

Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park

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Abstract

Cheetah *Acinonyx jubatus* home-range size and habitat use were analysed using radio-tracking data collected in the southern district of the Kruger National Park (KNP) between 1987 and 1990. Meaningful estimates of home-range size, using the 95% minimum convex polygon method, were 126 km² for a three-male cheetah coalition, 195 km² for a solitary male, and 150 km² and 171 km² for two female cheetahs. Although cheetahs used all habitats according to their availability, they did show a preference for open savanna habitat because their core or total home ranges centred on these habitats. Female cheetahs used denser woodland habitat more frequently than males, as they seemed to be influenced by the distribution of their main prey, impala *Aepyceros melampus*, which also preferred denser woodland habitat.

Key words: *Acinonyx jubatus*, cheetah, habitat, home range, impala, Kruger National Park

INTRODUCTION

Cheetahs *Acinonyx jubatus* are known as predators with a preference for open plains habitats (Dorst & Dandelot, 1970). This is not only because they are built for speed (Nowell & Jackson, 1996; Mills & Hes, 1997) but also 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,b; Laurenson, Weillnowski & Caro, 1995; Durant, 1998, 2000a,b; Kelly *et al.*, 1998). 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 areas. This is largely because of the logistical constraints associated with tracking and observing cheetahs in wooded habitats.

Recent studies in woodland savannas have increased our understanding of cheetah ecology in these areas (Zank, 1995; Hunter, 1998; Purchase & du Toit, 2000). To further extend the documented information on cheetah ecology

in woodland savannas we present a study conducted on the home-range size and habitat use of cheetahs in the Kruger National Park (KNP), South Africa. Cheetahs have never been studied in the KNP before and being an important conservation area for cheetahs, it will provide information useful to park management. This will also assist with cheetah conservation across a broader habitat scale as woodland savannas make up a large part of the cheetah's range (Skinner & Smithers, 1990).

In this study, the habitat requirements of the cheetahs in a woodland savanna are considered. In the Serengeti, adequate concentrations of Thomson's gazelle *Gazella thomsoni* and sufficient cover were the main determinants of male cheetah territory location as these features attracted females (Caro, 1994). Cover is required for stalking (Cohen, Scholtz & Reichel, 1978; Fitzgibbon, 1990; Caro, 1994), concealment from other predators and resting (Caro, 1994; Zank, 1995; Purchase, 1998), and would therefore be an important requirement for cheetahs in this open grassland habitat. In contrast, in woodland habitats, where there is considerable cover available, we hypothesize that cheetahs would seek out open areas to meet their hunting requirements. This is because they require open spaces for high-speed chases as bushes and trees may obstruct their hunting strategy (Myers, 1975; Bertram, 1979; Broomhall, 2001). Therefore, assuming that cheetahs need more open areas to hunt successfully, we predict that in woodland savannas they will prefer open habitats.

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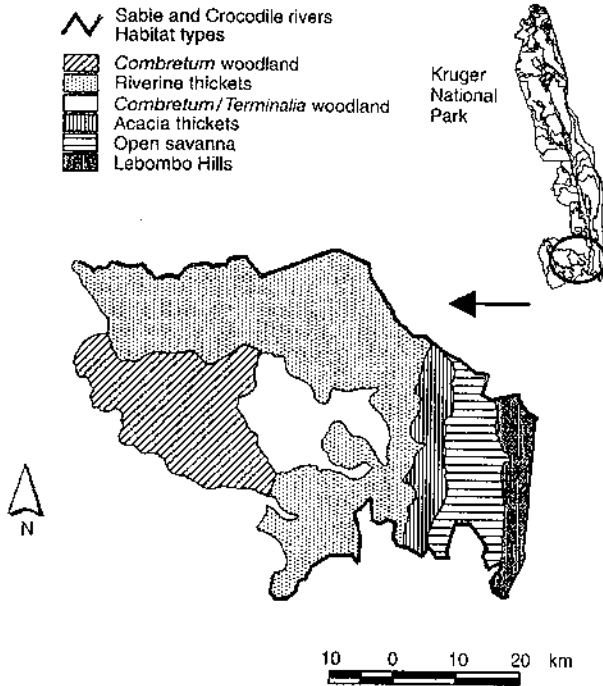


Fig. 1. Location of study areas in the Kruger National Park showing six different habitat types.

