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Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*)

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Abstract

Spotted hyaenas *Crocuta crocuta* were once considered mere scavengers; however, detailed research revealed that they are very efficient predators. Information on what spotted hyaenas actually prefer to prey on and what they avoid is lacking, as well as the factors that influence prey selection. Data from 14 published and one unpublished study from six countries throughout the distribution of the spotted hyaena were used to determine which prey species were preferred and which were avoided using Jacobs' index. The mean of these values for each species was used as the dependent variable in multiple regression, with prey abundance and prey body mass as predictive variables. In stark contrast to the rest of Africa's large predator guild, spotted hyaenas do not preferentially prey on any species. Also surprisingly, only buffalo, giraffe and plains zebra are significantly avoided. Spotted hyaena most prefer prey within a body mass range of 56–182 kg, with a mode of 102 kg. The dietary niche breadth of the spotted hyaena is similar to that of the lion *Panthera leo*, and the two species have a 58.6% actual prey species overlap and a 68.8% preferred prey species overlap. These results highlight the flexible and unselective nature of spotted hyaena predation and are probably a reason for the species' success throughout its range, despite a large degree of dietary overlap with lions.

Introduction

Spotted hyaenas *Crocuta crocuta* are common, large (45–80 kg), gregarious predators that occur throughout sub-Saharan Africa outside of tropical forests, alpine areas and true deserts (Frank, Holekamp & Smale, 1995; Mills & Harvey, 2001). Their body mass exceeds the 21.5 kg threshold that necessitates vertebrate carnivory (Carbone *et al*., 1999); however, the flexible foraging strategy that spotted hyaenas use and their catholic tastes mean that virtually any animate and inanimate object is potential food (Pienaar, 1969). To maintain their condition they need 3.8–4.0 kg of meat daily (Henschel & Tilson, 1988), and spotted hyaenas have been recorded as preying on fish and ostrich *Struthio camelus* eggs (Pienaar, 1969) up to prey the size of adult buffalo *Syncerus caffer* (Pienaar, 1969; Sillero-Zubiri & Gottelli, 1992*b*; di Silvestre, Novelli & Bogliani, 2000) and the calves of black rhinoceros *Diceros bicornis* (Berger & Cunningham, 1994) and giraffe *Giraffa camelopardalis* (Hirst, 1969).

Although originally considered a scavenger, it is now well known that spotted hyaenas are active hunters (Kruuk, 1966), scavenging only one-third of their diet in the Serengeti (Kruuk, 1972) and much less where other large, carcass-producing predators occur at lesser densities. They lose up to 5% of their kills to other carnivores (mostly lions *Panthera leo*) in the Serengeti and 20% in Ngorongoro Crater (Kruuk, 1972), and in agonistic encounters are often killed by lions (Kruuk, 1972; Whateley & Brooks, 1985).

Notwithstanding their scavenging behaviour, spotted hyaenas are flexible hunters, cooperating to bring down larger prey or steal carcasses from other predators, but foraging alone for smaller items (Kruuk, 1966, 1970) up to 75% of the time (Holekamp *et al*., 1997). Group hunts arise when several clan members assemble at a den and travel directly to a group of large ungulates while passing through herds of smaller prey, suggesting that the target prey species was selected in advance of the start of the hunt (Holekamp *et al*., 1997). Individual hyaenas hunting blue wildebeest *Connochaetes taurinus* calves in the Serengeti had a 15% hunt success rate, which increased to 23% for pairs and 31% for groups of three or larger (Kruuk, 1972). In the Masai Mara, adding a second hunter increased hunting success by 19% and a third hunter by a further 20% (Holekamp *et al*., 1997).

When hunting, spotted hyaenas rarely stalk but rather lope through a herd looking for a weakened individual before chasing it in the hunt (Mills & Harvey, 2001). Groups of up to 20 join forces and chase prey for up to 3 km at a speed of 65 km h^{-1} once a quarry has been selected (Kruuk, 1972). As a cursorial, pursuit predator, selection for sick prey occurs more frequently than for predators that rely on stealth, and *c*. 30–35% of all hunts end in kills (Kruuk, 1972; Cooper, 1990; Mills, 1990; Gasaway, Mossestad & Stander, 1991; Holekamp *et al*., 1997). They are nocturnal hunters, possibly because of their improved night vision compared with their prey (Bertram, 1979).

