Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive?

M. W. Hayward[1], M. Hofmeyr[2], J. O'Brien[3] & G. I. H. Kerley[1]

1 Terrestrial Ecology Research Unit, Department of Zoology, Nelson Mandela Metropolitan University, Eastern Cape, South Africa
2 Wildlife Veterinary Unit, Kruger National Park, Mpumulanga, South Africa
3 Shamwari Game Reserve, Eastern Cape, South Africa

Abstract

As a charismatic carnivore that is vulnerable to extinction, many studies have been conducted on predation by the cheetah *Acinonyx jubatus*. Cheetah are generally considered to capture medium-sized prey; however, which species are actually preferred and why has yet to be addressed. We used data from 21 published and two unpublished studies from six countries throughout the distribution of the cheetah to determine which prey species were preferred and which were avoided using Jacobs' index. The mean Jacobs' index value for each prey species was used as the dependent variable in multiple regression, with prey abundance and prey body mass as predictive variables. Cheetah prefer to kill and actually kill the most available prey present at a site within a body mass range of 23–56 kg with a peak (mode) at 36 kg. Blesbok, impala, Thomson's and Grant's gazelles, and springbok are significantly preferred, whereas prey outside this range are generally avoided. The morphological adaptations of the cheetah appear to have evolved to capture medium-sized prey that can be subdued with minimal risk of injury. Coincidentally, these species can be consumed rapidly before kleptoparasites arrive. These results are discussed through the premise of optimality theory whereby decisions made by the predator maximize the net energetic benefits of foraging. Information is also presented that allows conservation managers to determine which prey species should be in adequate numbers at cheetah reintroduction sites to support a cheetah population. Conversely, these results will illustrate which potential prey species of local conservation concern should be monitored for impact from cheetahs as several species are likely to be preyed upon more frequently than others.

Introduction

The cheetah *Acinonyx jubatus* is a highly specialized, cursorial felid that has evolved as a rapid pursuit specialist (Mills & Harvey, 2001). It once occurred throughout much of Africa, South Asia and the Middle East (Nowell & Jackson, 1996). This distribution has declined (Nowell & Jackson, 1996), and today the cheetah is listed as vulnerable (Cat Specialist Group 2002, 2004), largely through habitat loss (Marker, 1998; Frame, 1999).

As the fastest living land mammal, the cheetah is capable of speeds up to 104–112 km h^{-1} for short distances (Sharp, 1997; Mills & Harvey, 2001). This is possible through its highly flexible spine; hardened, grooved and pointed foot pads; shortened canine teeth that allow increased airflow; and semi-retractable claws (Eaton, 1974; Frame, 1999; Russell & Bryant, 2001). Despite these morphological adaptations, the wide distribution of the cheetah suggests it is

capable of killing a wide range of prey species. Reported prey range in mass from 2 kg hares *Lepus* sp. and warthog *Phacochoerus africanus* piglets to adult wildebeest *Connochaetes taurinus* and zebra *Equus burchelli* weighing up to 270 kg (Eaton, 1974) and even giraffe and buffalo calves (Pienaar, 1969). Adult cheetahs weigh between 30 and 72 kg (Stuart & Stuart, 2000), which means they need to prey upon large vertebrates (>45% of their own body mass) to satisfy their energetic demands (Carbone *et al*., 1999). Their relatively fragile teeth, skull and jaw musculature largely restricts cheetahs to feeding on flesh (van Valkenburgh, Teaford & Walker, 1990).

Approximately half of all cheetah pursuits end in kills (Frame, 1999). This high hunting success rate is thought to reflect a highly predictable outcome and the very high-energy expenditure during hunts that penalizes unsuccessful attempts (Bertram, 1979). Accurate prediction of the outcome of hunts may arise because cheetahs select less vigilant

individuals from the herds they are hunting (Fitzgibbon, 1989).

Hunting group sizes vary from solitary individuals, to females with cubs and coalitions of territorial males (Caro & Collins, 1986; Caro, 1994), with larger groups having a higher hunting success rate (Eaton, 1974) and taking larger prey (Caro, 1994). Hunting cheetah groups in Etosha exhibited coordination between members (Stander, 1990), although Caro (1994) rejects the evidence of cooperative hunting.

Cheetahs lose up to 12% of kills to kleptoparasites, particularly lion *Panthera leo* and spotted hyaena *Crocuta crocuta* (Kruuk, 1972; Schaller, 1972), and to reduce encounters with these competitors it is largely diurnal (Schaller, 1968; Stander, 1990). As it is competitively inferior to virtually all other large predators, even vultures (Frame, 1999), the cheetah only occasionally scavenges (Schaller, 1972) the 2.8 kg of meat it requires daily (Frame, 1999) and bolts down its food before competitors arrive (Kruuk & Turner, 1967). Cheetahs inhabiting areas of denser vegetation suffer lower levels of kleptoparasitism than conspecifics in more open areas (Mills, Broomhall & du Toit, 2004).

In this study, we aimed to use dietary and prey abundance data collected from various studies conducted throughout the distribution of the cheetah to determine which, if any,

prey species the cheetah prefers and those it avoids. Further, we attempt to explain why particular species are preferred or avoided using various ecological features of the prey and based on the premise of optimality (Pyke, Pulliam & Charnov, 1977; Krebs, 1978). We also investigated whether denser habitats afford cheetah refuge from kleptoparasitism and thereby make it worthwhile to capture larger prey than more open areas where the likelihood of kleptoparasitism is increased. Our analyses have followed that of Hayward & Kerley (2005) to allow direct comparison between the causes of prey preferences of lion and cheetah and, subsequently, the rest of Africa's large predatory guild.

