

# Habitat selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in thicket vegetation: is the cheetah a savanna specialist?

C. Bissett & R. T. F. Bernard

Wildlife and Reserve Management Research Group, Department of Zoology & Entomology, Rhodes University, Grahamstown, South Africa

## Keywords

*Acinonyx jubatus*; habitat selection; adaptability; diet.

## Correspondence

Ric T. F. Bernard, Wildlife and Reserve Management Research Group, Department of Zoology & Entomology, Rhodes University, Grahamstown 6139, South Africa.  
Email: R.bernard@ru.ac.za

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## Abstract

Habitat selection and feeding ecology of a reintroduced population of cheetahs *Acinonyx jubatus* were studied in a 16 000 ha game reserve in the Eastern Cape Province (South Africa). Seventy per cent of the reserve is characterized by very dense thicket vegetation (valley bushveld) and the remainder is open and savanna-like. The results illustrated a strong effect of sex and group size on the behaviour of cheetahs. The coalition (three adult males) killed significantly larger animals (55% of kills weighed more than 65 kg) than single female cheetahs (less than 2% of kills weighed more than 65 kg). Female cheetahs showed temporal and spatial avoidance of lions by hunting at dawn and dusk and positioning their home ranges [95% utilization distribution (UDs)] significantly farther from the pride of lions than did the coalition. The coalition hunted earlier and later than female cheetahs, and 46% of their kills were made in darkness. In addition, their home range overlapped that of the lions and they showed neither temporal nor spatial avoidance of the lions. The rates of kleptoparasitism were lower and the kill retention times were longer than those reported elsewhere in Africa, and it is suggested that this is a consequence of the cover provided by the thicket vegetation and prey size. The home ranges (95% UD) of female cheetahs incorporated more thicket vegetation than that of the coalition, indicating that the coalition is less susceptible to predation than single females. These data suggest that cheetahs possess greater behavioural flexibility than previously reported, that they can hunt successfully in thicket vegetation, sometimes in darkness, that they are not restricted to killing small to medium-sized prey, and that they may not be savanna specialists.

## Introduction

Historically, the cheetah *Acinonyx jubatus* occurred widely through much of non-forested Africa, the Middle East and southern Asia (Guggisberg, 1975; Caro, 1994; Sunquist & Sunquist, 2002; Hunter & Hamman, 2003), suggesting that the species might have a wide habitat tolerance. However, early studies of the biology and ecology of the cheetah, which were concentrated in the Serengeti plains of East Africa, pointed towards the species being highly specialized and requiring open savanna vegetation in which it could use its high speed to chase small to medium-sized prey (see e.g. Schaller, 1972; Caro & Collins, 1986, 1987; Durant *et al.*, 1988; Fitzgibbon, 1990; Caro, 1994; Laurenson, 1994, 1995; Laurenson, Weilebnowski & Caro, 1995; Durant, 1998a). Having sacrificed strength for speed and agility, cheetahs almost always lose when in competition with larger carnivores (lions and spotted hyaenas; Durant, 1998b). Consequently, cheetahs typically show temporal and spatial avoidance behaviour, feeding during the day and occupying

competition refuges (Durant, 1998b, 2000a,b). Recently, the reliance of cheetahs on open, savanna-type habitats has been questioned and, based on increased cub survival in thicket vegetations, Durant (1998a) suggested that thicket vegetations may be key to the survival of the species. In the woodland savanna of the Kruger National Park (KNP), Phinda Resource Reserve (South Africa) and Matusadona (Zimbabwe), cheetahs position their territories and prefer to hunt in more open habitats where the success rate is higher (Hunter, 1998; Purchase & du Toit, 2000; Broomhall, Mills & du Toit, 2003; Mills, Broomhall & du Toit, 2004). However, in these denser habitats, all cheetahs use the vegetation for cover; the females may use it for hunting and suffer reduced kleptoparasitism. Thus, Mills *et al.* (2004) conclude that the cheetah is more adaptable than previously thought.

