELECTION

INTRODUCTION

The feeding biology of cheetah has received extensive attention in the scientific literature with most studies focussing on diet, feeding behaviour and hunting patterns (see for example Mitchell *et al.* 1965; Kruuk & Turner 1967; Pienaar 1969; Schaller 1972; Eaton 1974; Mills 1984; Durant *et al.* 1988; Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990; Caro 1994; Nowell & Jackson 1996; Hofmeyr & van Dyk 1998; Hunter 1998; Purchase & du Toit 2000). This type of information is important in understanding the general behaviour and ecology of cheetah and the potential impact that they may have on their prey (Caro 1994). From previous studies it appears that cheetah feed predominantly on the most abundant medium sized antelope in any one area, although they are also able to utilise both larger and smaller prey (Mills 1996). For example on the Serengeti Plains Thomson's gazelle is the most abundant ungulate and the cheetah's most important prey species (Caro 1994); in the Kruger National Park impala are the most abundant and they form a far greater proportion of the cheetah's diet than any other species (Mills *et al.* 2004); in Phinda Resource Reserve nyala are the most abundant species and the most common prey species in the cheetah's diet (Hunter 1998) and in the Kalahari springbuck are cheetah's most important prey species as well as the most abundant medium sized ungulate (Mills 1984).

Cheetah have an unusual 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 cheetah in coalitions can hunt larger prey than lone males or single females and hunting larger prey is one adaptation that male cheetah use to meet the increased energetic demands of group living (Schaller 1972; Caro 1994). By contrast, solitary female cheetah and females with cubs generally hunt smaller prey than male cheetah in coalitions (Eaton 1974; Hunter 1998; Caro 1994; Mills *et al.* 2004).

Sex and age ratios of prey vary considerably in the literature, for example Schaller (1972) found that 55% of Thomson's gazelle killed by cheetah in the Serengeti were subadult and that there appeared to be no selection for sex in the adult class, whereas Kruuk and Turner (1967) found a preference for adult females in the same species in the Serengeti. In contrast to this, cheetah select male Thomson's gazelle in the Serengeti (Fitzgibbon 1990), male springbok in the Kalahari (Mills 1990) and male impala in the Kruger National Park (Mills *et al*. 2004). In Nairobi National Park (Eaton 1970) and Suikerbosrand Nature Reserve (Pettifer 1981b) there is a selection for females and juveniles of prey species, while in Phinda Resource Reserve and Kruger National Park cheetah select juveniles over adults and particularly juveniles from large prey species (Hunter 1998; Mills *et al.* 2004). This variation in predation highlights the need to analyse different areas and situations individually and to compare areas with similar features.

Kill rates for cheetah vary from 51 kills/cheetah/year (Pettifer 1981b) to 341 kills/cheetah/year (Schaller 1972) and daily consumption rates vary from 1.4kg meat/cheetah/day (Mills *et al.* 2004) to 5.3kg meat/cheetah/day (Schaller 1972). The variation in kill rate will be a result of differences in predator to prey ratios, size of selected prey, levels of kleptoparasitism, group size and presence of cubs (Pettifer 1981a; Caro 1994; Durant 2000a; Mills *et al.* 2004). It will also be affected by the method used to establish kill rate (i.e. casual observations versus intense observations). In the Serengeti, where many of the herbivores migrate, cheetah experience large fluctuations in local abundance of certain prey species (Caro1994). Durant *et al.* (1988) found that the movements of female cheetah and non-resident male cheetah correspond closely to the movements of Thomson's gazelles, but those of resident male cheetah are relatively independent of the gazelle migration. It has been suggested that the kill rates of female cheetah in the Serengeti are very high because of the continuous abundance of prey (Schaller 1972) and the high percentage of kleptoparasitism (Schaller 1972; Caro 1994).

The variation in daily consumption rates reflects the kill rate and size of the species selected, but it is also due to the methods used to estimate intake. In most studies the edible percentage of carcasses is determined and then the proportion of each carcass consumed is monitored (Schaller 1972; Pettifer 1981b; Mills *et al.* 2004). However, problems arise with the estimation of the percentage edible biomass as different researchers have used different estimates (Schaller 1972; Pettifer 1981b; Mills 1992; Hunter 1998; Mills *et al.* 2004).

Riney (1982) suggested that the physical condition of an animal is a sensitive and easily measured response to the condition of its habitat. The physical condition of prey selected by predators has important implications in predator-prey studies, particularly when the condition of the prey population is known (Davis *et al.* 1987; Gallivan & Culverwell 1995; Takatsuki 2000; Oosthuizen 2004). The selection of young, healthy individuals over old, malnourished or diseased animals from a prey population that contains animals in both good and poor condition, by predators like cheetah, could lead to important consequences for management. The likely impact of cheetah on their prey species within a reserve could be estimated more accurately by monitoring the condition of animals killed by cheetah. Fat deposits are a convenient indicator of the nutritional status of animals and have been used for various species of wild ungulates (Riney 1955; Anderson 1985; Gallivan & Culverwell 1995; Takatsuki 2000; Oosthuizen 2004). In these studies, fat from three different organs was used; subcutaneous, mesentery and bone marrow fat (Takatsuki 2000). In general, kidney fat is the most reliable and most commonly used indicator of condition (Riney 1955; Anderson *et al.* 1972; Mitchell *et al.* 1976), while subcutaneous fat is not often used as it is difficult to sample (Riney 1955; Anderson *et al.* 1972; Mitchell *et al.* 1976). Bone marrow fat is easier to collect than other fat types and a high correlation exists between kidney fat index and femur bone marrow dry weight (Gallivan & Culverwell 1995; Takatsuki 2000; Husseman *et al.* 2003; Oosthuizen 2004). In predator-prey studies bone marrow fat is the most suitable method as the bones are often the only remains at a kill and therefore it is possible to get an estimate of the condition of the prey of predators such as cheetah.

The majority of cheetah studies have focused on grassland savannahs (Schaller 1972; Durant *et al.* 1988; Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990; Caro 1994; Laurenson 1994), with more recent studies in woodland habitats (Marker *et al.* 2003a, b; Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003; Radloff & du Toit 2004), but little work has been done on the diet of cheetah in non-grassland habitats. The vegetation types on Kwandwe, referred to as Valley Bushveld (Acocks 1988), are quite different from those in any other area in which cheetah have been studied. Although there are some savannah-like vegetation types (for example karroid shrubland), these are not characterized by the long grass, which would usually offer the cheetah cover. Much of the rest of the reserve is covered by vegetation types, which are characterized by very thick, succulent, and thorny bush which is quite different from the type of habitat selected elsewhere by cheetah. Thus the aim of this chapter was to establish the diet of cheetah in Valley Bushveld, looking particularly at prey selection in terms of age, size and species and how this differed between different cheetah social groups.

METHODS

Data collection

All cheetah on Kwandwe were fitted with either a radio collar or an implanted radio transmitter (as detailed in Chapter 2). I collected data on feeding ecology by four means; the daily location of all cheetah and opportunistic observation of kills, faecal analysis, body condition analysis and continuous observation of selected animals.

Daily location of all cheetah

All cheetah were located each day and, where possible, I followed the cheetah for extended periods in an attempt to observe kills as they were made. Cheetah which had already made a kill, were often located and in this case it was assumed that the cheetah on the carcass made the kill as cheetah very rarely scavenge (Schaller 1972; Caro 1994). These direct observations are likely to artificially increase the contribution of large kills to the diet, because cheetah are more likely to spend more time on larger kills and thus large kills are more likely to be found than smaller ones. In an attempt to fill these gaps in the observations, I collected faeces and undertook two-week continuous observations. It was hoped that the faecal analysis would give a more accurate indication of the species killed by cheetah, while the continuous observations would give a better indication of kill frequency and daily consumption.

Faecal Analysis

Cheetah faeces, which could be allocated to a particular cheetah, were collected opportunistically throughout the study. Hairs were extracted, washed with water, filtered and air-dried using standard methods. Cuticle scale imprints were made from the extracted hair samples using a method discussed in Keogh (1983). Gelatin (Royal) was added to hot water to make a final concentration of 5%. Clean slides were thinly coated with the gelatin solution and the hairs were placed in position using fine forceps. Six randomly selected hairs were placed on each slide and 4 slides were made for each faecal sample. The slides were allowed to dry for approximately 24 hours before the hairs were removed. Cross sections were made using a method proposed by Douglas (1989). A random selection of 10-20 hairs from each faecal sample were placed in a disposable pipette and the tube was filled with molten wax (Paraplast Plus, Sherwood Medical Co. St Louis). Once filled, the tubes were cooled rapidly in a beaker with ice cubes. The pipette was cut into sections of 1-2mm thick and ~ 8 of these sections were fixed onto microscope slides using the molten wax. A reference collection of all possible prey species on Kwandwe was produced from hair samples collected from museum specimens (Amathola Museum, King Williams Town, Eastern Cape Province) and prepared following the same method mentioned above. For each faecal sample, hairs were identified to species by comparison of cuticle scale imprints and cross sections with the reference collection and presence of a species recorded.

Bone Marrow Samples

Intact bones were collected from cheetah kills for bone marrow analysis to determine the condition of the prey. Only bones from sub adult (> 2 years old) and adult (reproductive) animals were analyzed due to the variable and age-dependent nature of juvenile fat stores (Ballard & Whitman 1987). Bones from the cheetah kills were collected as soon as the cheetah had moved out of the area where the kill had been made. All samples were frozen in plastic bags with a label indicating the species, bone, the date the bone was collected, the date the kill was made and the location of the kill. Bones remained frozen until analysis (Neiland 1970; Anderson 1985; Fuller *et al.* 1987; Davis *et al.* 1987; Takatsuki 2000), which was sometimes several weeks after collection. For the analysis, a portion of the bone marrow was removed from the central area of the bone, avoiding the hemopoietic end regions (Neiland 1970; Brooks *et al.* 1977; Davis *et al.* 1987; Takatsuki 2000). The sample was obtained by cracking the middle of the bone with a hammer and chisel. Samples of 5-15g, measured to the nearest 0.01g, were used. The samples were placed in crucibles and oven dried at 60-70ºC. Each sample was weighed on a daily basis until there was no change in the weight. This took 5-8days, which was similar to what Davis *et al.* (1987) found. The bone marrow fat index was then calculated by expressing the dry weight as a percentage of the wet weight. It is difficult to predict at what percentage bone marrow fat an animal will suffer reproductively or physiologically or when death is inevitable, due to the variable nature in the responses of animals to resource shortage. In this study the condition of an animal is characterized as good when the marrow fat index is > 85%; moderate when the marrow fat index is between 50% - 85% and poor when the marrow fat index is < 50% (Brooks *et al.* 1977; Brooks 1978; Takatsuki 2000).

Continuous Observations

Because of time constraints, it was not possible to follow each of the social groups of cheetah nor to replicate observations as often as necessary. The male coalition was observed continuously from 19 January to 4 February 2004 and from May 1 to 15 2004, and a single female was observed continuously from 28 February to 13 March 2004. I usually followed the cheetah at a distance of about 100-200m in open regions and 40-50m in more dense areas, so as not to interfere with the hunt. For the three male coalition of cheetah, which did most of their hunting at night, I used a spotlight, with a red filter that I switched off when the cheetah encountered prey and waited until a kill had been attempted before I relocated them again. If I lost the cheetah in thick bush and they remained stationery in the bush it often meant that they had killed. I determined the location of the kill using triangulation and attempted to walk into the site once the cheetah had left the area. In this way I often located fresh kill remains.

For all kills found the date, species, sex and, where possible, age (juvenile, sub-adult, adult) of the prey were recorded. Age categories were defined as follows: juvenile was a small and dependent calf; sub-adult was a young, independent animal not fully grown and not reproductively active and adult was a full grown, reproductive animal. 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.

Using three of these methods, kill lists for Kwandwe were recorded for a total of 18 months beginning in February 2003. In this study the months have been divided as follows: Year 1 – February 2003 to December 2003 and Year 2 – January 2004 to July 2004.

Data Analysis

Kills were analyzed in terms of species of ungulate killed, age, sex, size and body condition in order to determine the diet and preferences of the cheetah. Species were assigned to a size class according to the age of the prey taken and categories used by Hunter (1998; Table 3.1). Kills were analyzed seasonally (summer: December to February; autumn: March to May; winter: June to August; spring: September to November) and each year of study was analyzed separately. Kills made by the different social groups of cheetah (coalition, females with cubs, single females & independent cubs) were analyzed separately so that comparisons could be made between the groups.

Table 3.1: Prey size categories (used by Hunter 1998) and typical examples. Totals are the total number of kills (all cheetah for all months) in each size class.

Kill Size	Weight Range	Typical Examples	Total
Small	< 30kg	Grey Duiker, Steenbok, Scrub Hare and juvenile Springbok, Bushbuck, Impala	47
Medium	30 – 65kg	Springbok, Bushbuck, Impala and juvenile Kudu, Waterbuck, Ostrich, Gemsbok, Blue Wildebeest, Red Hartebeest, Blesbok	134
Large	> 65kg	Kudu, Waterbuck, Red Hartebeest, Blesbok Burchell's Zebra and Eland	43

Prey Preference Index

To determine whether cheetah at Kwandwe selected certain ungulate species preferentially, a preference index was calculated for each prey species (Pienaar 1969). The preference indices were calculated as follows:

$$\text{Preference Index} = \frac{\text{kill frequency of prey}}{\text{relative abundance of prey}}$$

Kill frequency was calculated as the number of individuals of a particular species, killed by the cheetah, relative to the number of individuals of all species killed. The relative abundance of prey was based on game counts derived from the annual aerial census method and is the abundance of a particular species relative to the abundance of all prey species. A preference index of one indicates that the species was killed according to its abundance on the reserve. An index above one shows that the cheetah were preferentially selecting for the species and an index below one indicates that the prey species was not actively hunted and was avoided when it was encountered opportunistically. Prey preference indices were calculated for all cheetah on Kwandwe (i.e. at a reserve level) and separately for each vegetation type and for certain groups and individuals at a home range level. For the latter analyses a kernel utilisation distribution (95% UD, H=1000; ArcView 3.2; Animal Movement Analysis Extension; Hooge and Eichenlaub 1997) was used to determine the cheetah's home ranges. Using the aerial game counts for each year, the ungulate composition was calculated within each cheetah group's home range and these data were used to calculate the preference indices of each cheetah group. Species such as forest dwelling ungulates like duiker and bushbuck tend to be underestimated using aerial game counts (Bothma 2002) and this may result in an artificially elevated preference index.

Calculation of Daily Food Intake and Kill Rate

The total biomass consumed by all cheetah was calculated from the kill list. The edible biomass from a carcass was estimated from personal observations and the categories suggested by Blumenschine & Caro (1986) of carcass weight > 80kg = 67%, carcass weight 40-80kg = 75%, carcass weight 5-40kg = 90%, carcass weight <5kg =99%. The carcass weight was estimated for every kill, according to age, sex and species using published data on herbivore weights (Bothma 2002; Meissner 1982).

Because many kills were missed during the daily direct observations, average kill rates and daily intake rates (kg of meat/cheetah/day) were calculated from the two-week continuous observations on the coalition and single female.

Statistical Analyses

MANOVAs were used to test the effect of social group, season and year on the size, age and sex of kills made by the cheetah on Kwandwe. Chi-squared tests were used to asses whether cheetah were selecting certain prey by comparing availability of prey species to the rate they were killed by cheetah and by comparing availability of prey species in each habitat type to the numbers killed. All statistical analyses were done using Statistica.

RESULTS

General analysis of diet

A total of 224 kills, representing 15 species, were recorded over a period of 18 months for the entire cheetah population on Kwandwe (Table 3.2). 98.7% of cheetah kills were mammals and cheetah always ate from all species they killed.

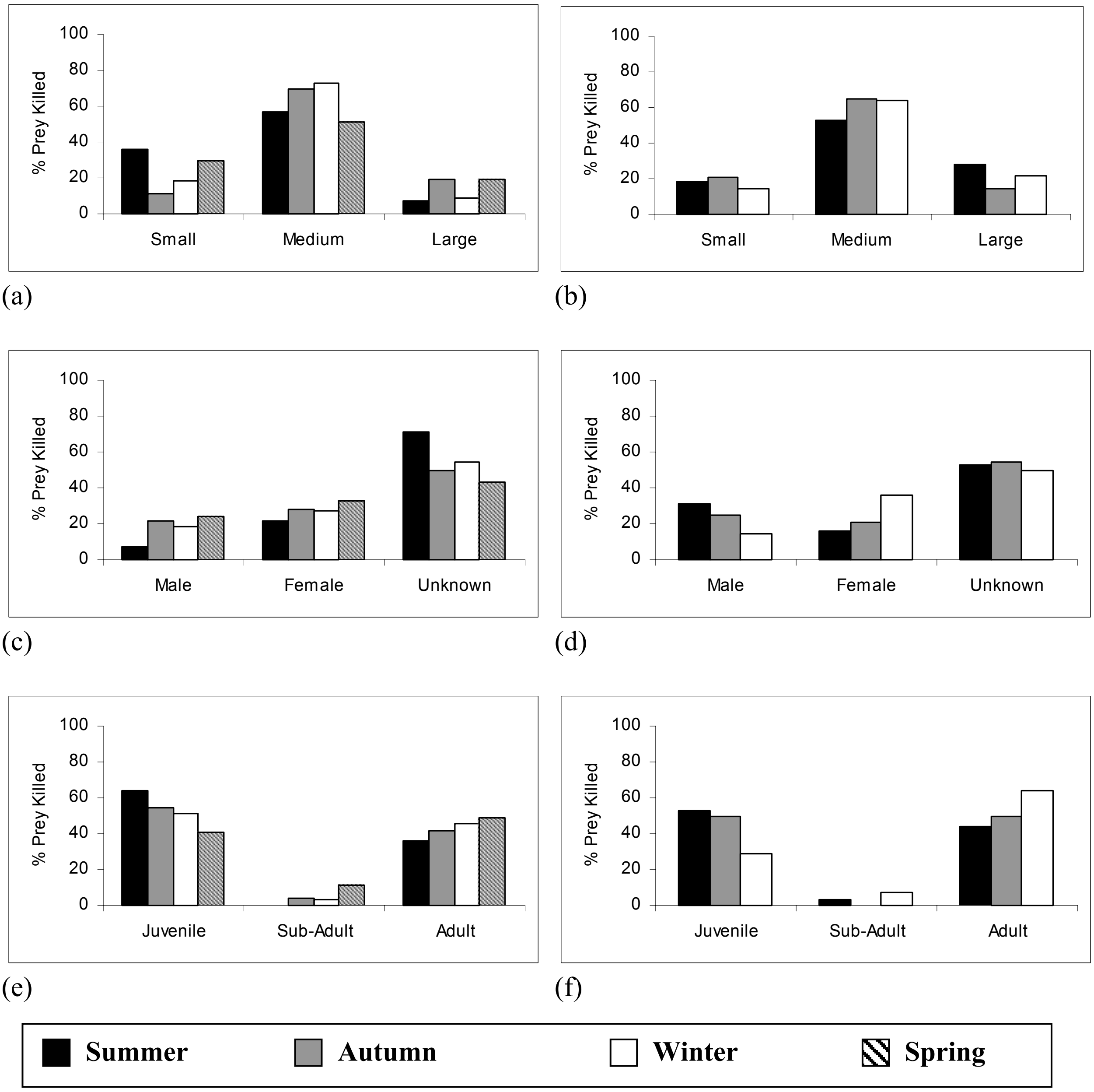
Table 3.2: Complete list and edible biomass of all prey species killed by cheetah. Mass of individuals is from Bothma (2002) and Meissner (1982). The edible biomass for all the individuals of each species is estimated from the categories suggested by Blumenschine & Caro (1986) and takes into account the age of the kills.

Prey species	Kills		Mass of indiv. (kg)			Edible Biomass	
	No	%	Juvenile	Male	Female	Kg	%
Kudu	96	42.9	55	220	155	4836.2	54.5
Springbok	28	12.5	12	41	31	721.7	8.1
Grey Duiker	27	12.1	8	17	21	403.4	4.5
Bushbuck	17	7.6	17	60	36	601.3	6.8
Impala	16	7.1	19	60	45	469	5.3
Blesbok	11	4.9	23	75	67	550.9	6.2
Red Hartebeest	7	3.1	30	150	120	434.5	4.9
Burchell's Zebra	6	2.7	95	335	290	402.9	4.5
Steenbok	4	1.8	5	11	11	33.2	0.4
Ostrich	3	1.3	35	120	120	89.8	1.0
Waterbuck	3	1.3	50	260	180	107.2	1.2
Scrub Hare	2	0.9	0.5	4.5	3	8.5	0.1
Gemsbok	2	0.9	55	240	210	81	0.9
Eland	1	0.4	160	650	460	107.2	1.2
Blue Wildebeest	1	0.4	51	200	160	30.9	0.3
Total	224	100				8877.7	100.0

Five of the 15 species (kudu, springbok, grey duiker, impala and bushbuck) preyed on by the cheetah at Kwandwe comprised 82.2% of the animals killed and 79.2% (7031.6kg) of the total edible biomass of the kills (Table 3.2). Analysis of both numbers of animals killed and their edible biomass is necessary since a small number of large kills may make a similar contribution to the cheetah's energetic and nutrient requirements as a larger number of smaller kills. Kudu formed a far greater proportion of the diet (42.9%; Table 3.2) than any other species.

In terms of size of the prey, more than half of the kills recorded over the study period, for all seasons, by the entire cheetah population on Kwandwe, were of the medium size class (Figure 3.1a, b). However there was a significant difference in the way in which male, female, female cheetah with cubs and independent cubs utilized prey of different size classes ($p < 0.001$; compare Figures 3.2, 3.3, 3.4 & 3.5). The male cheetah's (coalition) diet consisted of a significantly greater proportion of larger prey items in all seasons except for the winter of year 1, when more medium sized prey were consumed (Figure 3.2a,b). The coalition killed very few small prey (Figure 3.2a, b). Female cheetah and females with cubs preyed more on medium and small sized prey (Figures 3.3a, b & 3.4a, b) and independent cubs concentrated on smaller prey items in winter and medium and small prey items in spring and summer (Figure 3.5a).

The number of kills where the sex was not known was high (Figure 3.1c, d) and this was due to the high percentage of juveniles killed by the cheetah. A large number of juvenile kudu were killed and it is very difficult to determine the sex of kudu in this age class. Overall, there was no significant difference in the number of male and female ungulates killed ($p > 0.05$; Figure 3.1c, d). There was however a significant interaction between cheetah group and the number of males and females killed ($p < 0.05$). Independent cheetah cubs killed significantly more males than females ($p < 0.05$) and the coalition killed more females than males. Although there were some seasonal differences in the predation on male and female ungulates (compare Figures 3.2c, d; 3.3c, d; 3.4c, d; 3.5b), these were not significant ($p > 0.05$). Overall, significantly more juveniles and adults were killed than sub-adults ($p < 0.001$; Figure 3.1e, f) and this pattern was shown by all the cheetah groups (compare Figures 3.2e, f; 3.3e, f; 3.4e, f; 3.5c). 77% of all kudu killed were juvenile. Although the differences between the cheetah social groups were not significant, the single female cheetah killed a higher proportion of juveniles, than females with cubs, the coalition and independent cubs. Whether or not these differences represent a preference for a particular age or gender can only be established by comparison of the kills with the available prey. Data on the age and gender structure were only available for kudu, impala and bushbuck (Table 3.3), which happened to be three of the five most important prey species. Predation on juvenile kudu was significantly greater than expected from the availability of juveniles in year 1 and 2 (year 1: χ^2=266.7, df=1, $p < 0.05$; year 2: χ^2=982, df=1, $p < 0.05$; Tables 3.3 & 3.4). Similar analyses were not possible for impala and bushbuck, because the game counts were done out of the impala lambing season and although bushbuck lamb throughout the year juveniles are very often hidden and were missed during aerial census. Cheetah killed significantly more adult female kudu in year 1 than expected (χ^2=5.9, df=1, $p < 0.05$; Table 3.5), whereas in year 2 adult female kudu were killed according to availability (χ^2= 0, df=1, $p > 0.05$; Table 3.5). In both years 1 and 2, cheetah killed significantly more adult male impala and bushbuck than expected (year 1: χ^2=138.5, df=1, $p < 0.05$; year 2: χ^2=14.7, df=1, $p < 0.05$; Table 3.5).