METHODS

Study area

The field study was conducted in the southern district of the KNP ($24^{\circ}96' - 25^{\circ}44'E$, $31^{\circ}30' - 32^{\circ}00'S$) between the Sabie and Crocodile rivers (Fig. 1). The southern district covers an area of c. 3786 km² (Bowland, 1994). Two focal study areas were located in this district: (1) the main focal study area in the south-eastern region (6 radio-collared cheetahs were tracked in this area); (2) a secondary focal study area to the west of the main study site in a more central region of the southern district (1 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).

The main study area comprises 3 broad habitat types, identified using the landscape system developed by Gertenbach (1983) (Fig. 1). The main landscape is classified as *Sclerocarya birrea*/*Acacia nigrescens* tree savanna (an area covering c. 250 km²) 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 lines (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.

The Lebombo Hills border the open savanna to the east, covering an area of c. 148 km². This is an undulating, broken landscape with north-south rhyolite ridges and

bottomlands, 100 m 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).

The landscape bordering the open savanna to the west is the *Acacia welwitschii* thickets on Karoo sediments (170 km²) 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 in the dry season (Gertenbach, 1983).

The banks of Sabie and Crocodile rivers, which cut through all 3 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 3 broad habitat types (Fig. 1). The thickets of the Sabie and Crocodile rivers (1148 km²) are low-lying, relatively flat areas, characterized by dense woody vegetation, with *A. nigrescens*/*C. apiculatum* dominating (Gertenbach, 1983). The *Combretum collinum*/*C. zeyheri* woodland (454 km²) and mixed *Combretum* spp./*Terminalia sericea* woodland (257 km²) 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).

Data collection

Seven adult cheetahs were radio-tracked for 3 years between 1987 and 1990 (data collection by MGLM) in the southern district of the KNP (see Table 1). All cheetahs, except M3, were darted from a vehicle by slowly approaching close enough to a distance of c. 15–20 m. M3 was trapped in a 2-door cage trap set at a latrine with the access closed off by a thorn bush barrier around the tree so that the only way the cheetah could get there was through the trap. A rag dipped in urine from an oestrus female in captivity was hung in the trap (Mills, 1996). Cheetahs were immobilized with 150–200 mg CI-744 Park Davis (a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride), or a combination of 75 mg CI-744 and 15 mg xylazine and fitted with Telonics MOD-315 collars weighing 100 g, except for M3 who was fitted with a MOD-400 collar weighing 170 g. The duration of the tracking period for each cheetah varied depending on circumstances. M1 was only tracked until his collar stopped transmitting. M2 was found dead after both he and his companion had contracted sarcoptic mange, and the collar from M3 was removed. F1's collar was removed, F2 could not be relocated after her radio stopped transmitting after just over 1 year, F3 disappeared and is believed to have died, as did F4, who might have emigrated as she was a young adult when caught.

Table 1. Home-range estimates (km²) of radio-tracked cheetahs *Acinonyx jubatus* in the southern district of the Kruger National Park using the minimum convex polygon method (MCP). 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 ^a	Estimates of home-range size		
				MCP 100%	MCP 95%	MCP 50%
M3	25 Feb 87–15 Apr 90	177	Yes	170	126	14.1
M2	11 Jul 88–14 May 89	21	No	438	242	^b
M1	14 Oct 88–02 May 90	27	Yes	261	195	21.5
F1	29 Nov 88–17 Apr 90	70	Yes	192	150	36
F2	16 Sep 87–07 Oct 88	25	Yes	179	171	35.7
F3	18 Aug 87–23 Oct 87	14	No	118	118	^b
F4	29 Aug 89–28 Apr 90	9	No	102	102	^b

^a 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).

^b Sample sizes too small to estimate 50% MCP.

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 h; (3) long-term continuous observations, when cheetahs were followed continuously for 14 days. All 3 data collection types were recorded for a 3-male cheetah coalition (M3) and a female cheetah (F1). Two 14-day observation periods were recorded for M3 and 1 14-day period was recorded for F1. Radio-locations only were recorded for a 2-male cheetah coalition (M2); a solitary, territorial male cheetah (M1); and 3 female cheetahs F2, F3 and F4. M2 and F4 were dispersing, sub-adult cheetahs.