Methods

Data collection

Nineteen published studies and two theses found in the literature were combined with two unpublished studies that described the diet of the cheetah along with some measure of prey abundance (either actual or relative; Table 1). Several of these studies were conducted over a long term and these allowed temporally separated prey preferences to be calculated as prey abundance changed over time (Table 1). Others provided such information from different study regions

Table 1 Sites and sources of prey preference data used in this study

Country	Site	Years/period	No. of kills	Source
Kenya	Nairobi National Park	1966	53	Eaton (1974)
		1966–1967	13	Foster & McLaughlin (1968)
		1967–1969	183	McLaughlin (1970)
Namibia	Etosha National Park	1975–1978	63	Berry (1981)
South Africa	Hluhluwe-Umfolozi Park	Early 1980s	144	Whateley & Brooks (1985)
	Kalahari Gemsbok National Park	1974–1988	229	Mills (1990)
	Klaserie Private Nature Reserve	1979–1981	27	Kruger (1988)
	Kruger National Park	1956–1965 South	458	Pienaar (1969)
		1956–1965 Central	417	As above
		1956–1965 North	222	As above
		1987–1990	68	Broomhall (2001)
		Early 1990s	61	Mills & Biggs (1993)
	Kwandwe Game Reserve	2003	127	Bissett (2004)
		2004	94	As above
	Madikwe Game Reserve	1996–1998	56	M. Hoffmyer (unpubl. data)
	Phinda Resource Reserve	1992–1996	325	Hunter (1998)
	Pilanesberg National Park	1997	16	Hofmeyr & van Dyk (1998)
	Shamwari Game Reserve	2003	29	J. O'Brien (unpubl. data)
		2004	65	As above
		2005	33	As above
	Timbavati Game Reserve	1964–1966	47	Hirst (1969)
Tanzania	Serengeti National Park	Late 1950s	[a]	Wright (1960)
		1965–1966	23	Kruuk & Turner (1967)
		1966–1967	138	Schaller (1968)
		1970s	443	Frame (1986) in Caro (1994)
		Late 1980s	417	Caro (1994)
Zambia	Kafue National Park	1960–1963	33	Mitchell, Shenton & Uys (1965)
Zimbabwe	Wankie (Hwange) National Park	1969–1973	39	Wilson (1975b)

[a]Only percentages provided.

(Table 1). Such partitioning has been used previously in studies of carnivore ecology (see Creel & Creel, 2002). Consequently, a total of 28 assessments of prey preference were calculated from sites throughout the distributional range of the cheetah (Table 1). We do not believe that autocorrelation exists by using data from the same area at different prey abundance, as one of the fundamental rules of whether a species is captured and killed is the probability of coming in contact with the predator and this varies with prey density.

The unpublished data come from two sites in South Africa. Shamwari Game Reserve (J. O'Brien, unpubl. data) covers 19 746 ha in the Eastern Cape Province where cheetah were reintroduced in 2000. The 55 000 ha Madikwe Game Reserve in the North West Province was gazetted in 1991 with a small population of cheetah extant (Hofmeyr et al., 2003). This population was supplemented from 1994 onwards and contains 19 individuals (Hofmeyr & van Dyk, 1998).

Numerous studies provided excellent descriptive information on cheetah diet but insufficient information on prey abundance (Graham, 1966; McVittie, 1979; Stander, 1990; Purchase & du Toit, 2000; Cronje, Reilly & MacFadyen, 2002; Marker et al., 2003; Radloff & du Toit, 2004). Unless other sources could be found that provided prey abundance for the relevant time (Table 2), these studies could not be used in this analysis.

The data collected in these studies were derived from both incidental observations and continuous follows. Continuous follows are widely regarded as the superior method of ascertaining the diet of a predator (Bertram, 1979; Mills, 1992); however, because of the relatively brief period cheetahs spend on kills, there is no difference between the two methods in measuring the diet of cheetahs (Mills, 1992; Hunter, 1998).

Data analysis

Prey preference

Jacobs' index (Jacobs, 1974) minimizes the problems associated with many preference indices (non-linearity, bias to rare food items, increasing confidence intervals with increasing heterogeneity, being unbound or undefined, and lacking symmetry; Chesson, 1978; Strauss, 1979; Norbury & Sanson, 1992; Hayward & Kerley, 2005) and we chose this method. Jacobs' index

$$D = \frac{r - p}{r + p - 2rp} \quad (1)$$

standardizes the relationship between prey relative abundance p (i.e. the proportion that each species makes up of the total abundance of censused prey species at a site) and the relative proportion that each species comprises as cheetah kills r to between $+1$ and -1, where $+1$ indicates maximum preference and -1 maximum avoidance.

A Jacobs' index value was calculated for each prey species at each site using prey abundance and kill data presented for that site in the literature (Tables 1 and 2). The mean Jacobs' index of each prey species across studies was then calculated (± 1 SE wherever the mean is shown) and these values were tested for significant preference or avoidance using t-tests against a mean of 0 if they conformed to the assumptions of normality (Kolmogorov–Smirnov test) (Palomares et al., 2001; Hayward & Kerley, 2005; Hayward, de Tores & Banks, 2005; Hayward et al., 2006a). Where transformation could not satisfy these assumptions, the sign test was used (Zar, 1996).

If a species was killed more frequently than its relative abundance then it was considered preferred, whereas if a species was killed less frequently than its relative abundance it was considered avoided. Obviously, this is a simplification as this reflects not just the predator's preference but also the prey's vulnerability and the ease with which it is captured.

