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# Prey preferences of the leopard (*Panthera pardus*)

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## Keywords

character displacement; Carnivora; diet; Jacobs' index; optimal foraging; predation preference; preferred prey weight range; prey susceptibility.

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## Abstract

Leopards *Panthera pardus* have a catholic diet and are generally thought to prey on medium-sized ungulates; however, knowledge on which species are actually preferred and avoided is lacking, along with an understanding of why such preferences arise. Twenty-nine published and four unpublished studies of leopard diet that had relative prey abundance estimates associated with them were analysed from 13 countries in 41 different spatial locations or temporal periods throughout the distribution of the leopard. A Jacobs' index value was calculated for each prey species in each study and the mean of these was then tested against a mean of 0 using *t* or sign tests for preference or avoidance. Leopards preferentially prey upon species within a weight range of 10–40 kg. Regression plots suggest that the most preferred mass of leopard prey is 25 kg, whereas the mean body mass of significantly preferred prey is 23 kg. Leopards prefer prey within this body mass range, which occur in small herds, in dense habitat and afford the hunter minimal risk of injury during capture. Consequently, impala, bushbuck and common duiker are significantly preferred, with chital likely to also be preferred with a larger sample size from Asian sites. Species outside the preferred weight range are generally avoided, as are species that are restricted to open vegetation or that have sufficient anti-predator strategies. The ratio of mean leopard body mass with that of their preferred prey is less than 1 and may be a reflection of their solitary hunting strategy. This model will allow us to predict the diet of leopards in areas where dietary information is lacking, also providing information to assist wildlife managers and conservation bodies on predator carrying capacity and predator–prey interactions.

## Introduction

The leopard *Panthera pardus* is the most widespread member of the large felids (Myers, 1986), occurring throughout sub-Saharan Africa, India and southern Asia (Nowell & Jackson, 1996). This is largely due to its highly adaptable hunting and feeding behaviour (Bertram, 1999). Leopards are catholic in their use of habitat, which ranges from tropical rainforest to arid savanna, and from alpine mountains to the edges of urban areas, but reach their highest densities in riparian zones (Bailey, 1993), illustrating that they can live wherever there is sufficient cover and adequately sized prey animals (Bertram, 1999).

Leopards are highly variable morphologically (Mills & Harvey, 2001), with adults weighing between 20 and 90 kg (Stuart & Stuart, 2000). They require between 1.6 and 4.9 kg of meat per day to maintain body mass (Bothma & le Riche, 1986; Bailey, 1993; Stander *et al.*, 1997). To achieve this food intake they kill around 40 prey items per year in

Londolzi Game Reserve, on the border of Kruger National Park (le Roux & Skinner, 1989), 50 in Kruger (Bailey, 1993) and 60 in the Serengeti (Schaller, 1972). The leopard's body mass largely exceeds the 21.5 kg threshold of obligate vertebrate carnivory (Carbone *et al.*, 1999); however, the leopard's variable body mass may enable it to exist for short periods on invertebrates or small vertebrates in areas where large vertebrate prey is absent. It is not surprising, therefore, that leopards have been recorded preying on species as small as birds and rodents (Ott, 2004), catfish and hares (Mitchell, Shenton & Uys, 1965) up to the size of giraffe calves and adult male eland (Hirst, 1969; Kingdon, 1977; Scheepers & Gilchrist, 1991). Leopards also have the broadest diet of the larger predators with 92 prey species recorded in sub-Saharan Africa, although it is thought to focus on the 20–80 kg range (Mills & Harvey, 2001).

Leopards are almost entirely solitary, with the territories of females being overlapped by larger territories of similarly solitary males (Bertram, 1999). In open habitat they hunt

alone at night (Bailey, 1993), where their camouflage allows them to stalk exceedingly close to their quarry (mean of  $4.4 \pm 0.25$  m in semi-arid, savanna woodland in Kaudom, Namibia: Stander *et al.*, 1997) before initiating a short sprint of up to 120 m, but which averages  $10.3 \pm 1.3$  m in Kaudom (Stander *et al.*, 1997), at up to  $60 \text{ km h}^{-1}$  (Bertram, 1979). Conversely, leopards in rainforest hunt diurnally with crepuscular peaks (Henschel & Ray, 2003; Jenny & Zuberbühler, 2005) by ambushing prey at fruiting trees and along game trails rather than stalking (Hart, Katembo & Punga, 1996). Attempts only end in kills in 5% of hunts in the Serengeti (Bertram, 1979), 16% of hunts in Kruger (Bailey, 1993) and 38% of hunts in Kaudom (Stander *et al.*, 1997). Furthermore, between 5 and 10% of kills are lost to other predators, particularly lions *Panthera leo*, which is compensated for by similar levels of scavenging (Bertram, 1979). Leopards minimize kleptoparasitism by caching carcasses (Bertram, 1999). Although caching behaviour generally protects the carcass, 57% of tree cached carcasses in Kruger had scavengers in attendance, particularly spotted hyaenas *Crocuta crocuta* (Bailey, 1993), whereas only 9% of carcasses dragged into thick vegetation in Kaudom attracted competitors (Stander *et al.*, 1997). Records of giraffe calves cached in trees reflect the leopard's strength (Stevenson-Hamilton, 1947).

The leopards' hunting method requires dense cover to be successful, although edge habitats are also beneficial (Karanth & Sunquist, 1995). Therefore, there is no benefit to group hunting as a leopard must capture its prey before it can flee (Bertram, 1979) and, once detected, leopards have very little chance of successfully capturing prey (Rice, 1986). A successful hunt for a stalking predator is largely determined by chance, and the low predictability of the outcome necessitates a leopard embarking on unpromising hunts, which results in a lower success rate (Bertram, 1979). In theory, stalking predators do not select animals in poor body condition (see Fitzgibbon & Fanshawe, 1989); therefore, over 70% of leopard kills ( $n = 21$ ) in Kafue were of animals in good condition (Mitchell *et al.*, 1965).

The richness of leopard prey suggests that they are largely unselective; however, it seems likely that their morphology and solitary hunting strategy imposes limitations on the prey they can capture. We have previously found that the large body mass and group hunting strategy of lions led to larger prey species being optimally foraged upon, irrespective of the threat of injury during the hunt, herd size or habitat use of the prey (Hayward & Kerley, 2005). Injuries may be more common in smaller, solitary predators if they hunt dangerous prey, and prey body mass may therefore affect rates of predation. For solitary predators, even a minor injury can be life threatening and therefore consideration of the injury risk associated with hunting a prey item must be taken into account. The solitary, stalking hunting of the leopard may also impose some habitat limitations upon where it can capture prey.

In this study, we aimed to use dietary and prey abundance data collected from various studies conducted throughout the leopard's distribution to determine which prey species it

prefers and which it avoids. If a species is killed relatively more frequently than it exists in the prey population then it is considered preferred, whereas if it is taken less frequently it is avoided. Obviously, this is a simplification as it reflects not just the predator's preference but also the ease with which prey is captured (Schaller, 1972). Furthermore, we attempted to explain why particular prey species were preferred or avoided using various ecological and behavioural features, such as prey body mass, mean relative abundance, herd size, habitat use and injury threat. We know that prey size is an important consideration for leopards when selecting prey (Seidensticker, 1976) and that leopard biomass is correlated with that of prey weighing between 15 and 60 kg (Stander *et al.*, 1997), but what other variables are important and what prey size is actually preferred? Our analyses have followed that of Hayward & Kerley (2005) to allow direct comparison between the determinants of prey preferences of lion and leopard and, subsequently, the rest of Africa's large predatory guild.

## Methods

A literature survey revealed 29 published and four unpublished studies from 25 different conservation areas in 13 countries describing the diet of the leopard, which included 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 detailed information on leopard prey and their abundance in different study regions (Table 1). Such partitioning has been used previously in the study of carnivore ecology (see Creel & Creel, 2002). Consequently, a total of 41 assessments of prey preference were calculated from sites throughout the distributional range of the leopard. We do not believe that autocorrelation exists by using data from the same area at different levels of prey abundance, as one of the fundamental rules of whether a species is captured and killed is the probability of it coming in contact with the predator, and this varies with prey density (Hayward & Kerley, 2005).

The unpublished data come from three sites in South Africa and one in Gabon. The Shamwari Game Reserve covers 18 546 ha in South Africa's Eastern Cape Province and leopards were reintroduced there in 2003. The 55 000 ha Madkiwe Game Reserve is in the North-West Province and leopards occurred naturally before the reintroduction of huge numbers of wildlife during the creation of the park in the early 1990s (Hofmeyr *et al.*, 2003). The Munyawana Conservancy, which includes Phinda Game Reserve, covers 20 300 ha in kwaZulu-Natal and had an extant leopard population before the creation of the reserve. Ivindo National Park was created in 2002 and covers 300 000 ha of equatorial forest straddling the equator in north-east Gabon.