In this study, I aimed to use dietary and prey abundance data collected from studies conducted throughout the distribution of the spotted hyaena to determine which, if any, prey species it prefers and which it avoids. If a species is killed more frequently than it occurs in the prey population then it can be considered preferred, whereas if it is taken less frequently then it is avoided. Obviously, this is a simplification as it reflects not just the predator's preference but also the ease with which a prey species is captured.

I subsequently attempted to explain why particular prey species were preferred or avoided using various ecological features (similar to that conducted by Jaksic *et al*., 1992). My analyses have followed that of Hayward & Kerley (2005) to allow direct comparison between the causes of prey preferences of Africa's large predatory guild. Finally, I compared the diet of spotted hyaenas with published information on lions (Hayward & Kerley, 2005) to determine the degree of dietary overlap between them to ascertain whether this is likely to affect the conservation status of the spotted hyaena.

Methods

A literature survey revealed 14 published and one unpublished study describing the diet of the spotted hyaena, which included some measure of prey abundance (either actual or relative; Table 1). Several of these studies reported diet and prey abundance from more than one site, in different years or at differing prey abundances (migrations), allowing 21 assessments of prey preference to be calculated from sites throughout the distribution of the spotted hyaena.

The unpublished data come from the Addo Elephant National Park (33°30′S, 25°45′E) in South Africa's Eastern Cape (M. W. Hayward, unpubl. data). Eight spotted hyaenas have been released in the Main Camp section of the park since late 2003, and continuous follows and incidental sightings revealed 35 kills in the 12 months following the initial release (Table 2).

Other studies provided excellent descriptive information on spotted hyaena diet but insufficient information on prey abundance (Dean, 1960; Eloff, 1964; Smuts, 1979; Gasaway *et al*., 1991; Breuer, 2005). Unless other sources could be found that provided prey abundance (see Table 2), these studies could not be used.

The data collected in these studies were derived from incidental observations, continuous follows and identification of prey guard hairs found in spotted hyaena faeces. Continuous follows are widely regarded as the superior method of ascertaining the diet of a predator (Bertram, 1979). Incidental observations are biased towards larger prey; however, this bias against smaller items is generally counteracted by the undercounting of small prey species in aerial counts. Conversely, faecal studies are biased towards smaller prey that may have a faster rate of passage through the gut (Mills, 1992) and the differential passage of different body parts (e.g. fur or bone) through the gut resulting in double counting of a single prey item (Hiscocks

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

Country	Site	Years/period	No. of kills	Source
Botswana	Moremi Game Reserve	1986–1988	93	Cooper (1990)
Kenya	Aberdare National Park	1986–1987	311	Sillero-Zubiri & Gottelli (1992*a*)
	Masai Mara National Reserve	1988–1995 January–June	355[a]	Cooper *et al*. (1999)
		1988–1995 July–September	355[a]	As above
		1988–1995 October–December	355[a]	As above
Namibia	Namib-Nauklauf Park	1976–1977	621	Tilson, von Blottnitz & Henschel (1980)
		1989	129	Skinner *et al*. (1992)
Senegal	Niokolo Koba National Park	1995–1996	[b]	di Silvestre *et al*. (2000)
South Africa	Addo Elephant National Park	2004	35	M. W. Hayward (unpubl. data)
	Hluhluwe-Umfolozi Park	1989	162	Skinner *et al*. (1992)
	Kalahari Gemsbok National Park	1974–1988	346	Mills (1990)
	Kruger National Park	1956–1965	170	Pienaar (1969)
		1982–1984	24	Henschel & Skinner (1990)
		Early 1990s	27	Mills & Biggs (1993)
	Mkuze Game Reserve	1989	190	Skinner *et al*. (1992)
	Timbavati Game Reserve	1964	35	Hirst (1969)
		1965	24	As above
		1973–1975	749	Bearder (1977)
Tanzania	Ngorongoro Crater	1965–1969	240	Kruuk (1972)
		1996–1999	82	Höner *et al*. (2002)
	Serengeti National Park	1965–1969	220	Kruuk (1972)

[a]Three hundred and fifty-five kills were observed during the 7-year study period.
[b]Data presented as percentages.