(a) (b)

(c) (d)

(e) (f)

Figure 3.1: Seasonal variation in size, sex and age classes preyed upon by all cheetah on Kwandwe. (a, c, e = Year 1; b, d, f = Year 2; no data available for spring in Year 2; n=224).

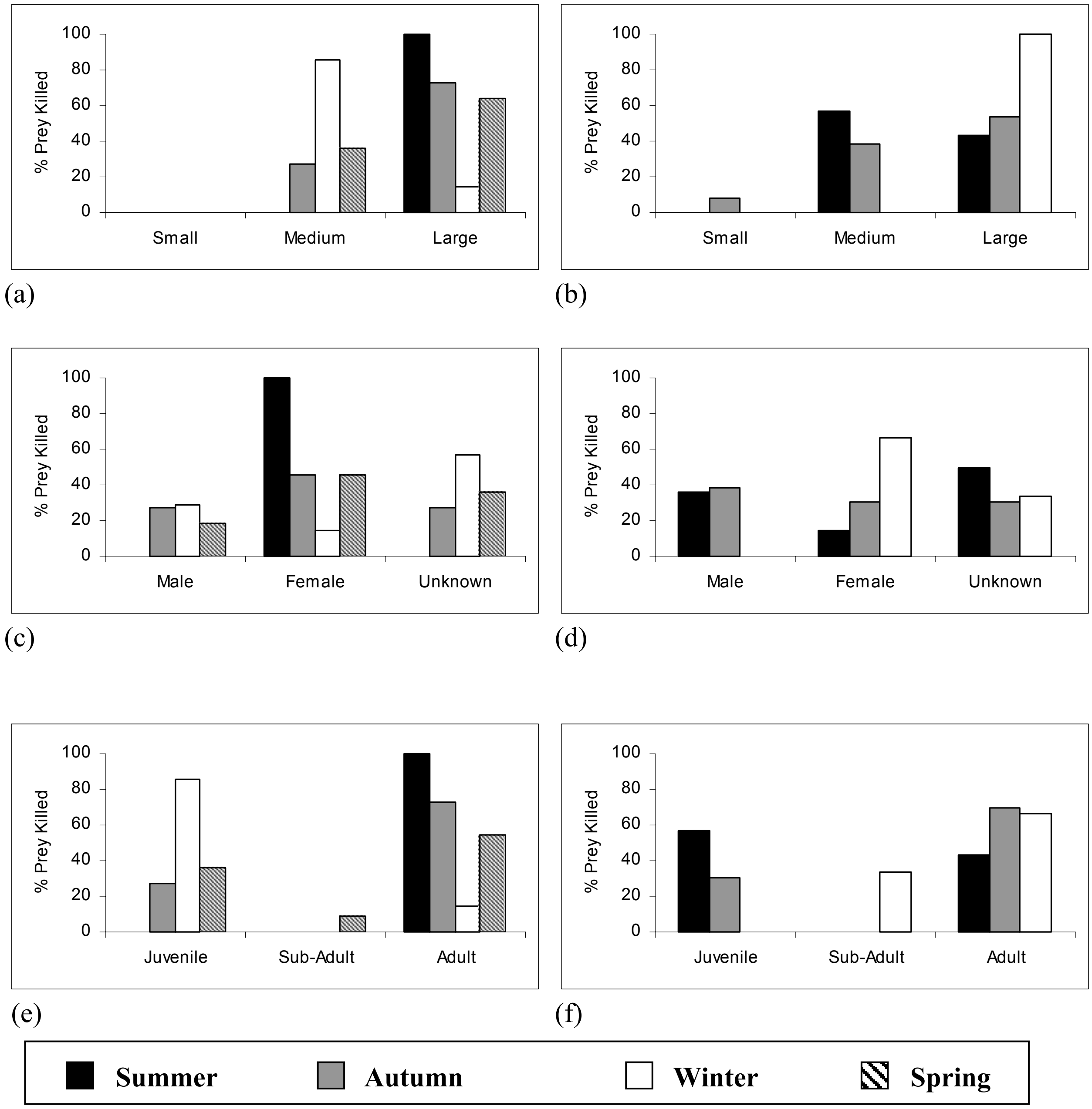


Figure 3.2: Seasonal variation in size, sex and age classes preyed upon by the 3 male coalition.

(a, c, e = Year 1; b, d, f = Year 2; no data available for spring in Year 2; n=60).

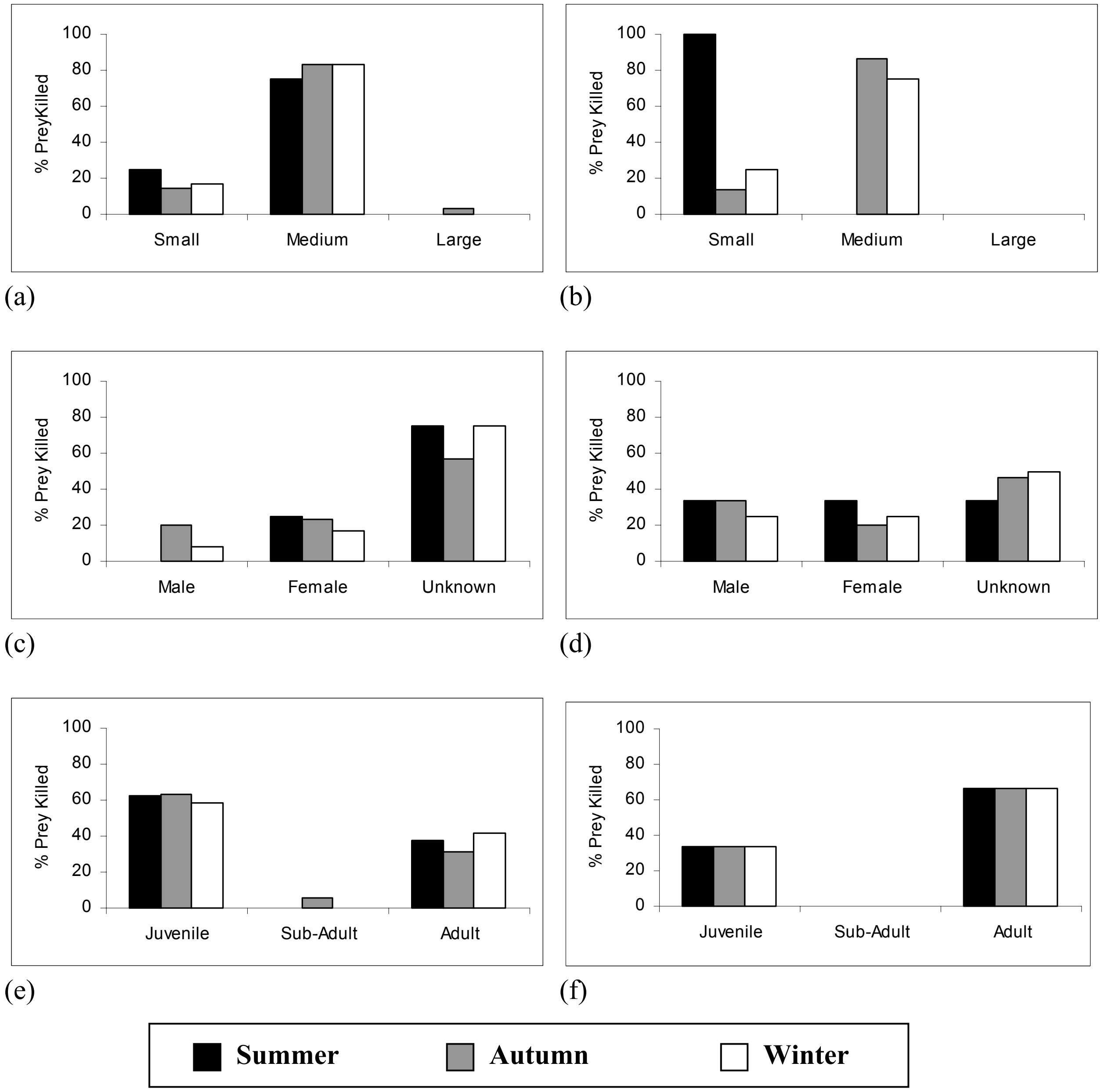
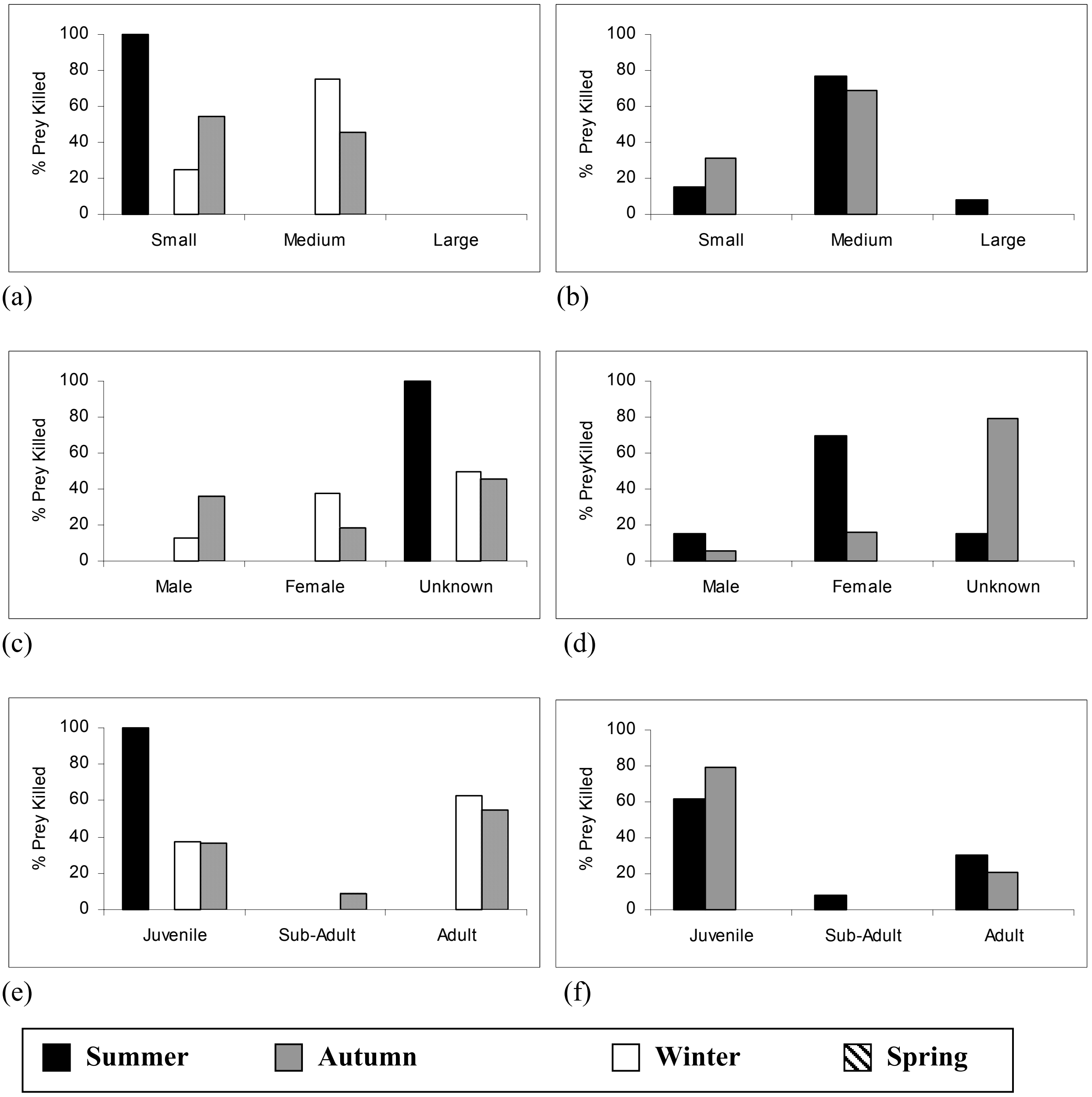


Figure 3.3: Seasonal variation in size, sex and age classes preyed upon by females with cubs. (a, c, e = Year 1; b, d, f = Year 2; no females with cubs in spring of Year 1; no data available for spring in Year 2; n=85; kills for 6 different female plus cub groups).



(a) (b)

(c) (d)

(e) (f)

Figure 3.4: Seasonal variation in size, sex and age classes preyed upon by single female cheetah. (a, c, e = Year 1; b, d, f = Year 2; no single females in autumn of Year 1 and winter of Year 2; no data available for spring in Year 2; n=53; kills for 4 different single females).

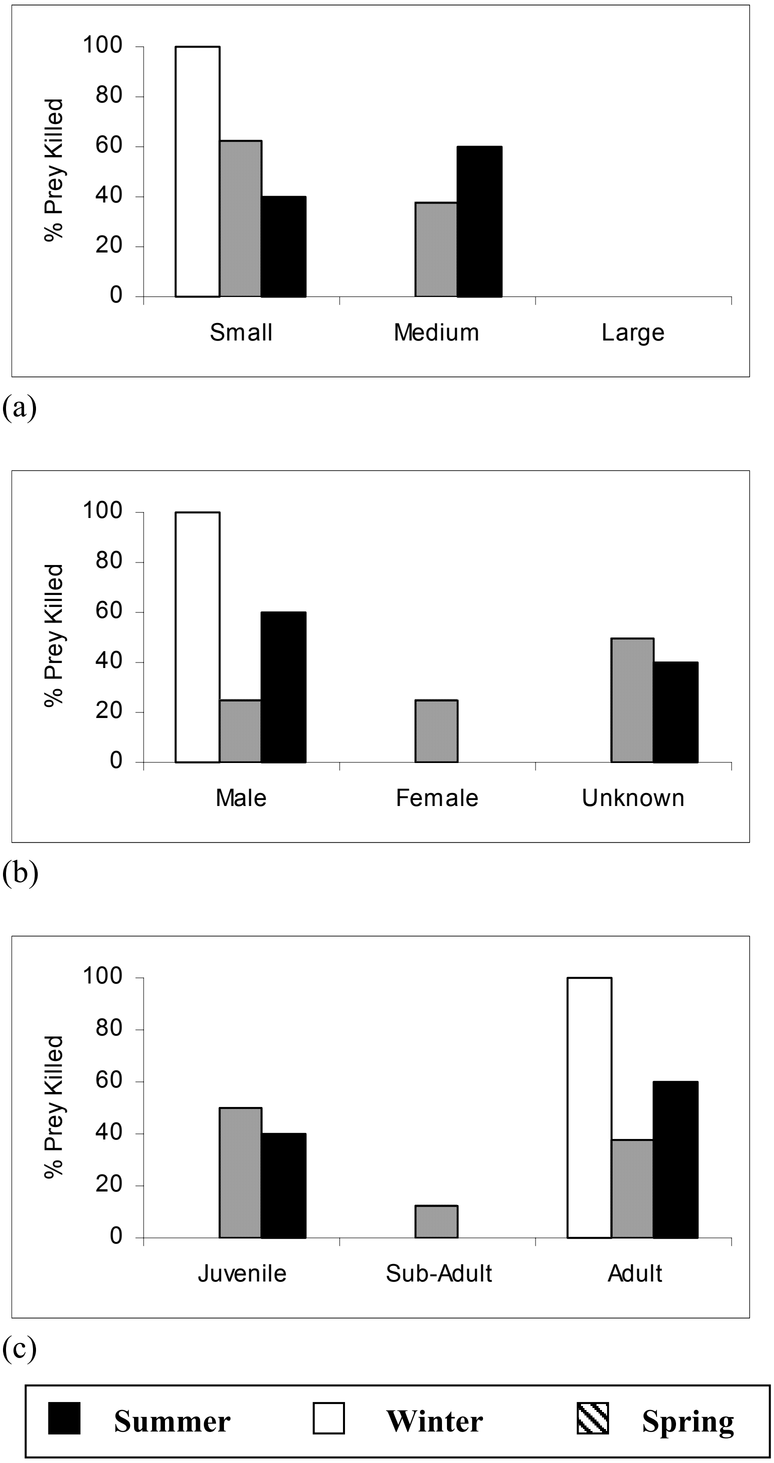


Figure 3.5: Seasonal variation in size, sex and age classes preyed upon by independent cubs. (a,b,c = Year 1; no independent cubs in autumn of Year 1 & 2; no data available for spring in Year 2; n=14; kills for one set of independent cubs).

Table 3.3: Ungulate population data for three of the five most important prey species of cheetah on Kwandwe.
Figure in parenthesis is the percentage of each sex class present in the population. Juveniles could not be sexed and the number in parenthesis is the number of juveniles as a percentage of the total. Data are from annual game counts.

SPECIES	Year 1 (2003)				Year2 (2004)			
	TOTAL	FEMALE	MALE	JUVENILE	TOTAL	FEMALE	MALE	JUVENILE
KUDU	1602	950 (70.2)	403 (29.8)	249 (15.5)	1422	934 (70.0)	401 (30.0)	87 (6.1)
BUSHBUCK	204	130 (63.7)	74 (36.3)	0	166	92 (55.4)	74 (44.5)	0
IMPALA	434	348 (80.2)	86 (19.8)	0	306	208 (67.9)	98 (32.1)	0

Table 3.4: Cheetah prey by age classes.

Figure in parenthesis is the percentage of each age class preyed on by the cheetah.

SPECIES	Year 1 (2003)				Year 2 (2004)			
	TOTAL	ADULT	SUB-ADULT	JUVENILE	TOTAL	ADULT	SUB-ADULT	JUVENILE
KUDU	59	10 (16.9)	5 (8.5)	44 (74.5)	37	7 (18.9)	0	30 (81.1)
BUSHBUCK	12	9 (75)	1 (8.3)	2 (16.2)	5	4 (80)	0	1(20)
IMPALA	11	5 (45.5)	1 (9.1)	5 (45.5)	5	5 (100)	0	0

Table 3.5: Cheetah prey by gender.

Figure in parenthesis is the number of each gender preyed on by the cheetah as a percentage of the total that could be sexed.

SPECIES	Year 1 (2003)				Year 2 (2004)			
	TOTAL	FEMALE	MALE	Unknown	TOTAL	FEMALE	MALE	Unknown
KUDU	59	13 (81.3)	3 (18.7)	43(73)	37	7 (70.0)	3 (30)	27(73)
BUSHBUCK	12	6 (54.5)	5 (45.5)	1(8.3)	5	1(20)	4 (80)	0
IMPALA	11	2 (33.3)	4 (66.7)	5(45)	5	2 (50)	2 (50)	1(20)

Faecal Analysis

Ninety seven cheetah faecal samples were analysed, of which 53% were from the coalition, 37% from females with cubs, 8% from single females and 2% from independent cubs. Twelve species of prey were found in the cheetah faeces analysed. The species composition in the faeces was very similar to that found in the observed kills, with only two new additions to the kill list, being an unidentified rodent and black backed jackal (Table 3.6). A higher percentage of kudu (63.9%), blesbok (6.2%) and waterbuck (5.2%) were found in the cheetah faeces compared to the observed kills (Table 3.6). Overall, the five dominant prey species in the observed kills represented 80.5% of specimens in the cheetah faeces analysed. Most faeces contained hair from a single species and only six faecal samples had hair from two or more species.

Table 3.6: Results of the faecal analysis showing the species found in the faecal samples. The prey species recorded by direct observations have been included to allow comparison.

Prey species	Obs.Kills		Faeces	
	No	%	No	%
Kudu	96	42.9	62	63.9
Springbok	28	12.5	6	6.2
Grey Duiker	27	12.1	2	2.1
Bushbuck	17	7.6	2	2.1
Impala	16	7.1	6	6.2
Blesbok	11	4.9	6	6.2
Red Hartebeest	7	3.1	1	1.0
Burchell's Zebra	6	2.7	0	0.0
Steenbok	4	1.8	0	0.0
Ostrich	3	1.3	0	0.0
Waterbuck	3	1.3	5	5.2
Scrub Hare	2	0.9	1	1.0
Gemsbok	2	0.9	0	0.0
Eland	1	0.4	0	0.0
Blue Wildebeest	1	0.4	1	1.0
Rodent	0	0.0	1	1.0
Black Backed Jackal	0	0.0	4	4.1
Total	224	100.0	97	100.0

Kudu was the most abundant species identified in the faeces of the coalition (54.9%), followed by blesbok (11.8%) and waterbuck (7.8%; Table 3.7). By contrast, in the faeces of the female cheetah with cubs, kudu (75%) was the most abundant species identified, followed by impala (11.1%) and bushbuck (5.6%; Table 3.7). For the coalition, faecal analysis added three new species to the kill list (an unidentified rodent species, scrub hare & black backed jackal); whereas only two new species were found in the faeces of the females with cubs (black backed jackal & waterbuck; Table 3.7). The sample size of faeces from single female cheetah and independent cheetah cubs was too low for detailed analysis.

Table 3.7: Results of the faecal analysis showing the percent occurrence of species found in the faecal samples and recorded by direct observation (Obs) for the various cheetah social groups on Kwandwe.

Prey species	**Coalition**		**Females with cubs**		**Single Females**		**Independent Cubs**	
	Obs	**Faeces**	**Obs**	**Faeces**	**Obs**	**Faeces**	**Obs**	**Faeces**
Kudu	40.0	54.9	47.6	75.0	48.1	75	21.4	50
Springbok	6.7	9.8	19.0	0.0	13.5	12.5	7.1	0
Grey Duiker	0.0	0.0	11.9	2.8	19.2	12.5	35.7	0
Bushbuck	0.0	0.0	7.1	5.6	7.7	0	21.4	0
Impala	1.7	2.0	10.7	11.1	5.8	0	14.3	50
Blesbok	18.3	11.8	0.0	0.0	0.0	0	0.0	0
Red Hartebeest	10.0	2.0	0.0	0.0	0.0	0	0.0	0
Burchell's Zebra	10.0	0.0	0.0	0.0	0.0	0	0.0	0
Steenbok	0.0	0.0	2.4	0.0	3.8	0	0.0	0
Ostrich	3.3	0.0	1.2	0.0	0.0	0	0.0	0
Waterbuck	3.3	7.8	0.0	2.8	1.9	0	0.0	0
Scrub Hare	0.0	2.0	1.2	0.0	1.9	0	0.0	0
Gemsbok	3.3	0.0	0.0	0.0	0.0	0	0.0	0
Eland	1.7	0.0	0.0	0.0	0.0	0	0.0	0
Blue Wildebeest	1.7	2.0	0.0	0.0	0.0	0	0.0	0
Rodent	0.0	2.0	0	0.0	0	0	0.0	0
Black Backed Jackal	0.0	5.9	0	2.8	0	0	0.0	0
Sample Size*	60	51	85	36	53	8	14	2

* Sample size is the number of kills made by the cheetah and the total number of faeces analysed for each group.

Condition of prey

Because of the small sample sizes, this analysis has been done for all cheetah and not for individual social groups. The overall condition of animals killed by cheetah was moderate with an average Bone Marrow Index (BMI) of ~ 61% (Table 3.8). The mean BMI of springbok was moderate, and the highest of all prey species while the mean BMI of bushbuck was poor and the lowest (~ 25%; Table 3.8). The condition of male and female animals was very similar with an average BMI of 65% (Table 3.9).

Table 3.8: Condition of cheetah kills analysed in terms of prey species with sample sizes and mean and standard deviations of BMI for each species.

Species	n	BMI
Bushbuck	6	24.7±7.3
Grey Duiker	3	42±30.3
Impala	8	79.7±27.3
Kudu	10	73.8±25.8
Springbok	8	83.3±11.7
Total	35	60.7±25.9

Table 3.9: Comparison of the condition of male and female animals killed by cheetah with sample sizes and mean and standard deviations of BMI.