The conservation of large carnivores, with their typically large home ranges (Kelly *et al.*, 1998), requires large tracts of suitable habitat and this will often compete with other forms of land use. In southern Africa, demands for land for

non-conservation purposes are high (Marker *et al.*, 2003), and it is thus important that land that has been set aside for conservation is fully used for the conservation of endangered species. This, in turn, requires a complete understanding of the habitat requirements of the endangered species. Thus, the question of the habitat requirements of the cheetah, or its behavioural adaptability, is both of fundamental interest and central to decisions about introductions to new areas. The Eastern Cape Province of South Africa is within the historical range of the cheetah and the last record for cheetahs in the region was in 1888 (Skead, 1987). Land use is changing from agriculture (mostly small livestock) to conservation and ecotourism with the development of many small (<30 000 ha) game reserves (Castley, Boschhoff & Kerley, 2001). These new reserves create opportunities to reintroduce species, such as the large felids, that had been extirpated from the region; however, in many cases the habitat may be unsuitable. The Eastern Cape Province is characterized by very diverse vegetation (Lubke, Everard & Jackson, 1986; Everard, 1987), much of which is denser than the open savannas on which cheetahs are usually found. In addition, the small size of many of these reserves might increase the intensity of competition between cheetahs and other large carnivores and reduce access to competition refuges (*sensu* Durant, 1998b). Thus, the aims of this project were to study the space use, habitat selection, diet and feeding behaviour of cheetahs in thicket vegetation to contribute to our understanding of the adaptability of the species and the role that small reserves in the region may play in conservation.

## Methods

### Study site

The study was undertaken on a 16 000 ha enclosed reserve (Kwandwe Private Game Reserve) in the Great Fish River Valley of the Eastern Cape Province, South Africa (c. 33°09'S and 26°37'E) between January 2003 and August 2004. The climate is warm temperate, with warm to hot summers (December–February); maximum daily temperatures often exceed 35°C and cold winters (June–August) with minimum nighttime temperatures often below 0°C. Rainfall is highly variable, with peaks between September and November, and February and April. The mean annual rainfall is 435 mm (climatic data from the reserve). The reserve is characterized by a central region of rolling hills (c. 30% of the total area), which is surrounded by a series of east–west orientated sandstone ridges with steep rising ground in the north (70% of total area). Although the vegetation is complex with 10 different vegetation types recognized, in this study we have combined these to form an open, savanna-like habitat and a grouping of denser, thicket vegetations. The open habitat occurs on the central rolling hills and thus comprises about 30% of the reserve, whereas the thicket habitat occurs on the slopes. The open habitat comprises old cultivated areas (2% of total area),

karroid shrubland (16%) and bushclump karroid thicket (12%). The old cultivated areas are dominated by a single species of grass (*Cynodon dactylon*, *Pennisetum clandestinum* or *Cenchrus ciliaris*), with different fields dominated by a different species, and no trees or shrubs. Karroid shrubland is dominated by a herbaceous layer comprising low (<20 cm high) karroid shrubs with little grass and few tall trees. Bushclump karroid thicket is characterized by clumps of bushes (typically <3 m tall) interspersed with extensive patches of grass and karroid shrubs. The thicket habitat falls into two categories. The first category is dominated by succulent plants, including *Portulacaria afra*, *Euphorbia bothae*, *Euphorbia tetragona* and *Euphorbia triangularis*, with a variety of tall trees and a variable herbaceous layer. These vegetation types, which have previously been classified as valley bushveld (Acocks, 1988) or valley thicket in the more moist areas and xeric succulent thicket in the drier regions (Low & Rebelo, 1996), comprise 60% of the total area and grow on the steeply sloping regions of the reserve. The second category includes the vegetation types that grow along drainage lines and rivers and are characterized by dense stands of trees such as *Acacia karroo*, *Rhus lancea* and *Rhus refracta* with a thick understorey of various grass species. These vegetation types comprise the remaining 10% of the reserve.

