The influence of large predators on the feeding ecology of two African mesocarnivores: the black-backed jackal and the brown hyaena

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Interactions between apex and mesopredators and their impacts on prey populations have been well documented, while the influence of apex predators such as lions on carrion availability and the subsequent impacts at lower trophic levels are not fully understood. Here we assess dietary overlap between two sympatric carnivores (brown hyaena, *Parahyaena brunnea,* and black-backed jackal, *Canis mesomelas*) in neighbouring reserves with and without apex predators (lions, *Panthera leo,* and wild dog, *Lycaon pictus*). We investigate whether apex predators facilitate niche partitioning between mesocarnivores by creating additional scavenging opportunities through predatory activity. We found that brown hyaena density was higher in the area with apex predators, while black-backed jackal density was higher in the area without apex predators. Black-backed jackal scats contained broadly similar dietary items at both sites, while large mammal remains occurred significantly more frequently in brown hyaena scats collected in the presence of apex predators. In the absence of apex predators there was a markedly higher degree of overlap between brown hyaena and jackal diets, suggesting increased levels of inter-specific competition. Our results suggest that apex predators potentially reduce levels of inter-specific competition for food between mesocarnivores by providing additional scavenging opportunities for specialist scavengers such as brown hyaena.

Key words: carnivore, diet, Africa, hyaena, jackal, predators, scavenger, competition.

INTRODUCTION

Competitive interactions among mammalian carnivores strongly influence the structure and dynamics of ecological communities and a thorough understanding of those interactions is important for practical management and conservation purposes (Linnell & Strand 2000; Caro & Stoner 2003; Ritchie & Johnson 2009). For example, the removal of apex predators can have negative effects at lower trophic levels by allowing populations of mesopredators to increase. This can intensify predation pressure on prey species and diminish ecosystem function (Crooks & Soule 1999; Prugh *et al.* 2009; Ritchie & Johnson 2009). Although apex predators can suppress populations of other carnivores through direct intraguild predation or interference competition (Mills & Mills 1982; Creel & Creel 1996; Durant 2000; Hayward & Kerley 2008), they may also facilitate the foraging activity of obligate scavengers such as vultures and carrion-dependent arthropods by leaving prey remains at kill sites (Houston 1979; Braack 1987). It has also been demonstrated that apex predators recolonizing an area stabilize carrion availability by reducing temporal variation in carcass abundance through regular predatory activity (Wilmers & Getz 2004), thereby allowing opportunistic mesocarnivores to switch from generalist or pred-

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atory diets to predominantly scavenging from predator kills (Wilmers & Getz 2004; van Dijk *et al.* 2008; Mattisson *et al.* 2011).

Although apex predators such as lions (*Panthera leo*) were extirpated from most of their range in South Africa in the early 20th century (Bauer & Van Der Merwe 2004), they have recently been reintroduced to many fenced reserves to attract tourists (Hayward *et al.* 2007a). These reintroductions have provided a framework within which impacts of apex predators on ecosystem dynamics can be tested experimentally. While the impacts of apex predators on prey species have been well documented (Power 2003; Hayward *et al.* 2007b; Hayward, O'Brien & Kerley 2007; Lehmann *et al.* 2008), their influence on the foraging ecology of other carnivores in fenced reserves is not fully understood (Hayward & Kerley 2009; Brassine & Parker 2012). Moreover, very little is known about interspecific interactions between mesocarnivores and large apex predators in South Africa prior to the extirpation of the latter.

Diet is an important part of carnivore ecology and conservation, and two preliminary studies in South Africa have examined whether the diets of mesocarnivores differed in the presence or absence of apex predators (van der Merwe *et al.* 2009; Brassine & Parker 2012). Brassine & Parker (2012) found no difference in black-backed jackal (*Canis mesomelas*) (hereafter referred to as jackal) diets from two neighbouring reserves, one that had apex predators and one that did not. Van der Merwe *et al.* (2009) found considerable overlap in jackal and brown hyaena (*Parahyaena brunnea*) diet from sites across the North West Province and they suggested apex predators facilitated niche partitioning in mesocarnivores by providing additional scavenging opportunities for brown hyaena.

Both brown hyaena and jackal are likely to be influenced by the presence and absence of apex predators. Both species alter their diets in relation to fluctuations in food availability (Kaunda & Skinner 2003; Maude & Mills 2005; Klare *et al.* 2010; Kamler *et al.* 2012), and it has been suggested that in the absence of large predators jackals occupy the niche of apex predators and prey more frequently on large (>15 kg) herbivores (Kamler *et al.* 2010; Klare *et al.* 2010; Kamler *et al*. 2012). Both jackal and brown hyaena have also been recorded as occasionally being killed by apex predators (Skinner & Chimimba, 2005; Mills, 1990). Further research is required to assess potential interactions between mesocarnivores and apex predators, particularly as predators and scavengers can have dramatic impacts on ecosystem function, economic sustainability and biodiversity (DeVault *et al.* 2003; Hayward *et al.* 2007a; Hayward *et al.* 2007; Klare *et al.* 2010; Kamler *et al.* 2012).

