Cheetah *Acinonyx jubatus* ecology in the Kruger National Park: a comparison with other studies across the grassland-woodland gradient in African savannas

by

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Dedicated to

The spirit of joy and nature

"i thank You God for most this amazing".... e.e. cummings

i thank You God for most this amazing day:
for the leaping greenly spirits of trees and a blue true dream of sky;
and for everything which is natural which is infinite which is yes
(I who have died am alive again today, and this is the sun's birthday;
this is the birthday of life and of love and wings:
and of the gay great happening illimitably earth)

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Abstract

Field data on home range size, habitat utilisation, prey selection and hunting behaviour of cheetahs in the Kruger National Park (KNP) were analysed. Data synthesised from this study and from the literature were then used in a comparative study across a variety of African savanna ecosystems. Home range size in the KNP averaged 217 km^2 for territorial male cheetahs, 186 km^2 for female cheetahs and 438 km^2 for a nomadic male cheetah coalition. Cheetahs preferred open savanna habitat, although females used thicker bush more frequently than males. The cheetah's main prey impala *Aepyceros melampus* preferred denser woodland habitat. Male cheetahs took larger prey than females. Cheetahs hunted and killed more frequently in open savanna habitat. Mean chase distance for successful hunts was 189 m and for unsuccessful hunts 96 m. Cheetah hunting success was 20.7%, kleptoparasitism was 11.8%, mean kill retention time was 165 min, and kill rate averaged 1 kill per 4.61 days.

Across African savanna ecosystems, female cheetah home range size was found to be significantly larger in areas with migratory than sedentary prey, while male cheetah territory size was significantly smaller. In areas with sedentary prey only, there was a significant negative relationship between medium-sized prey biomass and female cheetah home range size and significant positive correlation between female and male home range size. Across a range of African savannas, cheetahs preferred open habitat that provided some woody cover. Although medium-sized prey made up the largest proportion (60%) of the cheetahs' diet, there was a significant variation in the size and age groups of prey taken across ecosystems. Cheetahs in ecosystems with the least amount of cover appeared to have longer mean chase distances, and greater hunting success and incidents of kleptoparasitism.

A population viability analysis, using VORTEX, found that a woodland savanna cheetah population had a greater viability than a grassland savanna population, particularly at small population sizes. The grassland savanna population was most affected by changes in juvenile mortality while the woodland savanna population was most affected by changes in adult, followed by sub-adult mortality. Maximum annual litter size and female mortality rates had large impacts on population persistence.

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My praise and thanks to the spirit of nature and adventure of the wild. *it inspires….*

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1: Introduction

With a slight build, deep chest, narrow waist, small, streamlined head and long legs, the cheetah is the fastest mammal on earth over short distances (Skinner & Smithers 1990; Nowell & Jackson 1996; Mills & Hes 1997). Although previously occurring throughout the drier parts of sub-Saharan Africa (Nowell & Jackson 1996), it is now listed as Vulnerable by the World Conservation Union, defined as a species with a high risk of extinction in the wild in the medium-term future (Hilton-Taylor 2000). This is mostly because it has suffered from a serious loss of range due to competition with humans (Myers 1975; Anderson 1983; Marker-Kraus & Kraus 1997). The effects are loss of habitat, a declining prey base and competition with livestock interests (Marker-Kraus & Kraus 1997). In many countries, cheetahs are considered pests and are persecuted (Marker-Kraus, Barnett & Hurlbut 1996). Being wide-ranging asocial predators, they occur at low densities across their geographical range (Myers 1975; Hamilton 1986; Caro 1994; Kelly & Durant 2000). Cheetahs are thus particularly vulnerable to local extinction, as a fragmented range is less able to support viable populations (Gilpin & Diamond 1980; Shaffer 1987; Purvis et al. 2000). Lack of genetic variation, discovered during the 1980s, is considered another threat to cheetah populations (O'Brien et al. 1983; O'Brien et al. 1985; O'Brien, Wildt & Bush 1986; O'Brien et al. 1987). A greater concern, however, than a lack of genetic diversity is competition with other large predators (Caro & Laurenson 1994). Laurenson's (1994) studies on the Serengeti Plains in East Africa revealed that 95% of cubs born never reach independence, where predation by lion *Panthera leo* was chiefly responsible for the high cub mortality. Other competitive effects of predators on cheetahs are kleptoparasitism (Schaller 1972; Caro 1994), whereby cheetahs lose their kills to more powerful competitors, and even adult cheetahs can be killed by other members of the large carnivore guild (Hunter 1998).

The discovery of high cub mortality on the Serengeti Plains prompted a number of follow-up investigations into the co-existence of cheetahs with lion and spotted hyaena *Crocuta crocuta* (Durant 1998; Durant 2000a and b), and a series of demographic studies and population viability analyses on the Serengeti Plains' cheetah population (Laurenson 1995b; Crooks, Sanjayan, & Doak 1998; Kelly et al. 1998; Kelly & Durant 2000). These studies found that cheetahs manage to co-exist with competitors by seeking out 'competitive refuges' with low densities of lion and hyaena (Durant 1998), and actively avoiding competition with these large predators (Durant 2000a). Durant (1998) argued that the cheetah's mobility is the key to its continued co-existence with other large predators, and Kelly & Durant (2000) concluded that cheetahs would continue to live at low densities where other large predators occur in high numbers. Kelly & Durant (2000) proposed that the conservation of cheetahs may not rely solely on their protection inside national parks, but also on their protection in natural areas outside national parks where other large predators are absent. The largest population of cheetahs in Africa occurs on commercial livestock farmlands in Namibia where other large predators have been eradicated (Marker-Kraus et al. 1996).

There is, however, a skew in terms of the data collected on cheetahs. Most of our understanding on cheetah behaviour and ecology comes from the Serengeti Plains, which boasts 25 years of continuous research (Kruuk & Turner 1967; Schaller 1972; Bertram 1979; Frame & Frame 1980; Caro 1982; Caro & Collins 1986a and b, 1987; Durant et al. 1988; Caro 1989; Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990; Laurenson, Caro, & Borner 1992; Caro 1994; Laurenson 1994, 1995a and b; Laurenson, Weilbnowlski & Caro 1995; Kelly et al. 1998; Conniff 1999). The Serengeti Plains is a short to medium grassland ecosystem where its most abundant herbivores, the wildebeest *Connochaetes taurinus*, Burchell's zebra *Equus burchelli* and Thomson's gazelle *Gazella thomsonii* undertake large seasonal migrations; well known as the largest extant migrations in Africa. Cheetahs, however, also inhabit a wide range of woodland savanna habitats (Caro & Collins 1987; Skinner & Smithers 1990; Nowell & Jackson 1996; Mills & Hes 1997). In these areas, the prey base is mostly sedentary, the density of prey is generally far lower than on the Serengeti Plains, and the main prey species varies across ecosystems (Mills 1998).

The density and distribution of the cheetah's main prey, suitable habitat and competing predators are the main ecological factors affecting the behaviour, density and distribution of cheetahs (Mills 1990; Caro 1994; Nowell & Jackson 1996; Mills 1998). Considering the unique ecology and dynamics of the Serengeti Plains, this area cannot be widely representative of all ecosystems within the cheetah's range. Cheetahs are considered to need open habitat for hunting (Bertram 1979), but occur in woodland habitats across a large part of its range (Skinner & Smithers 1990). Differences in the dispersion patterns of the prey base may also affect the cheetah's ranging behaviour (Caro 1994). Furthermore, there is evidence that the exceptionally high cub mortality observed on the Plains does not occur in other areas (Hunter 1998; Purchase 1998). Therefore, threats facing the cheetah population on the Serengeti Plains may be of lesser importance compared to other more immediate dangers elsewhere. For example, bush encroachment in large parts of the South African Lowveld may be a threat to cheetah populations (Pienaar 1969; Pettifer 1981a)

Because of the status of the cheetah and the growth of the ecotourism industry in Africa, the cheetah is a focus of several captive breeding programmes and is increasingly becoming the focus of re-introduction programmes into lucrative game ranches and smaller parks (Penzhorn 1999). There is a considerable controversy associated with the success of large carnivore re-introduction programmes (Linnell et al. 1997). Any problems associated with re-introduction and management are compounded further when an understanding of the behaviour and ecology of the species is limited (Caro & Durant 1995). Trying to estimate viable cheetah densities or delineate reserve boundaries based on ranging patterns of cheetahs on the Serengeti Plains would be of little use to smaller reserves. To date, a proper assessment of the viability of cheetah populations in woodland savannas has been impossible as population viability models are simulated using long-term data collected on the Serengeti Plains (Zank 1995; Purchase 1998; Hunter 1998). There is even speculation that the Plains may be a sink for cheetahs and not a source and that woodland habitat may be more favourable to cheetahs (Kelly et al. 1998). This may have large implications regarding the conservation and status of the cheetah. Pulliam (1988) warned that conservation research and management decisions based on 'sink' habitats alone can be misleading and lead to undesirable results. In Suikerbosrand Nature Reserve, where the cheetah was the top predator, it was found that introduced cheetahs were so successful that they eventually had to be removed because of drastic declines in their main prey types (Pettifer 1981b). Mills (1998) warned of the danger of extrapolating from one area to another when making management decisions due to the flexibility of carnivore behaviour under different ecological conditions. Therefore, greater attention given to cheetah ecology and behaviour in woodland savannas may assist and improve the re-introduction, management and conservation of cheetahs in Africa.

Recently, ecological studies have been conducted in woodland savannas in Matusadona National Park, Zimbabwe (Zank 1995; Purchase 1998; Purchase & du Toit 2000) and Phinda Resource Reserve, South Africa (Hunter 1998). A study was also conducted in the Kruger National Park (KNP), South Africa between 1987 and 1990 (Mills unpubl. data). With these additional studies, the database was large enough for me to conduct a comparative study across a variety of different African savanna ecosystems.

1.1. OBJECTIVES

The main objectives of my study are:

1. To add to the existing knowledge on cheetah ecology in woodland savannas by analysing a data-set concerning the home range size, habitat utilisation, prey selection and hunting behaviour of cheetahs in the Kruger National Park, and
2. To conduct a comparative analysis on the above aspects of cheetah ecology across a range of African savanna ecosystems using existing data synthesised from literature.

The overriding theme of my study is to extend the range of documented information on cheetah ecology across the grassland-woodland gradient in African savannas. Since the KNP is an important conservation area for the cheetah, knowledge of its ecological requirements and role within the ecosystem would provide important information for management of the park.

1.2 KEY QUESTIONS

1. How does cheetah home range size differ across African savanna ecosystems?
2. What are the habitat preferences of cheetahs across a range of grassland and woodland savanna ecosystems?

3. What is the prey composition, expressed as prey size classes and age structure, of cheetahs across a range of African savanna ecosystems?
4. How does hunting success, kill rate, chase distance, kill retention time and kleptoparasitism vary with availability of cover?
5. For a given population size, is cheetah population viability higher in a woodland savanna than a grassland savanna?

1.3 APPROACH

The key questions listed above were addressed by analysing:

1. The home range size and habitat preferences of cheetahs in the KNP (Chapter 3).
2. Differences in home range size across different African savanna ecosystems, based on predictions concerning the effects of prey dispersion patterns and density on female cheetah home range size and female cheetah density on male cheetah territory size (Chapter 3).
3. Differences in habitat utilisation and preferences across a range of grassland and woodland savannas ecosystems (Chapter 3);
4. Cheetah predation, hunting behaviour and use of habitats for hunting in the KNP (Chapter 4).
5. Differences in prey composition (in terms of prey size categories and age classes) across selected African savanna study sites (Chapter 4).
6. The effect of cover availability on hunting success, kill rate, chase distance, kill retention time and kleptoparasitism using data available from African savanna study sites (Chapter 4).
7. The viability of cheetah populations in a grassland and woodland savanna by varying life history and demographic variables for each ecosystem (Chapter 5).

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Chapter 2: Kruger National Park study area

2.1 LOCATION AND CLIMATE

The field study was conducted by M.G.L. Mills in the southern district of the KNP (24°96'- 25°44'E, 31°30'- 32° 00'S) between the Sabie and Crocodile Rivers (Fig. 2.1). The southern district covers an area of approximately 3786 km^2 (Bowland 1994). Two focal study areas were located in this district: 1) the main focal study area in the south eastern region (six radio-collared cheetahs were tracked in this area), and 2) a secondary focal study area to the west of the main study site in a more central region of the southern district (one cheetah was tracked in this area). The KNP study area lies in a summer rainfall region, with a mean annual rainfall averaging 600 mm rising to 700 mm in the Lebombo Hills (Gertenbach 1980).

2.2 VEGETATION

The main study area comprises three broad habitat types, identified using the landscape system developed by Gertenbach (1983). The central landscape in main study area is classified as *Sclerocarya birrea*/*Acacia nigrescens* tree savanna (an area covering approximately 250 km^2) occurring on fairly flat undulating terrain (Gertenbach 1983). It is an open to semi-wooded savanna with a moderate shrub layer and dense grass layer, which is intersected by several well-defined and broad (50 – 200 m) drainage channels (Gertenbach 1983; Funston 1999). The sides of the drainage lines are lined with a denser shrub and tree layer than the rest of the open savanna (this was observed from aerial photographs taken of the study area).

The Lebombo Hills border the open savanna to the east, covering an area of approximately 148 km^2. This is an undulating, broken landscape with north/south running rhyolite ridges and bottomlands, 100 metres higher than the basalt plains in the open savanna (Gertenbach 1983). The vegetation is heterogeneous dense to moderate bush, dominated by *Combretum apiculatum*, with a less dense field layer (Gertenbach 1983; Mills & Gorman 1997).

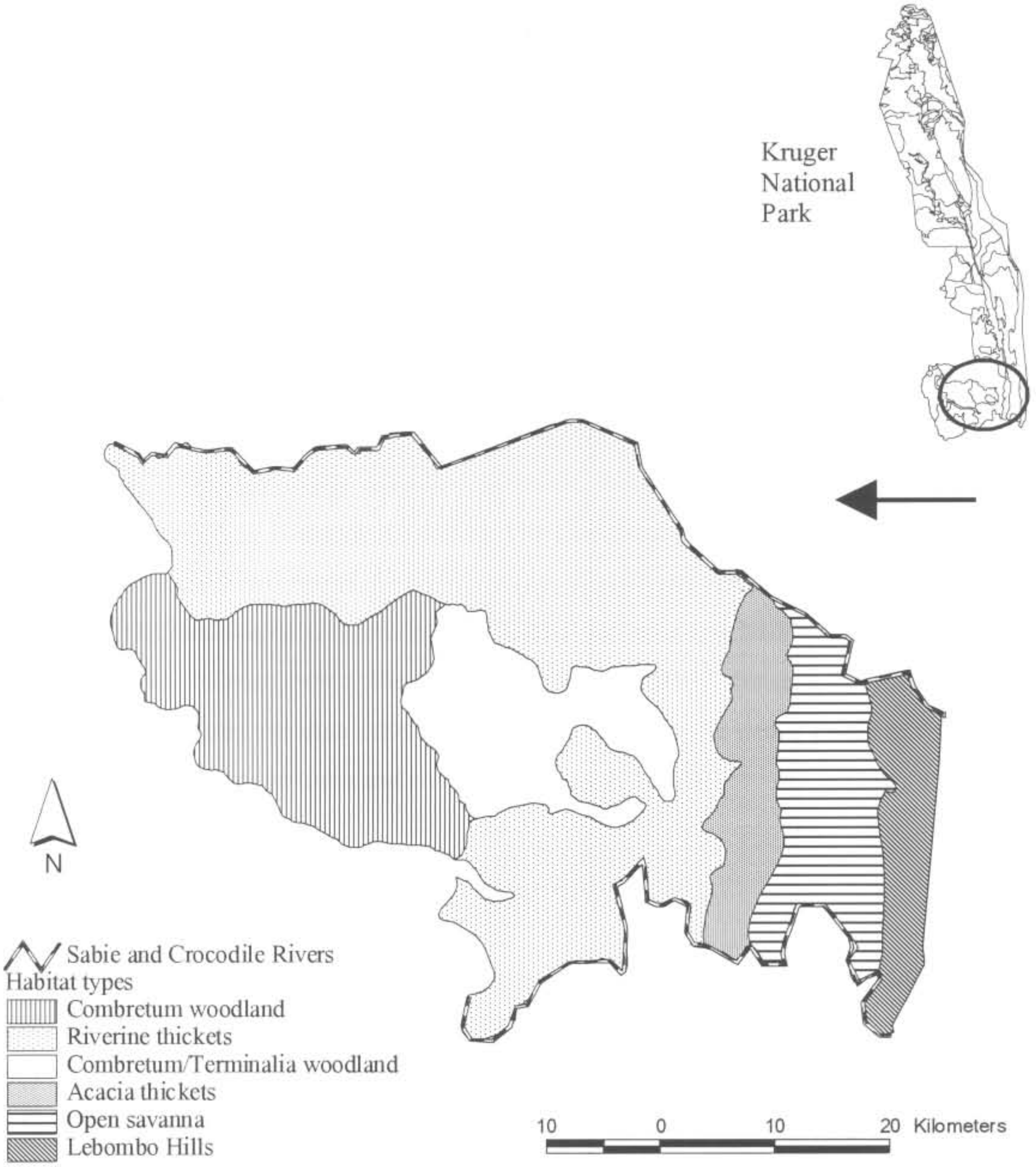

Figure 2.1. Location of study areas in the Kruger National Park showing six distinct habitat types.

The landscape bordering the open savanna to the west is the *Acacia welwitschii* thickets on Karoo Sediments (170 km^2) described as dense thorny bush thickets (Gertenbach 1983). The structure of the woody component is a moderate tree savanna with tall shrubs and sparse low shrubs (Gertenbach 1983). The grass cover is less dense and sometimes disappears altogether in the dry season (Gertenbach 1983).

The banks of Sabie and Crocodile Rivers, which cut through all three landscapes in the main study area, are densely overgrown with woody species and the grass layer is usually absent (Gertenbach 1983).

The secondary study area comprises a further three broad habitat types (Fig. 2.1). The thickets of the Sabie and Crocodile Rivers (1148 km^2) are low-lying, relatively flat areas, characterised by dense woody vegetation, with *Acacia nigrescens/Combretum apiculatum* dominating (Gertenbach 1983). The *Combretum collinum/Combretum zeyheri* woodland (454 km^2) and mixed *Combretum spp./Terminalia sericea* woodland (257 km^2) are undulating landscapes on granite with distinct uplands and bottomlands (Gertenbach 1983). In both habitat types, the uplands have relatively dense bush savanna, the bottomlands are open savanna with a dense grass layer, while dense riverine vegetation line the banks of drainage lines and rivers (Gertenbach 1983).

2.3 OTHER MAMMALS

The *Sclerocarya caffra/Acacia nigresens* open savanna is the centre of the wildebeest and Burchell's zebra habitat (Gertenbach 1983). Buffalo *Syncerus caffer*, kudu *Tragelaphus strepsiceros*, giraffe *Giraffa camelopardalis* and waterbuck *Kobus ellipsiprymnus* occur in large numbers. Lion *Panthera leo* and spotted hyaena *Crocuta crocuta* are abundant. In the Lebombo Hills, kudu, impala *Aepyceros melampus*, giraffe, buffalo bulls, waterbuck and klipspringer *Oreotragus oreotragus* are most common (Gertenbach 1983). The *Acacia welwitschii* thickets carry a large biomass of game: large numbers of impala, wildebeest and zebra occur (Gertenbach 1983). Giraffe, kudu, waterbuck, steenbok *Raphicerus campestris*, grey duiker *Sylvicapra grimmia* and elephant *Loxodonta africana* breeding herds are present. Because of the high density of prey species, lion and spotted hyaena are plentiful (Mills & Biggs 1993). The thickets of the Sabie and Crocodile

Rivers may support the largest impala population in the park while other common game species occurring are kudu, duiker, steenbok, bushbuck *Tragelaphas scriptus* and giraffe (Gertenbach 1983). Lion, leopard *Panthera pardus*, wild dog *Lycaon pictus* and spotted hyaena are the most important predators, especially the former two species, which are relatively abundant. The undulating *Combretum* woodlands support sable antelope *Hippotragus niger*, kudu, giraffe, elephant, white rhino *Ceratotherium simum* and buffalo, and smaller antelope such as steenbok and duikers are frequently encountered (Gertenbach 1983). Wildebeest and zebra occur in limited numbers and impala are restricted to the drainage lines and smaller rivers where water is available.

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Chapter 3: Home range and habitat use of cheetahs in the Kruger National Park and a comparison with other studies across the grassland-woodland continuum in African savannas.

3.1 INTRODUCTION

Cheetahs are known as predators with a preference for open plains habitats (Dorst & Dandelot 1970). This is because most previous studies on cheetah ecology were conducted in open grassland savannas, with a particular focus on the Serengeti Plains in East Africa (Schaller 1972; Frame & Frame 1980; Caro & Collins 1986, 1987; Durant et al. 1988; Fitzgibbon 1990; Caro 1994; Laurenson 1994, 1995a and b; Laurenson, Weilbnowlski & Caro 1995; Durant 1998). This focus on grassland savannas has largely been due to the logistical constraints associated with tracking and observing cheetahs in wooded habitats. Cheetahs, however, also occur across a wide range of woodland savannas (Myers 1975; Skinner & Smithers 1990; Mills & Hes 1997), though in comparison far less is known about cheetah ecology and behaviour in these habitats. Previously, the scant availability of data prevented the analyses of variation in cheetah ecology across different ecosystems (Stander 1991). Recent studies, however, in woodland savannas (Zank 1995; Hunter 1998; Purchase & du Toit 2000) have increased our understanding of cheetah ecology in these areas and contributed sufficiently to the database to allow for a comparative study across a variety of different African savanna ecosystems.

The objective of this chapter is to extend the documented information on cheetah ecology across the grassland-woodland continuum by: (1) adding to the existing knowledge on cheetah ecology in woodland savannas by analysing data on home range size and habitat use of cheetahs in the Kruger National Park (KNP), South Africa; (2) synthesizing available information from other studies on home range size and habitat use; and (3) comparing home range size and habitat use patterns across eight protected areas in southern and East Africa (see Table 3.2 for brief description of each area).