### Vegetation density and visibility

For each vegetation type, we assessed the density of the vegetation and visibility within the vegetation using a modified point centred quarter method (Phillips, 1959; Pellew, 1983) and a checkerboard method (MacArthur & MacArthur, 1961), respectively. In each of the original 10 vegetation types, we completed ten 100-m-long transects. At 20-m intervals along each transect, we marked a cross on the ground and, in each quarter, we measured the distance to the nearest plant or structure that was more than 50 cm tall. We chose a height of 50 cm as providing sufficient cover for a hunting cheetah. Objects at a distance greater than 10 m from the point were not counted so as to ensure that the same object was not counted twice. To calculate the density of objects, we used the mean of the four distances at each point of the transect to calculate the area of the circle that had been sampled at that point. For each transect, we summed the areas and expressed the number of objects relative to that area. For the checkerboard method we used a checkerboard that was 90 cm high and 60 cm wide with 10 × 10 cm red and white squares. Using the same transects and in the same quarters as above, the checkerboard was placed on the ground at a distance of 10 m from the point. With the observer's head at about 70 cm from the ground, the percentage of the board that was visible was estimated. A height of 70 cm represents the head height of a cheetah. We calculated the mean percentage of the checkerboard that was visible for each transect and each vegetation type and used this to calculate a visibility index for each of the two habitats.

## Animals and observations

We recognized four types of social groups of cheetahs on the reserve, and the numbers and make-up of the social groups changed through the study as a result of births and deaths. A single coalition of adult males (two brothers and an unrelated male) was present throughout the study. We collected data for four single females (solitary adult female cheetahs that may or may not have been pregnant), six females with cubs (single adult females with dependent cubs) and one set of four independent cubs (a group of cubs that had separated from their mother but were still together). All adult females were fitted with very high frequency (VHF) radio-collars and each member of the coalition had an implanted VHF radio-transmitter. Radio-collars and implants were manufactured by Africa Wildlife Tracking cc (Rietondale, Gauteng, South Africa) and incorporated Telonics high-power transmitters (Telonics, Mesa, AZ, USA). Cheetahs were immobilized and anaesthetized in the field with Zolatil (im), delivered using a gas-powered dart gun, under the guidance of a registered veterinarian. Implants were inserted into the abdominal cavity, through a mid-ventral incision in the inguinal region, by the veterinarian. Because of the ongoing nature of this research, collars and implants were replaced when necessary following the same procedure. No cheetahs have died as a result of these procedures. We located all animals by radio-telemetry (Telonics TR-4 receiver and Telonics RA-2A directional antenna) and confirmed the location visually every day. Once located, we took a global positioning system (GPS) fix (Garmin 72 GPS; Garmin Ltd, Olathe, KS, USA) and, if the cheetah was on a kill, we recorded the species, sex and age (juvenile, subadult or adult) and amount consumed. In the second year of the study, we supplemented these data by tracking individual animals (the coalition twice and a single female once) continuously for 14 days in an attempt to obtain a complete record of all kills and to collect more accurate estimates of kill rate (number of kills per day), daily consumption (kg of prey per cheetah per day), kill retention time, kleptoparasitism and hunting behaviour. For the analysis of kill size, each kill was assigned to a size class (small, <30 kg; medium, 30–65 kg; large, >65 kg) based on the species and age of the animal (Hunter, 1998). The sample size of one for the coalition and independent cubs precludes the use of ANOVA for analysis of differences between the types of social groups, and  $\chi^2$  analyses were used. However, in order to illustrate the variability between members of the same type of social group, data are presented as means  $\pm$  1SD in the tables for the single females ( $n = 4$ ) and females with cubs ( $n = 6$ ).

## Habitat selection and use

Habitat selection was analysed at the reserve and home range levels. Home range was calculated using ArcView 3.2 and the Animal Movement Extension (Hooge & Eichenlaub, 1997). We used the fixed kernel utilization distribution method (UD; Worton, 1989; Powell, 2000) because it is less

affected by outlying fixes and includes less unused space than does the more commonly used minimum convex polygon method (Harris *et al.*, 1990). We calculated the smoothing factor ( $H$ ) using the least-squares cross validation available in the Animal Movement Extension, and this value (1000) was used for all analyses. We used the 95% UD to represent the home range of each animal. To calculate habitat selection at a reserve level, we used a digital vegetation map of the reserve and compared the area of the two habitat types (open and thicket) in the home range with their availability on the reserve. At a home range level, we calculated the number of GPS fixes in each habitat type within the 95% UD (using ArcView 3.2). Expected habitat use, assuming habitat use to be random, was calculated by multiplying the total number of GPS fixes in the 95% UD by the percentage of each habitat type in the home range for each individual or each cheetah group. We compared observed and expected values using  $\chi^2$  tests.

