Spotted hyaenas switch their foraging strategy as a response to changes in intraguild interactions with lions

S. Périquet[1]*, M. Valeix[1], J. Claypole[2], N. Drouet-Hoguet[3], J. Salnicki[4], S. Mudimba[5], E. Revilla[6] & H. Fritz[1]

1 Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Université Claude Bernard Lyon 1, Villeurbanne Cedex, France
2 Centre for Wildlife Management, Mammal Research Institute, University of Pretoria, Pretoria, South Africa
3 CNRS-CIRAD HERD Programme – Hwange LTER, Main Camp Research, Dete, Zimbabwe
4 Hyaena Research and Conservation Project, Woollahra, Australia
5 Zimbabwe Parks and Wildlife Management Authority, Harare, Zimbabwe
6 Departamento Biología de la Conservación, Estación Biológica de Doñana (CSIC), Sevilla, Spain

Abstract

Large carnivores are keystone species and their foraging strategies may be a determinant in the functioning of communities and ecosystems. The plastic foraging behaviour of carnivores is likely to be influenced by a suite of factors. Here, we studied spotted hyaena diet during two contrasting periods in terms of lion population abundance to investigate the changes in spotted hyaena foraging strategies in response to changes in expected intraguild interactions in Hwange National Park, Zimbabwe. The analysis of hyaena scats and feeding sites of GPS-tracked individuals revealed that during the period of high lion abundance, spotted hyaena consumption and preference for very large prey (elephant and giraffe) increased, while that of large (buffalo) and medium-sized prey (zebra, wildebeest and kudu) decreased, despite an increase in spotted hyaena foraging group size. These results suggest a shift from active predation to scavenging as the potential risk of kleptoparasitism by lions and intraguild competition increased. However, the likely increase of lion predation on very large prey due to the increased proportion of adult males in the lion population could also result in intraguild facilitation by providing spotted hyaenas with additional food sources and thus promote coexistence between these species. Our findings suggest that changes in the numerical abundance of competing species can affect their diet and prey preference, which could ultimately increase the intensity of competition (and facilitation) between carnivores and may thus impact prey populations and possibly ecosystem functioning.

Introduction

Carnivores can access food through predation, kleptoparasitism (i.e. displacing other carnivores from their kills; see Iyengar, 2008, for a review) or scavenging (Pereira, Owen-Smith & Moleón, 2014). In a community, the relative importance of predation versus scavenging and kleptoparasitism is a determinant for the structure and stability of food webs (Wilson & Wolkovich, 2011), and changes in the foraging strategy of one carnivore species have the potential to affect its interactions with other carnivores (Karanth & Sunquist, 1995), as well as prey populations (Owen-Smith & Mills, 2008). At the intraspecific level, carnivores can exhibit several foraging strategies, depending on the circumstances (Pereira et al., 2014). For example, fork-tailed drongos, Dicrurus adsimilis, normally forage alone for small insects, but

they shift to following other species that they kleptoparasitize for larger terrestrial prey when temperatures are cold (Flower, Child & Ridley, 2013). Within the mammalian carnivore guild, interference competition plays a significant role in carnivore ecology (Durant, 2000; Caro & Stoner, 2003; Broekhuis et al., 2013) and can reach the extreme level of intra-guild predation (Palomares & Caro, 1999; Caro & Stoner, 2003). These competitive interactions may lead to shifts in foraging strategies and diet composition in the subordinate species. In India, leopard (Panthera pardus) diet shifted towards small prey and livestock following the recovery of the tiger, Panthera tigris, population (Harihar, Pandav & Goyal, 2011). Carnivore interactions are complex, and trophic facilitation between carnivore species may also take place and influence carnivore prey selection and foraging strategy. For instance, wolves, Canis lupus, appear to increase

scavenging opportunities for wolverines (*Gulo gulo*; van Dijk *et al.*, 2008) and coyotes (*Canis latrans*; Wilmers *et al.*, 2003) inducing modifications of their diets. An understanding of foraging strategies and their determinants is thus key to predicting diet shifts in response to changes in the prey and predator communities.

In African savannas, lions, *Panthera leo*, and spotted hyaenas, *Crocuta crocuta* (hyaenas hereafter), are the largest and most numerous predators. Their diets overlap extensively as they both predominantly prey on and scavenge from large and medium-sized herbivores (Hayward & Kerley, 2005; Hayward, 2006; Périquet, Fritz & Revilla, 2014); these two species are thus likely to compete with each other. Additionally, both lions and hyaenas are capable of stealing kills from each other, with the presence of at least one adult male lion providing a substantial advantage to lions (Kruuk, 1972; Cooper, 1991; Trinkel & Kastberger, 2005). However, they can also benefit from unfinished carcasses left by the other predator, hence facilitating each other's resource acquisition. Very little is known about how these interspecific interactions affect the two species' foraging strategies and diet (but see Purchase, 2004). Further, for these social predators, group size may influence their foraging strategy as group hunting allows larger prey to be killed (Kruuk, 1972; Schaller, 1972), and larger groups are also capable of better defending their kills from competitors and their kleptoparasitism success is increased (Kruuk, 1972; Cooper, 1991).

