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Living near the edge: a review of the ecological relationships between large carnivores in the arid Kalahari

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Much of Africa comprises arid regions, yet little is known about the ecological interactions between large carnivores in these landscapes. A review of the densities, feeding and foraging ecology, as well as the relations between the large carnivores in the arid Kalahari, illustrates how they have successfully adapted to arid conditions, and highlights some of the differences in these relationships with those in more mesic areas. In the arid Kalahari, the relative densities of the large carnivores are more even, but community structure is different, with the inclusion of the brown hyaena (*Hyaena brunnea*) and the disappearance of the African wild dog (*Lycaon pictus*). Resource partitioning is more acute and diet flexibility is evident. The relative contribution to animals killed by predation is more equitably shared by the predator community, and high rates of food loss by smaller carnivores to larger ones has not been recorded. There is even an example of a smaller carnivore (brown hyaena) deriving benefits from a larger one (lion, *Panthera leo*). Arid regions are clearly important areas for large carnivores and more attention should be given to research and conservation of carnivores in arid areas.

Key words: ecological interactions, carnivores, arid regions.

INTRODUCTION

Ecological theory holds that carnivores limit herbivore abundance and thereby affect community structure at most trophic levels (Steneck, 2005). At the same time, the outcomes of interactions between carnivores may be important in limiting their abundance (Ritchie & Johnson, 2009). Coexistence and ecological relationships in large (>20 kg), terrestrial African carnivores have been studied widely in a number of habitats, especially on the Serengeti Plains and the woodland savanna regions of southern Africa (Bertram, 1979; Broekhuis, Cozzi, Valeix, McNutt & Macdonald, 2013; Cozzi *et al.*, 2012; Durant, 1998; Hayward & Kerley, 2008; Hayward, O'Brien & Kerley, 2007; Hayward & Slotow, 2009; Mills & Biggs, 1993; Owen-Smith & Mills, 2008a; Owen-Smith & Mills, 2008b; Radloff & Du Toit, 2004; Schaller, 1972; Sinclair, Mduma & Brashares, 2003; Vanak *et al.*, 2013). These studies have made important contributions to our understand-

ing of the dynamics of African large carnivore communities and have reinforced the concept that African systems are characterized by the numerical, predatory and competitive dominance of the spotted hyaena, *Crocuta crocuta*, and lion, *Panthera leo*, and the subordinate position of smaller species, especially cheetahs, *Acinonyx jubatus*, and African wild dogs, *Lycaon pictus*.

The above-mentioned research has taken place in areas that receive 450 mm or more rainfall per annum. However, a substantial part of Africa (~43%) (www.worldclim.org) covers more arid areas, where annual rainfall is below 350 mm, and where the biomass of herbivores is lower (Coe, Cumming & Phillipson, 1976). Lower herbivore biomass would be expected to have an impact on large carnivore impacts and relationships. For example, lower carnivore densities would be likely, because of the decrease in food biomass and availability, and this might affect the larger or more specialized species more, as arid ecosystems are dominated by smaller-sized herbivores compared to ecosystems with higher

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rainfall (East, 1984; Fritz & Duncan, 1994). Similarly, dietary habits and resource partitioning might change and prey species not often utilized in more productive areas might become more important. Foraging behaviour too could be different. Generalists, with the ability to utilize a wide range of food types, would be expected to be more successful. Finally, behavioural interactions between the carnivores might vary and the impact they have on each other could take on a different dynamic.

Globally, dry land areas have been sorely neglected at all levels by both scientists and conservationists, because of their relatively low productivity. Yet, they are home to species that are adapted to harsh and highly variable conditions (Durant *et al.*, 2012; Durant *et al.*, 2014). One arid area that has received more attention than most is the arid Kalahari, where the Kgalagadi Transfrontier Park (KTP) in South Africa and Botswana, is not only a well-conserved ecosystem that is well managed, but one where the large carnivore community has been relatively well studied (Mills & Mills, 2013a).

In this paper, I review ecological and behavioural patterns and processes between large carnivores in the arid Kalahari, using studies conducted in the KTP. I consider relative densities, aspects of the diet, feeding ecology and behaviour, and interactions between the species. I discuss these relationships within the framework of large carnivore ecological and behavioral theory, as set out in (Ray, Redford, Steneck & Berger, 2005) and conclude with an evaluation of the biodiversity and conservation implications of these studies.