We calculated the mean distance between the various cheetah social groups and the pride of lions (there is a single pride on the reserve) in ArcView 3.2 using only the GPS fixes that fell within the 50% UD of both cheetahs and lions. The visibility in the home range was estimated using the visibility indices for the open and thicket habitats and the percentage of the home range that the two habitat types comprised. We calculated the density of antelope in the home ranges using the annual game census data for those species that are preyed on by cheetahs. Annual game counts are done by helicopter using standard procedures and the localities of all animals are recorded using GPS equipment. We analysed the use of the open and thicket habitats for hunting by comparing the observed number of kills in each habitat type in the 95% UD with an expected number that was generated by multiplying the total number of kills in the 95% UD by the percentage of each habitat type in the 95% UD.

Statistical analyses were performed in SigmaStat (Jandel Scientific, San Rafael, CA, USA) and Statistica (StatSoft, Tulsa, OK, USA).

## Results

### Cheetah diet

Two hundred and twenty-four kills, representing 15 species, were recorded over a period of 18 months for all cheetahs on Kwandwe. The five species that were killed most often (kudu *Tragelaphus strepsiceros*, springbok *Antidorcas marsupialis*, grey duiker *Sylvicapra grimmia*, impala *Aepyceros melampus* and bushbuck *Tragelaphus scriptus*) comprised 82% of the kills (Table 1) and 79% of the edible biomass. Kudu comprised 43% of all kills; the remaining four species individually were far less frequently caught, but together formed 39% of kills (Table 1).

Sixty-three per cent of the kills (pooled data for all cheetahs) were of the medium size class, and there was a significant difference in the way in which the different cheetah social groups utilized prey of different sizes

( $\chi^2$  220.4; d.f. 6;  $P < 0.0001$ ; Table 2). Fifty-five per cent of the coalition's diet comprised large animals whereas only 2% were small. By contrast, for the other social groups, large kills were rare (1 or 2%) and small and medium-sized kills were much more common (Table 2). The availability of prey of different sizes was calculated using game count data, available weights for juveniles and adults (Table 1), and an assumption that 25% of the population was of juvenile size. Of 4429 potential prey animals on the reserve, 43% were large, 33% medium and 23% of small size. For each of the four different social groups of cheetahs, prey size was significantly different from expected assuming that prey of different sizes was killed based on availability (coalition,  $\chi^2$  20.4; females with cubs,  $\chi^2$  106.5; single females,  $\chi^2$  92.4; independent cubs,  $\chi^2$  58.8; d.f. 2;  $P < 0.01$  for all). The abundance of juveniles will vary through a year, but it is unlikely that they will ever account for more than 25% of each species. To account for periods when juveniles are less abundant, and therefore small prey are less abundant, we recalculated availability assuming that 15% of the population was juvenile. Availability changed slightly (21% small, 31% medium and 48% large size), but this had no significant effect on the  $\chi^2$  analyses.

There was no significant relationship between the type of cheetah social group and the age of kills ( $\chi^2$  4.41; d.f. 3;  $P > 0.05$ ; Table 2). The subadult age class was excluded from this analysis as its inclusion resulted in too many of the cells in the contingency table including values less than five.

**Table 1** Pooled kill records for all cheetahs *Acinonyx jubatus* during the 18-month study

Prey species	Kills		Mass (kg)		
	No.	%	Juvenile	Male	Female
Kudu	96	43	55	220	155
Springbok	28	12	12	41	31
Grey duiker	27	12	8	17	21
Bushbuck	17	8	17	60	36
Impala	16	7	19	60	45

Body masses are from Bothma (2002) and Meissner (1982). The % column does not total 100 because data are for the five most often killed antelope.