Sex	n	BMI
Female	18	67.4±29.6
Male	17	63.1±29.3
Total	35	65.3±3.1

Prey Preference

Reserve level

The calculation of prey preference indices for all cheetah in all vegetation types in year 1 and year 2 has generated values from a maximum of 9.2 for blesbok in year 2 to a minimum of 0.0 for blue wildebeest and gemsbok (year 1) and eland and ostrich (year 2) (Tables 3.10 & 3.11). In this analysis, values below 0.8 have been interpreted as indicating avoidance, values between 0.8 and 2 as indicating that the prey was utilized according to its abundance on the reserve and values greater than 2 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. In terms of preference ratings kudu, which was by far the most common prey item, was killed according to its relative abundance in years 1 and 2. By contrast, blesbok which was not one of the top five prey species had the highest preference index in year 1 and year 2, suggesting that it was hunted preferentially. However, high preference indices should be interpreted with caution since, while they may reflect true preference, they can be artificially elevated. For example, if the population of a prey species on a reserve is very small then single predation incidents will produce a very high preference rating. This may be the case with blesbok, which were present in low numbers (see Chapter 2) on the reserve. Interestingly impala, which are the most common prey species of cheetah in other reserves (Kruger National Park, Pienaar 1969; Broomhall *et al.* 2003; Eaton 1974) and are abundant on Kwandwe, were avoided by cheetah on Kwandwe (Tables 3.10 & 3.11). Springbok and grey duiker were hunted opportunistically in year 1 and 2, while bushbuck were hunted preferentially in year 1. Chi-squared analyses of these data indicate a significant difference between observed and expected kills in year 1 and 2, assuming that the cheetah hunted at random (year 1: $\chi^2=27.6$, df=13, $p < 0.01$; year 2: $\chi^2=174.7$, df=13, $p < 0.001$).

Table 3.10: Preference indices for species killed by all cheetah on Kwandwe in 2003 (Year 1). The total number is the number of individuals of each species derived from the annual game count in Year 1.
Size categories of the prey species (L = large; M = medium; S = small) are included to allow comparison.

Species	Total No.	No. Killed	Preference Index	Size Category
Blesbok	58	4	2.4	L/M
Blue Wildebeest	252	0	0.0	L
Burchell's Zebra	175	3	0.6	L
Bushbuck	204	12	2.0	S/M
Grey Duiker	337	16	1.6	S
Eland	96	1	0.4	L
Gemsbok	131	0	0.0	M
Impala	434	11	0.9	S/M
Kudu	1602	59	1.3	M/L
Ostrich	77	3	1.3	S
Red Hartebeest	318	3	0.3	L/M
Springbok	510	13	0.9	S/M
Steenbok	69	1	0.5	S
Waterbuck	109	2	0.6	M/L
TOTAL	4372	128		

Table 3.11: Preference indices for species killed by all cheetah on Kwandwe in 2004 (Year 2). The total number is the number of individuals of each species derived from the annual game count in Year 2.
Size categories of the prey species (L = large; M = medium; S = small) are included to allow comparison**.**

Species	Total No.	No. killed	Preference Index	Size Category
Blesbok	29	7	9.2	L/M
Blue Wildebeest	173	1	0.2	L
Burchell's Zebra	172	3	0.7	L
Bushbuck	166	5	1.2	S/M
Grey Duiker	237	11	1.8	S
Eland	81	0	0.0	L
Gemsbok	166	2	0.5	M
Impala	306	5	0.6	S/M
Kudu	1422	37	1.0	M/L
Ostrich	91	0	0.0	S
Red Hartebeest	183	4	0.8	L/M
Springbok	403	15	1.4	S/M
Steenbok	50	3	2.3	S
Waterbuck	99	1	0.4	M/L
TOTAL	3578	94		

Prey preference in each habitat type

The analysis of prey preference at a reserve level does not take into account the fact that cheetah did not use all parts of the reserve and all vegetation types equally, or that the prey species were not spaced equally through the reserve. Using the game count data for 2003 and 2004 I characterized each vegetation type according to the ungulates that were present (Appendix B & C). Using this information and the data on kills in the different vegetation types (Tables 3.12 & 3.13); I calculated prey preferences within each vegetation type (Tables 3.14 & 3.15). In year 1 cheetah made most of their kills in karroid shrubland, short *Euphorbia* thicket, bushclump karroid thicket and *Euphorbia Portulacaria* mosaic (Table 3.12), whereas in year 2 the majority of kills were made in karroid shrubland, short *Euphorbia* thicket and medium *Portulacaria* thicket (Table 3.13). In year 1 cheetah selected kudu in bushclump karroid thicket, karroid shrubland and old lands, whereas in year 2 cheetah killed kudu according to their abundance in all vegetation types (Tables 3.14 & 3.15). In year 1, springbok were killed opportunistically in short *Euphorbia* thicket and avoided in all other vegetation types, whereas in year 2 springbok were selected in drainage line thicket and short *Euphorbia* thicket and killed opportunistically in bushclump karroid thicket (Tables 3.14 & 3.15). Grey duiker were selected for in karroid shrubland in year 1 and bushclump karroid thicket and riverine thicket in year 1 and 2, and killed opportunistically in *Euphorbia Portulacaria* mosaic and medium *Portulacaria* thicket in year 1 and 2 respectively (Tables 3.14 & 3.15). In year 1 bushbuck were selected for in bushclump karroid thicket, bushclump savannah thicket, karroid shrubland and short *Euphorbia* thicket and killed opportunistically in *Euphorbia Portulacaria* mosaic and riverine thicket, whereas in year 2 bushbuck were selected for in short *Euphorbia* thicket and riverine thicket and killed opportunistically in tall *Euphorbia* thicket and avoided in medium *Portulacaria* thicket (Tables 3.14 & 3.15). Impala were selected for in riverine thicket in year 1 and killed according to their abundance in bushclump karroid thicket, *Euphorbia Portulacaria* mosaic and karroid shrubland and avoided in all other vegetation types, whereas in year 2, impala were selected for in drainage line thicket, hunted opportunistically in bushclump karroid thicket and medium *Portulacaria* thicket and avoided in all other vegetation types (Tables 3.14 & 3.15). Chi-squared analyses of these data indicate a significant difference between observed and expected kills in all vegetation types in year 1 ($p < 0.05$ for all) and in all vegetation types except medium *Portulacaria* thicket in year 2 ($p < 0.001$; $p > 0.05$ for medium *Portulacaria* thicket; see Appendix G for chi-squared values).

Prey preference at a home range level

The data presented here are for kudu, the most important prey species on Kwandwe, and impala, an important prey species on many other reserves. The three male coalition selected for kudu in year 1, whereas in year 2 kudu were killed according to their abundance. Impala were avoided in both years by the coalition (Table 3.16). Females with cubs either avoided kudu or killed kudu according to their abundance, except for one female (CF6) which selected for kudu calves in year 1 (Table 3.16). CF6 with cubs selected mainly for juvenile kudu, although she was once found on an adult female kudu. Single females either avoided kudu or killed kudu according to their abundance (Table 3.16). Impala were avoided by all females with cubs and all single females in both years except for one female (CF6) who killed impala according to their abundance in her home range (Table 3.16). There are no comparable data for females with cubs in a den as these animals were not disturbed while their cubs were hidden and the sample size of the independent cubs was too small for comparison.

Table 3.12: Analysis of cheetah kills by vegetation type in 2003 (Year 1).
For each prey species in each vegetation type, the first number is the number of that species killed in the vegetation type as a percentage of all kills in that vegetation type. The number in parenthesis is the availability of that prey species in the vegetation type, as a percentage of all ungulates in the vegetation type.

PREY SPECIES	BKT	BST	DLT	EPM	KSL	MPT	OL	RT	SET	TET
Blesbok	0(2.5)	0(0.5)	0	0(0.1)	10.3(5.1)	0	0	0	0	0
Blue Wildebeest	0(10.8)	0	0(41.2)	0(2.1)	0(9.8)	0(0.3)	0(6.2)	0(4.6)	0(7.2)	0(3.5)
Burchell's Zebra	0	0(13.7)	0	0(2.6)	5.1(8.2)	0(2)	0	0(1.4)	4.3(1.8)	0(10.5)
Bushbuck	8.3(4.1)	33.3(7.7)	0	4.5(3.6)	2.6(0.4)	0(5.6)	0(6.1)	22.2(14.1)	17.4(1.2)	25(41.3)
Grey Duiker	29.2(3.2)	0(6.6)	0(17.6)	27.3(16.6)	5.1(0.6)	0(15.5)	0	11.1(3.9)	0(4.3)	0(4.2)
Eland	0(7)	0(5.5)	0	4.5(1)	0(4.6)	0	0	0	0(1)	0
Gemsbok	0(3.8)	0	0(2.9)	0(2.7)	0(1.4)	0(2)	0	0	0(7.2)	0
Impala	12.5(6.3)	33.3(34.4)	0	4.5(4.5)	7.7(5.8)	50(0.3)	0	11.1(3.5)	0(25)	25(0)
Kudu	37.5(13.7)	33.3(22.9)	100(2.9)	54.5(59.6)	33.3(11.3)	50(63.6)	100(27.2)	44.4(36.3)	56.5(34.4)	50(40)
Ostrich	4.2(5.1)	0(2.2)	0	0(0.4)	5.1(3.1)	0	0	0(1.1)	0(2.1)	0
Red Hartebeest	0(6)	0(3.3)	0	4.5(3.7)	1(12.2)	0(7.1)	0(3)	11.1(15.8)	0(6.9)	0
Scrub Hare	0	0	0	0	2.6(?)	0	0	0	4.3(?)	0
Springbok	4.2(26.7)	0	0(5.9)	0(0.1)	25.6(33.9)	0	0(33.3)	0(13.4)	8.7(5.9)	0
Steenbok	0(7.3)	0(2.2)	0(2.9)	0(0.6)	0(2.6)	0	0	0(1.1)	1(0.6)	0(0.7)
Waterbuck	4.2(3.5)	0(1.1)	0	0(2.4)	0(1.1)	0(4)	0(24.2)	0(4.9)	4.3(2.4)	0
Total*	24	3	2	22	39	2	2	9	23	4

* Total number of kills made by the cheetah in each vegetation type.
? Unknown abundance.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Table 3.13: Analysis of cheetah kills by vegetation type in 2004 (Year 2).

For each prey species in each vegetation type, the first number is the number of that species killed in the vegetation type as a percentage of all kills in that vegetation type. The number in parenthesis is the availability of that prey species in the vegetation type, as a percentage of all ungulates in the vegetation type.

PREY SPECIES	BKT	BST	DLT	EPM	KSL	MPT	OL	RT	SET	TET
Blesbok	0(1.7)	0	14.3(0)	0	17.2(3.4)	0	0	14.3(0.3)	0(0.1)	0
Blue Wildebeest	0(12.4)	0(1.5)	0	0(2.1)	3.4(6.1)	0(0.5)	0	0(1)	0(7.6)	0
Burchell's Zebra	0(4.3)	0(11.7)	14.3(2.4)	20(3.6)	0(6.1)	0(1.4)	0	0	6.3(5.7)	0(13.9)
Bushbuck	0(0.5)	0(10.7)	0(1.7)	0(3.6)	0(0.2)	5.3(9.7)	0	14.3(1.1)	12.5(1.4)	50(42.6)
Grey Duiker	22.2(3.1)	0(4.1)	0(6.8)	0(14.1)	0(0.7)	26.3(16.6)	0(2.1)	28.6(2.1)	6.3(4.2)	50(4.6)
Eland	0(1)	0(4.1)	0	0(6.2)	0	0	0	0	0(1.6)	0
Gemsbok	0(4.1)	0	0(32.2)	0(4.9)	6.9(4.4)	0(4.1)	0	0(3.5)	0(4.9)	0(3.7)
Impala	11.1(8.1)	0(32.1)	14.3(6.8)	0(1.7)	3.4(9.5)	5.3(5.1)	0	0	6.3(15.5)	0
Kudu	22.2(23.4)	0(30)	42.9(45.8)	80(54.8)	20.7(13.5)	63.2(57.1)	0(58.3)	42.9(58.7)	43.8(40.9)	0(32)
Ostrich	0(5.7)	0	0	0(1)	0(5.8)	0	0(8.3)	0(2.8)	0(1.6)	0
Red Hartebeest	0(13.6)	0(5.1)	0	0(4.6)	13.8(2.7)	0	0(29.2)	0(1.1)	0(5.6)	0
Scrub Hare	0	0	0	0	0	0	0	0	0	0
Springbok	22.2(16.9)	0	14.3(3.4)	0	34.5(42.6)	0	0	0(13.5)	12.5(5.3)	0
Steenbok	11.1(3.6)	0(0.5)	0	0(1.1)	0(1)	0(0.5)	0	0(1.4)	12.5(1.8)	0
Waterbuck	11.1(1.7)	0	0	0(2.3)	0(3.6)	0(5.1)	0(2.1)	0(2.1)	0(3.7)	0(2.8)
Total*	9	0	7	5	29	19	0	7	16	2

* Total number of kills made by the cheetah in each vegetation type.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Table 3.14: Preference indices for kills made by all cheetah in each vegetation type in 2003 (Year 1).

PREY SPECIES	BKT	BST	DLT	EPM	KSL	MPT	OL	RT	SET	TET
Blesbok	0.0	0.0	-	0.0	2.0	-	-	-	-	-
Blue Wildebeest	0.0	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Burchell's Zebra	-	0.0	-	0.0	0.6	0.0	0.0	0.0	2.4	0.0
Bushbuck	2.0	4.3	-	1.3	6.4	0.0	0.0	1.6	14.5	0.6
Grey Duiker	9.1	0.0	0.0	1.6	8.6	0.0	-	2.9	0.0	0.0
Eland	0.0	0.0	-	4.6	0.0	-	-	-	0.0	-
Gemsbok	0.0	-	0.0	0.0	0.0	0.0	-	-	0.0	-
Impala	2.0	1.0	-	1.0	1.3	166.7*	-	3.2	0.0	1.0
Kudu	2.7	1.5	34.5*	0.9	2.9	0.8	3.7	1.2	1.6	1.3
Ostrich	0.8	0.0	-	0.0	1.7	-	-	0.0	0.0	-
Red Hartebeest	0.0	0.0	-	7.3	0.2	0.0	0.0	0.7	0.0	-
Scrub Hare	-	-	-	-	-	-	-	-	-	-
Springbok	0.2	-	0.0	0.0	0.8	-	0.0	0.0	1.5	-
Steenbok	0.0	0.0	0.0	0.0	0.0	-	-	0.0	7.3	0.0
Waterbuck	1.2	0.0	-	0.0	0.0	0.0	0.0	0.0	1.8	-

* very high preference indices where the total number of kills in that vegetation type was only 2.
- ungulates not counted in the vegetation type.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Table 3.15: Preference indices for kills made by all cheetah in each vegetation type in 2004 (Year 2).

PREY SPECIES	BKT	BST	DLT	EPM	KSL	MPT	OL	RT	SET	TET
Blesbok	0.0	-	1.0	-	5.1	-	-	47.6	0.0	-
Blue Wildebeest	0.0	0.0	-	0.0	0.6	0.0	-	0.0	0.0	-
Burchell's Zebra	0.0	0.0	5.9	5.6	0.0	0.0	-	-	1.1	0.0
Bushbuck	0.0	0.0	0.0	0.0	0.0	0.5	-	13.0	8.9	1.2
Grey Duiker	7.2	0.0	0.0	0.0	0.0	1.6	0.0	13.6	1.5	10.9*
Eland	0.0	0.0	-	0.0	-	-	-	-	0.0	-
Gemsbok	0.0	-	0.0	0.0	1.6	0.0	-	0.0	0.0	0.0
Impala	1.4	0.0	2.1	0.0	0.4	1.0	-	-	0.4	-
Kudu	1.0	0.0	0.9	1.5	1.5	1.1	0.0	1.5	1.1	0.0
Ostrich	0.0	-	-	0.0	0.0	-	0.0	0.0	0.0	-
Red Hartebeest	0.0	0.0	-	0.0	5.1	-	0.0	0.0	0.0	-
Scrub Hare	-	-	-	-	-	-	-	-	-	-
Springbok	1.3	-	4.2	-	0.8	-	-	0.0	2.4	-
Steenbok	3.1	0.0	-	0.0	0.0	0.0	-	0.0	6.6	-
Waterbuck	6.5	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0

* very high preference indices where the total number of kills in that vegetation type was only 2.

- ungulates not counted in the vegetation type.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Table 3.16: Preference indices for kudu and impala killed by each cheetah group, within its home range (95% UD).

Cheetah ID	Year 1		Year 2	
	Kudu	Impala	Kudu	Impala
Males				
Coalition	2.4	0.0	1.4	0.3
Females with cubs				
CF5 + 3	1.1	0.6	-	-
CF7 + 1	1.3	0.0	-	-
CF6 + 2	2.1	1.4	-	-
CF6 + 4	-	-	1.1	1.9
CF11 + 2	-	-	0.0	0.0
CF10 + 4	-	-	0.0	0.0
Single females				
CF6	0.9	1.3	-	-
CF18	-	-	0.7	0.0
CF10	-	-	1.7	0.0
CF11	-	-	1.3	0.0

- female cheetah that did not have cubs or were not single in that year.

Calculation of Daily Food Intake and Kill Rate

In the first continuous observation of the coalition, seven kills were made in 18 days: two blesbok (one adult male & one juvenile); two red hartebeest (one adult male & one juvenile); one blue wildebeest (juvenile); one kudu (juvenile) and one Burchell's zebra (juvenile), giving a total edible biomass of 337.6 kg and a daily consumption of 5.3kg per cheetah per day (Table 3.17). The kill rate was one kill per 2.6 days (see detail in Appendix D). In the second observation of the coalition, five kills were made in 16 days: two kudu (adult females); two gemsbok (juveniles) and one impala (adult male), giving a total edible biomass of 325.6kg and a daily consumption rate of 6.2kg per cheetah per day. The kill rate was one kill per 3.2 days (see detail in Appendix E). In the observation of the single female (CF10), six kills were made (16 days): five kudu (all juveniles) and one grey duiker (juvenile), giving a total edible biomass of 127.3kg and a daily consumption rate of 8kg per cheetah per day. The kill rate was one kill per 2.7 days (see detail in Appendix F). If the consumption and kill rates are calculated from the kills recorded opportunistically over a full year, the daily consumption rate for the coalition and CF10 for year 1 was 1.8kg and 1.6kg meat/cheetah/day respectively (Table 3.17).

Table 3.17: Daily consumption rate (kg/cheetah/day) for the coalition and a single female cheetah at Kwandwe. Data from other studies have been included to allow comparison.

ID	Daily Consumption Rate			Reference
Cheetah in general	4-5kg	-	-	Hunter *et al.* (2003)
Serengeti cheetah	4kg	-	-	Schaller (1974)
ID	**Year 1***	**2-Week Cont. Obs.**		**Reference**
3 male coalition (Kruger NP)	-	1.4kg	1.4kg	Mills *et al.* (2004)
3 male coalition	1.8kg	5.3kg	6.2kg	Kwandwe
Single female	1.6kg	8.0kg	-	Kwandwe

* Year 1 is the daily consumption rate of all kills made by the individual cheetah groups for the whole of 2003.

DISCUSSION

The cheetah on Kwandwe exhibited a similar diet to that which has been reported elsewhere. They killed a wide range of prey of all sizes, including non-mammalian species (ostrich). However, as many other studies have shown, the majority of the diet was made up of only a few species (Caro 1994; Hunter 1998; Mills *et al.* 2004). For example, in Kruger National Park, three species make up 69.2% of the diet (Mills *et al.* 2004), while in Mala Mala, three species make up 86.6% of the diet (Radloff & du Toit 2004) and in Phinda Resource Reserve, three species make up 81.6% of the diet (Hunter 1998), while in Kafue National Park three species make up 66.5% of the diet (Mitchell *et al.*1965). Although the cheetah on Kwandwe killed prey of different sizes, the majority of the cheetah's diet comprised medium sized species (30-65kg) and again, this is consistent with previous studies (Mills 1984; Caro 1994; Mills *et al.* 2004). However the different cheetah groups on Kwandwe killed different sized prey. There is some controversy over the extent to which coalitions of cheetah hunt cooperatively (Eaton 1970; Kruuk & Turner 1967; Caro 1994). However, on Kwandwe, the three male coalition accompanied one another on all hunts and actively co-operated in the hunts. On a number of occasions the cheetah drove prey toward concealed coalition partners (pers. obs). The co-operation in hunting by the three adult male coalition on Kwandwe enabled them to kill large prey (>65kg), and this has been reported in some previous studies (Caro 1994; Hunter 1998; Mills 1998; Mills *et al*. 2004). Male coalitions need a greater biomass of food per unit time than solitary cheetah (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 and that changes in group size are associated with change in the size of the prey (Caro 1994) and this appears to be the pattern at Kwandwe. More than a third of kills made by the coalition weighed more than a 100kg and in most cases the cheetah remained at their kills until they were satiated. However, the continuous observations on the coalition showed that the cheetah did adjust the kill rate to meet their energetic needs as they killed twice on the same day on more than one occasion. Significantly, on these occasions the kills were juveniles which would explain the need to increase the kill rate. Females with cubs preyed on more medium sized animals than single females and again this can be explained in terms of the increased needs of the group over a solitary female. However, unlike the coalition the adult females and their cubs do not have the power to kill large prey. As expected, single females preyed upon more medium sized prey whereas independent cubs preyed on more small sized prey. These results are different from those from the Kruger National Park and Mala Mala Private Game Reserve, where females preyed mostly on smaller sized prey like grey duiker and steenbok (Mills *et al.* 2004; Radloff & du Toit 2004). This difference could be enforced by a high kleptoparasite challenge at Kruger National Park and Mala Mala. McVittie (1979) found that in Namibia, in areas where potential kleptoparasites were rare or absent, cheetah killed larger prey than their counterparts existing within an intact large carnivore guild in East Africa. This could apply to the female cheetah on Kwandwe as kleptoparastism was very rarely recorded (see Chapter 5) and, due to the low number of predators, female cheetah were able to stay on larger prey for longer periods therefore making it more feasible for them to hunt larger prey.

Cheetah preferentially selected male ungulates in the Kruger National Park (impala: Mills *et al.* 2004), Serengeti (Thomson’s gazelle: Fitzgibbon 1990) and Kalahari Gemsbok Park (springbok: Mills 1984). This could be because male gazelles tend to occur on the periphery of groups, have greater nearest-neighbour distances, are less vigilant and are found in smaller groups than females (Fitzgibbon 1990). Impala and springbok show similar social structures to Thomson’s gazelle and therefore impala and springbok males could be more vulnerable to predation than females. In the present study cheetah showed a similar preference for males of the smaller prey species (impala and bushbuck) but not for kudu, where significantly more female were killed than expected. The selection of female kudu probably reflects the high risks associated with attempting to kill male kudu, which have long horns, while females do not have horns. The independent cubs killed significantly more male than female ungulates, but this should be analyzed carefully as the majority of prey killed by the independent cubs was bushbuck and grey duiker, which have very different social systems to gazelles (Estes 1991).

It has been suggested that direct observations of predators is likely to artificially increase the contribution of large kills (Mills 1996), because cheetah will spend more time on larger kills and thus large kills are more likely to be found than smaller ones. In addition, it is likely that smaller kills will be totally consumed and thus under-represented. Results from the faecal analysis have shown that small prey like rodents and scrub hares do not appear regularly in the cheetah diet on Kwandwe and only two new species (a rodent species and black backed jackal) were added to the kill list. Very few studies have shown black backed jackal to be part of cheetah’s diet but the high concentration of black back jackal on Kwandwe could have led to the consumption of these subordinate predators. Pienaar (1969) recorded cheetah killing jackal but they did not form part of the diet. I have seen cheetah chase black backed jackal on a number of occasions on Kwandwe but none of these chases resulted in a kill. The similarity between the results from the observations and faecal analysis suggest that at Kwandwe the very intensive direct observations have given an accurate reflection of the diet.

It has been suggested that predators select the old, weak and sick members of prey populations and that the degree of selection depends on the predator's hunting technique (Schaller 1972; Kruuk 1972; Fitzgibbon & Fanshawe 1989). Stalkers such as cheetah which tend to rely on surprise and short pursuits should have less time for prey selection and therefore should kill a more random sample of individuals compared to a coursing predator like the African wild dog (Fitzgibbon & Fanshawe 1989; Caro 1994; Creel & Creel 2002). In the Serengeti cheetah took gazelles with high and low marrow fat reserves (~BMI), although on average the gazelles taken by African wild dogs were in worse condition (Fitzgibbon & Fanshawe 1989). In Matusadona National Park the condition of prey killed by cheetah varied extensively with no consistent pattern (Purchase & du Toit 2000), whereas in Kafue National Park the prey killed by cheetah was in good condition (Mitchell *et al.* 1965). The condition of animals killed by cheetah on Kwandwe varied among species with bushbuck and grey duiker being in poor condition while impala, springbok and kudu were in moderate condition with some individuals in good condition. There was no difference in the condition of male compared to female animals killed. These results should be interpreted with care due to the small sample size and because the BMI of the living ungulates on Kwandwe is unknown. However, the results for Kwandwe support the suggestion that the hunting style of cheetah will not give them time to select individuals that are old or in poor condition.