Numerous studies provided excellent descriptive information on leopard diet but insufficient or no information on prey abundance (Wilson, 1966; Hamilton, 1976; Smith,

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

Country	Site	Years/period	Number of kills	Source
Central African Republic	Manovo-Gounda-St Floris National Park	1982–1984	23	Ruggiero (1991)
Côte d'Ivoire (Ivory Coast)	Tai National Park	1992–1994	200	Zuberbühler & Jenny (2002)
Congo	Ndoki National Park	1996–1997	104	Osofsky (1998)
Gabon	Lop National Park	1993–2001	196	Henschel <i>et al.</i> (2005)
	Ivindo National Park	1993–2001 north	83	P. Henschel (unpubl. data)
		1993–2001 south	65	As above
India	Bandipur Tiger Reserve	1976–1978	121	Johnsingh (1983, 1992)
	Eravikulam National Park	1979–1981	48	Rice (1986)
	Kanha National Park	Early 1960s	22	Schaller (1967)
	Nagarhole National Park	1986–1989	83	Karanth & Sunquist (1995)
Kenya	Lakapia Ranches	1989–1995	57	Mizutani (1999)
Namibia	Kaodom National Park	1990s	131	Stander <i>et al.</i> (1997)
South Africa	Hluhluwe-Umfolozzi Park	Early 1980s	64	Whateley & Brooks (1985)
	Kalahari Gemsbok National Park	1974–1988	80	Mills (1990)
		1976–1992	80	Bothma <i>et al.</i> (1997)
		1976–1983	20	Bothma & le Riche (1984)
	Klaserie Private Nature Reserve	1979–1981	95	Kruger (1988)
	Kruger National Park	1956–1965 south	1881	Pienaar (1969)
		1956–1965 central	1808	As above
		1956–1965 north	1798	As above
		1973–1975 Sabie River	151	Bailey (1993)
		1973–1975 Nwaswitchaka River	91	As above
		Early 1990s	63	Mills & Biggs (1993)
	Madikwe Game Reserve	1996–1998	26	M. Hofmeyr, (unpubl. data)
	Phinda Game Reserve	1992–1998	228	Walker (1999)
		2002–2005	187	L. T. B. Hunter & G. Balme (unpubl. data)
	Shamwari Game Reserve	2004	28	J. O'Brien (unpubl. data)
	Timbavati Game Reserve	1964	20	Hirst (1969)
		1965	86	As above
		1966	46	As above
		1967	16	As above
	Waterberg – Melk River	1986–1987	60	Grimbeek (1992)
	Waterberg – Naboomspruit	1986–1987	18	As above
Sri Lanka	Wilpattu National Park	1968–1969	29	Eisenberg & Lockhart (1972)
Tanzania	Serengeti National Park	Late 1950s	%	Wright (1960)
		1965–1966	55	Kruuk & Turner (1967)
		1968–1971	172	Schaller (1972)
		1972–1973	36	Bertram (1982)
Zambia	Kafue National Park	1960–1963	96	Mitchell <i>et al.</i> (1965)
Zaire (Congo)	Ituri Forest	1988–1989	222	Hart <i>et al.</i> (1996)
Zimbabwe	Wankie (Hwange) National Park	1972–1973	54	Wilson (1975)

% indicates that the number of kills was not provided but rather expressed as a percentage. Two studies in the Kalahari by Bothma *et al.* (1997) and Bothma & le Riche (1984) were included because the different time frames revealed different prey preferences.

1978; Busse, 1980; Santiapillai, Chambers & Ishwaran, 1982; Hoppe-Dominik, 1984; Norton *et al.*, 1986; Rice, 1986; le Roux & Skinner, 1989; Johnson *et al.*, 1993; Grassman, 1999; Ramakrishnan, Coss & Pelkey, 1999; de Ruiter & Berger, 2001; Ray & Sunquist, 2001; Cronje, Reilly & MacFadyen, 2002; Ott, 2004; Henschel, Abernethy & White, 2005). Unless other sources could be found that provided prey abundance at the appropriate time, these studies could not be used in this analysis (see Table 2).

The dietary data collected in these studies were largely derived from incidental observations, although faecal analysis and continuous follows were also used. Continuous follows are widely regarded as the superior method of ascertaining the diet of a predator (Bertram, 1979; Mills, 1992); however, these are extremely difficult with such secretive and elusive predators as the leopard. Consequently, very few studies have used such techniques, although the spoor follows in arid areas are probably as

**Table 2** Assumptions made in determining prey abundance for studies where it is not implicitly stated and also data used from unpublished studies

Study and section	Assumptions made or source of abundance data
Bertram (1982)	Abundance data come from Schaller (1972)
Bothma & le Riche (1984), Bothma <i>et al.</i> (1997)	Abundance data come from dune habitats published by Mills (1990)
Henschel <i>et al.</i> (2005)	Abundance data come from Tutin, White & Mackanga-Missandzou (1997)
P. Henschel (unpubl. data)	Photo-trapping over 1138 camera trap nights and scat analysis yielded one blue duiker (zero kills), 167 red duiker species ( <i>Cephalophus leucogaster</i> , <i>Cephalophus callypygus</i> , <i>Cephalophus dorsalis</i> and <i>Cephalophus ogilby</i> combined: 41 kills), 177 yellow-backed duiker (0), 80 bushpig (31), 67 forest buffalo (0), 27 bongo (0), 35 chimpanzee (2), 11 lowland gorilla (0), one water mongoose (1), 11 African civet (0), five golden cat (0), 73 leopard (0), three genet (1), 461 forest elephants (0) and one honey badger (0) in northern Ivindo. Camera trapping in southern Ivindo over 621 trap nights and scat analysis of 65 leopard scats revealed two blue duiker (three kills), 74 red duiker species combined (24), 53 yellow-backed duiker (3), one sitatunga (1), 16 bushpig (11), 44 forest buffalo (1), five chimpanzee (2), 39 lowland gorilla (4), one water mongoose (0), two African civet (0), three golden cat (0), 28 leopard (0), 150 forest elephant (0) and two aardvark (0)
M. Hofmeyr (unpubl. data)	Wildlife population estimates come from Hofmeyr <i>et al.</i> (2003). During 1996–1998, one blesbok, 14 impala, four kudu, four warthog, two waterbuck and one blue wildebeest kills attributed to leopard were recorded
L. T. B. Hunter & G. Balme (unpubl. data)	Aerial wildlife counts yielded estimates of 383 blue wildebeest (three kills), 81 buffalo (0), 23 bushpig (2), 22 common reedbuck (11), 19 elephant (0), 47 giraffe (0), 66 kudu (1), 190 plain zebra (2), two steenbok (0), four waterbuck (0) and 54 white rhinoceros (0). Driven transects yielded estimates of 99 common duiker (12 kills), 1268 impala (30), 3538 nyala (94), 411 red duiker (12) and 523 warthog (19). There are also an estimated 11 bushbuck (one kill) at Phinda
Karant & Sunquist (1995)	Abundance data were only presented for chital, sambar, gaur, wild pig, langur and muntjac
Kruuk & Turner (1967)	Abundance data come from Schaller (1972)
Mills & Biggs (1993)	Giraffe and hippopotamus were assumed to be in equal abundance from Fig. 3, and buffalo abundance came from Donkin (2000). Similarly kudu and waterbuck were assumed to be of equal abundance
J. O'Brien (unpubl. data)	Wildlife census data derived from driven transects and kills of leopards fitted with radio-transmitters were baboon 122 individuals/0 kills, blesbok 226/0, bontebok 22/0, buffalo 33/0, bushbuck 980/9, bushpig 270/0, cheetah 4/1, blue duiker 65/0, common duiker 925/5, eland 112/0, elephant 53/0, gemsbok 100/1, giraffe 25/0, Cape grysbok 50/0, hippopotamus 22/0, brown hyaena 15/0, impala 724/4, kudu 938/0, lechwe 25/0, nyala 37/0, ostrich 46/0, hartebeest 161/0, common reedbuck 4/0, mountain reedbuck 325/0, black rhinoceros 18/0, white rhinoceros 19/0, springbok 299/0, warthog 231/0, waterbuck 77/0, blue wildebeest 109/0, plains zebra 155/0 and Cape mountain zebra 18/0
Rice (1986)	Relative abundance is based on the maximum number of individuals observed in a group at one time
Mitchell <i>et al.</i> (1965)	Abundance data come from Dowsett (1966)
Schaller (1967)	Abundance data come from table 43 and prey data come from tables 50 and 51 combining scats and carcass observations
Walker (1999)	Abundance data come from Hunter (1998), where driven transects yielded estimates of 628 blue wildebeest (zero kills), 79 common reedbuck (5), 67 giraffe (0), 252 kudu (2), 512 plain zebra (3), 2124 nyala (99) and 852 warthog (44)
Zuberbühler & Jenny (2002)	Population estimates for ungulates from Newing (2001)

effective (Bothma & le Riche, 1989, 1990; Bothma, van Rooyen & le Riche, 1997; Stander *et al.*, 1997). Incidental observations are biased towards larger prey; however, this bias against smaller items is generally alleviated in preference assessments by the undercounting of small prey species in aerial counts. There was no difference in the proportion of small-sized kills to larger kills using continuous follows and incidental observations in Kaudom (Stander *et al.*, 1997). Faecal analysis is another valuable method used in ascertaining predator diets, although if used alone may overemphasize the importance of small prey items (e.g. Hamilton, 1976). The inclusion of studies using all these methods ensures that the majority of prey species of the leopard are assessed in our analysis.