In Hwange National Park (HNP), Zimbabwe, the long-term monitoring of hyaena diet and group size (1999–2013) associated with a moratorium on lion trophy hunting in the periphery of the park (2005–2008) affecting the lion population within the protected area (Loveridge *et al.*, 2010), provided a unique opportunity to study the changes in hyaena foraging strategies in response to changes in the abundance of the lion population, considered as a proxy for the level of intraguild interactions. Hyaena foraging strategies are extremely difficult to characterize from direct observations because the dense vegetation in HNP prevents continuous monitoring of their behaviour. However, changes in hyaena diet composition are also likely to reflect modifications of their foraging strategies. We used scat and carcass analyses as complementary methods (as in Bacon, Becic & Epp, 2011; Davidson *et al.*, 2013) to assess hyaena diet composition and prey selection, and ultimately to assess whether the main driver of hyaena foraging strategies was (1) the level of intraguild interactions with lions (assumed from the numerical changes of the lion population) or (2) hyaena foraging group size. Under the first scenario, an increase in the number of lions and, in particular, male lions (resulting in a possible increase in competition) would lead hyaenas to avoid medium-sized prey and prefer smaller ones that can be killed and eaten fast enough to minimize kleptoparasitism by lions. Additionally, very large prey killed by lions would increase scavenging opportunities for hyaenas. Under the second scenario, smaller foraging groups would kill smaller prey, while the scavenging of very large prey should not be influenced by hunting group size.

Materials and methods

Study area and populations

HNP is located in north-western Zimbabwe (19°00′S, 26°30′E) and covers an area of approximately 14 600 km². The study area (≈1 500 km²) comprised the Main Camp area, located in the northern part of HNP, characterized by Kalahari sand soils. The vegetation is primarily woodland and bushland savanna, interspersed with small patches of grassland (Rogers, 1993). HNP is semi-arid with a wet season from November to April and a dry season from May to October. The long-term mean annual precipitation is 600 mm (CV = 25%). Availability of surface water to animals is primarily from rainwater collected in natural depressions. However, most of these do not hold water during the dry season, when water is artificially supplied in about 50 waterholes spread throughout HNP. The hyaena population density has been stable since 1999 with an average (±SD) of 0.09 ± 0.02 indiv./km² (Périquet, 2014). Lion sport hunting focused mainly on adult males for their trophy occurred in areas surrounding HNP until 2004, when a moratorium banned lion hunting from 2005 to 2008. As a consequence, the lion population density within HNP, which was just above 0.02 indiv./km² before 2005, has reached 0.035 indiv./km² in 2010 with a very strong increase in the percentage of males in the population from 15 to 35% (Loveridge *et al.*, 2010). We thus divided our study into two distinct periods: the period 1999–2005 characterized by a low level of interactions with lions (period 1 hereafter) and the period 2008–2013 characterized by a high level of interactions with lions (period 2 hereafter).

Hyaena group size

As part of the baseline monitoring of the hyaena population, we drove at least five nights per week (from sunset to midnight and 04:00–08:00 h), and spent full nights at waterholes during the dry season to locate and observe hyaenas during both periods. Group size was systematically recorded. Additionally, we collected opportunistic data on group sizes whenever we saw hyaenas. We distinguished foraging groups (groups of hyaenas moving around the landscape, either hunting or looking for a carcass to scavenge) from feeding groups (groups of hyaenas feeding on a carcass). We classified foraging and feeding groups into the following size classes: alone, small (2–4), medium (5–7) and large (>7). We observed 678 foraging groups and 54 feeding groups during period 1, and 122 foraging groups and 42 feeding groups during period 2.

Scat data

We collected 226 and 300 scats during periods 1 and 2, respectively. Each scat was soaked for 30 min in water and bleach in a nylon stocking to extract the hair content. Hairs were then sundried and analysed to identify the prey species they belonged to. Most of the time, it was possible to identify prey

species simply by looking at the bulk of hairs. When this was not feasible, a sample of hair (five on average) was analysed under the microscope (scale patterns and cross section) and compared to a reference collection (Koegh, 1983; Buys & Koegh, 1984). Scats that contained either hair we could not identify or no hair at all were discarded in the following analyses ($n = 46$). For scats that contained hairs from two different species, they were counted as two samples, one with each prey species. To avoid any pseudo-replication, only one scat per prey species was taken into account from those collected on the same day at a given location (e.g. latrine, carcass). We eventually obtained a final sample size of 180 and 206 scats for periods 1 and 2, respectively.

Carcass data

Hyaenas were opportunistically observed feeding on 58 different carcasses during period 1 and on 22 carcasses during period 2. Prey species was recorded at each carcass. Additionally, during period 2, nine hyaenas (from four clans) were equipped with GPS (Global Positioning System) radio collars (African Wildlife Tracking, UHF 407, GPS collar with UHF download and VHF transmitter) that recorded hourly positions at night (from 18:00 to 6:00). Hyaenas were immobilized by a professional team (see Périquet, 2014, for details). We used these GPS data to search for potential feeding sites (either kill or scavenging sites) by identifying clusters of GPS fixes that included at least 3 h of successive locations within a 50 m radius. We identified 281 clusters and visited 263 on foot. Clusters were visited as soon as possible after hyaenas had left the site and maximum 2 months after. We searched for the feeding site, identified by the presence of a carcass, bones, horns or large amounts of hair, within a 100 m radius of the first GPS point of the cluster. However, it was not possible to assess if the prey animal had been killed or scavenged by hyaenas. At 90 sites, we found a carcass or identifiable prey remains and recorded the prey species for each. In total, we thus identified 112 carcasses on which hyaenas fed during period 2. Very small prey (~10 kg) consumed in less than 3 h were not detectable using our method and were thus excluded from the carcass analysis.