The chapter investigates the hypothesis that cheetah home range size and habitat use patterns vary predictably across the grassland-woodland continuum. Several predictions are made for the effects of (a) prey movement patterns, (b) prey density, and (c) mating opportunities on cheetah home range size (Table 3.1), based on the premise that food dispersion is the major resource affecting female home range size and female dispersion is the major factor affecting male home range size (Sandell 1989; Caro 1994). The predictions are: (1) female cheetahs with a migratory prey base have larger home ranges than female cheetahs with a sedentary prey base; (2) male cheetah territory size is not affected by whether the prey base is migratory or sedentary; (3) the greater the prey density, the smaller the female cheetahs home range; and (4) the greater the density of female cheetahs, the smaller the male cheetah's territory (Table 3.1).

A final prediction is made on the habitat requirements of cheetahs. Cheetahs require both open areas for high-speed chases (Myers 1975; Bertram 1979), but also cover for stalking (Cohen, Scholtz & Reichel 1978; Fitgibbon 1990; Caro 1994), concealment from other predators, and resting (Caro 1994; Zank 1995; Purchase 1998). Therefore, it is predicted that (5) cheetahs have distinct preferences for open habitats that are either adjacent to a woodland edge or else include scattered patches of woody cover.

3.2 METHODS

3.2.1 Data collection in the KNP

Seven adult cheetahs were radio-tracked over a period of four years between 1987 and 1990 (field data collection by M.G.L. Mills; see Table 3.3 for periods of time individual cheetahs were radio-collared) in the southern district of the KNP (see KNP study area in Chapter 2). Three types of data collection were used based on the duration of the observation period: (1) radio-location observations, when only a radio-fix of the animal was recorded; (2) short-term continuous observations, when radio-collared cheetahs were followed by vehicle for periods of 2 – 15 hours; and (3) three long-term

Table 3.1. Predicted effects of key ecological determinants (prey movement patterns, prey density and cheetah mating opportunities) on male and female cheetah home range size.

Determinants	**Predictions**	
	Female home range	**Male home range**
(a) Sedentary prey	(1) Decrease	(2) No effect
Migratory prey	Increase	
(b) High prey density	(3) Decrease	
Low prey density	Increase	
(c) High female density		(4) Decrease
Low female density		Increase

continuous observations, when cheetahs were followed continuously for 14 days. All three data collection types were recorded for a three-male cheetah coalition (M3) and a female cheetah (F1). Two 14-day observation periods were recorded for M3 and one 14-day period was recorded for F1. Radio-locations only were recorded for a two-male cheetah coalition (M2); a solitary, territorial male cheetah (M1); and three female cheetahs F2, F3 and F4. M2 and F4 were dispersing, sub-adult cheetahs.

Male cheetahs employ two alternative mating strategies: they either roam over large areas in search of females or hold a mating territory where females concentrate their activities (Caro 1994). In this study, territory and home range were used interchangeably when discussing territorial male cheetahs' range, but not for non-territorial cheetahs, which were called home ranges. All cheetahs used all or part of the main study area, except cheetah M1, which inhabited the central region of the southern district of the KNP. The dispersing, sub-adult male cheetah coalition (M2) and sub-adult female cheetah (F4) were radio-collared in the main study area, but ranged westwards into the central region. During the entire study period only one other cheetah, an adult male, observed once, was seen in the main study area (Mills pers. comm.). In 1987, M3, F2 and F3 inhabited the main study area, and in 1988 and 1989, M3, F1, F2 and F4 did.

3.2.2 Home range estimates in KNP

The home range sizes of seven radio-collared cheetahs were determined using the computer package Ranges V (Kenward & Hodder 1996) and an Arcview extension package Animal Movement (Hooge 1999). Location points from radio-tracking and direct observations recorded between 1987 - 1990 were used for home range analyses. The location points were recorded on an old grid reference system used by the KNP and converted to latitude and longitude for input into the models. Models were run using the Transverse Mercator co-ordinate system. Only location points taken approximately 24 hours apart were used to ensure independence of locations (Swihart & Slade 1985). The number of fixes needed to calculate home range size were analysed by plotting number of fixes against home range size until home range size reached an asymptote (Harris et al. 1990; Kenward & Hodder 1996).

Three non-parametric methods were chosen to estimate home range size. The minimum convex polygon (MCP) method (Jenrich & Turner 1969) is the most commonly used method in the literature (Harris et al.1990) and was used for comparison across studies. The biggest problem with this technique is that area and shape are heavily influenced by outlying fixes (Harris et al. 1990) and may include large unused areas. Two techniques were used to address these problems: the first, peeled minimum convex polygon method was used to remove 'outliers' or fixes showing 'excursive activity" (Mizutani & Jewell 1998), as Burt (1943) considered excursions outside the normal area not part of an individual's 'normal' home range. The method of Mizutani & Jewell (1998) was followed in retaining 95% of the plotted points lying closest to the arithmetic mean centre of the range, and 'peeling' the outlying 5%. The kernel method was the second technique used and is a robust model that has been demonstrated to give accurate estimates of home range size (Worton 1987, 1989, 1995, Kenward & Hodder 1996; Seaman & Powell 1996). Either the cross-validated fixed kernel or the cross-validated adaptive (tail or core-weighting) kernel (Worton 1995; Kenward & Hodder 1996; Seaman & Powell 1996; Hooge 1999) was chosen as the best method for estimating home range size depending on individual cheetahs. The 95% probability contours have been presented, which removes 'outliers' and is generally considered a close approximation of total range size (Jaremovic & Croft 1987; Harris et al. 1990; Worton 1995; Mizutani & Jewell 1998).

3.2.3 Habitat use in the KNP

A chi-square goodness of fit test (Zar 1996) was used to determine if the observed frequencies of habitat use differed significantly from expected frequencies based on the proportion of area contributed by each habitat within a cheetahs' home range. Radio-locations recorded during direct observations of four radio-collared cheetahs (M3, M1, F1 and F2) were used to determine frequencies of observed sightings per habitat type. Distinct vegetation types defined at the landscape level (according to Gertenbach's landscapes, see KNP study area in Chapter 2) are referred to from here on as habitat types. The 100% MCP area was used to delineate home ranges for calculating habitat availability (km^2) for individual cheetahs, since the MCP encompasses every location point of an animal. Habitat analyses were not conducted on female cheetahs F3 and F4 due to small sample sizes and dispersing male cheetahs (M2).

Habitat use by the cheetahs' main prey type in the study area, impala *Aepeceros melampus* (reference to Chapter 4), was also analysed using the same methods. The mean number of impala per habitat type was determined using KNP aerial census data collected every August between 1987 and 1990 (Joubert 1983). Habitat availability for impala in the main study area was calculated by measuring the total area of each habitat type lying between the Sabie and Crocodile Rivers. Bonferroni confidence intervals were performed thereafter, for those use/availability comparisons that were found to be significantly different in the chi-squared tests, to determine preference or avoidance of particular habitat types (Neu, Byers & Peek 1974; Byers & Steinhorst 1984) by cheetahs and impalas.

Differences in habitat use by the three-male coalition (M3) and female cheetahs (F1 and F2) were investigated using chi-square test on contingency tables (Zar 1996). Further differences were investigated within habitat types, as the sides of the drainage lines intersecting these habitats had thicker shrub and tree cover: two-sample t-tests were used to test for differences in mean distance from male and female cheetah locations to drainage lines and roads.

Impala herd locations, obtained from aerial census data collected during dry and wet months between 1986 and 1990 within the main study area, were digitised into Arcview. Using Arcview and a grid overlaying the study site (grid scale approximately 4 km^2 per cell), the frequencies of cheetah and impala herd locations within cheetah home ranges (100% MCP) were counted per grid cell. Frequencies of impala herd sightings per grid cell were averaged for wet and dry months. Spearman rank correlation (Zar 1996) was then used to test for relationships between distributions of impala herds and cheetahs (M3 and F1) in wet and dry seasons.

Whilst recording activities during direct observations of cheetahs M3 and F1, relative grass height and shrub cover were also recorded. Grass height was classified as (1) short < 20 cm, (2) medium 20 – 60 cm and (3) tall > 60 cm, and shrub cover was classified as (1) open, (2) moderate, and (3) dense (Funston, Mills & Biggs 2001). Nine different cover classes were created by all possible combinations of grass height and shrub cover eg. short grass, moderate bush etc.. A chi-squared test on a contingency table was used to determine if the cheetahs showed preferences for any vegetation classes based on the vegetation observed at the start of each observation period. To satisfy sample size requirements per cell for the chi-square test (Roscoe & Byars 1971), the vegetation classes were further combined into four categories of relative cover ranging from habitats with open to closed cover: (1) short grass, open to moderate shrub cover; (2) medium grass, open to moderate shrub cover; (3) short to medium grass, dense shrub cover; and (4) tall grass with any shrub cover.

The amount of time an animal spent walking, resting and hunting within the different shrub cover classes were also recorded for the same 14-day observation periods. Although the availability of each vegetation class could not be quantified, this was used as indication of habitat use by male and female cheetahs (observations could not be tested statistically due to small sample sizes).

Finally, the frequencies of scent markings by the three-male coalition (M3) along the road and off the road were recorded during a 14-day continuous observation period. The relative importance of roads to the coalition was analysed using a chi-square goodness of fit test by comparing the observed frequency of scent markings along and off the road to the expected frequency based on the total area of all roads (averaging 6 m wide) versus "off the road" area available within the cheetah coalition's home range.

3.2.4 Across-ecosystem comparisons of cheetah home range size

Two-sample t-tests were used for comparing home range sizes of male and female cheetahs with migratory or sedentary prey in eight protected areas of southern and East Africa (Appendix 3.1). Home range figures from the Serengeti Plains were used for areas with migratory prey as the cheetahs' main prey type there, Thomson's gazelle *Gazella thomsoni*, undertakes large seasonal migrations (Caro 1994). The remaining seven areas have a more sedentary prey base, except for the Kgalagadi Transfrontier Park (KTP), where the main prey, springbok *Antidorcas marsupialis*, are mostly nomadic, although some remain along the riverbeds during the dry season (Mills 1998). Despite this, the home ranges of the study animals were centred along the riverbeds (Labuschagne 1979; Mills 1998), although the amount of time spent in the dunes is unknown. Welch's correction factor or 'approximate t' was employed for comparisons in which an equal variance of samples could not be assumed (Zar 1996).

Further analyses excluded the Serengeti Plains home range figures for female cheetahs because of their migratory patterns, but included them for male cheetahs as territorial male cheetahs on the plains do not migrate (Caro 1994). Spearman rank correlation (Zar 1996) was used to test for relationships between the following: female cheetah home range size verses (1) medium–sized prey biomass (15 – 60 kg); male cheetah territory size verses (2) female cheetah density, (3) medium-sized prey biomass (15 – 60 kg), and (4) female cheetah home range size; and (5) male and female cheetah home range size versus cheetah density. Following the above analyses, female home range size and medium-sized prey biomass values were log transformed for regression analysis (Zar 1996). An F-test was used to determine whether the data differed significantly from the horizontal line (Zar 1996).

Cheetah home range data and density figures were calculated for the study area contained within each protected area (Table 3.2; Appendix 3.1). In some cases, this included the entire protected area. Cases where the study area included only part of the entire protected area were as follows: in the KTP, studies were conducted along the two main riverbeds, and the area was calculated by multiplying the 383 km of total riverbed (Knight 1999) by a width of 5 km, after Mills (1998). Estimates of home range size and cheetah density in the KTP were synthesised from Mills (1998) and Knight (1999) respectively. In Matusadona National Park (MNP), Purchase's (1998) study concentrated on the valley floor, a total area of 388 km^2, where cheetah home ranges were located. In the KNP, density figures were calculated for the main study area (approximately 350 km^2), and home range size estimates were only used for those cheetahs in the main study area with 25 or more radio-locations, as smaller sample sizes were not considered accurate estimates (see Results). The study area in the Serengeti National Park comprised the central region of the Serengeti Plains and plains-woodland border, approximately 2200 km^2 (Caro 1994; Laurenson 1994). Home range size figures were extracted from Caro's (1994) study on the Serengeti Plains and density estimates were synthesised from

Table 3.2. Brief description of the habitat types in eight cheetah study sites across southern and East Africa.

Study site	Size (km^2)	Description	Ref **
*Serengeti Plains, Tanzania	2200	Short to long, open grass plains (kopjes and drainage systems on the plains contain some wooded vegetation to differing extents), and plains-woodland border.	1
*Kgalagadi Transfrontier Park (KTP), South Africa (riverbeds only)	1915	*Acacia erioloba* and *Acacia haematoxylon* trees, tall shrubs and grasses. Limestone plains dominated by dwarf shrubs and perennial grasses flank riverbeds in most areas.	2
Suikerbosrand Nature Reserve (SNR), South Africa	134	Bankenveld – predominately open grassveld. Some *Acacia* savanna areas, wooded valleys and dense thickets in some ravines.	3, 4
Nairobi National Park (NNP), Kenya	115	Rolling *Themeda triandra* grassland-*Acacia* savanna, open grassland plains, and some heavy bush. (open grassland and *Acacia*-grassland savanna were of equal area in the study unit).	5, 6
Pilanesberg National Park (PNP), South Africa	550	Sour bushveld - open savanna of *Faurea saligna* trees in sour grassveld in less rocky areas, and a dense, mixed bush on rugged slopes, valleys and kloofs.	7
*Matusadona National Park (MNP), Zimbabwe (valley floor only)	388	Open grassland on foreshore bordered by woodland – jesse thickets, open woodland savanna and mopane scrub. Treeline vegetation, comprising predominantly of mopane scrub, forms boundary between woodland and foreshore.	8, 9
Phinda Resource Reserve (PRR), South Africa	170	Natal lowveld bushveld/coastal bushveld-grassland – overlapping open to closed bushveld, sandforest, grasslands, riparian woodland and palmveld.	10
*Kruger National Park (KNP), South Africa (south eastern region only)	350	Open *Sclerocarya birrea*/*Acacia nigrescens* tree savanna bordered to east by *Combretum* tree savanna in Lebombo Hills and to west by *Acacia welwitschii* thickets.	11

* Study area only included a part of the entire protected area.
** 1, Caro 1994; 2, Mills 1998; 3, Pettifer 1981, 4, Cohen et al. 1978, 5, Eaton 1970b; 6, Eaton 1974; 7, Acocks 1988; 8, Purchase 1998; 9, Zank 1995; 10, Hunter 1998; 11, Gertenbach 1983.

Laurenson (1994) and Kelly & Durant (2000). For the remaining protected areas, Nairobi National Park (NNP), Pilanesberg National Park (PNP), Phinda Resource Reserve (PRR), and Suikerbosrand Nature Reserve (SNR), study areas covered the entire park area (Eaton 1970b; McLaughlin 1970 cited by Schaller 1972; Eaton 1974; Pettifer 1981; Hofmeyer & van Dyk 1998; Hunter 1998).

Medium-sized prey biomass (prey in the size range 15 – 60 kg) was used for the analyses (Appendix 3.1) as this has shown to be significantly correlated with cheetah biomass (Stander 1991, Laurenson 1995a, Gros, Kelly & Caro 1996, Purchase 1998). Prey biomass data collated by Gros et al. (1996) were used for KTP, KNP and NNP. For SNR and PNP prey biomass was calculated according to Coe, Cumming & Phillipson (1976), using standard unit weights. Herbivore weights not listed in Coe et al. (1976) were calculated using figures obtained from Skinner & Smithers (1986), viz. grey rhebuck *Pelea capreolus* and mountain reedbuck *Redunca fulvorufula*. Biomass figures for PRR and MNP were provided by the authors (Hunter 1998; Purchase 1998).

3.2.5 Across-ecosystem comparisons of cheetah habitat use

The type of habitat available within eight cheetah study sites across southern and East Africa ranged from open grassland to dense thicket (Table 3.2). Habitat use and preferences by resident cheetahs were extracted from these studies, except KTP, as this information was unavailable. Habitat use was assessed in terms of the relative amount of available cover and open area in each study site. Information from PNP was particularly sparse and a proper assessment of cheetah habitat use in this area could not be made.

3.3 RESULTS

3.3.1 Home range size and habitat use in KNP

An asymptotic home range was not reached for female cheetahs with less than 25 fixes (Table 3.3). These were also considerably smaller than the other female cheetah home ranges and were therefore not considered accurate estimates (Table 3.3). The two-male cheetah coalition (M2) ranged widely and only 21 fixes were obtained for these animals, which may explain why an asymptote was not reached for their home range (Table 3.3). Additionally, these animals were young and may not have acquired a territory. The kernel method could also not give any meaningful estimates of home range size for cheetahs with less than 25 fixes. The 95% kernel method gave similar estimates to the 100% MCP method, even though outlying areas unused by the animals were removed. This may be because probability contours of the kernel method tended to balloon into other areas beyond the distribution of fixes. The 95% MCP method may be a more accurate estimate of home range size than the 95% kernel method, following the removal of outliers (Table 3).

With the exception of dispersing sub-adults F4 and M2, the cheetahs' home ranges centred on the open *Sclerocarya birrea/Acacia nigrescens* tree savanna in the main study area (Fig. 3.1), which comprised a large percentage of their home ranges (Table 3.4). The territorial three-male coalition (M3) had a similar home range size (100% MCP) to adult female cheetahs with sample sizes greater than 25 (Table 3.3). There was a large amount of overlap between the adult female cheetah's home ranges in the main study area, and the three-male cheetah coalition (Fig. 3.1). The single male cheetah (M1) radio-tracked in the central region of the southern district (Fig. 3.2) had a larger territory size than the three-male cheetah coalition (Table 3.3). Most of M1's territory was positioned on the *Combretum and Combretum/Terminalia* woodlands (Fig. 3.2). The sub-adult two-male coalition was first located in the open savanna of main study area, but dispersed westwards, moving over greater distances than all the other cheetahs (Fig. 3.2, Table 3.3).

Chi-square analyses showed that the observed habitat use by female cheetahs F1 and F2 and the single male cheetah M1 did not differ significantly from the expected based on habitat availability within their home ranges. The male cheetah coalition M3, however, showed a significant difference between the observed and expected habitat use ($\chi^2 = 12.8$; d.f. = 2; $p < 0.01$). Of the three available habitats within the male cheetahs' home range, Bonferroni confidence limits indicated that M3 preferred the open savanna,

Table 3.3. Home range estimates (km^2) of radio-tracked cheetahs in the southern district of the Kruger National Park using three different non-parametric techniques. M3 = three-male cheetah coalition; M2 = two-male cheetah coalition; M1 = single male cheetah; F1 - F4 = female cheetahs.

Cheetahs	Period tracked	No. of fixes	Asymptote reached ***	Estimates of home range size			
				MCP* 100%	MCP* 95%	Kernel 95%	Best model (for kernel)
M3	25/02/87 - 15/04/90	175	yes	173	120	188	adaptive (tail)
M2	11/07/88 - 14/05/89	21	no	438	243	**	
M1	14/10/88 - 02/05/90	27	yes	261	195	250	fixed
F1	29/11/88 - 17/04/90	70	yes	193	154	179	fixed
F2	16/09/87 - 07/10/88	25	yes	179	171	244	fixed
F3	18/08/87 - 23/10/87	14	no	118	105	**	
F4	29/08/89 - 28/04/90	9	no	102	102	**	

* MCP = Minimum convex polygon.

** Sample sizes too small to estimate home range size using this technique.

*** Number of fixes was plotted against home range size to determine if home range size reached an asymptote (Harris et al. 1990; Kenward & Hodder 1996).

Table 3.4. Percentage of habitat within a cheetah's home range in the south eastern region of the Kruger National Park using the 100% minimum convex polygon (MCP) method.

Habitat	% in cheetah's home range			
	M3	F1	F2	F3
Acacia thickets	21	10	12	10
Open savanna	75	74	67	90
Lebombo Hills	4	16	21	-

Table 3.5. Habitat selection by a three-male cheetah coalition (M3) and impala in the south eastern region of the Kruger National Park. Symbols indicate if use was significantly greater (+), less (-), or no different (0) to the expected based on proportion of habitat available in the home range of the male cheetah coalition, and between the Sabie and Crocodile Rivers for impala.

Habitat	Significance*	
	M3	impala
Acacia thickets	-	0
Open savanna	+	-
Lebombo Hills	0	+

* at the 0.05 level

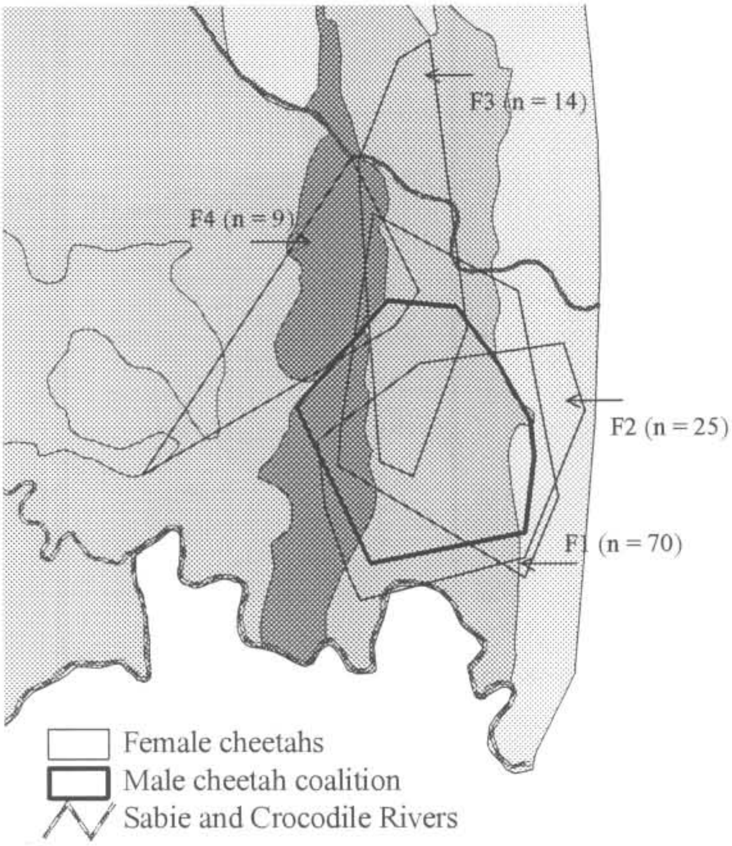

Figure 3.1. Home range of female cheetahs (F1, F2, F3, and F4 with number of location points indicated for each, as n) and a three-male cheetah coalition M3 (n = 175) in the south eastern region of Kruger National Park, estimated by the 100% minimum convex polygon (MCP) method. A = *Acacia* thickets; B = open savanna; C = Lebombo Hills.