Many selectivity indices have been described; however, none is considered superior to the rest or is without bias and increasing error at small proportions (Chesson, 1978; Strauss, 1979). Consequently, researchers have often overstated the accuracy of their preference results (Norbury & Sanson, 1992), particularly with the most commonly used techniques such as the forage ratio and Ivlev's electivity index (Ivlev, 1961). These two indices, and their variants, suffer from non-linearity, bias to rare food items, increasing confidence intervals with increasing heterogeneity, being unbound or undefined, and lacking symmetry between selected and rejected values (Jacobs, 1974). Confidence intervals also become excessive for proportions below about 10% (Strauss, 1979). There are methods that minimize these

biases (Krebs, 1989) and we have chosen Jacobs' index

$$D = \frac{r - p}{r + p - 2rp}$$

where  $r$  is the proportion of the total kills at a site made up by a species and  $p$  is the proportional abundance of that species of the total prey population (Jacobs, 1974). The resulting value ranges from +1 to -1, where +1 indicates maximum preference and -1 maximum avoidance (Jacobs, 1974). The mean Jacobs' index for each prey species across studies was calculated ( $\pm 1$  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 and Lilliefors test; Palomares *et al.*, 2001; Hayward, de Tores & Banks, 2005). Where transformation could not satisfy these assumptions, the sign test (Zar, 1996) was used, although the biological relevance of non-significant results stemming from several -1 (maximum avoidance) values being coupled with a fractionally positive is questionable.

The value of this kind of analysis is threefold. Firstly, this analysis is not biased by the results from one particular area. Secondly, it is not influenced by the available community of prey, because for a species to be significantly preferred or avoided it must be so in diverse communities throughout its range. Lastly, it is not biased by predation of particular

sexes or age classes as the data used arise from hunting by leopard populations that consist of both sexes and all age classes (Hayward & Kerley, 2005). This also applies to different studies that utilize different methods to census wildlife and determine diet, because for a species to be significantly preferred or avoided it must be so in several studies that are likely to have used different methods to collect the data. The number of species with relatively small sample sizes (i.e. few studies recording them as prey) means that significant preference and avoidance is less likely because at least five Jacobs' index values are required to obtain a significant result using the sign test. Consequently, plots of Jacobs' index with error bars illustrate which species are likely to be significantly preferred or avoided with a larger sample size, assuming the existing trend continues. Similarly, our use of studies with a small number of kills (Table 1) raised concerns and therefore we compared the Jacobs' index values obtained from the entire dataset with those obtained from studies that reported more than 100 leopard kills using linear regression.

Multiple regression was conducted on non-correlating, transformed variables to determine which factors influenced the prey preferences of the leopard. The variables used were prey relative abundance at a site, prey body mass, herd size, preferred habitat type and threat of injury to the predator (Table 3). Significant relationships were plotted using distance-weighted least-squares and linear regression fits of

**Table 3** Mean Jacobs' index value of each leopard prey species, 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 at a site, body mass (3/4 of mean adult female body mass) and categories of herd size, habitat density and injury threat to leopard used in modelling

Species	Jacobs' index ( $\pm 1$ SE)	$n_p$	$n_a$	Abundance (%) ( $\pm 1$ SE)	Kills (%) ( $\pm 1$ SE)	Body mass (kg)	Herd size	Habitat	Threat
Aardvark <i>Orycteropus afer</i>	-0.24 $\pm$ 0.53	3	2	0.2 $\pm$ 0	1.3 $\pm$ 0	40	1	2	0
Baboon <i>Papio cynocephalus</i> <sup>-</sup>	-0.56 $\pm$ 0.16	10	5	5.1 $\pm$ 3.6	2.8 $\pm$ 2.4	12	5	2	1
Barasingha <i>Cercus duvauceli</i>	0.46	1	1	1.7	4.5	54	1	2.5	0
Bat-eared fox <i>Otocyon megalotis</i>	0.00 $\pm$ 0.39	4	4	2.3 $\pm$ 1.5	5.0 $\pm$ 2.6	3	2	1	0
Bates's pygmy antelope <i>Neotragus batesi</i>	0.61 $\pm$ 0.39	2	2	1.0 $\pm$ 1.0	2.0 $\pm$ 1.0	2	1	3	0
Blackbuck <i>Antilope cervicapra</i>	-1	1	0	0.4	0	28	4	1	1
Blesbok <i>Damaliscus dorcas phillipsi</i>	-0.20 $\pm$ 0.46	4	2	1.9 $\pm$ 0.6	2.2 $\pm$ 1.3	52.5	3	1	0
Bontebok <i>Damaliscus dorcas dorcas</i>	-1	1	0	0.4	0	46.5	3	1	0
Bongo <i>Tragelaphus euryceros</i>	-0.79 $\pm$ 0.21	2	2	7.0 $\pm$ 5.0	2.0 $\pm$ 2.0	200	4	3	1.5
Buffalo, Asian water <i>Bubalus bubalis</i>	0.10	1	1	2.8	3.4	319	4	3	2
Buffalo, Cape <i>Syncerus c. caffer</i> <sup>-</sup>	-0.84 $\pm$ 0.10	17	6	8.0 $\pm$ 1.2	1.0 $\pm$ 1.0	432	5	2	2
Buffalo, forest <i>Syncerus c. nanus</i>	-0.71 $\pm$ 0.25	4	2	10.0 $\pm$ 0.1	1.0 $\pm$ 1.0	265	4	2.5	2
Bushbuck <i>Tragelaphus scriptus</i> <sup>+</sup>	0.45 $\pm$ 0.12	13	12	2.0 $\pm$ 0.1	6.0 $\pm$ 2.0	22.5	1	2.5	0
Bushpig/Red river hog <i>Potamochoerus</i> sp.	-0.17 $\pm$ 0.26	9	5	4.0 $\pm$ 1.2	7.0 $\pm$ 4.4	46	3	3	1
Cane rat, greater <i>Thryonomys swinderianus</i>	-0.78	1	1	21.5	3.3	1	1	1	0
Cape fox <i>Vulpes chama</i>	-0.41	1	1	2.9	1.3	2	1	1	0
Caracal <i>Caracal caracal</i>	-1	1	0	0.2	0	7	1	2	0.5
Cheetah <i>Acinonyx jubatus</i>	0.93 $\pm$ 0.05	3	3	0.07 $\pm$ 0.0	2.4 $\pm$ 0.6	30	1	1.5	1
Chimpanzee <i>Pan troglodytes</i>	-0.01 $\pm$ 0.24	6	5	1.0 $\pm$ 0	1.0 $\pm$ 0	22.5	4	2	1
Chital <i>Axis axis</i>	0.34 $\pm$ 0.31	3	3	45.8 $\pm$ 12.3	63.5 $\pm$ 10.3	30	5	1.5	0.5
Civet, African <i>Civetticus civetta</i>	-0.06 $\pm$ 0.42	6	3	1.1 $\pm$ 0.9	1.1 $\pm$ 0.9	7	1	2	0.5
Colobus monkeys <i>Colobus</i> sp.	-0.14 $\pm$ 0.27	7	6	9.3 $\pm$ 3.4	5.2 $\pm$ 1.4				
Colobus, black and white <i>Colobus angolensis/satanus</i>	-0.02 $\pm$ 0.35	3	3	6.0 $\pm$ 0.7	5.4 $\pm$ 2.1	7	4	3	0