This kind of analysis is not biased by the results from one particular area; is not overly influenced by the available community of prey species because for a species to be significantly preferred or avoided it must be so in diverse communities throughout its range; and it takes account of varying hunting group sizes and sex ratios by being collected in populations of males and females that hunt in various group sizes and compositions. Furthermore, variation in the effects of carnivore group size on components of predation cannot be made for a species living in the same habitat

Table 2 Assumptions made in determining kills and prey abundance for studies where it is not implicitly stated

Study and section	Assumptions made or source of abundance data
Broomhall (2001)	No abundance data were available for scrub hares
Caro (1994)	Prey data summed from appendices 8 and 11 for males and females combined
Frame (1986) in Caro (1994)	Prey abundance came from Houston (1979)
Kruuk & Turner (1967)	Prey abundance data came from Schaller (1972)
McLaughlin (1970)	Prey abundance data came from Foster & McLaughlin (1968)
Mills & Biggs (1993)	Giraffe and hippopotamus were assumed to be in equal abundance from Fig. 3; buffalo abundance came from Donkin (2000) Similarly, kudu and waterbuck were assumed to be of equal abundance
Mitchell et al. (1965)	Prey abundance data came from Dowsett (1966)
Schaller (1968)	Prey abundance data came from Schaller (1972)
Hofmeyr & van Dyk (1998)	Prey abundance data came from van Dyk & Slotow (2003)

(Caro, 1994); therefore, there is no justification for teasing apart group sizes and sexes of hunters, particularly where little such information is given in the literature.

Multiple regression analysis

Multiple regression was conducted on non-correlating, transformed variables to determine which factors influenced the prey preferences of the cheetah. Variables used were relative abundance of prey at a site (as an estimate of availability), prey body mass, herd size, preferred habitat type and threat of injury to the predator (Table 3). Categories were used for several of these variables, as has occurred previously (Funston, Mills & Biggs, 2001; Mills *et al.*, 2004; Hayward & Kerley, 2005); however, although we readily acknowledge that this is a simplification of very complex issues, we believe the use of such categories serves to illustrate general trends.

Cheetahs are generally thought to eat prey of medium body size (Schaller, 1968; Mills *et al.*, 2004). Three-quarters of the mean adult female body mass of prey species was used in order to take account of calves and sub-adults eaten. This value was used in previous studies (Hayward & Kerley, 2005; Hayward, 2006; Hayward *et al.* 2006*a,b*) following Schaller's (1972) example and we continue its use here. Weights were taken from Stuart & Stuart (2000).

Social organization is an indicator of the ability of prey to detect predators and the ability of predators to get close to prey. Cheetahs have a higher hunting success on herds of less than 30 individuals (Eaton, 1974), perhaps because larger groups can detect cheetahs at greater distances (Fitzgibbon, 1990), suggesting that there may be a relationship between cheetah prey preference and herd size. The dilution effect also acts to reduce the probability that an individual in a large herd will be preyed upon (Hamilton, 1971; Dehn, 1990). Such benefits of herding are counteracted as larger herds are easier to detect and allow closer approach (Dehn, 1990). We used a categorical variable to investigate this issue (Table 3).

Increased vegetation density reduces the detectability of prey and the speed of cheetah pursuit, and therefore habitat type may affect predation rates. Cheetahs occur in habitats ranging from desert to open grassland and woodland savanna (Eaton, 1970, 1974; Mills, 1998), suggesting that species preferring these habitats would be at greater risk of cheetah predation than those that rarely use them. Cheetahs also have a greater hunting success in more densely vegetated areas than the Serengeti short grass plains (Eaton, 1970), suggesting that prey in such areas are at even greater risk. Prey animals inhabiting dense vegetation generally adopt a silent, solitary, 'hider' strategy to evade detection, whereas prey on open grasslands are detected by sight rather than by sound and can exist in large herds (Geist, 1974; Leuthold & Leuthold, 1975). A categorical variable of habitat density was used and, while this was a simplification, this technique has been used successfully for cheetah previously (Mills *et al.*, 2004).

The anti-predatory strategy a species uses affects its chances of becoming prey. Cryptic coloration and patterning in predators is an obvious way of improving hunting success; however, there has been no scientific comparison of crypsis between prey species or their predators, although inhabitants of dense vegetation are often cryptic or of dull body coloration compared with grassland species (Geist, 1974). Similarly there has been little work on the evasion speed of prey species (but see Elliott *et al.*, 1977; Prins & Iason, 1989) and these issues meant the threat of injury to a hunter was all that could be analysed, where larger species are more likely to stand and fight predators than smaller ones (Geist, 1974) and an aggressive nature or dangerous weaponry are also factors. Again a categorical variable was used with information for each of these categories from Estes (1999) and Stuart & Stuart (2000).

Other analyses

Significant relationships were plotted using distance-weighted least-squares and linear regression fits of transformed data of the variables used in the multiple regression analysis. We also tested whether cheetahs were actually preying upon their preferred prey species using Spearman's rank order correlation and whether there was a significant difference between preferred and avoided species for each predictor variable used in multiple regression using the Mann–Whitney test (Zar, 1996).

Analysis of variance was used to test whether cheetahs in denser habitats preferred larger prey species due to the refuge from kleptoparasitism these habitats afforded. The habitat at several sites where Jacobs' index values were calculated was classified according to their vegetation density (i.e. 1, Serengeti; 2, Kgalagadi; 3, Nairobi; 4, Kruger; 5, Timbavati and Klaserie; from Mills *et al.*, 2004). Body mass was weighted by multiplying the body mass (three-quarters of adult female mass) of the prey species by the proportion it comprises of the total prey killed at a site.