We compared the dietary components of brown hyaena and jackal scats from two neighbouring study sites; one where apex predators (lions and African wild dogs, *Lycaon pictus*) have been reintroduced or were already present (leopards, *Panthera pardus*), and one where they have been extirpated. We predicted that brown hyaenas would consume large mammal remains more frequently in the presence of apex predators due to increased scavenging opportunities (van der Merwe *et al.* 2009), whereas the dietary components of jackal scats would be similar between both sites (Brassine & Parker 2012). We also predicted that brown hyaena density would be facilitated due to availability of more reliable carcass remains in the presence of apex predators, whereas jackal density would be suppressed due to increased competition from apex predators.

METHODS

Study sites

The study was conducted at two sites; Pilanesberg National Park (PNP), 25°24'S; 27°08'E; 570 km^2; and Mankwe Wildlife Reserve (MWR), 25°13'S; 27°18'E; 47 km^2, located approximately 6 km apart in North West Province, South Africa. PNP was established in 1978 to promote conservation and tourism and is enclosed by an electric predator-proof fence (van Dyk & Slotow 2003). MWR is a private game reserve that has been managed for conservation and ecotourism since 1982 and is surrounded by a non-predator proof fence designed to prevent the movements of wild herbivores (Yarnell *et al.* 2008). Predominant vegetation in both sites is open grassland with thickets of *Acacia* and broadleaf bushveld (Mucina & Rutherford 2006). Average annual rainfall is 639 mm at PNP (Magome *et al.* 2008) and 650 mm at MWR (Yarnell *et al.* 2008) with 80% falling between October and March. The predominant land use surrounding both areas is communal livestock grazing, although no domestic livestock are present in either study site. Both sites contain similar assemblages of large herbivores (Table 1), while lion, cheetah (*Acinonyx jubatus*) and African wild dog occur at PNP but are absent from MWR. Mesocarnivores present at both sites include brown hyaena, caracal (*Felis caracal*), serval (*Leptailurus serval*),

Table 1. Line-transect spotlighting survey effort (km) conducted at Pilanesberg National Park (PNP) and Mankwe Wildlife Reserve (MWR), North West Province, South Africa, between 2009 and 2011.

	PNP				MWR			
Transect No.	Transect length	2009	2010	2011	Transect length	2009	2010	2011
1	12.0	36.0	144.0	72.0	3.7	44.4	40.7	37.0
2	7.0	28.0	42.0	49.0	2.7	29.7	29.7	27.0
3	7.5	67.5	67.5	60.0	3.4	27.2	37.4	40.8
4	9.0	45.0	90.0	63.0	3.6	43.2	32.4	43.2
5	6.3	50.4	69.3	44.1	3.2	28.8	32.0	35.2
6	3.6	21.6	32.4	32.4	1.6	20.8	19.2	16.0
7	6.3	18.9	75.6	50.4	4.4	13.2	39.6	44.0
8	3.8	19.0	41.8	26.6	–	–	–	–
9	10.5	31.5	105.0	73.5	–	–	–	–
Total	66.0	317.9	667.6	471.0	22.6	207.3	231.0	243.2

jackal and civet (*Civettictis civetta*). Leopards are present in PNP and occasional visitors to MWR.

Large herbivores at PNP are monitored annually and the lions and wild dog are managed to maintain numbers (S.D., pers. obs. 2012). At MWR large herbivores are intensively managed by annual hunting and translocation (D.M., pers. obs. 2012). No mesocarnivore species are persecuted by management at either study site. A vulture restaurant was located at MWR where domestic livestock and wild ungulate carcasses were infrequently deposited.

Density estimates

We used a complete count of large herbivores from annual helicopter census at both sites. The 2010 census at PNP took place in August, and involved three replicated surveys, providing a mean count for each species (Knoop *et al.* 2010). The aerial census at MWR took place in September 2010, and involved one complete count.