Diet composition

Each prey species was assigned to a prey size class (Table 1) based on the adult female body weight (Coe, Cumming & Phillipson, 1976). Because of their low abundance, but also their similarities in size and ecology, sable was pooled with roan, and steenbok was pooled with duiker in subsequent analyses. We also grouped birds, small mammals (e.g. mongoose, rodents), springhare or *Pedetes capensis*, porcupine or *Hystricomorph hystricidae* and other carnivores into a class, 'other'. For each period, we calculated the proportion of each prey species in the diet by dividing the number of scats or carcasses of the given species by the total number of scats or carcasses. Elephant is a species that is not reliably identified from scat data as hyaenas may avoid feeding on the skin with very few hairs, and the proportion

of hair-less flesh in an elephant is large. Additionally, a bias may exist in our study for period 1 when most scats were collected from a clan living in close proximity to a National Park camp where hyaenas could access elephant meat and skin leftovers from a butchery processing staff ration. Consequently, comparison of diet composition (and prey preferences) based on scat analysis between the two periods was conducted excluding scats containing elephant hairs (20 scats for period 1 and 5 for period 2). We used chi-square tests to examine differences in prey community composition, hyaena group sizes and diet based on scats between the two periods and Fisher exact tests to examine hyaena diet based on carcasses.

Prey availability data and prey preference analyses

Prey densities for common species were estimated in the Main Camp area by using line transect surveys carried out in September/October (late dry season) and in May/June (early dry season). We used most of the available roads as transects. Data were analysed using Distance Sampling software (Thomas *et al.*, 2006). Details of the methodology used to analyse the data are provided in Chamaillé-Jammes *et al.* (2009), from which we extracted estimated densities of prey populations for period 1. We calculated the more recent densities for period 2 based on identical road surveys from 2008 to 2013. Overall prey abundance was estimated by averaging values for the late and early dry seasons. For each prey species we computed the Jacobs index (Jacobs, 1974) $D = (r - p)/(r + p - 2rp)$, which standardizes the relationship between the proportion of each species (or prey class) in the diet r and its proportion in the prey community p. D ranges from -1 maximum avoidance to $+1$ maximum preference. The Jacobs index was chosen as it minimizes bias in preference estimation, especially with proportions below 10% (see Hayward & Kerley, 2005, for details). The classes 'other' and sable + roan were not included in prey preference analyses as their availability was not known and their occurrence too rare to provide reliable density estimation, respectively. Averages are presented with their standard deviation ($\pm$SD), unless stated otherwise. We used the R software v. 3.0.2 for statistical analyses (R Core Team, 2014).

Results

Changes in prey community composition

The proportion of herbivore species in the community of potential prey significantly differed between the two periods ($\aleph^2 = 946.9$, df = 8, $P < 0.0001$). The overall prey biomass decreased from 7200 kg/km² during period 1 to 6762 kg/km² during period 2. The proportion of giraffe and wildebeest decreased from period 1 to period 2, whereas the proportion of buffalo and kudu increased (Fig. 1). All other species were stable in the prey community, with elephant being the

Table 1 Hyaena diet composition from scats and carcasses (i.e. feeding sites). Percentage in the diet from scats was not calculated for elephant as it is not reliable. Numbers in parentheses give the sample size and those in bold give the percentages of each prey size class in hyaena diet