Results

Jacobs' index scores were calculated from 3909 kills of 58 species recorded as prey of the cheetah. Impala were killed by cheetah in 26 out of 27 studies where they were present, while blesbok (6 out of 6 studies), kudu (18/19), steenbok (7/8), common duiker, Thomson's gazelle and springbok (8/9 for each) and hartebeest (17/19) were also commonly taken (Table 3; Fig. 1). Impala were also the most abundant species numerically (24.5% of available prey at 27 sites), followed by Thomson's gazelle (23.1% at nine sites), blue wildebeest (16.0% at 26 sites), springbok (18.6% at nine sites) and plains zebra (10.5% at 28 sites) (Table 3). Thomson's gazelle were the most frequently killed prey species (46.7% of kills from nine sites), followed by impala (32.0% at 27 sites), springbok (26.3% at nine sites) and Grant's gazelle (13.2% at eight sites) (Table 3). Each of these four species were killed proportionally more frequently than they were available. Irrespectively, there was a significant

Table 3 Jacobs' index values, number of studies recording the species as a potential (n_p) and actual prey item (n_a), mean percentage abundance of each species, mean percentage that each species comprised of the total kills recorded, body mass (three-quarters of mean female body mass) and categories of herd size, habitat density and injury threat to cheetah used in analyses

Species	Jacobs' index (±1 SE)	n_p	n_a	Abundance (%) (±1 SE)	Kills (%) (±1 SE)	Body mass (kg)	Herd size	Habitat	Threat
Baboon Papio cynocephalus⁻	−1 ± 0	8	0	1.0 ± 0.7	0 ± 0	12	5	2	1
Bat-eared fox Otocyon megalotis	−0.63 ± 0.37	2	1	0.7 ± 0.7	0.4 ± 0.4	3	2	1	0
Blesbok Damaliscus dorcas phillipsi⁺	0.62 ± 0.07	6	6	2.5 ± 0.7	9.0 ± 1.8	52.5	3	1	0
Bontebok Damaliscus dorcas dorcas	−1 ± 0	2	0	0.3 ± 0	0 ± 0	46.5	3	1	0
Buffalo Syncerus caffer⁻	−0.98 ± 0.01	22	3	4.5 ± 1.1	0.2 ± 0.1	432	5	2	2
Bushbuck Tragelaphus scriptus	−0.10 ± 0.16	13	9	4.9 ± 1.7	5.8 ± 2.5	23	1	3	0
Bushpig Potamochoerus larvatus⁻	−1 ± 0	9	0	1.9 ± 0.6	0 ± 0	46	3	3	1
Caracal Felis caracal	−1 ± 0	3	0	0.1 ± 0.1	0 ± 0	7	1	2	0.5
Cheetah Acinonyx jubatus	−1 ± 0	6	0	0.2 ± 0	0 ± 0	30	1	1.5	2
Duiker, blue Cephalophus monticola	−1 ± 0	3	0	1.1 ± 0	0 ± 0	3	2	3	0
Duiker, common Sylvicapra grimmia	0.18 ± 0.19	9	8	7.1 ± 2.1	10.6 ± 2.3	16	1	3	0
Eland Tragelaphus oryx⁻	−0.84 ± 0.06	20	6	1.9 ± 0.4	0.3 ± 0.2	345	5	2	2
Elephant Loxodonta africana⁻	−1 ± 0	9	0	4.2 ± 3.4	0 ± 0	1600	4	2	2
Gemsbok Oryx gazella⁻	−0.66 ± 0.19	10	3	2.2 ± 0.4	1.1 ± 0.7	158	4	1	2
Giraffe Giraffa camelopardalis⁻	−0.95 ± 0.04	22	2	1.7 ± 0.4	0.0 ± 0.0	550	3	2	2
Grant's gazelle Gazella granti	0.39 ± 0.22	8	7	4.9 ± 2.0	13.2 ± 4.6	38	4	1	0
Grant's gazelle (excluding Kruuk & Turner, 1967)⁺	0.59 ± 0.10	7	7	5.5 ± 2.3	14.9 ± 4.9				
Grysbok, Cape Raphicerus melanotis	−1 ± 0	3	0	0.9 ± 0	0 ± 0	7	1	2.5	0
Grysbok, Sharpe's R. sharpei	−0.83 ± 0.11	5	2	1.7 ± 0.9	0.1 ± 0.1	7	1	2.5	0
Hares Lepus sp.	−1 ± 0	2	0	0.1 ± 0.1	0 ± 0	1.5	1	1.5	0
Hartebeest Alcephalus busephalus	−0.18 ± 0.11	19	17	7.2 ± 2.4	4.8 ± 1.0	95	4	1.5	1
Hippopotamus Hippopotamus amphibius⁻	−1 ± 0	9	0	1.0 ± 0.8	0 ± 0	750	3	1.5	2
Honey badger Mellivora capensis	−1 ± 0	2	0	0.004 ± 0.003	0 ± 0	8	1	2	1
Hyaena, brown Hyaena brunnea	−1 ± 0	5	0	0.1 ± 0	0 ± 0	33.8	1	2	1
Impala Aepyceros melampus⁺	0.11 ± 0.08	27	26	24.5 ± 4.0	32.0 ± 5.4	30	4	2	0
Jackal, black-backed Canis mesomelas	−1 ± 0	5	0	1.3 ± 1.2	0 ± 0	6	2	1.5	0.5
Klipspringer Oreotragus oreotragus	−1 ± 0	6	0	0.7 ± 0.3	0 ± 0	10	2.5	3	0
Kudu Tragelaphus strepsicerus	−0.04 ± 0.10	19	18	8.9 ± 2.1	9.6 ± 2.8	135	3	2	0.5