Table 3 Continued

Species	Jacobs' index		Abundance (%)		Kills (%)	Body mass	Herd size	Habitat	Threat
	( $\pm 1$ se)	$n_p$	$n_a$	( $\pm 1$ se)	( $\pm 1$ se)	(kg)			
Colobus, western red <i>Procolobus badius</i>	-0.05 $\pm$ 0.68	3	3	13.0 $\pm$ 3.3	11.9 $\pm$ 4.6	6	4	3	0
Dik-dik, Kirk's <i>Madoqua kirkii</i>	0.89	1	1	0.3	5.3	3	1.5	2	0
Duiker, bay <i>Cephalophus dorsalis</i>	0.09 $\pm$ 0.56	2	2	6.1 $\pm$ 4.3	4.8 $\pm$ 1.1	14	1	3	0
Duiker, black-fronted <i>Cephalophus nigrifrons</i>	0.61 $\pm$ 0.35	2	2	0.5 $\pm$ 0.5	2.6 $\pm$ 0.9	10	1	3	0
Duiker, blue <i>Cephalophus monticola</i>	-0.02 $\pm$ 0.35	6	6	4.1 $\pm$ 1.9	8.9 $\pm$ 5.2	3	2	3	0
Duiker, common <i>Sylvicapra grimmia</i> <sup>+</sup>	0.42 $\pm$ 0.11	11	11	5.0 $\pm$ 1.9	10.6 $\pm$ 2.7	16	1	3	0
Duiker, Weyn's <i>Cephalophus weynsi</i>	-0.02	1	1	5.4	5.2	11	1	3	0
Duiker, white-bellied <i>Cephalophus leucogaster</i>	0.25	1	1	1.7	2.8	9	1	3	0
Duiker, yellow-backed <i>Cephalophus silvicultor</i>	-0.41 $\pm$ 0.31	6	3	5.8 $\pm$ 2.8	2.1 $\pm$ 0.8	34	1	2.5	0
Duikers, forest species	0.12 $\pm$ 0.23	8	7	3.8 $\pm$ 7.1	4.9 $\pm$ 0.4				
Duiker, red forest species	0.37 $\pm$ 0.21	5	5	11.7 $\pm$ 0.9	31.8 $\pm$ 9.6				
Eland <i>Tragelaphus oryx</i> <sup>-</sup>	-0.68 $\pm$ 0.16	14	4	1.4 $\pm$ 0.5	0.8 $\pm$ 0.4	345	5	2	2
Elephant, forest <i>Loxodonta cyclotis</i>	-1 $\pm$ 0	4	0	21.0 $\pm$ 10.0	0	1400	3	2	2
Elephant, savanna <i>Loxodonta africana</i> <sup>-</sup>	-1 $\pm$ 0	5	0	3.6 $\pm$ 2.5	0	1600	3	2	2
Elephant, Indian <i>Elephas maximus</i>	-1	1	0	1.2	0	1200	4	2.5	2
Four-horned antelope <i>Tetracornis quadricornis</i>	-1	1	0	2.2	0	17	2	2	0
Francolin <i>Francolinus</i> sp.	-0.97 $\pm$ 0.03	2	1	13.7 $\pm$ 3.9	0.3 $\pm$ 0.3	0.5	3	2	0
Gaur <i>Bos gaur</i>	-0.90 $\pm$ 0.10	3	1	8.4 $\pm$ 3.2	0.4 $\pm$ 0.4	700	3	2	2
Gazelle, Grant's <i>Gazella granti</i>	0.02 $\pm$ 0.29	3	3	5.4 $\pm$ 2.2	4.4 $\pm$ 0.8	38	4	1	0
Gazelle, Thomson's <i>Gazella thomsoni</i>	0.14 $\pm$ 0.21	5	5	22.0 $\pm$ 6.7	33.4 $\pm$ 10.4	15	5	1	0
Gemsbok <i>Oryx gazelle</i>	-0.33 $\pm$ 0.21	9	5	7.4 $\pm$ 4.0	4.7 $\pm$ 2.4	158	4	1	2
Genets <i>Genetta</i> sp.	0.03 $\pm$ 0.34	7	4	1.0 $\pm$ 0.9	2.1 $\pm$ 1.1	1	1	2.5	0
Gerenuk <i>Litocranius walleri</i>	-1	1	0	0.1	0	30	1	1.5	0
Giraffe <i>Giraffa camelopardalis</i> <sup>-</sup>	-0.95 $\pm$ 0.05	16	1	3.3 $\pm$ 1.0	0.4 $\pm$ 0.4	550	3	2	2
Golden cat <i>Felis aurata</i>	-1 $\pm$ 0	3	0	1.1 $\pm$ 0.2	0 $\pm$ 0	10	1	3	1
Gorilla, lowland <i>Gorilla gorilla</i>	-0.38 $\pm$ 0.42	4	2	3.1 $\pm$ 1.9	1.9 $\pm$ 0.8	120	3	3	1.5
Ground squirrel <i>Xerus inauris</i>	-0.19 $\pm$ 0.81	2	2	0.7 $\pm$ 0.4	0.6 $\pm$ 0.6	0.5	4	1	0
Grysbok, Cape <i>Raphicerus melanotis</i>	-1	1	0	0.8	0	7	1	2.5	0
Grysbok, Sharpe's <i>Raphicerus sharpei</i>	-0.56 $\pm$ 0.25	4	2	1.9 $\pm$ 1.1	1.4 $\pm$ 2.0	7	1	2.5	0
Guenon monkeys <i>Cercopithecus</i> sp.	0.24 $\pm$ 0.28	6	6	4.9 $\pm$ 0.3	2.8 $\pm$ 1.4				
Guenon, crowned <i>Cercopithecus pogonias</i>	0.44 $\pm$ 0.02	2	2	0.9 $\pm$ 0.4	2.2 $\pm$ 0.8	2.5	4	3	0
Guenon, l'Hoest's <i>Cercopithecus l'hoesti</i>	0.95	1	1	0.3	8.3	3	4	3	0
Guenon, owl-faced <i>Cercopithecus hamlyni</i>	0.84	1	1	0.1	0.7	3	3	3	0
Guenon, red-tailed <i>Cercopithecus ascanius</i>	-0.48	1	1	11.8	4.5	1.8	4	3	0
Guenon, wolf-dent <i>Cercopithecus wolfi-denti</i>	-0.75	1	1	14.5	2.4	2	4	3	0
Guinea fowl <i>Numida meleagris</i>	-0.95 $\pm$ 0.05	3	2	18.0 $\pm$ 11.3	0.2 $\pm$ 0.2	0.8	4	2	0
Hares <i>Lepus</i> sp.	-0.53 $\pm$ 0.07	9	4	5.7 $\pm$ 1.3	3.3 $\pm$ 0.9	1.5	1	1.5	0
Hartebeest <i>Alcephalus busephalus</i> <sup>-</sup>	-0.65 $\pm$ 0.11	14	8	4.8 $\pm$ 1.1	2.2 $\pm$ 0.8	95	4	1.5	1
Hippopotamus <i>Hippopotamus amphibius</i> <sup>-</sup>	-1 $\pm$ 0	6	0	1.0 $\pm$ 0.8	0	750	3	1.5	2
Honey badger <i>Mellivora capensis</i>	-1 $\pm$ 0	4	0	0.1 $\pm$ 0.0	0	8	1	2	1.5
Hyaena, brown <i>Hyaena brunnea</i>	-1 $\pm$ 0	1	0	0.2	0	33.8	1	2	1
Hyrax, rock <i>Procavia capensis</i>	0.81	1	1	1.9	15.8	2	3	3	0
Impala <i>Aepyceros melampus</i> <sup>+</sup>	0.36 $\pm$ 0.08	22	22	33.0 $\pm$ 3.9	48.2 $\pm$ 6.1	30	4	2	0
Jackal, black-backed <i>Canis mesomelas</i>	0.26 $\pm$ 0.34	5	4	1.3 $\pm$ 0.5	4.2 $\pm$ 1.4	6	2	1.5	0.5
Klipspringer <i>Oreotragus oreotragus</i>	-0.25 $\pm$ 0.25	7	5	2.8 $\pm$ 1.0	4.0 $\pm$ 1.8	10	2.5	3	0
Kob <i>Kobus kob</i>	-0.27	1	1	26.8	17.4	45	4	1	0
Korhaan <i>Eupodotis</i> sp.	-1	1	0	4.0	0	1	1	1	0
Kudu <i>Tragelaphus strepsiceros</i>	-0.31 $\pm$ 0.12	21	14	5.5 $\pm$ 1.1	4.2 $\pm$ 1.2	135	3	2	0.5
Lechwe <i>Kobus lechwe</i>	-1	1	0	0.4	0	60	4	1	1
Mangabey monkeys <i>Cerocebus</i> sp.	0 $\pm$ 0.33	3	3	2.1 $\pm$ 1.2	2.1 $\pm$ 1.2				
Mangabey, crested <i>Cerocebus galeritus</i>	-0.62	1	1	1.3	0.3	5	4	3	0
Mangabey, grey-cheeked <i>Cerocebus albigena</i>	-0.24 $\pm$ 0.64	2	2	3.3 $\pm$ 1.3	2.8 $\pm$ 2.1	5	4	3	0
Meerkat <i>Suricata suricatta</i>	-1	1	0	0.2	0	0.5	4	1	0
Mongoose species	-0.35 $\pm$ 0.32	7	4	1.8 $\pm$ 1.0	0.8 $\pm$ 0.4				
Monkey, blue <i>Cercopithecus mitis</i>	-0.85	1	1	15.1	1.4	4	4	3	0
Monkey, de Brazza's <i>Cercopithecus neglectus</i>	-1	1	0	0.3	0	4	4	3	0