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

Study	Assumptions made or source of abundance data
Cooper (1990)	Abundance from Viljoen (1993)
Cooper *et al*. (1999)	As only 12 of 526 pieces of carrion fed upon were identifiable (table 1 of their study), I have used the data presented on the proportion of kills from their table 3
M. W. Hayward (unpubl. data)	Aerial censuses in 2004 revealed the following wildlife populations and kills are shown in parentheses: buffalo 355 (5), bushbuck 103 (1), common duiker 55 (1), elephant 344 (0), eland 106 (2), Cape grysbok 1 (0), hartebeest 288 (5), kudu 706 (15), ostrich 261 (5), black rhinoceros 7 (0), warthog 298 (0) and plains zebra 36 (0)
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
Sillero-Zubiri & Gottelli (1992*a*)	Prey abundance was based on table 4 on p. 172 for buffalo, bushbuck, elephant, giant forest hog and warthog, but also included references in the text of 12 bushpig (p. 175) and suni, which were considered numerous (p. 174) and were concluded to be at the same density as bushbuck. Prey was based on scats in table 1 on p. 172 given that hyaenas were the dominant predator in the ecosystem.

& Bowland, 1989). Thus, the use of three methods to determine diet is likely to accurately reflect that of the spotted hyaena.

In accordance with previous studies conducted on the prey preferences of Africa's large predator guild (Hayward & Kerley, 2005; Hayward *et al*., 2006*a*), Jacobs' index was used because it minimizes problems associated with electivity indices (Jacobs, 1974). Jacobs' index

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

standardizes the relationship between the relative proportion that each species makes up of spotted hyaena kills r and prey relative abundance p (i.e. the proportion that each species makes up of the total abundance of all censused prey species at a site). The standardized values range from $+1$ to -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 in the literature (Tables 1 and 2). The mean Jacobs' index for each of these prey species was then calculated from all studies where that prey species was present (± 1 SE wherever 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, de Tores & Banks, 2005). Where transformation could not satisfy these assumptions, the sign test (Zar, 1996) was used to test preference or avoidance. The value of this kind of analysis is that it is not biased by the results from one area; it is not influenced by the community of available 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 that hunt as fission–fusion groups (Hayward & Kerley, 2005).

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

Spotted hyaena are generally thought to eat prey of medium to large body size (Mills & Harvey, 2001). Three-quarters of the mean adult female body mass of prey species was used to account for calves and subadults eaten. This value was used in a previous study (Hayward & Kerley, 2005) following Schaller's (1972) example, and I continue its use here to allow comparison between these studies. Weights were taken from Stuart & Stuart (2000).

Social organization of prey species is an indicator of the ability of prey to detect predators and the predators' ability to get close to prey (see the 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).

Habitat type may affect predation rates through the density of vegetation affecting prey detectability. Spotted hyaenas occur in habitats ranging from arid lands to open grassland to savanna and even forest (Kruuk, 1972; Mills, 1984; Sillero-Zubiri & Gottelli, 1992*b*), suggesting that irrespective of where a prey animal lives it is at risk of spotted hyaena predation. Prey animals inhabiting dense vegetation generally adopt a silent, solitary, hider strategy to evade detection, whereas prey in open grasslands are detected by sight rather than sound and can exist in large herds (Geist, 1974; Leuthold & Leuthold, 1975). Although inherently difficult to classify (Sunquist & Sunquist, 1997), a categorical variable of habitat density was used, with 1 referring to open grasslands, 2 to savannah 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 technique has been used in carnivore studies previously (e.g. Mills, Broomhall & du Toit, 2004).

Finally, the anti-predatory strategy a species employs will affect its chances of becoming prey. The evolution of

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 adult female body mass) and categories of herd size, habitat density and injury threat to spotted hyaena *Crocuta crocuta* used in modelling

