Brown hyaena feeding ecology on Namibian farmlands

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We identified the diet of brown hyaenas (*Hyaena brunnea*) on the farmlands of north-central Namibia based on scat analysis, den site orts, and evidence of scavenging at leopard (*Panthera pardus*) kills. In the absence of larger carnivores, which have been credited with providing larger food items for brown hyaenas elsewhere, we compared interspecific dietary overlap and activity patterns with the remaining large carnivores, leopards and cheetahs (*Acinonyx jubatus*). Where hyaenas and leopards were sympatric, diets of both nocturnal species (*n* = 212 hyaena scats and 41 leopard scats) were quite similar (both >89% wild, with some domestic ungulates), and only somewhat different from cheetahs in a previous study. Additionally, evidence of brown hyaena scavenging was found at 76% of 29 leopard kills available to them. Brown hyaenas occurring on Namibian farmlands likely find medium-sized to large ungulate prey by scavenging from leopards and perhaps cheetahs.

Key words: *Acinonyx*, cheetah, food, *Hyaena brunnea*, kills, leopard, orts, *Panthera pardus*, scats.

INTRODUCTION

Large carnivores are typically considered primary predators, but many will opportunistically scavenge instead of actively hunt (Bauer *et al.* 2005; Schrecengost *et al.* 2008). Brown hyaenas (*Hyaena brunnea*) scavenge medium-sized to large ungulates extensively where they co-occur with lions (*Panthera leo*; Owens & Owens 1978; Mills 1990; Maude & Mills 2005), but in many areas of Namibia and South Africa, brown hyaenas inhabit farmlands where only leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*) are present. There is evidence that brown hyaenas are dominant to cheetahs (Mills 1990) and that cheetahs can provide a substantial source of carrion for brown hyaenas (Mills 1991); also, either leopards or brown hyaenas can be dominant at an individual carcass (Owens & Owens 1978; Mills 1990).

On the farmlands of north-central Namibia, where brown hyaenas co-occur only with leopards and cheetahs, leopards rarely hoist kills into trees (11% of located kills; Stein 2008); this suggests that leopards could provide important feeding opportunities for brown hyaenas. During a concurrent study of leopard ecology and conservation in this area (Stein *et al.* 2010, 2011), we explored the feeding ecology of brown hyaenas because such areas, where the largest carnivores have been systematically exterminated, are an under-represented and increasingly important system in the brown hyaena's range. We evaluate brown hyaena diet based on scat analysis, den site orts (prey remains), and evidence of scavenging at leopard kills, estimate their dietary overlap by comparing scats with those collected from leopards and cheetahs, and discuss how dietary overlap may be a result of prey availability from sympatric carnivores.

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METHODS

Study area

We studied carnivore ecology on farmlands adjacent to the western edge of Waterberg Plateau Park (WPP) in north-central Namibia that are managed for livestock production but support populations of wildlife for game farming, trophy hunting and conservation (Stein 2008). Soils in the farmlands were characterized by deep sand near the Waterberg escarpment and mostly mixed clay and black cotton elsewhere (Schneider 1998). Mean annual rainfall is between 400 and 500 mm. A combination of large herbivore removal, increased livestock pressure and drought conditions have given rise to bush encroachment expressed by thick *Acacia* shrubland and woodland areas (Kaufman *et al.* 2007). The region is dominated by *Acacia mellifera* and *Dichrostachys cinerea*, characterized as the thornveld biome (Barnard 1998; Schneider 1998).

The commercial farmland north and southwest of the WPP are cooperatively managed through the Waterberg Conservancy. Ground water is pumped to the surface for livestock, but provides water year round for game, as well. The game species present included kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), warthog (*Phacochoerus africanus*), red hartebeest (*Alcelaphus buselaphus*), eland (*Taurotragus oryx*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Damara dik-dik (*Madoqua kirkii*). Road transect surveys indicated that kudus were most common (3.4/km^2), followed by warthogs (2.0/km^2) and gemsbok (1.7/km^2) (Stein 2008). Densities of cattle were about half the reported density of primary prey in the region (Stein 2008). A total of 240 head of cattle were reported for the sampled farms (3.2/km^2) but this included only ~50 calves (9 months of age or younger) vulnerable to depredation (0.7/km^2; Stein 2008). These cattle were kraaled at night and not herded during the day. Lions, spotted hyaenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) once occurred throughout the region but were essentially eliminated by the 1980s. Approximately, 38–43 medium-sized and large (≥1 kg, but including two mongoose species <1 kg) mammal species potentially occur in the study area (Stein *et al.* 2008).