Jackal, brown hyaena, scrub hare (*Lepus saxatilis*), and steenbok (*Raphicerus campestris*) density estimates were derived from line-transect spotlight distance sampling (Thomas *et al.*2006; Hounsome *et al.* 2005). Line-transect spotlight sampling was conducted in the months of February, June, August and November of each year, between 2009 and 2011. The minimum time between repeated transect sampling was one night and no transect was surveyed more than once per night. Spotlight survey effort is shown in Table 1. All transects were located on tourist or management roads. Random transect sampling was not possible in either reserve due to access restrictions, and therefore resulting estimates may be subject to road-induced bias (Buckland *et al.* 2001). However, any road-induced bias was likely to be similar across both sites allowing for a comparison of densities. Annual density estimates for each species were not possible due to low detection rates and consequently observations from 2009–2011 were pooled to allow estimates to be generated from the spotlight transects. Too few brown hyaena were detected at MWR to generate meaningful density estimates using DISTANCE. Model selection was based on the lowest Akaike's Information Criterion (AIC), Delta AIC values and % CV (Burnham & Anderson 2002).

Density estimates of lion and wild dog were taken from management reports (Knoop *et al.* 2010), and brown hyaena density from management estimates in Van Dyk & Slotow (2003) for PNP to help verify density estimates from this study. To estimate brown hyaena density at MWR we identified individuals based on physical characteristics (leg stripe patterns and scars) from the images recorded at the vulture restaurant camera trap between April and September 2010, to calculate minimum number alive (MNA) each month and to estimate the total number of individuals using the site during the study period. We also used a relative index of abundance (RIA) from scat transect lines (RIA = latrine count/km surveyed) to further compare brown hyaena and jackal abundance at both sites. Scat transect surveys are conducted annually for monitoring purposes along tourist and management roads at both sites (Thorn *et al.*2010).

Scat collection and analysis

Scats from both species were collected during the dry season in August 2010. Faecal standing crop is relatively high at this time of year due to low decomposition rates associated with a lack of rainfall and dung beetle activity (Stone 2005). Consequently, it is reasonable to assume that the scats collected in this study were possibly deposited at any time during the winter (May to August). Scats were identified to species level based on appearance and size (Stuart & Stuart 2000), and only scats that were identified with a high degree of confidence were included (Thorn *et al.* 2010). Fifty-four and 50 brown hyaena scats were collected and analysed from PNP and MWR, respectively, while 50 jackal scats were analysed from each site.

Scats were air dried in an oven at 80°C for four hours before being manually examined using forceps. Mammalian food items within the scats were identified to species level by comparing micro- and macroscopic hair morphology, teeth and bone fragments to available reference collections (Keogh 1983), and from known large and small mammal hair samples collected by RWY. The dietary items were divided into six broad categories: large mammals (adults >15 kg), small mammals (adults <15 kg), birds, invertebrates, seeds and anthropogenic items (van der Merwe *et al.* 2009). Remains of vegetation other than seeds (*e.g.* grass and leaves) were not included in the analyses as they were considered to function as an aid to digestion rather than being consumed for nutritional value (Vieira & Port 2007).

The frequency of occurrence for each dietary item was calculated separately for both species and both sites using the equation (Klare *et al.* 2011):

$$\text{Frequency occurrence} = (n_i/N) \times 100\ ,$$

where n_i is the number of times food item i occurs in diet at one study site and N is the number of scats analysed at that site. Ninety-five per cent confidence intervals were calculated from 1000 bootstrap simulations (Reynolds & Aebischer 1991; Andheria *et al.* 2007).

Dietary diversity for each species was estimated for both sites using the Brillouin index (H; Brillouin 1956) based on the six broad dietary categories described above using the formula:

$$H = (\ln(N!) - S \ln(n_i!))/N,$$

where H is the diversity, N is the total number of individual scat items recorded and n_i is the number of individual scat items in the ith category. Cumulative Brillouin diversity (H_k) values were plotted against sample size to determine whether the curve reached an asymptote, indicating that a sufficient number of samples were analysed to describe the diets of each species at both sites (Glen *et al.* 2011).

The overlap in frequency of occurrence of dietary categories (excluding anthropogenic items) between MWR and PNP was calculated for brown hyaena and jackal scats separately, as well as the overlap between brown hyaena and jackal diet categories at each site, using the Pianka index (Pianka 1973) calculated in EcoSim Software v7.72 (Gotelli & Entsminger 2004) using the formula:

$$O_{jk} = S\, P_{ij}P_{ik}/(S\, P_{ij}^2\ S\, P_{ik}^2)^{0.5}\ ,$$

where O_{jk} is the index of overlap, j and k are the species or sites being compared, and p_i is the frequency of occurrence of dietary item i (Glen *et al.* 2011). The index values range from zero, indicating no overlap, to one, indicating complete overlap. The amount of overlap between the large and small mammal dietary items between species and sites was also calculated separately.