Previous studies of the diet of cheetah have shown that the majority of the diet comprises the most abundant medium sized prey species in an area (for example Mills 1984; Caro 1994; Hunter 1998).

The results from Kwandwe support this and kudu, which comprise 37% of all ungulates on Kwandwe, were hunted according to their abundance on the property. In addition, the kudu on Kwandwe were naïve to predators and this plus the high numbers could have lead to the high percentage of kudu in the cheetah's diet. In most of the previous studies, the most important prey species (those killed most frequently) are small to medium sized ungulates and weigh less than 60kg (Mithell *et al.* 1965; Eaton 1970; Mills 1984; Caro 1994; Broomhall *et al.* 2003; Radloff & du Toit 2004). Exceptions have been reported for Phinda Resource Reserve (Hunter 1998) and Suikerbosrand Nature Reserve (Pettifer 1981b) where the most important prey species, nyala and blesbok, are large sized ungulates. Kudu, which weigh ~ 220kg in the males and ~ 160kg in the females are significantly larger ($p < 0.05$; Meissner 1982) and this may suggest that cheetah are not as restricted to small to medium sized prey as has previously been suggested. Bushbuck, grey duiker and springbok were hunted opportunistically further suggesting that on Kwandwe, the cheetah were not selecting the most important prey. Interestingly, impala, which are the most common prey species of cheetah in some other reserves (Purchase & du Toit 2000, Matusadona National Park; Broomhall *et al.* 2003, Kruger National Park; Radloff & du Toit 2004, Mala Mala) and are abundant on Kwandwe, were avoided by cheetah. Impala were most abundant in the short Euphorbia thicket (see Appendix B & C) and this vegetation type made up at least 20% of the home ranges of all cheetah (see Chapter 4). This avoidance of impala was especially evident in the coalition as on a number of occasions they ignored nearby impala herds while hunting kudu.

On Kwandwe, blesbok, which was not one of the most important prey species (in terms of numbers killed), had the highest prey preference index. Similar results have been reported from the Kruger National Park where impala are the most important prey species but reedbuck has the highest preference index of all cheetah prey (Pienaar 1969).

Specialisation on different prey by cheetah in the same area has been recorded and regional differences, though often reflecting prey abundance, may partially be the result of specialisation (Eaton 1970).

The majority of cheetah kills on Kwandwe were made in *Euphorbia Portulacaria* mosaic, karroid shrubland, bushclump karroid thicket, short *Euphorbia* thicket and medium *Portulacaria* thicket, which comprise 85.3% of Kwandwe. Within these vegetation types there was evidence of selective predation of each of the five most important prey species. In some instances this might have been an artefact of a small sample size, but in others it probably reflects true selective hunting. For example in year 1 there were 39 kills in karroid shrubland and cheetah selectively killed kudu (preference index (PI) of 2.95), bushbuck (PI of 6.41) and grey duiker (PI of 8.55). This analysis highlights a weakness of the broad, reserve level analysis of preference, which included prey individuals that the cheetah never encountered. Similarly, the analysis of prey preference at a home range level showed that different individuals or social groups selected different prey. For example, CF6 selected kudu calves in year 1 when she had two cubs and when her cubs became independent she selected bushbuck and grey duiker. Interestingly, her independent cubs (CF10&11) also selected for bushbuck and grey duiker before they separated, which could have been a result of learnt behaviour or because they remained in their natal range. Eaton (1970) has similarly reported that learnt behaviour in certain groups of cheetah lead to the selection of specific prey species in Nairobi National Park. CF6 selected springbuck in year 2 when she had four cubs and remained in the more open areas (karroid shrubland) where the springbuck were abundant. In summary, the analysis at the reserve level suggested that cheetah were not selecting for the five most often killed prey species but killing them based on their abundance. By contrast, analyses at a vegetation type level indicated that within certain vegetation types, cheetah were selecting for certain species. At a home range level there was also evidence of prey selection and for a single female (CF6), of changing prey preference when she was with or without cubs. Together this suggests that cheetah are adaptable predators and have the ability to modify their diet depending on the area they occupy.

Kill rates of cheetah are affected by group size, presence of cubs, prey size and availability, habitat structure and competition with other predators (Pettifer 1981b; Caro 1994; Durant 2000a; Mills *et al.* 2004). An increase in group size, through birth (*i.e.* presence of cubs), or the formation of a coalition brings with it increased nutritional requirements, which must be met. This can be done by increasing the kill rate and not changing the selection of prey, or by preying on larger species (or individuals), without changing the kill rate (Caro 1994), or a combination of the two. If hunting is a dangerous activity, possibly through increased exposure to superior predators, then there may be pressure not to increase the kill rate. Similarly, increasing food intake by killing a larger species requires that there is a suitably larger species, which occurs in habitats in which the cheetah can hunt. If this is not the case, then there may be no option but to increase kill rate. At a methodological level, different methods will generate quite different kill rates. It is widely accepted that opportunistic observations will miss kills (Mills 1992) and that the number missed will depend on the effort put into the observations. By contrast, periods of continuous observations will miss few if any kills but their accuracy depends on the duration of the observation and the number of times they are repeated. Variations found in cheetah kill rates across African ecosystems are therefore possibly due to one or more of the above factors. Three male coalitions have very low kill rates of 95 and 51 kills per year in Suikerbosrand Nature Reserve and Timbavati-Klaserie Nature Reserves respectively (Pettifer 1981a; 1981b). However, the cheetah were estimated to have consumed approximately 4.1kg of meat/cheetah/day in Suikerbosrand

Nature Reserve and approximately 2.2kg in Timbavati- Klaserie Nature Reserves (Pettifer 1981b). Schaller's (1972) estimate that a female (with two cubs) consumed approximately 4kg of meat/cheetah/day is similar to that found by Pettifer (1981b) in Suikerbosrand Nature Reserve, although this female had a far higher kill rate of 341 kills per year. The high estimate of kill rate (Schaller 1972) could be due to high kleptoparasitism recorded in the Serengeti, which would require the cheetah to hunt more often. A three male coalition in the Kruger National Park had a comparatively low kill rate of 79 kills per year and consumed approximately 1.4kg of meat/cheetah/day (Mills *et al.* 2004). Cheetah on Kwandwe had much higher kill rates (~ 126 kills per year) and a higher consumption rate of ~ 5.8kg of meat/cheetah/day for a three male coalition and ~ 8kg of meat/cheetah/day for a single female cheetah. The differences in the results for Kwandwe and the Kruger National Park could be a result of the high concentration of prey on Kwandwe and the low numbers of lion and other competitors, which would allow the cheetah to catch more often and consume more meat at each kill. However it is unlikely that similar groups of cheetah require such different amounts of food and it is more likely that the differences in daily consumption rate reflect differences in methodology. This is in spite of the fact that the reported methods in the above mentioned studies were very similar (Schaller 1972; Pettifer 1981b; Mills *et al.* 2004). Clearly, kill rates and daily food intake will vary from one study to another and interpretation of this variation is difficult. In some cases, differences may be due to the use of different methodologies while in others, differences may reflect differences in predator-prey ratios, prey size, and the threat of kleptoparasitism.

In conclusion, cheetah are regarded as the most specialised of all felids, preferring small to medium sized prey, particularly in open grasslands where most studies have been undertaken (Caro 1994; Nowell & Jackson 1996). However, the patterns observed at Kwandwe illustrate that cheetah are adaptable and successful hunters in Valley Bushveld and are not necessarily dependent on gazelle or impala-sized prey. Indeed, impala are abundant at Kwandwe but were not selected by the cheetah.

CHAPTER 4

CHARACTERISTICS OF HOME RANGE AND HABITAT USE BY DIFFERENT CHEETAH SOCIAL GROUPS ON KWANDWE

INTRODUCTION

Various factors will interact to determine the space use (home range and core area) and habitat selection of a carnivore. In most felids, the availability of cover, both for hunting and for concealment from superior predators, and water, particularly for lactating females, are important but the spacing patterns of females are generally dictated by the food supply and availability of denning sites for rearing young (Caro 1994; Laurenson 1995; Mizuntani & Jewell 1998; Sunquist & Sunquist 2002). In most species of felid, 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 prey of a suitable size and how the prey is distributed in time and space (Sunquist & Sunquist 2002). By contrast, the spacing patterns of male felids are thought to be driven more by female distribution (Sunquist & Sunquist 2002) and to a lesser extent by access to food, suitable hunting grounds and cover. For example, in the Serengeti, territorial cheetah males may vacate their territories when Thomson's gazelle numbers are low, but these absences are thought to be related to the lack of females on their territories rather than lack of food. This is because some resident Grant's and Thomson's gazelles remain within the males' territories and thus the territories are only worth defending when the reproductive returns are sufficiently high (Caro & Collins 1986). Considerable variation has been reported in the space used by cheetah in different parts of their geographical range and this has often been explained in terms of resource availability. In the Serengeti the main determinants of territory location are a combination of adequate cover and adequate densities of Thomson's gazelles (Caro 1994). Thomson's gazelles make up 90 percent of the cheetah's diet and female cheetah which follow the migratory movements of the gazelles have larger home ranges (833km^2) than the resident males (37.4km^2) (Schaller 1972; Durant *et al.* 1988; Caro 1994). In Kruger National Park and Phinda Resource Reserve where prey are non-migratory, and in Matusadona National Park where the density of prey is high, male and female cheetah have smaller overlapping ranges which are similar in size (Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003).

The social system of the species will play a role in space use and habitat selection. Most members of the Family Felidae tend to be solitary except when courting or when a female has young (Schaller 1972). The exceptions to this are lion and cheetah, which display a far greater degree of sociality than most other felids (Caro & Collins 1986; Hunter 1998). Cheetah have a variable social organization that is unique among the felids. Adult females are solitary or accompanied by dependent young, adult males are either solitary or live in stable coalitions of two to four males, and independent adolescents of varying sex stay together for approximately six months after leaving their parents (Sunquist & Sunquist 2002). Coalitions of male cheetah mate with many females and in this way differ from the coalitions formed by male lions, which typically remain attached to and mate with the females in a single pride (Estes 1991; Caro 1994; Sunquist & Sunquist 2002). This variable social organization results in different groups of cheetah, based on gender, size and age, having different space and habitat requirements. Female cheetah generally occupy larger home ranges than do males (Caro 1994; Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003; Marker *et al.* 2003a) and the home range of a coalition of males will often overlap with the home ranges of several females (Caro & Collins 1986; 1987; Sunquist & Sunquist 2002; Broomhall *et al.* 2003). Furthermore, female cheetah tend to select habitats that offer more cover than do male cheetah (Hunter 1998; Sunquist & Sunquist 2002; Broomhall *et al*. 2003).

There appears to be a relationship between home range size and the amount of suitable space, as compared to total space, and studies in which suitable space is limited have reported relatively small home ranges (Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.*2003). However interpreting the significance of available space is problematic because of variation in other factors such as prey density, between the different reserves.

An important factor that may affect both space use and habitat selection is the presence of other carnivores (Durant 2000a; 2000b). Cheetah may be negatively affected through interactions with superior predators (for example lions and spotted hyenas) and there are several reports of kleptoparasitism injury and death (Schaller 1972; Caro 1994; Hunter 1998; Durant 2000a; 2000b). It would therefore be surprising if the presence of superior predators was not an important factor in determining space use and habitat selection, and that this effect will vary between different groups of cheetah. Indeed, it is likely that the influence of superior predators will be exaggerated in spatially limiting conditions as found in "small" reserves because of the reduced opportunities for evasion.

Thus the aims of this study were to examine the space use and habitat selection of cheetah in a small reserve; to ascertain how space use and habitat selection may vary between different cheetah social groups and to analyze the factors that may be influencing habitat selection and space use. In addition, since this study is in an area and vegetation type in which there has been no previous research, the study will provide data on space use and habitat selection in Valley Bushveld.

METHODS

Data collection

Daily location of all cheetah

All cheetah were located by radio-telemetry on a daily basis from February 2003 to August 2004 and their positions were recorded using a global positioning system (GPS). 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 or cheetah group (Gehrt & Fritzell 1998; Boydston *et al.* 2003; Broomhall *et al.* 2003). One day allowed enough time for cheetah groups to cross their home ranges and was thus sufficient for statistical independence of observations (Mizutani & Jewell 1998).

Home range characterization

Home range size

The home range sizes of all the cheetah groups were determined using an ArcView 3.2 extension package Animal Movement (Hooge & Eichenlaub 1997). Location points from triangulation and direct observations were used for home range analyses. Two non-parametric methods were used; the minimum convex polygon (MCP) method (White & Garrott 1990) and the fixed kernel utilization distribution (UD) method (Worton 1989; Powell 2000). The MCP was used to facilitate comparisons with previous studies many of which have used only this method. The biggest problem with this technique is that the area and shape are heavily influenced by outlying fixes (Harris *et al.* 1990) and the MCP often includes unused space. 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 spent in that area. Kernel UDs more accurately reflect habitat use and are therefore more appropriate for studies of habitat selection than are MCPs. In addition, while the MCP method generates a single polygon at each level (50% and 95%), the UD method will generate more than one polygon where appropriate. The UD method is an accurate way to meaningfully calculate home range size (Worton 1995; Seaman & Powell 1996), it is increasingly being adopted over more traditional methods (Worton 1995) and has been used for analysis of home range patterns in large carnivores (Seaman & Powell 1996; Bothma *et al*. 1997). For these reasons the UD method was used for data analysis while MCPs have been calculated to allow comparison with other studies.

The key variable in the UD method is the smoothing factor (H). In this study, H was calculated once using the least squares cross validation available in the Animal Movement extension. This value was then tested on a number of data sets and then modified slightly to reduce the extent to which the polygons overlapped the reserve boundary. An H value of 1000 was used in all analyses.

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 respectively (Mizutani & Jewell 1998). The 95% and 50% UDs were calculated directly in the Animal Movement extension. For the MCPs, 5% and 50% of outliers were removed using the harmonic mean method (Animal Movement extension) and the remaining points used to calculate the 95% and 50% MCPs. Where necessary, the UDs and MCPs were clipped to exclude regions outside the reserve boundaries and the areas were recalculated. The 50% UD and MCP and 95% UD and MCP were calculated for the coalition (CM1-3), females with cubs (n=6), single females (n=4), females with cubs in a den (n=3) and independent cubs (n=1). The data for the females with cubs in a den were calculated for approximately two months, from when the female gave birth until she moved her cubs out of the area.

Habitat use

The vegetation of Kwandwe has been fully described in Chapter 2. In summary, the reserve had ten vegetation types (Figure 4.1) of which four (*Euphorbia Portulacaria* mosaic; short *Euphorbia* thicket; karroid shrubland and bushclump karroid thicket) made up 77% of the study area with *Euphorbia Portulacaria* mosaic (dominated by *Portulacaria afra* and *Euphorbia bothae*) and short *Euphorbia* thicket (dominated by *Euphorbia bothae*) covering 27.3% and 21.2% of the study site respectively. Karroid shrubland covered 15.9% of the reserve and generally supported scattered trees and bushes (dominated by *Pappea capensis* and *Rhus refracta*). Bushclump karroid thicket (*Rhus* spp, *Euclea undulata* and *Maytenus polyacantha*) covered 12.6% of the area. Medium *Portulacaria* thicket (dominated by *Portulacaria afra* and *Pappea capensis*), tall *Euphorbia* thicket (dominated by *Euphorbia tetragona* and *Euphorbia triangularis*), bushclump savannah thicket (characterized by *Cussonia spicata, Scutia myrtina,Olea europea* and *Pteroxylon obliquum* and occurring at higher altitudes), old lands (rehabilitated cultivated areas, lacking trees or shrubs), drainage line thicket (dense stands of *Rhus refracta*) and riverine thicket (dominated by *Acacia karroo, Rhus lancea* and *Combretum caffrum*) each covered less than 8% of the study area.

The vegetation map of Kwandwe was used to determine habitat availability, defined as the proportion of each home range covered by each vegetation type (Creel & Creel 2002) using ArcView 3.2. Observed habitat use was then calculated as the proportion of GPS fixes for each cheetah group that fell into each vegetation type within that cheetah's home range. Expected habitat use, assuming habitat use to be random, was calculated by multiplying the

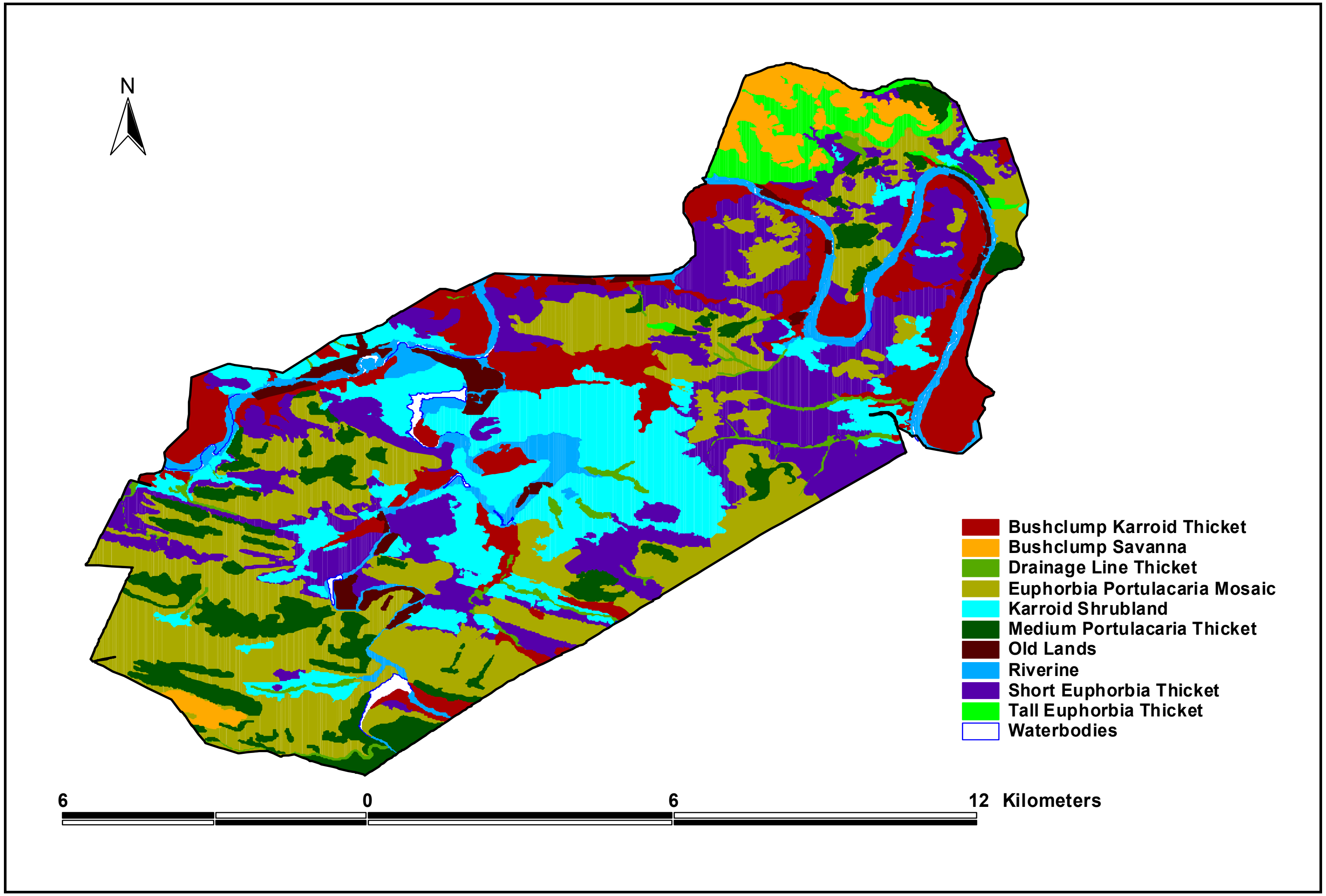


Figure 4.1: Distribution of the vegetation types of Kwandwe Private Game Reserve.

total number of fixes by the percentage of each vegetation type occurring in the 95% UD for each individual of each cheetah group. To test if cheetah preferred certain habitats, habitat use was compared to expected use using chi-squared tests.

Further habitat characterization

The altitude and slope for each GPS fix was determined using Surface Tools (Jenness 2004) in ArcView 3.2. These values were then used to calculate mean altitude and slope for each cheetah group.

The distances of each GPS fix in the 95% UDs from drainage lines and roads were calculated in ArcView 3.2 and these values were used to calculate the mean distance for each cheetah group from the nearest drainage line and road. Where there was more than one example of a social group, mean values for each example were used to generate a mean for that social group. To allow comparison of these measurements with those for "animals" using the reserve at random, an identical set of measurements were made for five sets of random points within the reserve and these were used to calculate mean values. The mean distances between the various cheetah groups and the pride of lions and the coalition were calculated in ArcView 3.2 using only the GPS fixes that fell within the 50% UDs.

The visibility in the home range and core areas was estimated using the visibility indices for each vegetation type (Chapter 2) and the percentages of the home range or core areas that the vegetation types occupied. The abundance of ungulates in the home range and core areas of all the cheetah social groups was calculated using the annual game count data and ArcView 3.2. Only ungulate species preyed upon by cheetah on Kwandwe were counted to work out the density of potential prey species in each home range and core area. The abundance of the five most dominant cheetah prey species on Kwandwe within each vegetation type was calculated using the annual game counts and ArcView 3.2.

Statistical analyses

One-way ANOVAs were used to test the effect of social group on the home range and core area size and on the distance from drainage lines, roads, the coalition and the pride of lions (Statistica). Chi-squared tests were used to asses whether the cheetah were selecting certain vegetation types by comparing the habitat available to the cheetah, to the habitat they utilised (Statistica). The relationship between the cheetah social groups and the elevation and slope of the area utilised was tested using one-way ANOVAs (Sigma Stat; Jandel Scientific).

RESULTS

Size of Home Range and Core Area

Independent cubs had the largest 95% UD (93.93km²) and 95% MCP (110.07 km²), which covered more than two thirds of the reserve (Tables 4.1 & 4.2), while females with cubs in a den had the smallest 95% UD (mean = 11.05km²) and 95% MCP (mean =2.03 km²), which covered less than 8% of the reserve (Tables 4.1 & 4.2).

Table 4.1: Home range and core area sizes of cheetah on Kwandwe as calculated by the fixed kernel method and the percentage of the reserve used by each group. Data are means ± 1sd except where n = 1.

		Area (km²)		**% of reserve**	
Cheetah Group	**Sample Size**	**50%**	**95%**	**50%**	**95%**
Coalition	453(n=1)	6.0	32.7	4.3	23.6
Female with cubs	544(n=6)	9.4±2.2	62.3±21.0	6.8±1.5	44.9±13.8
Single females	349(n=4)	9.7±4.3	65.6±23.3	7.0±3.1	47.3±16.8
Females with cubs (den)	170(n=3)	3.9±0.1	11.1±0.9	2.8±0.1	8.0±0.6
Independent cubs	138(n=1)	26.6	93.9	19.1	67.7

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

Table 4.2: Home range and core area sizes of cheetah groups on Kwandwe as calculated by the minimum convex polygon method and the percentage of the reserve used by each group. Data are means ± 1sd except where n = 1.