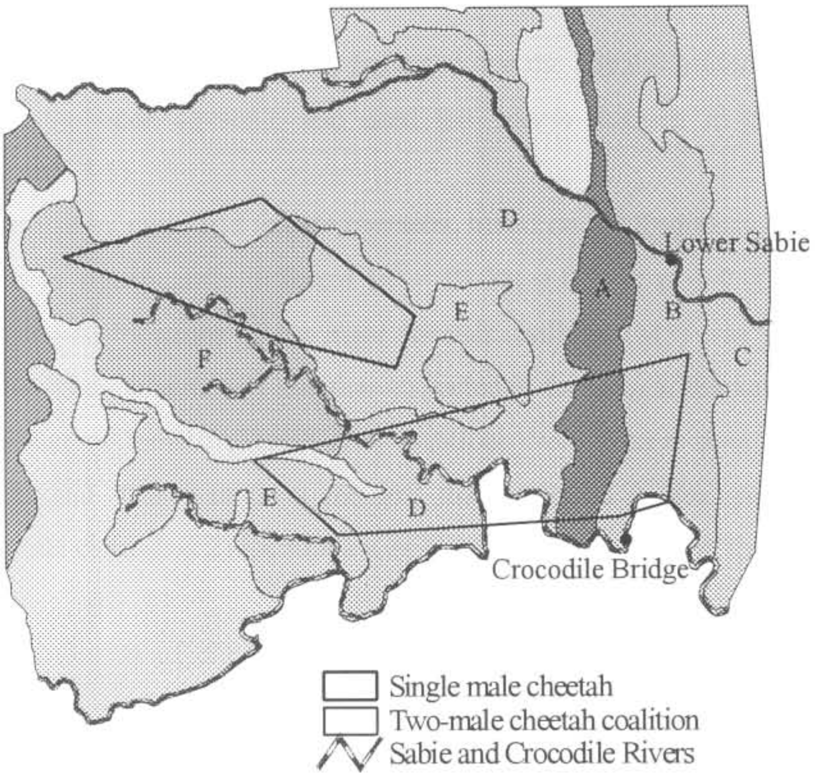

Figure 3.2. Home range of a single male cheetah M1 (n = 27 location points) and two-male cheetah coalition M3 (n = 21) in the southern district of the Kruger National Park, estimated by the 100% minimum convex polygon (MCP) method. A = *Acacia* thickets; B = open savanna; C = Lebombo Hills; D = Riverine thickets; E = *Combretum/Terminalia* woodland; F = *Combretum* woodland

avoided the *Acacia* thickets, and used the Lebombo Hills in proportion to its availability (Table 3.5). The observed habitat use by impala differed significantly from the expected, based on habitat availability between the Sabie and Crocodile Rivers ($\chi^2 = 185$; d.f. = 2; $p < 0.0001$). Bonferroni confidence limits indicated that the impalas preferred the Lebombo Hills, avoided the open savanna, and used the *Acacia* thickets in proportion to its availability (Table 3.5).

Habitat use by male and female cheetahs, based on the frequency of locations per habitat type, was significantly different ($\chi^2 = 25.75$; d.f. = 2; $p < 0.0001$). While the number of observed locations of the male cheetah coalition (M3) was greater than the expected in the open savanna and less than expected in the *Acacia* thickets and Lebombo Hills, the number of female cheetah (F1) locations were greater than expected in the Lebombo Hills and *Acacia* thickets and less than expected in the open savanna. The number of female cheetah (F2) locations was greater than expected in the Lebombo Hills only.

The distribution of cheetah radio-locations in the study area revealed that the three-male cheetah coalition was closely associated with the roads, while the female cheetah locations (F1 and F2) followed the drainage lines (Fig. 3.3). Unpaired t-tests showed M3 was significantly closer to the roads than the drainage lines ($t = 2.42$; d.f. = 352; $p < 0.05$), while F1 and F2 were significantly closer to the drainage lines than the roads ($t = 4.64$, d.f. = 138; $p < 0.0001$ and $t = 2.55$; d.f. = 48; $p < 0.05$ respectively, Fig. 3.4). The mean distance to drainage lines and roads between males and females were also significantly different (Fig. 3.4). Female cheetahs F1 and F2 were significantly closer to the drainage lines than the male cheetah coalition ($t = 3.92$; d.f. = 245; $p < 0.0001$ and $t = 4.37$; d.f. = 200; $p < 0.0001$ respectively), and the male cheetah coalition was significantly closer to the roads than F1 ($t = 3.6$; d.f. = 245; $p < 0.001$), but not F2.

There was a significant positive correlation between impala herd and female cheetah F1 locations in both the wet ($r_s = 0.401$; $p < 0.05$; $n = 39$) and dry ($r_s = 0.488$; $p < 0.01$; $n = 39$) seasons. No correlations were found between impala herd and male cheetah (M3) locations at any time (wet: $r_s = 0.161$; $n = 43$, dry: $r_s = -0.189$; $n = 43$). There was

Figure 3.3. Three-male cheetah coalition M3 (•) and female cheetah F1 (▲) radio-location points in the south eastern region of the Kruger National Park.

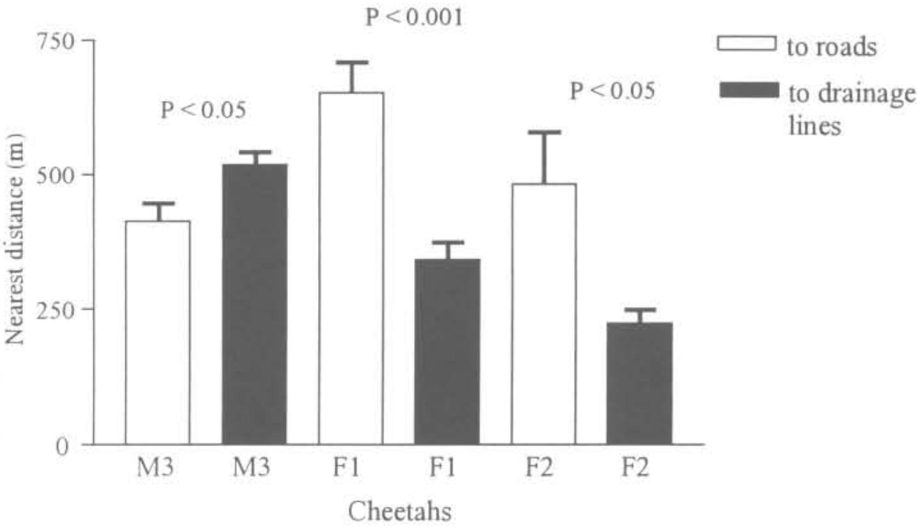

Figure 3.4. Mean nearest distance (±SE) of male and female cheetah locations to drainage lines and roads in the south eastern region of the Kruger National Park. M3 = three-male cheetah coalition; F1 and F2 = female cheetahs.

a strong significant difference between the frequency of scent markings by M3 along and off the road, based on the area available for scent marking within their home range ($\chi^2 = 13736$; d.f. = 1; $p < 0.0001$). The frequency of scent markings was greater than expected along the road (observed: 265, expected: 5) and less than expected off the road (observed: 52, expected: 312).

Chi-squared analysis based on frequency of observations in different vegetation-cover categories showed the three-male cheetah coalition to be using significantly different vegetation categories for different activities (Table 3.6). The coalition preferred medium to tall grass areas for hunting, but not in areas with dense shrub cover. Short to medium grass, regardless of shrub cover, was preferred for resting, while moderate to more dense shrub cover was preferred for walking, but not areas with tall grass. Female cheetah F1 did not show any preferences for different vegetation categories for different activities.

The percentage of time recorded in different shrub cover classes indicated some differences between the male cheetah coalition M3 and female cheetah F1. The female spent 72% of her time in moderate shrub, 14% in dense shrub and 14% in open shrub, while the males spent 51% of their time in moderate shrub and 49% in open shrub.

3.3.2 Across-ecosystem comparisons of cheetah home range size

Female cheetahs with a migratory prey base had significantly larger home ranges than female cheetahs with a sedentary base ($t = 8.41$; d.f. = 19; $p < 0.0001$, Fig. 3.5). Male cheetahs with a migratory prey base had significantly smaller territories than male cheetahs with a sedentary prey base ($t = 3.848$; d.f. = 29; $p < 0.001$, Fig. 3.5). Female cheetahs with migratory and sedentary prey had mean home range sizes of 833 km^2 (SE = 85.1; n = 19) and 105 km^2 (SE = 16.2; n = 13) respectively. Male cheetahs with migratory and sedentary prey had mean territory sizes of 37.4 km^2 (SE = 5.2; n = 22) and 108 km^2 (SE = 26.1; n = 9). There was no significant difference between male and female home range size in areas with sedentary prey ($t = 0.099$; d.f. = 20; $p = 0.922$).

Table 3.6. Chi-squared test for use of different vegetation categories for different activities by a three-male cheetah coalition (M3) in the south eastern region of the Kruger National Park. $\chi^2 = 26.1$; d.f. = 6; $p < 0.01$

Observations		short grass; open to moderate shrub	medium grass; open to moderate shrub	short-medium grass; dense shrub	Tall grass; Open to dense shrub
Walk	observed	9	26	21	2
	expected	9	26	15	8
Rest	observed	14	24	18	6
	expected	10	27	16	9
Hunt	observed	6	32	9	19
	expected	10	29	17	10

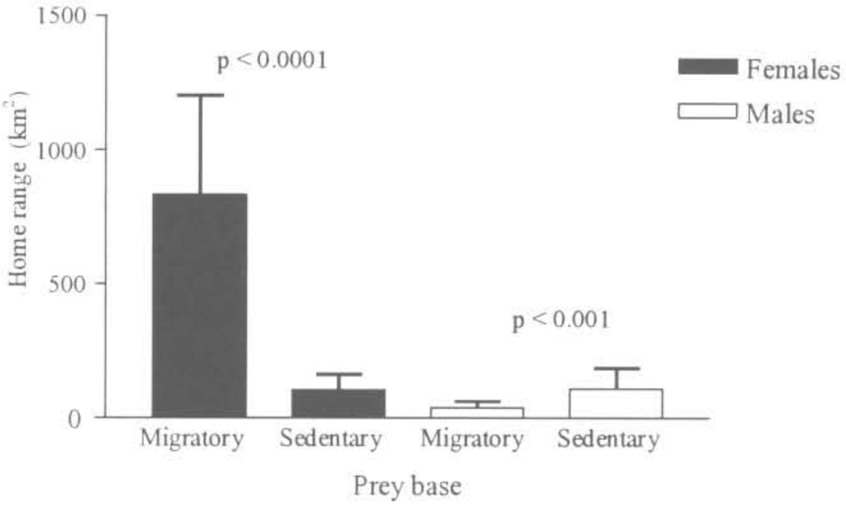

Figure 3.5. Mean home range size (±SE) of female and male cheetahs in areas with migratory and sedentary prey.

There was a significant negative relationship between medium-sized prey biomass and female cheetah home range size (Fig. 3.6). No other correlations (see Methods) were found except a significant positive correlation between male and female home range size when PNP was excluded from the analysis (Fig. 3.7). The data from PNP was excluded because the male home range estimate was only based on occasional sightings of a known coalition (van Dyk pers. comm.). While home ranges were of similar size in each protected area, female home ranges in the KTP were much larger than male home ranges (Fig. 3.7).

3.3.3 Across-ecosystem comparisons of cheetah habitat use

In seven cheetah study sites across southern and East Africa, cheetahs utilised habitats that provided both woody cover and open areas (Table 3.7). On the open grassland plains in the Serengeti, cheetahs used areas where there is some available woody cover. In SNR and MNP, where both open grassland and woodland habitats are available, cheetahs preferred the wooded areas. Although there is an equal availability of open grassland and *Acacia*-grassland savanna in NNP, the cheetahs preferred the latter. In PNP, the cheetahs appeared to prefer the grasslands to the woodlands (although they were frequently found in the woodlands), however a proper study on habitat preferences has not been undertaken for this area. In PRR and KNP, where the habitat is predominantly woodland savanna, cheetahs sought out more open areas, i.e. the open savanna in KNP, and grassland areas in the case of PRR. There was generally an avoidance of dense habitat types when available in the study areas.

3.4 DISCUSSION

3.4.1 Home range and habitat use in the KNP

Meaningful estimates of home range size for cheetahs in the KNP were 173 km^2 for a three-male cheetah coalition, 261 km^2 for a solitary male cheetah, 438 km^2 for a sub-adult, two-male cheetah coalition, and 193 km^2 and 179 km^2 for female cheetahs F1

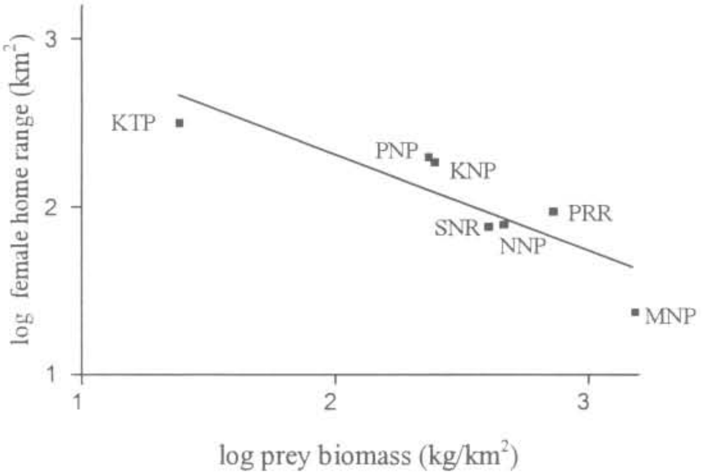

Figure 3.6. Linear regression showing relationship between medium-sized prey biomass and female home range size, across seven protected areas of southern and East Africa ($r^2 = 0.759$; $F_{1,5} = 15.8$; $p < 0.05$). KTP Kgalagadi Transfrontier Park; KNP Kruger National Park; MNP Matusadona National Park; NNP Nairobi National Park; PRR Phinda Resource Reserve; PNP Pilanesberg National Park; SNR Suikerbosrand Nature Reserve.

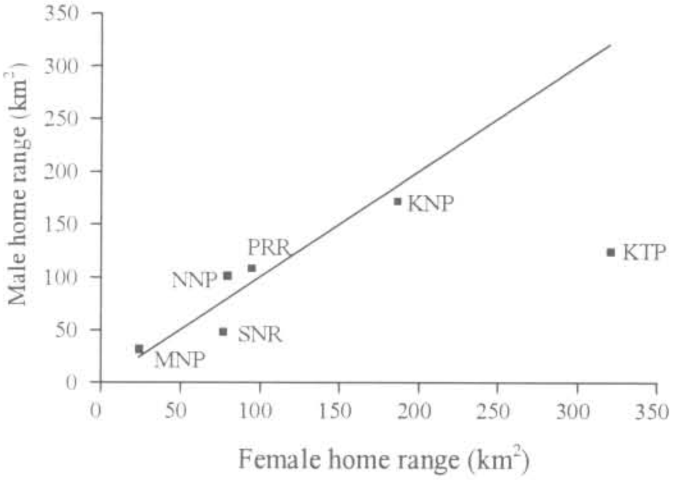

Figure 3.7. The relationship between female and male home range size, across six protected areas of southern and East Africa ($r_s = 0.943$; $p < 0.02$; $n = 6$). A forced line of perfect fit appears on the graph for comparison across areas. KTP Kgalagadi Transfrontier Park; KNP Kruger National Park; MNP Matusadona National Park; NNP Nairobi National Park; PRR Phinda Resource Reserve; SNR Suikerbosrand Nature Reserve.

Table 3.7. Habitat use and preference by cheetahs in seven study sites across southern and East Africa (with reference to Table 3.2, which provides a brief description of habitat available within each study site).

Area*	Habitat use and preference	Ref**
SP	Territories situated in areas with some wooded cover - on the plains-woodland border, along drainage lines and kopjes. Avoided areas devoid of trees and bushes.	1
SNR	Utilised open grassveld and *Acacia* savanna areas, preferred wooded slopes and ravines as opposed to the plains.	2, 3
NNP	Preferred *Acacia*-grassland savanna.	4
PNP	Appeared to prefer flat pediment grasslands, but were frequently located on the plateau's and slopes.	5
MNP	Utilised foreshore and woodland; preferred treeline vegetation and open woodland.	6, 7
PRR	Preferred grassland; tendency to occupy open mixed bushveld and palmveld. Avoided dense habitat types.	8
KNP	Preferred open savanna habitat.	This study

* SP Serengeti Plains; SNR Suikerbosrand Nature Reserve; NNP Nairobi National Park; PNP Pilanesberg National Park; MNP Matusadona National Park; PRR Phinda Resource Reserve; KNP Kruger National Park.

** 1, Caro 1994; 2, Pettifer 1981; 3, Cohen et al. 1978; 4, Eaton 1970b; 5, Hofmeyer & van Dyk 1998; 6, Purchase 1998; 7, Zank 1995; 8, Hunter 1998.

and F2 (Table 3.3). Bowland's (1994) photographic survey in the KNP estimated male and female cheetah home range size to vary between 104 km^2 and 1848 km^2. These estimates were taken from very small sample sizes and the social status of the animals was not determined. Therefore, non-territorial or dispersing cheetahs may be partly responsible for the large home ranges recorded in Bowland's (1994) study. However, the variation in cheetah home range size, including those observed between M1 and M3 in this study, may also be associated with the variation in habitat structure and prey availability across the different landscapes or habitat types in the KNP.

The adult cheetahs' home ranges in the main study area of the KNP were centred on the open savanna (Fig. 2.1, Table 3.4), suggesting a preference for it, relative to other available habitats. Pienaar (1969) recorded that cheetahs showed a decided preference for open or lightly wooded savannas across the KNP. In the Timbavati and Klaserie Private Nature Reserves, where the habitat varies from open savanna to moderately dense or riparian woodland, cheetahs also preferred the *Acacia nigrescens-Sclerocarya birrea* woodland (Kruger 1988). The solitary male cheetah in the central study area positioned his territory in the *Combretum* woodlands (Fig. 3.2), which is characterised by open savanna habitat in the bottomlands (see description of KNP study area in Chapter 2).

While the male cheetah coalition confirmed a strong preference for the open savanna (Table 3.5), the adult females (F1 and F2) used all habitat types according to their availability within their home ranges, although most of the home range was open savanna (Table 3.4). When comparing male and female cheetahs' habitat selection, the females showed greater use and preference than males throughout for denser vegetation types, such as the drainage lines and more woody Lebombo Hills and *Acacia* thickets. The cheetahs' main prey impala also preferred the Lebombo Hills and *Acacia* thickets (Table 3.5) and occurred at greater densities in these two habitat types than the open savanna (Chapter 4). Impala also prefer the denser vegetation along drainage lines and rivers (Gertenbach 1983; Ben-Shahar 1995). Therefore, females may be using dense vegetation because encounters with impala are greater. This is supported by the significant positive correlation found between female cheetah F1's distribution and impala distribution, while no correlations were found between impala and the male coalition M3. In the KNP, the open savanna is important habitat to the cheetahs in that it is the preferred habitat for hunting (Chapter 4). Therefore, it seems that female cheetahs must reach a compromise between the habitat best suited for hunting and the one supporting the highest impala densities.

Wooded habitats are nevertheless preferred for walking and moving between hunting and resting sites (Cohen et al. 1978; Zank 1995; Purchase 1998). The KNP three-male cheetah coalition selected moderate to dense shrub cover for walking (Table 3.6) and female F1 seemed to use denser shrub cover for all activities. Considering that the open savanna in this area is also the preferred habitat of lions (Mills & Gorman 1997), this may indicate predator avoidance and a selection for habitats that provide greater concealment. Durant (1998) found in the Serengeti that cheetahs seek out "competitive refuges" with low densities of lions and hyaenas, as they are both directly responsible for cub mortalities (Laurenson 1994) and both steal kills from cheetahs (Caro 1994). This argument is further strengthened by the fact that female cheetah F1 was accompanied by cubs in 77% of the observations. However, cheetahs in SNR used the kloofs and large wooded valleys for movement (Pettifer, de Wet & Muller 1979; Pettifer 1981), despite the fact that they were, artificially, the top predator on the reserve. The open savanna in the KNP is not without cover as it contains a moderate shrub layer and moderate to dense grass layer (Gertenbach 1983), therefore, it is questionable whether cheetahs were using the denser bush mainly to hide from predators.

Preferences for thicker bush may also be for stalking as cover is considered an important requirement for efficient hunting (Eaton 1970b; Fitzgibbon 1990), especially where it borders more open areas. Purchase & du Toit (2000) suggested that cheetahs in MNP preferred to hunt from woodland edges onto the open foreshore grassland where their main prey occurred, as this cover prevented early detection. Cheetahs in the KNP used the denser sides to hunt from into the open centre of the drainage lines (Mills pers. comm.). The male cheetah coalition also used more open areas with medium to tall grass cover for hunting (Table 3.6), which suggests that they are using this tall grass cover for concealment during the hunt. Cheetahs in the Serengeti used sparse riparian vegetation, deep drainage lines, and steeply rolling topography for stalking prey on the open plains (Fitzgibbon 1990). Therefore, the benefits of thicker bush to cheetahs may be three-fold, by maximising (1) encounters with prey, by using habitat preferred by the prey, (2) hunting efficiency, through cover for stalking, and (3) concealment from competitors. The role the latter two benefits may play in habitat preferences of the cheetahs could not be determined and would require further investigation. The benefits of cover, however, must be counter balanced by the impediment of thick bush to cheetahs being able to utilise their explosive hunting speed.

The behavioural patterns of male and female cheetahs in the Serengeti and KNP appear to be similar, except that they operate at different spatial scales. In both areas, female cheetahs follow the distributions of their main prey types. In the Serengeti, females follow the gazelle migration (Caro 1994) and in KNP, they move to areas where impala densities are the highest, both within the open savanna habitat but also in the bordering habitats. The males, in both areas, centre their home ranges where the females range, but habitat use differs both between and within the sexes. Unlike the females in the KNP, the male coalition was less concerned with cover and impala distribution. They preferred the open savanna habitat, used more open vegetation when resting compared to other activities (Table 3.6), and concentrated their activities along the roads (Fig. 3.3). Therefore, the male coalition may be less concerned than the females about other predators. A cheetah coalition is more able to deter other predators than a solitary animal (Caro 1994). Male coalitions also prey on larger food items (Caro 1994; Chapter 4) and are less dependent on impala than female cheetahs in the KNP (Chapter 4). In addition, staying in open habitat might make it easier for them to detect intruding cheetah males. The greater dependency of female cheetahs on impala may be due to the high nutritional demands placed on females during pregnancy, lactation and cub growth (Laurenson 1995b). The frequency of hunting attempts per prey encounters by females was significantly greater than the males (Chapter 4). Kruuk (1986) suggests that females must exploit a less profitable but more predictable food supply, i.e. impala, than the males, which further supports the argument that females in KNP are required to distribute themselves according to impala distribution and not necessarily for the most suitable hunting habitat or predator avoidance.