Species	Jacobs' index ± SE	n_p	n_a	Kills (%) ± SE	Abundance (%) ± SE	Mass	Herd size	Habitat	Threat
Baboon *Papio* sp.	−0.99 ± 0.01	2	1	0.75 ± 0.75	26.12 ± 26.04	12	5	2	1
Buffalo *Syncerus caffer*[−]	−0.39 ± 0.17	11	9	6.04 ± 1.91	11.2 ± 3.33	432	5	2	2
Bushbuck *Tragelaphus scriptus*	0.10 ± 0.19	4	4	10.89 ± 6.57	7.45 ± 2.67	23	1	3	0
Bushpig *Potamochoerus larvatus*	−0.12 ± 0.88	2	1	2.11 ± 2.11	0.3 ± 0.3	46	3	3	1
Duiker, common *Sylvicapra grimmia*	−0.45 ± 0.23	7	4	2.13 ± 1.08	2.86 ± 0.93	16	1	3	0
Duiker, red *Cephalophus natalensis*	−0.70 ± 0.30	2	1	0.53 ± 0.53	1.26 ± 1.18	10	1	3	0
Eland *Tragelaphus oryx*	−0.34 ± 0.33	6	3	2.54 ± 1.60	1.17 ± 0.64	345	5	2	2
Elephant *Loxodonta africana*	−1 ± 0	3	0	0 ± 0	7.66 ± 5.78	1600	4	2	2
Gemsbok *Oryx gazella*	0.62 ± 0.25	3	3	63.85 ± 8.58	30.26 ± 15.20	158	4	1	2
Giraffe *Giraffa camelopardalis*[−]	−0.59 ± 0.20	9	4	5.66 ± 4.41	4.99 ± 1.28	550	3	2	2
Grant's gazelle *Gazella granti*	−0.19 ± 0.5	2	2	2.22 ± 1.39	3.96 ± 2.20	38	4	1	0
Grysbok *Raphicerus* sp.	−0.12 ± 0.88	2	1	0.29 ± 0.29	0.06 ± 0.02	7.5	1	2	0
Hartebeest *Alcephalus busephalus*	−0.36 ± 0.24	8	5	4.20 ± 2.33	2.57 ± 1.30	95	4	1.5	1
Hippopotamus *Hippopotamus amphibius*	0.28 ± 0.53	2	2	3.58 ± 0.58	2.67 ± 2.20	750	3	1.5	2
Impala *Aepyceros melampus*	−0.09 ± 0.15	13	13	28.29 ± 7.75	35.06 ± 7.53	30	4	2	0
Klipspringer *Oreotragus oreotragus*	−0.84 ± 0.16	2	1	0.56 ± 0.56	2.93 ± 2.84	10	2.5	3	0
Kudu *Tragelaphus strepsiceros*	0.11 ± 0.19	11	10	10.42 ± 3.66	6.28 ± 2.38	135	3	2	0.5
Nyala *Tragelaphus angasi*	−0.33 ± 0.35	3	2	15.37 ± 9.65	14.58 ± 7.67	47	3	2	0.5
Ostrich *Struthio camelus*	−0.41 ± 0.59	2	1	7.14 ± 7.14	5.14 ± 5.06	70	3	1.5	1
Reedbuck sp. *Redunca* sp.	−0.52 ± 0.48	4	1	0.81 ± 0.81	0.46 ± 0.27	32	3	1.5	0
Roan *Hippotragus equines*	−0.56 ± 0.44	3	1	1.20 ± 1.20	0.74 ± 0.58	220	3.5	2	1.5
Sable *Hippotragus niger*	−1 ± 0	2	0	0 ± 0	0.45 ± 0.19	180	4	2	1.5
Springbuck *Antidorcas marsupialis*	−0.81 ± 0.05	3	3	6.27 ± 3.12	33.93 ± 12.91	26	5	1	0
Steenbuck *Raphicerus campestris*	−0.56 ± 0.26	4	3	6.79 ± 6.08	7.17 ± 4.09	8	1.5	1.5	0
Thomson's gazelle *Gazella thomsoni*	−0.46 ± 0.12	4	4	20.64 ± 9.66	36.12 ± 13.09	15	5	1	0
Topi/Tsessebe *Damaliscus lunatus*	0.01 ± 0.40	6	5	4.41 ± 2.08	2.13 ± 1.18	94.5	4	1.5	1
Warthog *Phacochoerus aethiops*	−0.20 ± 0.21	14	10	4.45 ± 1.51	4.61 ± 1.67	45	3	2	1.5
Waterbuck *Kobus ellipsiprymnus*	−0.02 ± 0.19	10	8	2.31 ± 1.07	1.33 ± 0.29	188	3.5	2	1.5
Wildebeest *Connochaetes taurinus*	0.02 ± 0.13	15	13	26.92 ± 6.76	22.03 ± 5.00	135	5	1	1.5
Zebra *Equus burchelli*[−]	−0.44 ± 0.12	16	12	9.10 ± 2.38	14.82 ± 2.91	175	3	2	1.5

Specifics of each category are described in the text and their details were derived from Stuart & Stuart (2000) and Estes (1999).
[−]Indicates significantly avoided.

cryptic coloration and patterning in predators is an obvious way of improving hunting success; however, primate prey can recognize 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 predators and/or their prey species, although inhabitants of dense vegetation are often cryptic or of dull body coloration compared with the conspicuous patterning of grassland species (Geist, 1974). Similarly, there has been little comparative work on prey evasion speed (Elliott, Cowan & Holling, 1977; Prins & Iason, 1989 excepted). This dearth of comparative information 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 were 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 of predators caused by this species) (Table 3). Information for each of these categories comes from Estes (1999) and Stuart & Stuart (2000).

