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Source: Wildlife Biology, 10(3) : 177-186

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2004.024

Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains?

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Mills, M.G.L., Broomhall, L.S. & du Toit, J.T. 2004: Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? - Wildl. Biol. 10: 177-186.

The literature on cheetah *Acinonyx jubatus* ecology is dominated by studies on the Serengeti Plains (SNP) in East Africa. Because of this and the cheetah's hunting strategy it is generally considered to be a predator that prefers open grassland plains. However, cheetahs also inhabit a range of bush, scrub and woodland habitats. A field study using direct observations of radio-collared individuals in the woodland savanna habitat of the Kruger National Park (KNP), South Africa, and a literature review of studies across savanna habitats examined cheetah predation, hunting behaviour and habitat use in relation to prey composition, cover availability and kleptoparasitism. The cheetah's main prey is medium-sized herbivores, with a bias towards male prey. The group size and sex of the hunting cheetah may influence the results of prey selection studies as male coalitions tend to take larger prey than females. Cheetahs initiated more hunts and had a higher success rate in the open woodland savanna of the KNP compared to other available habitats with thicker bush, and in other wooded savanna areas they also prefer more open habitat for hunting. Although they appear to have shorter chase distances in more wooded habitats, hunting success appears to be slightly higher in open grassland habitat. Woody vegetation appears to obstruct the cheetah's high-speed hunting strategy, thereby lowering hunting success. However, cheetahs use cover for stalking prey and open habitats with bordering woodlands, or patches of cover are considered preferred cheetah habitats. In these habitats, cheetahs can stalk closer to their prey using available cover, but also successfully pursue their prey into available open spaces. Across African savanna ecosystems, cheetahs appear to be kleptoparasitised less in more wooded habitats. Therefore they may also prefer these habitats because they provide greater concealment from kleptoparasites. Our study suggests that the cheetah is more adaptable to habitat variability than is often thought and is not only a successful hunter on open grassland plains.

Key words: Acinonyx jubatus, African savannas, cheetah, feeding ecology, predation

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Received 28 November 2002, accepted 31 October 2003

Associate Editor: Urs Breitenmoser

The cheetah *Acinonyx jubatus* can easily reach a speed of 100 km per hour when hunting (Nowell & Jackson 1996). Such high-speed chases require good visibility and freedom from obstruction (Bertram 1979). Therefore, it is reasonable to assume that cheetahs require open habitats for successful hunting. The literature on cheetah ecology, which is dominated by studies conducted on the open grassland Serengeti Plains (SNP) in East Africa (Schaller 1972, Frame & Frame 1980, Caro 1986, Caro & Collins 1986, 1987, Durant, Caro, Collins, Alawi & Fitzgibbon 1988, Fitzgibbon & Fanshawe 1989, Fitzgibbon 1990, Laurenson, Caro, & Borner 1992, Caro 1994, Laurenson 1994, 1995a,b, Laurenson, Weilbnowlski & Caro 1995, Durant 1998), supports this assumption.

However, cheetahs also inhabit a wide range of bush, scrub and woodland habitats (Myers 1975, Marker-Kraus, Kraus, Barnett & Hurlbut 1996, Nowell & Jackson 1996, Purchase & du Toit 2000), although relatively little is known about their ecology and behaviour in these habitats. Woodland savannas, with a greater availability of cover than open plains, might inhibit cheetahs from attaining high speeds, but may confer other advantages not provided by grassland habitats. Cover is considered advantageous to cheetahs for stalking prey (Caro 1994, Purchase & du Toit 2000), because it enables them to get closer to the quarry before the chase, thereby reducing chase distance and improving hunting success (Eaton 1970, Fitzgibbon 1990, Caro 1994). Furthermore, cheetahs suffer from competition with the other large carnivores and are easily robbed of their prey (Schaller 1972, Bertram 1979, Mills 1990, Caro 1994, Nowell & Jackson 1996), so cover may also provide increased concealment to cheetahs after the hunt thereby reducing kleptoparasitism (Myers 1975, Zank 1995, Purchase & du Toit 2000).

As most cheetah studies have focused on grassland savannas, the comparative benefits of open spaces and cover in woodland savannas have not been fully explored. Additionally, no quantitative analysis has been done on variations in the use of prey by cheetahs across ecosystems. In this paper we aim to address these imbalances by: 1) adding to the existing knowledge on cheetah ecology and behaviour in woodland savannas by analysing data on cheetah predation, hunting behaviour and habitat use for hunting in the Kruger National Park (KNP), South Africa; 2) synthesising available information on cheetah predation in relation to prey composition, cover availability and kleptoparasitism from other studies (see Table 1); and 3) comparing this information across different African savanna ecosystems. Our hypothesis is that cheetah hunting behaviour varies as a function of habitat, and that the species is not exclusively a hunter on open plains. It is able to hunt adequately in savanna woodland habitats, which may even provide benefits not found on open plains. Testable predictions of this hypothesis are: (i) chase distances vary with habitat and are shorter in woodlands; (ii) hunting success rates (kills/hunting attempts) are comparable across habitats, but will be higher in more open habitats; and (iii) cheetah kills are kleptoparasitised less in wooded habitats than in open habitats.