On the Serengeti Plains, the males position their territories where there is some form of vegetation cover (Caro 1994). Caro (1994) considered that the availability of sufficient cover for stalking and resting determines cheetah territory location. The apparent preferences for open areas and close proximity to roads by the male coalition in the KNP (Fig. 3.3) and cover by the males on the Serengeti Plains may also be associated with scent marking behaviour of territorial male cheetahs. Scent marking plays an integral role in territory maintenance as a warning to other males of their presence (Eaton 1970a) but is also considered important to males and females for communicating their reproductive status to one another (Marker-Kraus et al. 1996). Scent marks are usually placed on conspicuous objects or frequently used places where encounter rates are maximised (Gorman & Trowbridge 1989), such as large trees or shrubs and dirt mounds (Eaton 1970a), and roads or game paths or around waterholes (Funston 1999). Male cheetahs in the KNP scent marked significantly more frequently along the roads and Mills (pers. comm.) observed that they preferred the large trees on the sides of roads rather than the bushes for scent marking. Cheetahs on the open grassland plains (Caro 1994) use prominent landmarks throughout their territory, such as solitary trees, rocks and termite mounds far from others (Caro 1994). In NNP, Eaton (1970a) found that the distance between scent marking locations halved with greater densities of woody plants, indicating the need for trees or bushes for scent marking. Cheetah scent marking behaviour and the importance of habitat for scent marking and territorial advertisement, however, remains relatively unexplored.

To conclude this section, the study in the KNP found that cheetahs prefer more open habitat compared to other available habitats with denser woodland. Bowland's (1994) photographic study in the KNP, however, showed that cheetahs occupy a wide range of habitats across the park, although limited observations suggest that they occur at lower densities in more wooded habitats (Mills pers. comm.). The study has also shown that the male and female cheetahs utilise the habitat and vegetation structure differently, which reflects their different requirements. It is conceded, however, that larger sample sizes would be required to show more conclusive differences in habitat use between male and female cheetahs in the KNP.

3.4.2 Across-ecosystem comparisons

As predicted, across protected areas, female cheetahs with a migratory prey base had significantly larger home range sizes than female cheetahs with a sedentary prey base (Prediction 1; Table 3.1, Fig. 3.5). Female cheetahs on the Serengeti Plains, with migratory prey, have a mean home range size of 833 km^2 as they follow their migrating prey. The mean home range size of female cheetahs in areas with sedentary prey was 105 km^2. The same pattern has been observed in other large carnivores, such as lion, wild dog *Lycaon pictus* and mountain lion *Felis concolor* (Hanby, Bygott, & Packer 1995; Mills & Gorman 1997; Pierce et al. 1999). Contrary to Prediction 2, male cheetah territory size was significantly smaller in areas with migratory than sedentary prey (Prediction 2; Table 3.1, Fig. 3.5). Male cheetahs with a migratory prey base had a small mean territory size of 37 km^2 compared to male cheetahs with a sedentary prey base, with a mean territory size of 108 km^2. In most felids, male home ranges are usually larger than those of females, as males must overlap with as many females as possible presumably to increase mating opportunities (Kruuk 1986; Mizutani & Jewell 1998). Female cheetahs on the Serengeti Plains, however, have considerably larger home ranges than territorial males as they follow their seasonally migrating prey, while territorial males do not (Caro 1994). Larger home ranges are often associated with a greater overlap, and on the Plains up to 20 female home ranges overlapped extensively (Caro 1994). Therefore, male cheetah territories may be smaller because of a greater access to females. On the Serengeti Plains, male territories are found in certain hotspots where they have access to migrating females (Caro 1994). Conversely, in areas with sedentary prey, there was no significant difference between male and female cheetahs' home range size (Fig. 3.5). In these areas, with smaller female home ranges and fewer numbers of female ranges overlapping (i.e. in the KNP, only 2 - 3 females were available to the male cheetah coalition at any one time), male home ranges must be larger to ensure sufficient mating opportunities.

There was a significant negative relationship between medium-sized prey biomass and female cheetah home range size (Prediction 3; Table 3.1, Fig. 3.6). MNP, with high prey densities had small home ranges averaging 24 km^2, while the KTP with very low prey densities had larger home ranges of 320 km^2. This has also been observed in spotted hyaena, lion and leopard *Panthera pardus*, which have much larger home ranges in more arid than mesic areas, attributed to the low prey densities in the former (Mills 1990;

Stander 1991; Bothma et al. 1997). While female cheetah home range size was affected by the availability of prey, male cheetah territory size was affected by the availability of female cheetahs (Caro 1994). No relationship, however, was found between female cheetah density and male cheetah territory size in this study (Prediction 4; Table 3.1). This may be because the density of female cheetahs does not directly reflect the availability of females for mating opportunities (as discussed above). The extent of overlap between female cheetah home ranges may also affect the availability of females. This argument may be further supported by the significant positive correlation found between male and female home range size across protected areas (Fig. 3.7). While male and female home ranges were of a similar size in each protected area, female cheetahs in the KTP were estimated to have much larger home ranges than males (Fig. 3.7). The low density and nomadic nature of the prey occurring in the KTP (Mills 1998; also see Methods) explains the much larger female home ranges compared to other areas. These larger home ranges are probably associated with greater home range overlap; therefore male territories can be smaller while still encountering sufficient mating opportunities. Further consideration is also be made regarding the restriction of park size or fencing on cheetah home range size, where home ranges are almost as large as the protected area and therefore, range size may be an underestimate.

The resource dispersion hypothesis predicts that territory size is determined by the dispersion pattern of food patches (McDonald 1983) or other resources. Therefore, cheetah home range size may also be influenced by the distribution of their main prey and suitable habitat. Mills (1990) found that spotted and brown hyaena *Hyaena brunnea* home range size was determined predominantly by the average distance between food sites. In the Serengeti, the patchiness of prey accounted for expanded home ranges of the female cheetahs, not low prey density (Caro 1994). Similarly, the nomadic nature of springbok in KTP (Mills 1998) and concentrated distribution of prey in MNP (Purchase & du Toit 2000) may have influenced home range size in these two areas (Fig. 3.6; Appendix 3.1). In the KNP, impala were concentrated in habitats less preferred by the cheetahs, i.e. the *Acacia* thickets and Lebombo Hills, which formed the edges of the cheetahs' home ranges. Therefore, the cheetahs may have had to expand their home ranges into these bordering habitats in order to include sufficient availability of prey or 'food patches'. Similarly, the distribution of suitable habitat for hunting may affect cheetah home range size. Kruuk (1986) states the distribution of such places would be more important in determining the size of home ranges in felids, than the number of potential prey moving around an area. PRR had larger home ranges compared to NNP and SNR even though prey densities were higher in the former (Appendix 3.1). In PRR, cheetahs sought out open grassland patches in the woodland for hunting, but since grasslands only made up 8.6% of the entire reserve (Hunter 1998) cheetahs may have needed to expand their home ranges to include as much of these habitat patches as possible to ensure sufficient hunting opportunities.

From studies across a variety of woodland and grassland savannas in southern and East Africa, cheetahs showed distinct preferences for habitats that offered both open spaces and woody cover. (Prediction 5). Cheetahs generally avoided dense habitat types and areas devoid of trees and bushes (Table 3.7). Mitchell, Shenton & Uys (1965) also found that cheetahs in Kafue National Park did not venture onto extensive open plains but occupied savanna woodlands, tree savannas and smaller grasslands. In Uganda, a GIS analysis of vegetation structure in areas where cheetahs were observed and in those where none were reported suggested that cheetahs favoured habitats with 25 - 50% woody cover (Gros & Rejmánek 1999). Nowell & Jackson (1996) suggested that habitat with a mosaic of woodland and grassland savannas would meet the cheetah's requirements. In summary, this may be described as areas providing open spaces for high-speed pursuit of prey, but with some availability of woody cover for stalking their prey and escaping detection from predators (Myers 1975; Gros & Rejmánek 1999; Purchase & du Toit 2000).

To conclude, the comparative study across African savanna ecosystems found that female cheetah home range size is determined by the movement patterns and density of their main prey. Although it was predicted that male cheetah territory size would be affected by the availability of female cheetahs, no relationship was found between male cheetah territory size and female cheetah density. This raises a question for further study i.e. the relationship between female cheetah density and the availability of mating opportunities for males.

Cheetahs prefer open savanna habitats that offered some woody cover and in woodland savannas sought out more open areas. Therefore, optimal cheetah habitat is probably a heterogeneous mix of grassland and woodland savanna or open woodland savanna, with a sufficient availability of medium-sized prey. The spatial distribution of prey and suitable habitat may also influence the size of the cheetahs' home ranges, which may be as small as 24 km^2 (Purchase & du Toit 2000 in MNP). The small range sizes of cheetahs in MNP were attributed to the high density of prey concentrated on the foreshore grassland, combined with the easily accessible cover bordering the grassland (Purchase & du Toit 2000). While cover may confer benefits to cheetahs for protection against predators, the effects of dense or encroaching bush on cheetah densities in woodland savannas (like the KNP) requires some investigation, considering that preferred cheetah habitat is open woodland savanna (also see Chapter 4). Bush encroachment may lower cheetah density and therefore reduce the viability of cheetah populations. Bush encroachment has been identified as one of the main factors responsible for changes in distribution and abundance of vertebrate populations in southern Africa (MacDonald 1992).

Finally, while cheetah research on the Serengeti Plains in East Africa continues to expand (Durant 2000a and b; Kelly & Durant 2000), cheetah research in woodland savannas is comparatively neglected. Woodland savannas may be an important source of cheetahs for 'sink' or depleted populations (Chapter 5); therefore, cheetah populations in woodland savannas require more attention. The utilisation of the vegetation structure within woodland habitats, the benefits of cover to cheetahs, and the influence of these on cheetah density are suggested areas for future study.

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Appendix 3.1

Data collated for eight protected areas of southern and East Africa. FHR = female home range; MHR = male home range (MNP male, SNR male, NNP male, KNP female, PRR, and SP home range sizes are mean values.

Area *	**Size** (km^2)**	**FHR size (km^2)**	**MHR size (km^2)**	**Medium-sized prey biomass (kg/km^2)**	**Female cheetah per km^2**	**Cheetah per km^2**	**Reference *****
MNP	388	23.6	32.5	1517	0.017	0.044	1
SNR	134	76.6	48.8	400.4	0.045	0.216	2, 3
NNP	115	79	102	461	0.039	0.152	4, 5, 6
PRR	170	94.4	109.1	724.2	0.035	0.094	7, 8
KNP	350	185.9	173	246	0.007	0.023	6, this study
PNP	550	200	100	232.6	0.006	0.031	9, 10, 11
KTP	1915	320	125	24	0.01	0.044	6, 12, 13
SP	2200	833	37.4		0.019	0.136	14, 15, 16

* MNP Matusadona National Park; SNR Suikerbosrand Nature Reserve; NNP Nairobi National Park; PRR Phinda Resource Reserve; KNP Kruger National Park; PNP Pilanesberg National Park; KTP Kgalagadi Transfrontier Park; SP Serengeti Plains.

** Size (km^2) of the study area only (see Methods)

*** 1, Purchase 1998; 2, Pettifer et al. 1979; 3, Pettifer 1981; 4, McLaughlin 1970 cited by Schaller 1972; 5, Eaton 1974; 6, Gros et al. 1996; 7, Hunter 1998; 8, Butchart 1999; 9, van Dyk 1995; 10, Adcock 1996; 11, Hofmeyer & van Dyk 1998; 12, Mills 1998; 13, Knight 1999; 14, Caro 1994; 15, Laurenson 1994; 16, Kelly & Durant 2000.

Chapter 4: Cheetah predation in relation to prey composition, cover availability and kleptoparasitism in the Kruger National Park, including a comparison across African savanna study sites.

4.1 INTRODUCTION

The literature on cheetah ecology is dominated by studies conducted on the Serengeti Plains in East Africa (Schaller 1972; Frame & Frame 1980; Caro 1986; Caro & Collins 1986, 1987; Durant et al. 1988; Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990; Laurenson, Caro, & Borner 1992; Caro 1994; Laurenson 1994, 1995a and b; Laurenson, Weilbnowlski & Caro 1995; Durant 1998). As a result, cheetahs are considered to be predators that prefer the open plains, particularly because of their hunting strategy, which involves a high-speed chase (Bertram 1979). Cheetahs are adapted for speed, with a slight build, narrow chest, long legs and specialised internal organs, they can reach speeds of up to 100 km per hour (Nowell & Jackson 1996). Such high-speed chases probably require good visibility and freedom from obstruction (Bertram 1979), and may explain the cheetah's diurnal hunting behaviour (Mills & Biggs 1993). Therefore, open habitats may be required by cheetahs to attain high speeds, both for successful hunting and for presenting sufficient hunting opportunities.

Cheetahs, however, also inhabit a wide range of bush, scrub and woodland habitats (Myers 1975; Skinner & Smithers 1990; Nowell & Jackson 1996; Mills & Hes 1997), although in comparison relatively little is known about their ecology and behaviour in these habitats. Woodland savannas, with a greater availability of cover, may inhibit cheetahs from attaining high speeds, although may confer other advantages not provided by grassland habitats. Cover is considered advantageous to cheetahs for stalking prey (Cohen, Scholtz & Reichel 1978; Caro 1994; Purchase & du Toit 2000) because it enables closer proximity to the quarry before the chase, thereby reducing chase distance and improving hunting success (Eaton 1970; Fitzgibbon 1990; Caro 1994). Concealment is considered another advantage of cover (Myers 1975; Caro 1994; Zank 1995; Purchase & du Toit 2000). Because cheetahs are built for speed, rather than strength, they suffer from competition with all the other large carnivores, such as lion *Panthera leo*, spotted hyena *Crocuta crocuta* and leopard *Panthera pardus* (Nowell & Jackson 1996; Mills & Hes 1997) and are easily robbed of their prey (Schaller 1972; Caro 1994). Therefore, a greater availability of cover may provide increased concealment to cheetahs after the hunt, thereby reducing the chances of kleptoparasitism.

As most cheetah studies have focused on grassland savannas, requirements for open spaces and benefits of cover in woodland savannas have not been fully explored. Although it has been observed that the cheetahs' principal food is medium-sized prey (Schaller 1972; Stander 1991; Laurenson 1995b; Mills 1984, 1998), no quantitative analysis of the variations in the use of prey across ecosystems has been conducted. The objectives of this chapter are: (1) to add to the existing knowledge on cheetah ecology and behaviour in woodland savannas by analysing data on cheetah predation, hunting behaviour and use of habitats for hunting in the Kruger National Park (KNP), South Africa; (2) to synthesise available information on cheetah predation in relation to prey composition, cover availability and kleptoparasitism from other studies (see Table 4.1 for description of study sites); and (3) to compare these across different African savanna ecosystems. The approach is to extend the range of information available on cheetah ecology across the spectrum between grassland and woodland savanna habitats. The proposed hypothesis is that cheetah ranging and hunting behaviour varies as a function of cover availability. Testable predictions of this hypothesis are that: (i) cheetahs initiate more hunts and kill more frequently in more open habitats; although (ii) chase distances are shorter in more wooded habitats, and (iii) hunting success rates (kills/hunting attempts) are higher in more wooded habitats; and (iv) cheetah kills are kleptoparasitised less in more wooded habitats.

4.2 METHODS

4.2.1 Data collection in the KNP

Seven adult cheetahs were radio-tracked between 1987 and 1990 (field data collection by M.G.L. Mills) in the southern district of the KNP (see KNP study area in Chapter 2).

Individuals included a three-male coalition (M3); a single male cheetah (M1); a two-male cheetah coalition (M2); and four female cheetahs with or without cubs (F1, F2, F3 and F4). Three types of data collection were used, based on the duration of the observation period: (1) radio-location observations, which included recording the radio-fix and any kill data, i.e. habitat, prey species, sex and approximate age of prey, for the cheetah, (2) short-term continuous observations, when radio-collared cheetahs were followed by vehicle for periods of 2 – 15 hrs; and (3) three long-term continuous observations, when cheetahs were followed continuously for 14 days (two periods for M3 and one for F1).

All three types of data were collected for M3 and F1; data types (1) and (2) for F2; and radio-locations were only recorded for the remaining animals. For data collection types (2) and (3), the following data were recorded every time cheetahs encountered potential prey: the habitat; prey species, sex and approximate age of prey; chase distance (i.e. the estimated distance the cheetah was observed chasing its prey); kill retention time (i.e. length of time 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. Age of prey was measured according to tooth eruption (Mills pers. comm.). Juveniles had erupting teeth and adults full permanent dentition.

Prey encounters were classified as (1) a kill; (2) a failure, i.e. where cheetah either stalked or moved towards the prey at a faster than normal walking speed, but the animals escaped; or (3) no attempt, where the cheetah detected prey but did not attempt to hunt in the manner described above. Habitat was recorded at the (1) landscape level - according to Gertenbach's landscapes (see KNP study area in Chapter 2) - and referred to from here on as habitat types, and (2) vegetation level: grass height and shrub cover, which were classified as: (1) short < 20 cm, (2) medium 20 – 60 m and (3) tall >60 cm, and (1) open, (2) moderate and (3) dense, respectively (Funston, Mills & Biggs 2001).

4.2.2 Analyses of KNP data

The radio-location and direct observation kill data of seven cheetahs were combined for analyses as Mills (1992) and Hunter (1998) both found no significant differences between these two methods in terms of bias for larger kills. To analyse for differences between male and female cheetah's diets, prey items were separated into small < 18 kg, medium 18 - 65 kg, and large > 65 kg weight classes, using two methods: (a) the estimated weight of the prey item, and (b) the average weight of adult male and female animals of the prey item. Prey weight figures were obtained from Meissner (1982) and Owen-Smith (1988). A chi-square test on a contingency table (Zar 1996) was used to determine if male and female cheetahs were taking prey classes, based on average adult size, at different frequencies. A chi-square goodness of fit test (Zar 1996) was used to determine if cheetahs were taking male and female impala *Aepyceros melampus* according to their relative availability. Relative availability of male and female impala was calculated using the average sex ratio recorded for impala (1.68 females per male) between 1986 and 1989 in the KNP (Mason 1990).

A prey preference rating (PPR) was calculated for each prey species (Pienaar 1969), where

$$\text{PPR} = \frac{\text{kill frequency of prey species}}{\text{relative abundance of prey species}}$$

PPR is considered to be a true indication of real food preferences irrespective of the density of its various prey species (Pienaar 1969). Annual aerial surveys conducted every August between 1987 and 1990 by the KNP were used to determine prey availability for impala, kudu *Tragelaphus strepsiceros*, warthog *Phacochoerus aethiopicus*, waterbuck *Kobus ellipsiprymnus* and zebra *Equus burchelli* only. Although reedbuck *Redunca arundinum* were censused, they were omitted from the analyses because of the very small number of sightings (total of eight), which could bias results (Jacobs 1974).

Percentage hunting success, average kill rate, mean chase distance, mean kill retention time and percentage kleptoparasitism were determined using data collected from continuous observation periods (see Data collection in the KNP). Chi-square tests on contingency tables were used to compare male (M3) and female (F1 and F2) cheetahs' hunting attempts versus no attempts, hunting success versus failure, and incidents of kleptoparasitism (M3 and F1 only for the latter). Average kill rates were determined using 14-day continuous observation periods only as Mills (1992) found that long-term direct observation periods were less likely to inflate kill frequency. To convert kill rate into kg of meat consumed/cheetah/day, the total weight of the prey items killed by the cheetahs were estimated using weight values obtained from Meissner (1982) and Skinner & Smithers (1990). Blumenschine & Caro's (1986) estimated weight of flesh of an eviscerated adult Thomson's gazelle *Gazella thomsonii* carcass agreed with Schaller's (1972) estimate that cheetahs consume 60% of the animal. To facilitate comparison, therefore, it was assumed that approximately 65% of the total weight of an adult impala and 60% of juvenile prey (Blumenschine & Caro 1986) and 90% of very small prey, in this case a scrub hare *Lepus saxatilis*, which weighs approximately 2 kg is edible to cheetahs. The Mann-Whitney U test (Zar 1996) was used to compare chase distances of successful and unsuccessful hunts of male (M3) versus female (F1 and F2) cheetahs. Successful verses unsuccessful hunts of the pooled chase distances of all cheetahs (M3, F1 and F2) were compared using an unpaired t-test (Zar 1996). Mean kill retention time was calculated by combining data for M3, F1 and F2 for only those kills not kleptoparasitised.

A chi-square goodness of fit test was used to analyse the frequencies of hunting and killing locations across habitat types in relation to the expected values based on the relative availability of habitat types within the cheetahs' home ranges. Habitat types - open savanna, *Acacia* thickets and Lebombo Hills - in the main study area were used in the analyses (see Fig. 2.1 in Chapter 2). Frequency data for hunting and killing were derived by combining the hunting locations of three cheetahs (M3, F1 and F2) and kill locations of four cheetahs (M3, F1, F2 and F3). For each analysis, a minimum convex polygon was drawn around the cheetahs' home ranges to determine the area (km^2) available for hunting and killing in the three habitat types using GIS Arcview. A chi-square goodness of fit test was used to determine if cheetahs were killing impalas in proportion to their relative availability in the different habitat types (Hunter 1998). Relative availability was determined by using the annual aerial impala census data (described above) to calculate the mean number of impala per habitat type for the area (km^2) lying between the Sabie and Crocodile Rivers. Impala density (animals/km^2) was calculated for each habitat type. Following any significant results from the above chi-square tests, Bonferroni confidence intervals were performed to determine preference or avoidance of particular habitat types (Neu, Byers & Peek 1974; Byers & Steinhorst 1984) by the cheetahs. Finally, chi-square tests on contingency tables were used to compare hunting attempts versus no attempts and hunting success versus failure of cheetahs M3, F1 and F2 in different habitat types and vegetation classes.