All cheetahs used all or part of the main study area, except cheetah M1, who 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, only 1 other cheetah, an adult male, observed once, was seen in the main study area. In 1987, M3, F2 and F3 the main study area, and in 1988 and 1989 it was inhabited by M3, F1, F2 and F4.

Home range

The home-range sizes of 7 radio-collared cheetahs were determined using an ArcView extension package Animal Movement (Hooge, 1999). Location points from radio-tracking and direct observations recorded between 1987 and 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 Universal Transverse Mercator (UTM) co-ordinate system. Only location points taken *c.* 24 h apart were used to ensure independence of locations (Swihart & Slade, 1985). The number of fixes needed to calculate home-range size were analysed using the computer package RangesV (Kenward & Hodder, 1996) by plotting number of fixes

against home-range size until home-range size reached an asymptote (Harris *et al.*, 1990).

Two non-parametric methods were chosen to estimate home-range size. The minimum convex polygon (MCP) method (Jenrich & Turner, 1969) is the most widely used method in the literature (Harris *et al.*, 1990) and is presented for comparison with other 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. To address these problems, the peeled minimum convex polygon method was used to remove 'outliers' or fixes showing 'excursive activity' (Mizutani & Jewell, 1998), because Burt (1943) considered excursions outside the normal area not part of an individual's 'normal' home range. Animal Movement's harmonic mean method for outlier removal was used to plot the 50% and 95% MCPs (Hooge, 1999). The 50% and 95% home ranges were selected as they are generally considered the most robust estimators of an animal's centre of activity (core home range) and a close approximation of total range size, respectively (Jaremovic & Croft, 1987; Harris *et al.*, 1990; White & Garrott, 1990; Mizutani & Jewell, 1998).

Habitat use

A chi-square goodness of fit test (Zar, 1999) 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 4 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) are referred to in this paper as habitat types. The 95% MCP was used to delineate home ranges for calculating habitat availability (km²) for individual cheetahs, as this method was considered to provide the best estimates of home range for these cheetahs. Habitat analyses were not conducted

on female cheetahs F3 and F4 owing to small sample sizes and dispersing male cheetahs (M2).

Impala were the cheetahs' main prey in the study area, and their habitat use 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 3-male coalition (M3) and female cheetahs (F1 and F2) were investigated using chi-square test on contingency tables (Zar, 1999). Further differences were investigated within habitat types, as the sides of the drainage lines intersecting these habitats had thicker shrub and tree cover: 2-sample *t*-tests were used to test for differences in mean distance from all male and female cheetah locations to the nearest drainage line and road.

Impala herd locations, obtained from aerial census data collected during dry and wet months between 1986 and 1990 within the main study area, were digitized into ArcView. Using ArcView and a grid overlaying the study site (grid scale *c.* 4 km² per cell), the frequencies of cheetah and impala herd locations within cheetah home ranges (using the 100% MCP as this included all cheetah fixes) were counted per grid cell. Frequencies of impala herd sightings per grid cell were averaged for wet and dry months. Spearman rank correlation (Zar, 1999) 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, (3) tall > 60 cm; shrub cover was classified as: (1) open, (2) moderate, (3) dense (Funston, Mills & Biggs, 2001). Nine different cover classes were created by all possible combinations of grass height and shrub cover, e.g. 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 4 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; (4) tall grass with any shrub cover.

The amount of time a cheetah 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 owing to small sample sizes).

The frequencies of scent markings by the 3-male coalition (M3) along the roads and off the roads 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 roads to the expected frequency based on the total area of all roads (averaging 6 m wide) vs 'off the roads' area available within the home range of the cheetah coalition.

RESULTS

Home range

An asymptotic home range was not reached for female cheetahs with < 25 fixes (Table 1). These were also considerably smaller than the other female cheetah home ranges and were therefore not considered accurate estimates (Table 1). 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 1). Additionally, these animals were young and had not acquired a territory.