Methods

Data collection in the KNP

We radio-tracked seven adult cheetahs during 1987-1990 in the southeastern region of the KNP (Broomhall 2001). These were a three-male coalition (M3), a single male (M1), a two-male coalition (M2), and four females with or without cubs (F1, F2, F3 and F4). Three types of data collection were used, based on the duration of the observation period (Mills 1992): 1) radio-location observations, which included recording the position of the animal, the habitat it was in, and kill data where applicable; 2) short-term continuous observations, when radio-collared cheetahs were followed by vehicle for periods of 2-15 hours; and 3) three long-term continuous observations, when cheetahs were followed more or less continuously for 14 days each (two periods for M3 and one for F1). All methods of data collection have biases, but where possible direct observations of animals have obvious advantages. However, following animals in a vehicle particularly, in wooded environments, needs to be carefully executed, as the observers have to keep relatively close to the animal in order to maintain visual contact. We are unable to measure the influence this may have had on our results, but we were always careful to be as unobtrusive as possible and to hold back when the cheetahs located prey. As the observations were mainly made in daylight and the animals were radio collared it was possible to do this without missing any kills. The study area has a very high tourism impact so that most of the animals, both predator and prey, are well habituated to vehicles.

All three types of data were collected for M3 and F1, data types 1) and 2) for F2 and data type 1) only for the remaining animals. The following parameters for data types 2) and 3), were recorded when cheetahs encountered potential prey: habitat, prey species, sex and approximate age of prey, chase distance (estimated using the vehicle's odometer), kill retention time (i.e. length of time spent at the carcass, including resting periods at the carcass), and whether the carcass was appropriated by other predators (i.e. kleptoparasitism). Kills were observed until the cheetah left the carcass or the kill was kleptoparasitised. Age of prey was estimated according to tooth eruption; juveniles had erupting teeth and adults full permanent dentition.

Prey encounters were classified as: 1) a kill, 2) a failure, where cheetahs either stalked (i.e. spent at least three minutes intently watching the prey from a concealed position, and/or moved at least 5 m closer to the prey while seemingly trying not to be detected by the prey), or moved towards the prey at a faster than normal walking speed, including fast chases, but the prey escaped, or 3) no attempt, where the cheetah detected prey, but did not attempt to hunt in the manner described above. Habitat was recorded at the landscape level (Gertenbach 1983), as 1) open tree savanna plains with a moderate shrub and dense grass layer, 2) dense *Acacia* thickets and 3) undulating to steep Lebombo Hills with dense to moderate bush.

Analysis of KNP data

Kill data collected through radio locations and direct observations were combined for analyses as Mills (1992) and Hunter (1998) found no significant differences between these two methods in terms of bias for kills. To analyse for differences between male and female cheetah diets, prey items were separated into small (< 18 kg), medium (18-65 kg), and large (> 65 kg) weight classes, at two levels: 1) the estimated weight of the prey item according to the species, sex and age, and 2) the average weight of adult male and female animals of the prey species. Prey weights were obtained from Meissner (1982) and Owen-Smith (1988). Relative availability of male and female impala *Aepyceros melampus* (the dominant prey) was calculated using the average sex ratio recorded for impala (1.68 females/male) between 1986 and 1989 in the KNP (Mason 1990).

Average kill rates were determined using the three 14-day continuous observation periods only as Mills (1992) found that long-term direct observation periods were least likely to inflate kill frequency. To convert kill rate into kilogrammes of meat consumed/cheetah/day, the total weight of the prey items killed by the cheetahs were estimated using weight values for the different species according to sex and ages obtained from Meissner (1982) and Smithers (1983). Blumenschine & Caro's (1986) estimated weight of flesh of an eviscerated adult Thomson's gazelle *Gazella thomsonii* carcass agreed with Schaller's (1972) estimate that cheetahs consume 60% of the animal. To facilitate comparison, therefore, it was assumed that approximately 60% of the total weight of an adult impala, 65% of juvenile prey (Blumenschine & Caro 1986) and 90% of very small prey, in this case a scrub hare *Lepus saxatilis*, was edible.

Frequency data for hunting and killing across habitat types were derived by combining the hunting locations of three cheetahs (M3, F1 and F2) and kill locations of four cheetahs (M3, F1, F2 and F3). For each analysis, a minimum convex polygon was drawn around the cheetahs' home ranges to determine the area (in km^2) available for hunting and killing in the three habitat types using GIS Arcview (Broomhall, Mills & du Toit 2003). A chi-square goodness-of-fit test was used to determine if cheetahs were killing impala in proportion to their relative availability in the different habitat types (Hunter 1998). Relative availability was determined by using the unpublished annual aerial impala census data (Viljoen, Rochat & Wood 1994) to calculate the mean number of impala per habitat type for the study area. Impala density (animals/km^2) was calculated for each habitat type. Following any significant results from the above chi-square tests, Bonferroni confidence intervals were performed to determine preference or avoidance by cheetahs of particular habitat types (Neu, Byers & Peek 1974, Byers & Steinhorst 1984).

Across-ecosystem comparisons

For a comparison of prey composition (prey size and age) across different savanna ecosystems, suitable data were synthesised from 10 different studies in southern and East Africa. Study sites were as follows: East Africa (Graham 1966), a broad survey conducted across Uganda, Tanzania and Kenya, Serengeti National Park (SNP; Kruuk & Turner 1967), Kafue National Park (Kafue NP; Mitchell, Shenton & Uys 1965), Matusadona National Park (MNP; Zank 1995), the Kgalagadi Transfrontier Park (KTP; Mills 1984), Suikerbosrand Nature Reserve (SBNR; Pettifer 1981a), Phinda Resource Reserve (PRR; Hunter 1998), Mala Mala Game Reserve (MM; Radloff & du Toit 2004); Timbavati & Klaserie Private Nature Reserves (TNR; Pettifer 1981b), and KNP (this study).