THE ARID KALAHARI

The Kalahari is a large, sand filled basin stretching from 28°S to 1°N in the west of Africa. The arid Kalahari is in the extreme south of the region where the sand is piled into vegetated, linear or seif dunes fixed by vegetation. The data used in this review were collected in an area of approximately 15 000 km², encompassing the South African side and a 40 km strip along the Nossob riverbed on the Botswana side of the KTP (24°S and 27°S and 20°E and 22°E). Two riverbeds run through the KTP which only flow for short periods and distances during abnormally wet years (Leistner, 1967). There is no naturally occurring permanent water, but boreholes have been introduced along the riverbeds and in the dunes on the South African side of the KTP (Anonymous, 2008). However, the

natural fauna of this area, including the large carnivores, are adapted to survive without surface water.

Annual rainfall in the study area increases from 150 mm in the southwest to 250 mm in the north (Anonymous, 2008). Therefore, the climatic conditions comply with the criteria of Durant *et al.* (2014) for a desert ecosystem. The vegetation type is classified as Kalahari Duneveld (Mucina & Rutherford, 2006) and is predominantly a shrubby grassland, except along the riverbeds where an open *Acacia erioloba* and *Acacia haematoxylon* tree savanna is found. Ecological conditions dictate that herbivorous animals are generally thinly distributed and need to be mobile. Gemsbok (*Oryx gazella*), blue wildebeest (*Connochaetes taurinus*) (along the riverbeds), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Ostrich (*Struthio camelus*) are sedentary species, whereas springbok (*Antidorcas marsupialis*), red hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*) and wildebeest (away from the riverbeds) are more nomadic (Mills, 1990). Herbivores tend to concentrate along the riverbeds during the wet season and disperse in the dry season (Mills & Retief, 1984; van der Walt, Retief, le Riche, Mills & de Graaff, 1984). Smaller carnivores, such as black-backed jackals (*Canis mesomelas*), bat-eared foxes (*Otocyon megalotis*), African wild cats (*Felis sivestris*) are well represented (Mills, 1990; Mills & Mills, 2013a). One of the major biodiversity characteristics of the KTP is that it represents a relic of a nomadic large herbivore community in an arid ecosystem, supporting a functional large carnivore predator/prey system (Anonymous, 2008).

THE STUDIES

Two features of the KTP lend themselves to making it possible to record many aspects of the behaviour of large carnivores – the fact that it is largely covered with sand, and with sparse vegetation. The sand and sparse vegetation provide unique conditions for tracking spoor over long distances with experienced Bushman trackers (Bothma & le Riche, 1984, 1990; Bothma, van Rooyen & le Riche, 1997; Eloff, 1973, 1984; Mills, 1990). The sparse vegetation and open landscape also make it possible to visually follow habituated animals in a vehicle for long periods (Mills, 1990). This has made it possible to compile accurate profiles of the diets of these animals, as continuous follows are widely regarded as the most accurate method of ascertaining the diet

of a predator, without having to resort to more biased measures, such as radio-tracking and opportunistic observations (Bertram, 1979; Mills, 1996; Mills & Shenk, 1992).

In the 1960s, Eloff began to document the feeding habits of lions in the arid Kalahari. Over the years, he made numerous short visits to the area to continue this work into the late 1980s. He and the trackers documented 195 complete 24 h movements of various lion groups, tracking lions for approximately 2300 km, which provided a sample of 92 kills (Eloff, 1973, 1984). In the early 1970s, Bothma and le Riche initiated a similar type of study on leopards (*Panthera pardus*). During this study, 136 complete 24 h movements of leopards were made, totalling about 2150 km of spoor followed, from which a sample of 80 kills was collected (Bothma & le Riche, 1984; Bothma & Le Riche, 1986; Bothma & le Riche, 1990; Bothma *et al.*, 1997).

My own work in the arid Kalahari was over two periods. From 1972–1984, I conducted intensive studies on the brown (*Hyaena brunnea*) and spotted hyaenas, using a combination of following spoor and direct observations. I followed brown hyaena spoor for nearly 1200 km and directly followed them for about 4445 km, during which time I recorded 794 feeding events on anything from termites to eland carcasses. Spotted hyaenas were tracked for approximately 3500 km and followed for 3660 km, and 346 feeding events, of which 110 were kills, were documented (Mills, 1990). The second period was from 2006–2012 when I studied cheetahs. Again, I used a combination of tracking spoor (965 km) and following (2340 km) during which I documented 411 cheetah kills. This work is presently being written up, so the data presented here are previously unpublished.

