

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, Weillknowlski & 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		

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 *Aepyceros 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 versus (1) medium-sized prey biomass (15 – 60 kg); male cheetah territory size versus (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 km², where cheetah home ranges were located. In the KNP, density figures were calculated for the main study area (approximately 350 km²), 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 km² (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	<i>Acacia erioloba</i> and <i>Acacia haematoxylon</i> 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 <i>Acacia</i> savanna areas, wooded valleys and dense thickets in some ravines.	3, 4
Nairobi National Park (NNP), Kenya	115	Rolling <i>Themeda triandra</i> grassland- <i>Acacia</i> savanna, open grassland plains, and some heavy bush. (open grassland and <i>Acacia</i> -grassland savanna were of equal area in the study unit).	5, 6
Pilanesberg National Park (PNP), South Africa	550	Sour bushveld - open savanna of <i>Faurea saligna</i> 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 <i>Sclerocarya birrea</i> / <i>Acacia nigrescens</i> tree savanna bordered to east by <i>Combretum</i> tree savanna in Lebombo Hills and to west by <i>Acacia welwitschii</i> 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 (km²) 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

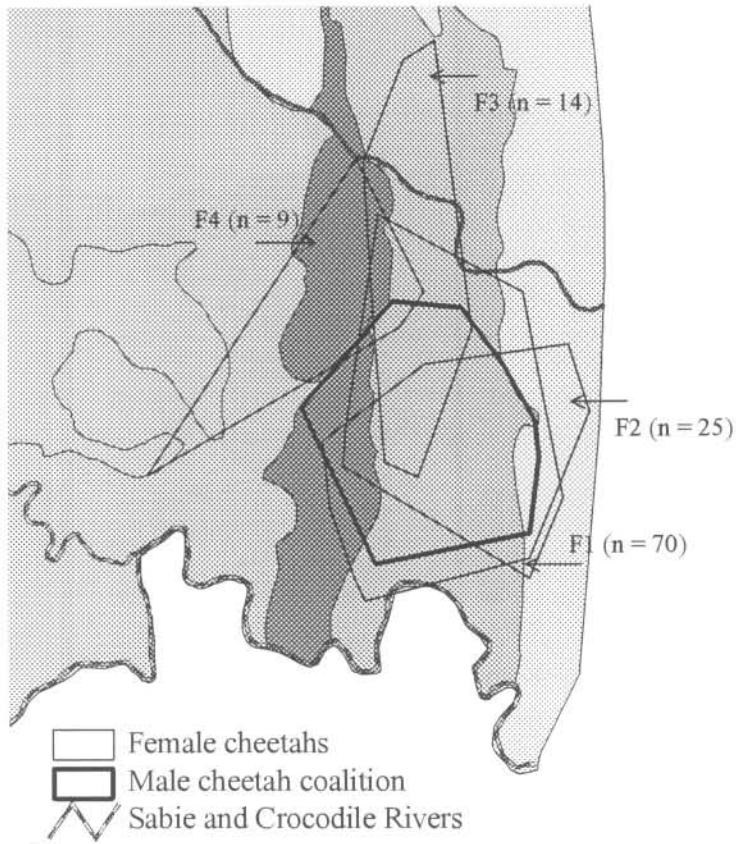


Figure 3.1. Home range of female cheetahs (F1, F2, F3, and F4 with number of location points indicated for each, as n) and a three-male cheetah coalition M3 (n = 175) in the south eastern region of Kruger National Park, estimated by the 100% minimum convex polygon (MCP) method. A = *Acacia* thickets;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