		Area (km²)		% of reserve	
Cheetah Group	**Sample Size**	**50%**	**95%**	**50%**	**95%**
Coalition	453(n=1)	1.9	62.4	1.4	45.0
Female with cubs	544(n=6)	9.4±6.5	57.6±30.8	6.8±4.3	41.5±20.3
Single females	349(n=4)	7.8±6.3	60.8±29.2	5.6±4.5	43.8±21.1
Females with cubs (den)	170(n=3)	0.002±0.004	2.0±1.7	0.002±0.003	1.5±1.2
Independent cubs	138(n=1)	26.2	110.1	18.9	79.3

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

Excluding the females with cubs in a den, where the very small areas were due to the adult female rarely moving far from the den, the 3 male coalition had the smallest 95% UD (32.71km²), which covered less than a quarter of the reserve. In comparison, single cheetah females had a much larger 95% UD (mean = 65.59km²), which covered just less than half of the reserve. There was no significant difference between the 95% UDs of the females with cubs and the single females which were both significantly greater than that of the cubs in dens ($p < 0.001$). The 95% MCP for the coalition, which was almost twice the size of the 95%UD, was similar to the 95% MCPs of the single females and females with cubs which were significantly larger than the 95% MCP of the females with cubs in a den ($p < 0.001$; Table 4.2). Core areas (50% UDs) of the different cheetah groups differed significantly in size ($p < 0.05$) and ranged from 3.85km² for females with cubs in a den to 26.55km² for the independent cubs (Table 4.1) and from 0.002km² to 26.21km² for the 50% MCP (Table 4.2). Excluding the females with cubs in a den, the coalition had the smallest 50% UD (6.00km²) and 50% MCP (1.91km²). The 50% UDs and MCPs of the single females and females with cubs were similar ($p > 0.05$) and were larger than those of the coalition (Tables 4.1 & 4.2).

Location of Home Ranges and Core Areas

In this analysis, data for replicates of the same social group have not been pooled because, for example, the different single females used different regions of Kwandwe. Furthermore, the data for the same animal (CF6) in different stages of cub rearing have been treated separately. The home range and core area of the coalition were positioned within the centre of the reserve throughout the study (Figure 4.2). The home ranges of the four single females spanned a vast area of the reserve (Figure 4.3) and overlapped the home range of the coalition to a variable extent. However, there was no overlap between the core areas of the single females and that of the coalition (compare Figures 4.2 and 4.3).

Single females CF10 and CF11 were siblings and were born on the reserve to CF6. Their home ranges were both on the south western side of the reserve which was close to part of their mother's home range (compare Figure 4.3a, b, c), and their core areas overlapped. By contrast, the home range of female CF18, who was not related to the other females, was on the north eastern side of the reserve (Figure 4.3d) and showed the least overlap with the home range of the coalition.

Females with cubs in a den had very small home ranges and core areas (Figure 4.4). The two siblings CF10 and CF11 chose very similar areas for their den sites, which overlapped, with one of the core areas of their mother CF6 (compare Figures 4.4a, b; 4.3a and 4.5a). This overlap was in an area, which was utilized when they were still dependent on their mother (Figure 4.5a). However, CF10 and CF11 had their cubs at the same time and their mother (CF6) avoided this area during that time, as she had another litter of cubs of three months old and utilized the centre of the reserve (Figure 4.5b). In this study there was no evidence of female cheetah moving cubs from one den to another.

The home ranges of females with cubs overlapped yet there was almost no overlap between the core areas (compare Figure 4.5a-f). The core areas of CF10+4 and CF5+3 (Figure 4.5c, e) and CF6+4 and CF7+1 (Figure 4.5b, f) did overlap but they had cubs in different years and therefore no interaction would have occurred between the two females. There appears to be no fixed relationship between the den site and the space used by the females and cubs once they have left the den. CF6+4 kept her cubs in a similar area to the location of the den (compare Figures 4.4c and 4.5b), while CF10+4 moved her cubs well away from the den site (compare Figures 4.4a and 4.5c).

The independent cubs utilized the south western and the north eastern ends of the reserve (Figure 4.6) and their home ranges were in similar areas to that utilized when they were with their mother before they became independent (compare Figures 4.5a and 4.6). They spent the first three months on the southwestern side of the reserve and the second three months before they split up on the northeastern side of the reserve (Figure 4.6).

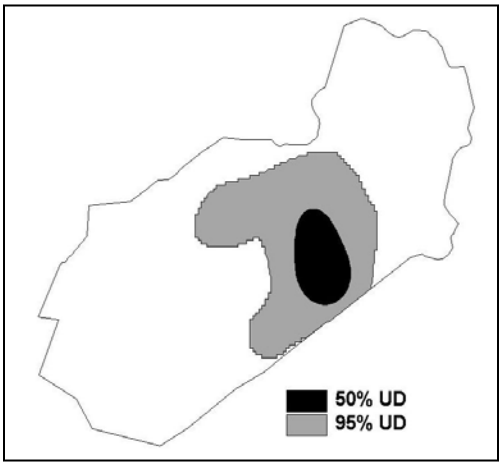
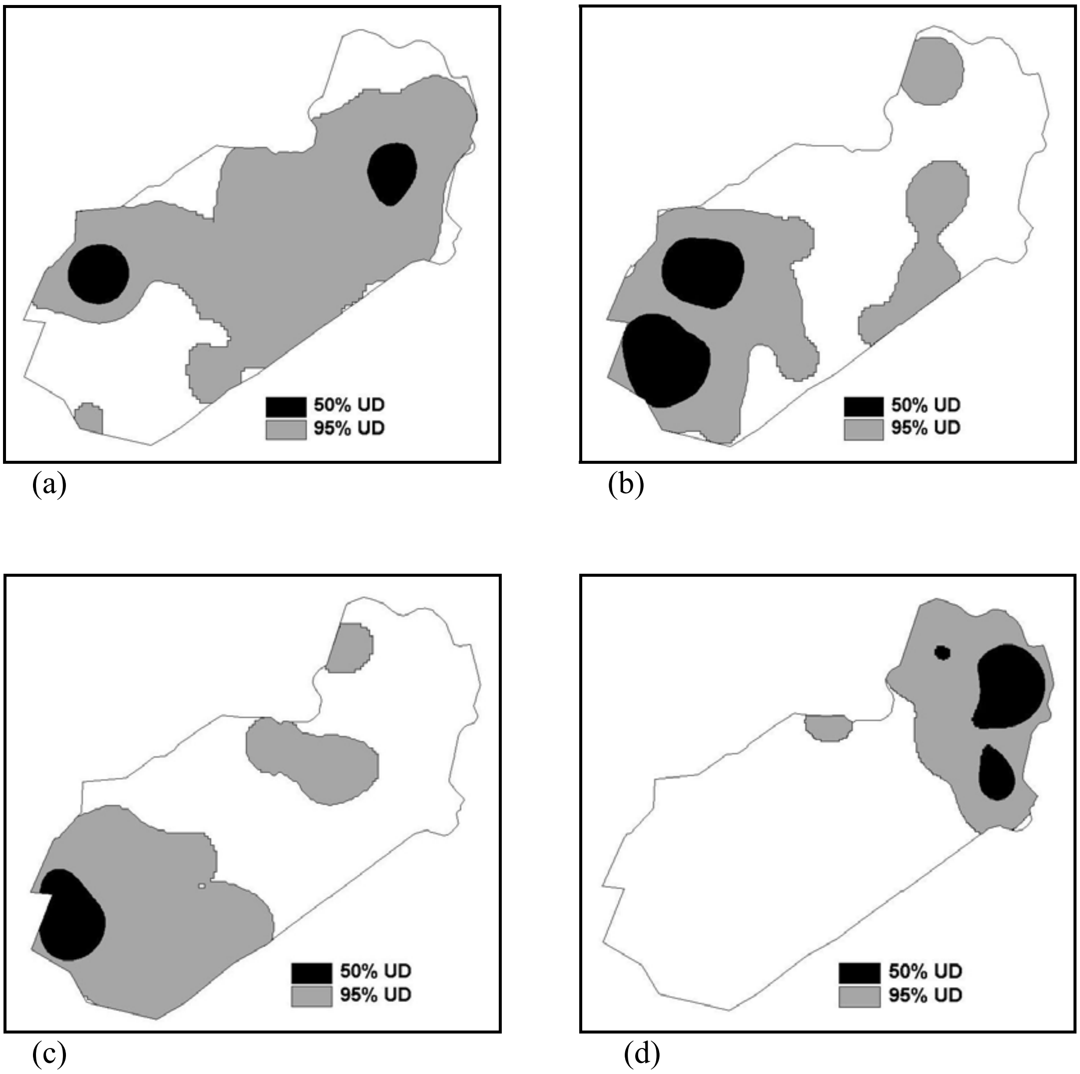


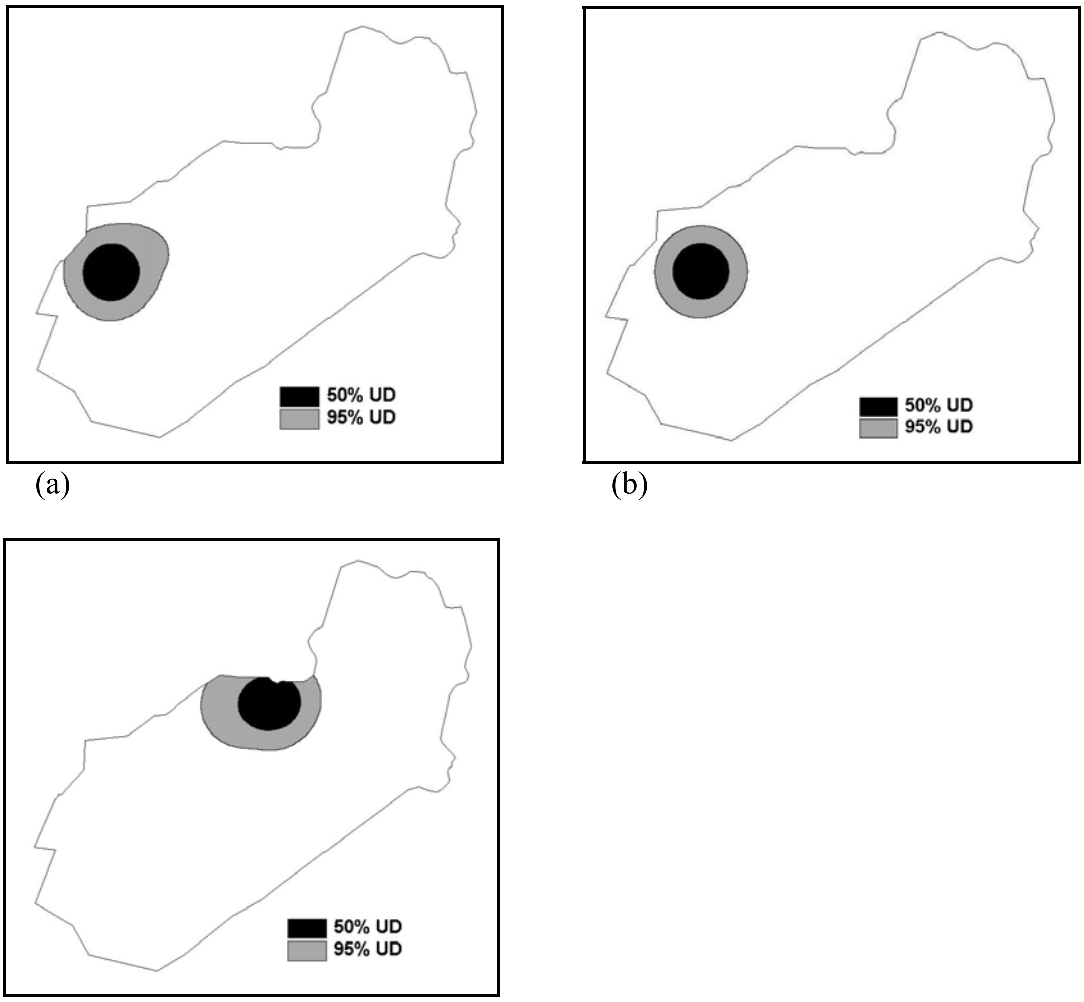
Figure 4.2: Home range and core areas for the coalition (CM1-3), 95% and 50% UDs determined by the fixed kernel method.



(a) (b)

(c) (d)

Figure 4.3: Home range and core areas for single female cheetah, 95% and 50% UDs determined by the fixed kernel method. (a = CF6; b = CF10; c = CF11; d = CF18).



(a) (b)

(c)

Figure 4.4: Home range and core areas for female cheetah with cubs in a den, 95% and 50% UDs determined by the fixed kernel method. (a = CF10+4; b = CF11+2; c = CF6+4).

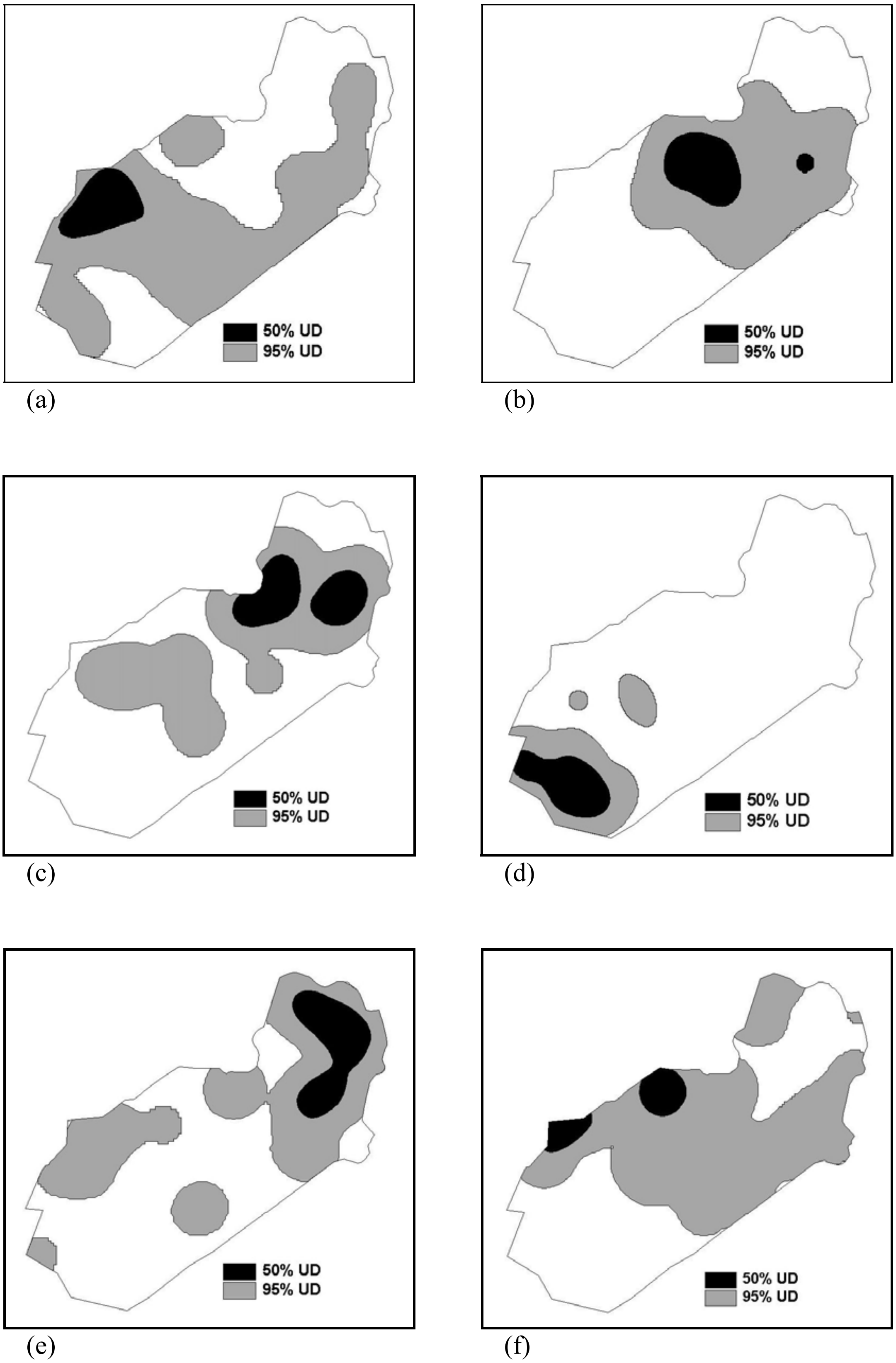


Figure 4.5: Home range and core areas for female cheetah with cubs, 95% and 50% UDs determined by the fixed kernel method. (a = CF6+2; b = CF6+4; c = CF10+4; d = CF11+2; e = CF5+3; f = CF7+1).

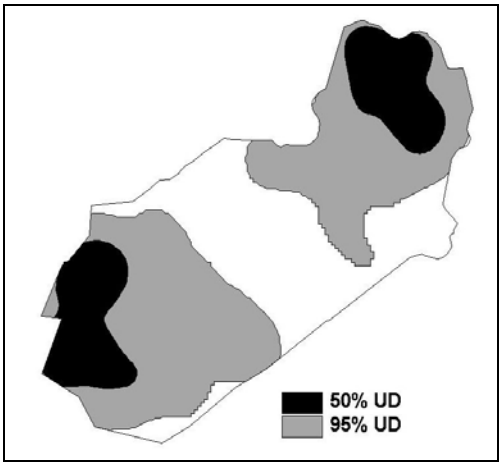


Figure 4.6: Home range and core areas for independent cubs (CF10 & 11), 95% and 50% UDs determined by the fixed kernel method.

Habitat use

The coalition's home range was characterized by three main vegetation types (karroid shrubland, short *Euphorbia* thicket and *Euphorbia Portulacaria* mosaic) which made up 80.4% of the home range (Table 4.3). Within this home range, the coalition did not use the available vegetation types at random (χ^2=100.5, df=9, p < 0.001) but showed a strong preference for karroid shrubland and a strong avoidance of *Euphorbia Portulacaria* mosaic (Table 4.5). The observations of preference or avoidance are subjective and are based on the difference between observed and expected use of the main vegetation types in each home range and core area.

The home ranges of the single female cheetah were characterized by four major vegetation types (*Euphorbia Portulacaria* mosaic, short *Euphorbia* thicket, bushclump karroid thicket and karroid shrubland) which made up 76.2% of their home ranges (Table 4.3), and which they used at random (χ^2=10.64, df=9, p > 0.05; Table 4.5).

The home ranges of the female cheetah with cubs in a den were characterized by three main vegetation types (*Euphorbia Portulacaria* mosaic, short *Euphorbia* thicket and bushclump karroid thicket), which made up 76.6% of their home ranges (Table 4.3). Female cheetah with cubs in a den did not use the available vegetation at random (χ^2=85.21, df=8, p < 0.001) and showed a strong preference for *Euphorbia Portulacaria* mosaic, a weak avoidance of short *Euphorbia* thicket and avoided bushclump karroid thicket (Table 4.5).

The home ranges of the females with cubs were characterized by four major vegetation types (*Euphorbia Portulacaria* mosaic, short *Euphorbia* thicket, karroid shrubland and bushclump karroid thicket), which made up 79.9% of their home ranges (Table 4.3). These animals did not use the available vegetation at random (χ^2=46.76, df=9, p < 0.001) but selected for bushclump karroid thicket and short *Euphorbia* thicket and avoided riverine thicket (Table 4.5). The home ranges of the independent cubs were characterized by four major vegetation types (*Euphorbia Portulacaria* mosaic, short *Euphorbia* thicket, bushclump karroid thicket and medium *Portulacaria* thicket), which made up 77.5% of their home ranges (Table 4.3). Independent cubs did not use the available vegetation at random (χ^2=32.62, df=9, p < 0.001) but selected for bushclump savannah thicket and avoided the other major vegetation types (Table 4.5).

The three vegetation types that characterized the coalition's home range (karroid shrubland, short *Euphorbia* thicket and *Euphorbia Portulacaria* mosaic), also made up 90% of the core area (Table 4.4). Within their core area, the coalition did not use the available vegetation types at random (χ^2=58.28, df=5, p < 0.001) and showed a strong preference for karroid shrubland, a weaker preference for short *Euphorbia* thicket and avoided the other vegetation types (Table 4.6).

The core areas of the single female cheetah were dominated by *Euphorbia Portulacaria* mosaic and to a lesser extent, short *Euphorbia* thicket and bushclump karroid thicket, which made up 71.2% of their core area (Table 4.4). The single female cheetah did not use the available vegetation at random (χ^2=86.41, df=9, p < 0.001) but selected for bushclump karroid thicket and avoided *Euphorbia Portulacaria* mosaic and short *Euphorbia* thicket (Table 4.6).

The core areas of the females with cubs in a den were dominated by *Euphorbia Portulacaria* mosaic which made up more than half the core area, and short *Euphorbia* thicket (Table 4.4). Females with cubs in a den did not use the available vegetation at random (χ^2=34.86, df=8, p < 0.001) and showed a strong preference for *Euphorbia Portulacaria* mosaic and avoided short *Euphorbia* thicket (Table 4.6). The core area of the females with cubs was dominated by *Euphorbia Portulacaria* mosaic, short *Euphorbia* thicket and bushclump karroid thicket, which made up 71.5% of the core area (Table 4.4). Females with cubs did not use the available vegetation at random (χ^2=36.26, df=8, p < 0.001) and showed a strong preference for bushclump karroid thicket and avoided *Euphorbia Portulacaria* mosaic (Table 4.6). The core area of the independent cubs was dominated by *Euphorbia Portulacaria* mosaic and to a lesser extent short *Euphorbia* thicket, medium *Portulacaria* thicket and tall *Euphorbia* thicket which made up 78.1% of the core area (Table 4.4). Independent cubs did not use the available vegetation at random (χ^2=23.97, df=9, p < 0.001; Table 4.6) and showed a preference for karroid shrubland and bushclump karroid thicket, and avoided medium *Portulacaria* thicket and *Euphorbia Portulacaria* mosaic.

In general, female cheetah tended to select denser vegetation types such as *Euphorbia Portulacaria* thicket and bushclump karroid thicket compared to the males, which predominantly selected karroid shrubland, which was the most open vegetation type. This trend was particularly apparent at the 50% UD level.

Table 4.3: Characteristics of the home ranges (95% UD) of the various cheetah groups.

Data are means ± 1sd except where n = 1.

	Cheetah Group				
	Coalition	**Single Females**	**Females + Cubs (den)**	**Females + Cubs**	**Independent Cubs**
Characteristics					
HR Size (km^2)	32.7	65.6±23.3	11.1±0.9	62.3±21.0	93.9
Vegetation Types (%)					
BKT	9.8	12.2±7.4	15.6±17	13.5±6.0	9.6
BST	0	3.3±3.1	0.0	1.8±1.6	3.6
DLT	2	1.4±0.4	0.7±0.2	1.5±0.5	1.3
EPM	25.3	30.0±12.7	40.4±9.8	26.9±14.4	35.1
KSL	29.2	11.9±5.7	7.3±2.1	16.6±6.1	7.8
MPT	3.9	8.2±4.3	10.4±8.2	7.1±6.9	9.4
OL	1.8	1.4±0.2	0.8±1.4	1.8±0.8	1.3
RT	1.8	5.2±2.0	3.8±1.1	6.0±1.8	4.4
SET	25.9	22.1±4.5	20.6±2	22.9±7.1	23.4
TET	0.2	4.2±4.3	0.2±0.3	2.0±2.4	4.1
Prey Density (animals/ha)	2.2	3.7±1.1	1.5±0.2	3.0±0.8	3
Visibility Index	68.6	62.1±31	59.5±6.5	65.6±6.5	59.1
Altitude (m)	365.9	370.3±52.1	379.1±23.7	352.7±42.8	386.9
Slope (º)	2.6	6.8±6.6	4.8±4.7	4.8±4.6	6.0
Distance (m)					
Drainage lines	270.2±158.4	248.4±58.8	180.9±21.5	267.9±39.8	259.8±215.8
Roads	86.5±83.4	110.6±10.7	130.1±23.7	96.5±10.9	106.5±100.6

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Table 4.4: Characteristics of the core areas (50% UD) of the various cheetah groups.
Data are means ± 1sd except where n = 1.