For the purposes of comparing aspects of feeding ecology it has been found that it is feasible to combine data from the two techniques used, especially those involved in foraging (Mills, 1990). Because the raw data from the lion and leopard data were not available, statistical comparisons of most aspects discussed were not possible. However, I believe that the qualitative comparisons are useful.

LARGE CARNIVORE DENSITIES

Resource dispersion and the composition of the prey populations play an important role in determining carnivore densities (Carbone & Gittleman, 2002). Table 1 shows large carnivore densities in

Table 1. Large carnivore densities from the Kgalagadi Transfrontier Park (KTP) and other large protected areas. ? = no reliable data found _ = species does not occur in the area.

Area	Density (number/100 km ²) and reference					
	Spotted hyaena	Lion	Leopard	Wild dog	Cheetah	Brown hyaena
Kgalagadi Transfrontier Park	0.9 (Mills, 1990)	1 (Funston, 2011)	0.2 (Funston, 2001)	–	0.7 (M. Mills, unpubl.)	1.8 (Mills, 1990)
Selous Game Reserve	32 (Creel & Creel, 2002)	11 (Creel & Creel, 2002)	?	4 (Creel & Creel, 2002)	?	–
Hluhluwe-Imfolosi Park	36 (Graf <i>et al.</i> , 2009)	12.4 (Bauer & van der Merwe, 2004)	7 (Balme <i>et al.</i> , 2009)	1.6 (Somers <i>et al.</i> , 2007)	?	–
Serengeti National Park	60 (Hofer & East, 1995)	16 (Bauer & van der Merwe, 2004)	9 (Bertram, 1979)	0.1 (Creel & Creel, 2002)	1 (Caro, 1994)	–
Kruger National Park	13.3 (Mills <i>et al.</i> , 2001)	8.4 (Ferreira & Funston, 2010)	3.4 (Bailey, 1993)	1.3 (Maddock & Mills, 1994)	2.1 (Marnewick <i>et al.</i> , 2014)	–
Moremi Game Reserve	14.4 (Cozzi <i>et al.</i> , 2013)	5.8 (Cozzi <i>et al.</i> , 2013)	?	4 (Creel & Creel, 2002)	0.6 (Broekhuis, 2012)	–

Table 2. The ratio of lion plus spotted hyaena densities to cheetah, wild dog and brown hyaena densities in some large African protected areas. ? = no reliable data found; x = species does not occur in the area.

	Cheetah	Wild dog	Brown hyaena
Kgalagadi Transfrontier Park	2.7	x	1.1
Selous Game Reserve	?	10.8	x
Hluhluwe-iMfolosi Park	?	43.8	x
Serengeti National Park	76.0	760.00	x
Kruger National Park	10.3	16.7	x
Moremi Game Reserve	33.7	5.1	x

the KTP, as well as from some other large protected areas in less arid regions of Africa for comparison. Table 2 shows various ratios of these densities to further analyse this. These data clearly illustrate the numerical dominance of the spotted hyaena, lion and, to a lesser extent the leopard, in all areas except for the arid Kalahari. Cheetah and wild dog densities, are always low, and do not vary as much as the other three species. In terms of the composition of the large carnivore guild, a new species, the brown hyaena, appears in the arid Kalahari. (In north Africa the striped hyaena, *Hyaena hyaena*, is marginally present at unknown densities in the Serengeti and Selous, but becomes prevalent in the arid regions (Mills & Hofer, 1998; Wagner, 2013)).

