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

4.1 INTRODUCTION

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

Cheetahs, however, also inhabit a wide range of bush, scrub and woodland habitats (Myers 1975; Skinner & Smithers 1990; Nowell & Jackson 1996; Mills & Hes 1997), although in comparison relatively little is known about their ecology and behaviour in these habitats. Woodland savannas, with a greater availability of cover, may inhibit cheetahs from attaining high speeds, although may confer other advantages not provided by grassland habitats. Cover is considered advantageous to cheetahs for stalking prey (Cohen, Scholtz & Reichel 1978; Caro 1994; Purchase & du Toit 2000) because it enables closer proximity to the quarry before the chase, thereby reducing chase distance and improving hunting success (Eaton 1970; Fitzgibbon 1990; Caro 1994). Concealment is considered another advantage of cover (Myers 1975; Caro 1994; Zank 1995; Purchase & du Toit 2000). Because cheetahs are built for speed, rather than strength, they suffer

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from competition with all the other large carnivores, such as lion *Panthera leo*, spotted hyena *Crocuta crocuta* and leopard *Panthera pardus* (Nowell & Jackson 1996; Mills & Hes 1997) and are easily robbed of their prey (Schaller 1972; Caro 1994). Therefore, a greater availability of cover may provide increased concealment to cheetahs after the hunt, thereby reducing the chances of kleptoparasitism.

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

4.2 METHODS

4.2.1 Data collection in the KNP

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

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

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

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

4.2.2 Analyses of KNP data

The radio-location and direct observation kill data of seven cheetahs were combined for analyses as Mills (1992) and Hunter (1998) both found no significant differences between

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these two methods in terms of bias for larger kills. To analyse for differences between male and female cheetah's diets, prey items were separated into small < 18 kg, medium 18 - 65 kg, and large > 65 kg weight classes, using two methods: (a) the estimated weight of the prey item, and (b) the average weight of adult male and female animals of the prey item. Prey weight figures were obtained from Meissner (1982) and Owen-Smith (1988). A chi-square test on a contingency table (Zar 1996) was used to determine if male and female cheetahs were taking prey classes, based on average adult size, at different frequencies. A chi-square goodness of fit test (Zar 1996) was used to determine if cheetahs were taking male and female impala *Aepyceros melampus* according to their relative availability. Relative availability of male and female impala was calculated using the average sex ratio recorded for impala (1.68 females per male) between 1986 and 1989 in the KNP (Mason 1990).

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

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

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

Percentage hunting success, average kill rate, mean chase distance, mean kill retention time and percentage kleptoparasitism were determined using data collected from continuous observation periods (see Data collection in the KNP). Chi-square tests on contingency tables were used to compare male (M3) and female (F1 and F2) cheetahs' hunting attempts versus no attempts, hunting success versus failure, and incidents of kleptoparasitism (M3 and F1 only for the latter). Average kill rates were determined using 14-day continuous observation periods only as Mills (1992) found that long-term

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direct observation periods were less likely to inflate kill frequency. To convert kill rate into kg of meat consumed/cheetah/day, the total weight of the prey items killed by the cheetahs were estimated using weight values obtained from Meissner (1982) and Skinner & Smithers (1990). Blumenschine & Caro's (1986) estimated weight of flesh of an eviscerated adult Thomson's gazelle *Gazella thomsonii* carcass agreed with Schaller's (1972) estimate that cheetahs consume 60% of the animal. To facilitate comparison, therefore, it was assumed that approximately 65% of the total weight of an adult impala and 60% of juvenile prey (Blumenschine & Caro 1986) and 90% of very small prey, in this case a scrub hare *Lepus saxatilis*, which weighs approximately 2 kg is edible to cheetahs. The Mann-Whitney U test (Zar 1996) was used to compare chase distances of successful and unsuccessful hunts of male (M3) versus female (F1 and F2) cheetahs. Successful verses unsuccessful hunts of the pooled chase distances of all cheetahs (M3, F1 and F2) were compared using an unpaired t-test (Zar 1996). Mean kill retention time was calculated by combining data for M3, F1 and F2 for only those kills not kleptoparasitised.

A chi-square goodness of fit test was used to analyse the frequencies of hunting and killing locations across habitat types in relation to the expected values based on the relative availability of habitat types within the cheetahs' home ranges. Habitat types - open savanna, *Acacia* thickets and Lebombo Hills - in the main study area were used in the analyses (see Fig. 2.1 in Chapter 2). Frequency data for hunting and killing were derived by combining the hunting locations of three cheetahs (M3, F1 and F2) and kill locations of four cheetahs (M3, F1, F2 and F3). For each analysis, a minimum convex polygon was drawn around the cheetahs' home ranges to determine the area (km^2) available for hunting and killing in the three habitat types using GIS Arcview. A chi-square goodness of fit test was used to determine if cheetahs were killing impalas in proportion to their relative availability in the different habitat types (Hunter 1998). Relative availability was determined by using the annual aerial impala census data (described above) to calculate the mean number of impala per habitat type for the area (km^2) lying between the Sabie and Crocodile Rivers. Impala density (animals/km^2) was calculated for each habitat type. Following any significant results from the above chi-square tests, Bonferroni confidence intervals were performed to determine preference or

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avoidance of particular habitat types (Neu, Byers & Peek 1974; Byers & Steinhorst 1984) by the cheetahs. Finally, chi-square tests on contingency tables were used to compare hunting attempts versus no attempts and hunting success versus failure of cheetahs M3, F1 and F2 in different habitat types and vegetation classes.