**Table 2** Size and age of kills made by the four types of cheetah *Acinonyx jubatus* social groups and by all cheetahs (pooled data)

Kill size/age	Available	Pooled data	Coalition	Females + cubs	Single females	Independent cubs
Social group sample size			1	6	4	1
Small (%)	23	21 (44)	2 (1)	21.9 $\pm$ 8.3	34.2 $\pm$ 13.6	57 (8)
Medium (%)	33	63 (133)	43 (26)	77.4 $\pm$ 7.8	63.8 $\pm$ 10.3	43 (6)
Large (%)	43	16 (35)	55 (60)	0.5 $\pm$ 1.2	2.1 $\pm$ 4.2	0
Juvenile (%)	Unknown	49 (111)	42 (25)	52.3 $\pm$ 10.2	66.0 $\pm$ 19.7	43 (6)
Subadult (%)	Unknown	4 (9)	3 (2)	1.6 $\pm$ 3.1	3.2 $\pm$ 4.1	7 (1)
Adult (%)	Unknown	47 (104)	55 (33)	45.9 $\pm$ 18.3	30.9 $\pm$ 21.6	50 (7)
Total			60	85	53	14

The availability of prey of different sizes (Available column) in the reserve is given. Data are given as % rounded to the nearest whole number, with absolute values in parentheses for social groups where  $n = 1$  and as mean  $\pm$  1SD where sample size is greater than 1.

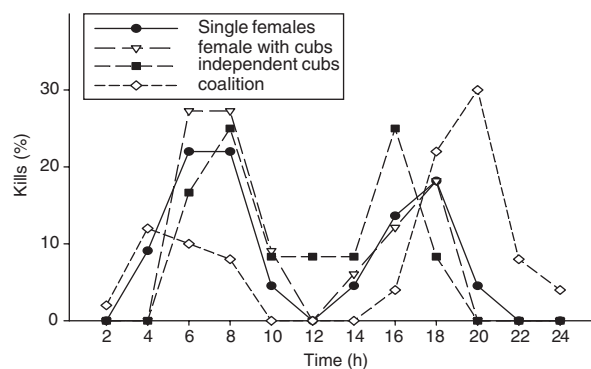
Comprehensive demographic data were not available for the antelope on the reserve and it was not possible to compare observed kills with expected values.

## Time of hunting

Single females, females with cubs and independent cubs were most active just after dawn and just before dusk (Fig. 1). However, the coalition was active earlier and later, and 42% (21 of 50 kills for which the time was known) of kills by the coalition occurred between 20:00 and 24:00 h (Fig. 1). To account for annual changes in the time of sunrise and sunset, we converted the time of each kill by the coalition to time (in min) before or after dawn or dusk, and this analysis revealed that 23 kills (46%) were made in darkness (from 40 min after sunset to 40 min before sunrise) and 12 kills were made between 2 and 4 h after sunset.

## Kleptoparasitism and kill retention time

The rates of kleptoparasitism (observed incidences of kleptoparasitism as a percentage of all kills for a particular social group) were low, with the coalition losing two kills to lions, and females with cubs losing three kills to the coalition and lions. The mean kill retention time differed significantly between the social groups, with the single females and



**Figure 1** Timing of hunting activity by the four types of social groups of cheetahs *Acinonyx jubatus*. Data are the number of kills in 2 h as a percentage of all kills made by each social group.

females with cubs spending significantly more time at kills than the coalition and independent cubs (ANOVA,  $F$  7.3; d.f. 3;  $P < 0.001$ ; Table 3).