For each study site, prey was divided into adults and juveniles for small, medium and large prey species as above. Laurenson (1995b) classified medium-sized prey

Table 1. Habitat description in selected cheetah study sites across southern and East Africa. Each study site was ranked subjectively for cover availability, where the site with the least amount of cover was given a value of one; see Fig. 1.

Study sites	Habitat description	Rank	Source
Serengeti Plains (SNP), Tanzania	Short to long, open grass plains (kopjes and drainage systems on the plains contained some wooded vegetation)	1	Caro 1994
Kgalagadi Transfrontier Park (KTP), South Africa & Botswana (riverbeds only)	*Acacia erioloba* and *Acacia haematoxylon* trees, tall shrubs and grasses. Limestone plains dominated by dwarf shrubs and perennial grasses flank riverbeds in most areas	2	Mills 1998
Nairobi National Park (NNP), Kenya	Rolling *Themeda triandra* grassland-*Acacia* savanna, open grassland plains, and some heavy bush	3	Eaton 1970, 1974
Kruger National Park (KNP), South Africa (south-eastern region only)	Open *Sclerocarya birrea*/*Acacia nigrescens* tree savanna bordered to east by *Combretum* tree savanna in Lebombo Hills and to the west by *Acacia welwitschii* thickets	4	Gertenbach 1983
Mala Mala Game Reserve (MM), South Africa	Mixed *Combretum* sp./*Terminalia sericea* woodland. Dense bush savanna on the uplands, open tree savanna in the bottomlands and dense riverine vegetation	5	Gertenbach 1983
Timbavati & Klaserie Private Nature Reserves (TNR), South Africa	Heterogeneous bushveld varying from open woodland to moderately dense riparian woodland. *Acacia nigrescens*, *Combretum* spp. and *Colophospermum mopane* woodlands dominate	5	Kruger 1988 De Villiers 1995

as ranging within 15-60 kg, so this was adjusted slightly to facilitate analysis in this study. Prey weights were obtained from Owen-Smith (1988) where the average weight of adult males and females determined the size category of the prey. The adults and juveniles of small prey were combined because studies often did not classify small prey items in this manner; particularly when considering prey items such as birds, hares, rodents and small carnivores. Studies with no reported kills of small prey were excluded from the analysis as small prey are known to form a significant part of the cheetah's diet (Labuschagne 1979), but are often underrepresented in studies due to the method of data collection used by the researcher (Mills 1992).

Further comparisons across ecosystems were conducted concerning hunting success, chase distance, kleptoparasitism, kill retention time and kill rates. Study sites for these analyses were SNP (Schaller 1972, Caro 1994), Nairobi National Park (NNP; Eaton 1970, McLaughlin 1970 cited by Schaller 1972), KTP (Labuschagne 1979), MM (G.T. Radloff, unpubl. data), PRR (Hunter 1998), TNR (Pettifer 1981b), Suikerkop Nature Reserve (SNR; Pettifer 1981b), and KNP (this study). The relationships between cover availability and various parameters pertaining to feeding ecology, i.e. chase distance, hunting success and kleptoparasitism, were explored. For these analyses, study areas were ranked according to cover availability (open to closed cover), where the area with the least amount of cover was given a value of one (Table 1). Kleptoparasitism values were not standardised to control for variation in predator density because the SNP and KNP had similar total densities of lion *Panthera leo* and spotted hyaena *Crocuta crocuta* (Stander 1991), and it was assumed that MM, which adjoins the KNP and is unfenced, had the same predator density as the KNP.

Results

Cheetah in the KNP

Of the nine prey species observed to be killed by cheetahs in the southeastern KNP, impala were the most frequent for both males and females (Table 2). For all prey species, cheetahs took more juveniles (61%) than adults (39%), particularly of large prey species, although male

Table 2. Cheetah prey composition in the Kruger National Park.

	Male cheetahs				Female cheetahs				All cheetahs	
Prey	Adult	Juvenile	Unknown	Total	Adult	Juvenile	Unknown	Total	Total	%
Large	1	14		15		1		1	16	23.5
Zebra		5		5		1		1	6	8.8
Waterbuck	1	5		6				0	6	8.8
Kudu		4		4					4	5.9
Medium	9	6		15	10	9		19	34	50.0
Impala	9	4		13	9	9		18	31	45.6
Reedbuck				0	1			1	1	1.5
Warthog		2		2				0	2	2.9
Small		3	1	4	6	7	1	14	18	26.5
Grey duiker		3		3	2	3		5	8	11.8
Steenbok				0	4	4		8	8	11.8
Scrub hare			1	1			1	1	2	2.9
Total	10	23	1	34	16	17	1	34	68	100

Table 3. Cheetah hunting behaviour and density of impala in different habitat types in the southeastern region of the Kruger National Park.

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

cheetahs took impala adults more frequently than juveniles. Of the 18 adult impala killed, 78% were male and 22% were female. Cheetahs preyed on male and female impala at significantly higher and lower frequencies, respectively, than their availability would predict (χ^2 = 12.7, df = 1, P < 0.001).

There was a difference in the way in which male and female cheetahs utilised prey of different weight and size classes. The male cheetahs' diet consisted of a greater proportion of larger prey items (21, 68 and 12% large-, medium- and small-weighted prey, respectively), while female cheetahs caught smaller prey items (44 and 56% of medium- and small-weighted prey, respectively). When comparing male and female cheetah selection of prey based on average adult size, there was a significant difference (χ^2 = 18.3, df = 2, P < 0.0001). The males' diet consisted of larger prey species, such as kudu *Tragelaphus strepsiceros*, waterbuck *Kobus ellipsiprymnus* and zebra *Equus burchelli*, whereas the females caught common duiker *Sylvicapra grimmia* and steenbok *Raphicerus campestris*.