4.2.3 Across-ecosystem comparisons

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

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

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proportions across study sites. To meet the assumption of normal distribution for an ANOVA, the proportional data were arcsine transformed (Zar 1996).

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

4.3 RESULTS

4.3.1 Cheetahs in the KNP

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

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

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

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

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

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

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

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

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

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

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

There was no significant difference in mean chase distance of successful and unsuccessful hunts between male (M3) and female cheetahs (F1 and F2). Using the pooled data of males and females, a significant difference was found between the mean chase distance of successful versus unsuccessful hunts ($t = 4.36$; d.f. = 113, $p < 0.0001$). The mean chase distance for successful hunts was 189 m (SE = 22.9, n = 26) and

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unsuccessful hunts was 95.7 m (SE = 9.41, n = 89). The mean kill retention time was 165 min (SE = 59, n = 9). There was no significant difference between incidents of kleptoparasitism for the male cheetah coalition (9.1%) and female cheetah F1 (16.7%). When combining data of males and females, kleptoparasitism was 11.8% (n = 34).

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

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

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

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

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

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

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

* Significance at the 0.05 level

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

4.3.2 Across-ecosystem comparisons

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

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

4.4 DISCUSSION

4.4.1 Cheetah predation

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

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

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

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

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

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

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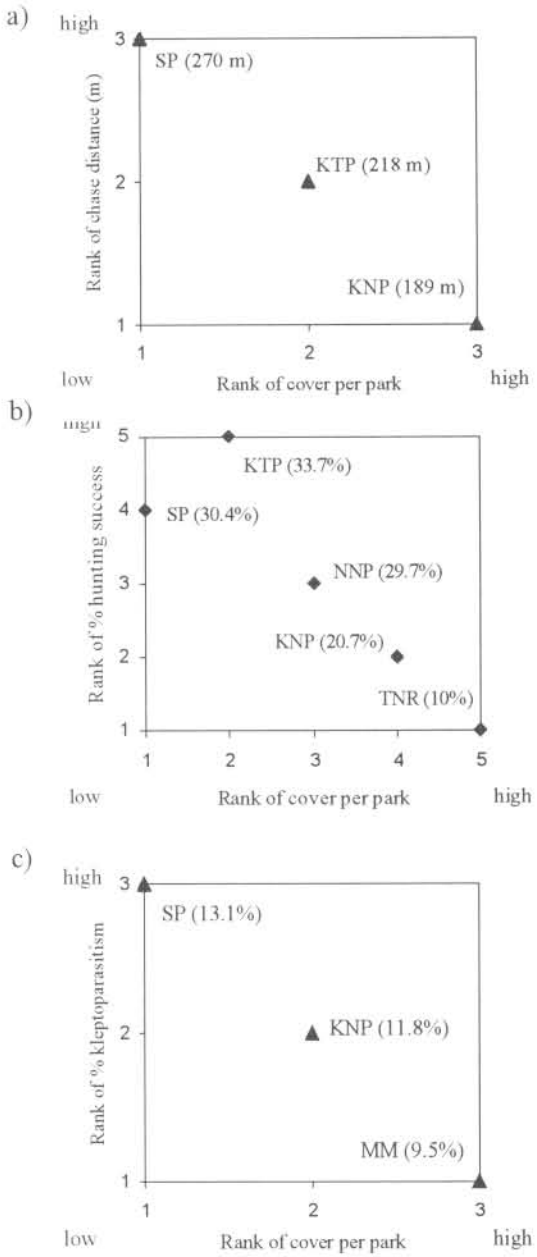

Figure 4.1. Relationship between rank of cover per park and (a) rank of mean chase distance (m), (b) rank of % hunting success, and (c) rank of % kleptoparasitism across protected areas in southern and East Africa. SP = Serengeti Plains; KTP = Kgalagadi Transfrontier Park; NNP = Nairobi National Park;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

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

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

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

** no data available

[1] cited by Schaller (1972)

[2] impala only

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

The size and composition of the cheetahs' hunting group may affect prey size and species preyed upon (Eaton 1974; McVittie 1979; Caro 1994). In PRR, Hunter (1998) found that male cheetah coalitions killed mostly male nyala (120 – 130 kg) while female

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

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

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

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

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

4.4.2 Kill retention time

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

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4.4.3 Kill rates and consumption rates

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

4.4.4 Hunting and killing frequencies

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

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grasslands for hunting (Hunter 1998) and in MNP, cheetahs used the open foreshore grassland predominantly for hunting (Purchase & du Toit 2000).

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

4.4.5 Chase distance and hunting success

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

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as did the KTP and Serengeti Plains (Table 4.8). The success of longer chase distances indicates that in these circumstances cheetahs persisted in catching their quarry rather than giving-up early in the chase because of a predicted failure.

4.4.6 Kleptoparasitism

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

4.5 CONCLUSIONS

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

Cheetahs in the KNP, PRR and MNP prefer open habitat for hunting. Although cheetahs appear to have shorter chase distances in more wooded habitats, hunting success

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

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

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