### Habitat selection and home range characteristics

The visibility indices and density measures for the 10 original vegetation types were strongly correlated ( $r^2$  0.8;  $F$  33.4;  $P < 0.001$ ), and only visibility indices are presented here. The visibility index of the open habitat was 94 whereas that for the thicket habitat was 55. The home ranges (95% UD) of the different cheetah social groups differed in size (Table 4) and in the percentages of open and thicket habitat types ( $\chi^2$  13.0; d.f. 3;  $P < 0.005$ ). The home range of the coalition included the greatest percentage of open habitat

(41%), whereas the home ranges of the single females and independent cubs included the greatest percentages of thicket (Table 4). However, for no social group were the percentages of open and thicket habitat significantly different from expected, assuming that habitat selection reflected overall availability on the reserve ( $P > 0.05$  for all). There was no significant difference in the visibility index (ANOVA,  $F$  1.2; d.f. 3) or the prey density (ANOVA,  $F$  0.9; d.f. 3) of the home ranges of the different social groups ( $P > 0.05$  for both; Table 4). The coalition was significantly closer to the core area of the pride of lions than all the other social groups, which were at least twice as far from the lions (Table 4;  $F$  9.8; d.f. 3;  $P < 0.05$ ). There was no significant difference in the distances of the various social groups from the coalition (Table 4;  $F$  1.0; d.f. 2;  $P > 0.05$ ).

Within their home ranges, the coalition did not use the two habitats at random and showed a strong preference for the open habitat ( $\chi^2$  18.4; d.f. 1;  $P < 0.0001$ ; Table 5). The other social groups used the habitats available at random ( $P > 0.05$  for all).

**Table 3** Confirmed incidences of kleptoparasitism (as a % of all kills in parentheses) and kill retention time for the four types of social groups of cheetahs *Acinonyx jubatus*

	Kleptoparasitism	Mean kill retention time (min)
Coalition	2 (3.3%)	417 $\pm$ 356 ( $n=21$ )
Females with cubs	3 (3.5%)	939 $\pm$ 535 ( $n=16$ )
Single females	0	1253 $\pm$ 774 ( $n=10$ )
Independent cubs	0	495 $\pm$ 383 ( $n=6$ )

Mean kill retention time  $\pm$  1sd is given with the number of kills from which the mean was calculated in parentheses.

### Habitat use and hunting

The different social groups used the available habitats in their home ranges significantly differently for hunting ( $\chi^2$  49.19; d.f. 3;  $P < 0.0001$ ; Table 5), with the coalition making the greatest percentage of kills in the open habitat and the single females and independent cubs making the greatest percentage of kills in thicket habitat (Table 5).

**Table 4** Summary of the characteristics of the home ranges (95% UD) of the four types of social groups of cheetahs *Acinonyx jubatus*

Home range characteristics	Cheetah social group (sample size)			
	Coalition ( $n=1$ )	Single females ( $n=4$ )	Females + cubs ( $n=6$ )	Independent cubs ( $n=1$ )
Home range size (km <sup>2</sup> )	32.7	65.6 $\pm$ 23.3	62.3 $\pm$ 21.0	93.9
Habitat types				
Open (%)	41	25.3 $\pm$ 7.9	31.5 $\pm$ 12.1	19
Thicket (%)	59	74.7 $\pm$ 8.1	68.5 $\pm$ 12.1	81
Visibility index	68.6	62.1 $\pm$ 3.1	65.6 $\pm$ 6.5	59.1
Prey density (animals per ha)	0.25	0.32 $\pm$ 0.07	0.28 $\pm$ 0.03	0.30
Distance from lions (m)	1990	6272 $\pm$ 1236	5056 $\pm$ 287	7121
Distance from coalition (m)	N/A	7161 $\pm$ 1967	5185 $\pm$ 2538	7480

Where sample size for the social group is greater than 1, data are means  $\pm$  1sd UD, utilization distribution; N/A, not applicable.