Although the hunting success for the three male coalition (M3) was higher (25%) than for the two female groups (16 and 17%, respectively) this was not significant (χ^2 = 2.32, df = 1, P > 0.05). However, the frequency of hunting attempts per prey encounter (45 vs 69 and 71%, respectively) was significantly higher in the female groups (χ^2 = 5.758, df = 1, P < 0.05). Kill rates for M3 were 1 kill/7 days (or 1.4 kg meat/cheetah/day) and 1 kill/3.5 days (or 1.4 kg meat/cheetah/day) for two 14-day continuous observation periods. Although F1 accompanied by two large cubs was followed for one 14-day continuous observation period, the kill and consumption rates were not accurately determined as contact was lost with these animals for 17 hours. However, judging by their stomach sizes when relocated they had obviously not made a big kill, although a small kill may have been made. At least two kills were made during the 14-day period, giving a minimum kill rate of 1 kill/4.6 days. One of the kills was kleptoparasitised by a spotted hyaena, so the minimum amount of meat consumed by the three animals was approximately 0.4 kg meat/cheetah/day. Using the pooled data for males and females, a significant difference was found between the mean chase distance of successful ($\bar{x}$ = 189 m, SE = 22.9, N = 26) versus unsuccessful ($\bar{x}$ = 96 m, SE = 9.41, N = 89) hunts (t = 4.36, df = 113, P < 0.0001). The mean kill retention time was 165 minutes (SE = 59, N = 9). When combining data of males and females, kleptoparasitism was 12% (N = 34).

In Table 3 aspects of the cheetahs' hunting behaviour in the three habitat types are analysed. Once prey was detected, cheetahs attempted more hunts per prey encounter in the open savanna than in *Acacia* thickets and the Lebombo Hills, with significantly more hunts than expected in the open savanna and less than expected in the *Acacia* thickets (χ^2 = 153, df = 1, P < 0.0001). Hunting success (kills/hunting attempt) was also greater, but not significantly so, in the open savanna than in the *Acacia* thickets. The frequency of kills per habitat type was significantly different from the expected based on habitat available for killing within the cheetahs' home ranges (χ^2 = 11.3, df = 2, P < 0.01), most kills being made in the open savanna. The frequency of hunting attempts per habitat type also differed significantly from the expected based on habitat available for hunting within the cheetahs' home ranges (χ^2 = 14.9, df = 2, P < 0.001), with most hunting attempts also occurring in the open savanna. Of the three available habitat types, Bonferroni confidence limits indicated that the open savanna was used significantly more and the Lebombo Hills significantly less than expected for killing and hunting. The *Acacia* thickets were used significantly less than expected for killing but were used in proportion to availability for hunting (Table 4). Impala were killed at significantly different frequencies to those predicted based on their occurrence across different habitat types (χ^2 = 22.5, df = 2, P < 0.0001), with more being killed

Table 4. Habitat selection by cheetahs for killing, hunting and hunting impala in the southeastern region of the Kruger National Park. The symbols indicate whether use was significantly greater (+), less (-) or no different (0) to the expected use based on the proportion of habitat available within the cheetahs' home ranges for killing and hunting, and the proportion of impala available in the different habitat types. The level of significance was set at 0.05.

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

Table 5. Proportions (in %) of size categories and age classes of cheetah prey in 10 study sites across southern and East Africa. The size categories include: small- (< 18 kg), medium- (18-65 kg) and large-sized prey (> 65 kg).

Study site[1]	N	Small	Medium		Large		Source
			Adult	Juvenile	Adult	Juvenile	
East Africa	173	15.8	52.0	13.5	7.0	11.7	Graham 1966
SNP	33	4.3	52.2	4.3	8.7	30.4	Kruuk & Turner 1967
KTP	229	1.7	65.8	18.1	6.8	7.6	Mills 1984
Kafue NP	33	3.8	11.5	15.4	42.3	26.9	Mitchell et al. 1965
MNP	41	14.6	53.7	24.4	4.9	2.4	Zank 1995
SBNR	215	11.9	56.3	31.8	0.0	0.0	Pettifer 1981b
PRR		8.1	22.1	23.4	22.1	24.3	Hunter 1998
KNP	68	27.3	27.3	22.7	0.0	22.7	This study
MM		24.4	25.9	42.9	0.4	6.4	Radloff & du Toit 2004
TNR	36	10.5	36.8	5.3	10.5	36.8	Pettifer 1981a
Mean		12.2	40.4	20.2	10.3	16.9	
Standard error		2.71	5.69	3.70	4.12	4.06	

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

in the open savanna. Bonferroni confidence limits indicated that cheetah killed significantly more impala in the open savanna and significantly less impala in the Lebombo Hills than expected, while they were killed in proportion to their availability in the *Acacia* thickets (see Table 4). The densities of impala were higher in the Lebombo Hills and *Acacia* thickets than the open savanna.

Across-ecosystem comparisons

In 10 study sites across southern and East Africa, the adults of medium-sized prey (18-65 kg) occurred most frequently in the cheetah's diet, followed by the juveniles of medium- and large-sized prey (Table 5). There was, however, a significant variation in the size and age groups of prey taken by cheetahs across study sites (ANOVA: $F = 7.406$, $df = 49$, $P < 0.0001$). In the KNP, impala were the most abundant prey and the most common species in the cheetah's diet (see Table 2). On the SNP, it was Thomson's gazelle (Kruuk & Turner 1967, see also Caro 1994) and in KTP springbok *Antidorcas marsupialis* (Mills 1984). All these species are in the medium-sized prey category.