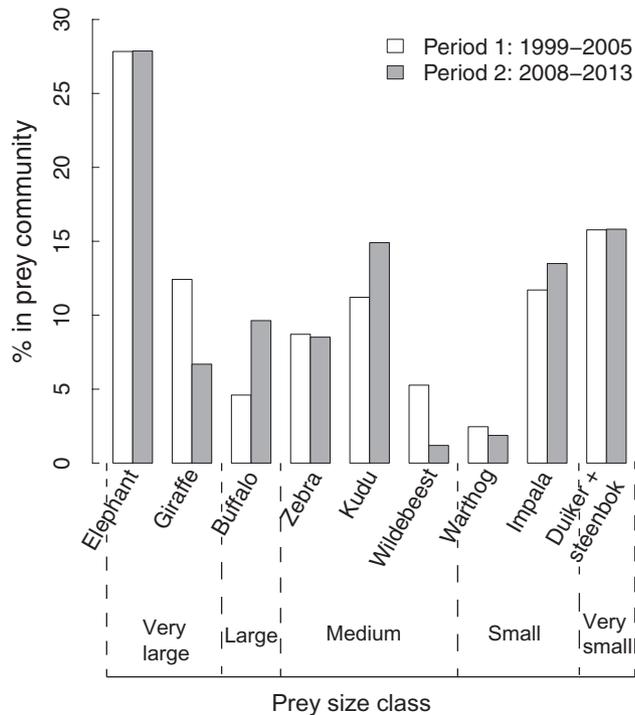| Size class	Species (*Latin name*)	Frequency of occurrence from scats in % (sample size)		Frequency of occurrence from carcasses in % (sample size)	
		Period 1 1999–2005 Low interaction level	Period 2 2008–2013 High interaction level	Period 1 1999–2005 Low interaction level	Period 2 2008–2013 High interaction level
Very large >800 kg		**8.8 (34)**	**18.4 (42)**	**41.4 (24)**	**79.5 (89)**
	Elephant (*Loxodonta africana*)	–(20)	–(5)	37.9 (22)	67 (75)
	Giraffe (*Giraffa camelopardalis*)	8.8 (14)	18.4 (37)	3.4 (2)	12.5 (14)
Large 400–800 kg		**8.1 (13)**	**5.5 (11)**	**13.8 (8)**	**3.6 (4)**
	Buffalo (*Syncerus cafer*)	8.1 (13)	3.5 (7)	13.8 (8)	3.6 (4)
	Eland (*Taurotragus oryx*)	0	2 (4)	0	0
Medium 120–400 kg		**41.3 (66)**	**38.8 (78)**	**32.8 (19)**	**13.4 (15)**
	Zebra (*Equus quagga*)	16.3 (26)	11.4 (23)	5.2 (3)	0
	Roan (*Hippotragus equinus*) and sable (*Hippotragus niger*)	1.9 (3)	6.5 (13)	0	0
	Greater kudu (*Tragelaphus strepsiceros*)	13.8 (22)	15.9 (32)	15.5 (9)	9.8 (11)
	Wildebeest (*Connochaetes taurinus*)	6.9 (11)	2.5 (5)	12.1 (7)	0.9 (1)
	Waterbuck (*Kobus ellipsiprymnus*)	2.5 (4)	2 (4)	0	0
	Tsessebe (*Damaliscus lunatus*)	0	0.5 (1)	0	0
	Antelope species unknown	–	–	0	2.7 (3)
Small 20–120 kg		**14.4 (23)**	**16.9 (34)**	**12.1 (7)**	**3.6 (4)**
	Bushpig (*Potamochoerus larvatus*)	0.6 (1)	0	0	0
	Warthog (*Phacochoerus aethiopicus*)	1.3 (2)	6.5 (13)	0	0.9 (1)
	Bushbuck (*Tragelaphus scriptus*)	1.9 (3)	2.5 (5)	0	0
	Impala (*Aepyceros melampus*)	10.6 (17)	8 (16)	12.1 (7)	2.7 (3)
Very small <20 kg		**20 (32)**	**19.4 (39)**	**0**	**0**
	Steenbok (*Raphicerus campestris*) and common duiker (*Sylvicapra grimmia*)	20 (32)	19.4 (39)	0	0
Other	Birds, small mammals, porcupine, springhare and carnivores	7.5 (12)	1 (2)	0	0

Figure 1 Prey community composition (in % of total number of individuals) during period 1 (white) with low level of interspecific interactions with lions, *Panthera leo*, and period 2 (grey) with high level of interspecific interactions with lions.

dominant species with 28% of the herbivore individuals and 75–77% of the biomass.

Changes in hyaena group sizes

Foraging group size differed between the two periods (x^2 = 10.15, df = 3, P = 0.02) with hyaenas foraging less on their own and more in small and medium groups during period 2 (Fig. 2a). However, once at a carcass, they fed significantly more alone and less in large groups during period 2 than during period 1 (x^2 = 10.24, df = 3, P = 0.02, Fig. 2b).

Changes in hyaena diet composition

Hyaenas fed on at least eight different species based on carcass data (one white rhinoceros, *Ceratotherium simum*; carcass is excluded from the analysis due to the extreme rarity of these species in HNP) and 17 species based on scat data (Table 1). Diet composition was different between the two periods based on both carcasses (Fisher exact test P < 0.0001) and scats (x^2 = 21.56, df = 7, P = 0.003). Based on scat data (and excluding elephants), the major changes from period 1 to period 2 for common prey species were that hyaenas fed 2.1 times more on giraffe, 2.3 times less on buffalo, 2.8 times less on wildebeest and 5 times more on warthog (Table 1, Fig. 3a). Based on carcass data, the major changes from period 1 to
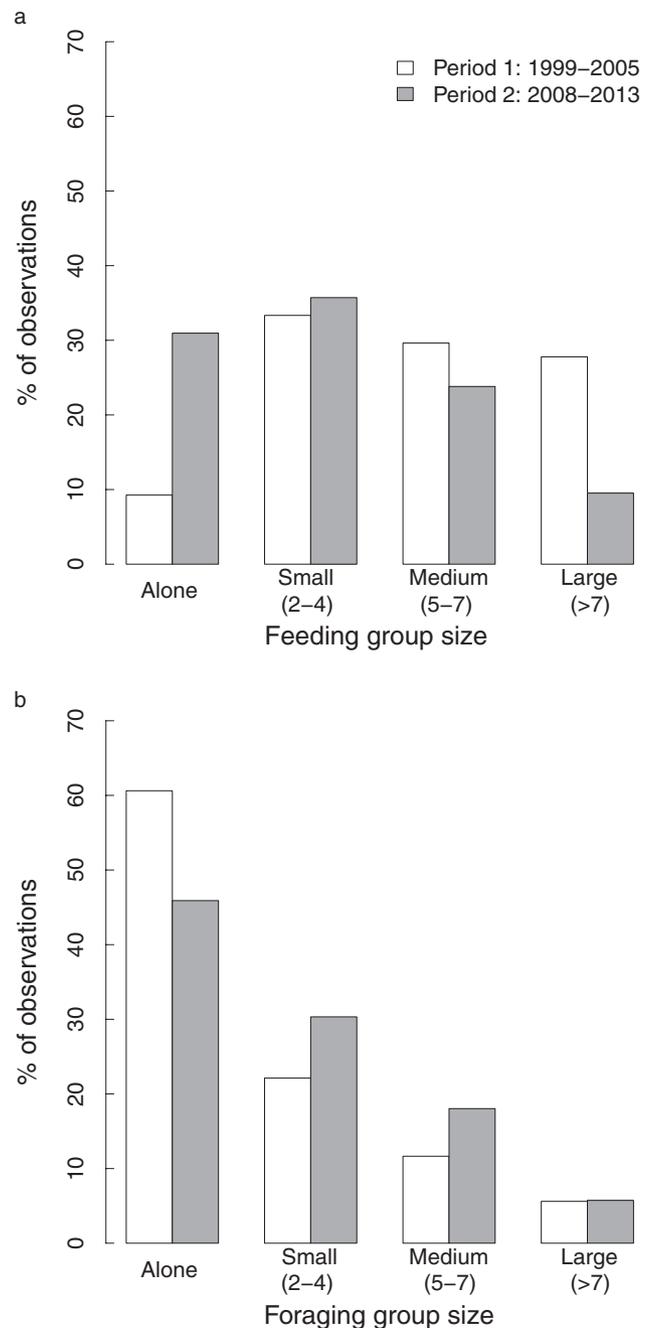