In the lion and spotted hyaena high-density areas, competition from these species may be partly responsible for wild dogs and cheetahs living at low densities (see for example Creel & Creel, 1996; Durant, 1998), and for the absence of the brown hyaena in Kruger National Park (Mills & Funston, 2003). At the same time, in the arid Kalahari, where spotted hyaenas and lions occur at low densities, cheetahs and brown hyaenas are able to maintain densities to the point that they occur at similar densities to their larger competitors. Indeed, the brown hyaena is the most common large carnivore species in the KTP. The wild dog, however, is only sporadically seen in the KTP, and although it has been observed to occasionally breed successfully there, it is not known to have done so for the last 20 years (Mills & Mills, 2013a). Its absence is unlikely to be through interspecific competition because of the low density of lions and spotted hyaenas. Rather, due to its exceptionally high metabolic demands (Gorman, Mills, Raath & Speakman, 1998), and selective hunting behaviour (Davies-Mostert, Mills & Macdonald, 2013), the prey base may not be sufficient to sustain a resident population.

DIET AND PREY SELECTION

Table 3 summarizes the diets of the five species in the KTP, showing those species that make up 5% or more of their food. The two hyaena species differ markedly in diet. The brown hyaena has the widest diet, supplementing carrion of almost any origin, which makes up 69% of the diet, with wild fruits which make up 23% of the diet, especially the tsama melon (*Citrullus lunatus*) and gembok cucumber (*Acanthosicyos naudianus*). To a lesser extent it also eats reptiles, insects and birds eggs, especially Ostrich eggs. Many feeding events involve picking up small items such as bone chips and beetles. Hunting is almost irrelevant for this species in the KTP and contributes only about 2% of the biomass of its food. Although an accomplished and opportunistic scavenger, the spotted hyaena is predominantly a hunter of gembok calves and wildebeest of all ages; kills contributing 65% of the biomass eaten. It tends to be the most specialized hunter in the arid Kalahari, with only two species making up 68% of kills.

The lion has a similar diet to the spotted hyaena, although the two species tend to prey on different segments of the gembok population; adults in the case of lions, and calves in the case of spotted hyaenas. Although it could be argued that this enhances scramble competition (Allaby, 1999), as the hyaenas may be removing gembok that might later become available to lions, it could also be seen as resource partitioning (Mills, 1990), as lions are better equipped to capture adult gembok than spotted hyaenas and so are able to dominate this food source.

The outstanding feature of the lion's diet is the preponderance of porcupines (*Hystrix africae-australis*) killed, far more than has been recorded anywhere else (Hayward & Kerley, 2005). This is testimony to the low density of large herbivores in this arid region and to the adaptability of the lion. The leopard also capitalizes on porcupines far

Table 3. The diets of the large carnivores in the Kgalagadi Transfrontier Park (KTP).

	Lion	Leopard	Cheetah	Spotted hyaena	Brown hyaena
Number of kills/food items*	92	80	411	346 (65%**)	794 (2%**)
Species making up >5% of the diet	Porcupine 34% Gemsbok 26% (60% adults) Springbok 11% Hartebeest 9%	Porcupine 20% Gemsbok calves 19% Duiker 10% Black-backed jackal 9% Bat-eared fox 9% Steenbok 8% Genet 6%	Steenbok 36% Hare 19% Springbok 15% Springhare 7% Ostrich 7% Gemsbok calf 6%	Gemsbok 50% (80% calves) Wildebeest 18%	Wild fruits*** 25%

*For spotted hyaena carcasses fed on, for brown hyaena food items eaten.

**% biomass killed.

***Tsama and gemsbok cucumber.

more often in the arid Kalahari than anywhere else so far studied (Hayward *et al.*, 2006). However, in line with the leopard's reputation for killing carnivores, especially in less productive areas (Hunter, Henschel & Ray, 2013), small carnivores comprised 24% of its kills. These were the abundant and widespread canids; black-backed jackals and bat-eared foxes, which are killed in equal proportions, and small-spotted genets (*Genetta genetta*). Additionally, more typical antelope species were often utilized.

The most important prey of cheetahs is the widespread steenbok, which does not feature in the diet of leopards to anything like the same extent. Other important prey for the cheetah are hare (*Lepus* sp.), springbok and springhare (*Pedetes capensis*), and, for coalition males, gemsbok calves and adult Ostriches. Most of these species are also not usually associated as important prey for cheetahs in other areas (Hayward, Hofmeyr, O'Brien & Kerley, 2006).