Cheetah home ranges using the 100% MCP method are presented in Figs 2 & 3 as this method could be used to represent all cheetah home ranges regardless of sample size or male social status. With the exception of the dispersing sub-adults F4 and M2, the home ranges of cheetahs centred on the open *S. birrea*/*A. nigrescens* tree savanna in the main study area (Fig. 2), which also made up a large percentage of their home ranges (Table 2). The territorial three-male coalition (M3) had smaller total and core home-range sizes than adult female cheetahs with adequate sample sizes (Table 1). There was a large amount of overlap between adult cheetah home ranges in the main study area (Fig. 2), although there was no overlap in core home ranges between M3 and F1 and some overlap with F2 (Fig. 4). The core home ranges of all the cheetahs were located in the open savanna, although the core ranges of both female cheetahs bordered onto and extended into the Lebombo Hills (Fig. 4). The single male cheetah (M1) radio-tracked in the central region of the southern district (Fig. 3) had a far larger home range than the three-male cheetah coalition in the open savanna (Table 1). Most of the home range of M1 was positioned in the *Combretum* and *Combretum/Terminalia* woodlands (Fig. 3). 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, Table 1).

Habitat use

Chi-square analyses showed that the observed habitat use by female cheetah F2, the single male cheetah M1 and

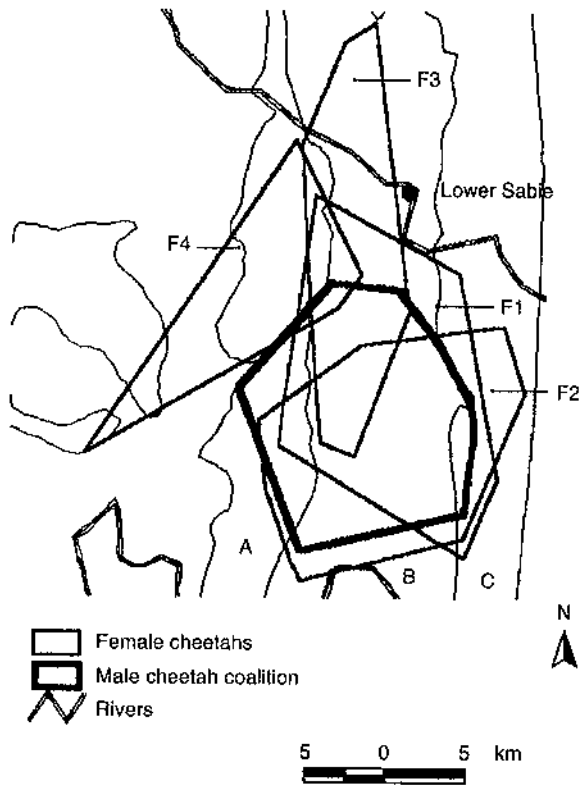


Fig. 2. Home range of female cheetahs *Acinonyx jubatus* (F1, F2, F3 and F4) and a three-male cheetah coalition M3 in the south-eastern region of Kruger National Park, estimated by the 100% minimum convex polygon (MCP) method. A, *Acacia* thickets; B, open savanna; C, Lebombo Hills.

Table 2. Percentage of habitat within the home range of a cheetah *Acinonyx jubatus* in the south-eastern region of the Kruger National Park using the 95% minimum convex polygon (MCP) method

Habitat	% in cheetah's home range			
	M3	F1	F2	F3
<i>Acacia</i> thickets	10	15	8	10
Open savanna	86	69	63	90
Lebombo Hills	4	16	29	—

male cheetah coalition M3 did not differ significantly from that expected based on habitat availability within their home ranges (95% MCP). The female cheetah F1, however, showed a significant difference between the observed and expected habitat use ($\chi^2 = 9.6$, d.f. = 2, $P < 0.05$) (Table 3). The *Acacia* thickets were used more than expected and the open savanna and Lebombo Hills less than expected. Bonferroni confidence intervals, however, indicated that F1 showed no significant differences between observed versus expected utilization of available habitat types. The expected value for the *Acacia* thickets (Table 3) may be the cause of the discrepancy as the Chi-squared goodness of fit test can be sensitive to small values (Zar, 1999). The observed habitat use by impala differed significantly from the