Figure 2 Changes in hyaena (a) foraging and (b) feeding group sizes during period 1 (white) with low level of interspecific interactions with lions, *Panthera leo*, and period 2 (grey) with high level of interspecific interactions with lions.

period 2 were that hyaenas fed 1.8 times more on elephant, 3.7 times more on giraffe, 3.8 times less on buffalo, zebras disappeared from their diet, 1.6 times less on kudu, 13.4 times less on wildebeest and 4.5 times less on impala (Table 1; Fig. 3b). The contribution of very large prey to hyaena diet increased
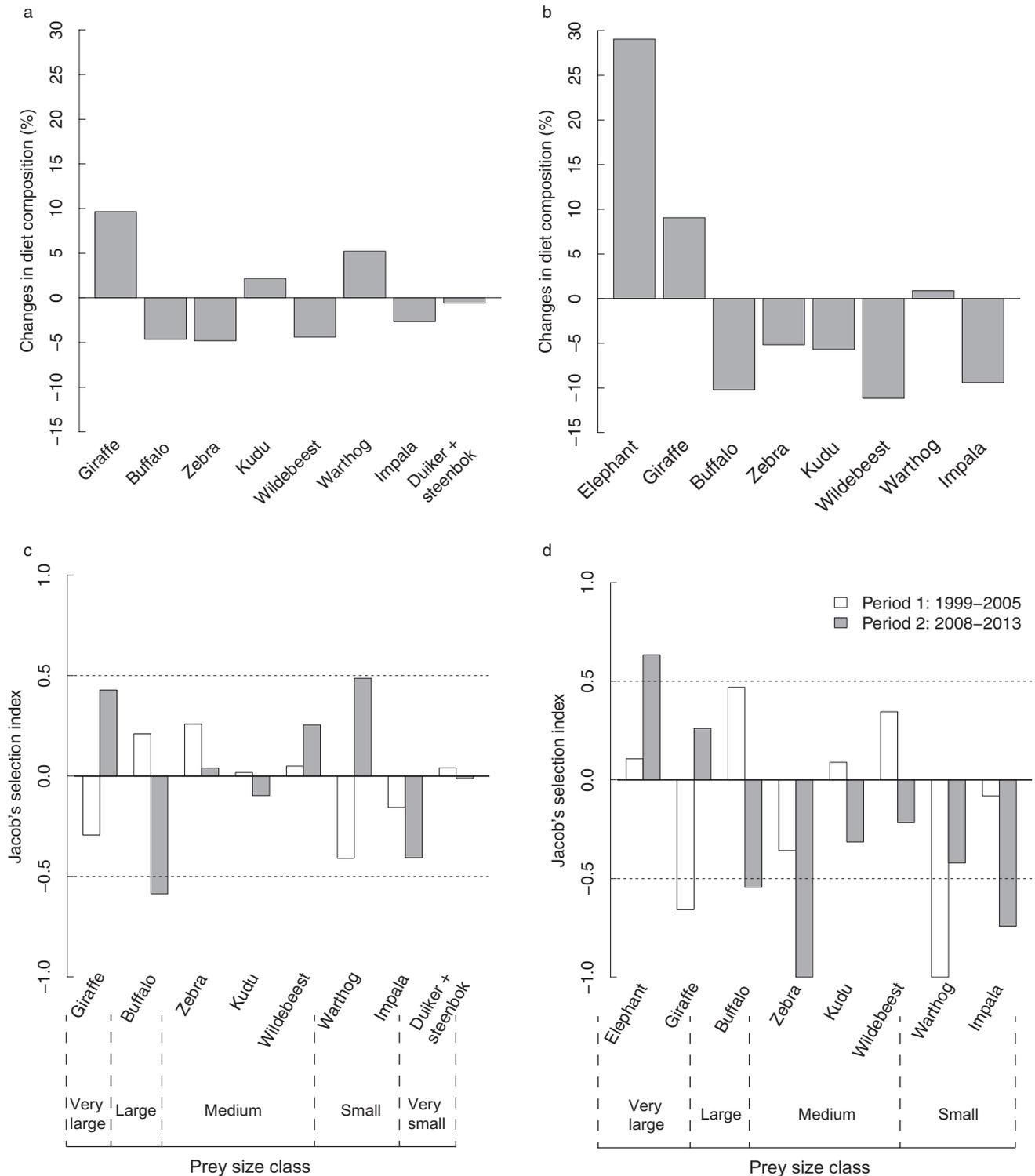
Figure 3 Changes of (a,b) hyaena diet composition and (c,d) prey preferences between period 1 (white), with low level of interspecific interactions with lions, *Panthera leo*, and period 2 (grey), with high level of interspecific interactions with lions. The results are from analyses of both scat data (a,c) and carcass data (b,d). (a) and (b) show the difference in diet composition between the 2 periods, i.e. for a given species, it is % in the diet during period 2 − % in the diet during period 1. (c) and (d) are the Jacobs selection indices with negative indices indicating avoidance while positive ones indicating selection. Elephant (*Loxodonta africana*) results are not presented for analyses on scat data (see text for details) and very small antelopes results are not presented for analyses on carcass data (see text for details).