In Kafue NP, SBNR and PRR, cheetahs selected a large proportion of adults in the large-size category (> 65 kg), namely puku *Kobus vardoni*, blesbok *Damaliscus pygargus* and nyala *Tragelaphus angasi*, respectively (Mitchell et al. 1965, Pettifer 1981a, Hunter 1998), compared to others areas. The average weight of male and female puku, however, is 67 kg, and therefore borders close to the division between medium- and large-sized prey. In SBNR there was a preferred selection for blesbok females (60 kg) and juveniles, which Pettifer (1981a) explained may have been due to males weighing up to 80 kg. Hunter (1998) suggested that the behaviour of nyala (average weight: 85 kg) browsing in more open areas near cover and their sluggish nature made them more vulnerable to cheetah predation.

In the SNP, Kafue NP, PRR, KNP and TNR cheetahs utilised a greater proportion of juveniles of large prey, and in KNP and MM cheetahs took a greater proportion of small-sized prey compared to other areas.

Relationships between the rank of cover per study site and chase distance in successful hunts, percent hunting success and percent kleptoparasitism are shown in Figure 1 and Table 6. This small data set suggests that chase distances, hunting success and amount of klep-

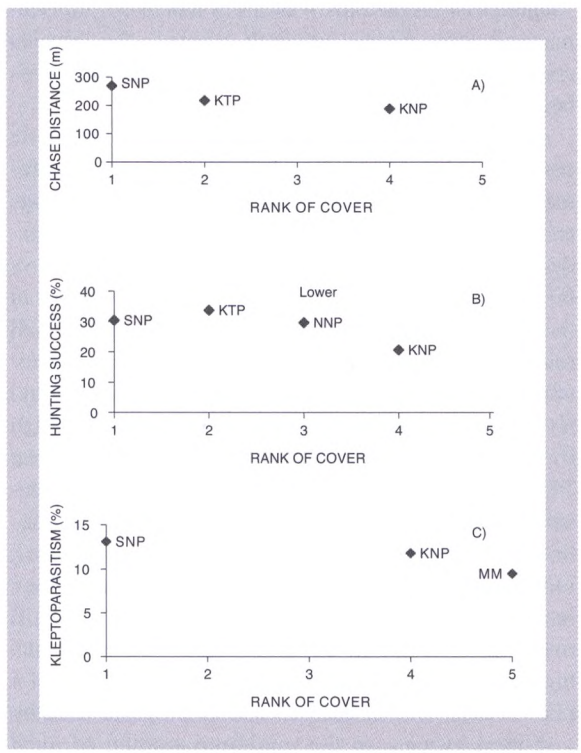

Figure 1. Relationship between rank of cover at a study site and mean chase distance (A; in m) in successful hunts, hunting success (B; in %), and kleptoparasitism (C; in %). See Table1 for key to protected area initials and brief descriptions of the habitat in each area.

Table 6. Aspects of cheetah hunting behaviour and incidents of kleptoparasitism in eight study sites across southern and East Africa. ** indicate that no data are available.

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

[1] *SP*: Serengeti Plains; *KTP*: Kgalagadi Transfrontier Park; *NNP*: Nairobi National Park; *KNP*: Kruger National Park; *MM*: Mala Mala Game Reserve; *PPR*: Phinda Resource Reserve; *TNR*: Timbavati & Klaserie Private Nature Reserves; *SNR*: Suikerkop Nature Reserve.
[2] cited by Schaller (1972)

toparasitism are higher in more open areas, but that the differences between habitats are not great. Study sites with the least cover had the longest mean chase distance, while those with greatest cover had the shortest mean chase distance. All study sites had longer chase distances for successful hunts (see Table 6). No patterns were found in mean kill retention time and kill rate across study sites (see Table 6).

Discussion

Prey selection

Diet preferences of cheetahs in different areas reflect differences in prey species and their abundance (Stander 1991, Caro 1994, Mills 1998; see Table 5). The cheetah's main food, however, is medium-sized prey, which represents an average of 60% of the diet across ecosystems (see Table 5). The juveniles of large-sized prey also form an important part of the diet in many areas, most of these fall into the medium-sized prey category (18-65 kg).

In the KNP study, smaller prey formed a significantly more important part of the female cheetah group's diets than of the three-male cheetah coalition (see Table 2). This is at least partially explained by the fact that the size and composition of the hunting group may affect prey size and species (Eaton 1974, McVittie 1979, Caro 1994). In PRR, Hunter (1998) found that male cheetah coalitions killed mostly male nyala (120-130 kg) while female cheetahs killed mostly female nyala (60-70 kg). In the SNP, Caro (1994) also found that larger groups of cheetah hunted wildebeest *Connochaetes taurinus* more often than did smaller groups. Therefore, the group size and sex of the animals observed may influence the results of prey selection studies.

Small prey represented an average of 12% in the cheetah's diet across the African savanna study sites (see Table 5). Small prey, however, are usually underrepresented (Stander 1991, Mills 1992) because studies often depend on data from carcass remains (Pienaar 1969, Pettifer 1981a) or opportunistic observations (Mitchell et al. 1965). Kills of small prey are usually unobserved because of the rapid consumption time and lack of remains (Mills 1992). The large percentage of small prey recorded in the cheetah's diet in this study (27%) and in Radloff & du Toit's (2004) study in Mala Mala (24%) are probably more representative of the proportion of small prey because these studies relied mainly on continuous observation data (see Methods). Alternatively, these are the areas with the highest cover values (see Table 1), and so the habitat structure may also account for the higher kill rate of smaller prey.