Table 3 Continued

Species	Jacobs' index (±1 SE)	n_p	n_a	Abundance (%) (±1 SE)	Kills (%) (±1 SE)	Body mass (kg)	Herd size	Habitat	Threat
Lechwe Kobus leche	−1±0	3	0	0.5±0.1	0±0	60	4	1	1
Lion Panthera leo	−1±0	4	0	0.4±0.1	0±0	110	3	1.5	2
Mongoose species	−1±0	2	0	2.3±2.1	0±0	0.5	1	2	0
Nyala Tragelaphus angasi	−0.58±0.26	7	2	10.3±6.1	13.4±8.5	47	3	2	0.5
Oribi Ourebia ourebi	−0.85±0.15	4	1	2.5±1.4	0.8±0.8	14	2	1	0
Ostrich Struthio camelus	−0.61±0.15	16	5	1.2±0.2	0.6±0.3	70	3	1.5	1
Porcupine Hystrix africaeaustralis	−1±0	2	0	0.3±0.2	0±0	10	1	2	2
Puku Kobus vardoni	0.99	1	1			52	4	1	1
Reedbuck, Bohor Redunca redunca	0.99	1	1			35	3	1	0.5
Reedbuck, common Redunca arundinum	0.12±0.24	11	9	2.0±1.4	4.2±1.3	32	3	1.5	0.5
Reedbuck, mountain Redunca fulvorufula	−0.39±0.24	8	4	2.6±0.9	4.0±1.8	23	3	2.5	0
Rhinoceros, black Diceros bicornis[−]	−1±0	8	0	0.1±0.1	0±0	800	1	2	2
Rhinoceros, white Ceratotherium simum[−]	−1±0	5	0	0.3±0.1	0±0	1400	2	1.5	2
Roan Hippotragus equines	−0.79±0.21	5	1	0.6±0.3	0.1±0.1	220	3.5	2	1.5
Sable Hippotragus niger[−]	−0.61±0.18	7	3	1.3±0.5	0.6±0.4	180	4	2	1.5
Springbok Antidorcas marsupialis	0.26±0.19	9	8	18.6±8.2	26.3±12.5	26	5	1	0
Springbok (excluding Shamwari 2003; J. O'Brien, unpubl. data)[+]	0.41±0.11	8	8	18.6±9.1	30.0±14.7				
Springhare Pedetes capensis	−1±0	2	0	0.1±0.1	0±0	1.5	1	1	0
Steenbok Raphicerus campestris	−0.02±0.25	8	7	1.9±0.7	2.9±1.4	8	1.5	1.5	0
Thomson's gazelle Gazella thomsoni	0.33±0.19	9	8	23.1±5.3	46.7±9.3	15	5	1	0
Thomson's gazelle (excluding Foster & McLaughlin, 1968)[+]	0.50±0.10	8	8	25.0±5.6	52.5±8.9				
Topi/tsessebe Damaliscus lunatus[−]	−0.65±0.15	11	5	1.6±0.3	0.7±0.3	90	3	2	1
Vervet monkey Cercopithecus aethiops	−1±0	3	0	1.1±0.8	0±0	3.5	4	2	0
Warthog Phacochoerus africanus[−]	−0.41±0.11	26	17	4.8±0.9	3.5±0.7	45	3	2	1.5
Waterbuck Kobus ellipsiprymnus	−0.13±0.14	25	17	1.9±0.4	3.5±1.0	188	3.5	2	1.5
Wildebeest, black Connochaetes gnou	−1±0	3	0	1.9±0.1	0±0	100	4	1	1.5
Wildebeest, blue Connochaetes taurinus[−]	−0.63±0.07	26	19	16.0±2.9	4.7±1.2	135	5	1	1.5
Zebra, plains Equus burchelli[−]	−0.69±0.07	28	17	10.5±1.4	2.0±0.5	175	3	2	1.5
Zebra, Cape mountain Equus zebra	−1±0	3	0	0.2±0.1	0±0	179	3	1.5	1.5

Details of each category were derived from Stuart & Stuart (2000) and Estes (1999). Herd size categories range from 1 relating to solitary individuals, 2 to species that exist in pairs, 3 to small family grouping species, 4 to small herds (10–50) and 5 to large herds (>50). Habitat categories ranged from 1 referring to open grasslands, 2 to savannah and 3 to densely vegetated areas. Obviously a species may overlap these habitat types and, in such cases, an average of habitat use was applied. Threat to the hunting cheetah was also categorized ranging from 0 (no threat), 1 (minor threat or active defence of young) and 2 (severe threat; known deaths attributed to predators caused by this species). Intermediary categories were also used to separate the threat status of certain species.

[+]Indicates significantly preferred.
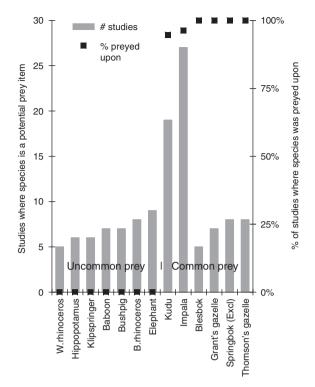
[−]Indicates significantly avoided.

Figure 1 Commonly killed and avoided prey of cheetah *Acinonyx jubatus.*

positive relationship between the abundance of cheetah prey and the proportion with which it is killed (Spearman's rank order correlation coefficient $R = 0.840$, $n = 34$, $P < 0.050$), although there were no such relationships for individual species.