from 41.4 to 79.5% based on carcass data (Table 1), which represents the most important difference (Fig. 3b).

Changes in hyaena prey preference

We found that hyaenas did not take prey in proportion to their availability and prey preference changed from period 1 to period 2 (Fig. 3c and d). There was a switch from avoiding very large prey (giraffe) or consuming them as available (elephant) to being preferred. Large prey (buffalo) were preferred during period 1 but were avoided during period 2. For medium-sized prey (zebra, kudu and wildebeest), there has been an overall trend from preference during period 1 to avoidance during period 2, except for wildebeest based on scat data. No clear trend was detected for small prey. Very small prey (duiker and steenbok) were consistently taken in proportion to their availability during the two periods.

Discussion

We found that hyaenas are generalist foragers feeding on a wide range of available prey, which is consistent with previous studies (e.g. Kruuk, 1972, Mills, 1990, Hayward, 2006). However, hyaenas in HNP did not consume prey relative to their availability, similar to observations of hyaena feeding ecology at other sites (e.g. Moremi Game Reserve, Cooper, 1990; Ngorongoro Crater, Höner *et al.*, 2002; Addo Elephant National Park, Wentworth, Tambling & Kerley, 2011). All these studies show that hyaenas have site-specific prey preferences. In HNP, elephants contribute a large percentage to hyaena diet (up to 67% of their diet), a clear adjustment of hyaenas to this ecosystem where elephants represent over 75% of the herbivore biomass (this study; Chamaillé-Jammes *et al.*, 2009). While hyaenas have been reported to kill newborn elephants (Salnicki *et al.*, 2001), there is no doubt that the large majority of the elephant biomass they consumed was scavenged (only 11 elephant carcasses were calves). While most of the very large (elephant and giraffe) and large prey (buffalo) were most probably scavenged, medium-sized prey (kudu, wildebeest and zebra) have a greater chance to have been actively hunted and killed by hyaenas. Several studies have shown that hyaenas are efficient hunters and capable of taking down relatively heavy prey (Kruuk, 1972; Mills, 1990; Périquet *et al.*, 2014), and this is also the case in HNP (Salnicki *et al.*, 2001; Drouet-Hoguet, 2007; Périquet, 2014).

Our results revealed a significant change in hyaena diet composition and prey preference in terms of size class consumed between the two study periods. Whereas in period 1 large and medium-sized prey were selected by hyaenas, and hence represented an important contribution to their diet, this was not the case in period 2. These trends were consistent based on both scat and carcass analyses. In parallel, a striking result of our study is the strong increase of very large species contribution to hyaena diet and the preference for these prey in period 2. Our results suggest there has been a switch in hyaena foraging strategy from predominantly hunting medium-sized prey and scavenging/kleptoparasiting large prey during period 1 to mostly scavenging very large prey during period 2. These results do not support the hypothesis that hyaena foraging strategy was driven by hyaena foraging group size. Since hyaenas foraged in larger groups in period 2, we would have expected the proportion of medium and large prey hunted by hyaenas to have increased. Additionally, the consumption of giraffe increased while their abundance decreased, and we found the opposite pattern for buffalo. Thus changes in prey community composition cannot explain the changes in hyaena diet. Finally, the number of animals dying from natural causes unrelated to predation (drought, disease) was unlikely to have changed between the two periods (both had above-average rainfall and no disease outbreak was reported). Hence, these changes are compatible with the hypothesis that the level of interspecific interactions with lions is a main driver of hyaena foraging strategy.