4.2.3 Across-ecosystem comparisons

For a comparison of prey composition (prey size and age) across different savanna ecosystems, data were synthesised from 10 different studies in southern and East Africa. Study sites were as follows: East Africa (Graham 1966) - a broad survey conducted across Uganda, Tanzania and Kenya; Serengeti National Park (SNP) in Tanzania (Kruuk & Turner 1967); Kafue National Park (Kafue NP) in Zambia (Mitchell, Shenton & Uys 1965); Matusadona National Park (MNP) in Zimbabwe (Zank 1995); and in South Africa - the Kgalagadi Transfrontier Park (KTP, Mills 1984); Suikerbosrand Nature Reserve (SBNR, Pettifer 1981b); Phinda Resource Reserve (PRR, Hunter 1998); Mala Mala Game Reserve (MM, Radloff unpubl. data); Timbavati & Klaserie Private Nature Reserves (TNR, Pettifer 1981a); and KNP (this study).

For each study site, prey was divided into adults and juveniles for small (< 18 kg), medium (18 – 65 kg) and large (> 65 kg) weight categories. Medium-sized prey for cheetahs are recorded as ranging between 15 – 60 kg (Laurenson 1995b), however this was adjusted slightly to facilitate analysis in this study. Prey weights were obtained from Owen-Smith (1988), where the average weight of adult males and females determined the size category of the prey. The adults and juveniles of small prey were combined because studies often did not classify small prey items in this manner, particularly when considering prey items such as birds, hares, rodents and small carnivores. Studies with no reported kills of small prey were excluded from the analysis as small prey are known to form a significant part of the cheetah's diet (Labuschagne 1979), but are often underrepresented in studies due to the method of data collection used by the researcher (Mills 1992). Prey frequency values in each category of each study area were converted into proportions for comparison. A single-factor ANOVA (Zar 1996) was used to test whether cheetahs were taking prey size categories and age classes in the same proportions across study sites. To meet the assumption of normal distribution for an ANOVA, the proportional data were arcsine transformed (Zar 1996).

Further comparisons across ecosystems were conducted concerning chase distance, hunting success, kleptoparasitism, kill retention time, and kill rates. Study sites were as follows: Serengeti Plains in Tanzania (Schaller 1972, Caro 1994); Nairobi National Park (NNP) in Kenya (Eaton 1970; McLaughlin 1970 cited by Schaller 1972); and in South Africa - KTP (Labuschagne 1979); MM (Radloff unpubl. data); PRR (Hunter 1998); TNR (Pettifer 1981a); Suikerkop Nature Reserve (SNR, Pettifer 1981a); and KNP (this study). The relationships between cover availability versus chase distance, hunting success and kleptoparasitism were explored; however, small sample sizes prevented any statistical analyses. For these analyses, study areas were ranked according to cover availability (open to closed cover), where the area with the least amount of cover was given a value of one (Table 4.1). Chase distance, hunting success, and kleptoparasitism were also ranked, where areas with the shortest mean chase distance for successful hunts, and the lowest percentage hunting success and kleptoparasitism were given values of one (Table 4.1). Kleptoparasitism values were not standardised to control for the variation in predator density because the Serengeti Plains and KNP had the same total density of predators i.e. lion and spotted hyaena (Stander 1991), and it was assumed that MM had the same predator density as KNP as this reserve borders the KNP, is unfenced from the KNP, and occupies the same broad vegetation type (classified by Acocks 1988).

4.3 RESULTS

4.3.1 Cheetahs in the KNP

Of the eight prey species killed by cheetahs in the southern KNP, impala occurred most frequently in the diet of both male and female cheetahs (Table 4.2). Overall, cheetahs took more juveniles (60.6%) than adults (39.4%), particularly of large prey species, although male cheetahs took impala adults more frequently than juveniles. The prey

Table 4.1. Habitat description in selected cheetah study sites across southern and East Africa. Each study site was ranked subjectively for cover availability, where the site with the least amount of cover was given a value of one, and sites with the shortest mean chase distance (m), and the lowest hunting success (%) and incidents of kleptoparasitism (%) were given values of one (no data were available for some areas). A = rank of cover; B = rank of chase distance; C = rank of hunting success; D = rank of kleptoparasitism. See Fig. 4.1.

Study sites	**Habitat description**	**A**	**B**	**C**	**D**
Serengeti Plains, Tanzania	Short to long, open grass plains (kopjes and drainage systems on the plains contained some wooded vegetation) [1]	1	3	4	3
Kgalagadi Transfrontier Park (KTP), South Africa (riverbeds only)	*Acacia erioloba* and *Acacia haematoxylon* trees, tall shrubs and grasses. Limestone plains dominated by dwarf shrubs and perennial grasses flank riverbeds in most areas [2]	2	2	5	
Nairobi National Park (NNP), Kenya	Rolling *Themeda triandra* grassland-*Acacia* savanna, open grassland plains, and some heavy bush [3, 4]	3		3	
Kruger National Park (KNP), South Africa (south eastern region only)	Open *Sclerocarya birrea*/*Acacia nigrescens* tree savanna bordered to east by *Combretum* tree savanna in Lebombo Hills and to west by *Acacia welwitschii* thickets [5]	4	1	2	2
Mala Mala Game Reserve (MM), South Africa	Mixed *Combretum* sp./*Terminalia sericea* woodland. Dense bush savanna on the uplands, open tree savanna in the bottomlands and dense riverine vegetation [5]	5			1
Timbavati & Klaserie Private Nature Reserves (TNR), South Africa	Heterogeneous bushveld varying from open woodland to moderately dense riparian woodland. *Acacia nigrescens*, *Combretum spp*. and *Colophospermum mopane* woodlands dominate [6, 7]	5		1	

1, Caro 1994; 2, Mills 1998; 3, Eaton 1970; 4, Eaton 1974; 5, Gertenbach 1983; 6, Kruger 1988; 7, De Villiers 1995.

Table 4.2. Cheetah prey composition in the Kruger National Park.

Prey	**Males**				**Females**				**All cheetahs**	
	Adult	**Juvenile**	**Unknown**	**Total**	**Adult**	**Juvenile**	**Unknown**	**Total**	**Total**	**%**
Impala	9	4		13	9	9		18	31	45.6
Grey duiker		3		3	2	3		5	8	11.8
Steenbok				0	4	4		8	8	11.8
Waterbuck	1	5		6				0	6	8.8
Zebra		5		5		1		1	6	8.8
Kudu		4		4				0	4	5.9
Warthog		2		2				0	2	2.9
Scrub hare			1	1			1	1	2	2.9
Reedbuck				0	1			1	1	1.5
Total	10	23	1	34	16	17	1	34	68	100

Table 4.3: The availability and kill frequency of five common prey species in the diet of cheetahs in the Kruger National Park.

	Impala	**Kudu**	**Zebra**	**Waterbuck**	**Warthog**
Total number	6219	333	757	125	178
Relative abundance	81.7	4.4	9.9	1.6	2.3
Total kills	31	4	6	6	2
Percentage of total	63.3	8.2	12.2	12.2	4.1
Preference Rating	0.8	1.9	1.2	7.6	1.8

Cheetahs preyed on male and female impala at significantly higher and lower frequencies respectively than their availability would predict ($\chi^2 = 12.7$; d.f. = 1; $p < 0.001$). Of the 18 adult impala killed, 77.8% were males and 22.2% were females.

There was a difference in the way in which male and female cheetahs utilised prey of different weight and size classes. The male cheetahs' diet consisted of a greater proportion of larger prey items (20.6%, 67.6% and 11.8% large-, medium- and small-weighted prey respectively), while the female cheetahs caught smaller prey items (44.1% and 55.9% of medium- and small-weighted prey respectively). When comparing male and female cheetahs' selection of prey based on average adult size, there was a significant difference ($\chi^2 = 18.3$; d.f. = 2; $p < 0.0001$). The male cheetahs' diet consisted of larger prey species, such as kudu, waterbuck and zebra, while the females caught grey duiker *Sylvicapra grimmia* and steenbok *Raphicerus campestris*.

While the hunting success (kills/hunting attempts) of male and female cheetahs did not differ significantly, the frequency of hunting attempts (per prey encounters) of males and females did ($\chi^2 = 5.758$; d.f. = 1; $p < 0.05$). The hunting success for M3, F1 and F2 was 24.7%, 16.1% and 16.7% respectively, and the frequency of hunting attempts per prey encounters was 44.5%, 69.4% and 70.6% respectively. Kill rates for M3 were 1 kill per 7 days (or 1.35 kg meat/cheetah/day) and 1 kill per 3.5 days (or 1.41 kg meat/cheetah/day) for two 14–day continuous observation periods, and 1 kill per 4.61 days for F1 for one 14-day continuous observation period. One kill, however, was kleptoparasitised from F1 by a spotted hyaena, therefore, meat consumed was calculated at 1.37 kg meat/day. Cheetah F1, however, was accompanied by two large cubs, so by dividing the meat equally among them, meat consumed was approximately 0.43 kg meat/cheetah/day. This figure, however, may be an underestimate as F1 may have made an additional kill during 17 unobserved hours of the 14-day observation period (Mills pers. comm.).

There was no significant difference in mean chase distance of successful and unsuccessful hunts between male (M3) and female cheetahs (F1 and F2). Using the pooled data of males and females, a significant difference was found between the mean chase distance of successful versus unsuccessful hunts ($t = 4.36$; d.f. = 113, $p < 0.0001$). The mean chase distance for successful hunts was 189 m (SE = 22.9, n = 26) and unsuccessful hunts was 95.7 m (SE = 9.41, n = 89). The mean kill retention time was 165 min (SE = 59, n = 9). There was no significant difference between incidents of kleptoparasitism for the male cheetah coalition (9.1%) and female cheetah F1 (16.7%). When combining data of males and females, kleptoparasitism was 11.8% (n = 34).

Once prey was detected, cheetahs attempted considerably more hunts per prey encounters in the open savanna than *Acacia* thickets and Lebombo Hills (Table 4.4). There was a significant difference in the frequency with which hunting attempts to no attempts were made in the *Acacia* thickets and open savanna ($\chi^2 = 153$; d.f. = 1; $p < 0.0001$). Cheetahs attempted more hunts than expected in the open savanna and less than expected in the *Acacia* thickets. Hunting success (kills/hunting attempt) was also greater in the open savanna than in the *Acacia* thickets (Table 4.4), although there was no significant difference.

Cheetahs made most of their kills in the open savanna (Table 4.4). The frequency of kills per habitat type was significantly different from the expected based on habitat available for killing within the cheetahs' home ranges ($\chi^2 = 11.3$; d.f. = 2; $p < 0.01$). Most hunting attempts also occurred in the open savanna (Table 4.4). The frequency of hunting attempts per habitat type differed significantly from the expected based on habitat available for hunting within the cheetahs' home ranges ($\chi^2 = 14.9$; d.f. = 2; $p < 0.001$). Of the three available habitat types, Bonferroni confidence limits indicated that the open savanna was used significantly more and the Lebombo Hills significantly less than expected for killing and hunting, while the *Acacia* thickets were used significantly less than expected for killing but were used in proportion to availability for hunting (Table 4.5).

More impala were killed in the open savanna than the other two habitat types (Table 4.4). Impala were killed at significantly different frequencies to those predicted based on their occurrence across different habitat types ($\chi^2 = 22.5$; d.f. = 2; $p < 0.0001$). Bonferroni confidence limits indicated that cheetahs killed significantly more impala in the open savanna and significantly less impala in the Lebombo Hills than expected, while they were killed in proportion to their availability in the *Acacia* thickets (Table 4.5). The densities of impala were higher in the Lebombo Hills and *Acacia* thickets than the open savanna (Table 4.4).

Table 4.4. Cheetah hunting behaviour and the density of impala in different habitat types in the south eastern region of the Kruger National Park.

Hunting and prey	***Acacia* thickets**	**Open savanna**	**Lebombo Hills**
Hunting attempts/prey encounters (%)	20	95	14
Kills/hunting attempts (%)	11	23	0
Frequency of kills (%)	8	85	6
Frequency of hunting attempts (%)	18	81	1
Frequency of impala kills (%)	21	76	3
Impala/km^2	12.5	8.8	12.7

Table 4.5. Habitat selection by cheetahs for a) killing and hunting and b) hunting impala in the south eastern region of the Kruger National Park. Symbols indicate if use was significantly greater (+), less (-), or no different (0) to the expected based on a) the proportion of habitat available within the cheetahs' home ranges for killing and hunting, and b) the proportion of impala available in the different habitat types.

Habitat	**Killing***	**Hunting***	**Hunting impala***
Acacia thickets	-	0	0
Open savanna	+	+	+
Lebombo Hills	-	-	-

* Significance at the 0.05 level

Cheetahs initiated more hunts, and had a greater hunting success in long grass followed by medium grass, while hunting success was lowest in short grass (Table 4.6). More hunting attempts occurred in moderate and dense bush, but hunting success was greater in open bush (Table 4.6). The females were responsible for the high rates of initiating hunts (82%) in dense shrub cover compared to the males (46%), with 70% verses 46% in moderate and 61% verses 41% in open shrub cover respectively. No significant differences were found between any of the vegetation classes.

4.3.2 Across-ecosystem comparisons

In 10 study sites across southern and East Africa, the adults of medium-sized prey (18 – 65 kg) occurred most frequently in the cheetahs' diet, followed by the juveniles of medium- and large-sized prey (Table 4.7). There was, however, a significant variation in the size and age groups of prey taken by cheetahs across study sites (ANOVA, F = 7.406; d.f. = 49; $p < 0.0001$). In Kafue NP and PRR, cheetahs selected a large proportion of adults in the large-size category (> 65 kg) compared to others areas. In the SNP, Kafue NP, PRR, KNP and TNR cheetahs utilised a greater proportion of juveniles of large prey, and KNP and MM cheetahs took a greater proportion of small-sized prey compared to other areas.

When plotting the rank of cover per park against rank of chase distance, study sites with the least cover had the longest mean chase distance while those with greatest cover had the shortest mean chase distance (Fig. 4.1a, Table 4.1 and 4.8). Study sites with the least cover had the greatest hunting success (Fig. 4.1b, Table 4.1 and 4.8) and greater incidences of kleptoparasitism (Fig. 4.1c, Table 4.1 and 4.8). Study sites had longer chase distances for successful hunts (Table 4.8). No patterns were found in mean kill retention time and kill rate across study areas (Table 4.8).

4.4 DISCUSSION

4.4.1 Cheetah predation

Table 4.6. Rates of hunting attempts and hunting success in different vegetation classes in the south eastern region of the Kruger National Park.

Grass height	**< 20 cm**	**20 – 60 cm**	**> 60 cm**
Kills/hunting attempts (%)	14.7	18.4	25
Hunting attempts/prey encounters (%)	44.7	54.3	64.4
Shrub cover	**Open**	**Moderate**	**Dense**
Kills/hunting attempts (%)	27.6	17.2	17.8
Hunting attempts/prey encounters (%)	46.8	54.5	63.6

Table 4.7. Proportions (%) of size categories and age classes of cheetah prey in 10 study sites across southern and East Africa. Size categories: small (< 18 kg), medium (18 – 65 kg) and large (> 65 kg).

Study site*	**Small**	**Medium**		**Large**		**Ref****
		Adult	**Juvenile**	**Adult**	**Juvenile**	
East Africa	15.8	52.0	13.5	7.0	11.7	1
SNP	4.3	52.2	4.3	8.7	30.4	2
KTP	1.7	65.8	18.1	6.8	7.6	3
Kafue NP	3.8	11.5	15.4	42.3	26.9	4
MNP	14.6	53.7	24.4	4.9	2.4	5
SBNR	11.9	56.3	31.8	0.0	0.0	6
PRR	8.1	22.1	23.4	22.1	24.3	7
KNP	27.3	27.3	22.7	0.0	22.7	8
MM	24.4	25.9	42.9	0.4	6.4	9
TNR	10.5	36.8	5.3	10.5	36.8	10
Mean	12.2	40.4	20.2	10.3	16.9	
Standard error	2.71	5.69	3.70	4.12	4.06	

* East Africa: a broad survey across Uganda, Tanzania and Kenya; SNP Serengeti National Park; KTP Kgalagadi Transfrontier Park; Kafue NP Kafue National Park; MNP Matusadona National Park; SBNR Suikerbosrand Nature Reserve; PRR Phinda Resource Reserve; KNP Kruger National Park; MM Mala Mala Game Reserve; TNR Timbavati & Klaserie Private Nature Reserves.

**1, Graham 1966; 2, Kruuk & Turner 1967; 3, Mills 1984; 4, Mitchell et al. 1965; 5, Zank 1995; 6, Pettifer 1981b; 7 Hunter 1998; 8, This study; 9, Radloff unpubl. data; 10, Pettifer 1981a.

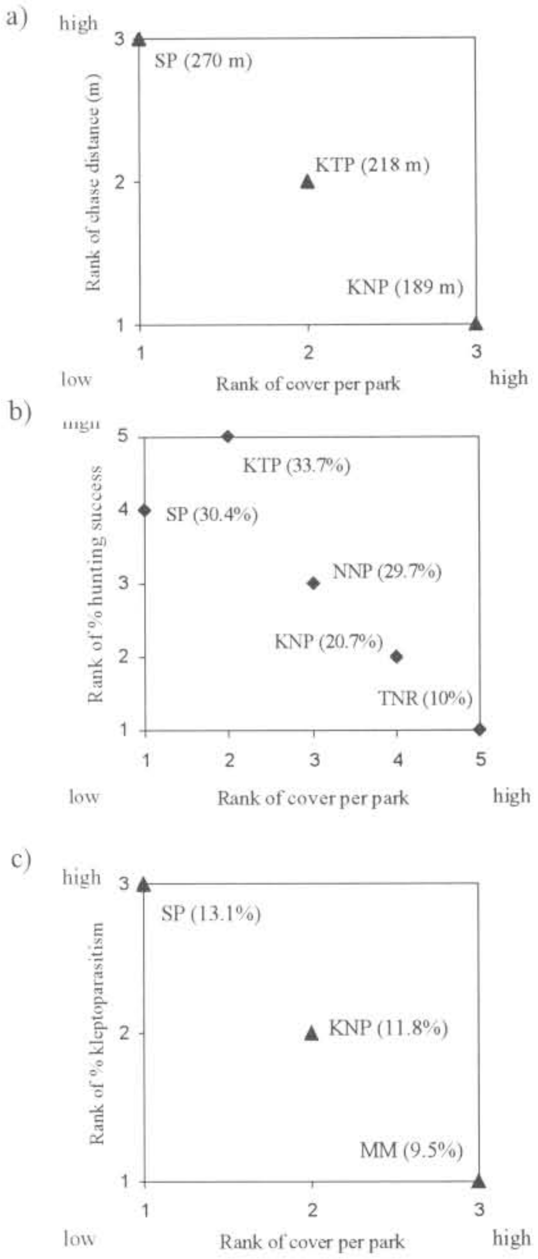

Figure 4.1. Relationship between rank of cover per park and (a) rank of mean chase distance (m), (b) rank of % hunting success, and (c) rank of % kleptoparasitism across protected areas in southern and East Africa. SP = Serengeti Plains; KTP = Kgalagadi Transfrontier Park; NNP = Nairobi National Park; KNP = Kruger National Park; TNR = Timbavati & Klaserie Private Nature Reserves; and MM = Mala Mala Game Reserve. See Table 4.1 for brief habitat description of each area.

Table 4.8. Aspects of cheetah hunting behaviour and incidents of kleptoparasitism in eight study sites across southern and East Africa.

Protected Area*	Hunting success (%)	Mean chase distance (m)	Klepto-parasitism (% of kills)	Mean kill retention (min)	Mean kill rate (kills/year)	Reference
SP	30.4	290 success 270 fail	13.1	136	341	Caro 1994; Schaller 1972
KTP	33.7	218 success 122 fail	**	**	146	Labuschagne 1979
NNP	29.7	**	**	**	150	Eaton 1970; McLaughlin 1970[1]
KNP	20.7	189 success 96 fail	11.8	165	79	This study
MM	**	**	9.5	**	**	Radloff unpubl. data
PRR	**	**	**	720 - 840	**	Hunter 1998
TNR	10[2]	**		1944	51	Pettifer 1981a
SNR	**	**	**	1031	95	Pettifer 1981a

*SP Serengeti Plains; KTP Kgalagadi Transfrontier Park; NNP Nairobi National Park; KNP Kruger National Park; MM Mala Mala Game Reserve; PPR Phinda Resource Reserve; TNR Timbavati & Klaserie Private Nature Reserves; SNR Suikerkop Nature Reserve.

** no data available

[1] cited by Schaller (1972)

[2] impala only

Diet preferences of cheetahs have been found to differ between study locations, reflecting differences in prey species and their abundance (Stander 1991; Caro 1994; Mills 1998). The significant variations found in the cheetah's diet across 10 different study sites reflect this (Table 4.7). In the KNP study site, impala were the most abundant prey in the study area and the most common prey item in the cheetahs' diet (Table 4.2). On the Serengeti Plains it was Thomson's gazelle (Caro 1994), in KTP the springbok *Antidorcas marsupialis* (Mills 1984), in SBNR blesbok *Damaliscus pygargus* (Pettifer 1981b), in PRR nyala *Tragelaphus angasi* (Hunter 1998), and in Kafue NP puku *Kobus vardoni* (Mitchell et al. 1965). The cheetah's main food, however, was medium-sized prey, which represented an average of 60% in the cheetah's diet across ecosystems (Table 4.7). The juveniles of large-sized prey also formed an important part of the diet in many areas, although most probably fall into the medium-sized prey category (18 – 65 kg). In SBNR, where blesbok were the most frequently caught prey item, there was a preferred selection for blesbok females (60 kg) and juveniles, which Pettifer (1981b) explained may be due to blesbok males weighing up to 80 kg. Cheetahs, however, will take large-sized prey, such as nyala and puku in PRR and Kafue NP respectively (those areas mainly responsible for 10% recorded in large-sized prey category, Table 4.7). The average weight of male and female puku, however, is 67 kg (Owen-smith 1988), and therefore bordered between medium- and large-sized prey. Hunter (1998) suggested that the habit of nyala (average weight: 85 kg) browsing in more open areas near cover and their sluggish nature made them more vulnerable to cheetah predation. In Namibia, cheetahs were recorded taking unusually large prey items, such as adult kudu (McVittie 1979). These may be a result of individual specialisations (Mills 1984) or a type of predator release in the absence of other dominant predators (McVittie 1979). In areas where Namibian cheetahs were translocated, such as PRR and Pilanesberg National Park (Hofmeyer & van Dyk 1998), cheetahs also hunted larger prey items. These studies along with McVittie's (1979) study may indicate that Namibian cheetahs are transferring learned behaviour to other areas that result in this selection for larger prey.