**Table 3** Continued

Species	Jacobs' index ( $\pm 1$ SE)	$n_p$	$n_a$	Abundance (%) ( $\pm 1$ SE)	Kills (%) ( $\pm 1$ SE)	Body			
						mass (kg)	Herd size	Habitat	Threat
Monkey, langur <i>Presbytis entellus</i>	0.06 $\pm$ 0.51	3	3	11.7 $\pm$ 7.9	12.1 $\pm$ 7.7	7	4	2	0
Monkey, moustached <i>Cercopithecus cephus</i>	0.23 $\pm$ 0.43	2	2	4.1 $\pm$ 4.1	3.9 $\pm$ 1.8	2.5	4	3	0
Monkey, patas <i>Erythrocebus patas</i>	-1	1	0	0.1	0	4	4	2	0
Monkey, putty-nosed <i>Cercopithecus nictitans</i>	-0.53 $\pm$ 0.43	3	1	5.4 $\pm$ 4.1	7.9 $\pm$ 7.9	4	4	3	0
Monkey, vervet <i>Cercopithecus aethiops</i>	-0.06 $\pm$ 0.26	5	3	3.3 $\pm$ 1.0	3.1 $\pm$ 1.0	3.5	4	2	0
Mouse deer <i>Tragulus meminna</i>	-1	1	0	6.2	0	2.5	1	3	0
Muntjac <i>Muntiacus muntjak</i>	-0.67 $\pm$ 0.33	3	1	3.7 $\pm$ 1.0	1.0 $\pm$ 1.0	14	1	2.5	0
Nilgai <i>Boselaphus tragocamelus</i>	-0.74 $\pm$ 0.30	2	2	0.5 $\pm$ 0	0 $\pm$ 0	135	3	2	2
Nilgiri tahr <i>Hemitragus hylocrius</i>	-0.74	1	1	73.5	29.2	80	4	2	1
Nyala <i>Tragelaphus angasi</i>	-0.37 $\pm$ 0.23	7	4	16.0 $\pm$ 7.7	18.8 $\pm$ 8.7	47	3	2	0.5
Okapi <i>Okapia johnstoni</i>	0.77	1	1	0.3	2.4	158	1	3	1
Oribi <i>Ourebia ourebi</i>	-0.41 $\pm$ 0.33	4	3	3.0 $\pm$ 1.3	0.6 $\pm$ 0.5	14	2	1	0
Ostrich <i>Struthio camelus</i> <sup>-</sup>	-0.64 $\pm$ 0.22	10	3	1.4 $\pm$ 0.4	0.6 $\pm$ 0.4	70	3	1.5	1
Pangolin <i>Manis temmincki</i>	-1	1	0	0.001	0	5	1	2	0
Polecat, striped <i>Ictonyx striatus</i>	-1	1	0	0.7	0	0.6	1	1.5	0
Porcupine <i>Hystrix africaeaustralis</i>	-0.22 $\pm$ 0.29	6	4	4.3 $\pm$ 3.2	7.7 $\pm$ 6.4	10	1	2	1.5
Puku <i>Kobus vardoni</i>	0.98	1	1	0.3	15.6	52	4	1	1
Reedbuck, bohor <i>Redunca redunca</i>	-0.43 $\pm$ 0.57	2	2	7.7 $\pm$ 6.6	10.1 $\pm$ 9.9	35	3	1	0.5
Reedbuck, common <i>Redunca aruninum</i>	0.04 $\pm$ 0.27	9	6	0.8 $\pm$ 0.3	2.7 $\pm$ 1.1	32	3	1.5	0.5
Reedbuck, mountain <i>Redunca fulvorufula</i>	-0.58 $\pm$ 0.17	5	4	3.8 $\pm$ 1.5	1.6 $\pm$ 1.0	23	3	2.5	0
Rhinoceros, black <i>Diceros bicornis</i>	-1 $\pm$ 0	3	0	0.2 $\pm$ 0.1	0	800	1	2	2
Rhinoceros, white <i>Ceratotherium simum</i>	-1 $\pm$ 0	4	0	0.3 $\pm$ 0.1	0	1400	2	1.5	2
Roan <i>Hippotragus equines</i>	-0.78 $\pm$ 0.18	7	2	1.3 $\pm$ 0.3	0.2 $\pm$ 0.2	220	3.5	2	1.5
Sable <i>Hippotragus niger</i>	-0.80 $\pm$ 0.15	7	2	1.4 $\pm$ 0.5	0.6 $\pm$ 0.5	180	4	2	1.5
Sambar <i>Cervus unicolor</i>	0.23 $\pm$ 0.30	4	4	14.9 $\pm$ 7.7	6.9 $\pm$ 1.9	200	3.5	2	1.5
Sitatunga <i>Tragelaphus spekii</i>	0.80 $\pm$ 0.07	2	2	0.1 $\pm$ 0.0	1.1 $\pm$ 0.4	48	3	2.5	1
Springbok <i>Antidorcas marsupialis</i>	-0.59 $\pm$ 0.31	4	2	16.6 $\pm$ 11.0	16.9 $\pm$ 16.1	26	5	1	0
Springhare <i>Pedetes capensis</i>	-1 $\pm$ 0	2	0	1.6 $\pm$ 1.6	0	2.5	3	1	0
Steenbok <i>Raphicerus campestris</i>	-0.18 $\pm$ 0.18	10	10	12.3 $\pm$ 6.6	4.6 $\pm$ 1.4	8	1.5	1.5	0
Topi/Tsessebe <i>Damaliscus lunatus</i> <sup>-</sup>	-0.55 $\pm$ 0.16	10	5	2.8 $\pm$ 1.0	1.0 $\pm$ 0.4	90	3	2	1
Warthog <i>Phacochoerus africanus</i>	-0.20 $\pm$ 0.13	21	15	4.0 $\pm$ 0.7	4.7 $\pm$ 1.0	45	3	2	1.5
Water chevrotain <i>Hyemoschus aquaticus</i>	0.82 $\pm$ 0.17	3	3	0.1 $\pm$ 0.1	2.4 $\pm$ 1.1	8	1	3	0
Waterbuck <i>Kobus ellipsiprymnus</i> <sup>-</sup>	-0.39 $\pm$ 0.17	19	8	2.6 $\pm$ 0.6	2.0 $\pm$ 0.6	188	3.5	2	1.5
Wild cat, African <i>Felis sylvestrus</i>	0.07	1	1	1.1	1.3	2.5	1	2	0.5
Wild boar, Asiatic <i>Sus scrofa</i>	-0.39 $\pm$ 0.61	3	1	3.4 $\pm$ 0.2	9.2 $\pm$ 9.2	47	3	2.5	1.5
Wildebeest, black <i>Connochaetes gnou</i>	-1	1	0	1.8	0	100	4	1	1.5
Wildebeest, blue <i>Connochaetes taurinus</i> <sup>-</sup>	-0.77 $\pm$ 0.06	22	14	15.4 $\pm$ 3.0	2.8 $\pm$ 0.3	135	5	1	1.5
Zebra, mountain <i>Equus zebra</i>	-1 $\pm$ 0	2	0	0.3 $\pm$ 0.0	0	179	3	1.5	1.5
Zebra, plains <i>Equus burchelli</i> <sup>-</sup>	-0.80 $\pm$ 0.06	23	9	7.3 $\pm$ 1.0	1.4 $\pm$ 0.3	175	3	2	1.5

Specifics of each category are described in the text and their details were derived from Stuart & Stuart (2000), Estes (1999) and Nowak (1999).

\*Indicates significantly preferred.

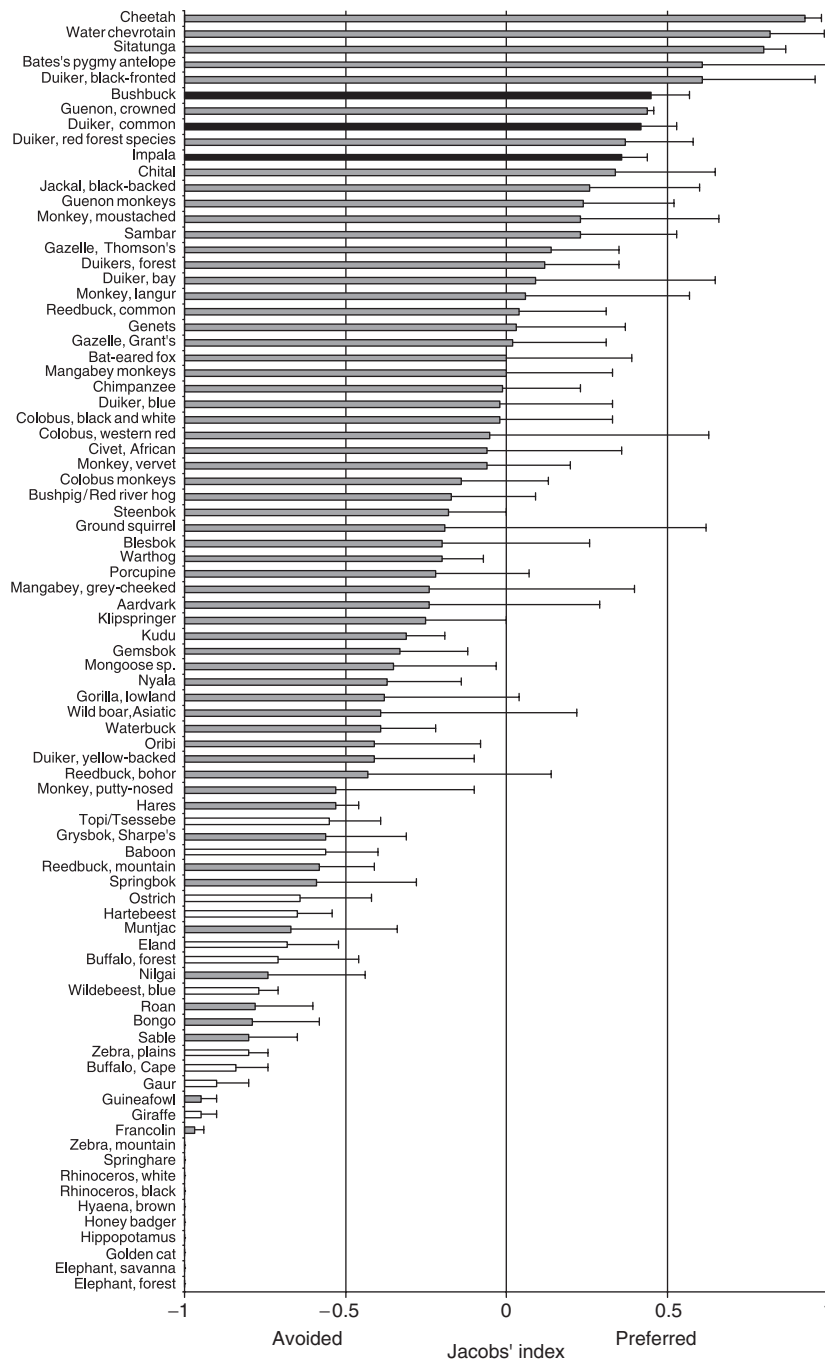
<sup>-</sup>Indicates significantly avoided.

transformed data. Spearman rank correlation was used to determine if there was a relationship between the prey species that leopards prefer to capture and the species they actually capture.