The relative frequency of occurrence of large (>1kg) mammalian herbivore species remains was also calculated to ascertain the relative importance of different species to brown hyaena and jackal diets at both sites as follows (Klare *et al.* 2011):

$$\text{Relative frequency of occurrence} = (n_i/N_s) \times 100$$

where n_i is the number of times mammalian species i occurs in diet at one study site and N_s is total occurrences of all herbivore species (>1 kg) that density estimates were available for (Loveridge & Macdonald, 2003). A Pearson's product correlation was performed between the relative frequency of occurrence of dietary remains and the relative abundance of each herbivore species at each site to determine whether jackal and brown hyaena diets reflected the relative abundance of those species. Only herbivores that were identified in scats were included to reduce bias caused by the inclusion of herbivores that were not consumed.

RESULTS

Densities

The 2010 census estimates for large herbivore species showed 19 species at PNP and 14 at MWR (Table 2). Density of large herbivores was twice as high at MWR compared to PNP.

Thirty brown hyaena, 101 jackal, 213 scrub hare and 99 steenbok sightings were made at PNP,

Table 2. Abundance, density (individuals/km^2) and relative index of abundance (RIA) estimates of large herbivores, medium-sized mammals and large mammalian predators at Pilanesberg National Park (PNP;570 km^2) and Mankwe Wildlife Reserve (MWR; 47 km^2), North West Province, South Africa, in 2010.

	PNP			MWR		
Species	Abundance	Density	RIA	Abundance	Density	RIA
Large herbivores (>15 kg)*	7370	12.929		1450	30.851	
Blesbok	0	0		178	3.787	
Buffalo	166	0.291		0	0	
Common reedbuck	4	0.008		20	0.426	
Eland	83	0.145		71	1.511	
Elephant	208	0.364		0	0	
Gemsbok	2	0.004		30	0.638	
Giraffe	125	0.219		15	0.319	
Hartbeest	50	0.088		78	1.660	
Impala	2237	3.925		496	10.553	
Kudu	516	0.906		78	1.660	
Mountain reedbuck	89	0.157		0	0	
Sable	5	0.009		0	0	
Springbok	58	0.102		0	0	
Tsessebe	68	0.119		31	0.660	
Warthog	189	0.331		32	0.681	
Waterbuck	144	0.252		37	0.787	
Wildebeest	1720	3.018		226	4.809	
Zebra	1706	2.993		158	3.362	
White rhino	P	P		P	P	
Black rhino	P	P		0	0	
Ostrich*	46	0.081		22	0.468	
Medium-sized mammals (1–15 kg)+						
Steenbok	216 (128-365)	0.379 (0.224-0.640)		33 (17-60)	0.695 (0.364-1.269)	
Scrub hare	992 (666-1476)	1.740 (1.169-2.589)		52 (17-155)	1.104 (0.370-3.293)	
Mammalian predators						
Lion#	39	0.068		0	0	
Wild dog#	8	0.014		0	0	
Brown hyaena	50-100#	0.088-0.175		2-5^A	0.04-0.11	
Brown hyaena	34 (14-80)+	0.06 (0.025-0.141)	3.04	DD	DD	0.80
Jackal	211 (119-374)+	0.37 (0.208-0.657)	0.43	54 (29-100)	1.152 (0.621-2.137)	3.26

*Abundance and density estimates are calculated from aerial counts.

+ indicates DISTANCE sampling.

^ = minimum number alive from camera trapping.

= management estimates (Knoop *et al*. 2010; van Dyk & Slotow 2003).

RIA indicates the number of scats/km of road transect.

DD indicates that brown hyaena density estimates from DISTANCE at MWR were data-deficient.

P indicates the presence of black and white rhino.

Value in brackets are the 95% confidence intervals.

Table 3. The best fit DISTANCE models used to estimate brown hyaena, jackal, scrub hare and steenbok abundance from distance sampling at Pilanesberg National Park (PNP) and Mankwe Wildlife Reserve (MWR) using the Akaike's Information Criterion (AIC) and % coefficient of variation (% CV). Details of truncated data to improve model fit are also given.

Site	Species	Model	Truncation	AIC	% CV
PNP	Brown hyaena	Negative exponential cosine	Left 5m	136.99	42
	Jackal	Half normal cosine	Right 100 m, left 20 m	327.63	29
	Scrub hare	Hazard rate cosine	Right 80 m, left 10 m	943.96	19
	Steenbok	Half normal cosine	Right 200 m, left 20 m	684.34	25
MWR	Brown hyaena	N/A	N/A	N/A	N/A
	Jackal	Half normal cosine	Right 150 m, left 20 m	543.6	29
	Scrub hare	Negative exponential cosine	Right 70 m	309.53	46
	Steenbok	Half normal cosine	none	640.23	27

while 2 brown hyaena, 123 jackal, 53 scrub hare and 72 steenbok sightings were made at MWR during spotlight transects between 2009 and 2011. Density estimates generated in DISTANCE all had good fitting models and relatively low % CV indicating precise estimates (Table 3). Steenbok density estimates were higher at MWR than PNP, with scrub hare density higher at PNP compared to MWR.