I have not separated the analysis of these data by gender or group size of the hunting spotted hyaenas as no study looked solely at the prey of solitary hunters or groups of either sex. I expect these results to reflect the mean hunting group size at a site and the variation in hunting group size of males and females. The data available never indicated the group size or gender of each kill and I leave such detailed analyses to individual study sites where data have been collected with this in mind (e.g. Radloff & du Toit, 2004). Similarly, studies I used looked at seasonal variation (e.g. Cooper, 1990) and others looked at the same site in varying climatic conditions (Kruuk, 1972; Höner, Wachter & East, 2002). I expect the mean Jacobs' index value for a species to reflect the variable susceptibility of prey in drought or above average rainfall.

Levin's niche breadth and percentage niche overlap (Krebs, 1989) were calculated for the spotted hyaena using the derived Jacobs' index values, and for the lion *P. leo* using data presented in Hayward & Kerley (2005; Table 3). A log-likelihood test (G^2) was used to test if there were any significant differences between the overall preferences of these two dominant predators.

Results

Jacobs' index scores were derived from 3478 kills of 30 prey species recorded as prey of the spotted hyaena (Table 3 shows the scientific names). Impala (11 studies), Thomson's and Grant's gazelles (six studies), bushbuck (four studies), springbok and gemsbok (three studies each) were killed by spotted hyaenas wherever they occurred at a site (Fig. 1). Kudu, blue wildebeest, hartebeest, waterbuck and buffalo are also common prey items (Fig. 1). Except for elephant, every potential prey species recorded in more than two studies was preyed upon by spotted hyaenas (Fig. 1).

Gemsbok was the most frequently killed prey species where it occurred (63.9% at three sites), followed by impala (28.3% at 13 sites), Thomson's gazelle (20.6% at four sites), blue wildebeest (26.9% at 15 sites), nyala (15.4% at three sites) and kudu (10.4% at 11 sites) (Table 3). This contrasts with the most abundant prey species, which were Thomson's gazelle (36.1% of available prey at the four sites it occurred at) impala (35.1% at 13 sites), springbok (33.9% at three sites), gemsbok (30.3%), baboon (26.1% at two sites) and blue wildebeest (22.0%). Although there is variation as to the proportion that a species is preyed upon and its relative abundance, there is a significant correlation between what spotted hyaenas kill and what is available (Spearman's rank order correlation $r = 0.89$, $n = 19$, $P < 0.05$).

No prey species are significantly preferred by spotted hyaenas. Gemsbok may be eventually with a larger sample size if the existing trends continue (Fig. 2).

Hippopotamus, kudu, topi/tsessebe, bushpig, waterbuck, bushbuck, blue wildebeest, impala, grysbok, warthog, Grant's gazelle, nyala and ostrich are all taken in proportion

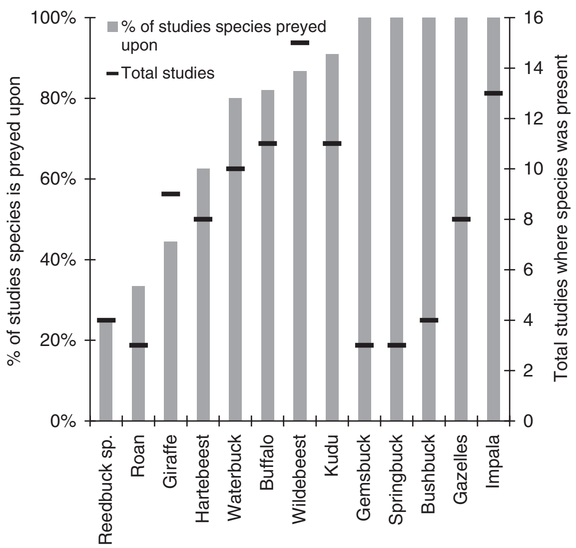

Figure 1 Common and infrequently killed prey of spotted hyaena *Crocuta crocuta*.

with their abundance (Fig. 2). Eland, common duiker, hartebeest, reedbuck, steenbok, roan, red duiker, springbok, klipspringer, baboon, sable and elephant are currently taken in proportion with their relative abundance, but a larger sample size is likely to see them classed as avoided (Fig. 2). Only buffalo ($t = -2.234$, d.f. = 10, $P = 0.049$), giraffe ($Z = 89$, $n = 9$, $P = 0.046$) and plains zebra ($t = -4.79$, d.f. = 13, $P < 0.001$) are significantly avoided by spotted hyaenas.