Leopards are generally thought to kill prey of medium body size (Santiapillai *et al.*, 1982; Bailey, 1993; Hart *et al.*, 1996; Bothma, 1997; Ramakrishnan *et al.*, 1999; Mills & Harvey, 2001), and  $3/4 \times$  mean adult female body mass of prey species was used in order to take account of calves and subadults eaten. This value was used in a previous study

(Hayward & Kerley, 2005) following Schaller's (1972) example, and we continue its use here to allow comparison between these studies. Weights were taken from Stuart & Stuart (2000) and Nowak (1999).

Social organization of prey species is an indicator of the ability of the prey to detect predators and vice versa (see review in Hayward & Kerley, 2005). This was a categorical variable, with 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; Table 3).



**Figure 1** Leopard prey preferences determined with Jacobs' index (mean  $\pm$  1 SE of species with > 2 Jacobs' index estimates) calculated from 41 leopard 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 taken significantly less frequently than expected based on their abundance (avoided).

Obviously, this is a simplification as large herding species may also have solitary males among them; however, this technique has been used previously (Funston, Mills & Biggs, 2001; Hayward & Kerley, 2005).

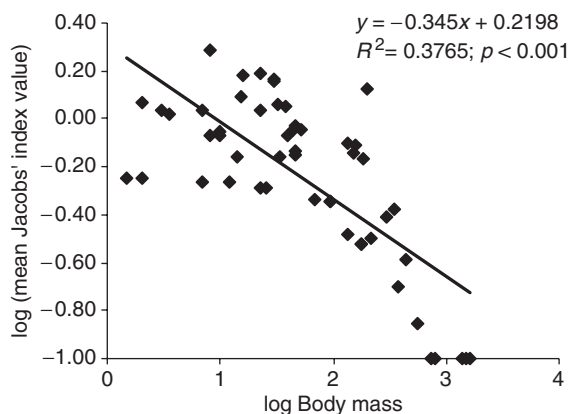
Habitat type may influence predation rates as the density of vegetation can affect the detectability of both predator and prey. Animals inhabiting dense vegetation generally

adopt a silent, solitary, hider strategy to evade detection, whereas prey on open grasslands are detected by sight rather than sound and often exist in large herds (Geist, 1974; Leuthold & Leuthold, 1975). On this basis we would expect solitary leopards to predominately hunt prey in denser habitat types. Although inherently difficult to classify (Sunquist & Sunquist, 1997), a categorical variable of habitat

**Table 4** Regression statistics for the multiple regression model  $\text{Jacobs' index} = 0.163 + 0.112(\log(\text{abundance})) - 0.002(\log(\text{habitat use})) - 0.426(\log(\text{body mass}))$  for species with more than two estimates of Jacobs' index

Variable	Coefficient	SE	$T_{42}$	Probability
Constant			0.713	0.479
$\log(\text{abundance})$	0.112	0.132	0.800	0.403
$\log(\text{habitat use})$	-0.002	0.133	-0.021	0.984
<i><math>\log(\text{body mass})</math></i>	-0.426	0.132	-3.215	0.002

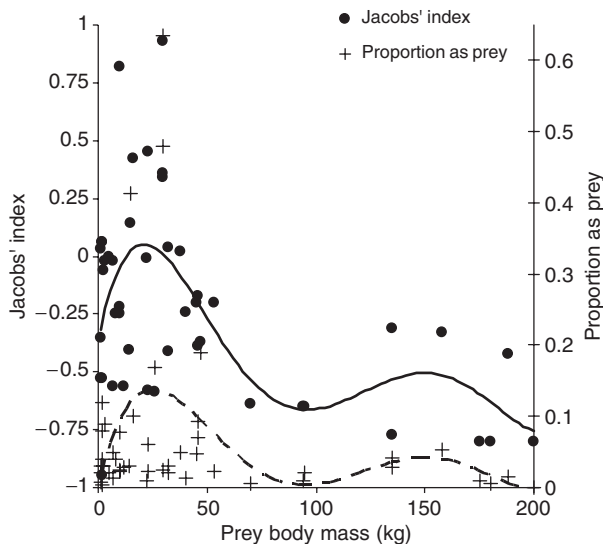
Standard error (SE) of estimate = 0.427;  $R^2 = 0.200$ ; analysis of variance  $F_{3, 46} = 3.759$ ;  $P = 0.017$ . Only prey body mass (*italicized*) predicted the Jacobs' index value at  $\alpha = 0.05$ .



**Figure 2** Linear plot of the relationship between leopard prey preference  $\log(\text{Jacobs' index value} + 1)$  and  $\log(\text{body mass})$  for species with more than two Jacobs' index estimates and excluding carnivores.

density was used, with 1 referring to open grasslands, 2 referring to savannah or open woodland, and 3 to densely vegetated areas. Obviously, a species may overlap these habitat types, and in this case an average of habitat use was applied (Table 3). Again by necessity, this is a simplification; however, this approach has been successfully used previously (e.g. Mills, Broomhall & du Toit, 2004).

Finally, the anti-predatory strategy a species uses will affect its chances of becoming prey. The evolution of cryptic coloration and patterning in predators is an obvious way of improving hunting success; however, primate prey can recognize both coat pattern and texture (Coss & Ramakrishnan, 2000; Zuberbühler, 2000), particularly when the face of the predator is visible (Coss, Ramakrishnan & Schank, 2005). There have been no comparisons of crypsis between prey species, although inhabitants of dense vegetation are often cryptic or of dull body coloration compared with grassland species that have conspicuous patterning (Geist, 1974). Unfortunately, this lack of comparative studies of crypsis, as well as evasion speed of prey species (Elliott, Cowan & Holling, 1977; Prins & Iason, 1989) meant that the threat of injury to a hunter was the only parameter that could be analysed, where larger species are more likely to stand and fight predators than smaller ones (Geist, 1974)



**Figure 3** Distance-weighted least-squares relationship between leopard prey preference (mean Jacobs' index: circles) and the proportion that each species actually occurs as leopard prey (crosses) against prey body mass for species weighing less than 200 kg. Regression statistics for the Jacobs' index–prey body mass relationship are  $r = -0.336$ ,  $n = 43$ ,  $P = 0.031$  and for proportion as prey are  $r = -0.108$ ,  $n = 43$ ,  $P = 0.502$ .

and an aggressive nature or dangerous weaponry are also factors. The categories of threat used were 0 (no threat), 1 (minor threat or active defence of young) and 2 (severe threat; known deaths attributed to predators caused by this species) following Hayward & Kerley (2005) (Table 3). Information for each of these categories comes from Estes (1999) and Stuart & Stuart (2000).

## Results

Jacobs' index scores ( $n = 532$ , mean per species =  $4.85 \pm 0.47$ ) for 8643 kills of 111 species recorded as leopard prey in the literature are shown in Fig. 1 and Table 3, along with their scientific names. When species with only one Jacobs' index estimate were excluded, the mean number of estimates per species rose to  $6.57 \pm 0.59$  (range 2–23).

The most frequently taken prey of leopards are impala (preyed upon in 22/22 studies where they occur), followed by common duiker (11/11), steenbok (10/10), bushbuck (12/13), warthog (15/21), blue wildebeest (14/22) and kudu (14/21) (Table 3). Small carnivores are also commonly taken (20/35) and this is particularly so for felids (4/5) and canids (9/10). Conversely, elephant, hippopotamus, honey badger, black and white rhinoceros, springhare and mountain zebra are never preyed upon by leopards in any of the studies assessed here (Fig. 1).

The proportionally most common prey of leopards are chital deer (64% of kills where they occur), impala (48%), Thomson's gazelle (33%), nyala (19%), springbok (17%), langur monkey (12%) and common duiker (11%) (Table 3).

Red forest duikers (Table 2) are also common prey (22%) in African rainforests (Table 3). Four of these species are also the most abundant at the study sites, with chital accounting for 46% of available prey at the sites where it occurs, impala 33%, Thomson's gazelle 22% and springbok 17% (Table 3). As these percentages attest, these species are preyed upon more often than expected on the basis of their relative abundance, and there was a significant positive relationship between the abundance of leopard prey and the proportion with which it is killed (Spearman's rank order correlation  $r = 0.569$ ;  $n = 60$ ;  $P < 0.001$ ).

Leopards significantly prefer impala [Jacobs' index (JI) =  $0.36 \pm 0.08$ ;  $t = 4.99$ ; d.f. = 21;  $P < 0.001$ ], bushbuck (JI =  $0.45 \pm 0.12$ ;  $t = 3.08$ ; d.f. = 12;  $P = 0.006$ ) and common duiker (JI =  $0.42 \pm 0.11$ ;  $t = 2.11$ ; d.f. = 7;  $P = 0.020$ ) (Fig. 1). If only studies that reported more than one hundred leopard kills are assessed, these species are still highly preferred (impala =  $0.26 \pm 0.12$  and bushbuck =  $0.51 \pm 0.05$ ). In fact, there is a highly significant relationship between the Jacobs' index values of leopard prey species calculated using all available studies and using only the six studies that recorded more than one hundred leopard kills ( $r^2 = 0.851$ ;  $n = 15$ ;  $P < 0.001$ ;  $y = 0.77x - 0.09$ ). Larger sample sizes for black-fronted duiker, red forest duikers, chital, water chevrotain and smaller carnivores may also see them significantly preferred if the existing pattern is maintained in additional studies (Fig. 1).