All estimates of brown hyaena density were higher at PNP than MWR (Table 2). A total of five brown hyaena were identified on camera traps at MWR vulture restaurant, with mean 2.5 (±1.25 S.D.) MNA/month. The brown hyaena abundance estimates from DISTANCE sampling indicate 34 (14–80 95% CI) individuals at PNP. Latrine surveys also showed a higher relative index of brown hyaena abundance at PNP compared with MWR. By contrast, all estimates of jackal density were higher for MWR than PNP (Table 2). The density estimates for jackal and brown hyaena were consistent and are therefore likely to reflect actual differences between the sites.

Diet composition

A total of 21 and 20 different food items were identified for brown hyaena and jackals respectively, from both study sites. We identified 14 and 17 food items in brown hyaena and jackal scats collected at PNP, respectively, compared to 19 and 18 at MWR (Table 4). On average fewer dietary categories were recorded per brown hyaena scat collected at PNP, while the number of categories per scat was similar between sites for jackals (Table 4). Diversity of dietary remains was higher in brown hyaena scats collected at MWR than at PNP, whereas the dietary diversity of jackals was similar between sites (Table 4). Cumulative dietary diversity curves reached asymptotes for both species at both sites (Fig. 1).

Large mammal remains were the most frequently recorded dietary components in brown hyaena and jackal scats at both sites (Table 5). Large mammal remains occurred significantly more frequently in brown hyaena scats at PNP than at MWR (Fisher's exact test: $c^2 = 10.109$, d.f. = 1, $P = 0.002$), while small mammal remains occurred significantly less frequently (Fisher's exact test: $c^2 = 13.523$, d.f. = 1, $P < 0.001$; Table 5). There was no significant difference between the frequency of occurrence of large (Fisher's exact test: $c^2 = 1.449$, d.f. = 1, $P = 0.316$) or small (Fisher's exact test:

Table 4. Total number of dietary items, number of mammal species, mean number of dietary categories per scat and Brillouin index of dietary diversity (*H*) recorded for brown hyaena and jackal scats collected at Mankwe Wildlife Reserve (MWR) and Pilanesberg National Park (PNP) in North West Province, South Africa.

	Brown hyaena		Black-backed jackal	
	MWR	PNP	MWR	PNP
Total items	19	14	18	17
Mammal species	14	9	12	11
Mean ± S.D. categories/scat	1.50 ± 0.81	1.19 ± 0.44	0.82 ± 0.72	0.84 ± 0.65
Dietary diversity (*H*)	1.29	0.68	1.06	1.20

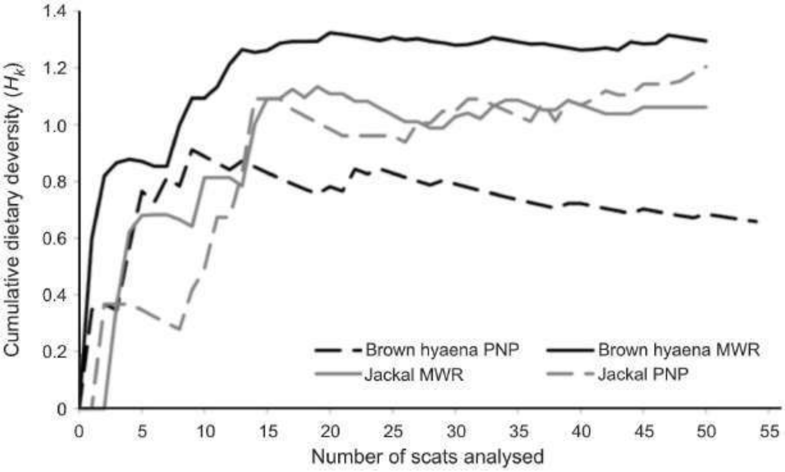

Fig. 1. Cumulative dietary diversity (Brillouin index, H_k) of brown hyaena and jackal diet based on scat samples from Pilanesberg National Park (PNP) and Mankwe Wildlife Reserve (MWR).

c^2 = 0.071, d.f. = 1, *P*= 0.121) mammal remains in jackal scat at either site (Table 5). There was no significant difference in the frequency of occurrence of bird remains in either brown hyaena (Fisher's exact test: c^2 = 3.171, d.f. = 1, *P*= 0.103) or jackal (Fisher's exact test: c^2 = 0.211, d.f. = 1, *P*> 0.999) scats and no significant difference in invertebrate remains in brown hyaena (Fisher's exact test: c^2 = 0.193, d.f. = 1, *P*= 0.801) or jackal (Fisher's exact test: c^2 = 0.444, d.f. = 1, *P*= 0.741) scats at both sites. Seeds occurred significantly more frequently in brown hyaena scats at MWR compared to PNP (Fisher's exact test: c^2 = 7.790, d.f. = 1, *P* = 0.007), while the difference between the sites was not significant for jackals (Fisher's exact test: c^2 = 0.543, d.f. = 1, *P*= 0.715).