Preferences by cheetahs for male impala in the KNP study are paralleled by cheetahs' preferences in SNP for male Thomson's gazelle (Fitzgibbon 1990) and in KTP for male springbok (Mills 1990). Fitzgibbon (1990) describes how male gazelle are more vulnerable than females and preferentially selected by cheetahs because they tend to occur on the periphery of groups, have greater nearest-neighbour distances, are less vigilant and are found in smaller groups than females. The same conditions may apply to male impala and springbok as they show similar social structures and behaviour (Estes 1991). As males are more expendable than females, this greater vulnerability of males to predation has the effect of lessening the impact of predation on prey populations.

Kill rate and consumption

Group size, presence of cubs, prey size and availability, habitat structure and competition with other predators affect kill rates (Pettifer 1981a, Caro 1994, Durant 2000, this study). These probably explain the large variations found in cheetah kill rate across African

savanna ecosystems (see Table 6). The rate of food consumption needed to keep a cheetah in healthy condition in a zoological garden is 1.3-1.8 kg/day (Crandall 1964). Although the calorific needs of zoo animals are lower than those of wild cheetahs, captive animals are usually fatter; therefore the male cheetah coalition in the KNP appeared to be obtaining an adequate diet (1.4 kg/cheetah/day). The female cheetah's (F1) consumption rate, with two large cubs, was considerably lower (0.4 kg/day), although as explained this figure may be slightly lower than the actual figure. However, Caro (1994) estimated that cheetah mothers with old offspring ate as little as 0.5 kg/day because of direct competition from their large cubs.

Kill retention time

Kill retention time may be affected by group size, prey size, predator densities, knowledge of competing predators (Schaller 1972, Pettifer 1981b, Hunter 1998), or amount of available cover. These may explain the large variation found in kill retention times across ecosystems (see Table 6). In SNR, TNR and PRR, cheetahs were acquired from captive-breeding programmes (Pettifer 1981b) or Namibia (Hunter 1998) for re-introductions, and had not been subjected to competition from other large predators. Pettifer (1981b) discussed this as the reason for the exceptionally long kill retention times in SNR and TNR. Hunter (1998) attributed the lack of direct competition in PRR to the long hours cheetahs spent at carcasses. Differences in kill retention time between the SNP and KNP, with similar densities of competing predators (Stander 1991) were similar, although differences in availability of cover would have predicted shorter retention times in more open habitat.

Hunting and habitat

Cheetahs initiated more hunts and killed more frequently in the open savanna of the KNP than in other available habitats with thicker bush (see Table 3). It is important to note, however, that KNP open savanna is not like the open grassland plains of the Serengeti. It is an open woodland with a moderate shrub layer and tall grass throughout. The preference by cheetahs for the most open habitat in the KNP for hunting (see Table 4) is particularly evident when considering that the cheetah's main prey (impala) occurred at greater densities in the *Acacia* thickets and Lebombo Hills (see Table 3), yet were hunted and killed significantly more in the open savanna (see Table 4). In PRR, which consists of overlapping open to closed bushveld habitat, cheetahs also preferred the open grasslands for hunting (Hunter 1998) and in MNP, cheetahs used the open foreshore grassland predominantly for hunting (Purchase & du Toit 2000).

Chase distance and hunting success

Chase distances and hunting success are difficult to measure (Mills 1990), and comparisons between studies are difficult to make. Nevertheless, chase distances appear to be shorter in more wooded habitats, the average for KNP was 2.3 times less than the average for SNP (Prediction I; see Fig. 1A and Table 1). Caro's (1986) study on the SNP and Eaton's (1974) study in Nairobi National Park found that cheetahs were more likely to be successful at hunting when they were able to get closer to their prey before rushing. Compared to the KTP and SNP, cheetahs in the KNP had significantly longer chase distances in successful (189 m) than in unsuccessful hunts (96 m; see Table 6). The success of longer chase distances indicates that cheetahs are able to quickly gauge their chances of success in a chase and give-up early if failure is predicted.

Hunting success rates between studies did not vary greatly but appeared to be higher in more open habitats (Prediction ii; see Fig. 1B and Table 1). In the KNP, cheetahs also appeared to have a greater hunting success and hunted more often in the open savanna habitat (see Tables 3 & 4). Therefore, greater tree and shrub cover in woodland habitats may obstruct the cheetah's high-speed hunting strategy, thereby lowering hunting success.

Kleptoparasitism

Across African savanna ecosystems, cheetahs appeared to be kleptoparasitised less in more wooded habitats (Prediction iii; see Fig. 1C and Table 1). Paulson (1985) considered four effects that open habitat has on host and parasite, three of which are relevant to cheetahs: 1) kleptoparasites can observe and follow hosts more easily, 2) kleptoparasites can observe prey capture and carrying, and 3) hosts are less able to hide from kleptoparasites. Considering these effects, cheetahs in an open grassland ecosystem like the SNP, with a short to medium grass layer, are expected to be more vulnerable to kleptoparasitism than in areas like the KNP (Myers 1975).