Blesbuck ($t = 8.61$, d.f. = 5, $P < 0.001$) and impala ($Z = 26.9$, $n = 26$, $P = 0.031$) were the only species that were significantly preferred by cheetah when all data were used. The exclusion of Kruuk & Turner's (1967) data from the Serengeti led to Grant's gazelle being significantly preferred ($t = 5.66$, d.f. = 6, $P = 0.001$). Similarly, excluding Foster & McLaughlin's (1968) small sample from Nairobi National Park data led to Thomson's gazelle being significantly preferred ($t = 4.76$, d.f. = 7, $P = 0.002$). The exclusion of one year's data (2003) from the newly reintroduced cheetah population at Shamwari resulted in springbok ($t = 3.65$, d.f. = 7, $P = 0.008$) being significantly preferred also. Justification for this is discussed below. An increased sample size for common reedbuck and common duiker may also result in them being significantly preferred if the existing trends continue (Fig. 2).
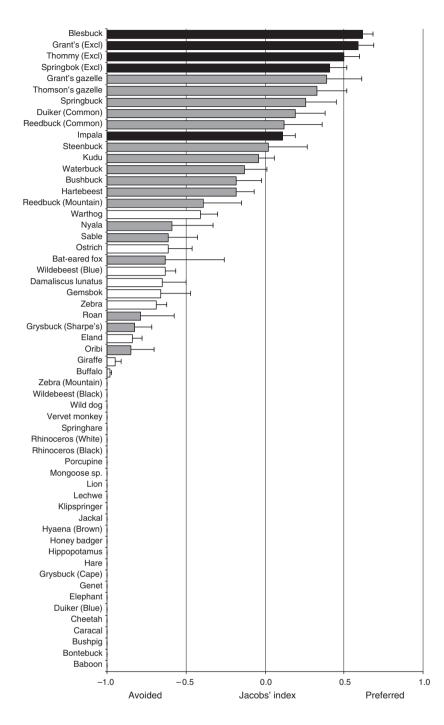
Baboon ($Z = 100$, $n = 9$, $P < 0.001$), buffalo ($Z = 100$, $n = 22$, $P < 0.001$), bushpig ($Z = 100$, $n = 9$, $P < 0.001$), topi/tsessebe ($Z = 91$, $n = 11$, $P = 0.016$), eland ($Z = 100$, $n = 20$, $P < 0.001$), elephant ($Z = 100$, $n = 9$, $P < 0.001$), gemsbok ($Z = 90$, $n = 10$, $P = 0.027$), giraffe ($Z = 100$, $n = 22$, $P < 0.001$), hippopotamus ($Z = 100$, $n = 6$, $P = 0.031$), ostrich ($Z = 81$, $n = 16$, $P = 0.024$), rhinoceros (black and white combined; $Z = 100$, $n = 13$, $P < 0.001$),

sable ($t = -3.40$, d.f. = 6, $P = 0.014$), warthog ($Z = 81$, $n = 26$, $P = 0.003$), blue wildebeest ($t = -9.40$, d.f. = 25, $P < 0.001$) and plains zebra ($Z = 93$, $n = 28$, $P < 0.001$) were all significantly avoided (Fig. 2). Bontebok, black wildebeest, blue duiker, bushbuck, hartebeest, klipspringer, kudu, lechwe, nyala, oribi, porcupine, roan, Cape and Sharpe's grysbok, steenbok, waterbuck, common and mountain reedbuck, monkey, mountain zebra and bat-eared fox were all taken in accordance with their abundance (Fig. 2). A larger sample size, however, may lead to hartebeest, nyala, bat-eared fox, mountain reedbuck, roan, Sharpe's and Cape grysbok, oribi, bontebok, blue duiker, klipspringer, lechwe, porcupine, vervet monkey, black wildebeest, mountain zebra and several carnivore species being avoided if the existing trends continue (Fig. 2).
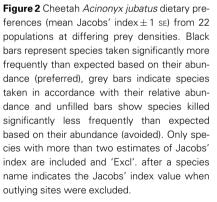
A multiple linear regression analysis was performed on species with more than two Jacobs' index estimates using prey abundance, body mass and habitat type variables (Table 3) after increased prey abundance was found to correlate with increased herd size (Spearman's rank order correlation coefficient $R = 0.37$, $n = 36$, $P < 0.05$) and decreased threat ($R = -0.37$, $n = 36$, $P < 0.05$). The Jacobs' index value of a species was predicted by the equation Jacobs' index $= 1.09 + 0.45(\log(\text{abundance})) - 0.23(\log(\text{body mass})) - 0.25(\text{habitat})$ ($R^2 = 0.458$, $F_{3,32} = 9.001$, $P < 0.001$). Proportional prey abundance and body mass were significant predictive variables ($P < 0.001$; Table 4; Fig. 3). When these five potential predictive variables are viewed independently, only the threat of injury to the hunting cheetah differs significantly between preferred and avoided prey species (Mann–Whitney $U = 2.93$, $n = 30$, $P = 0.002$; Fig. 4).

A more detailed look at the relationship between Jacobs' index and prey body mass (i.e. for body masses less than 200 kg) using distance-weighted least-squares (DWLS) regression shows that the most preferred prey of cheetah weigh between 23 and 56 kg with an ideal weight range (mode) of 36 kg (DWLS $r = 0.350$, $n = 30$, $P = 0.058$; Fig. 5). There is another rise in the plot of Jacobs' index values at 120 kg (Fig. 5). This distribution is reflected in the range of prey body mass cheetahs actually take, and there is a significant relationship between what cheetahs prefer and what they actually kill (Spearman's rank order correlation coefficient $R = 0.891$, $n = 30$, $P < 0.05$) despite the maximum of the prey killed plot occurring somewhat lower than that preferred at 25 kg (Fig. 5).