The size and composition of the cheetahs' hunting group may affect prey size and species preyed upon (Eaton 1974; McVittie 1979; Caro 1994). In PRR, Hunter (1998) found that male cheetah coalitions killed mostly male nyala (120 – 130 kg) while female cheetahs killed mostly female nyala (60 – 70 kg). In the Serengeti, Caro (1994) also found that larger groups of cheetahs hunted wildebeest more often than did smaller groups. In the KNP study, smaller prey formed a significantly more important part of the female cheetah's diet compared to the three-male cheetah coalition (Table 4.2). Therefore, the group size of the study animals selected for observation will influence the size and species of prey items found in the diet. These considerations do not explain the unusually large-sized prey hunted by cheetahs in Namibia (McVittie 1979).

Small prey represented an average of 12% in the cheetah's diet across African savanna study sites (Table 4.7). Small prey, however, are usually underrepresented (Stander 1991; Mills 1992) because studies often depend on data from carcass remains (Pienaar 1969; Pettifer 1981b) or opportunistic observations (Mitchell et al. 1965). Kills of small prey are usually unobserved because of the rapid consumption rate and lack of remains (Mills 1992). The large percentage of small prey recorded in the cheetahs' diet in this study (27%) and in Radloff's (unpubl. data) study in Mala Mala (24%) are probably more representative of the proportion of small prey because this study used continuous observation data (see Methods) and Radloff (unpubl. data) recorded predation over all seasons of 13 years. Radloff's data (Radloff pers. comm.) revealed seasonal switches in the diet, as cheetahs were found to take mostly impala lambs during the impala breeding season, but larger prey at other times. Long-term studies in the Serengeti showed that hares represented 28% of the female cheetahs diet (Laurenson 1991, in Stander 1991). Therefore, the degree to which small prey items are recorded in the cheetah's diet may depend largely on the season and duration of the cheetah study, and the type of data collection used.

While medium-sized, abundant prey occurred most frequently in the cheetahs' diet, preference indices across studies indicate that cheetahs strongly preferred waterbuck and/or reedbuck (Pienaar 1969, Eaton 1970; Whateley & Brooks 1985; Zank 1995; Hunter 1998, Purchase 1998, this study). However, the accuracy of this is questionable as preference indices based on food availability depend on the extent of selection and relative abundance of different food types (Jacobs 1974), and depend markedly upon the array of components deemed by the investigator to be available (Johnson 1980). Census data are also unreliable as large species are easier to spot than smaller ones (Mills pers.

comm.). This study found that the presence or absence of certain prey items influenced the rating of others. Waterbuck and reedbuck are always recorded in very low numbers, and often small prey items commonly eaten by cheetahs, such as steenbok and duiker, are left out of the calculations because population censuses of these small ungulates are usually impossible. It is recommended, therefore, that cheetah re-introduction projects should assess the availability of abundant, medium-sized prey to cheetahs rather than whether the 'preferred' prey items are present.

Preferences by cheetahs for male impala in the KNP study are paralleled by cheetah preferences in Serengeti for male Thomson's gazelle (Fitzgibbon 1990) and in KTP for springbok (Mills 1990). Fitzgibbon (1990) describes how male gazelles were more vulnerable than females and preferentially selected because they tended to occur on the periphery of groups, had greater nearest-neighbour distances, were less vigilant and were found in smaller groups than females. The same conditions may apply to male impala and springbok as they show similar social structures and behaviour (Jarman 1979; Moss 1989; Skinner & Smithers 1990). Males are also more expendable than females, which lessens the impact of predation on prey populations.

4.4.2 Kill retention time

Kill retention time may be affected by group size, prey size, predator densities, knowledge of competing predators (Schaller 1972; Pettifer 1981a; Hunter 1998) or amount of available cover. These may explain some of the large variations found in kill retention times across African savanna ecosystems (Table 4.8). In SNR, TNR and PRR, cheetahs were acquired from captive-breeding programmes (Pettifer 1981a) or Namibia (Hunter 1998) for re-introductions, therefore, cheetahs had not been subjected to competition from other large predators. Pettifer (1981a) discussed this as the reason for the exceptionally long kill retention times in SNR and TNR. Hunter (1998) attributed the lack of direct competition in PRR to the long hours cheetahs spent at carcasses. Differences in kill retention time between the Serengeti Plains and KNP, with similar densities of competing predators (Stander 1991), may potentially be due to availability of cover and therefore the reason for longer kill retention times in the latter (Table 4.8).

4.4.3 Kill rates and consumption rates

Group size, presence of cubs, prey size and availability, and competition with other predators affect kill rates (Wrogemann 1975; Pettifer 1981b; Caro 1994; Durant 2000). These probably explain the large variations found in cheetah kill rate across African savanna ecosystems (Table 4.8). Pettifer's (1981b) study found that a re-introduced three-male cheetah coalition had very low kill rates of 95 and 51 kills per year in SNR and TNR respectively. However, Pettifer (1981a) estimated that the cheetahs consumed approximately 4.06 kg of meat per cheetah per day in SNR and approximately 2.17 kg in TNR. The former equals Schaller's (1972) estimate that a female (with two cubs) consumed approximately 4 kg/day, although this female had a far higher kill rate of 341 kills per year. The high estimate of kill rate, given by Schaller (1972), however was influenced by the sample size, which was recorded once over six consecutive days. Cheetahs in the KNP had comparatively low kill rates (79 kills/year), although the 14-day continuous observation method used in this study is a more accurate reflection of kill rate (Mills 1992). The rate of food consumption needed to keep a cheetah in healthy condition in a zoological garden is 1.3 to 1.8 kg/day (Crandall 1964); therefore the male cheetah coalition in the KNP appeared to be obtaining an adequate diet (1.4 kg/cheetah/day). The female cheetah's (F1) consumption rate, with two large cubs, was considerably lower (0.4 kg/day), although Caro (1994) estimated that cheetah mothers with old offspring ate as little as 0.5 kg/day because of direct competition from their large cubs.

4.4.4 Hunting and killing frequencies

Cheetahs initiated more hunts and killed more frequently in the open savanna of the KNP compared to other available habitats with thicker bush (Prediction i, see introduction in section 4.1; Table 4.4). The preference by cheetahs for open habitat for hunting (Table 4.5) is particularly evident when considering that the cheetah's main prey (impala) occurred at greater densities in the *Acacia* thickets and Lebombo Hills (Table 4.4), yet were hunted and killed significantly more in the open savanna (Table 4.5). In PRR, which consists of overlapping open to closed bushveld habitat, cheetahs also preferred the open grasslands for hunting (Hunter 1998) and in MNP, cheetahs used the open foreshore grassland predominantly for hunting (Purchase & du Toit 2000).

In the KNP, the high frequency of hunting attempts by female cheetahs recorded in areas with moderate and dense shrub cover is probably because this is the preferred habitat of impala (Chapter 3). The frequency of hunting attempts per prey encounters, however, was far higher in the open savanna (Table 4.4). Female cheetahs may have attempted more hunts than the male coalition in the KNP because females were accompanied by cubs during most observation periods. Laurenson (1995a) found that female cheetahs with denned cubs doubled their food intake by hunting prey at a higher rate and increasing the success rate of hunts.

4.4.5 Chase distance and hunting success

Across African savanna ecosystems, chase distances appeared shorter in more wooded habitats (Prediction ii, see introduction in section 4.1; Fig. 4.1a, Table 4.1). Caro's (1986) study on the Serengeti Plains and Eaton's (1974) study in Nairobi National Park found that cheetahs were more likely to be successful at hunting when they were able to get closer to their prey before rushing. Successful hunts averaged 53 m from the prey and unsuccessful hunts averaged 198 m (Eaton 1974). In the KNP, cheetahs appeared to have attempted more hunts and had a greater hunting success in taller grass cover (Table 4.6; Chapter 3). Fitzgibbon (1990) found that cheetahs in the Serengeti hunted a significantly greater proportion of gazelle in high (>30 cm) than low (<30 cm) vegetation. Across African savannas, hunting success rates, however, appeared higher in more open habitats (Prediction iii, see introduction in section 4.1; Fig. 4.1b, Table 4.1). In the KNP, cheetahs also appeared to have a greater hunting success in the open savanna habitat (Table 4.4) and in areas with open shrub cover (Table 4.6). Therefore, greater tree and shrub cover in woodland habitats may obstruct the cheetah's high-speed hunting strategy, thereby lowering hunting success. As the density of the woody vegetation increases, the more likely the cheetahs are to lose sight of their prey or are prevented from reaching or maintaining high speeds needed for successful hunts. Cheetahs in the KNP had significantly longer chase distances in successful (189 m) than unsuccessful hunts (96 m), as did the KTP and Serengeti Plains (Table 4.8). The success of longer chase distances indicates that in these circumstances cheetahs persisted in catching their quarry rather than giving-up early in the chase because of a predicted failure.

4.4.6 Kleptoparasitism

Across African savanna ecosystems, cheetahs appeared to be kleptoparasitised less in more wooded habitats (Prediction iv, see introduction in section 4.1; Fig. 4.1c, Table 4.1). The sample sizes, however, are very small and further studies need to be undertaken to show conclusive evidence for this. Paulson (1985) considered four effects that open habitat has on host and parasite, three of which are relevant to cheetahs: (1) kleptoparasites can observe and follow hosts more easily, (2) can observe prey capture and carrying, and (3) hosts are less able to hide from kleptoparasites. Considering these effects, one would expect that cheetahs in an open grassland ecosystem like the Serengeti Plains, with a short to medium grass layer, are more vulnerable to kleptoparasitism than in areas like the KNP. On the Serengeti Plains, Myers (1975) considered that cheetahs were more likely to be harassed by other predators and have their prey stolen because of the openness of the habitat.

4.5 CONCLUSIONS

Across a variety of African savanna ecosystems, cheetahs prefer abundant, medium-sized prey (18 – 65 kg). In areas where large-sized prey species (> 65 kg) are more abundant these make up a greater proportion of the cheetah's diet, however, these species either border on medium-sized prey or are more susceptible to predation because of the particular nature of the prey species. Small prey probably form an important part of the cheetah's diet, particularly at certain times of the year, however due to different methods of data collection used across studies a more accurate reflection of this could not be established.

Cheetahs in the KNP, PRR and MNP prefer open habitat for hunting. Although cheetahs appear to have shorter chase distances in more wooded habitats, hunting success appears higher in more open habitat. Therefore, woody vegetation appears to obstruct the cheetah's high-speed hunting strategy, thereby lowering hunting success. Cheetahs, however, actively use cover for stalking prey (Fitzgibbon 1990) and open habitats with bordering woodlands or patches of woody cover are considered preferred or optimal cheetah habitats. Similar conclusions applied when habitat preferences were assessed across a wide range of African savannas (Chapter 3). Gros & Rejmánek (1999) conducted a habitat study in Uganda, based on presence/absence in particular habitat types, which suggested that cheetahs favoured habitats with 25 - 50% woody cover and grasses of medium height (50 – 100 cm). In these habitats, cheetahs can stalk closer to their prey using available cover, but also successfully pursue their prey into available open spaces. Cheetahs may also prefer these habitats because they provide greater concealment and may reduce the risk of kleptoparasitism.

Considering that cheetahs prefer open habitat for hunting, the impact of bush encroachment may be an important factor limiting their range, particularly in the KNP and PRR with predominantly woodland savanna habitat. Pettifer (1981a) considered bush encroachment in most parts of the South African Lowveld to have a negative impact on cheetah hunting success and density. This study is the first attempt at understanding cheetah requirements across a variety of different African savanna ecosystems. Small sample sizes and varying ecological factors across study sites, however, made comparisons difficult. It is conceded too that small sample sizes in the KNP study may have potentially biased results to the idiosyncrasies of those particular individuals chosen for study. Further cheetah studies are required in woodland habitats to expand the database and to obtain a greater understanding of the use and benefits of woodlands to cheetah populations.

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Chapter 5: Population viability of cheetahs in two contrasting habitats

5.1 INTRODUCTION

Cheetahs occur at low densities (Myers 1975; Hamilton 1986; Kelly & Durant 2000) across an increasingly restricted range in sub-Sahelian Africa, inhabiting both woodland and open plains habitat (Caro & Collins 1987a). The main threats to cheetah populations are loss of habitat and persecution by humans (Myers 1975; Anderson 1983; Marker-Kraus et al. 1996); competition from other large predators (Caro & Laurenson 1994; Laurenson 1995; Laurenson, Wielebnowski & Caro 1995); and lack of genetic diversity (O'Brien et al. 1983; O'Brien et al. 1985; O'Brien, Wildt & Bush 1986; O'Brien et al. 1987). Competition with other large predators was identified as a major threat to cheetah populations when Laurenson (1994) found that the exceptionally high cub mortality (95%) on the Serengeti Plains was chiefly due to predation by lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). Lions were the main predator accounting for 73% of cheetah cub deaths (Laurenson 1994). The extremely high rates of cheetah cub predation in the Serengeti, an open grassland system, may be associated with a shortage of available refuge sites for cubs and their extreme vulnerability on the short grass plains (Caro & Durant 1995; Laurenson 1995). Therefore, conditions in woodland habitats may be more favourable to cheetahs for avoidance of predation, because of increased availability of cover for refuges and concealment. In fact, cheetah populations in woodland savannas seem to have lower juvenile mortality rates (Hunter 1998; Purchase 1998), and therefore indeed may be exposed to less threat from predation than grassland savanna populations are.

Because animal species occurring in distinct habitat types may experience different development rates, life spans, and birth and death rates (Pulliam & Danielson 1991), different populations of the same species may show different rates of population growth and persistence across a spectrum of habitat conditions. In this chapter, a population viability analysis (PVA) was conducted, using the computer simulation model

VORTEX (Miller & Lacy 1999), to explore the population dynamics of cheetahs occupying contrasting habitats – a woodland and grassland savanna. The question asked here is: for a given population size, is cheetah population viability higher in a woodland savanna than a grassland savanna? A long-term data set from the Serengeti Plains in East Africa (Kelly & Durant 2000) provided the demographic data required to simulate the dynamics of a grassland savanna cheetah population. The Kruger National Park (KNP), having a population size (Pienaar 1969; Bowland 1994) similar to the Serengeti Plains population (Kelly & Durant 2000), was a hypothetical woodland savanna population. A cheetah study in the KNP (1987 – 1990; see Chapters 3 and 4) provided some demographic data for woodland savanna cheetahs; the remaining data were gathered from other cheetah studies in southern African woodland savannas (Berry et al. 1997; Hunter 1998; Purchase 1998).

The main objectives of this chapter are to: (1) assemble life history and demographic data on cheetahs inhabiting grassland and woodland savannas respectively; and (2) conduct a PVA to compare the viability of cheetah populations in those two contrasting habitats. Sensitivity analyses were used when demographic data were uncertain and for comparing viability under different scenarios. In this way, the PVA helps to identify parameters that the populations may be particularly vulnerable to (Lacy 1993). It is important to note that the model outcomes in this PVA are not meant to make any precise predictions or give absolute answers about the long-term persistence of the two cheetah populations. The value, however, lies in being able to compare the model outcomes of the two cheetah populations to understand how varying demographic parameters affects population viability and what implications this has for managing and conserving cheetahs. Demographic models are commonly used to make decisions for managing wild populations of threatened or endangered species (Beissinger & Westphal 1998), which has an important application for cheetah re-introductions into small parks and nature reserves. Finally, the relationship between cheetah cub mortality and cover availability is discussed.

5.2 METHODS

Population viability analysis is a process in which the probability that a population will become extinct is assessed within a specific period and under specific circumstances (Shaffer 1981). The computer simulation model VORTEX, version 8 (Miller & Lacy 1999) was used to perform the PVA. VORTEX models the deterministic and stochastic processes that determine population performance (Miller & Lacy 1999). In these analyses, general species and population specific parameters were assembled for cheetah populations in a grassland and woodland savanna (Table 5.1). Demographic data for the woodland cheetah population were collated from cheetah studies in the south eastern region of the Kruger National Park, South Africa (field data collected by M.G.L. Mills, 1987 – 1990); Matusadona National Park (MNP), Zimbabwe (Purchase 1998); Phinda Resource Reserve (PRR), South Africa (Hunter 1998); and on commercial livestock farmlands, Namibia (Berry et al. 1997) for the woodland savanna population. Data from the Serengeti Plains in East Africa were used for the grassland savanna population (Laurenson 1995; Kelly & Durant 2000).

5.2.1 General species parameters used in VORTEX for both populations

The VORTEX program was set for 500 reiterations projected at 100 years into the future. A population with a 95% probability of surviving over 100 years was assumed to be viable with an acceptable risk of extinction (Shaffer 1981). The following assumptions were made for the models: (1) no inbreeding depression was incorporated into the simulations; (2) no catastrophes were assumed for both populations; (3) environmental variation in survival was correlated with environmental variation in reproduction as cheetah mothers are known to abandon cubs if they cannot obtain enough food (Laurenson 1995; Purchase 1998); (4) populations were considered isolated and immigration was not included in the simulations as data for this were unavailable for both areas. Emigration, however, is incorporated into sub-adult and adult mortality rates (see below); (5) reproduction was assumed to be density independent as there is no evidence from previous cheetah studies to that show that the number of females which breed and

Table 5.1. Values for life history and demographic parameters used for input into VORTEX for simulating the population dynamics of two cheetah populations in contrasting habitats. Figures in brackets under mortality rates represent variations from baseline scenarios for sensitivity analyses. Data for the baseline scenario for the woodland savanna population were obtained from cheetah studies conducted in the south eastern region of Kruger National Park (this study); Matusadona National Park (Purchase 1998); Phinda Resource Reserve (Hunter 1998) and commercial livestock farmlands in Namibia (Berry et al. 1997). Data from the Serengeti Plains (Kelly & Durant 2000) were used for the baseline scenario for the grassland savanna population.

VORTEX parameter	**Woodland savanna**	**Grassland savanna**
Age at first reproduction	2 years*	2 years*
Maximum annual litter size	6 (1 litter)	18* (3 litters)
Litters size distribution*	1 – 6 cubs: 3.75, 3.75, 40, 32, 20 and 0.5 respectively.	1 – 18 cubs: 1.6, 2, 20, 16, 10, 8, 11.5, 11.5, 7, 4.5, 3.5, 2.4, 1.4, 0.5, 0.1, 0, 0, 0 respectively.
Proportion of females breeding per year (%)	68 ± 6.8	87.4* ± 8.74
Mortality rates (%)		
0 – 1 years	50 (and 25)	90* (85 – 95)
1 – 2 years	15 (– 65)	35* (30 – 40)
Adult > 3 years	15 (– 25)	15* (10 – 20)
Age of senescence	12*	12*

* Kelly & Durant (2000)

produce cubs decreases with increasing population size (Purchase 1998; Kelly & Durant 2000); and (6) all males were assumed to be in the breeding pool for both populations. Caro (1994) found in the Serengeti that male cheetahs display two behavioural tactics for acquiring mates: either holding a mating territory or roaming in search of females. Therefore, it was assumed that most males would find and mate with at least one female (Purchase 1998).

Age at first reproduction for a single female cheetah in KNP was approximately 2.6 years. In Namibia, the average age of first reproduction for females was estimated at about three years in the wild farmland cheetah population or Etosha National Park (Berry et al. 1997). The average age of first reproduction in the Serengeti is 2.4 years (Kelly et al. 1998). Females are, however, capable of producing their first litters at two years of age (Schaller 1972; Berry et al. 1997; Kelly & Durant 2000). Therefore, Kelly & Durant's (2000) 'optimistic estimate' of two years for age of first reproduction for females was used for both populations as VORTEX does not allow fractional ages (Miller & Lacy 1999). Age of first breeding for males was also set at two years as male cheetahs are physiologically capable of breeding at this age (Caro 1994), but social constraints may limit breeding to older animals (Berry et al. 1997). Being a polygynous species, however, reproductive age is not considered to have a significant demographic effect on the model unless populations are extremely small (Berry et al. 1997). Differences in fecundity, such as the age at first reproduction, appeared to have little effect on the potential number of cubs produced compared with increasing cub survival by avoiding predators (Laurenson 1995). Age of first reproduction also appear similar for both cheetah populations, and therefore any effect on outcome would be applied to both populations.

A stable starting age distribution was used for both populations, wherein VORTEX assigns individuals to each age-sex class proportionate to the stable age distribution (Miller & Lacy 1999). In the initial analyses, a starting population size of 250 was used for both populations, as these are approximate to estimates established by Pienaar (1969) and Bowland (1994) for the KNP population and Kelly & Durant (2000) for the Serengeti Plains population. Starting population sizes of 15, 25, 50, 150 and 200 were also used to analyse for effects on extinction risk.

Carrying capacity was set at 500 individuals. This is an arbitrary selection that allows room for population growth before truncation (Kelly & Durant 2000). The cheetah population in the Serengeti also appears to show no signs of density dependence (Kelly & Durant 2000), and this was assumed for the woodland savanna cheetah population.

5.2.2 Population specific parameters

Female cheetahs are considered to produce between one and six cubs per litter (Berry et al. 1997; Purchase 1998; Kelly & Durant 2000; and KNP study). In the KNP, a female cheetah with four successive litters of cubs only produced a maximum of one litter per year (or six cubs per year). Berry et al. (1997) and Hunter (1998) used maximum litter sizes of five and six cubs respectively per year. Adult females, however, in the Serengeti with exceptionally high rates of cub mortality (estimated at 95%) conceive again rapidly (Laurenson, Caro & Borner 1992). Females mated, on average, within three weeks of losing the previous litter (Laurenson et al. 1992). Kelly & Durant (2000) assumed in their viability model that a cheetah mother in the Serengeti could give birth to a maximum of three litters per year, therefore producing a maximum of 18 cubs a year (VORTEX defines this as maximum annual litter size). They calculated probabilities for annual litter sizes ranging from 0 – 18, which were adapted slightly for use in the VORTEX model. Probabilities of giving birth to litter sizes of one to six cubs for woodland savanna cheetahs were obtained from Laurenson (1992, in Kelly & Durant 2000). Litter size distributions for both populations considered average litter size at birth to be approximately 3.5 cubs. This mean, however, is probably an underestimate as litters were only examined on average 15 days after parturition (Laurenson et al. 1992). Reports vary depending on when litter size was calculated. The average litter size in MNP was estimated at three cubs (Purchase 1998). Field data in Namibia yielded a mean litter size of 3.4 cubs (Berry et al. 1997). Both, however, appear to be underestimates, as litter sizes were estimated after emergence from the lair. Hunter (1998) recorded a mean litter size of 4.4 ± 0.94 cubs in PRR. The sex ratio at birth was set at 0.5 (Pettifer 1981; Laurenson et al. 1992; Berry et al. 1997).