Conclusion

In this study, sample size in relation to the number of individual animals observed in the KNP and the number of areas available for comparison are small. Notwithstanding, the data suggest that in addition to being a suc-

cessful open plains hunter the cheetah is also able to function efficiently in more wooded areas. However, in woodland areas cheetahs prefer the more open habitats for hunting. Apparently shorter chase distances in more wooded habitats is offset by higher hunting success in more open habitat. Woody vegetation appears to obstruct the cheetah's high-speed hunting strategy, but cover is useful for stalking prey (Fitzgibbon 1990). Open habitats with bordering woodlands or patches of woody cover may be optimal cheetah habitats. Gros & Rejmánek (1999) conducted a cheetah habitat study in Uganda, based on presence/absence in particular habitat types, which suggested that cheetahs favoured habitats with 25-50% woody cover and grasses of medium height (50-100 cm). Cheetahs may also prefer these habitats because they provide greater concealment and may reduce the risk of kleptoparasitism. Further studies are required in woodland habitats to expand the database and to obtain a greater understanding of the use and benefits of woodlands to cheetah populations.

Acknowledgements - we thank South African National Parks, National Research Foundation, Mammal Research Institute, University of Pretoria and the Endangered Wildlife Trust for financial support to carry out the study and the Tony and Lisette Lewis Foundation for support to M.G.L. Mills. The late Ross English, Bryan Havemann, John Mabaso, Louis Olivier and Heather Wildi helped with field work. Jaco Barendse, Human Buirski, Elmarie Cronje, Michelle Greyling, Martin Haupt and Pat Flectcher helped during the analyses and write up.

References

Bertram, B.C.R. 1979: Serengeti predators and their social systems. - In: Sinclair, A.R.E. & Arcese, P. (Eds.); Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, pp. 221-249.

Blumenschine, R.J. & Caro, T.M. 1986: Unit flesh weights of some East African bovids. - African Journal of Ecology 24: 273-286.

Broomhall, L.S. 2001: Cheetah Acinonyx jubatus ecology in the Kruger National Park: A comparison with other studies across the grassland-woodland gradient in African savannas. - Unpublished M.Sc. thesis, University of Pretoria, South Africa, 115 pp.

Broomhall, L.S., Mills, M.G.L. & du Toit, J.T. 2003: Home range and habitat use by cheetahs (Acinonyx jubatus) in the Kruger National Park. - Journal of Zoology (London) 261: 119-128.

Byers, C.R. & Steinhorst, R.K. 1984: Clarification of a technique for analysis of utilization-availability data. - Journal of Wildlife Management 48: 1050-1053.

Caro, T.M. 1986: The functions of stotting in Thomson's gazelles: some tests of the predictions. - Animal Behaviour 34: 663-684.

Caro, T.M. 1994: Cheetah of the Serengeti Plains: Group living in an asocial species. - The University of Chicago Press, Chicago, 478 pp.

Caro, T.M. & Collins, D.A. 1986: Male cheetahs of the Serengeti. - National Geographic Research 2: 75-86.

Caro, T.M. & Collins, D.A. 1987: Ecological characteristics of territories of male cheetahs (Acinonyx jubatus). - Journal of Zoology (London) 211: 89-105.

Crandall, L.S. 1964: The management of wild animals in captivity. - University of Chicago Press, Chicago, 761 pp.

De Villiers, P.A. 1995: Aspects of the behaviour and ecology of elephant (Loxodonta africana, Blumenbach, 1797) in the eastern Transvaal Lowveld with special reference to environmental interactions. - Unpublished PhD thesis, University of the Orange Free State, Bloemfontein, 269 pp.

Durant, S.M. 1998: Competition refuges and coexistence: an example from Serengeti carnivores. - Journal of Animal Ecology 67: 370-386.

Durant, S.M. 2000: Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. - Behavioural Ecology 11: 624-632.

Durant, S.M., Caro, T.M., Collins, D.A., Alawi, R.M. & Fitzgibbon, C.D. 1988: Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. - African Journal of Ecology 26: 257-268.

Eaton, R.L. 1970: Hunting behaviour of the cheetah. - Journal of Wildlife Management 34: 56-67.

Eaton, R.L. 1974: The cheetah: the biology, ecology and behaviour of an endangered species. - Van Nostrand Reinhold Company, New York, 178 pp.

Estes, R.D. 1991: The behaviour guide to African mammals. - The University of California Press, Berkeley, 611 pp.

Fitzgibbon, C.D. 1990: Why do cheetahs prefer hunting male gazelles? - Animal Behaviour 40: 837-45.

Fitzgibbon, C.D. & Fanshawe, J.H. 1989: The condition and age of Thomson's gazelle killed by cheetahs and wild dogs. - Journal of Zoology (London) 218: 99-108.

Frame, G.W. & Frame, L.H. 1980: Cheetahs: In a race for survival. - National Geographic 157: 712-28.

Gertenbach, W.P.D. 1983: Landscapes of the Kruger National Park. - Koedoe 26: 9-121.

Graham, A. 1966: East African Wildlife Society cheetah survey: extracts from the report by wildlife services. - East African Wildlife Journal 4: 50-55.

Gros, P.M. & Rejmánek, M. 1999: Status and habitat preferences of Uganda cheetahs: An attempt to predict carnivore occurrence based on vegetation structure. - Biodiversity and Conservation 8: 1561-1583.

Hunter, L.T.B. 1998: The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa. - PhD thesis, University of Pretoria, 206 pp.

Kruger, J.E. 1988: Interrelationships between larger carnivores

of the Klaserie Private Nature Reserve with special reference to the leopard (Panthera pardus (Linnaeus, 1758)) and the cheetah (Acinonyx jubatus, Schreber, 1775). - M.Sc. thesis (Wildlife Management), University of Pretoria, 227 pp.

Kruuk, H & Turner, M. 1967: Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. - Mammalia 31: 1-27.