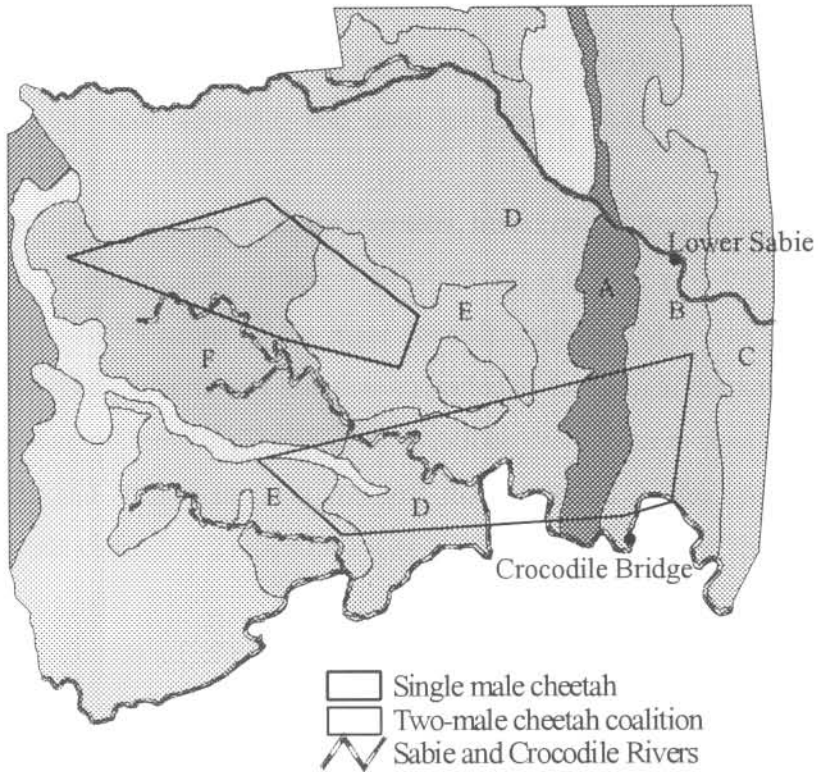


Figure 3.2. Home range of a single male cheetah M1 (n = 27 location points) and two-male cheetah coalition M3 (n = 21) in the southern district of the Kruger National Park, estimated by the 100% minimum convex polygon (MCP) method. A = *Acacia* thickets; B = open savanna; C = Lebombo Hills; D = Riverine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

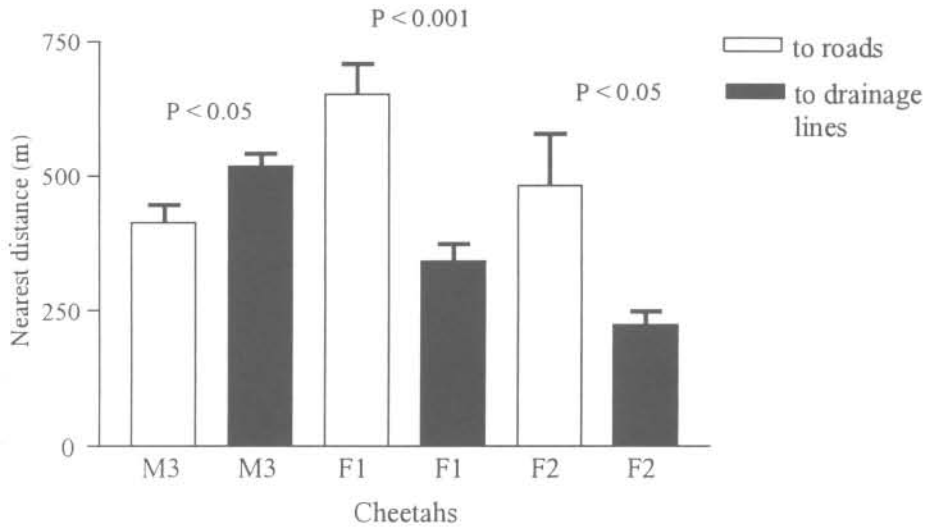


Figure 3.4. Mean nearest distance (\pm SE) of male and female cheetah locations to drainage lines and roads in the south eastern region of the Kruger National Park. M3 = three-male cheetah coalition; F1 and F2 = female cheetahs.