In PRR, one female with three litters had an inter-litter interval of 16.5 months. In the KNP a female with three successive litters had a mean inter-litter interval of 18.6 ± 1.25 (SD) months. Combining the two areas, the average inter-litter interval was estimated at 17.6 months; i.e. 68% of female cheetahs will produce a litter in a given year. Berry et al. (1997) used estimates of 75% and 60% of the proportion of females producing litters in a given year. The standard deviation (SD) used by VORTEX for the percent females producing litters of offspring reflects environmental variation in reproduction (Miller & Lacy 1999). Insufficient data, however, prevented an estimation of this. Kelly & Durant (2000) were also unable to obtain a direct measure of this variation in the Serengeti, but entered a range of values in SD from 5% to 40% of the mean proportion breeding, and found no effect on extinction risk. Consequently, they set the SD equal to 10% of the mean, and the same was applied for the woodland savanna cheetah population.

No data were available regarding age of senescence for KNP and PRR cheetahs, therefore, 12 years of age was used as the maximum age (Kelly & Durant 2000) in the model for both cheetah populations, and assumes that the animals can breed (at normal rates) throughout adult life.

Data for age-specific mortality rates for woodland savanna cheetahs are exceptionally sparse. The KNP data were able to provide some estimate of juvenile mortality rate from a single adult female cheetah with three successive litters of cubs. Here, juvenile mortality for 0 – 12 months was estimated at 45% (n = 3 litters). Litter size was estimated when cubs were approximately six weeks of age. Hunter's (1998) mortality rate for 0 – 12 months was 25%. Purchase's (1998) observations in MNP estimated mortality 0 – 2 years at 60% (n = 2 litters). Cub mortality from emergence to maturity was estimated by Pienaar (1969) as 50% in the KNP, and by Eaton (1970) and McLaughlin (1970, in Caro 1994) as 50% and 43% respectively in Nairobi National Park. Cub mortality of Namibian ranchland cheetahs between three months to one year of age was estimated at 46%, however, due to the absence of other predators in these areas, this statistic was disregarded. Considering the above, juvenile mortality (0 – 12 months) in the woodland savanna was set at 50% (for the baseline scenario) and 25%. These values may be considered optimistic, however, as mortality rates were not measured immediately from birth. Laurenson (1994) estimated that 94.4 – 96% of cubs die before reaching independence at 14 months of age. The conservative figure, however, of 90% adopted by Kelly & Durant (2000) for the age-specific mortality rate 0 – 12 months was used in the VORTEX model for the grassland savanna cheetah population.

A three year study in the Serengeti by Laurenson (1995) estimated age-specific mortality for female cheetahs as 15.3% (adolescent, < 3 years), 22.7% (prime, 3 – 9 years) and 55% (old, > 9 years). Kelly & Durant's (2000) long-term data set on Serengeti cheetahs over 20 years, which estimates adolescent (1 – 2 years) and adult (> 2 years) female mortality as 35% and 15% respectively, however was used for the baseline scenario for simulating the grassland savanna cheetah population. While Laurenson's (1995) mortality estimates includes only those female cheetahs that died, Kelly & Durant (2000) estimates were based upon time of last sighting, which therefore includes those cheetahs that emigrated or dispersed out of the study area. This may explain the higher mortality estimates documented by the latter. The grassland savanna population was also modelled with Laurenson's (1995) sub-adult mortality estimate of 15%.

Data for sub-adult survival in woodland savannas proved the most problematic as no real studies have been conducted to estimate mortality rates for this cohort. Hunter (1998) used sub-adult mortality rates of 12.5% and 10% for males and females respectively, based on natural mortality estimates of Namibian cheetahs (Berry et al 1997). Berry et al. (1997), however, considers total annual mortality to range up to 30% with removal on farmlands by humans. A radio-telemetry study on 18 male and 8 female Namibian cheetahs reported by Berry et al. (1997) estimated crude annual death rates for cheetahs over one year of age to be 38.6% for males and 19.2% for females, of which four of the males were shot. Purchase (1998) estimated annual adult and sub-adult mortality at 20.5% using projected and actual population sizes observed over three years of study. These estimates also include those cheetahs that dispersed out of the study area. Considering the above statistics, baseline sub-adult mortality for the woodland savanna cheetah population was modelled at 15%, which was considered to exclude rates of emigration and dispersal. Mortality rates were then increased to include a percentage of cheetahs that may have dispersed or emigrated out of the population (Table 5.1).

The only recorded adult mortalities available for the woodland savanna population were from Hunter's study (1998) in PRR, which estimated male and female mortality at 17.85% and 12.5% respectively. The baseline scenario in this study used an average of 15% for the adult mortality rate. Sub-adult and adult mortality rates (including dispersion and emigration) were then predicted by varying the mortality rates until the population reached a stable or self-replacing state, i.e. growth rate (r) is close to zero and probability of extinction is less than 5%. Positive values of 'r' are necessary for a population to survive or grow, and, in principle, a zero value characterises a stable population (Berry et al. 1997). No statistics were available for male cheetahs in either of the two habitats, although survival is considered to be lower for adult males than for females (Caro & Collins 1987b; Kelly & Durant 2000). This is mostly a result of intra-specific combat between males (Caro & Collins 1986), but also because non-territorial males are usually behaviourally and physiologically stressed and in poor health due to their nomadic lifestyle (Caro, Fitzgibbon & Holt 1989; Caro & Collins 1987a; Caro 1994). Males are also more likely to disperse out of the area than females, which further decreases measured survival rates (Frame & Frame 1980; Caro 1994; Kelly & Durant 2000). Evidence of this was observed in some woodland savanna cheetah populations. In PRR, sub-adult males were excluded from existing territories of other males and were killed on two occasions by cheetah coalitions (Hunter 1998). In the KNP, two nomadic, sub-adult male cheetahs moving through the study area were found to be in poor condition with mange - one died and the other disappeared. Therefore, males were considered to have higher mortality rates than females, but were initially modelled with equal age-specific mortality rates as females. Thereafter, sensitivity testing was used to assess the effects differential mortality rates may have on persistence by independently varying mortality rates of males and females. Sensitivity analyses were also used to assess the influence varying age-specific mortality rates may have on persistence by independently increasing and decreasing each mortality rate by 5% while holding all others constant (male and females with equal age-specific mortality rates were used for this set of simulations).

The environmental variation (EV) in mortality rates is reflected by the input of a standard deviation into the model for all mean age-specific mortality rates. These variances, although shown in Kelly & Durant's (2000) viability study on the Serengeti cheetahs, were not available for woodland savanna cheetahs. Therefore, it was assumed that the differences in environmental variation between the two habitats, e.g. in predator and prey densities, were reflected by differences in the age-specific mortality rates. Therefore, EV was kept constant throughout by assigning zero standard deviations values to all age-specific mortality rates. The simulations varying each age-specific mortality rate by 5% will provide some measure of the effect further EV in mortality rates may have on population viability.

5.3 RESULTS

The results of the following set of simulations are presented in Table 5.2. When simulating the baseline scenarios for both cheetah populations, the *grassland savanna* population, although viable, showed a negative growth rate (r) and a 3% chance of extinction. In comparison, the *woodland savanna* population showed a high positive mean growth rate with no chance of extinction. When juvenile mortality of the woodland savanna population was lowered to 25%, mean growth rate climbed even higher. The grassland savanna population showed a positive mean growth rate when sub-adult mortality was lowered to 15%, according to Laurenson's (1995) estimate, and no chance of extinction. When increasing sub-adult mortality rates to 35%, according to Kelly & Durant's (2000) estimate, using the baseline scenario for the woodland savanna population, mean growth rate was still considerably higher than the grassland population with no chance of extinction. Comparing across all scenarios, lower cub mortalities produced higher mean growth rates. A hypothetical self-replacing woodland savanna cheetah population was generated when sub-adult and adult mortality was set at 60% and 23% respectively (with a 50% juvenile mortality), and 68% and 28% respectively (with a 25% juvenile mortality). Exchanging maximum litter size and litter size distribution between the two cheetah populations, while holding all other parameters constant, had a large impact on model outcomes. The probability of persistence for the grassland savanna population (using the baseline scenario) dropped to 0% (Fig. 5.1), while mean growth

Table 5.2. The results of population viability analyses using VORTEX simulating two cheetah populations in contrasting habitats. Demographic parameters used for input into the model are summarised in Table 5.1. Mortality rates are the same for both sexes. r = mean stochastic growth rate over 100 years; SD = standard deviation of r; PE = mean probability of extinction over 100 years for extant and extinct populations; N = mean population size (across all extant and extinct populations) after 100 years.

Mortality rates			**VORTEX results**				**Comments***
Juvenile	**Sub-adult**	**Adult**	**r**	**SD**	**PE**	**N**	
			Grassland savanna				
90	35	15	-0.012	0.07	0.03	99	Baseline
90	15	15	0.04	0.036	0	498	Decrease sub-adult
90	35	15	-0.100	0.152	1.00	0	Adjust litter size = 6
			Woodland savanna				
50	15	15	0.230	0.049	0	500	Baseline
25	15	15	0.339	0.058	0	500	25% juvenile
50	35	15	0.164	0.053	0	500	Increase sub-adult
25	35	15	0.266	0.064	0	500	Increase sub-adult
50	60	23	0.000	0.082	0	277	Hypothetical self-replacing population
25	68	28	0.004	0.098	0.01	334	Hypothetical self-replacing population
50	60	23	0.119	0.085	0	498	Adjust litter size = 18

* Comments indicate two baseline scenarios simulated for each population. Thereafter, alternative scenarios simulated with adjusted sub-adult mortalities; maximum litter size; and to generate hypothetical self-replacing populations.

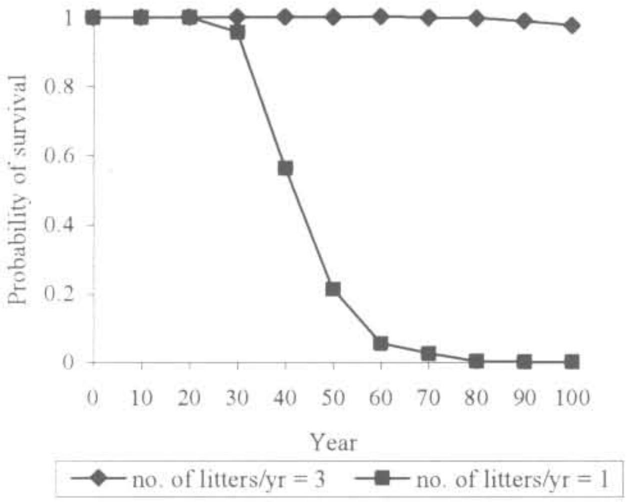

Figure 5.1. The effect of varying maximum litter size on the probability of a grassland savanna cheetah population surviving over 100 years. Three litters per year = maximum litter size of 18 while one litter per year = maximum litter size of six.

rate of the hypothetical self-replacing woodland savanna population increased from 0 to 11.9%. When independently increasing and decreasing age-specific mortality rates by 5% for both populations, mean growth rate and persistence of the *grassland savanna* cheetah population was most affected by changes in juvenile followed by adult mortality (Fig. 5.2a), while the *woodland savanna* population, with 50% juvenile mortality, was most affected by changes in adult followed by sub-adult mortality (Fig. 5.2b). The woodlandsavanna population, with 25% juvenile mortality, showed adult and sub-adult mortality to have an equal and larger effect on growth and persistence than juvenile mortality (Fig. 5.2c).

Using the baseline scenario (Table 5.1) and decreasing starting population size of the *grassland savanna* cheetah population, the probability of survival dropped below the threshold of 95% at a starting population size of 200 (Fig. 5.3). At a starting population size of 50 animals or less, there was a sharper decline in the probability of survival compared to other projections with larger population sizes (Fig. 5.3). The same scenario was then simulated but with sub-adult mortality of the grassland population adjusted to 15%, according to Laurenson's (1995) estimate. The results now showed that the grassland savanna population was still viable at a starting population size of 25 (probability of extinction (PE) = 3%), but not at a starting population size of 15 (PE = 14%). Comparatively, the *woodland savanna* cheetah population, using the baseline scenario (Table 5.1), still had a 100% chance of persistence at a starting population size of 15.

When modelling differential adult and sub-adult mortality rates for male and female cheetahs in the grassland and woodland savanna, female cheetahs had a considerably greater effect on mean growth rate and persistence than males. Increasing and decreasing female mortality rates by 5% resulted in the same outcomes to those observed in Fig. 5.2a for the grassland savanna and Fig. 5.2b and c for the woodland savanna cheetah population. In contrast, increasing adult or sub-adult male mortalities independently to 90%, for both populations, had little effect on PE and mean growth rate. When increasing them simultaneously in 10% increments, the probability of survival dropped below the 95% threshold for the grassland savanna population when adult and sub-adult mortality reached 55% and 75% respectively (PE = 9%), and when the

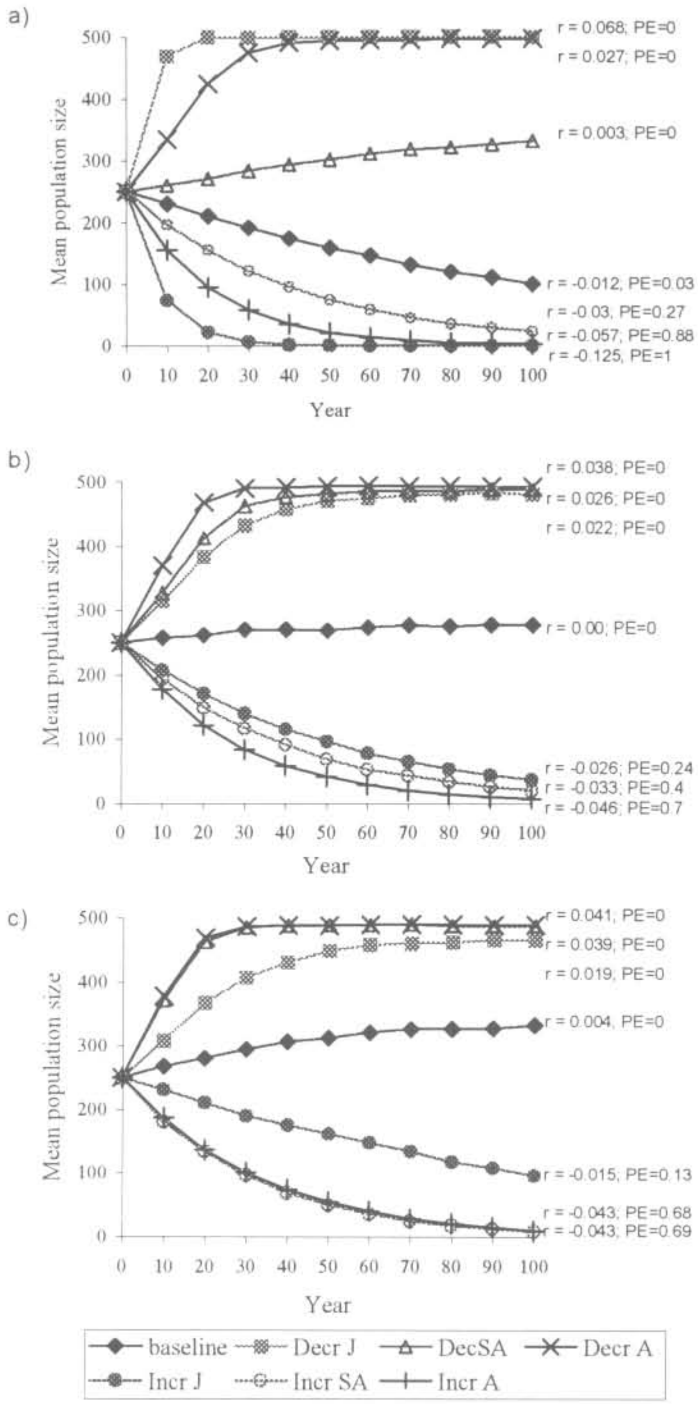

Figure 5.2. The effects of varying age-specific mortality rates by 5% on mean population size of cheetahs in a) grassland savanna with 90% juvenile mortality; b) woodland savanna with 50% juvenile mortality; and c) woodland savanna with 25% juvenile mortality. Baseline = 90%, 35%, 15% for grassland population; and 50%, 60%, 23% and 25%; 68%, 28% for woodland populations for J, SA and A mortality respectively. Decr = decrease 5%; Incr = increase 5%; J = juvenile; SA = sub-adult; A = adult; r = mean stochastic growth rate; PE = mean probability of extinction for extant and extinct populations.

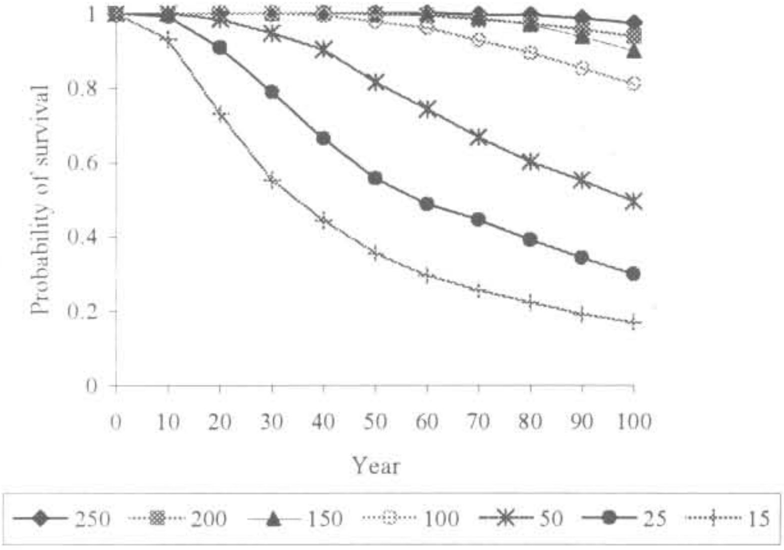

Figure 5.3. The effects of decreasing starting population size (from 250 individuals) on the probability of a grassland savanna cheetah population surviving over 100 years.

woodland savanna population reached 70% and 90% respectively (PE = 7%). There were no changes in mean growth rate for the woodland savanna population and only a slight reduction in mean growth rate (r = -1.1%) for the grassland savanna population when increasing sub-adult and adult mortalities simultaneously.

5.4 DISCUSSION

5.4.1 Population Viability Analysis

The woodland savanna cheetah population appeared to have a greater viability than the grassland savanna population over 100 years, using demographic data gathered from the literature and KNP study. The woodland savanna population had high positive mean growth rates and was viable at small population sizes, while the Serengeti Plains population had a negative mean growth rate and was not viable at population sizes smaller than 200. A population size of less than 100 cheetahs on the Serengeti Plains appears to be the population size whereby stochastic processes begin to have a greater impact on the ability of the population to persist (Miller & Lacy 1999). This appears evident because of the steeper decline in survival probabilities compared to other projections using larger starting population sizes (Fig. 5.3). A population size of 250 cheetahs in the grassland savanna with no change in mortality rates may not persist in the long-term, as a sustained negative growth rate inevitably leads to extinction (Berry et al. 1997). When lowering the sub-adult dispersal rates on the Serengeti Plains to those recorded by Laurenson (1995), which seemed to exclude those cheetahs that dispersed or emigrated (following Kelly & Durant 2000), the grassland population reflected a positive mean growth rate, and was viable at a starting population of 25 cheetahs over a 100 years. Therefore, in this PVA and possibly in Kelly & Durant's (2000) viability study, including emigration without immigration rates into the simulations will result in pessimistic predictions for population persistence. The difference between the two mortality rates may indicate some measure of emigration and dispersal of cheetahs on the Serengeti Plains (20%).

The high growth rates shown by the woodland savanna population (Table 5.2) are reflected by the low juvenile mortality rates coupled with low adult and sub-adult to those estimated by Kelly & Durant (2000) in the Serengeti still showed high positive mean growth rates. In order to generate hypothetical self-replacing cheetah populations, with mean growth rates close to zero and PE < 0.05, sub-adult mortality had to be increased substantially. Sub-adult mortalities were raised to 60% and 68% for populations with 50% and 25% juvenile mortality respectively (Table 5.2). Like the grassland savanna population, the difference between the natural mortality rates estimated by Berry et al. (1997) and those predicted for sub-adult mortality in this PVA may provide an indication of the dispersal rates of sub-adult cheetahs in woodland savannas (45% and 54% when juvenile mortalities are 50% and 25% respectively). Although probably an overestimate, because of certain parameters 'optimistically' used or excluded in the PVA (see Methods), this high sub-adult mortality rate is feasible as high emigration probabilities have been recorded in other large carnivores. Lindzey et al. (1988) recorded a 50% dispersal rate for mountain lions (*Felis concolor*), with more males dispersing than females. Waser (1998) tabulates emigration probabilities for lions (87% males, 38% females); gray wolves *Canis lupus* (29% males, 26% females), spotted hyaenas (43% males, 6% females) and coatis *Nasua narica* (46% males, 23% females). Waser (1998) also found that significantly more males than females emigrate, as is the case in cheetahs (Caro 1994; Kelly et al. 1998), which is significant because the model allowed for far higher mortality rates in males than females without increasing extinction risk. The cheetah, being a polygynous breeder probably allows for this.