In period 1, due to the lower abundance of lions in the ecosystem and the lower probability of encountering adult male lions, hyaenas were more likely to retain the medium-sized prey they killed. During this period, lions were also likely to be more sensitive to kleptoparasitism from hyaenas due to the low number of adult males in the lion population (Cooper, 1991; Trinkel & Kastberger, 2005). As a consequence, hyaenas might have been able to steal numerous buffalo carcasses, which are the main prey of lions in HNP (Davidson *et al.*, 2013). Conversely, the risk of hyaenas losing their carcasses to lions is expected to increase in period 2 while their ability to steal lion kills is expected to decrease. Further, the cost of kleptoparasitism by lions was likely to be higher for large and medium-sized prey as hyaenas expend more energy while hunting and have a high risk of attracting lions in the process because of the noise (Kruuk, 1972). This might be responsible for the decrease in hyaena consumption and preference for these prey size classes between periods 1 and 2. The decrease in hyaena feeding group size might also be a response to the increased competition with lions, as fewer clan members at feeding sites will decrease the level of hyaena interactions while feeding and ultimately will result in less noisy feeding to remain undetected by lions (see Webster, McNutt & McComb, 2010 for the role of eavesdropping in large carnivores). Therefore, changes in lion population composition might have induced changes in the fission–fusion dynamics of hyaena clans, which is consistent with the conclusion of Smith *et al.* (2008).

During period 2, males were more often present in lion prides (Loveridge *et al.*, 2010); hence lion groups had a better chance of success in hunting elephant, giraffe and buffalo, and they thus might have increased their predation of these rewarding species. In HNP, some lion groups have specialized in killing elephants including large sub-adults and weak adults (S. Périquet, pers. obs.) and giraffe are also common lion prey (Davidson *et al.*, 2013). This ultimately provides more very large carcasses available in the landscape, increasing scavenging opportunities for hyaenas. Leftovers from lion on these carcasses are likely to be very beneficial for hyaenas. The increase of lion predation may provide hyaenas with

additional food sources. Our results are in accordance with those from Höner *et al.* (2002) showing that in the Ngorongoro, hyaenas switched from hunting to scavenging as the availability of buffalo carcasses killed by lions increased.

Another mechanism operating at the intraguild level might have played a role also in the observed changes in hyaena diet. Cursorial predators such as hyaenas tend to concentrate disproportionally on old as well as young animals when killing relatively large prey (Husseman *et al.*, 2003). If a larger ambush predator like the lion removes a substantial proportion of prime-aged adults from these populations, fewer adults survive into the age range where they could be readily killed by hyaenas. Hence, if lions are abundant, hyaenas may scavenge carcasses of species they would normally have killed when those species reached the geriatric age class.

Resource diversity and heterogeneity have been shown to promote species coexistence (Durant, 1998, in large carnivores; Cromsigt, Prins & Olff, 2009, in ungulates). Karanth & Sunquist (1995) also showed that the availability of large prey for tigers greatly reduces their competition with leopards. The abundance of elephant carcasses, especially during the dry season, might act as an alternative food resource for hyaenas, releasing the competitive pressure with lions. The use of these carcasses might be a compensatory mechanism for the reduction in large- and medium-sized prey hunting in response to increasing competition with lions. This might also be why hyaena density remained stable through the period of increasing competition from lions. While intraguild competition is known to influence large carnivore habitat use and behaviour (Creel & Creel, 1996; Durant, 2000; Périquet *et al.*, 2014), this study shows that an increase in the lion population abundance may have led to an increase in the intensity of interactions between lions and hyaenas and ultimately may have affected diets through changes in foraging strategies. The associated changes in predation pressure on the various prey body sizes could ultimately impact the dynamics of prey populations and the functioning of the ungulate community (Fritz *et al.*, 2011), and possibly the whole ecosystem functioning through trophic cascades (Fritz *et al.*, 2011; Ripple *et al.*, 2014) or shifts in food web structures (Wilson & Wolkovich, 2011).

Acknowledgements

References

Bacon, M.M., Becic, G.M. & Epp, M.T. (2011). Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. *Wildl. Soc. Bull.* **35**, 409–415.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013). Risk avoidance in sympatric large carnivores: reactive or predictive? *J. Anim. Ecol.* **82**, 1098.

Buys, D. & Koegh, H.J. (1984). Notes on the microstructure of hair of the Orycteropodidae, Elephantidae, Equidae, Suidae and Giraffidae. *S. Afr. J. Wildl. Res.* **14**, 111–119.

Caro, T.M. & Stoner, C. (2003). The potential for interspecific competition among African carnivores. *Biol. Conserv.* **110**, 67–75.

Chamaillé-Jammes, S., Valeix, M., Bourgarel, M., Murindagomo, F. & Fritz, H. (2009). Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. *Afr. J. Ecol.* **47**, 804–808.

Coe, M.J., Cumming, D.H. & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* **22**, 341–354.

Cooper, S.M. (1990). The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. *Afr. J. Ecol.* **28**, 131–141.

Cooper, S.M. (1991). Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *Afr. J. Ecol.* **29**, 130–136.

Creel, S. & Creel, N.M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conserv. Biol.* **10**, 526–538.

Cromsigt, J.P.G.M., Prins, H.H.T. & Olff, H. (2009). Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. *Divers. Distrib.* **15**, 513–522.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2013). Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PLoS ONE* **8**, e55182.

van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H. & Landa, A. (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *J. Anim. Ecol.* **77**, 1183–1190.