The mean body mass of the preferred prey species (i.e. blesbok, impala, Grant's and Thomson's gazelles, and springbok) was 27.3 ± 4.8 kg. If we take 30 kg as three-quarters of the adult female body mass of the cheetah (Stuart & Stuart, 2000), then the ratio of predator to preferred prey is 1:1.2 based on the ideal body mass of prey or 1:0.9 based on the mean body mass of preferred prey.

There was no significant difference between the weighted body mass of prey species in different habitat densities (Fig. 6). Thus there is no preference for larger prey items in more densely vegetated areas that offer refuge from kleptoparasitism.

Figure 2 Cheetah *Acinonyx jubatus* dietary preferences (mean Jacobs' index ± 1 SE) from 22 populations at differing prey densities. Black bars represent species taken significantly more frequently than expected based on their abundance (preferred), grey bars indicate species taken in accordance with their relative abundance and unfilled bars show species killed significantly less frequently than expected based on their abundance (avoided). Only species with more than two estimates of Jacobs' index are included and 'Excl'. after a species name indicates the Jacobs' index value when outlying sites were excluded.
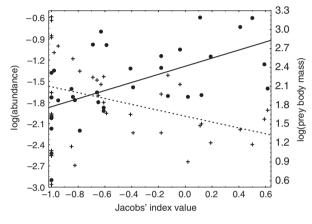
Discussion

Cheetahs prefer abundant prey within a range of 23–56 kg and that have a mean mass of 27 kg, and actually take prey of similar, although slightly smaller, dimensions (Fig. 5). Prey inhabiting open grasslands seem particularly susceptible to cheetah predation (Fig. 4), suggesting that cheetahs are highly adapted to this niche as a predator of gazelles and the larger blesbok. The once great migrations that crossed the southern African highveld grasslands with springbok and blesbok herds numbering millions (Skead, 1987) may have been the ideal environment for the cheetah, depending upon the density of larger competitors. Similarly, the decline of the Thomson's gazelle population in the Serengeti in the 1970s and 1980s (Borner *et al.*, 1987; Ottichilo *et al.*, 2000; but questioned by Dublin *et al.*, 1990) may have caused the decline in cheetah reproductive success observed over that period (Kelly *et al.*, 1998) and led to a decline in cheetah abundance there.
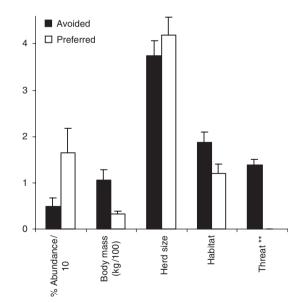
Table 4 Regression statistics for the multiple regression model Jacobs' index = 1.088+0.451(log(abundance))−0.225(log(body mass)) −0.252 habitat: using prey species with more than two estimates of Jacobs' index and excluding carnivores

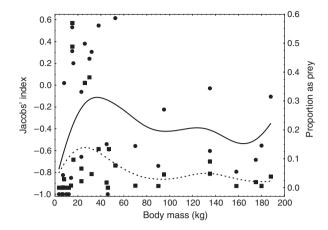| Variable	Coefficient	SE	t_{32}	Probability
Constant	1.088	0.319	3.313	0.002
log(abundance)	*0.451*	*0.142*	*3.171*	*0.003*
log(body mass)	*−0.225*	*0.106*	*−2.113*	*0.043*
Habitat	−0.252	0.124	−2.025	0.052

Standard error of estimate = 0.328; r^2 = 0.458; $F_{3, 32}$ = 9.001; $P < 0.001$. Prey abundance and body mass (italicized) significantly predicted the Jacobs' index value at $\alpha = 0.05$.
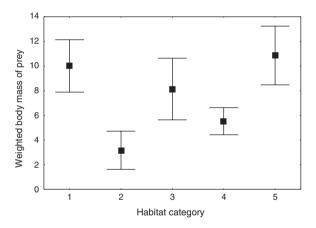

Figure 3 Linear plot of the relationship between cheetah *Acinonyx jubatus* prey preference (mean Jacobs' index value) against prey abundance (filled circles and line; r^2 = 0.34, n = 36, $P < 0.001$) and prey body mass (crosses and dashed line; r^2 = 0.13, n = 36, P = 0.031).

Figure 4 Comparison between significantly preferred prey of cheetahs *Acinonyx jubatus* and significantly avoided prey using the five potential predictor variables considered in the multiple regression. Preferred prey of cheetahs has a significantly lower threat category than avoided prey.

Figure 5 Distance-weighted least-squares relationship between the percentage that each species is killed by cheetah *Acinonyx jubatus* (black boxes) and the prey preference (Jacobs' index) value (black circles) plotted against the body mass of that species for prey species weighing less than 200 kg (three-quarters mean adult female body mass).

Figure 6 Weighted mean (±1 SE) body mass of prey species captured by cheetah *Acinonyx jubatus* in each habitat category (1, open; 5, densely vegetated based on categories derived by Mills *et al.*, 2004). Body mass was weighted by multiplying the body mass of the prey species by the proportion it comprises of the total prey at a site. There was no significant difference between the body mass of prey in each habitat density category (ANOVA $F_{4,148}$ = 1.186, P = 0.319).