	Cheetah Group				
	Coalition	**Single Females**	**Females + Cubs (den)**	**Females + Cubs**	**Independent Cubs**
Characteristics					
Core Area Size (km²)	6	9.7±4.3	3.8±0.1	9.4±2.2	26.6
Vegetation Types (%)					
BKT	3.1	10.1±12.1	4.9±8.6	19.1±15.4	5.2
BST	0	0.7±0.8	0.0	0.9±1.8	8
DLT	1.6	0.8±0.5	1.0±07	0.7±0.5	1.3
EPM	20.2	44.2±23.1	58.4±5.2	29.0±20.9	37.1
KSL	45.9	5.3±3.1	4.1±3.8	10.5±10.7	4
MPT	5.2	14.9±10	11.4±9.1	6.8±8.2	13.7
OL	0	0.5±0.8	1.3±2.2	1.2±1.3	0.2
RT	0	6.1±6.9	0.9±0.8	6.1±4.7	3.4
SET	23.9	16.9±10	18.2±1.5	23.4±16.8	16.5
TET	0	0.7±1.4	0.1±0.2	2.3±5.2	10.8
Prey Density (animals/ha)	1.2	2.4±2.9	1.9±2.4	2.1±1.9	2.3
Visibility Index	72.8	56.6±7.2	55.4±3.4	63.4±8.4	56.4
Distance (m)					
Lions	1990.3±365.8	6272.7±1236.3	3915.7±44.1	5056.7±287.2	7121.2±1468.3
Coalition	-	7161.1±1967.7	5372.9±11.4	5185.3±2538.8	7480.9±1857.7

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Table 4.5: Habitat use by cheetah. The observed figure is the actual number of locations per vegetation type. The expected figure was calculated by multiplying the total number of locations by the percentage of each vegetation type occurring in the 95% UD of each individual.

Individual Group	BKT	BST	DLT	EPM	KSL	MPT	OL	RT	SET	TET	χ^2 Results
Coalition											
expected	38.1		7.9	98.7	113.9	15.3	7.2	6.9	101.4	0.7	χ^2=100.5, df=8
observed	22		4	51	193	3	6	3	110	0	$p < 0.001$
Single Females											
expected	42.3	9.6	4.9	98.2	43.7	25.8	4.7	17.8	76.2	12.2	χ^2=10.6, df=9
observed	52	5	4	103	40	28	9	18	66	13	$p > 0.05$
Females with cubs in den											
expected	23.8		1.1	69.9	12.7	18.8	1.2	6.3	34.9	0.3	χ^2=85.2, df=8
observed	2		0	126	3	16	0	1	21	0	$p < 0.001$
Females with cubs											
expected	76.2	6.8	8.6	125.3	95.3	29.1	9.6	32.6	128.7	7.6	χ^2=46.8, df=9
observed	111	9	15	113	83	18	7	12	152	6	$p < 0.001$
Independent cubs											
expected	12.62	4.69	1.7	45.94	10.14	12.3	1.71	5.69	30.6	5.39	χ^2=32.62, df=9
observed	16	15	1	38	15	9	0	4	26	8	$p < 0.001$

- Areas left blank are when a vegetation type did not occur in the 95% UD of that particular animal.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Table 4.6: Habitat use by cheetah. The observed figure is the actual number of locations per vegetation type. The expected figure was calculated by multiplying the total number of locations by the percentage of each vegetation type occurring in the 50% UD of each individual.

Individual Group	BKT	BST	DLT	EPM	KSL	MPT	OL	RT	SET	TET	χ^2 Results
Coalition											
expected	8.6		4.5	56.2	127.8	14.3			66.5		$\chi^2=58.3$, df=5
observed	1		2	24	171	0			80		$p < 0.001$
Single Females											
expected	16.9	1.1	1.1	65.7	8.6	22.3	0.7	10.3	27.3	1.2	$\chi^2=86.4$, df=9
observed	29	2	2	49	13	24	4	14	18	1	$p < 0.001$
Females with cubs in den											
expected	5.3		1.3	87.9	6.9	19.4	1.4	1.3	27.1	0.1	$\chi^2=34.9$, df=8
observed	1		0	122	2	15	0	1	10	0	$p < 0.001$
Females with cubs											
expected	48.9	1.9	1.6	74.7	33.9	17.4	9.0	14.2	54.2	4.8	$\chi^2=36.3$, df=9
observed	75	0	2	58	38	12	3	4	63	2	$p < 0.001$
Independent cubs											
expected	4.4	6.8	1.1	31.7	3.4	11.7	0.1	2.9	14.1	9.2	$\chi^2=23.9$, df=9
observed	9	10	1	27	10	5	0	3	14	7	$p < 0.001$

- Areas left blank are when a vegetation type did not occur in the 50% UD of that particular animal.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

Further characterization of home ranges

Distance to drainage lines

There was no statistically significant difference between the mean distances of the five cheetah groups and the random points from the drainage lines ($p > 0.05$). However, females with cubs at dens were closer to drainage lines (mean distance = 180.9m) than the other groups of cheetah, which were all about 250m from drainage lines (Figure 4.8).

Distance to Roads

There was a statistically significant difference between the mean distances to roads of the five cheetah groups and the random points ($p < 0.05$). Females with cubs at dens were the furthest from any roads (mean distance = 130.1m), the coalition of cheetah were the closest to roads (86.5m) and the other groups were about 100m from roads (Figure 4.8).

Distance to lions

The core area of the coalition was significantly closer to the core area of the pride of lions (Figure 4.7) than all other social groups of cheetah, which were at least twice as far from the lions (Figure 4.9; $p < 0.05$). The independent cubs and single females were significantly further from the lions than the other social groups ($p < 0.05$).

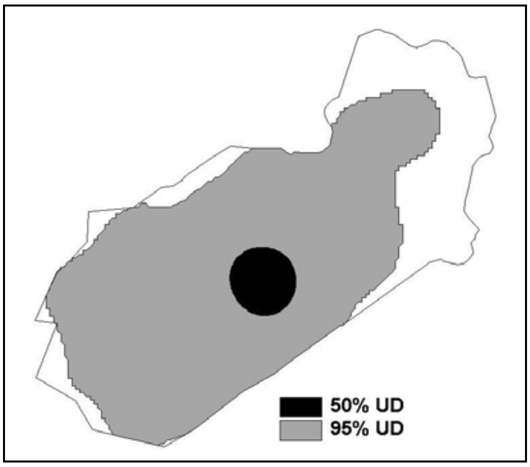


Figure 4.7: Home range and core areas for the pride of lions on Kwandwe, 95% and 50% UDs determined by the fixed kernel method. (Data are from the reserve records for the period January 2003 to August 2004).

Distance to the coalition

The core areas of the female cheetah were situated between 5000-7000m from the core area of the coalition (Figure 4.9) and the independent cubs were furthest from the coalition. However, there was no statistically significant difference in the distances of the different groups of female cheetah from the coalition ($p > 0.05$).

Slope and altitude

Single female cheetah occupied steeper slopes (mean slope = 6.8°) compared to the other females, while the coalition occupied flatter and low lying areas. The females with cubs in a den and the independent cubs occupied areas with the highest altitude (Table 4.3). However, these differences were not statistically significant ($p > 0.05$).

Prey density and visibility

The core area of the coalition had the most open vegetation with a visibility index of 72.8 and nearly 50% of the core area comprised karroid shrubland which had the highest visibility index of all vegetation types (Table 2.1 from Chapter 2). By contrast, the core area of the females with cubs in a den had the densest vegetation with a visibility index of 55.4 (Table 4.4) and nearly 60% of the core area comprised *Euphorbia Portulacaria* mosaic which had one of the lowest visibility indices (Table 2.1 in Chapter 2). There was no statistically significant difference between the mean visibility indices of the home ranges and core areas of the different groups of cheetah ($p > 0.05$).

The density of ungulates was greatest in the home range (3.7 animals/ha) and the core area (2.4 animals/ha) of the single females and lower in the home range (2.2 animals/ha) and the core area (1.2 animals/ha) of the coalition (Tables 4.3 and 4.4). There was no statistically significant difference between the mean abundance of ungulates in the home ranges and core areas of the different groups of cheetah ($p > 0.05$ for both).

In addition, although the abundances of the five dominant prey species (kudu, springbok, grey duiker, bushbuck and impala) varied between the different vegetation types (Table 4.7) these differences were not significant (p>0.05 for all). The highest densities of kudu were in *Euphorbia Portulacaria* mosaic, medium *Portulacaria* thicket and riverine thicket and the lowest in karroid shrubland and bushclump karroid thicket (Table 4.7). The highest densities of springbok were in karroid shrubland and riverine thicket; whereas the denser vegetation types for example *Euphorbia Portulacaria* mosaic and medium *Portulacaria* thicket had no springbok present (Table 4.7). Grey duiker densities were the highest in tall *Euphorbia* thicket, *Euphorbia Portulacaria* mosaic and medium *Portulacaria* thicket, whereas the more open vegetation types had no grey duiker present (Table 4.7). The highest bushbuck densities were in tall *Euphorbia* thicket, riverine thicket and bushclump savannah, whereas 50% of the vegetation types on Kwandwe had no bushbuck (Table 4.7). The highest densities of impala were in bushclump savannah thicket, whereas no impala were present in tall *Euphorbia* thicket and old lands (Table 4.7).

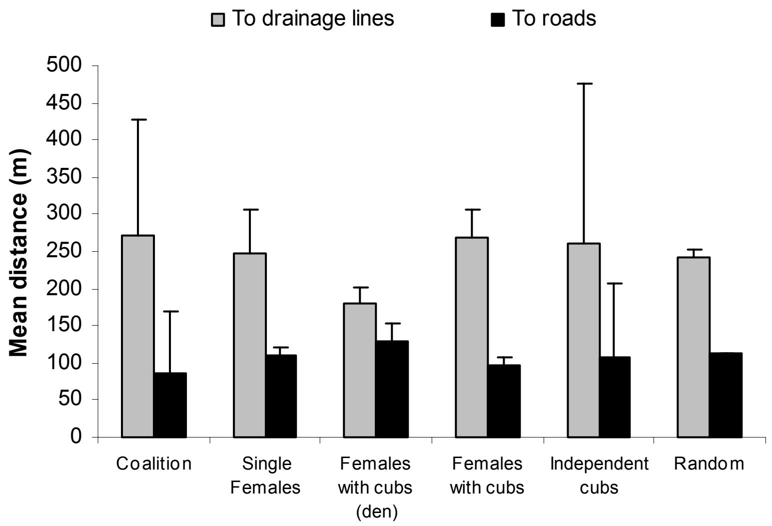


Figure 4.8: Mean distance (± 1sd) of cheetah locations, within the home range, to drainage lines and roads.

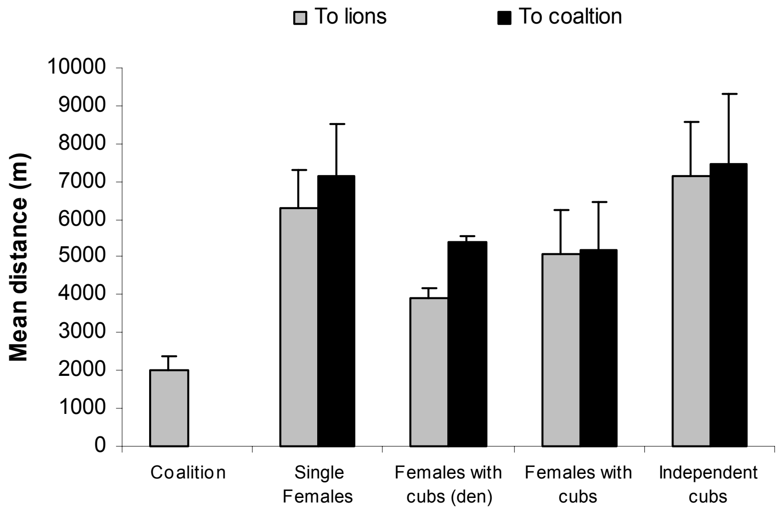


Figure 4.9: Mean distance (± 1sd) of cheetah core areas to the Kwandwe lion pride core area and mean distance (± 1sd) of the female cheetah core areas to the coalition core area.

Table 4.7: Prey density (animals/ha) in each vegetation type for the five most dominant cheetah prey species on Kwandwe.

Vegetation Type	Kudu	Springbok	Grey Duiker	Bushbuck	Impala
BKT	0.04	0.04	0.01	0.00	0.02
BST	0.14	0.00	0.03	0.05	0.18
DLT	0.09	0.01	0.02	0.00	0.01
EPM	0.16	0.00	0.04	0.01	0.01
KSL	0.04	0.13	0.00	0.00	0.03
MPT	0.15	0.00	0.04	0.02	0.01
RT	0.18	0.05	0.01	0.05	0.01
SET	0.11	0.02	0.01	0.00	0.06
TET	0.12	0.00	0.05	0.13	0.00
OL	0.07	0.02	0.01	0.00	0.00

Vegetation types as described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah thicket; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket; OL = old lands.

Summary of home range characteristics

In summary, the 95%UD of the coalition was small and was characterized by open flat areas dominated by karroid shrubland with a visibility index of 98.5 and a prey density of 2.2 animals/ha. Adjacent *Euphorbia Portulacaria* mosaic and short *Euphorbia* thicket provided areas of increased cover. The 95% UD of the coalition was closest to the space used by the pride of lions.

The home range of the single female cheetah was characterized by dense vegetation on steeper slopes dominated by *Euphorbia Portulacaria* mosaic with a visibility index of 53.2 and a prey density of 3.7 animals/ha. The mean distance to the pride of lions was greater than for all other cheetah except the independent cubs.

The home range of the female cheetah with cubs at a den was very small, relatively high lying and had the closest proximity to drainage lines. It was dominated by *Euphorbia Portulacaria* mosaic and had a prey density of 1.5 animals/ha and low visibility.

The 95% UD of the females with cubs was characterized by areas dominated by *Euphorbia Portulacaria* mosaic with a prey density of 3.0 animals/ha.

The home range of the independent cubs was the largest and was characterized by the highest altitude (386.9m) with relatively steep slopes (6°) dominated by *Euphorbia Portulacaria* mosaic with a prey density of 3.0 animals/ha and low visibility. The distance to the pride of lions and the coalition was greater than for the other groups of cheetah.

These trends were typically exaggerated in the core areas.

DISCUSSION

Space use

Previous studies of space use by cheetah have shown that the 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.* 2003a). 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 reflect gender differences in home range size. This is evident in the Serengeti where the large home ranges of female cheetah (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 cheetah and non-territorial male cheetah in the Serengeti mirror the migration patterns of the 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 cheetah 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 (37.4km²) (Caro & Collins 1986; 1987; Durant *et al*. 1988; Caro 1994). In Namibia, where the majority of the cheetah are found on private farm land, the lack of suitable hunting habitat and low availability of prey has lead to the home ranges of the male and female cheetah being as large as 1500km² (McVittie 1979; Marker *et al*. 2003a). Similarly the nomadic nature of the springbok in the Kalahari Gemsbok Park may be partly responsible for the large home ranges of female cheetah in this area. In this example the male coalition of cheetah had a smaller territory size compared to the females (Mills 1984; 1998). In Kruger National Park, a three male coalition had a home range (95% MCP) of 126 km^2 while the mean home range size of four females was 135 km^2 (Broomhall *et al.* 2003). These relatively small home ranges are probably a consequence of the nature of the environment where thickets on one side and hills on the other flank a region of open savannah. The small home ranges of cheetah in Matusadona National Park are explained in terms of the high density of prey on the foreshore grasslands (200-300 impala per km^2), combined with the easily accessible cover provided by the adjacent woodland (Purchase & du Toit 2000). In addition, the water on one side and very thick bush on the other may act as barriers, reducing the available space and thus resulting in small home ranges. The study at Matusadona National Park further illustrates the roles of space and prey abundance as factors influencing space use. Between 1995, when cheetah were released onto Matusadona National Park and 1998 when a second study was undertaken, home range size decreased by more than 50%. Over the same period, the level of Lake Kariba rose, the area of the foreshore decreased by about 50% and the density of impala increased by a similar amount (Purchase & du Toit 2000). It is possible that the home range was initially large as the cheetah explored their new surroundings after which the home range decreased as they settled into suitable habitat. However, it seems likely that the decrease in available space and the increase in prey density were possibly more important factors.

Other factors such as the distribution of suitable habitat for hunting and restrictive boundaries of small reserves may affect cheetah home range size (Hunter 1998; Broomhall *et al.*2003). Small patches of a widely dispersed habitat that is required for hunting will result in a large home range and an example is discussed below as part of the discussion of habitat selection. In the present study the relatively small home ranges of the female cheetah on Kwandwe is attributed to a combination of high prey density (150-300 animals/km²), the sedentary nature of the prey, restrictive boundaries of the reserve and availability of suitable habitat. The sizes of the home range and core area of the three male coalition were smaller than those of the females, which is unusual in felids (Ewer 1973; Sandell 1989; Mizutani & Jewell 1998) but may be typical for cheetah. Male cheetah defend much smaller areas than females which will visit the male home range in order to obtain resources (Caro 1994). In other groups of birds and mammals large female home ranges tend to be associated with reduced male territory size since large female home ranges are no longer defensible by males (Caro 1994). However, whether or not this reasoning applies to cheetah is questionable since there is little or no evidence of male cheetah defending the space used by the females. Nevertheless, the trend holds true in the Serengeti and to a lesser extent in Kruger National Park where female cheetah have large home ranges which overlap the much smaller home ranges of the males presumably to increase mating opportunities (Sandell 1989; Caro 1994; Broomhall *et al.* 2003). In the present study the home range of the coalition overlapped the home ranges of all the female groups to some extent, except for females with cubs in a den. However, whether this was due to the coalition selecting space so as to ensure that they encountered all the females, or due to the females attempting to ensure that they encountered the coalition, or both, cannot be answered with the data collected in this study. There was little overlap between the core areas of the female cheetah and in only one case (one female with cubs) was there any overlap between the coalition and a female. Thus, while there was extensive overlap in space use at the home range level, the cheetah also seemed to avoid each other and showed exclusive use of certain areas, which is more typical of asocial felids (Sandell 1989; Caro 1994; Broomhall *et al.* 2003). As reported by Caro (1994) and in the present study, much of the apparent overlap in home ranges represents sequential and not simultaneous residence.

Habitat selection

Because many of the previous studies of the ecology of cheetah have been in savannah habitats, the cheetah has been characterized as a species that prefers open, grassland habitats on which it uses its speed to catch prey (Schaller 1972; Caro & Collins 1986; Durant *et al.* 1988; Fitzgibbon 1990; Caro 1994; Laurenson 1994; 1995; Laurenson *et al.* 1995; Nowell & Jackson 1996; Durant 1998; Durant 2000a; 2000b). However, the historic distribution of cheetah includes a range of more heavily wooded habitats and recent studies in some of these woodland savannahs have added to our understanding of habitat selection. In an area of woodland savannah in Kruger National Park, a three male coalition of cheetah had a home range and core area that was centered in an area of open savannah while females used denser woodland habitats more often (Broomhall *et al.* 2003). In Matusadona National Park, the cheetah prefer the open grassland of the lake foreshore for hunting and eating and use the adjacent dense woodland for resting and moving through the area (Purchase & du Toit 2000). Although the sample size in Matusadona National Park study (two adult male cheetah and one adult female) was too small for a comparison of male and female habitat selection, the home range of one male included much more of the open grass on the foreshore than did the home ranges of the second male and the female. In Phinda Resource Reserve cheetah select open areas, particular grassland patches in the woodland, for hunting. These spaces, which constitute less than 10% of available habitat, are distributed as small, discreet, widely spaced patches and it is suggested that the availability of these spaces rather than the abundance of prey is the key factor in habitat selection and home range size (Hunter 1998).

The results from Kwandwe are strikingly similar to those from Kruger National Park. Female cheetah on Kwandwe selected denser vegetation types found on steeper slopes and at higher elevation while the coalition selected the most open and flat vegetation type (karroid shrubland) on the reserve. The three male coalition on Kwandwe selected what would perhaps be regarded as the most ‘typical’ cheetah habitat, being flatter low lying areas with open vegetation, with adjacent cover. Their core area was the closest to that of the pride of lions, suggesting that the location of the lion pride did not have a major influence on habitat selection. By contrast, the females used space and selected habitats that were much denser and undulating and almost as far away from the lion pride and the coalition as possible within the confines of the reserve. This pattern was particularly evident in the location of the core areas of the females. It is likely that various factors were important in habitat selection by female cheetah. The positioning of the core areas away from the pride of lions suggests that avoidance of lions played a major role. It is well documented that lions will steal prey from cheetah (Caro 1994; Durant 2000a; 2000b) and that they can kill cubs and adults (Durant 2000a; 2000b). It is thus not surprising that the core areas were almost as far from the lions as possible. In addition, the female cheetah selected denser vegetation types (as seen in Kruger National Park), which would have offered more cover, and steep areas, which would have offered better vantage points. In Kruger National Park, the main prey of female cheetah are impala which also prefer the more dense woodland habitats and Broomhall *et al*. (2003) suggest that the habitat selection by female cheetah is influenced by the distribution of the prey. In the present study, kudu were abundant in the denser habitats selected by the female cheetah but it is not possible to separate the roles of prey distribution from the cover offered by the habitat. Finally, it is likely that the space occupied by the coalition was important in female habitat selection as their home ranges overlapped with that of the males.

Habitat selection by the coalition suggests that the group of three males was far less susceptible to interference from the lions and similar observations have been made in the past (Caro 1994; Hunter 1998; Durant 2000b). It is thus likely that habitat selection was based on the availability of suitable habitat for hunting, the abundance of prey of a suitable size, and the availability of cover, more than the presence of lions. Thus the selection of a home range in which the most open vegetation type on Kwandwe (karroid shrubland) and adjacent regions of denser vegetation (*Euphorbia Portulacaria* mosaic and short *Euphorbia* thicket) predominated can be explained. Prey density in both the home range and core area of the coalition was amongst the lowest and it is therefore unlikely that the availability of prey of a suitable size was an important factor. Mills *et al.* (2004) demonstrated that prey of a suitable size was an important factor in determining habitat selection in Kruger National Park. However, the relatively high density of prey on Kwandwe probably precluded the importance of this factor in the present study. Prey density of kudu on Kwandwe was 11 kudu/ km^2

compared to the density of impala in the Kruger National Park which ranged from a minimum of 3.9 impala/km^2 to a maximum of 5.9 impala/km^2 (M.G.L Mills pers. comm.). The above mentioned impala densities were not from the same years as the study (Broomhall *et al.* 2003) but they were the only data available.

Habitat selection by females with cubs in a den represents an extreme form of selection as the space occupied was very small and the threats are perhaps greater than for any other group of cheetah. Female cheetah with cubs in a den selected higher lying areas with the densest vegetation and lowest ungulate density (1.5 animals/ha), and their den sites were furthest away from roads and closest to drainage lines compared to the other cheetah social groups. Generally female cheetah give birth to cubs in a concealed den with long, dense grass or under a thornbush (Laurenson 1995). Access to water is an important factor in den choice, as lactating cheetah significantly increase the time they spend drinking (Laurenson 1995; Sunquist & Sunquist 2002). The distance of the den sites from the lions and the coalition, and their proximity to the edge of the reserve, suggest that avoidance of the lions and the coalition played an important role. Cub predation by lions has been previously reported (Durant 2000a; 2000b) and in the present study, 4 cubs and a litter of unknown number were killed by lions. Many previous studies have reported that female cheetah will move their cubs from one den to another, presumably in an effort to reduce the chances of the cubs being detected and killed (Adamson 1969; Laurenson 1995; Sunquist & Sunquist 2002). This widely used anti-predator behaviour was not used in the present study, possibly because of the thickness of the vegetation and the low density of superior predators.

The single set of independent cubs had the largest home range and core area and ranged widely through the reserve. They used vegetation types with low visibility and were further from the lions and coalition than any other group of cheetah. Independent cubs may be susceptible to predation from adult cheetah and lions and this may explain their habitat use.

It has been suggested that learnt behaviour may play a role in habitat selection (Davis & Stamps 2004) and results from the present study support this. Females CF10 and CF11 were born to CF6 at a den site in the west of the reserve. This group remained together with a core area in the west of the reserve while the cubs were dependent on their mother. As independent cubs, CF10 and CF11 remained in the west and then moved to the opposite end of the reserve where CF6 had another core area. CF10 and CF11 returned to the west of the reserve and established dens in a very similar area to the one in which they had been born.

In conclusion, habitat selection by cheetah varied between social groups depending on their susceptibility to predation by lions, their need for cover and need for water. In this case (Kwandwe) it is unlikely that the distribution or abundance of prey played an important role in habitat selection because prey abundance was relatively high throughout the reserve.