Drouet-Hoguet, N. (2007) *Influence des activités anthropogéniques sur le régime alimentaire et la réponse numérique de la hyène tachetée en savane arborée dystrophique dominée par l'éléphant*. PhD Thesis, Université Claude Bernard Lyon 1.

Durant, S.M. (1998). Competition refuges and coexistence: an example from Serengeti carnivores. *J. Anim. Ecol.* **67**, 370–386.

Durant, S.M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behav. Ecol.* **11**, 624–632.

Flower, T.P., Child, M.F. & Ridley, A.R. (2013). The ecological economics of kleptoparasitism: pay-offs from self-foraging versus kleptoparasitism. *J. Anim. Ecol.* **82**, 245–255.

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M. & Clobert, J. (2011). A food web perspective on large herbivore community limitation. *Ecography* **34**, 196–202.

Harihar, A., Pandav, B. & Goyal, S.P. (2011). Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *J. Appl. Ecol.* **48**, 806–814.

Hayward, M.W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *J. Zool.* **270**, 606–614.

Hayward, M.W. & Kerley, G.I.H. (2005). Prey preferences of the lion (*Panthera leo*). *J. Zool.* **267**, 309–322.

Höner, O.P., Wachter, B., East, M.L. & Hofer, H. (2002). The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *J. Anim. Ecol.* **71**, 236–246.

Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R. & Quigley, H. (2003). Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos.* **101**, 591–601.

Iyengar, E.V. (2008). Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. *Biol. J. Linn. Soc.* **93**, 745–762.

Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia* **14**, 413–417.

Karanth, K.U. & Sunquist, M. (1995). Prey selection by tiger, leopard and dhole in tropical forests. *J. Anim. Ecol.* **64**, 439–450.

Koegh, H.J. (1983). A photographic reference system of the microstructure of the hair of southern African bovids. *S. Afr. J. Wildl. Res.* **13**, 89–132.

Kruuk, H. (1972). *The spotted hyena: a study of predation and social behavior*: Chicago: University of Chicago Press.

Loveridge, A.J., Hemson, G., Davidson, Z. & Macdonald, D.W. (2010). African lions on the edge: reserve boundaries as 'attractive sinks'. In *Biology and conservation of wild felids*: 283–304. Macdonald, D.W. & Loveridge, A.J. (Eds). Oxford: Oxford University Press.

Mills, M.G.L. (1990). *Kalahari hyaenas: comparative behavioural ecology of two species*. Caldwell: The Blackburn Press.

Owen-Smith, N. & Mills, M.G.L. (2008). Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology* **89**, 1120–1133.

Palomares, F. & Caro, T.M. (1999). Interspecific killing among mammalian carnivores. *Am. Nat.* **153**, 492–508.

Périquet, S. (2014) *Sharing the top: how do spotted hyaenas cope with lions? Apex predator coexistence in a wooded savanna*. PhD Thesis, Université Claude Bernard Lyon 1.

Périquet, S., Fritz, H. & Revilla, E. (2014). The Lion King and the Hyaena Queen: large carnivore interactions and coexistence. *Biol. Rev.* (doi: 10.1111/brv.12152).

Pereira, L.M., Owen-Smith, N. & Moleón, M. (2014). Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Rev.* **44**, 44–55.

Purchase, G.K. (2004) *Factor affecting the ratio of lions (*Panthera leo*) to spotted hyaenas (*Crocuta crocuta*) in protected areas in Africa: competition and/or available prey*. PhD Thesis, University of Aberdeen.

R Core Team (2014). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014). Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484.

Rogers, C.M. (Eds) (1993). A woody vegetation survey of Hwange National Park. Harare: Department of National Parks and Wildlife Management.

Salnicki, J., Teichmann, M., Wilson, V. & Murindagomo, F. (2001). Spotted hyaenas *Crocuta crocuta* prey on new-born elephants calves in Hwange National Park, Zimbabwe. *Koedoe* **44**, 79–83.

Schaller, G.B. (1972). *The Serengeti lion – a study of predator-prey relations*: Chicago: University of Chicago Press.

Smith, J.E., Kolowski, J.M., Graham, K., Dawes, S.E. & Holekamp, K.E. (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Anim. Behav.* **76**, 619–636.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F., Buckland, S.T., Borchers, D.L., Anderson, D., Burnham, K., Hedley, S.L., Pollard, J.H., Bishop, J. & Marques, T.A., (2006) Distance 6.0. Research Unit for Wildlife Population Assessment. University of St Andrews, UK.

Trinkel, M. & Kastberger, G. (2005). Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. *Afr. J. Ecol.* **43**, 220–224.

Webster, H., McNutt, J.W. & McComb, K. (2010). Eavesdropping and risk assessment between lions, spotted hyenas and African wild dogs. *Ethology* **116**, 233–239.

Wentworth, J., Tambling, C.J. & Kerley, G. (2011). Evidence for prey selection by spotted hyaena in the Eastern Cape, South Africa. *Acta Theriol. (Warsz)* **56**, 389–392.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M. & Getz, W.M. (2003). Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *J. Anim. Ecol.* **72**, 909–916.

Wilson, E.E. & Wolkovich, E.M. (2011). Scavenging: how carnivores and carrion structure communities. *Trends Ecol. Evol.* **26**, 129–135.