Telemetry

To identify home ranges and general range sympatry, and to find hyaena den and latrine sites, we caught and radio-collared three leopards between February 2004 and November 2008 (one adult male and one adult female with VHF collars and one adult female with a GPS collar; Stein *et al.* 2011) and two brown hyaenas (one adult female and one subadult male with VHF collars) in cage traps set for leopards (University of Massachusetts, Amherst IACUC Protocol #24-02-09). We located these marked animals *via* VHF triangulations (usually 1–3 times/week) and from downloaded GPS locations (~4 locations/day), then mapped the locations (Animal Movements Extension, ArcView 3.2, Environmental Systems Research Institute Inc., Redlands, CA) (Stein *et al.* 2011).

Food habits

Food habits of leopards and hyaenas were identified in three ways. First, when encountered individually during radio tracking forays or, for hyaenas, at latrine sites and while investigating den sites, we identified faeces of each species by the size, shape and colour (Stuart & Stuart 2000), as well as by associated tracks, and then collected and dried them (Marker *et al.* 2003). We placed dried samples onto a 30 × 20 cm tray with a six-cell grid at the bottom and evenly spread hairs across the grid. A random hair selected from each was placed on a plastic cover slip between two glass slides and clipped with four paper clamps. The six hairs were placed within a conventional toaster oven at high power for 10 minutes to melt the cuticular mosaic pattern onto the plastic cover slip, then removed from the plastic cover slip. Both the hair and cover slip were taped to a datasheet and examined under magnification. The gross appearance of the hairs and the cuticular mosaic patterns were compared to a reference collection of hairs from all local potential prey species, with samples representing various regions of the body (Keogh 1983). Some hairs from kudu and eland could not be distinguished from one another and are identified as such in our tabulations. Results were tested by season and location, and frequencies of occurrence calculated for comparison. We also visited an active brown hyaena den, as identified from telemetry, each month to collect and identify the accumulation of orts presumably provisioned to young. During each visit, the species, age and sex of new orts were recorded, and the total assorted by frequency of occurrence. Finally, we located presumed kill sites of the GPS-collared leopard by analysing GPS locations. Where two or more consecutive locations were recorded within 100 m or each other, the midpoint was recorded and the site was investigated to find any remains an average of 12 days (median = 11, range = 2 to 27) after the kill was suspected to have taken place (Anderson & Lindzey 2003; Martins *et al.* 2011). We recorded the date, species, age, sex and location of carcasses we found. To assess the extent to which these carcasses might provide food for hyaenas, we also recorded tracks and signs of brown hyaena scavenging. For comparison, food habits of cheetahs were taken from a previous study of cheetah scats from the same study area (Marker *et al.* 2003, 2010). Results are indicated as relative percentage of remains in scats (thus totalling to 100%).

We recognize that we have limited sample sizes of radio-collared animals, assess food habits using

Table 1. Percentage occurrence of various prey items within scats of brown hyaenas (collected in wet and dry seasons at the den and away from the den) and leopards collected during February 2004 to November 2006 and cheetahs collected during 2002 (from Marker *et al.* 2010), and within a collection of orts identified at a brown hyaena den site during 2004–2005, on north-central Namibian farmlands. Sample sizes indicated in brackets.

	Brown hyaena [b]						
	Dry		Wet				
Prey item	Away (59)[a]	Den (69)	Away (60)	Den (24)	Den orts (44)	Leopard[c] (41)	Cheetah[d] (47)
Kudu	51	36	32	50	5	46	21
Warthog	20	23	47	29	20	20	2
Gemsbok	7	10	5	8	2	15	4
Eland	5	4		4	5	12	15
Eland-kudu[e]	2	3					26
Red hartebeest			2		5		6
Large antelope					7		
Steenbok			2		2		9
Duiker					2		
Dik-dik					2		
Small antelope					7		
Domestic livestock							
Calf	5	4	7				4
Sheep	2					2	2
Goat			2	4		2	
Horse					2		
Donkey					2		
Scrub hare			3				6
Leopard				4	5		
Jackal		1			14	2	
Bird		4	2		5[f]		4
Insects		1					
Vegetation	9	13					
Other					16[g]		