CHAPTER 5

CHEETAH HUNTING BEHAVIOUR ON KWANDWE

INTRODUCTION

Cheetah are predominantly diurnal, with peaks of activity around sunrise and sunset (Kruuk & Turner 1967; Schaller 1972; Skinner & Smithers 1990; Laurenson 1995). In cold weather cheetah sun themselves in the early morning, moving later than in warm weather (Pettifer 1981b), and lying up in the shade during the hottest hours of the day (Schaller 1972; Skinner & Smithers 1990; Sunquist & Sunquist 2002; Marker *et al.* 2003a). Cheetah normally choose an elevated resting place with a clear view of the surrounding area so as to see potential prey and approaching predators or competitors (Skinner & Smithers 1990). It is thought that cheetah mostly hunt by day, to avoid competition from larger nocturnal predators (for example lion and hyena), but the hours vary from area to area depending on the climate, presence of other predators and possibly the topography (Skinner & Smithers 1990; Estes 1991; Sunquist & Sunquist 2002). Family groups (mother and her cubs) generally spend the night resting in open areas and are usually found in the same place in the morning, whereas male coalitions and juveniles sometimes continue to move during the night (Estes 1991; Caro 1994). In the Sahara, where daytime temperatures can reach 43ºC, cheetah do most of their hunting at night and in the relatively cool hours after daybreak (Dragesco-Joffé 1993). Cheetah use various techniques to minimize direct interactions with lions and hyenas. They reduce visual and audio cues by killing silently by asphyxiation after a short chase, hunting during the day when many of their competitors are inactive, and dragging kills immediately into cover to avoid attracting vultures to carcasses (Caro 1994; Durant 2000a). This is evident in the Serengeti where cheetah hunt slightly later in the morning and earlier in the afternoon than lions and hyenas, presumably as a strategy to avoid these larger carnivores (Schaller

1972; Caro 1994; Durant 2000a; Sunquist & Sunquist 2002). Cheetah have been seen hunting at night in the Serengeti and Namibia (Schaller 1972; Stander 1990), but there is a general lack of information on their nighttime activities. Although cheetah mainly hunt during the day to avoid other predators they do encounter predators such as lions, leopards and hyenas which all represent a threat to them. These larger and more aggressive carnivores kill adult cheetah and cubs and cheetah may lose a certain percentage of their kills to lion, leopard and hyena (Caro 1994; Laurenson 1995; Durant 2000a; 2000b; Sunquist & Sunquist 2002).

As mentioned in previous introductions, much of the research on cheetah has been conducted in open habitats (Schaller 1972; Caro & Collins 1986; 1987; Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990; Caro1994; Laurenson 1994; 1995) and more recently in more wooded habitats (Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003; Marker *et al.* 2003a; Mills *et al.* 2004). These studies have shown that cheetah select open savannah-like habitats for hunting, even in the more wooded areas and that available cover, often on the fringes of the open areas is used both in hunting and for refuge. Together these studies have shown that hunting style, chase distance, kill retention time and levels of kleptoparasitism will be influenced by the density of the vegetation (Schaller 1972; Eaton 1974; Fitzgibbon 1989; Pettifer 1981b; Caro 1994; Hunter 1998; Purcase & du Toit 2000; Mills *et al.* 2004; Radloff & du Toit 2004).

Valley Bushveld, which characterizes Kwandwe, has very few open, savannah-like vegetation types and the major aim of this research was to study the activity patterns and hunting behaviour of cheetah in a particularly dense vegetation type. However, the thickness of the vegetation and the nocturnal hunting of the coalition made this very difficult and the results can only be regarded as preliminary and incomplete. Nevertheless, since this is the first study of cheetah in Valley Bushveld the results are presented here and compared with feeding behaviour from other studies in more open habitats.

METHODS

Data Collection

All cheetah were located by radio-telemetry on a daily basis, and where possible I followed the cheetah for extended periods of time to observe kills as they were made. Direct observations and continuous observations were used to record the hunting behaviour of the various cheetah groups (see Chapter 3 for details). Following animals in a vehicle in denser vegetation types like the Valley Bushveld found on Kwandwe, needs to be carefully executed, as the observers need to keep relatively close to the animal in order to maintain visual contact. It is difficult to measure the influence this may have had on my data, but I was always careful to be as unobtrusive as possible and hold back when the cheetah located prey. The following data were recorded when cheetah encountered potential prey: habitat or vegetation type, time of kill, prey species, sex and approximate age of prey, chase distance (estimated by using a Nikon Laser 800 Rangefinder with a 8x magnification), kill retention time (i.e. the length of time the cheetah spent at the carcass, including resting periods at the carcass), and whether the carcass was appropriated by other predators (i.e. kleptoparasitism). Kills were observed until the cheetah left the carcass or the kill was kleptoparasitised.

Statistical Analyses

The relationship between the cheetah social groups and their chase distances and kill retention times were tested using one way ANOVAs (Sigma Stat; Jandel Scientific). The relationship between successful and unsuccessful hunts within each social group was tested using student t-tests (Sigma Stat, Jandel Scientific).

RESULTS

Timing of hunting

Peak activity periods for all the cheetah were in the morning and evening between 05h00 and 10h00 and 16h00 and 19h00, and the single females, females with cubs and the independent cubs made more kills in the morning than the coalition (Figure 5.1). Single female cheetah and females with cubs spent most of the middle of the day (between 10h00 and 15h00) resting and a very small percentage of kills were made during this time. Independent cubs were active throughout the day and made 24% of their kills during the midday hours (Figure 5.1). The hunting activities of the three male coalition were very different to the females, with 26% of kills made in the late afternoon and early evening between 16h00 and 20h00, 42% of kills at night (between 20h00 and 24h00), 32% in the morning and no hunting attempts during the middle of the day (Figure 5.1).

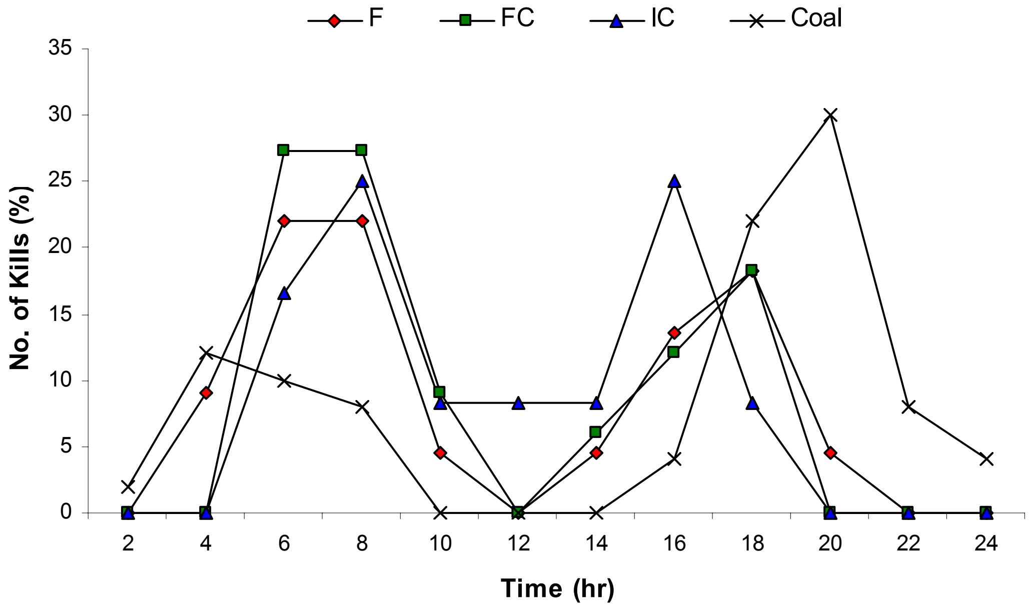


Figure 5.1: The number of kills as a percentage of all kills made during the various times of day for the coalition (Coal), single female cheetah (F), cheetah with cubs (FC) and independent cubs (IC). (On the X axis, 2 = kills made between 24h00 and 02h00, 4 = kills made between 02h01 and 04h00 etc).

To further examine the relationship between the timing of kills and the day length, and to establish how many kills were made in the dark, kills by the coalition that occurred just before or after sunset and before and just after sunrise were re-analyzed by calculating the time in minutes of the kill in relation to the time of sunset or sunrise for that particular day (Figures 5.2 & 5.3).

All kills made after sunrise were in partial or full sunlight however, kills made more than 60 minutes before sunrise were made in darkness. Similarly, kills made before sunset and within 60 minutes after sunset were made in full or partial light. However kills made more than 60 minutes after sunset were made in darkness. Based on this, 19 kills were made in darkness, 14 being made at night and 5 in the early morning (Figures 5.2 & 5.3).

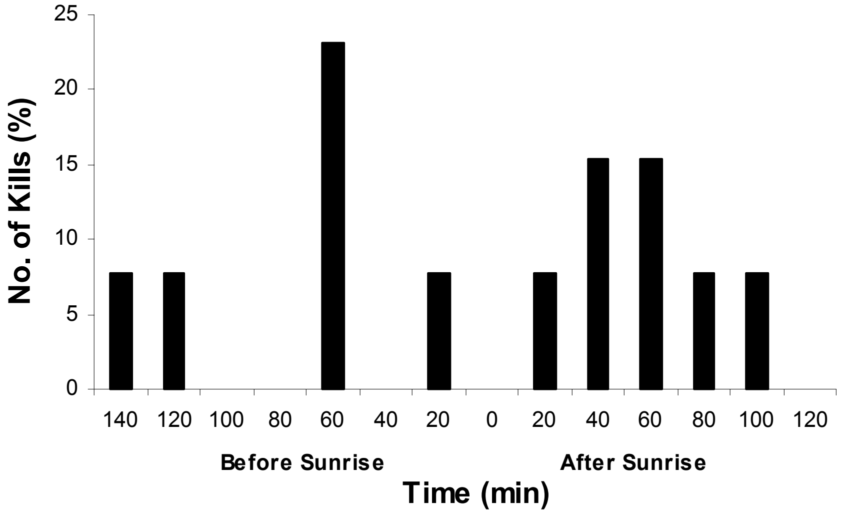


Figure 5.2: Number of kills, as a percentage of all kills made before and after sunrise, by the coalition of male cheetah.

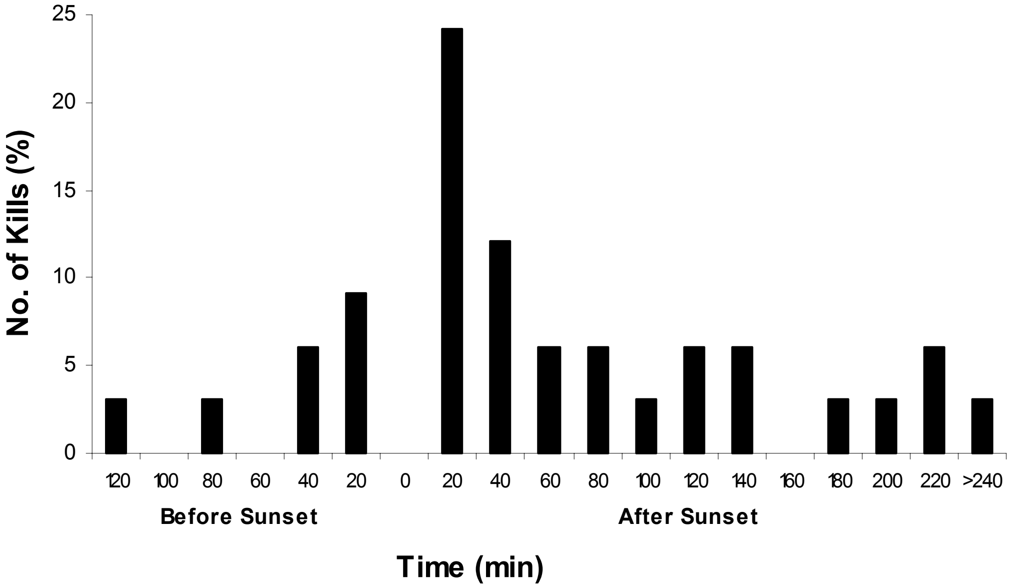


Figure 5.3: Number of kills, as a percentage of all kills made before and after sunset, by the coalition of male cheetah.

Chase distance, kleptoparastism and kill retention time

There was no significant difference between the chase distances of the various cheetah social groups ($p > 0.05$ for both successful and unsuccessful hunts). However, the chase distance of successful hunts was much shorter in single female cheetah compared to the other cheetah social groups, and independent cubs had the longest chase distance for successful hunts (Table 5.1). The coalition of cheetah and females with cubs had significantly longer chase distances for successful hunts compared to unsuccessful hunts ($p < 0.05$; Table 5.1). Chase distances for successful hunts by the independent cubs were longer than unsuccessful hunts, while for the single females the opposite was recorded. However, these differences were not statistically significant ($p > 0.05$; Table 5.1).

The percentage of cheetah kills that were kleptoparasitised on Kwandwe was very low with the three male coalition and females with cubs being the only social groups that lost any kills to other predators (Table 5.1). All kills kleptoparasitised from the coalition on Kwandwe were by lion whereas the majority of kills kleptoparasitised from the female cheetah with cubs was by the three male coalition.

The mean kill retention time was significantly longer for single female cheetah, with the three male coalition spending significantly less time at a kill compared to the other cheetah groups ($p < 0.001$; Table 5.1).

Table 5.1: Aspects of cheetah hunting behaviour and incidents of kleptoparastism on Kwandwe. Data are means ± 1sd.

ID	Mean chase distance (m)		Kleptoparastism (%)	Mean kill retention (min)
	Success	Fail		
Coalition	245.7±120.2(n=7)	129.3±73.6(n=7)	3.3	417±356(n=21)
Females with cubs	296.8±71.2(n=5)	101.7±53.1(n=6)	3.5	939±535(n=16)
Single Females	89.1±63.0(n=3)	250.3±177.0(n=3)	0.0	1253±774(n=10)
Independent cubs	465.5±297.3(n=4)	122.8±96.3(n=4)	0.0	495±383(n=6)

Hunting and habitat

The coalition of cheetah hunted 11 times in karroid shrubland (79.0% of all observed hunts) and of these, five were successful and six unsuccessful (Table 5.2). Two successful hunts were observed in short *Euphorbia* thicket, and one unsuccessful hunt was observed in bushclump savannah thicket (Table 5.2). Karroid shrubland and short *Euphorbia* thicket comprised 29.2% and 25.9% of the home range of the coalition. Although *Euphorbia Portulacaria* mosaic (25.3%) was a dominant vegetation type in the coalition's home range, no hunts were observed in this vegetation type. The coalition employed open pursuit in karroid shrubland and cover provided by denser vegetation for concealment while stalking.

Female cheetah with cubs were observed hunting 10 times of which half were successful (Table 5.2). Similar numbers of successful and unsuccessful hunts were made in karroid shrubland, *Euphorbia Portulacaria* mosaic and short *Euphorbia* thicket and these vegetation types comprised 16.6%, 26.9% and 22.9% of their home range respectively (Table 5.2). One unsuccessful hunt was observed on the old lands. Bushclump karroid thicket (13.5%) was one of four dominant vegetation types in the home range of the females with cubs, yet no hunts were observed in this vegetation type.

Single female cheetah were observed hunting six times with a 50.0% success rate (Table 5.2). Successful hunts were made in karroid shrubland and in old lands, vegetation types that comprised 11.9% and 1.4% of their home range respectively (Table 5.2). Unsuccessful hunts were made in short *Euphorbia* thicket, *Euphorbia Portulacaria* mosaic and old lands, which comprised 22.1%, 30.0% and 1.4% of their home range respectively (Table 5.2). Bushclump karroid thicket (12.2%) was one of four dominant vegetation types in the home range of the single female cheetah, but no hunts were observed in this vegetation type.

Four successful hunts were observed by the independent cubs with two of these in karroid shrubland, one in *Euphorbia Portulacaria* mosaic and one in bushclump savannah thicket. These vegetation types comprised 7.8%, 35.1% and 3.6% of their home range respectively (Table 5.2). Four unsuccessful hunts were observed and of these, 75.0% were in karroid shrubland and 25.0% in old lands, vegetation types that comprised 7.8% and 1.3% of their home range respectively (Table 5.2). Although short *Euphorbia* thicket was a dominant vegetation type in the home range of the independent cubs, no hunts were observed in this vegetation type.

For all cheetah, 38 hunts were observed and 19 were successful. Twenty two of the hunts were in karroid shrubland.

Table 5.2: Total number of hunts made in the various vegetation types for each cheetah social group. Figure in parenthesis is the percentage of each vegetation type found within the 95% UDs of each cheetah social group.

	Coalition		**Females with cubs**		**Single Females**		**Independent cubs**	
Successful hunts	KSL	5 (29.2)	KSL	2 (16.6)	KSL	2 (11.9)	KSL	2 (7.8)
	SET	2 (25.9)	SET	1 (22.9)	OL	1 (1.4)	EPM	1 (35.1)
			EPM	2 (26.9)			BST	1 (3.6)
Unsuccessful hunts	KSL	6 (29.2)	KSL	2 (16.6)	SET	1 (22.1)	KSL	3 (7.8)
	BST	1(0)	SET	1 (22.9)	EPM	1 (30)	OL	1 (1.3)
			EPM	1 (26.9)	OL	1 (1.4)		
			OL	1 (1.8)				

Vegetation types are described in chapter 2: KSL = karroid shrubland; SET = short *Euphorbia* thicket; EPM = *Euphorbia Portulacaria* mosaic; BST = bushclump savannah thicket; OL = old lands.

DISCUSSION

The importance of continuous field observations in arriving at an accurate assessment of predatory behaviour and ecology is obvious (Eaton 1970). By following individual cheetah, females with cubs or male coalitions, it is possible to establish the similarities and differences in hunting behaviour of the different social groups in an area and from these data to make comparisons with other areas. However, the very thick vegetation which characterizes Valley Bushveld made observations of hunting behaviour difficult and the results must be seen as preliminary. Cheetah hunting behaviour varies between different areas, with variation in the habitat type, prey species; size of hunting group and the cheetah's hunting experience (Eaton 1970; Eaton 1974). For example in open, short grass plains like the Serengeti, cheetah employ open pursuit, where they walk up to the prey, pausing motionless from time to time if the prey shows anxiety (Fitzgibbon 1990; Skinner & Smithers 1990; Caro 1994; Laurenson 1995), whereas in woodland or scrub areas cheetah may use cover for concealment while stalking (Skinner & Smithers 1990; Caro 1994; Purchase & du Toit 2000; Mills *et al.* 2004). On

Kwandwe the cheetah hunting behaviour varied depending on the social group and the habitat in which the hunts occurred. The male coalition mainly hunted in the open karroid shrubland plains were they employed open pursuit, although the use of cover for concealment in stalking was used when available, whereas the female cheetah mainly used cover for concealment in stalking as they hunted in the thicker vegetation types.

In Kruger National Park cheetah initiated more hunts and killed more frequently in the open savannah than in other available habitats with thicker bush (Mills *et al.* 2004) and in Phinda Resource Reserve, which consists of overlapping open and closed bushveld habitats, cheetah also preferred the open grasslands for hunting (Hunter 1998). In Matusadona National Park, cheetah hunted predominantly in the open foreshore grasslands (Purchase & du Toit 2000). It is important to note that the open savannahs mentioned above are not like the open grassland plains of the Serengeti. The same pattern seems to emerge on Kwandwe where male and female cheetah hunted in the more open karroid shrubland areas even though the percentage of karroid shrubland available to the cheetah was very low in certain home ranges. However, the data must be interpreted with care since the apparent preference for hunting on the most open habitat might simply reflect the fact that cheetah were easiest to observe in this habitat type.

Chase distances are difficult to measure and therefore comparisons between studies are difficult to make (Mills 1990; Mills *et al.* 2004). Average chase distances appear to be shorter in more wooded habitats for example in Kruger National Park the average chase distance (189m) was 2.3 times less than the average chase distance (290m) for the Serengeti (Caro 1994; Mills *et al.* 2004). Based on this one might expect that in the dense vegetation of Kwandwe, the chase distance would have been even shorter, however this was not the case and chase distances were longer in Kwandwe than in Kruger National Park. While these differences might be real, different techniques were used to measure chase distances in

Kruger National Park compared to Kwandwe and comparisons should be made with care. Cover is not only important in that it may result in a reduced chase distance, but it may also increase the likelihood of success. In the Serengeti and Nairobi National Parks, cheetah are more likely to be successful at hunting when they are able to use cover to get closer to their prey before rushing (Eaton 1974; Caro & Collins 1986). Chase distances in Kruger National Park are significantly longer in successful (189m) than unsuccessful hunts (96m) and similar results have been reported for the Kalahari and the Serengeti (Schaller 1972; Labuschagne 1979; Caro 1994; Mills *et al.* 2004). In the present study the average chase distances for the various cheetah social groups varied considerably, and the chase distance for successful hunts was longer than for unsuccessful hunts for all groups except single female cheetah. The sample sizes for successful and unsuccessful hunts for single female cheetah were very small and the results may be unreliable. However, the sample sizes for independent cubs was only one larger and they showed the same trend of longer chase distances in successful hunts. The very long chase distances for the independent cubs probably reflect their inexperience. Caro (1994) found that cheetah cubs in the Serengeti were poor hunters at the time of separation from their mothers and therefore the most dramatic development in hunting skills developed after independence.

Cheetah are predominantly diurnal with peaks of activity around sunrise and sunset and very little or no activity at night (Schaller 1972; Eaton 1974; Pettifer 1981b; Skinner & Smithers 1990; Caro 1994). The activity of the cheetah at Kwandwe conform to this with the exception of the coalition which were active earlier in the morning and later at night than the other social groups. Although cheetah are known to hunt at night in some areas, especially where maximum day temperatures are very high (Dragesco-Joffé 1993), there is a lack of information on their night-time activities. The diurnal behaviour of cheetah, especially in the Serengeti is thought to have developed for avoidance of larger carnivores like lion and hyena which have a negative impact on cheetah, stealing carcasses and accounting for the high mortality of cubs (Schaller 1972; Caro 1994; Durant 2000a; 2000b). In addition, it is accepted that vision is the primary sense of cheetah (Eaton 1970) and this must be partly responsible for their diurnal activity. Numerous factors could be responsible for the nocturnal hunting behaviour seen by the coalition on Kwandwe; for example the low density of competitors, the absence of spotted hyena, the relatively open habitat they hunt in, cooperative hunting and the increased vigilance of three adult animals. Nocturnal hunting could be beneficial due to the fact that cheetah prey are diurnal and would therefore be less active at night. Additional studies in other Valley Bushveld regions and of other factors including the species killed at night are needed to gain a better understanding of this behaviour.

Cheetah lose 13.1% of their prey to lions and hyenas in the Serengeti (Schaller 1972; Caro 1994) compared to 11.8% in Kruger National Park (Mills *et al.* 2004), 9.5% in Mala Mala Game Reserve (Radloff & du Toit 2004) and 3-4% on Kwandwe (present study). The differences in levels of kleptoparasitism could be due to different densities of larger predators like lion and hyena or differences in the habitat. Across African savannah ecosystems, cheetah are less prone to kleptoparasitism in more wooded habitats (Schaller 1972; Caro 1994; Mills *et al.* 2004; Radloff & du Toit 2004). In open habitat, kleptoparasites can observe and follow hosts more easily, prey capture and carrying can be observed and hosts are less able to hide from kleptoparasites. Therefore cheetah in an open grassland ecosystem like the Serengeti are expected to be more vulnerable to kleptoparasitism than in areas like Kruger National Park (Caro 1994; Mills *et al.* 2004) and Kwandwe. All kills kleptoparasitised from the coalition on Kwandwe were by lion whereas the majority of kills' kleptoparasitised from the female cheetah with cubs was by the three male coalition.