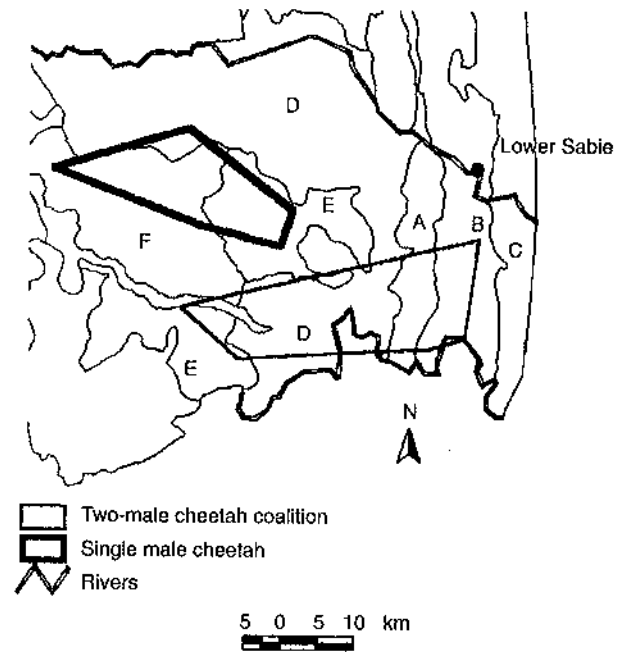


Fig. 3. Home range of a single male cheetah *Acinonyx jubatus* M1 and two-male cheetah coalition M3 in the southern district of the Kruger National Park, estimated by the 100% minimum convex polygon (MCP) method. A, *Acacia* thickets; B, open savanna; C, Lebombo Hills; D, riverine thickets; E, *Combretum/Terminalia* woodland; F, *Combretum* woodland.

Table 3. Chi-squared test for use of different habitat types by the cheetah *Acinonyx jubatus* female F1 in the south-eastern region of the Kruger National Park

Habitat	Observed	Expected
<i>Acacia</i> thickets	10	4
Open savanna	46	50
Lebombo Hills	11	13

expected, based on habitat availability between the Sabie and Crocodile rivers ($\chi^2 = 185$, d.f. = 2, $P < 0.0001$). Bonferroni confidence intervals indicated that the impalas preferred the Lebombo Hills, avoided the open savanna, and used the *Acacia* thickets in proportion to its availability.

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 was 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 less than expected in the open savanna and greater than expected in the Lebombo Hills.

When plotting radio-locations in the main study area, the distribution of fixes revealed that the three-male

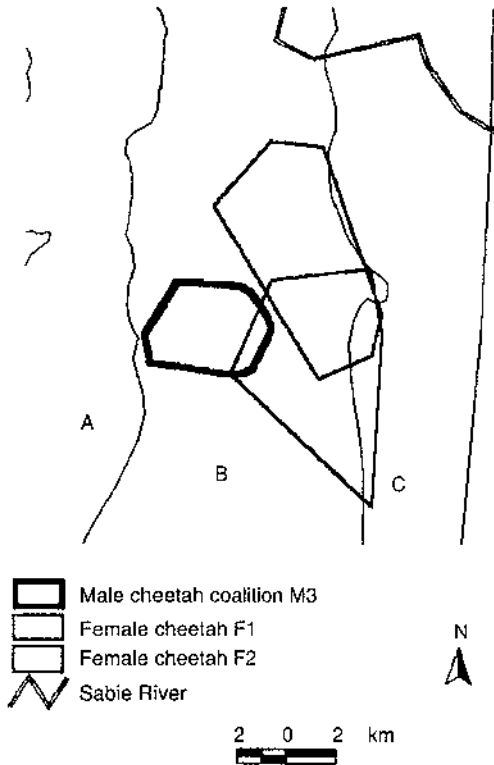


Fig. 4. Core home ranges of male (M3) and female cheetahs *Acinonyx jubatus* (F1 and F2) in the south-eastern region of the Kruger National Park, estimated by the 50% minimum convex polygon (MCP) method. A, *Acacia* thickets; B, open savanna; C, Lebombo Hills.