The frequency of occurrence of large mammal remains was significantly higher in brown hyaena scats (93%) compared to jackal scats (40%) at PNP (Fisher's exact test: c^2 = 32.634, d.f. = 1, *P*< 0.001), while there were no significant differences in the frequency of occurrence of the six broad dietary categories between brown hyaena and jackal scats collected at MWR (Table 5).

At the species level for mammalian dietary items, impala (*Aepyceros melampus*) (Fisher's exact test: c^2 = 7.820, d.f. = 1, *P*= 0.006) and blue wildebeest (*Connochaetes taurinus*) (Fisher's exact test: c^2 = 13.757, d.f. = 1, *P* < 0.001) remains occurred significantly more frequently in brown hyaena scats at PNP, whereas fewer rodent remains (Fisher's exact test: c^2 = 11.949, d.f. = 1, *P*< 0.001) occurred compared to MWR.

Dietary overlap between brown hyaenas and jackals was higher at MWR than at PNP (Table 6). Dietary overlap was low between brown hyaena scats collected at both sites, while the overall level of dietary overlap for jackals between the two sites was relatively high (Table 6).

Table 5. Frequency of occurrence (%) of six categories of dietary remains from brown hyaena and jackal scats collected at Pilanesberg National Park (PNP) and Mankwe Wildlife Reserve (MWR). 95% confidence intervals are given in brackets.

Dietary category	Frequency of occurrence (%)			
	Brown hyaena		Jackal	
	MWR	PNP	MWR	PNP
Large mammals	68 (54-80)	93 (85-98)	52 (38-64)	40 (26-54)
Small mammals	34 (22-58)	6 (0-13)	16 (6-28)	18 (8-28)
Birds	10 (2-20)	2 (0-6)	6 (0-12)	4 (0-10)
Invertebrates	20 (10-32)	17 (7-26)	8 (2-16)	12 (4-22)
Seeds	18 (8-28)	2 (0-6)	6 (0-12)	10 (2-20)
Anthropogenic matter	0	0	4 (0-10)	0

Table 6. Dietary niche overlap (Pianka's index, *O*; Pianka 1973) between brown hyaena and jackals at Mankwe Wildlife Reserve (MWR) and Pilanesberg National Park (PNP) based on frequency of occurrence of dietary remains in scats.

Site/species	Overlap	Total diet	All mammal	Large mammal	Small mammal
MWR	Brown hyaena:jackal	0.869	0.913	0.913	0.819
PNP	Brown hyaena:jackal	0.525	0.467	0.539	0.809
Brown hyaena	MWR:PNP	0.488	0.433	0.493	0.603
Jackal	MWR:PNP	0.724	0.683	0.581	0.901

Diet selection

There was a significant positive correlation (Pearson's correlation coefficient = 0.875, *P*= 0.004) between relative percentage occurrence of herbivores (>1 kg) in scats of brown hyaena and relative abundance of herbivores at PNP but not at MWR (Pearson's correlation coefficient = 0.138, *P*= 0.745; Fig. 2A,B); and there was a near significant positive correlation between relative percentage occurrence of herbivores (>1 kg) in scats of jackal and relative abundance of herbivores at MWR (Pearson's correlation coefficient = 0.778, *P*= 0.069) and no correlation at PNP (Pearson's correlation coefficient = –0.408, *P*= 0.364; Fig. 2C,D).

DISCUSSION

Mammalian carnivore diets are often determined by the abundance and dispersion of prey resources (*e.g.* Kruuk & MacDonald, 1983; Maude & Mills, 2005; Hayward, 2006; Klare *et al.* 2010). In this study, both study sites had similar communities of indigenous large herbivores, with MWR having higher densities compared to PNP. Despite this, no significant difference was detected in the frequency of occurrence of large herbivores in the diet of jackals at MWR or PNP, indicating a versatile, generalist foraging strategy, consuming small and large mammals and other food items when available (Loveridge & MacDonald 2003; Klare *et al.*2010; Brassine & Parker, 2012). However, we were unable to determine whether dietary items in the scats were obtained by scavenging or via direct predation.