Leopards significantly avoid preying upon elephant (sign test  $Z = 100$ ;  $n = 9$ ;  $P = 0.001$ ), hippopotamus ( $Z = 100$ ;  $n = 6$ ;  $P = 0.001$ ), Cape buffalo ( $Z = 94.1$ ;  $n = 17$ ;  $P < 0.001$ ), giraffe ( $Z = 100$ ;  $n = 16$ ;  $P < 0.001$ ), eland ( $Z = 85.7$ ;  $n = 14$ ;  $P = 0.016$ ), plains zebra ( $Z = 100$ ;  $n = 23$ ;  $P < 0.001$ ), ostrich ( $Z = 88.9$ ;  $n = 10$ ;  $P = 0.046$ ), blue wildebeest ( $Z = 95.5$ ;  $n = 22$ ;  $P < 0.001$ ), topi/tsessebe ( $Z = 90$ ;  $n = 10$ ;  $P = 0.013$ ), baboon ( $Z = 90.0$ ;  $n = 10$ ;  $P = 0.027$ ) and hartebeest ( $Z = 92.9$ ;  $n = 14$ ;  $P = 0.003$ ). A larger sample size is likely to see black and white rhinoceros, forest buffalo, forest elephant, francolin, gaur, golden cat, grysbok, guineafowl, hares, honey badger, mountain reedbuck, roan, sable, springbok, springhare and waterbuck significantly avoided also (Fig. 1).

Jackal, most monkey species, sambar, Grant's and Thomson's gazelle, forest duikers, common reedbuck, genets, bat-eared fox, chimpanzee, civet, bushpig, blesbok, warthog, porcupine, aardvark, klipspringer, steenbok, kudu, gemsbok, nyala, mongoose, gorilla and wild boar are all taken in accordance with their abundance (Fig. 1). Despite being frequently taken when grouped together, other carnivores and particularly felids and canids are also taken only in accordance with their abundance.

A multiple linear regression analysis was performed on prey relative abundance, body mass and habitat use, after increased herd size was found to correlate positively with increased prey abundance ( $r = 0.52$ ;  $n = 65$  and  $P < 0.05$  for all other correlations) and body mass ( $r = 0.32$ ), and threat positively correlated with body mass ( $r = 0.77$ ) and negatively with prey abundance ( $r = -0.43$ ). The Jacobs' index value of a species was

predicted by the equation Jacobs' index =  $0.16 + 0.11 \log(\text{abundance}) - 0.002 \log(\text{habitat use}) - 0.43 \log(\text{body mass})$  ( $R^2 = 0.200$ ;  $F_{3,46} = 3.759$ ;  $P = 0.017$ ), although only prey body mass was a significant predictive variable ( $P < 0.001$ ; Table 4).

When all available prey species are considered, leopards preferred prey of small to medium body mass (Fig. 2). A more detailed look at this (between 0 and 200 kg) shows a left-skewed distance-weighted least-squares fit with preferred range from 10 to 40 kg and a peak at 25 kg (Fig. 3). This left-skewed distribution of preferred prey body mass is reflected in the plot of actual leopard diet (Fig. 3), such that the preferred and actual prey of leopards is highly correlated (Spearman's  $r = 0.629$ ;  $n = 41$ ;  $P < 0.05$ ). Leopards also avoid prey with a higher injury threat category ( $r^2 = 0.317$ ;  $n = 58$ ;  $P < 0.001$ ); however, this variable was not included in the multiple regression because of its relationship with body mass and prey abundance.

The mean body mass of preferred prey species, that is those species with two or more Jacobs' index estimates where the mean ( $\pm 1$  SE) exceeded 0, was  $20 \pm 5$  kg, and the mean body mass of significantly preferred prey species was  $23 \pm 4$  kg (Table 3). On the basis of a leopard body mass of 29 kg ( $3/4 \times$  mean adult female body mass from Stuart & Stuart, 2000), the ratio of predator body mass to that of their preferred prey was 1:0.79 and that of their ideal prey (based on Fig. 3) was 1:0.86. Significantly preferred prey species occurred in significantly smaller herds (category  $2 \pm 1$ ) than significantly avoided species ( $4 \pm 1$ ;  $t = -2.45$ ; d.f. = 12;  $P = 0.031$ ), in significantly denser vegetation (category  $3 \pm 0$  compared with  $2 \pm 0$ ;  $t = 2.98$ ; d.f. = 12;  $P = 0.01$ ) and afforded no threat (category  $0 \pm 0$  compared with  $2 \pm 0$ ;  $t = -5.51$ ; d.f. = 12;  $P < 0.01$ ) (Table 3).

## Discussion

Leopards are catholic predators of over one hundred prey species but prefer to kill, and actually kill, common prey between 10 and 40 kg with an optimum weight of 23 kg based on significantly preferred prey. This body mass range is much smaller than previously reported (Stander *et al.*, 1997; Mills & Harvey, 2001). Preferred prey species occur in small herds, in dense habitat and afford solitary leopards minimal risk of injury during hunting (Table 3).

Like the puma *Felis concolor* (Iriarte *et al.*, 1990), the leopard is morphologically adapted to kill large prey, but may depend heavily on locally abundant small prey in difficult times, and this is reflected in the richness of leopard prey (Table 3). Thus, we concur with Hart *et al.* (1996) that leopards are not non-selective predators, as asserted by Hoppe-Dominik (1984), but do show preferences in selecting prey.

Given the leopard's preferred weight range, it is not surprising that leopard biomass is significantly correlated with that of prey weighing between 15 and 60 kg (Stander *et al.*, 1997). Reanalysis with our 10–40 kg range, or against the biomass of significantly preferred prey species, may yield improved predictive results. Leopards also invest more

effort in capturing prey within this range (Bothma & le Riche, 1989; Bothma *et al.*, 1997), particularly when they are hungry (Bothma & le Riche, 1990). They also protect large carcasses by dragging them to more distant cover than small carcasses (Smith, 1978). The larger body mass of males probably causes them to invest more energy in capturing larger prey than females (Bothma & le Riche, 1984), and the marked sexual dimorphism in skull morphology, including the prominent sagittal crest of males, might be an adaptation for different food habits from females (Sunquist & Sunquist, 2002).

The leopard is renowned for its stealth, and its pelage seems ideally adapted for the dappled light of dense vegetation, such that 90% of kills in Kruger occur in dense vegetation and leopards never hunt in short grasslands there (Bailey, 1993). As a solitary hunter, the leopard cannot be sustained by pride or pack mates if injured and hence preys upon species where the risk of injury is minimal. These characteristics of prey (body mass, threat, habitat type and herd size) are far more specific than those found in the lion (Hayward & Kerley, 2005). The ability to kill such a broad range of food items is undoubtedly a reason why leopards survive close to urban areas (Pienaar, 1969), and they are still classified as having a lower risk of extinction by the IUCN (Cat Specialist Group, 2004) compared with so many other fur-bearing felids (Nowell & Jackson, 1996).

Impala, bushbuck and common duiker are all species that satisfy the criteria for leopard predation and hence are preferred prey items. Leopards in Letaba Ranch (Cronje *et al.*, 2002) and Londolozi Game Reserve (le Roux & Skinner, 1989), both adjoining Kruger, predominantly preyed on impala, which is likely to increase the preference value of this species if prey abundance data were available. Similarly, leopards at Londolozi (le Roux & Skinner, 1989) and in Zambia are also considered major predators of common duiker (Wilson, 1966). Bailey (1993) suggested that the leopard's preference for these species resulted from the denseness of their preferred habitat, their ideal size and, for bushbuck and duiker, their largely solitary nature. Larger sample sizes from Asia reporting chital predation may lead to their being considered preferentially preyed upon, particularly considering they comprised 67% of the leopard's diet in Mudumalai and 24% in Mundanthurai, India (Ramakrishnan *et al.*, 1999), where prey abundance data were unavailable.

Leopards regularly kill smaller competitors, such that cheetah (Jacobs' index = 0.93), African civet (0.81), black-backed jackal (0.26) and genets (0.13) are taken more frequently than expected (Table 3). These preference values may be underestimates, as there are numerous anecdotes of leopards killing other carnivores (Estes, 1967; Pienaar, 1969; Hamilton, 1976; Bertram, 1982; le Roux & Skinner, 1989; Bailey, 1993; Bothma, 1997; Stander *et al.*, 1997; Mills & Funston, 2003). Individual preferences are thought to dictate whether leopards eat other predators (Hunter, Henschel & Ray, in press); however, the reasons for interspecific killing among predators remain unclear (Palomares & Caro, 1999).