cheetah coalition M3 was closely associated with the roads, while female cheetahs (F1 and F2) followed the drainage lines (Fig. 5). 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. 6). The mean distance to drainage lines and roads between males and females were also significantly different (Fig. 6). Female cheetahs F1 and F2 were significantly closer to the drainage lines than the male cheetah coalition M3 ($t=3.92$, d.f.=245, $P<0.0001$ and $t=4.37$, d.f.=200, $P<0.0001$, respectively), and M3 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 a strong significant difference between the frequency of scent markings by M3 along and off the roads, 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 roads (observed 265, expected 5) and less than expected off the roads (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

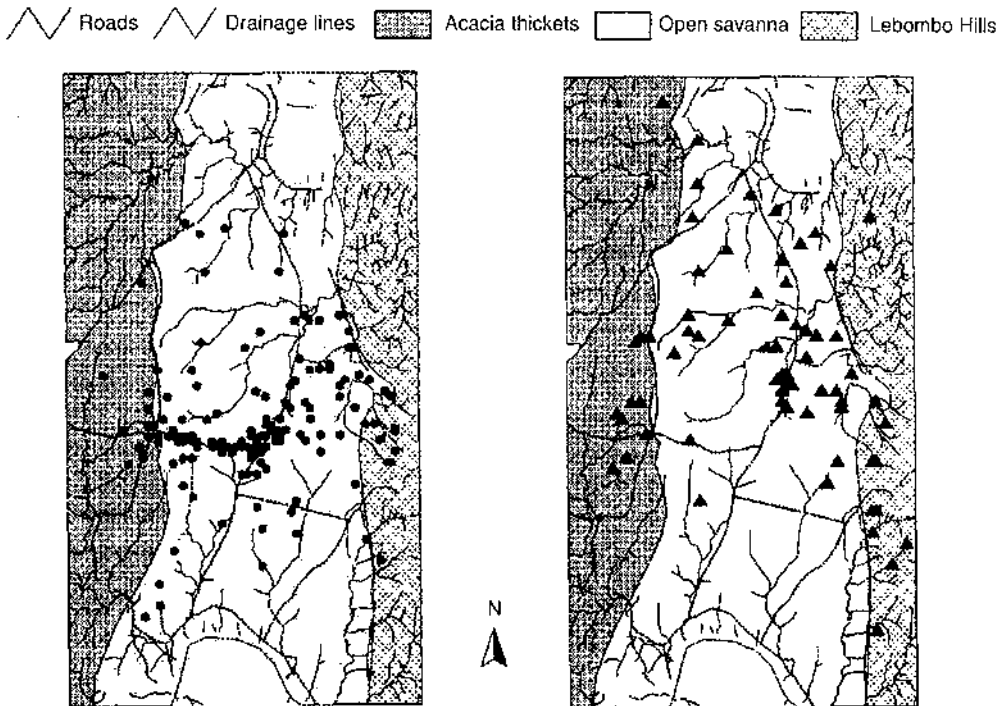


Fig. 5. Radio-location points of a three-male cheetah *Acinonyx jubatus* coalition M3 (●) and female cheetahs F1 and F2 (▲) in the south-eastern region of the Kruger National Park.

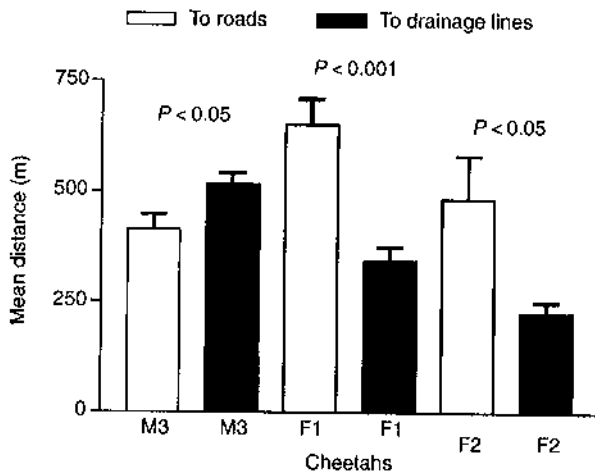


Fig. 6. Mean distance (\pm SE) of male and female cheetah *Acinonyx jubatus* locations to drainage lines and roads in the south-eastern region of the Kruger National Park. M3, three-male cheetah coalition; F1 and F2, female cheetahs.

different vegetation categories for different activities ($\chi^2 = 26.1$, d.f. = 6, $P < 0.01$). 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.