A multiple linear regression analysis to predict the Jacobs' index value was conducted using prey abundance, body mass and habitat as independent variables, after prey body mass was found to correlate significantly with herd size (Spearman's $r = 0.42$) and threat category ($r = 0.87$, $n = 29$, $P < 0.05$ for both). The resulting non-significant equation was Jacobs' index $= -0.07 - 0.16 \text{Arc Sin}\sqrt{\text{abundance}} - 0.11\,\text{habitat use} - 0.02 \log \text{body mass}$ (Table 4). No individual variable significantly predicted the Jacobs' index value.

A distance-weighted least-squares regression was used to investigate the body mass of prey that is most preferred and most frequently killed by spotted hyaenas. Although non-significant for both Jacobs' index ($r = -0.112$, $n = 29$, $P = 0.562$) and prey actually killed ($r = 0.007$, $n = 29$, $P = 0.971$), it has been included to allow comparison with previous studies. This plot shows the ideal prey body mass for spotted hyaena to be 102 kg, with a range from 56 to 182 kg (Fig. 3). There are only six potential prey species within this 126 kg range, and none are significantly preferred (Table 3). Given that three-quarters of adult female spotted hyaena body mass is about 60 kg (Stuart & Stuart, 2000), the ratio of predator body mass to that of their most preferred prey is 1:1.7.

The log-likelihood ratio revealed that there were no significant differences between the preference values for spotted hyaena and lion prey ($G = 10.86$, d.f. = 34, $P > 0.999$). There were, however, significant differences in the percentage of prey that was actually taken by each species ($G = 67.97$, d.f. = 34, $P < 0.001$). Levin's dietary niche breadth for prey preferences of spotted hyaenas was 21.56 and for lions was 21.90. Using actual kill data (% prey), the niche breadth for spotted hyaenas was 8.57 and for lions was 14.05. These two predators also had an actual dietary overlap of 58.6% and a preferred dietary overlap of 68.8%. The niche breadth and overlap values are greatest using the prey preference data.

Discussion

The results highlight the eclectic nature of spotted hyaena predation and are in stark contrast to the predatory behaviour of the rest of Africa's large predatory guild. It seems most likely that very few prey species are free from the threat of spotted hyaena predation and larger, common prey are generally taken. That there was no relationship between prey abundance and hyaena prey preference may be due to the effects of seasonal or localized changes in prey abundance due to migrations or birth seasons; however, this does