By contrast, brown hyaena diet consisted of

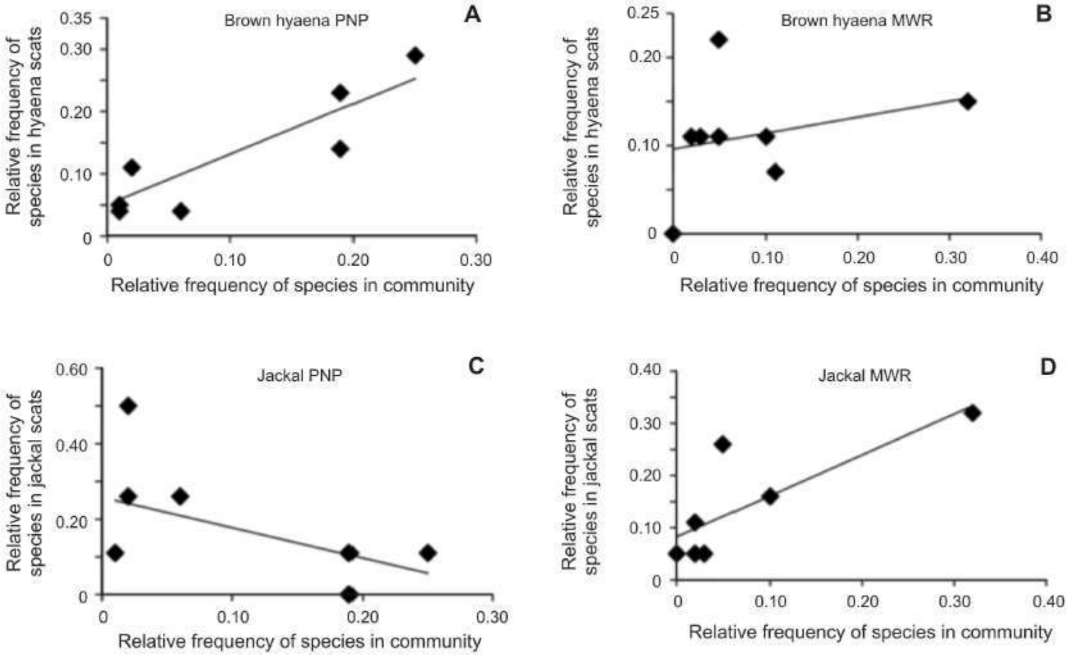

Fig. 2. Relative frequency of occurrence of mammalian herbivore (>1 kg) species in the scats of two mesocarnivore species (brown hyaena **A–B**, and jackal **C–D**) in relation to their relative abundance in Pilanesberg National Park (PNP) and Mankwe Wildlife Reserve (MWR), South Africa.

greater proportions of large herbivores in PNP where the densityof large herbivores was lower. In addition, brown hyaena consumed the most abundant prey in PNP, probably in response to scavenging opportunities created by apex predators which were likely to be taking the most abundant prey, but no such significant correlation was found at MWR. Consequently, we suggest that the predatory activity of apex predators at PNP facilitated facultative scavenging by brown hyaena of large herbivores more frequently than at MWR, where herbivore density was higher, but large apex predators were absent.

In PNP the restricted movements of herbivores and high numbers of apex predators have resulted in herbivore populations being regulated by high predation rates rather than seasonal productivity of the ecosystem (Mduma *et al*. 1999; van Dyk & Slotow 2003;Tambling &Du Toit 2005;Hayward*et al.*2007). Large mammal carcass availability was therefore likely to be more regular and predictable in PNP comparedtoMWR where ungulate mortality was dependent primarily on stochastic, climatic factors (Sinclair *et al.*2003). As a consequence, brown hyaena in PNP are likely to have accessed scavenging opportunities derived from predator-killed large mammal carcasses, whereas their diet in MWR was more flexible and they consumed small mammals and other food items more frequently, resulting in increased dietary overlap with jackals. Similar changes in foraging behaviour in response to increased carcass availability in the presence of apex predators have been recorded before in brown hyaena in Botswana (Owens & Owens 1978; Maude & Mills 2005), and in other opportunistic carnivores (Arjo, Pletscher & Ream 2002; Wilmers *et al.*2003b; van Dijk *et al.*2008), highlighting an important role that areas with apex predators play in terms of providing scavenging opportunities for other species in the ecosystem.

The greater frequency of occurrence of small mammal remains in brown hyaena scats in the absence of apex predators resulted in a greater level of dietary niche overlap between brown hyaena and jackal diet at MWR, which may indicate that both species potentially compete for the same food at MWR (Owens & Owens 1978). Differences in the small mammal component of the diet between sites may have resulted from differences in small mammal abundance, which were not quantified in this study. However, small mammal abundance in the region is heavily regulated by rainfall (Yarnell*et al.*2007), and due to the close proximity of sites we assume small mammal abundance would be similar at both study sites. We therefore suggest the difference in the proportion of small mammals in brown hyaena diet at MWR reflected a shift in foraging behaviour in response to a relatively low abundance of large mammal carcasses from which they could scavenge. In addition, the higher frequency of occurrence of large mammal remains in scats collected at PNPinthe presenceofapex predators gave rise to a lower degree of overlap of mammalian dietary components between jackals and hyaena (van der Merwe*et al.*2009). It is possible therefore that the predatory activity of apex predators might result in greater niche partitioning between the two species, but further research is required to test this hypothesis.