DISCUSSION

Estimates of home-range size for cheetahs in the KNP were presented in this study (Table 1). Bowland's (1994) photographic survey estimated that the home-range size of male and female cheetahs in the KNP varies between 104 km² and 1848 km². These estimates, however, were taken from small sample sizes and the social status of the animals was unknown. Therefore, non-territorial or dispersing cheetahs may be partly responsible for the large home ranges recorded in Bowland's (1994) study. When compared with other studies in other woodland savannas, cheetah home-range sizes varied widely from 24 km² in Matusadona National Park (MNP) to 320 km² in Kgalagadi Transfrontier Park (KTP) (Mills, 1998; Purchase & du Toit, 2000; Broomhall, 2001). 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 different landscapes or habitat

types. The resource dispersion hypothesis predicts that territory size is determined by the dispersion pattern of food patches (Macdonald, 1983) or other resources. In the Serengeti, the large female home ranges (averaging 833 km²) are attributed to the patchiness of their main prey, not low prey density, as Thomson's gazelle undertake large seasonal migrations (Caro, 1994). Similarly, the nomadic nature of springbok *Antidorcas marsupialis* in the KTP (Mills, 1998) and concentrated distribution of high prey density on the foreshore grassland in MNP (Purchase & du Toit, 2000) may have influenced the home-range size of female cheetahs in these areas. 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. In Phinda Resource Reserve (PRR), cheetahs sought out open grassland patches in the woodland for hunting, which constituted only 8.6% of available habitat and were distributed as small, discreet, widely spaced patches (Hunter, 1998). Hunter (1998) considered that suitable habitat for hunting, rather than prey, may have been the 'patchy' resource that gave rise to cheetah movements.

In this study, total and core territory sizes of the three-male cheetah coalition M3 were smaller than the adult female home ranges (Figs 2 & 4, Table 1). Although it is unusual in carnivores for the territory size of males to be smaller than the range size of females (Sandell, 1989; Mizutani & Jewell, 1998), increasing female home-range size is associated with reduced male territory size, since very large female areas are no longer defensible by males (Caro, 1994). This is true in the Serengeti (Caro, 1994) and is probably the situation in the KNP as female cheetahs have large home ranges. Cheetah home ranges in the main study area of this study overlapped extensively (Fig. 2) and the territory of the male cheetah coalition overlapped those of both adult female cheetahs, presumably to increase opportunities for mating (Sandell, 1989; Caro, 1994). However, core home ranges of the male coalition M3 and female F1 did not overlap and may not have overlapped with female F2 had the sample size for F2 been > 25 (Table 1, Fig. 4). Thus, although home ranges showed extensive overlap, the cheetahs also seemed to avoid each other and showed exclusive use of certain areas, which is more typical of asocial felids (Caro, 1994; Mizutani & Jewell, 1998).

Although chi-squared analyses showed that cheetahs had no preferences for any particular habitat types, the home ranges of adult cheetahs in the main study area were centred on the open savanna (Fig. 2, Table 2), suggesting a preference for this relative to other available habitats. The core home ranges of cheetahs M3, F1 and F2 were also positioned in the open savanna (Fig. 4). 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 *A. nigrescens*/*S. birrea* woodland (Kruger,

1988). The solitary male cheetah in the central study area, positioned his territory in the *Combretum* woodlands (Fig. 3), which is characterized by open savanna habitat in the bottomlands (see Methods). In the woodland savanna of PRR, the core areas of the territorial male cheetahs with the longest tenure were all centred in regions with the most extensive grasslands and all females used these same grasslands extensively (Hunter, 1998). In MNP, home ranges of cheetahs included both woodland and grassland habitat, where they preferred the open grassland for hunting (Purchase & du Toit, 2000).