The preferred prey species offer minimal injury risk (Fig. 4) and their small size means cheetahs can bolt down their meat before kleptoparasites arrive (as reflected by the speed with which they eat: Mills, 1992; Hunter, 1998), without risking losing too much food. This is probably an artefact of the morphological limitations of cheetahs to the size of prey they can capture given that cheetahs in denser habitats that afford refuge from, and lower levels of, kleptoparasitism do not prefer larger prey than those in more open areas (Fig. 6). Other morphological features, such as the wide nares, may also be adaptations to assist

rapid feeding. As no study we used lacked dominant competitors of the cheetah, we were unable to test directly whether cheetah select larger prey in the absence of lions or spotted hyaenas, as occurs in Namibian rangelands (McVittie, 1979). Given the apparent selective forces acting on the cheetah from these dominant competitors (Laurenson, 1995; Durant, 1998, 2000*a*), there seems no impetus for cheetahs to kill prey larger than they can consume before kleptoparasites arrive.

All these features highlight the importance of optimality (Pyke *et al.*, 1977; Krebs, 1978) to cheetah foraging. The small body size, semi-retractile claws and gracile limbs of the cheetah impose morphological limitations on the size of prey that can be captured (energetic benefit), with ease and with minimal risk of injury (energetic costs). Kleptoparasitism imposes another cost that cheetahs must consider when foraging, and this explains their avoidance of lions and spotted hyaenas (Durant, 2000*a,b*). These species are also predation threats to cheetah, which imposes another limitation to optimality (Krebs, 1980). Although regular opportunistic predation acts to cloud evidence of optimality, this in itself is further substantiation that decisions made by the predator about the energy obtainable from a prey item after consideration of the energy expended during the hunt, the likelihood of success and the risk of injury, act to direct the predator to hunt or not. Unfortunately, we cannot test whether decisions made to optimize the net energetic benefits of a hunt result in increased reproductive fitness, and thereby suffer the limitations of all studies based on the premise of optimal foraging (Pierce & Ollason, 1987).

The causes of cheetah prey preferences stand in stark contrast to those of the lion (Hayward & Kerley, 2005). Where the cheetah preferentially preys upon medium-sized prey (23–56 kg), the lion prefers much larger prey species (190–550 kg). Where cheetah select prey based on its abundance, lions select prey based on its body mass. Given the differences in body mass between the two species, niche theory suggests that they should segregate the dietary niche available to them in Africa (Hutchinson, 1959; Wilson, 1975*a*); however, there is substantial overlap in their diets (Table 3; Hayward & Kerley, 2005). Rather, these two predators prefer to prey upon different species (based on the significantly preferred prey unique to each), but opportunistic predation acts to create dietary overlap.

The preferred weight range of cheetahs (23–56 kg) encompasses 15 prey species, but only five are significantly preferred. These are blesbok, impala, springbok, and Thomson's and Grant's gazelles (Fig. 1). Common and bohor reedbuck, and common duiker are also largely within this weight range and all regularly inhabit areas where cheetah predominantly hunt (Mills *et al.*, 2004). Increased sample size is also likely to see these species significantly preferred if the current trends continue (Fig. 2), and other data support this as cheetah predation led to a precipitous decline in reedbuck numbers in Phinda (Hunter, 1998, p. 149). As Thomson's gazelles are below the preferred weight range

(based on three-quarters of adult female body mass), it is not surprising that cheetahs take adult male Thomson's gazelles most frequently (Fitzgibbon & Fanshawe, 1989)

Thomson's gazelle is taken preferentially on the Serengeti plains over impala and Grant's gazelle (Kruuk & Turner, 1967; Schaller, 1968), but in Nairobi Grant's gazelle and impala are preferred over Thomson's gazelle (Foster & McLaughlin, 1968). The numerical dominance of Thomson's gazelle in the Serengeti indicates that it may be uneconomical to hunt anything else (Eaton, 1974), and the higher hunting success rate in the Serengeti woodlands (Eaton, 1970) reinforces that Thomson's gazelles may be almost all that can be captured in open areas, despite being sub-optimal (Fig. 5). This is particularly the case during the breeding season when Thomson's gazelle fawns are captured in almost every hunting attempt (Schaller, 1968). The preference for larger impala and Grant's gazelle in denser vegetation suggests that increased habitat density (as found in Nairobi compared with the Serengeti plains) affords cheetah stalking cover that allows them to capture larger, more profitable, prey items, but this is likely to reduce the maximum speed cheetahs and their prey can reach in dense vegetation.

As preferred prey of cheetahs, Thomson's gazelles are likely to avoid them and point scans show that gazelles are in fact less common in the vicinity of cheetahs than they are in the vicinity of lions *P. leo* and spotted hyaenas *C. crocuta* (Durant, 1998), both of which significantly avoid gazelles as prey (Hayward & Kerley, 2005; Hayward, 2006; Hayward *et al.*, 2006*b*). Therefore, whether cheetahs occur in areas supporting a low density of Thomson's gazelle through avoidance of encounter competition (as suggested by Creel, Spong & Creel, 2001) or through the localized predator avoidance movements of the gazelle away from their most serious predator is unknown.

Finally from a conservation viewpoint, strategies to increase the density of cheetah, and other threatened predators, can now be made with a knowledge of what prey species need to increase in abundance to see a corresponding increase in a specific predator. Such a strategy has been suggested for tiger *Panthera tigris* and leopard *P. pardus* in India (Ramakrishnan, Coss & Pelkey, 1999) and wolves *Canis lupus* in Europe (Meriggi & Lovari, 1996); however, the results here provide detailed information as to what species are required for cheetah. Our results will also prove useful for conservation managers in India who are considering reintroducing cheetah (Marker, 1998) by illustrating the body mass of prey that are likely to be preferentially killed, and therefore required, by cheetah. Similarly, research into the remnant cheetah population in Iran may also benefit from this information.

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