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

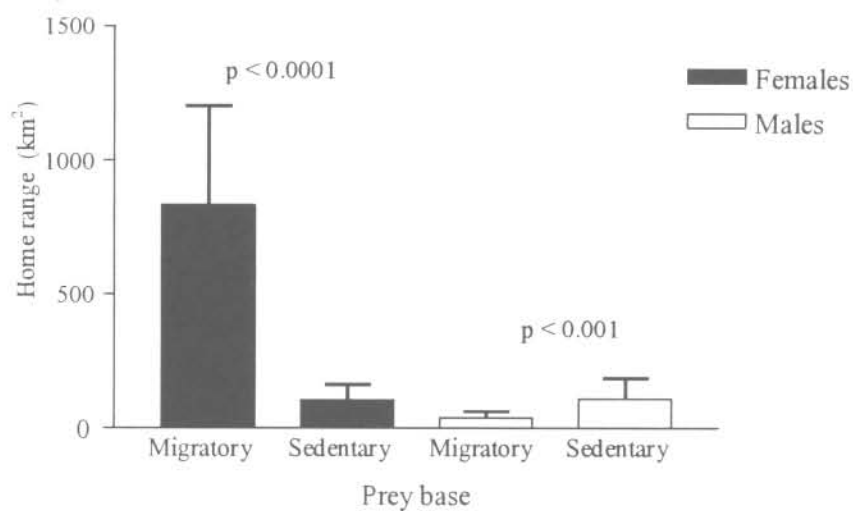


Figure 3.5. Mean home range size (\pm SE) of female and male cheetahs in areas with migratory and sedentary prey.

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 km² for a three-male cheetah coalition, 261 km² for a solitary male cheetah, 438 km² for a sub-adult, two-male cheetah coalition, and 193 km² and 179 km² for female cheetahs F1

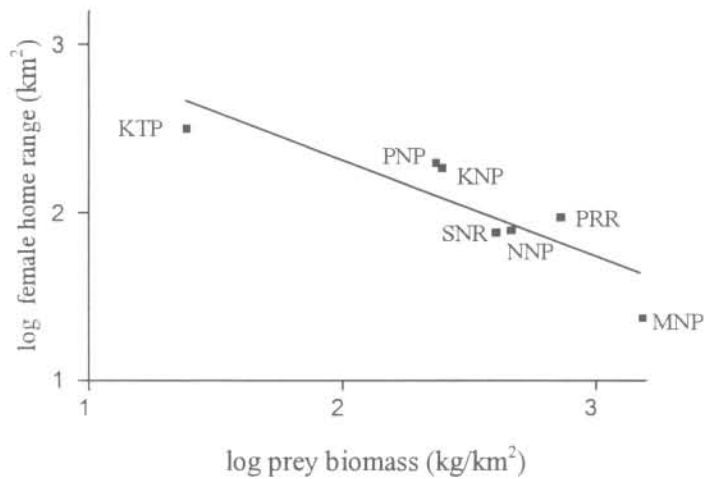


Figure 3.6. Linear regression showing relationship between medium-sized prey biomass and female home range size, across seven protected areas of southern and East Africa ($r^2 = 0.759$; $F_{1,5} = 15.8$; $p < 0.05$). KTP Kgalagadi Transfrontier Park; KNP Kruger National Park; MNP Matusadona National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

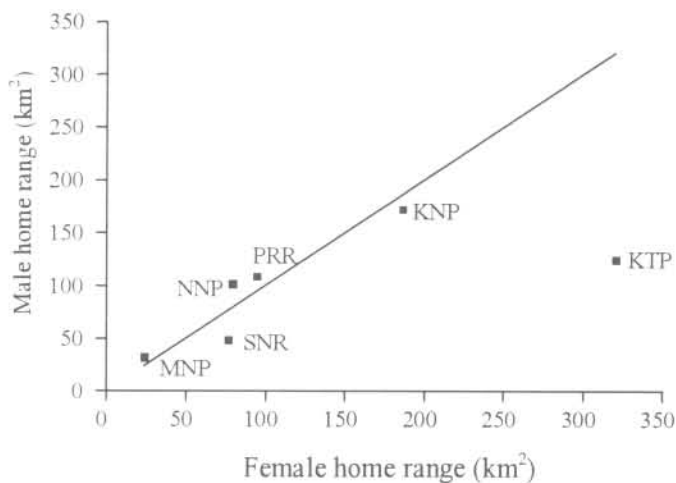


Figure 3.7. The relationship between female and male home range size, across six protected areas of southern and East Africa ($r_s = 0.943$; $p < 0.02$; $n = 6$). A forced line of perfect fit appears on the graph for comparison across areas. KTP Kgalagadi Transfrontier Park; KNP Kruger National Park; 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 <i>Acacia</i> savanna areas, preferred wooded slopes and ravines as opposed to the plains.	2, 3
NNP	Preferred <i>Acacia</i> -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 km² and 1848 km². 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 km² as they follow their migrating prey. The mean home range size of female cheetahs in areas with sedentary prey was 105 km². 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 km² compared to male cheetahs with a sedentary prey base, with a mean territory size of 108 km². 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 km², while the KTP with very low prey densities had larger home ranges of 320 km². 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 km² (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 (km²) 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.