Labuschagne, W. 1979: 'n Bio-ekologiese an gedradstudie van die jagluiperd Acinonyx jubatus jubatus (Schreber, 1776). - M.Sc. thesis, University of Pretoria, 132 pp. (In Afrikaans).

Laurenson, M.K. 1994: High juvenile mortality in cheetahs (Acinonyx jubatus) and its consequences for maternal care. - Journal of Zoology (London) 234: 387-408.

Laurenson, M.K. 1995a: Behavioural costs and constraints of lactation in free-living cheetahs. - Animal Behaviour 50: 815-826.

Laurenson, M.K. 1995b: Implications of high offspring mortality for cheetah population dynamics. - In: Sinclair A.R.E & Arcese, P. (Eds.); Serengeti II: Dynamics, Management and Conservation of an Ecosystem. University of Chicago Press, Chicago, pp. 385-399.

Laurenson, M.K., Caro, T.M. & Borner, M. 1992: Female cheetah reproduction. - National Geographic Research and Exploration 8: 64-75.

Laurenson, M.K, Weilbnowlski, N. & Caro, T.M. 1995: Extrinsic factors and juvenile mortality in cheetahs. - Conservation Biology 9: 1329-1331.

Marker-Kraus, L., Kraus, D., Barnett, D. & Hurlbut, S. 1996: Cheetah survival on Namibian farmlands. - Cheetah Conservation Fund, Windhoek, 85 pp.

Mason, D. 1990: Monitoring of ungulate population structure in the Kruger National Park. - Unpublished report, SAN Parks, 32 pp.

McVittie, R. 1979: Changes in the social behaviour of South West African cheetah. - Madoqua 2: 171-184.

Meissner, H.H. 1982: Classification of farm and game animals to predict carrying capacity. - In: Farming in South Africa C3, Department of Agriculture and Fisheries, Pretoria, 4 pp.

Mills, M.G.L 1984: Prey selection and feeding habits of the large carnivores in the southern Kalahari. - Koedoe 27 (Suppl.): 281-294.

Mills, M.G.L. 1990: Kalahari hyenas: the comparative behavioural ecology of two species. - Chapman & Hall, London, 304 pp.

Mills, M.G.L. 1992: A comparison of methods used to study food habits of large African carnivores. - In: McCullough, D.R. & Barrett, R.H. (Eds.); Wildlife 2001: Populations. Elsevier Applied Science, London and New York, pp. 1112-1124.

Mills, M.G.L. 1998: Cheetah ecology and behaviour in East and South Africa. - In: Penzhorn, B.L. (Ed.); Cheetahs as game ranch animals. Proceedings of a symposium on cheetahs as game ranch animals, Onderstepoort, 23-24 October, pp. 18-22.

Mitchell, B.L., Shenton, J.B. & Uys, J.C.M. 1965: Predation on large mammals in the Kafue National Park, Zambia. - Zoologica Africana 1: 297-318.

Myers, N. 1975: The cheetah Acinonyx jubatus in Africa. - IUCN Monograph No. 4. IUCN, Morges, Switzerland, 88 pp.

Neu, C.W., Byers, C.R. & Peek, J.M. 1974: A technique for analysis of utilization-availability data. - Journal of Wildlife Management 38: 541-545.

Nowell, K & Jackson, P. 1996: Wild Cats: Status survey and conservation action plan. - IUCN, Gland, Switzerland, The Burlington Press, Cambridge, 382 pp.

Owen-Smith, R.N. 1988: Megaherbivores: the influence of large body size on ecology. - Cambridge University Press, Cambridge, 369 pp.

Paulson, D.R. 1985: The importance of open habitat to the occurrence of kleptoparasitism. - Auk 102: 637-639.

Pettifer, H.L. 1981a: Aspects on the ecology of cheetah (Acinonyx jubatus) on the Suikerbosrand Nature Reserve. - In: Chapman, J.A. & Punsley, D. (Eds.); Proceedings of the First World Furbearer Conference. University of Maryland, Frostburg, Virginia, pp. 1121-1142.

Pettifer, H.L. 1981b: The experimental release of captive bred cheetah into the natural environment. - In: Chapman, J.A. & Punsley, D. (Eds.); Proceedings of the First World Furbearer Conference. University of Maryland, Frostburg, Virginia, pp. 1001-1013.

Pienaar, U. De V. 1969: Predator-prey relationships amongst the larger mammals of the Kruger National Park. - Koedoe 12: 108-176.

Purchase, G. & du Toit, J.T. 2000: The use of space and prey by cheetahs in Matusadona National Park, Zimbabwe. - South African Journal of Wildlife Research 30: 1-6.

Radloff, F.G. & du Toit, J.T. 2004: Large predators and their prey in a southern African savanna: a predators body size determines prey size range. - Journal of Animal Ecology 73: 410-423.

Schaller, G.B. 1972: The Serengeti Lion: A study of predator-prey relations. - The University of Chicago Press, Chicago, 480 pp.

Smithers, R.H.N. 1983: The mammals of the southern African subregion. - University of Pretoria, Pretoria, 736 pp.

Stander, P.E. 1991. Aspects of the ecology and scientific management of large carnivores in sub-Saharan Africa. - M.Sc. thesis, University of Cambridge, 118 pp.

Viljoen, P.C., Rochat, M.A. & Wood, C.A. 1994: Ecological aerial survey in the Kruger National Park 1993. - Unpublished National Parks Board Scientific Report 1/94, 47 pp.

Zank, C.M. 1995: Population viability analysis for cheetah in Matusadona National Park, Zimbabwe. - M.Sc. thesis, University of Zimbabwe, 126 pp.