Whereas cheetah and leopard diets are similar in the Serengeti (Bertram, 1979) and Kruger (Mills & Biggs, 1993; Owen-Smith & Mills, 2008a), only one species, the steenbok, is represented in over 5% of their kills in the arid Kalahari. However, the steenbok is utilized four times more frequently by the cheetah than the leopard. The cheetah is well adapted to arid regions. Its ability to survive on small, cryptic and solitary species such as steenbok, hare and springhare is noteworthy and somewhat at odds to the conclusion of Hayward *et al.* (2006) that it prefers to kill prey within a body mass range of 23–56 kg.

Although, judging from spoor counts, the porcupine is less common than other potential prey species of similar size such as steenbok, common duiker, black-backed jackal and bat-eared fox (Mills, 1990), it is less agile, albeit equipped with formidable defence structures through its quills. It is therefore easier for the more robust cats like lions and leopards to catch (the spotted hyaena has also been observed killing it occasionally). The cheetah's small jaws and teeth and adaptations for speed (Kitchener, Van Valkenburgh & Yamaguchi, 2010), preclude its ability to kill a porcupine. The ubiquitous steenbok, on the other hand, is most vulnerable to the swift cheetah, but less so to the other hunters. The reason for springbok being a less important prey than might be expected is because of their limited distribution. They are exclusively confined to the river-beds (van der Walt *et al.*, 1984).

Table 4. Aspects of the foraging ecology and behaviour of large carnivores in the Kgalagadi Transfrontier Park (KTP).

	Lion	Leopard	Cheetah	Spotted hyaena	Brown hyaena
Mean % 24 h active	?	?	10.3	31	42.6
Mean distance (km) moved/24 h	11.8	13.9	11.0	27.1	31.1
Mean distance moved (km) between meals	25.2	24.5	15.9	32.7	9.2
Mean amount of food available at each meal (kg)	58	22	15	59	1.7
Mean consumption rate (kg eaten/kg mass /day)	0.08	0.11	0.1	0.1	0.09
% chases successful	39 (n = 148)	18 (n = 110)	43 (n = 730)	35 (n = 136)	9 (n = 70)

FORAGING BEHAVIOUR

Table 4 summarizes aspects of the foraging behaviour of the five species in the KTP. Because the lion and leopard studies relied solely on tracking spoor, it was impossible to measure the amount of time they spent active. However, cheetahs were active for much less time than both hyaena species, and while the hyaenas are strongly nocturnal (Mills, 1990), the cheetah is mainly diurnal, although more nocturnal than is often taken to be the case, not least because that is when they hunt the obligatory nocturnal springhare (Butynski, 1984). Lions and leopards are widely accepted as being predominantly nocturnal (Hunter *et al.*, 2013; West & Packer, 2013). As has been shown in a recent study (Cozzi *et al.*, 2012), temporal activity partitioning in large carnivores for complete avoidance may not always be as important as has been suggested (Hayward & Slotow, 2009).

Because they are active for longer periods than the cheetah, and probably the other cats as well, hyaenas are generally more mobile and cover longer distances over a 24 h period than the cats. For the brown hyaena this is an important adaptation for their scavenging strategy, where food items are often widely scattered and quite small. Mobility for the spotted hyaena is important because, not only does it scavenge about one third of its food, it is also the most selective hunter of the large carnivores in the arid Kalahari. Additionally, it has the challenge of having to locate gemsbok calves, which only make up approximately 10% of the relatively thinly dispersed gemsbok population (M.G.L. Mills, unpubl. data), but on which it relies heavily for food. The cats make up for their limited mobility by being able to catch a larger range of prey (Table 3). Additionally,

cats typically hunt by stealth, employing a sit and wait or ambush foraging strategy, followed by a stalk and short chase (Macdonald, Loveridge & Nowell, 2010), whereas the spotted hyaena follows a widely foraging and cursorial hunting strategy of running down prey over quite long distances (Mills, 1990).

Estimations of the average size of a meal for lions, leopards, and cheetahs (Table 4) were calculated by assuming that the average mass of food from a kill was three quarters of the average size of an adult female of the species, a measure often used for these type of calculations (Hayward *et al.*, 2007), summing the total for all kills, and dividing that by the number of kills recorded. For the hyaena species, the figures were taken from data in Mills (1990). The average travel distances between meals of over 1 kg for all species is related to the size of the meal (Spearman's rank correlation: $r_s = 1.00$, d.f. = 3, $P < 0.05$). The brown hyaena tends to find several small meals per night, whereas the spotted hyaena and the lion eat fewer, but substantially larger meals, and the cheetah and leopard intermediate sized meals, although leopards move nearly twice as far as cheetahs do between meals.