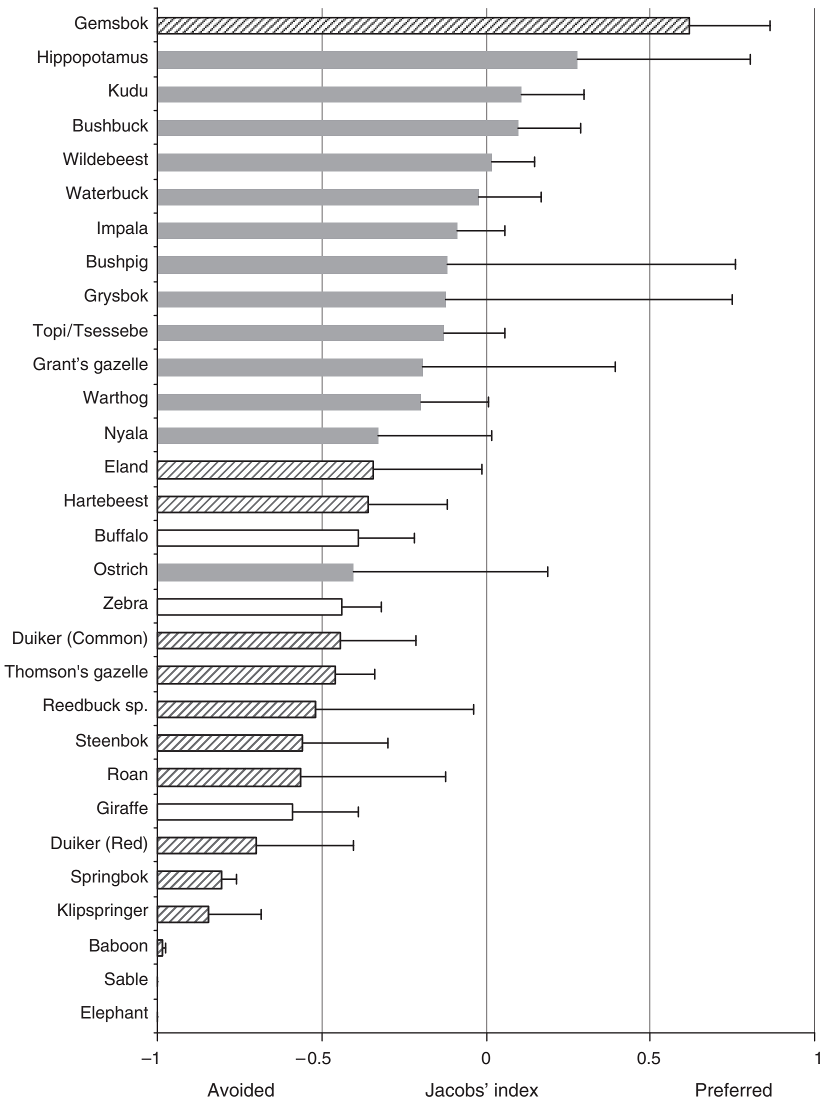

Figure 2 Spotted hyaena *Crocuta crocuta* prey preferences based on Jacobs' index (mean ± 1 SE) of 21 spotted hyaena populations at differing prey densities. Black stippled bars represent species that are likely to be significantly killed more frequently than expected based on their relative abundance (preferred) with a larger sample size assuming the existing trends continue. Grey bars indicate species taken in proportion to their relative abundance and unfilled bars show species taken significantly less frequently than expected based on their relative abundance (avoided). Grey stippled bars indicate species that are likely to be significantly avoided with a larger sample size if the existing trends continue.

not seem to be a factor for other large predators (M. W. Hayward, unpubl. data).

Spotted hyaenas do not exhibit a significant preference for any prey species and avoid very few, and this reflects their ability to hunt cooperatively in groups, to hunt alone or to satisfy their dietary requirements through scavenging. Conversely, lions *P. leo* significantly prefer five prey species (gemsbok, buffalo, blue wildebeest, giraffe and plains zebra; Hayward & Kerley, 2005), leopard *Panthera pardus* prefer three species (impala, bushbuck and common duiker; Hayward *et al*., 2006*a*), cheetah *Acinonyx jubatus* prefer five species (Hayward *et al*., 2006*b*) and African wild dog *Lycaon pictus* prefer four species (Hayward *et al*., 2006*c*). Although spotted hyaenas only significantly avoid buffalo, plains zebra and giraffe (Fig. 2), lion and leopard significantly avoid 11 prey species (Hayward & Kerley, 2005; Hayward *et al*., 2006*a*), cheetah avoid 16 species (Hayward *et al*., 2006*b*) and wild dog significantly avoid 16 prey species (Hayward *et al*., 2006*c*). Finally, multiple regression analysis revealed that there were no factors that significantly predicted the Jacobs' index value of spotted hyaena prey (Table 4). The same analysis revealed that lion and leopard prey preferences are significantly predicted by the body mass of their prey (Hayward & Kerley, 2005; Hayward *et al*., 2006*a*), whereas cheetah and wild dog prey preferences are significantly predicted by the body mass of their prey and its relative abundance (Hayward *et al*., 2006*b,c*).

The non-specific nature of spotted hyaena predation undoubtedly contributes to its relatively secure conservation status (Hyaena Specialist Group, 2004). Its morphology and behavioural opportunism allow it to capture anything it can overpower, from springhares to giraffes (Cooper, 1990). The lack of significant preference of any prey species by the spotted hyaena as a species found here probably relates to local variation in hunting behaviour in individual populations because localized prey preferences have been

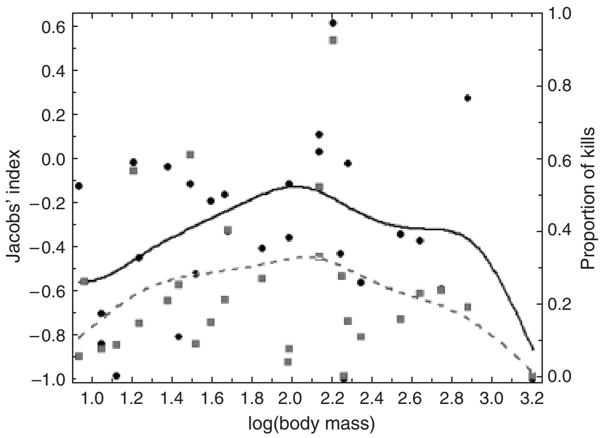

Figure 3 Distance-weighted least-squares relationship between spotted hyaena *Crocuta crocuta* prey preference (mean Jacobs' index in black) and the proportion that each species actually occurs as spotted hyaena prey (in grey) against prey body mass for species weighing less than 200 kg. Regression statistics for Jacobs' index—prey body mass relationship are $r=-0.366$, $n=58$, $P=0.011$ and for proportion as prey are $r=-0.119$, $n=58$, $P=0.422$.