A large variation is found in kill retention time across ecosystems as kill retention time may be affected by group size, prey size, predator densities, awareness of competing predators or amount of available cover (Schaller 1972; Caro 1994; Pettifer 1981b; Hunter 1998; Mills *et al*. 2004). In the Timbavati-Klaserie Private Nature Reserves, and Suikerbosrand Nature Reserve the mean kill retention time was 1944min and 1031min respectively (Pettifer 1981b), compared to 720-840min in Phinda Resource Reserve (Hunter 1998), 165min in Kruger National Park (Mills *et al.* 2004) and 136min in the Serengeti (Schaller 1972; Caro 1994). In Timbavati-Klaserie Private Nature Reserves, Suikerbosrand Nature Reserve and Phinda Resource Reserve, cheetah were acquired from captive-breeding programmes (Pettifer 1981b) or Namibia (Hunter 1998) for re-introductions, and had not been subjected to competition from other large predators. The exceptionally long kill retention time in the Timbavati-Klaserie Private Nature Reserves and Suikerbosrand Nature Reserve can therefore be explained by the fact that the cheetah had never been subjected to competition from other predators or scavengers while in captivity (Pettifer 1981b). In addition, there are no other large carnivores on Suikerbosrand Nature Reserve and thus no threat of kleptoparasitism. However, there are lions on Timbavati-Klaserie Private Nature Reserves but the studies were done from introduction of the cheetah which had no prior experience of kleptoparasitism (Pettifer 1981a, b). It has been suggested that the long kill retention time at Phinda is due to low densities of competitors such as lion and hyena (Hunter 1998). Kill retention times in the Serengeti and Kruger National Park, with similar densities of competing predators, are similar (Schaller 1972; Caro 1994; Mills *et al.* 2004). The slightly shorter retention time in the Serengeti can probably be explained in terms of the reduced amount of cover compared with Kruger National Park (Schaller 1972; Caro 1994; Mills *et al.* 2004). In the present study, kill retention times were longer than those recorded for the Serengeti and Kruger National Park, similar to those of Phinda Resource Reserve and shorter than those of the Timbavati - Klaserie Private Nature Reserves and Suikerbosrand Nature Reserve. The relatively long kill retention times at Kwandwe can be explained by the low density of direct competitors, as in

Phinda Resource Reserve, and the density of the vegetation. There was a large variation in kill retention times across the different cheetah social groups, with the three male coalition having the shortest kill retention time (420min). The home range of the coalition on Kwandwe was dominated by a relatively open habitat type (karroid shrubland) and this may have been partly responsible for the shorter kill retention times. In addition, the home range of the coalition was closest to that of the pride of lions and this plus the nocturnal hunting behaviour of the coalition on Kwandwe probably played a significant role in the kill retention time. Finally the fact that three animals were feeding on a single carcass would of reduced the kill retention time. The independent cubs were inexperienced and vulnerable to predation and kleptoparasitism and this may explain their short kill retention time. In addition the majority of the prey they killed was small and therefore would be consumed in a relatively short period of time.

In conclusion, cheetah activity patterns and hunting behaviour varied between cheetah social groups depending on competition from larger predators like lion, their need for cover for hunting and the availability of suitable habitat within their home ranges. Further studies on the cheetah activities and hunting behaviour on Kwandwe and other reserves with similar habitats, need to be conducted to increase the robustness of the data set and to give a better understanding of the nocturnal hunting behaviour seen in the three male coalition.

CHAPTER 6

FINAL DISCUSSION AND MANAGEMENT IMPLICATIONS

The present study has revealed several interesting aspects of the behaviour of cheetah in Valley Bushveld. However, the possibility that these behaviours were a result of the small, enclosed system, rather than the habitat, should be considered. The coalition on Kwandwe developed a home range that incorporated the most open vegetation type (karroid shrubland) with surrounding denser vegetations, and consequently exhibited similar habitat selection to that reported for other more wooded habitats (Hunter 1998; Purchase & du Toit 2000; Broomhall *et al.* 2003). It is thus unlikely that their habitat selection and use was an artifact of the size of the system. Their diet was also similar to what has been previously reported (small number of species comprising the majority of kills with the most important species being the most abundant in the area). However, it differed in that the most important prey species (kudu) fell into the large prey size category, weighing ~ 220kg for males and ~ 160kg for females, rather than medium or small categories. In addition, 38% of the kills made by the coalition were made in darkness. The majority of hunts by the coalition were observed in karroid shrubland and this preference for hunting in the most open vegetation type was supported by the fact that more than half the kills (55%, based on location of cheetah at a kill) were made in the same habitat. Thus, it is unlikely that the observation of hunts was heavily biased by the open nature of karroid shrubland and it is more likely that the coalition preferred to hunt in this vegetation type. These results are similar to what has previously been described for cheetah and thus are probably a true reflection of the hunting behaviour of cheetah in Valley Bushveld. The ability to kill adult female kudu and the nocturnal hunting of the coalition are unlikely to be artifacts of the enclosed system and it is more likely that they reflect a level of adaptability that has not often been described.

Female cheetah on Kwandwe established home ranges that overlapped with that of the coalition and included areas of denser vegetation, which is similar to what has been reported previously (Hunter 1998; Broomhall *et al.* 2004). However, they only made a few kills in the open and used the denser vegetation types more than expected (62.3% of kills were made in denser vegetation types such as bushclump karroid thicket, *Euphorbia Portulacaria* mosaic and short *Euphorbia* thicket; see Chapter 3). It is possible that this was an artifact of the system in that the preferred open vegetation type was occupied by the coalition and the pride of lions and the females were forced to use less preferred vegetation types for hunting. However, previous studies have shown that female cheetah select vegetation types with greater cover than do males (Hunter 1998; Sunquist & Sunquist 2002; Broomhall *et al.* 2003). It would be interesting to establish the habitat selection of female cheetah in areas without lions or male cheetah as this would help determine if the habitat selection of cheetah represented a real preference or a form of Ideal Despotic Distribution (see Chapter 1).

The core areas of all female cheetah and the independent cubs were positioned close to the boundary fence and this may be an artifact of the system. Had the fence not been present, the home ranges may have been larger and the core areas further away from the pride of lions. However, in a larger system other lions and male cheetah may be present and a larger system should not necessarily be expected to result in larger home ranges.

The positioning of den sites on Kwandwe in thick vegetation and close to water was typical for cheetah. However, their proximity to the boundary fence and distance from the pride of lions suggests that should the boundary fence not have been present the females may have established dens even further from the lions. Thus, while the selection of a den site was typical for cheetah, the position of the dens may have been affected by the enclosed nature of the reserve.

Together, the results from Chapters 3 – 5 suggest that while cheetah in general have preferred vegetation types (open savannah with adjacent denser bush), hunting techniques (stalk and short chase in open flat areas in daylight), and prey size (small to medium) the species is more adaptable than some previous studies have suggested. This adaptability may have important implications for conservation of cheetah and may, at least in part, explain the observation that many introductions of cheetah to small reserves have been successful (Caro 1994).

Management implications

Carrying capacity for large carnivores

The carrying capacity of a reserve for large carnivores can be calculated in several ways based on food requirements (Power 2002) but an understanding of the spatial requirements of the carnivores and the nature of any interspecific interactions is equally important. Interspecific killing is common among mammalian carnivores (Palomares & Caro 1999) and mortality from interspecific killing can be high. This is particularly true for cheetah and African wild dogs, and for both species, in open or large systems, there is an inverse relationship between their densities and the densities of lions and spotted hyenas (Laurenson 1995; Creel & Creel 1996; Palomares & Caro 1999). In the Serengeti interspecific killing is limiting the population density of cheetah by lions (Laurenson 1995). 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. Thus management of a guild of large predators in a small, enclosed system is very important so as to minimize the effect on subordinate predators such as the cheetah. On Kwandwe seven cheetah were killed by lions throughout the study period (see Chapter 2) but the absence of comparable studies makes it difficult to determine whether this is a high or low rate of predation. However, the low percentage of cheetah kills that were kleptoparasitised by lions and the long kill retention time of cheetah on Kwandwe suggest that interspecific interactions were not a common occurrence and that the structure of the guild of carnivores is appropriate for the space available. This is supported by the observation that female cheetah on Kwandwe did not move their cubs from one den to another as has been reported in previous literature (Caro 1994; Laurenson 1995).

Studies of the home ranges of the female cheetah revealed that the core areas were positioned in relatively dense vegetation at a distance from the pride of lions and the coalition, and that there was little overlap. This suggests that a reserve such as Kwandwe will only be able to maintain a small number of adult, breeding females and highlights the importance of an understanding of space use.

Clearly the guild of carnivores on Kwandwe is dynamic with recruitment through reproduction and loss through deaths and while the guild structure may be appropriate now, it may not remain so. Therefore ongoing studies of the behaviour of the carnivores are necessary if the reserve is to make informed management decisions.

Effect of large predators on their prey

Although not a central component of this study, the interactions between predators and their prey populations is another important factor to consider. In Phinda Resource Reserve (170km²) the impact of growing populations of re-introduced lion and cheetah led to the decline of some herbivore species (Hunter 1998), which lead to a management decision to reduce the numbers of both lions and cheetah. In small, enclosed systems with resident populations of herbivores, long term population control of large carnivores will be necessary to avoid excessive impact on prey species. On Kwandwe the large number of young kudu being killed by cheetah will have a knock on effect on the kudu population and with the lions preying on a large number of adult kudu (unpublished reserve records), the population may be threatened. However, the results from this and many other studies suggest that cheetah kill the most abundant ungulate in the small to medium size range (Mills 1984; Caro 1994; Hunter 1998). If this is the case, then as the kudu numbers decline so the diet of the cheetah should change. On Kwandwe there are several other small to medium sized species including grey duiker, springbok and impala and it would be interesting to establish if the diet of the cheetah changes over the next ten years. If there is a change in diet that mirrors a reduction in abundance of kudu then this might provide a natural opportunity for the kudu population to recover. And, if this is the case then it might be possible for management to be less intensive and to allow prey populations to cycle naturally.

Maintenance of genetic diversity

The re-introduction of carnivores into enclosed systems is typically initiated with a small number of founders and therefore these small populations may suffer from limited genetic variability. If these animals reproduce and if inbreeding is not prevented there will be further loss of genetic variability which is associated with a reduced ability to cope with environmental changes and disease (Hunter 1998; Caro 2000). The prevention of inbreeding and maintenance of genetic diversity is a particular problem on small reserves which cannot support a large enough population to ensure natural maintenance of genetic diversity. In this case, management interventions to maintain genetic diversity are essential if the reserve wishes to contribute to conservation rather than just ecotourism. On Kwandwe, the adult, breeding female cheetah are closely related, being CF6 and two of her daughters. Since the only adult males on Kwandwe form the coalition, of whom two are brothers, there is a chance that the daughters were mated by their father. To increase genetic diversity on Kwandwe it will be necessary to bring in new animals. An analysis of the predation records suggests that the female cheetah that were born on the reserve were less susceptible to predation than re-introduced animals that were not familiar with the vegetation nor superior predators such as lions. It is thus more feasible to consider bringing in new coalitions of males which are less susceptible to predation by lions. It is unlikely that Kwandwe is large enough to support a second coalition and it will be necessary to replace the existing coalition with another group of males in the next few years. In this way, populations of cheetah on small reserves are treated as a sub-division of the entire population and genetic and demographic exchange is mediated by human management (Hunter 1998).

Research and monitoring

If small, enclosed ecosystems are to play a role in conservation rather than simply function as ecotourism destinations, then ongoing research is essential to inform management decisions. The dynamic nature of multi-carnivore systems means that habitat selection, space use and diet should be continuously monitored and short term studies after initial release of predators are not sufficient.

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APPENDIX A

Common and scientific names of mammalian species found on Kwandwe Private Game Reserve

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Order Primate	
Chacma Baboon	*Papio ursinus*
Vervet Monkey	*Cercopithecus aethiops*
Order Lagomorpha	
Scrub Hare	*Lepus saxatilis*
Smith’s Red Rock Rabbit	*Pronolagus rupestris*
Order Rodentia	
Springhare	*Pedetes capensis*
Greater Canerat	*Thryonomys swinderianus*
Cape Porcupine	*Hystrix africaeaustralis*
Order Hyracoidea	
Rock Hyrax	*Procavia capensis*
Order Insectivora	
South African Hedgehog	*Atelerix frontalis*
Order Tubulidentata	
Aardvark	*Orycteropus afer*
Order Carnivora	
Small Grey Mongoose	*Galerella pulverulenta*
Yellow Mongoose	*Cynictis penicillata*
Water Mongoose	*Atilax paludinosus*
Suricate	*Suricata suricatta*
Small Spotted Genet	*Genetta genetta*
Striped Polecat	*Ictonyx striatus*

Cape Clawless Otter	*Aonyx capensis*
Cape Fox	*Vulpes chama*
Bat-eared Fox	*Otocyon megalotis*
Aardwolf	*Proteles cristatus*
African wild dog	*Lycaon pictus*
Black-backed jackal	*Canis mesomelas*
Cheetah	*Acinonyx jubatus*
Caracal	*Felis caracal*
Serval	*Felis serval*
Leopard	*Panthera pardus*
Lion	*Panthera leo*
Brown Hyena	*Hyaena brunnea*
Order Proboscidea	
Elephant	*Loxodonta africana*
Order Perissodactyla	
Black Rhino	*Diceros bicornis*
White Rhino	*Ceratotherium simum*
Burchell's Zebra	*Equus burchelli*
Order Artiodactyla	
Warthog	*Phacochoerus aethiopicus*
Bushpig	*Potamochoerus porcus*
Giraffe	*Giraffa camelopardalis*
Bushbuck	*Tragelaphus scriptus*
Greater Kudu	*Tragelaphus strepsiceros*
Eland	*Taurotragus oryx*
Buffalo	*Syncerus caffer*
Waterbuck	*Kobus ellipsiprymnus*
Gemsbok	*Oryx gazella*
Mountain reedbuck	*Redunca fulvorufula*
Grey Rhebuck	*Pelea capreoulus*
Red Hartebeest	*Alcelaphus buselaphus*

Blesbok	*Damaliscus dorcas phillipsi*
Blue Wildebeest	*Connochaetes taurinus*
Steenbok	*Raphicerus campestris*
Grey Duiker	*Sylvicapra grimmia*
Impala	*Aepyceros melampus*
Springbok	*Antidorcas marsupialis*
Cape Grysbok	*Raphicerus melanotis*

APPENDIX B

Ungulate composition in the various vegetation types in 2003.
(Figure in parenthesis is percentage of the ungulate composition in each vegetation type)

Habitat Type	Blesbuck	Blue Wildebeest	Burchell's Zebra	Bushbuck	Grey Duiker	Eland	Gemsbuck	Red Hartebeest	Impala	Kudu	Ostrich	Springbok	Steenbok	Waterbuck	Total
BKT	8(2.5)	34(10.8)	0	13(4.1)	10(3.2)	22(7)	12(3.8)	19(6)	20(6.3)	43(13.7)	16(5.1)	84(26.7)	23(7.3)	11(3.5)	315
BST	1(0.5)	0	25(13.7)	14(7.7)	12(6.6)	10(5.5)	0	6(3.3)	63(34.4)	42(22.9)	4(2.2)	0	4(2.2)	2(1.1)	183
DLT	0	14(41.2)	0	0	6(17.6)	0	1(2.9)	0	0	10(2.9)	0	2(5.9)	1(2.9)	0	34
EPM	1(0.1)	24(2.1)	30(2.6)	41(3.6)	191(16.6)	12(1)	31(2.7)	43(3.7)	52(4.5)	687(59.6)	5(0.4)	1(0.1)	7(0.6)	28(2.4)	1153
KSL	48(5.1)	92(9.8)	77(8.2)	4(0.4)	6(0.6)	43(4.6)	13(1.4)	115(12.2)	55(5.8)	106(11.3)	29(3.1)	319(33.9)	24(2.6)	10(1.1)	941
MPT	0	1(0.3)	7(2)	20(5.6)	55(15.5)	0	7(2)	25(7.1)	1(0.3)	224(63.3)	0	0	0	14(4)	354
OL	0	2(6.1)	0	2(6.1)	0	0	0	1(3)	0	9(27.3)	0	11(33.3)	0	8(24.2)	33
RT	0	13(4.6)	4(1.4)	40(14.1)	11(3.9)	0	0	45(15.8)	10(3.5)	103(36.3)	3(1.1)	38(13.4)	3(1.1)	14(4.9)	284
SET	0	67(7.2)	17(1.8)	11(1.2)	40(4.3)	9(1)	67(7.2)	64(6.9)	233(25)	321(34.4)	20(2.1)	55(5.9)	6(0.6)	22(2.4)	932
TET	0	5(3.5)	15(10.5)	59(41.3)	6(4.2)	0	0	0	0	57(40)	0	0	1(0.7)	0	143

Total is the total number of ungulates in each vegetation type.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

APPENDIX C

Ungulate composition in the various vegetation types in 2004.

(Figure in parenthesis is percentage of the ungulate composition in each vegetation type)

Habitat Type	Blesbuck	Blue Wildebeest	Burchell's Zebra	Bushbuck	Grey Duiker	Eland	Gemsbuck	Red Hartebeest	Impala	Kudu	Ostrich	Springbuck	Steenbuck	Waterbuck	Total
BKT	7(1.7)	52(12.4)	18(4.3)	2(0.5)	13(3.1)	4(1)	17(4.1)	57(13.6)	34(8.1)	98(23.4)	24(5.7)	71(16.9)	15(3.6)	7(1.7)	419
BST	0	3(1.5)	23(11.7)	21(10.7)	8(4.1)	8(4.1)	0	10(5.1)	63(32.1)	59(30)	0	0	1(0.5)	0	196
DLT	0	0	2(2.4)	1(1.7)	4(6.8)	0	19(32.2)	0	4(6.8)	27(45.8)	0	2(3.4)	0	0	59
EPM	0	19(2.1)	33(3.6)	33(3.6)	129(14.1)	57(6.2)	45(4.9)	42(4.6)	16(1.7)	501(54.8)	9(1)	0	10(1.1)	21(2.3)	915
KSL	20(3.4)	39(6.6)	36(6.1)	1(0.2)	4(0.7)	0	26(4.4)	16(2.7)	56(9.5)	80(13.5)	34(5.8)	252(42.6)	6(1)	21(3.6)	591
MPT	0	1(0.5)	3(1.4)	21(9.7)	36(16.6)	0	9(4.1)	0	11(5.1)	124(57.1)	0	0	1(0.5)	11(5.1)	217
OL	0	0	0	0	1(2.1)	0	0	14(29.2)	0	28(58.3)	4(8.3)	0	0	1(2.1)	48
RT	1(0.3)	3(1)	0	31(10.8)	6(2.1)	0	10(3.5)	3(1.1)	8(2.8)	169(58.7)	8(2.8)	39(13.5)	49(17)	6(2.1)	288
SET	1(0.1)	56(7.6)	42(5.7)	10(1.4)	31(4.2)	12(1.6)	36(4.9)	41(5.6)	114(15.5)	301(40.9)	12(1.6)	39(5.3)	13(1.8)	27(3.7)	735
TET	0	0	15(13.9)	46(42.6)	5(4.6)	0	4(3.7)	0	0	35(32)	0	0	0	3(2.8)	108

Total is the total number of ungulates in each vegetation type.

Vegetation types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.

APPENDIX D

Details of continuous observations done on the coalition from the 19 January to 4 February, 2004

			KILL								
DATE	**ACTIVITY**	**TIME OF KILL**	**SPECIES**	**SEX**	**AGE**	**% EATEN**	**LIVE MASS(kg)**	**EDIBLE MASS(kg)**	**MASS EATEN(kg)**	**CONSUMPTION/CHEETAH**	**KILL RET. TIME**
19/01/2004	-										
20/01/2004	-										
21/01/2004	kill	22H50	blesbuck	male	adult	85	75	56.3	47.8	15.9	7hrs
22/01/2004	mating(pm)	22H00									
23/01/2004	mating										
24/01/2004	mating										
25/01/2004	-										
26/01/2004	kill	7h15	red hartebeest	-	juv	100	30	27.0	27	9	35min
27/01/2004	kill	20h00	red hartebeest	male	adult	70	150	100.5	70.4	23.5	6hrs
28/01/2004	-										
29/01/2004	kill	20h26	blue wildebeest	-	juv	98	35	31.5	30.9	10.3	2hrs
30/01/2004	-										
31/01/2004	kill	9h00	kudu	-	juv	75	55	41.3	30.9	10.3	-
01/02/2004	-										
02/02/2004	kill	6h40	blesbuck	-	juv	100	23	20.7	20.7	6.9	40min
02/02/2004	kill	19h10	Burchell's zebra	-	juv	95	90	60.3	57.3	19.1	3hrs
03/02/2004	-										
04/02/2004	mating										
TOTAL									285	95	
									15.8kg/coal/day	**5.3kg/cheetah/day**	

APPENDIX E

Details of continuous observations done on the coalition from May 1 to 15, 2004

			KILL								
DATE	**ACTIVITY**	**TIME OF KILL**	**SPECIES**	**SEX**	**AGE**	**% EATEN**	**LIVE MASS(KG)**	**EDIBLE MASS (kg)**	**MASS EATEN(kg)**	**CONSUMPTION/CHEETAH**	**KILL RET. TIME**
01/05/2004	-										
02/05/2004	kill	7h58	impala	male	adult	95	60	45	42.7	14.3	5hrs
03/05/2004	-										
04/05/2004	-										
05/05/2004	-										
06/05/2004	-										
07/05/2004	kill	17h50	kudu	female	adult	90	155	103.9	93.5	31.2	8hrs
08/05/2004	-										
09/05/2004	-										
10/05/2004	-										
11/05/2004	-										
12/05/2004	kill	16h00	kudu	female	adult	85	155	103.9	88.3	29.4	15hrs
13/05/2004	-										
14/05/2004	kill	21h15	gemsbuck	-	juvenile	100	55	41.3	41.3	13.8	2hrs
14/05/2004	kill	23h40	gemsbuck	-	new born	100	35	31.5	31.5	10.5	2.5hrs
15/05/2004	-										
TOTAL									297.3	99.2	
									18.6kg/coal/day	**6.2kg/cheetah/day**	

APPENDIX F

Details of continuous observations done on a single female cheetah (CF10) from 28 February to 13 March, 2004

			KILL								
DATE	ACTIVITY	TIME OF KILL	SPECIES	SEX	AGE	% EATEN	LIVE MASS(kg)	EDIBLE MASS(kg)	MASS EATEN(kg)	CONSUMPTION/CHEETAH	KILL RET. TIME
28/02/2004	-										
29/02/2004	kill	9h00	kudu	-	juv	85	55	41.3	35	35	33h45min
01/03/2004	-										
02/03/2004	-										
03/03/2004	kill	10h30	kudu	-	new born	90	30	27	24.3	24.3	18hrs
04/03/2004	-										
05/03/2004	kill	9h00	kudu	-	new born	90	30	27	24.3	24.3	17hrs
06/03/2004	-										
07/03/2004	-										
08/03/2004	-										
09/03/2004	kill	20h00	kudu	-	new born	60	30	27	16.2	16.2	
10/03/2004	-										
11/03/2004	-										
12/03/2004	kill	8h45	duiker	-	juv	100	8	7.2	7.2	7.2	1h45min
12/03/2004	kill	18h30	kudu	-	new born	75	30	27	20.3	20.3	
13/03/2004	-										
TOTAL										127.3	
										8.0kg/cheetah/day	

APPENDIX G

Results of chi-squared analysis of prey preference of 15 prey species within each vegetation type

Year 1

Vegetation Type	Chi-Squared	Degrees of Freedom	P-Value
BKT	319.6	14	$p < 0.01$
BST	124.9	14	$p < 0.01$
DLT	332.1	14	$p < 0.01$
EPM	30.9	14	$p < 0.01$
KSL	128.9	14	$p < 0.01$
MPT	8273	14	$p < 0.01$
OL	267.6	14	$p < 0.01$
RT	64.2	14	$p < 0.01$
SET	293.2	14	$p < 0.01$
TET	27.8	14	$p < 0.01$

Year 2

Vegetation Type	Chi-Squared	Degrees of Freedom	P-Value
BKT	231.4	14	$p < 0.01$
BST	99.8	14	$p < 0.01$
DLT	143.1	14	$p < 0.01$
EPM	127.9	14	$p < 0.01$
KSL	130.9	14	$p < 0.01$
MPT	19.9	14	$p > 0.13$
OL	100	14	$p < 0.01$
RT	1175.8	14	$p < 0.01$
SET	193.3	14	$p < 0.01$
TET	501.8	14	$p < 0.01$

Habitat types are described in chapter 2: BKT = bushclump karroid thicket; BST = bushclump savannah; DLT = drainage line thicket; EPM = *Euphorbia Portulacaria* mosaic; KSL = karroid shrubland; MPT = medium *Portulacaria* thicket; OL = old lands; RT = riverine thicket; SET = short *Euphorbia* thicket; TET = tall *Euphorbia* thicket.