In terms of foraging efficiency, measured as kg of food eaten /kg of mass of carnivore/day (Table 4), there is little to choose between the species, suggesting that all are adequately meeting their energy demands.

Defining hunting success is subjective (Schaller, 1972; Mills, 1990). In the KTP, hunting was defined as the moment the predator was noted, either visually or by spoor, to have run towards the prey. Using this criterion, the data in Table 4 show a significant difference in the ratio of successful to unsuccessful chases ($\chi^2 = 34.47$, d.f. = 3,

$P < 0.0001$), with lion, cheetah and spotted hyaena hunting success being similar, but leopard lower. This might be overcome to an extent by the leopard's broader diet (it has the most prey species making up more than 5% of its diet from the smallest kill sample). On the other hand, the leopard appears to exist at the lowest density of the large carnivores in the KTP (Table 1), and may therefore be the least well adapted species to this area. As hunting plays an insignificant role in the brown hyaena's foraging behaviour, at least in the arid Kalahari, it was omitted from this analysis.

INTERSPECIFIC RELATIONS

Because of the relatively low densities of the large carnivores in the KTP, interactions between the species are comparatively rare, but that does not necessarily mean that they are trivial.

The spotted hyaena and the lion are potentially serious competitors, as they have the largest measure of overlap in diet and activity regime. Interactions between lions and spotted hyaenas in the KTP, although infrequent, are intense. In the spotted hyaena study (Mills, 1990), 33 interactions between these two species were observed; 20 around food and 13 away from food. Some interactions lasted over an hour, especially when initiated by spotted hyaenas, as was the case in 64% of the interactions. Lions twice lost almost an entire carcass to hyaenas and hyaenas lost one to lions, in the remaining interactions the amount of food at stake was insignificant. In two instances lions killed a spotted hyaena cub.

When spotted hyaenas were the initiators of an interaction, the impression gained was that they were attempting to move the larger competitors away from the area, and were prepared to take risks to achieve this. It seems that in the KTP spotted hyaena/lion interactions are not as one-sided as they are in a highly productive area like the Ngorongoro Crater, where lions are clearly dominant (Kruuk, 1972). Perhaps in this arid region, where food resources are thinly distributed, the loss or gain of a kill is a more significant event. The smaller spotted hyaena has more to lose if lions steal a kill in the arid Kalahari than Ngorongoro and, therefore, is more prepared to take the risk of standing up to lions.

The low spotted hyaena density in the KTP results in few interactions between them and leopards and cheetahs. Only three kills were observed to be stolen from leopards in the spotted hyaena study (Mills, 1990) and one in the leopard

study, although on two occasions, spoor suggested that a large male leopard kept two spotted hyaenas away from its kill (Bothma & le Riche, 1984). Five cheetah kills, four at night, were taken by spotted hyaenas in the spotted hyaena study, and four, all at night, in the cheetah study, although in one case the cheetahs had all but finished eating. At least seven of these encounters took place within about 1 km from a spotted hyaena den.

The brown hyaena may lose food to the spotted hyaena through being displaced, or because spotted hyaenas locate a carcass before brown hyaenas do. Additionally, away from food spotted hyaenas may harass brown hyaenas and occasionally kill one. However, the brown hyaena outnumbered the larger and dominant spotted hyaena by about 2:1 in the KTP, so the detrimental effects of these interactions are localized, and mainly take place in the vicinity of spotted hyaena dens. A difference was found in the ratios with which these two species were counted in two areas. More spotted hyaenas (8.3:1) were counted in the core area of a spotted hyaena clan, whereas in an equal-sized area where there was no spotted hyaena den, the ratio was 0.5:1 (Mills, 1990).

The numerical dominance of the spotted hyaena in most African ecosystems is diminished in the arid Kalahari, and the rarer brown hyaena is better able to survive in an area where food resources, especially large ones, are scarce. However, the fact that even in the arid Kalahari the spotted hyaena appears to impact on the brown hyaena, at least locally in the vicinity of spotted hyaena dens, may explain the limited distribution of the brown hyaena and its exclusion from areas of higher rainfall. Once the spotted hyaena has the resources to reach higher densities, it is apparently able to limit the brown hyaena. It has been speculated that in the Kruger National Park an increase in spotted hyaena numbers, due to management interventions, may have led to the local extinction of the brown hyaena (Mills & Funston, 2003).