[a]Total number of scats in which prey remains were identified; does not include unidentified remains in 7, 1, 4 and 2 scats from dry season/field, dry season/den, wet season/field and wet season/den, respectively.
[b]Does not include unidentified remains in 16 other scats.
[c]Does not include unidentified remains in 3 other scats.
[d]Does not include unidentified remains in 18 other scats or cheetah hair in 13 others.
[e]Some kudu and eland hair could not be distinguished.
[f]Includes guinea fowl (1), unidentified raptor (1).
[g]Includes bat-eared fox (2), honey badger (1), African wild cat (1), genet (1), aardvark (1), rock hyrax (1).

different methods of data acquisition with inherent problems of detectability and loss of animal remains to scavengers, and found leopard kills up to 27 days *post mortem* (mean of 12 days) that may present biases to carcass persistence and actual hyaena consumption of remains. Thus, our results should be viewed with caution but still provide an interesting and important contribution to understanding food habits and potential interaction of the study species.

RESULTS

We collected and identified prey remains in 212 brown hyaena scats at the den site and in the field away from the den during wet and dry seasons (Table 1) within the range of radio-collared leopards (Fig. 1). The prevalence of the six most common prey items (i.e. prey identified in at least three of the four categories of season and location samples) varied between seasons (chi-square = 14.92, d.f. = 5, P = 0.01) but not by location (P = 0.46). During the dry season kudu were the most common prey item (~43%) followed by warthog (~22%); in the wet season, both kudu and warthog remains occurred most frequently and in similar overall percentage (~38%). No other seasonal differences in occurrence of prey remains were identified. Overall, kudu and

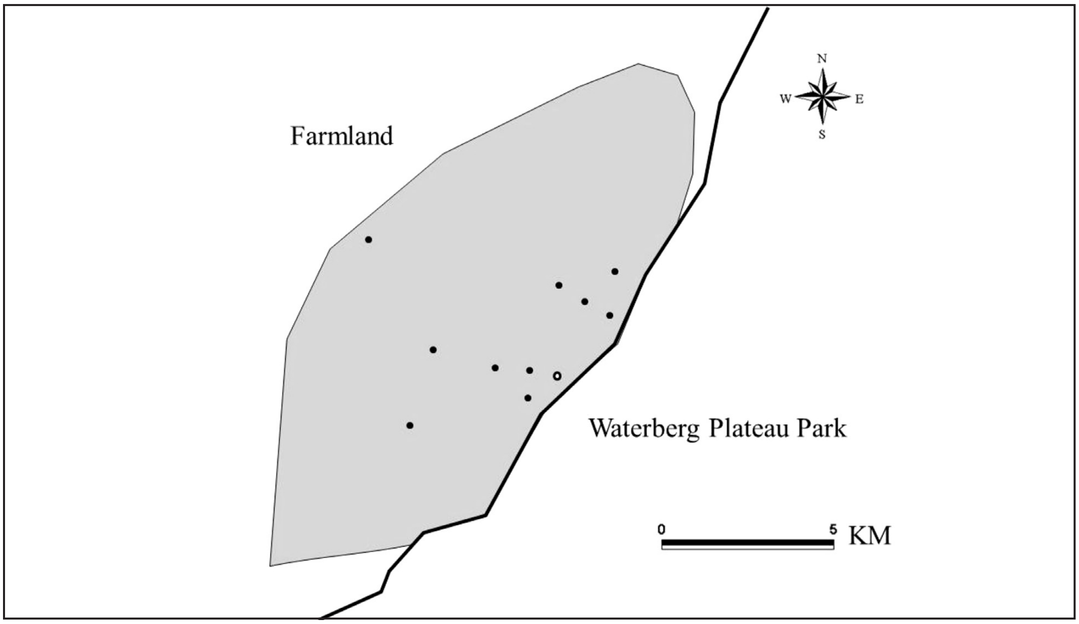

Fig. 1. The locations of brown hyaena latrines (•) and den site (○) within the composite ranges of three radio-collared leopards (grey polygon; Stein *et al.* 2011).

warthog remains occurred most commonly, and wild (79–91%) and domestic (4–9%) ungulate remains were the most prevalent food items (Table 1). Den orts, in contrast, included more species of ungulates and many more carnivore remains, both in number and species. Still, wild (57%) and domestic (4%) ungulate remains were the most commonly recorded.