When comparing the habitat selection of male and female cheetahs, 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. Impala also preferred these dense vegetation types (Gertenbach, 1983; Ben-Shahar, 1995; this study). Therefore, females may be using thicker vegetation because encounters with impala are greater. This is supported by the significant positive correlation found between distribution of female cheetah F1 and the distribution of impala, while no correlations were found between impala and the male coalition M3. In the KNP, the open savanna is an important habitat to the cheetahs as it is the preferred habitat for hunting (Broomhall, 2001). 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 areas are nevertheless preferred for walking and moving between hunting and resting sites (Cohen *et al.*, 1978; Zank, 1995; Purchase, 1998). The three-male cheetah coalition selected moderate to dense shrub cover for walking and female F1 seemed to use denser shrub cover for all activities. This may be because the cheetahs are avoiding predators by selecting habitats that provide greater concealment. In the Serengeti, Durant (1998) found that cheetahs seek out 'competitive refuges' with low densities of lions *Panthera leo* and spotted hyenas *Crocuta crocuta*, as they are both directly responsible for cub mortalities (Laurenson, 1994) and both species steal kills from cheetahs (Caro, 1994). The risk of cub predation may be another reason why the core ranges of female cheetahs bordered onto and extended into the Lebombo Hills (Fig. 4) because female cheetahs were accompanied by cubs in over two-thirds of observations. This habitat not only carries higher impala densities (Broomhall, 2001), but is also avoided by lion and spotted hyena (Mills & Biggs, 1993; Mills & Gorman, 1997). The *Acacia* thickets, on the other hand, are preferred by lion and spotted hyena (Mills & Biggs, 1993) and carry high densities of these predators (Mills & Gorman, 1997).

Unlike the female cheetahs in the KNP, the male coalition was less concerned with cover and impala distribution. They seemed to prefer the more open savanna habitat, used more open vegetation when resting compared to other activities, and concentrated their activities along the roads. The male coalition may be less concerned than the females about other predators as a cheetah coalition is more likely to deter other predators than a solitary animal (Caro, 1994). Male coalitions also prey

on larger food items (Caro, 1994; Broomhall, 2001) and seem less dependent on impala than female cheetahs in the KNP (Broomhall, 2001). 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 because of the high nutritional demands placed on females during pregnancy, lactation and cub growth (Laurenson, 1995*b*). Kruuk (1986) suggests that females must exploit a less profitable but more predictable food supply, i.e. impala, than the males, which may indicate that females in the KNP are distributing themselves according to impala distribution and are not only avoiding predators.

On the Serengeti Plains, where the males position their territories and where there is some cover, Caro (1994) considered that the availability of sufficient cover for stalking and resting determines territory location. In this study, we consider that scent-marking may also influence the habitat selection of territorial male cheetahs. Scent marking plays an integral role in territory maintenance as a warning to other males of their presence (Eaton, 1970), but is also considered important to males and females for communicating their reproductive status (Marker-Kraus *et al.*, 1996). Scent marks are usually placed on conspicuous objects or frequently used places where encounter rates are maximized (Gorman & Trowbridge, 1989), such as large trees or shrubs and dirt mounds (Eaton, 1970), and roads or game paths or around waterholes (Funston, 1999). The male cheetah coalition in the KNP scent marked significantly more frequently along the roads and MGLM 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 Nairobi National Park, Eaton (1970) 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.

Our study in the KNP found that cheetahs prefer more open habitat in woodland savannas. However, for female cheetahs this preference seems to be largely influenced by the distribution of impala. Predation may also play a significant role in habitat selection but this could not be determined in this study. The need for open areas for hunting may be the main determinant for cheetahs using the open savanna, which indicates the importance of open habitats to cheetahs. 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). The requirements by cheetahs for open areas in woodland savannas is important as the effects of dense or encroaching bush may lower cheetah densities and affect population viability in small reserves.

Finally, we concede that due to difficulties associated with tracking and observing cheetahs in this study the

cheetah observations were limited to small sample sizes. This study, however, provides a meaningful contribution to our knowledge of cheetah ecology in woodland savannas, which to date has been largely unexplored. Further studies in woodland savanna ecosystems are required to substantiate any differences in habitat use by male and female cheetahs and to gain a better understanding of the effects of prey availability and their requirements for open areas and cover on home-range size and habitat use.

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