Baboon, brown hyaena, mountain reedbuck, oribi, springbok and yellow-backed duiker are all within the preferred prey weight range, but are avoided or may be with an increased sample size (Fig. 1 and Table 3). The arboreal refuge and group vigilance of primates affords them some protection from predation by large, terrestrial predators and this, coupled with the smaller body mass of most primates, explains why leopard predation has not influenced primate evolution (Zuberbühler & Jenny, 2002). The brown hyaena is occasionally killed by leopards (Owens & Owens, 1978), despite being competitively superior, possessing sufficient weaponry to minimize predation (Estes, 1999), and occurring at a low density that reduces encounter rates, which makes searching for them too energetically costly (Sunquist & Sunquist, 1997; Hayward & Kerley, 2005). Nonetheless, leopards still capture and kill the brown hyaena's more aggressive relative *C. crocuta* (Bailey, 1993). The avoidance of oribi and springbok is probably due to their use of more open habitats than those utilized by leopards and, for springbok, their large herd sizes, although over 50% of oribi predation in Kruger were attributed to leopards (Pienaar, 1969). The probable avoidance of mountain reedbuck is more surprising given that leopards regularly inhabit mountainous areas and rocky outcrops (Hes, 1997), which are the main habitats of this species (Norton, 1997*a,b*), and that over 50% of all mountain reedbuck kills in Kruger were attributed to leopards (Pienaar, 1969). It may be that leopards use these areas as refuge from more dominant competitors, in the same way as cheetah require competition refugia (Durant, 1998), and then forage in the denser vegetation of the valleys nearby where a higher prey density exists. Data from the mountains of the Cape Province suggest that in the absence of larger competitors, leopards take small mountain-dwelling ungulates (klipspringer, grey rhebok *Pelea capreolus*) frequently (Norton *et al.*, 1986; Ott, 2004). Similarly, competitive release may expand the body mass range of prey taken by leopards (Johnson *et al.*, 1993).

Eisenberg & Lockhart (1972) suggested that wild boar were too aggressive and dangerous to become prey of leopards in Sri Lanka, and similar conclusions come from India (Ramakrishnan *et al.*, 1999). The results here indicate that this may apply to all Suidae, with warthog and bushpig killed less frequently by leopards than expected on the basis of their abundance (Table 3). This is probably due to their exceeding the upper limit of the leopard's preferred weight range, as well as their ability to inflict significant injury, such that juveniles may make up the majority of predation events.

Baboons have long been considered preferred prey species of leopards, and over 77% of baboon kills in Kruger were attributed to leopards (Pienaar, 1969). Leopards hunt baboons actively during the night (Cowlshaw, 1994), when baboons climb to the outer branches of the tallest trees to escape rather than actively defending themselves as they do during the day (Busse, 1980). Leopards may be the baboon's primary enemy; however, it does not necessarily follow that the baboon is the leopard's chief prey (Hamilton, 1976). Seidensticker (1983) considered that leopards only prey on

primates when larger prey are scarce, and our data support this.

The preferred and actual weight range of leopard prey throughout its distribution extends from 10 to 40 kg with an optimal weight of 23 kg. This is close to the preferred weight determined in Mudumalai, India (Ramakrishnan *et al.*, 1999), Ruhuna, Sri Lanka (Santiapillai *et al.*, 1982), Serengeti (Schaller, 1972), Kruger (Bailey, 1993), the Kalahari (Bothma, 1997) and in the Ituri Forest (Hart *et al.*, 1996). The overall ratio of leopard to optimal prey body mass (based on  $0.75 \times$  mean adult female mass) is 1:0.79, which lends support to the prediction of Griffiths (1975) that vertebrate predators in prey-rich environments would be energy maximizers and is very similar to that found for leopards in Nagarhole, India (Karanth & Sunquist, 1995). This contrasts, however, with results from the resource-poor Kalahari, which showed that leopards were number maximizers that were unselective of prey type, age or sex, although the flexible hunting tactics indicated some degree of energy maximization (Bothma *et al.*, 1997).

The concept of preferred prey weight range we use here is essentially the same as Burbidge & McKenzie's (1989) critical weight range. This is a range of body mass of prey species that have been threatened with extinction in Australia, largely through predation by the European red fox *Vulpes vulpes*. Although the prey species within the leopard's preferred weight range have evolved alongside it, and are therefore not being driven to extinction by leopard predation, it is becoming increasingly apparent that each predator has a range of prey body masses that facilitate successful predation. For the red fox in Australia, this entails a range of prey species that have not evolved alongside it and are therefore highly susceptible to predation by it.

Where the prey preference–body mass plot of lions was skewed to the right (Hayward & Kerley, 2005), that of the leopard is skewed to the left (Fig. 3). We had hypothesized that predator–prey preference would follow a normal distribution when plotted against prey body mass based on optimality theory (see review by Pyke, Pulliam & Charnov, 1977) and energy maximization (Griffiths, 1975, 1980), with some species too small to obtain enough energy from hunting to be sustainable (Bourlière, 1963; Rosenzweig, 1966; Earle, 1987) and others too large to be easily and safely taken (Elliott *et al.*, 1977; Hayward & Kerley, 2005). Serengeti data support this as carnivores there are inefficient at catching prey outside their preferred size range (Sinclair, Mduma & Brashares, 2003). Similarly, pumas in Florida are deficient in available, suitably sized prey and hence are smaller, have lower reproductive rates and are in poorer condition than pumas elsewhere (Iriarte *et al.*, 1990). Furthermore, leopards invest more energy in hunting medium-sized prey rather than smaller or excessively large, suboptimal species (Bailey, 1993; Bothma *et al.*, 1997). We also hypothesized that the right-skewed distribution of lion preferred prey was due to its group hunting capability (Hayward & Kerley, 2005) and therefore suggest that the left-skewed distribution for the leopard may result from its solitary hunting.

One interesting factor relating to the prey selection of the leopard is its highly variable body mass. Animals in the south of its African range (e.g. Western Cape of South Africa), with adult males averaging 31 kg and females 21 kg (Stuart, 1981), are about half the size of those further north (Mills & Harvey, 2001). Whether this is a result of simple latitudinal body mass variation or evidence of a flexible body mass in response to variations in available prey body mass or both is unknown, although it is readily conceivable that where small prey are all that is available natural selection would favour a decline in predator body mass if smaller hunters can subsist on this smaller available prey after sufficient isolation time. Character displacement by way of divergence in size is important for larger carnivores where prey is difficult to partition except by size (van Valkenburgh & Wayne, 1994), and such character displacement may therefore occur in the absence of competition where it arises to fill a vacant niche in response to the size of locally available prey (as occurs in the puma, Iriarte *et al.*, 1990; and tiger *Panthera tigris*; Seidensticker & McDougal, 1993).

As the leopard's body mass range crosses the body mass threshold for obligate large vertebrate carnivory ( $>45\%$  of predator body mass; Carbone *et al.*, 1999), smaller body mass populations of leopards might be expected to prey on smaller vertebrates. Leopards in the Baviaanskloof Wilderness Area in South Africa's Eastern Cape Province support this, with rodents comprising 9% of the total prey species killed (Ott, 2004). Other populations of leopards that prey largely on suboptimally sized prey (Grobler & Wilson, 1972) may also be smaller in body mass than those preying on large ungulates. Limited data from Israel and Oman suggest that small leopards there largely prey on smaller body sized species (Ilani, 1981; Spalton & Willis, 1999).

A review such as this highlights problems with the collection of data. The 4 840 000 km<sup>2</sup> distribution of the leopard extends through sub-Saharan and North Africa, the Middle East and Asia (Nowell & Jackson, 1996). This range encompasses dozens of nations; however, data sufficient for inclusion in this study on the diet of the leopard have only been conducted in 13 of these (Table 1). Different habitats are also under study, notably Asian and African rainforest (with the exception of the studies of Hart *et al.*, 1996; Henschel *et al.*, 2005), where leopard diet but not prey abundance was frequently documented (e.g. Hoppe-Dominik, 1984; Ray & Sunquist, 2001). Clearly, there is a deficiency in the degree of research conducted or perhaps published on the ecology of the leopard.

The technique used here is highly robust, as evidenced by the strong linear relationship between Jacobs' index values of leopard prey calculated using all available data and using a subset of studies from savanna habitats that reported more than 100 kills. Consequently, this technique may provide answers to unsolved questions in predator–prey ecology. Karanth & Sunquist (1995) suggest that the unselective intake of small prey items by large predators reported in several tropical forests (Rabinowitz & Nottingham, 1986;

Emmons, 1987; Rabinowitz, 1989; Iriarte *et al.*, 1990) may simply be due to the absence of available large prey. By using electivity indices, as we have here, this issue could be resolved.

As well as being important for understanding the ecology of the leopard and predator–prey interactions, our research has important management and conservation implications. The Jacobs' index values calculated here can be used to predict the diet of leopards where their ecology is poorly known or where their reintroduction and translocation is planned. By solving the Jacobs' index equation using the values calculated here and using prey abundance data for the site in question, the relative proportion that each species will be taken as prey can be estimated. This means that wildlife managers can predict what leopards will kill in a reserve in the absence of any data on leopard feeding ecology and ensure they plan instead of merely responding to stochastic variations in prey abundance. Similarly, from a conservation viewpoint, when planning reintroductions and translocations of leopards, confirmation that there is a sustainable base of prey within the leopard's preferred weight range will maximize the chances of success. The data presented here, therefore, allow us to move from a simple description of leopard diet on to a predictive focus based on electivity and optimality theory.

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