**Table 5** Comparison of the use of open and thicket habitats for hunting by the four types of social groups of cheetah *Acinonyx jubatus*

Cheetah social group ( $n$ )	Habitat available		Habitat use		Kills	
	Open	Thicket	Open	Thicket	Open	Thicket
Coalition ( $n=1$ )	41%	59%	56%	44%	64 (38)	36 (22)
Females + cubs ( $n=6$ )	31.5 $\pm$ 12.1	68.5 $\pm$ 12.1	39.2 $\pm$ 11.7	60.8 $\pm$ 11.1	59.3 $\pm$ 17.0 (45)	40.7 $\pm$ 17.0 (40)
Single females ( $n=4$ )	25.3 $\pm$ 8.1	74.7 $\pm$ 8.1	29.8 $\pm$ 13.5	70.2 $\pm$ 13.5	25.0 $\pm$ 29.9 (18)	75.0 $\pm$ 29.9 (35)
Independent cubs ( $n=1$ )	19%	81%	23%	77%	29 (4)	71 (10)

Data include the per cent availability of the two habitats in the home ranges, the use of those habitats and the percentage of kills in each habitat type with numbers of kills in parentheses. Where sample size for the social group is greater than 1, data are means  $\pm$  1sd.

Within their home ranges, the independent cubs and the single females used the available habitats at random for hunting (females,  $\chi^2$  0.03; d.f. 1;  $P > 0.05$ ; independent cubs,  $\chi^2$  2.2; d.f. 1;  $P > 0.05$ ). The coalition and females with cubs made significantly more kills than expected in the open habitat (coalition,  $\chi^2$  9.7; d.f. 1;  $P < 0.005$ ; females with cubs,  $\chi^2$  12.6; d.f. 1;  $P < 0.001$ ). Although the above analysis was based on the observations of cheetahs at kills that had occurred, the nature of the vegetation made observation of hunting behaviour very difficult. The coalition was observed hunting 14 times, of which 11 (79%) were in the open habitat and of these five were successful. The remaining three hunts were in thicket habitat and two were successful. Female cheetahs with cubs were observed hunting 10 times with five hunts in the open, of which two were successful, whereas three of the five hunts in the thicket were successful. Single females made six hunts, of which four were in open habitats (three successful) and two (both unsuccessful) were in thicket habitat. Independent cubs made eight hunts, six in the open (two successful) and two (both unsuccessful) in the thicket. In total, 38 hunts were observed, and of these 19 were successful. Twenty-six hunts were in open habitats and 12 were successful. Twelve hunts were in thicket habitat and seven were successful.

## Discussion

Our results highlight a sex difference in various aspects of the space use, habitat selection and feeding biology of cheetahs in thicket vegetation. As has been reported in previous studies, members of the coalition killed significantly more large-sized animals than did the female groups and cubs, which killed mostly small and medium-sized animals (Caro, 1994; Hunter, 1998; Mills *et al.*, 2004; Radloff & du Toit, 2004). Although there is some controversy as to whether or not coalitions cooperate in hunting, our unpublished observations at Kwandwe indicate that they do and therefore the combined strength of the coalition has to be considered. However, it is unlikely that the significantly larger kill size of the coalition is simply a response to the increased or combined strength of the three males since single females killed (albeit very rarely) adult kudu. We suggest that it is more likely that coalitions of males kill larger prey to meet the increased nutritional demands of the group. The difference in prey size of the different social groups of cheetahs could be explained not only by the selection of different prey species but also by the selection of prey of different ages (see e.g. Mills *et al.*, 2004; Table 2). On Kwandwe, although male cheetahs killed more adult animals than female cheetahs, the difference was not significant. Rather, the significant difference in prey size reflects the selection of different prey species and this will be discussed fully in another paper.

The female cheetahs hunted in the early morning and late afternoon, showing the temporal avoidance of lions as described by Durant (1998b). However, the coalition hunted earlier and later than the other cheetah social groups, and made 46% of observed kills in darkness. The home range of

the coalition overlapped extensively with that of the lion pride, and by hunting at night they increased the likelihood of encountering or being encountered by the lions. Many of the previous studies have reported that cheetahs kill the most abundant antelope species which, in those systems, is typically a small to medium-sized diurnal species (impala at Matusadona, Purchase & du Toit, 2000, and the KNP, Pienaar, 1969; Mills *et al.*, 2004; Thomson's gazelle in the Serengeti, Schaller, 1972; and springbok in the Kalahari Gemsbok National Park, Mills, 1984). On Kwandwe, kudu is the most abundant antelope species (30% of all antelope), the most commonly killed prey species (43% of all kills), and is crepuscular. Although diurnal, medium-sized prey such as impala were abundant within the home range of the coalition, they comprised only 7% of all kills, and we suggest that the numerical dominance and crepuscular habits of kudu could have played a significant role in the nocturnal hunting and diet of the coalition.