The higher dispersal rates predicted for the woodland savanna cheetahs are probably due to a high recruitment of juveniles into the sub-adult cohort due to high cub survival. Greater cub survival in woodland savannas may be due to an increased availability of cover, which offers greater concealment from predators (this is discussed later). The greatest influence on population growth and persistence, detected in this PVA, is that females are able to produce up to three litters per year by rapid resumption of breeding following litter loss (Laurenson et al. 1992; Kelly & Durant 2000). This was evident when substituting the maximum litter size of 18 (three litters per year) to six (one litter per year) for the grassland savanna population, resulting in a 100% probability of extinction (Fig. 5.1). This is considered to be an evolutionary strategy of cheetahs compensating for their high cub mortality (Hamilton 1986; Caro 1994)

Crooks et al. (1998) and Kelly & Durant (2000) modelled demographic data of cheetahs on the Serengeti Plains and found that adult survivorship was the most important factor contributing to population increase, but that extinction risk was highly sensitive to both adult and juvenile survival. Kelly & Durant (2000), however, contended that it is typical for adult survival to exhibit the strongest influence on population growth in large, long-lived mammals, but such a finding says little about a population's risk of extinction. In this PVA, the grassland savanna population was most sensitive to 5% variations in juvenile mortality, while the woodland savanna population was more sensitive to variations in adult mortality, more so when juvenile mortality was low (i.e. 25%). These analyses seemed to show that when juvenile mortality is exceptionally high, adult mortality has a less important influence on viability. Vucetich & Creel's (1999) results of a PVA, using VORTEX, also suggested that population persistence was relatively insensitive to juvenile mortality in wild dogs *Lycaon pictus* unless it is severe (71%) and persistent.

The results of Kelly & Durant's (2000) viability study found a self-replacing cheetah population in the Serengeti with a deterministic growth rate of 0.997. This value, however, is largely affected by demographic or environmental stochasticity and excludes rates of immigration (Kelly & Durant 2000). It appears that a source of immigrating cheetahs, which this PVA also did not include, is the greatest security from extinction for the Serengeti Plains cheetah population. Vucetich & Creel (1999) found that population persistence of wild dogs increased substantially even at low immigration rates. A demographic study by Kelly et al. (1998) found that 60% of male and 50% of female cheetahs on the Serengeti Plains were of unknown origin. Kelly & Durant's (2000) study of the Serengeti cheetahs also indicated that the population had not reached carrying capacity. This implies that the Serengeti Plains may be a sink for cheetahs (Kelly et al. 1998). For many populations, a large fraction of the individuals may regularly occur in 'sink' habitats, where reproduction is insufficient to balance local mortality; however, populations may persist in such habitats being locally maintained by continued immigration from more-productive 'source' areas nearby (Pulliam 1988). With the predicted high rates of sub-adult dispersal, nearby woodland savannas may be this source. The relationships found between lion (Packer 1985; Hanby, Bygott & Packer 1995) and bank vole *Clethrionomys glareolus* (Mazurkiewicz 1994) populations in two contrasting habitats are striking examples of what may also be occurring between the grassland and woodland savanna cheetah populations in the Serengeti National Park.

Across both woodland and grassland savanna habitats, it is apparent that the survival of adult cheetahs, particularly females, needs to be ensured. A number of factors threaten adult survival and ultimately cheetah density; the most important identified as habitat loss and direct persecution by humans (Crooks et al. 1998). In Namibia, adult survival is a major concern to population persistence as cheetahs are considered 'pests' in the farming areas and shot (Marker-Kraus et al. 1996). Habitat suitability, however, may also affect cheetah densities (Chapter 3), as parks, particularly small, isolated parks, may not be able to support adequate densities for viable populations (Purchase 1998). High lion densities in restricted areas may also outcompete cheetahs, as cheetahs seek out spatio-temporal 'competitive refuges' with low predator densities, which enables them to coexist with their superior competitors (Durant 1998; Durant 2000a). Durant (1998) suggested that cheetahs, with high mobility and low competitive ability, may only be able to persist in areas that are large enough to sustain sufficient spatial heterogeneity.

5.4.2 Implications to management and conservation

A grassland savanna population (like the Serengeti Plains) may be threatened with extinction if cub mortality continues to increase or is persistently severe; but probably the greatest threat is a lack of immigrating cheetahs. 'Sink' habitats may support very large populations despite the obvious fact that the 'sink' population would eventually disappear without continued immigration (Pulliam 1988). Therefore, maintaining 'source' or highly cheetah-reproductive habitats would be of prime conservation consideration. Cheetahs are known to flourish outside protected areas, where other large predators have been removed (Laurenson et al. 1992; Laurenson & Caro 1994; Burney 1980 in Laurenson 1995), and therefore the conservation of cheetahs may rely on their protection outside as well as within national parks (Kelly & Durant 2000). Further demographic studies are required of woodland savanna cheetah populations, which may act as important 'source' habitats. Pulliam (1988) warns that species conservation based on 'sink' habitats alone can lead to very misleading conclusions and inappropriate management decisions. Autecological studies of populations in 'sink' habitats may yield little information on the factors regulating population size if population size in the sink is largely determined by the size and proximity of sources (Pulliam 1988).

According to this study and Hunter's (1998) PVA, re-introduced cheetahs into woodland savannas can establish viable populations, even at small population sizes. This is mostly due to rapid recruitment rates from high cub survival. The success of cheetah re-introductions, however, is questionable as high sub-adult recruitment and dispersal rates may lead to conflict with bordering land use areas, or else increased adult mortality rates or stress-related factors from competing for space with conspecifics and other predators. In PRR, MNP and Suikerbosrand Nature Reserve, re-introduced cheetahs were frequently reported snared, shot or in conflict with bordering areas (Cohen et al. 1978; Zank 1995; Hunter 1998; Purchase 1998) because of the natural tendency for cheetahs to disperse (Cohen et al. 1978; Frame & Frame 1980; Caro 1994). Conflict with people on reserve borders is a major cause of mortality in wide-ranging carnivores, so that border areas represent population sinks and may contribute more to their extinction than stochastic processes (Woodroffe & Ginsberg 1998). Although predators lower the reproductive success and density of cheetahs (Laurenson 1995; Durant 2000b; Kelly & Durant 2000), an absence of predators may result in a very opposite outcome. In Suikerbosrand Nature Reserve, where cheetahs were the top predator, an 85% cub survival rate led to a rapid increase in cheetahs and a decimation of abundant prey populations, which resulted in the cheetahs' eventual removal (Cohen et al. 1978, Pettifer et al. 1981). Similarly, the average litter size in Namibia of 10 month old cubs was four on ranchlands, where lion and hyenas have been eliminated (McVittie 1979). This gives an indication of the recruitment potential into the sub-adult cohort in the absence of predators. In order to counter balance high recruitment rates, sub-adults need to be "removed" from the population, either through dispersal, and if the system is a closed one then management intervention may be required. Dispersal opportunities may be provided by removing fences, enlarging reserves or creating corridors for movement. These are some of the considerations needed for re-introductions into small, isolated woodland savanna habitats. Re-introductions into small, isolated grassland savanna habitats with high predator densities and few refuges for escape and concealment may not produce viable cheetah populations, unless supplementation occurs. Zank (1995) ran a PVA using life history data from the Serengeti Plains, with 95% cub mortality, to establish the viability of re-introduced cheetahs in MNP and found that a founder population of 20 cheetahs required a supplementation of at least three cheetahs every three years to prevent probable extinction.

5.4.3 Juvenile survival and benefits of cover

Although records and observations of cub survival in woodland savannas are limited and poorly researched, these reports, including the few observations in the KNP indicate that cub survival is higher than on the Serengeti Plains. This may be due to the benefits of increased cover availability for concealment from predators. An increase in cub mortality, however, seems predominantly associated with an increase in predator density (Table 5.3). Lion density has a negative impact on cheetah density (Laurenson 1995) and reproductive success (Kelly et al. 1998; Durant 2000b; Kelly & Durant 2000). There is, however, no estimate of cub mortality for the Serengeti Plains during the early period (1967 – 1979), when lion density was lower than the later period (Table 5.3). Using the same proportionate decline in average lifetime reproductive success from early to late periods (Kelly et al. 1998), cub mortality may be estimated at approximately 70% for the early period. The Serengeti Plains, however, during the early period (1967 – 1979) had a similar lion density to the KNP but KNP cub mortality is only 45%. Similarly, one would expect juvenile mortality rates in KNP and Serengeti Plains during the later period (1985 – 1991) to be more similar, considering that differences in lion densities between these two areas were not that large. The differences in cub mortality may be associated with the greater availability of cover and refuges for concealment in woodland savannas. Furthermore, in MNP, Purchase (1998) estimated a 60% juvenile mortality between 0 – 2 years old (i.e. including the age of maturity and dispersal), which seems comparatively low judging from the exceptionally high lion density found there.

Table 5.3. Lion and spotted hyaena density and cheetah juvenile mortality across five protected areas of southern and East Africa.

Protected area	**Lion density*** **(animals per km^2)**	**Hyaena density*** **(animals/km^2)**	**Juvenile mortality** **0 – 12 months (%)**
Suikerbosrand Nature Reserve (SNR)	none	none	15
Phinda Resource Reserve (PRR)	0.08	0.05	25
Kruger National Park (KNP)	0.07 – 0.1	0.135	45
Matusadona National Park (MNP)	0.317	0.13	60 (up to 2 years)
Serengeti Plains (1967 - 1979)	0.079 - 0.094	0.12-0.17	No estimate**
Serengeti Plains (1985 – 1991)	0.14	0.82	95

*Densities collated from Stander (1991) and Creel & Creel (1996).

**Average lifetime reproductive success was higher during this period than 1980 – 1994 (Kelly et al. 1998).

These figures, however, must be interpreted with caution, as cub mortality estimates in the woodland savannas may be underestimates due to mortality rates not being recorded immediately following birth.

Cheetahs may benefit from a greater availability of cover when cubs are immobile and in the lair (< 2 months). Cubs in the lair are typically hidden in long grass, rocky outcrops or dense vegetation (Labuschagne 1979, Laurenson et al. 1992). Lions located female cheetahs with cubs in the lair by seeing them sit up in the lair, or by noticing the mothers resting nearby (Laurenson et al. 1992; Laurenson 1994). Laurenson (1994) found that lying low in the lair was a good anti-predator strategy. Cubs are most vulnerable just after emergence until four months as they are not yet fast enough to escape from predators (Laurenson 1994). On the short-grass plains, where cheetahs can be spotted from as far away as 2.5 km (Caro 1994), cubs are particularly vulnerable. Hanby & Bygott (1979) considered the reduction in dry-season fires over a ten-year period may have benefited cheetahs by providing more cover for safe concealment of cubs. Therefore, in woodland savannas, a greater availability of cover may substantially reduce cheetah mortality (most obviously before four months of age) when compared to an open grassland system like the Serengeti Plains. Woodlands may provide far greater concealment of the lair and the mother and a greater opportunity for escape. In PRR and MNP, cheetah cubs were observed escaping from predators into dense bush (Hunter 1998; Purchase 1998). The effects that other environmental factors may contribute to differences in cub mortalities are indeterminate, although they may not play a large role. Laurenson (1994) found that about 21% of juvenile mortality on the Serengeti Plains is due to environmental causes, such as abandonment, fire and exposure, while Pettifer (1981) recorded a 15% juvenile mortality in Suikerbosrand Nature Reserve (in the absence of other large predators). Finally, it must be noted that although cub survival may seem higher in the KNP than on the Serengeti Plains, further evidence is required before any such conclusions can be drawn.

5.4.4 Reflections on the model

Beissinger & Westphal (1998) believe predictions from quantitative models of endangered species are unreliable because of poor quality data. As with any other study, this PVA is open to the criticism that population persistence predictions are no more reliable than the data on which the predictions are based (Reed, Murphy & Brussard 1998; Miller & Lacy 1999). The aim of this PVA, however, was not to make any absolute predictions about either of the two cheetah populations, but was more interested in comparing cheetah population dynamics in contrasting habitats using different demographic and life history parameters. Unfortunately, environmental variation in mortality rates could not be included in the models for reasons explained above (see Methods). Extinction risk tends to increase with increasing environmental variation in survival rates (Mills et al. 1995; Kelly & Durant 2000). Therefore, excluding this variation probably produced overly optimistic estimates of persistence for both cheetah populations. Although most extinctions are a function of steady population decline due to deterministic causes rather than chance events (Caughley 1994), the random fluctuations that increase as populations become smaller can cause the final extinction (Beissinger & Westphal 1998). A positive population growth rate, without modelling environmental variation or catastrophes, can lead to a false sense of security (Bessinger & Westphal 1998). In a predictive capacity, including environmental variation would have either raised the extinction risk or resulted in lowered adult and sub-adult mortality rates to attain hypothetical self-replacing populations. Lowering sub-adult mortality rates was possible for the grassland savanna population as these mortality rates included those cheetahs that disappeared out of the study area, and had not necessarily died (Kelly & Durant 2000).

5.5 CONCLUSIONS

Overall, this PVA indicates that the persistence of cheetah populations depend on the ability of female cheetahs to conceive again rapidly after litter loss; adult survival, except when cub mortality is very high and persistent; and immigration into populations experiencing low cub survival rates. Similar conclusions were found from a PVA conducted on wild dogs, which is also a low density, wide-ranging carnivore that is highly sensitive to competition with lions (Vucetich & Creel 1999). The importance of the continued persistence of 'source' populations in the Serengeti National Park, either outside the park or from the woodland population within the park, may be paramount to the continued persistence of the Plains population. When compared to the Serengeti Plains cheetah population, very little is known about the population dynamics of cheetahs in woodland savannas. Demographic data on cub survival, sub-adult recruitment and dispersal, and adult survival in woodland savannas are required, as woodland savanna populations may be critical 'source' populations for other depleted areas. This information would also be more far more representative of cheetah populations inhabiting southern Africa, and may provide a better indication of the cheetah's ability to persist across a fragmented and diminishing range.

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Chapter 6: Synthesis

The literature is dominated by cheetah studies conducted on the Serengeti Plains in East Africa. As a result, current understanding of cheetah behaviour and ecology is based largely upon this grassland ecosystem. Therefore, the aim of this study was to extend the range of documented information on cheetah *Acinonyx jubatus* ecology across the grassland-woodland continuum in African savannas, by (1) analysing a data-set on cheetah home range size, habitat utilisation, prey selection and hunting behaviour in the Kruger National Park (KNP), and (2) synthesising data from this study and from the literature for a comparative study on the above aspects of cheetah ecology across a range of African savanna ecosystems. The data are presented in three central chapters of this thesis, which are (1) cheetah home range size and habitat use (Chapter 3); (2) cheetah predation in relation to prey composition, cover availability and kleptoparasitism (Chapter 4), and (3) population viability analysis (Chapter 5).

Home range sizes in the KNP averaged 217 km^2 for territorial male cheetahs, 186 km^2 for female cheetahs and 438 km^2 for a nomadic male cheetah coalition (Chapter 3). Cheetahs preferred open savanna habitat rather than other available habitats with denser woodland. Habitat use by female cheetahs, however, appeared to be influenced by the distribution of impala *Aepyceros melampus* as females used areas with thicker bush more frequently than males, which was also preferred impala habitat. Therefore, females may be maximising encounter rates with their main prey by using denser woodland habitat. Female cheetahs may also use areas with dense bush to conceal their cubs from their main competitors, lion *Panthera leo* and spotted hyaena *Crocuta crocuta*, which are abundant in the main study area (Mills & Biggs 1993). The male cheetah coalition used more open areas compared to females and concentrated their activities along roads, where they preferred to scent mark. Although no data could support this supposition, this may be where encounter rates with other cheetahs are more likely. Therefore, differences in habitat use by male and female cheetahs may reflect their different requirements.

Across African savanna ecosystems, female cheetahs with a migratory prey base had significantly larger home range sizes than female cheetahs with a sedentary prey base. Female cheetahs on the Serengeti Plains follow their migrating prey and as a result have huge home ranges averaging 833 km^2, compared to all other areas with mostly sedentary prey with a mean home range size of 105 km^2. Female home range size is also determined by prey density as a predictive relationship was found between medium-sized prey biomass and female cheetah home range size. The distribution of prey and suitable habitat may also influence female home range size. It was predicted that male cheetah territory size would be determined by female cheetah density, however, no relationship was found in this study. Female cheetah density, however, may not directly reflect the availability of females for mating opportunities. The size of the females' home ranges seem to determine the extent of overlap between female home ranges, and the possible number of ranges that may overlap. On the Serengeti Plains, where home ranges are huge with up to 20 female ranges overlapping extensively, male territories are small and located in hotspots where they have access to the greatest number of females (Caro 1994). In the KNP, where female home ranges are smaller with only 2 - 3 females overlapping, male territories are much larger covering a large proportion of the females' home ranges. This is supported by the significant difference found between male territory size in areas with migratory and sedentary prey (37 km^2 and 108 km^2 respectively). These conclusions are further supported by the positive correlation found between male and female home range size in areas with sedentary prey, where the Kgalagadi Transfrontier Park (KTP) was an outlier in the relationship. In the KTP, with a low density and nomadic prey base, female home ranges (320 km^2) are larger than males (125 km^2). In all other areas, male and female home range sizes are similar.

When comparing habitat use and preferences across a range of grassland and woodland savannas in southern and East Africa, cheetahs showed distinct preferences for habitats that offered both open spaces and woody cover. Cheetahs preferred open areas in woodland savannas and in grassland savannas preferred areas with some woody cover. Dense habitat types and areas devoid of trees and bushes were mostly avoided.

The analyses in Chapter 4 showed that impala are the cheetahs' main prey in the KNP, and male impala are preyed on more frequently than females. Male and female cheetahs showed differences in use of prey as males took larger prey species, such as zebra *Equus burchelli*, kudu *Tragelaphus strepsiceros*, and waterbuck *Kobus ellipsiprymnus*, while females took a larger proportion of steenbok *Raphicerus* *campestris* and grey duiker *Sylvicapra grimmi*. The cheetahs showed a definite preference for open savanna habitat for hunting, even though impala densities were higher in adjacent woodland habitats. Cheetahs in the KNP had longer chase distances for successful hunts (189 m) compared to unsuccessful hunts (96 m), probably because cheetahs abandon the chase early in the latter due to a predicted failure. They also had a greater hunting success in open savanna habitat although this was non-significant. Female cheetahs attempted significantly more hunts than a male cheetah coalition. This may be because females seem to have a lower hunting success than a three-male cheetah coalition, but may also be due to them having greater nutritional demands associated with reproduction. The male coalition appeared to experience less kleptoparasitism than females, suggesting that three male cheetahs may have a better chance at defending their kill than a single female.

When comparing cheetah predation across a variety of African savanna ecosystems, medium-sized prey (18 – 65 kg) occurred most frequently in the cheetahs' diet (60%). There was, however, a significant variation in the size and age groups of prey taken by cheetahs across ecosystems. In certain areas, cheetahs took a larger proportion of large-sized prey when more abundant or susceptible to predation. Cheetahs in Namibia seem to have specialised in hunting larger prey items than typically found in the diet (McVittie 1979). Although small prey (< 18 kg) appear to form an important part of the cheetah's diet, the extent of this could not be established due to the variations in data collection methods used by researchers.

When comparing various aspects of cheetah hunting behaviour across ecosystems, in order to attempt to establish the influence of cover availability on these, the following was found: mean chase distance was longer, and hunting success and incidents of kleptoparasitism was greater in habitats with less woody cover. Small sample sizes, however, prevented statistical analyses and further studies are required to establish more conclusive trends. Although kill retention time and mean kill rate were compared across ecosystems, no clear relationships or patterns were found with cover availability because of other influencing factors. A comparison of consumption rates with other studies seemed to indicate that the male cheetah coalition in the KNP was obtaining an adequate diet (approximately 1.4 kg meat/cheetah/day).

The final chapter found that the population viability of cheetahs in a woodland savanna (hypothetically modelled as the KNP) was greater than in a grassland savanna (Serengeti Plains). This was particularly evident with starting population sizes below 200, as extinction probabilities were high for the grassland savanna population while the woodland savanna population was still viable at small starting population sizes of 20 animals. Viability of the grassland savanna population was most affected by persistent and severe cub mortality (90 - 95%), while viability in the woodland savanna was most affected by adult mortality, followed by sub-adult mortality. The ability of cheetahs to reproduce rapidly after litter loss enables populations to persist when cub mortality is high. Immigration appears to play an important role in population persistence. The Serengeti Plains population, with its high cub mortality, may be a sink for cheetahs and may be strongly dependent on 'source' habitats nearby. Woodland savanna habitats may be these sources, because they appear to have higher cub survival rates (25 – 50%) and high sub-adult dispersal or emigration rates (45 – 54%). Areas with an absence of large predators are also important source habitats. The availability of cover in woodland savannas may play a role in reducing cub mortality by offering protection and concealment to mothers, cubs and lair sites. Re-introduction of cheetahs into small parks may not be successful for grassland savanna ecosystems when predator densities are high and there is a shortage of refuge sites, while conflict with bordering land use areas and dispersing sub-adults may be the greatest concern for re-introductions into woodland savanna ecosystems. Alternatively, a lack of competing predators may result in rapid recruitment rates and large impacts on prey populations.

In conclusion, this study demonstrated how cheetah ecology varies across African savanna ecosystems as a function of prey density and dispersion patterns and cover availability. Cheetah ecology on the Serengeti Plains cannot be considered representative of what occurs in most parts of the cheetah's range, as prey dispersion patterns here have a significant influence on the ranging patterns of cheetahs compared to all other areas. On the Serengeti Plains, although providing a high density of prey and extensive open habitat for hunting, cheetahs appear limited by high densities of lion and spotted hyaena and a paucity of available safe lair sites. In contrast, in woodland savannas, although offering plenty of safe refuge sites for cubs, cheetahs may be limited by a lack of available open habitat for hunting. Purchase & Du Toit (2000) have described the Matusadona National Park as optimal cheetah habitat with cover available for shelter, protection and stalking and open areas with high densities of medium-sized prey for hunting. A heterogeneous mix of grassland and woodland savanna or open woodland savanna habitat is preferred. More specifically, Gros & Rejmánek's (1999) study in Uganda suggested that 25 – 50% woody cover and grasses of medium height (50 – 100 cm) is preferred cheetah habitat. In a shifting dynamic across the grassland-woodland gradient in African savannas, cheetahs require habitats that provide (1) abundant, medium-sized prey, (2) open areas for high-speed chases, and (3) cover for stalking and concealment from predators. Any benefits of cover must be counter balanced by the impediment of thicker bush or grass cover to the cheetah's hunting strategy, while benefits of open areas must be counter balanced by the loss of cover for stalking, shelter and concealment. Bush encroachment in woodland savanna habitats, such as the KNP, may have a significant impact on the density and distribution of cheetahs in these areas, and this requires attention, especially when considering that woodland savannas may fulfil the important role of 'source' areas for 'sink' habitats or other depleted areas. The benefits of cover in terms of protection from and avoidance of competing predators also require further investigation. Future studies should give woodland habitats much more recognition than has been done up to now as important cheetah habitat. This will provide a far more accurate and balanced perspective on the cheetah's ecology and requirements and its ability to persist across a fragmented and threatened range.

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