Table 4 Regression statistics for the multiple regression model using data from Table 3

Variable	Coefficient	SE	t_{26}	Probability
Constant	−0.07	0.39	0.17	0.87
ArcSin$\sqrt{\text{Abundance}}$	−0.16	0.38	−0.16	0.69
Habitat use	−0.11	0.12	−0.96	0.37
log(body mass)	−0.02	0.10	0.16	0.87

log Jacobs' index = −0.07−0.16(ArcSin(Sqrt(relative abundance))) −0.11(habitat use) −0.02(log(body mass)). Standard error of estimate = 0.39; $R^2=0.03$; analysis of variance $F_{3,26}=0.28$; $P=0.84$. No variables predicted the Jacobs' index value at $\alpha=0.05$.

reported. It may be that the effect of hyaenas as predators of a particular species depends on factors such as hyaena population density, previous experience and the local abundance of prey (Cooper, 1990). For example, in Senegal's Niokolo Koba National Park buffalo are one of the most preferred prey species (di Silvestre *et al*., 2000); however, in the Savuti region of Botswana's Moremi Game Reserve they are considered almost immune to predation by hyaenas (Cooper, 1990). In such cases, preference for a prey species at one site is negated by avoidance of that species at another. Site-specific prey preferences have also been found for the Talek spotted hyaena clan in Kenya's Masai Mara National Reserve (Cooper, Holekamp & Smale, 1999).

Hyaena in Kenya's Masai Mara National Reserve tended to hunt whichever prey species was most abundant each season (Holekamp *et al*., 1997), and Kruuk (1972) hypothesized that seasonal fluctuations in spotted hyaena diet reflected changes in relative prey abundance. This may explain the absence of preference for any prey of the spotted hyaena that I found here, based on sites with migratory prey (e.g. Cooper *et al*., 1999); however, it does not explain the results for sites with sedentary prey. Variation in prey abundance in Ngorongoro Crater between the 1960s and 1990s led to increased predation of buffalo calves and adult wildebeest, which was used as evidence for a functional response by spotted hyaenas (Höner *et al*., 2002). This dietary flexibility, coupled with their mobility, makes spotted hyaenas the most successful of Africa's large predators (Mills & Harvey, 2001).

The body mass range of most preferred prey species (56–182 kg) encompasses the gemsbok, which is the only species that is likely to become significantly preferred with a larger sample size, if the existing trends continue (Fig. 2). As there are few other prey species within the spotted hyaena's most preferred prey range that are common in the environments where gemsbok live, it is not surprising that gemsbok have a high Jacobs' index value. Hartebeest, kudu, topi/tsessebe, blue wildebeest and plains zebra are the only other species that are within the most preferred weight range of spotted hyaena prey, yet all except the zebra (significantly avoided) are killed in proportion with their abundance (Table 3). In comparison, the lion has only four species in its 190–550 kg preferred prey range and significantly prefers two of them, although it takes each more frequently than the species' abundance would suggest (Hayward & Kerley, 2005).

This body mass range may be biased slightly towards larger prey items, given that spotted hyaenas generally take the young of larger prey items (Mills, 1990; Cronje, Reilly & MacFadyen, 2002); however, the greater effort spotted hyaenas invest in hunting larger prey (Cooper, 1990; Holekamp *et al*., 1997) confounds this. Similar body mass ranges are found in spotted hyaenas from Senegal (di Silvestre *et al*., 2000) and the Kalahari (Mills, 1990, p. 32).

The ratio of predator body mass to that of its most preferred prey indicates that spotted hyaenas prefer and actually take prey larger than themselves. This may be due to the cooperative hunting strategy often used by spotted hyaenas (Kruuk, 1972).

Spotted hyaenas have the fewest published studies reporting their diet (14 with abundance estimates associated and 19 without) of Africa's large predator guild. This does not inhibit the likelihood of non-parametric statistics returning a significant result ($n = 5$ required for sign test), and therefore my results and conclusions are likely to be valid. It is, however, important to increase the amount of research conducted on this valuable species, particularly given its impact on competitively inferior and threatened species like African wild dogs (Carbone, du Toit & Gordon, 1997; Mills & Gorman, 1997; Gorman *et al*., 1998; Woodroffe & Ginsberg, 1999) and cheetahs (Laurenson, 1995; Durant, 2000*a*,*b*).

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