The rates of kleptoparasitism were low for all cheetah groups and the kill retention time was significantly longer for single females and females with cubs than for the coalition and independent cubs. The rates of kleptoparasitism are higher in the savanna-like systems of the Serengeti (13.1%; Schaller, 1972; Caro, 1994), KNP (11.8%; Mills *et al.*, 2004) and Mala Mala (South Africa, 9.5%; Radloff & du Toit, 2004). Between these sites there is a trend for decreasing kleptoparasitism with increasing cover (Mills *et al.*, 2004), and this is supported by the results from our study where kleptoparasitism was recorded for the two social groups (coalition and females with cubs) that had the greatest percentages of open habitat in their home ranges and that made the greatest number of kills in the open habitat. Kill retention times in the Serengeti (136 min; Schaller, 1972) and KNP (165 min; Mills *et al.*, 2004) are much shorter than those at Kwandwe. It is likely that the lower rates of kleptoparasitism and the longer kill retention times in Kwandwe reflect the increased cover provided by the thicket vegetation, a lower level of competition from lions and the large size of the prey. Kill retention time will be affected by prey size, the number of cheetah feeding from the kill, the habitat in which the kill was made and the threat of kleptoparasitism. Therefore, while the coalition killed larger animals than single females, kill retention time was significantly shorter because the coalition comprised three adult males, many of the kills were made in the open and the coalition was the closest of all cheetahs to the pride of lions. By contrast, single adult females killed smaller animals that were concealed in thicket vegetation, and fed on by one adult animal for a longer period of time.

The home range of the coalition included the highest percentage of open habitat whereas the female groups and the independent cubs established home ranges with significantly more thicket habitat. Within these home ranges, the coalition spent more time, and the coalition and females with cubs hunted more in the open habitat than expected. This selection of open areas within a more densely vegetated region has been described previously for male cheetahs (Hunter, 1998; Purchase & du Toit, 2000; Broomhall *et al.*,

2003; Mills *et al.*, 2004) and has been interpreted as indicating that the species prefers open areas for hunting even when the prey density is lower than in adjacent more heavily wooded areas. The suggestion that habitat selection by male cheetahs is based on hunting requirements more than prey abundance is supported by results from the present study, where there was no significant difference in prey abundance in the home ranges of the different cheetah social groups. However, it seems likely that the home range of the coalition was positioned so as to incorporate a mix of open habitat for hunting and thicket habitat for cover. By contrast, female cheetahs make greater use of more heavily wooded habitats (Durant, 2000b; Broomhall *et al.*, 2003; present study), and this is widely interpreted as a predator avoidance strategy (Durant, 2000b). However, it should be noted that selection of more heavily wooded habitats need not be associated with decreased hunting success, and at Kwandwe hunting success was about 50% in the two habitat types. Thus, the factors that affect habitat selection differ for male and female cheetahs. Solitary females are more susceptible to predation and kleptoparasitism by lions and hyaenas and position their home ranges to include more heavily wooded areas than do adult males, who occur in functional groups and are less susceptible to predation. The home ranges of females were significantly farther from the pride than the home range of the coalition, and thus the females show both temporal (discussed earlier) and spatial predator avoidance (*sensu* Durant, 1998b, 2000a,b). By contrast, the coalition showed neither temporal nor spatial avoidance of the lions, supporting the suggestion that pressure from the lions was less intense than in many other systems.

We believe that these results provide strong support for the suggestion that the cheetah is more adaptable to habitat diversity than previously thought (Mills *et al.*, 2004). In particular, our results indicate that cheetahs can hunt successfully in thicket vegetation, where they have the additional benefit of reduced kleptoparasitism. The consequence of this is that nature reserves in the Eastern Cape Province (South Africa), with their characteristic valley bushveld vegetation, may be suitable sites for reintroductions of cheetahs.

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