The similarity between the dietary components in the jackal scats between the two sites indicates that the presence of apex predators did not cause them to significantly alter their foraging strategy, which is in agreement with Brassine & Parker (2012). It seems likely therefore that jackals foraged opportunistically both in the presence and absence of apex predators by both preying on small mammals and scavenging from the remains of, or hunting, large mammals depending on availability, as seen elsewhere (Rowe-Rowe 1983; Kaunda & Skinner 2003;Loveridge & Macdonald 2003;Klare *et al.*2010). Interestingly, there was a weak positive correlation between the relative frequency of occurrence of herbivores in jackal scats and herbivore abundance at MWR.Although not significant, it suggests that jackals may select prey more in relation to prey availability at MWR than at PNP. This difference between jackal prey selection in MWR and PNP might indicate that jackals are more of an apex predatorinMWR, whereas they are moreof a mesopredator in PNP (Thompson & Gese 2007). Further research into prey selection of jackals in areas with and without apex predators would help determine if jackal do indeed shift their functional role in response to competition with apex predators.

The ability of brown hyaena to exploit the kill remains of apex predators might explain their higher density at PNP compared to MWR. Differences in food availability (Hone *et al*. 2007), interspecific competition (Crooks & Soule 1999; Prugh *et al.*2009), and persecution (Balme *et al*. 2009) can influence carnivore density. It is therefore possible that the higher large herbivore densities (Klare *et al*. 2010), combined with reduced interspecific carnivore competition and a lack of predation from lions at MWR can explain the greater jackal density compared with PNP. By contrast, brown hyaena benefit from the presence of apex predators through the increased scavenging opportunities they provide. For example, lions provided 43% of carcasses accessed by brown hyaena in the Kalahari, compared to 30% of carcasses that were from non-violent deaths (Mills 1990). We argue that the higher relative abundance of carrion provided by apex predators in PNP might have increased the carrying capacity of the area for brown hyaena. This may explain the relatively high brown hyaena abundance when compared to MWR which lacks large apex predators.

This study suggests that brown hyaena density is higher in protected reserves that contain apex predators, where they are free from human persecution and can access scavenging opportunities. While in the unprotected rangelands of southern Africa where the majority of the global population lives, they face high levels of human persecution (St John *et al.*2011; Thorn *et al.*2012) and have limited access to scavenging opportunities provided by large predators (Thorn *et al*. 2010). Further empirical studies are required to evaluate which factors (persecution or the presence of apex predators) influence brown hyaena density which will have implications for their future persistence (Wiesel *et al.*2008).

There are a number of limitations to this study, such as a lack of replication of apex predator present and absent sites, food provisioning at the vulture feeding site and the seasonality of scat collection. To confirm that our results are representative of mesocarnivore diets across the region further replication is required and confounding factors controlled. For example, possible differences in leopard and caracal density at both sites may have resulted in differences in carcass availability. Further research is required to ascertain the impact that the presence of leopards and caracal have on the diets of other mesocarnivores in southern Africa. It is also possible that the vulture restaurant at MWR acted as a confounding factor when comparing the diets of mesocarnivores between these sites. However, we argue that the impactofthe vulture restaurantonthe diet ofjackal and hyaena in this study was limited as food provisioning was infrequent and brown hyaena rarely visited the restaurant according to camera trap data (WLP unpublished data). Finally, scats collected in the present study were from winter only, and for these findings to be truly representative of brown hyaena and jackal feeding ecology, scats from all seasons are required.

Despite these shortcomings, we argue that our results give an important insight into the possible dietary competition within the African mesocarnivore guild, and raise the possibility that the presence of apex predators may have an influence on the structure of the carnivore communities in the southern African sub-region, as reported in carnivore communities in North America (Wilmers*et al.* 2003a; Thompson & Gese, 2007). This study also adds further evidence to that suggests apex predators such as lions have an influence on brown hyaena diet (Maude & Mills, 2005; van der Merwe*et al.*2009), and that increased scavenging opportunities will be of benefit to brown hyaena densities. We recommend replicated studies that control for different levels of prey availability, persecution, and competition to further elucidate which variables determine brown hyaena density and the role of intra-specific competition in South Africa's rangelands in the absence of apex predators.

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