Prey remains in 41 leopard scats mirrored those in brown hyaenas scats, with kudu remains being most prevalent (46%), warthogs, gemsbok and eland remains common (12–20%), and some occurrence (4%) of domestic livestock remains (Table 1); other than a single occurrence of jackal (*Canis mesomelas*) remains, all leopard prey was ungulate. From a previous study in the area (Marker *et al.* 2010), cheetahs also fed on mostly wild (80%) and domestic (10%) ungulates, but less on warthogs and more on steenbok than either brown hyaenas or leopards we studied (Table 1).

Of 38 leopard kills located by GPS tracking of single collared leopard, nine were unavailable as a food resource to brown hyaenas at the time of data collection because they were hoisted into trees ($n = 4$) or small and presumably mostly or entirely consumed by the leopard ($n = 5$). Of the 29 remaining leopard kills, brown hyaenas occurred at and apparently scavenged 22 (76%), most of which were kudu and warthog (Table 2). There was no difference between the leopard scat and leopard kill/GPS-tracking food habits assessments (chi-square = 11.4, d.f. = 6, $P = 0.076$), though duiker, steenbok and cattle remains were identified only from kills.

DISCUSSION

On Namibian farmlands, brown hyaenas, leopards and cheetahs are the largest carnivores persisting where others have been systematically exterminated. In the absence of lions and with substantial overlap in diet, range and activity patterns, we believe that leopards and perhaps cheetahs provide a significant portion of medium-sized to large ungulate prey for brown hyaenas over a large portion of their shared range. Our evidence indicated that brown hyaenas fed on many of the same carcasses as leopards. Considering the evidence suggesting that brown hyaenas are primarily scavengers, unable to kill medium-sized and large ungulates (Owens & Owens 1978; Mills 1990; Maude & Mills 2005), it is likely that leopards and perhaps cheetahs provide these food items for brown hyaenas much like larger carnivores provide carrion for them in the Central Kalahari, Kgalagadi Transfrontier Park, and Makgadigadi National Park (Owens & Owens 1978; Mills 1990; Maude & Mills 2005). Without larger scavenging competitors, leopards likely hoist their kills less

Table 2. Number of carcasses from leopard kills (located through GPS tracking of an adult female leopard from September 2005 to February 2006, inclusive) available to (A)[a] and scavenged by (S) brown hyaenas on north-central Namibian farmlands.

	Age of prey killed									
	Calf		Subadult		Adult		Unknown		Total	
Species	A	S	A	S	A	S	A	S	A	S
Kudu	3	3	1	1	5	4			9	8
Warthog			5	2	2	2	1	1	8	5
Gemsbok		3	2						3	2
Eland			1	1					1	1
Steenbok					1	0			1	0
Duiker					4	3			4	3
Cattle	1	1							1	1
Unidentified			1	1	1	1			2	2
Total									29	22

[a]Does not include kills made by the leopard but not available to hyaenas because they were hoisted into trees (n = 1 kudu calf, 2 gemsbok calves, 1 subadult warthog) or were entirely consumed by the leopard (n = 2 duikers, 1 porcupine, 2 scrub hares).

often and brown hyaenas perhaps have greater access to the remains (Turnbull-Kemp 1967; Mills 1990; Bailey 1993).

Prey densities are drivers of carnivore abundance (Fuller & Sievert 2001) and without access to larger prey items, brown hyaenas likely do not reach high populations densities. In most areas, brown hyaenas depend on sympatric carnivores to provide access to carcasses (Owens & Owens 1978; Mills 1990). Namibian farmlands provide areas devoid of lions, wild dogs and spotted hyaenas but with substantial numbers of leopards and cheetahs and thus good potential for brown hyaena populations (Stuart *et al.* 1985). Such farmland areas may be strongholds for brown hyaenas because, as scavengers, they do not pose a critical threat to livestock operations (Stein *et al.* 2010) but are able to access carcasses as food. Neither leopards nor cheetahs appear to prey excessively on livestock, likely because of the abundance of wild ungulates relative to livestock. The fate of leopards and cheetahs on the farmlands we studied seems fairly secure for now; livestock losses are fairly low, and though some leopards and cheetahs are killed in response to losses, options for long-term conservation of leopards and cheetahs there (Marker *et al.* 2010; Stein *et al.* 2010) have been identified, and these should benefit brown hyaenas as well.

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