The brown hyaena derives considerable benefit by scavenging from lion kills in the KTP. Not only were 43% of the carcasses of known origin scavenged by brown hyaenas killed by lions, but the amount of food gained was relatively high, as these were large ungulates. On the other hand, lions may attack and kill or maim a brown hyaena (Apps, 1982), but this is rare. On balance, it would seem that the brown hyaena gains more than it loses from the presence of the lion in the KTP. In

the case of the leopard, neither species is influenced by the presence of the other, but the cheetah is an important contributor of food to the brown hyaena, especially along the riverbeds where springbok remains are frequently scavenged. However, only 6% ($n = 121$) of cheetah springbok kills observed during the intensive cheetah study were kleptoparasitized by a brown hyaena, and the hyaenas mostly ate the remains after the cheetahs had departed. The diurnal hunting behaviour of the cheetah and the nocturnal activity regime of the brown hyaena is a major reason for this; an example where temporal activity partitioning is important.

The cheetah (together with the wild dog) is often considered to be the most vulnerable of the large African carnivores to competition with larger carnivores, especially the lion and spotted hyaena (Durant, 2000; Laurenson, 1994). However, although predation on small cheetah cubs in the KTP is high, lions and spotted hyaenas were not found to be the culprits and a range of smaller carnivores including black-backed jackals and honey badgers *Mellivora capensis* were suspected. Cheetah cub survival in the KTP is considerably higher than in the Serengeti (where factors other than lion predation are also an important consideration) (Mills & Mills, 2013b). Furthermore, energetically the cheetah is better able to deal with kleptoparasitism than the wild dog (Scantlebury *et al.*, 2014) and the incidence of kleptoparasitism for cheetahs in the KTP is low; only 6.1% of carcasses were stolen, with an average percentage loss of meat of 65% per kill. Direct killing of cheetah adults by other carnivores was also found to be low; only two instances were observed, both by leopards, and both cheetahs were probably injured beforehand.

Interspecific interactions between carnivores has been held up as a major cause of density differences between large and smaller species (Ritchie & Johnson, 2009). In Africa, this has been especially well illustrated in the case of the wild dog (Creel & Creel, 1996; Mills & Gorman, 1997). However, the relative densities of carnivores are also determined by other factors. The availability of resources, not just the biomass of prey (Hayward *et al.*, 2007), but also the structure of the prey community is crucial. Arid ecosystems have a dominance of smaller-sized herbivores, while the more mesic savanna ecosystems are dominated by larger-bodied herbivores (East, 1984; Fritz & Duncan, 1994). When these are in short supply, it

may even up the differences in relative densities between large and smaller carnivores.

CONCLUSION

A major difference between the dynamics of large carnivore communities in mesic compared to arid savannas like the arid Kalahari, is that larger carnivores are not the numerically dominant species in the arid systems as they are in the more mesic systems. Furthermore, the wild dog seems to be the first species to disappear as aridity increases, and the brown (and in the north, the striped) hyaena appears. In the KTP, the generalist brown hyaena is numerically the dominant species.

Resource partitioning appears to be more acute in arid systems. Where prey is less abundant, dietary selection becomes more finely tuned, and each species tends to concentrate on the prey species and foraging strategy it is best adapted to utilize. For example, the cheetah, because of its superior acceleration, and ability to successfully follow the rapid twist and turns of fleeing steenbok (Wilson *et al.*, 2013), is the major predator of this wide ranging and common species in the arid Kalahari. The brown hyaena, with its ability to move long distances, is the chief scavenger, whereas the spotted hyaena hunts more and scavenges less than it does in areas where the brown hyaena is absent, such as the Kruger National Park. In the Kruger National Park, the spotted hyaena broadens its diet, taking on more of a scavenging role (Henschel & Skinner, 1990; Mills & Biggs, 1993). At the same time, some species show flexibility in diet and are able to make use of prey that, although abundant in other systems, are not often killed, e.g. porcupines by lions and leopards, and springhares by cheetahs.

Interspecific relations between carnivores in arid systems may also take on a different dynamic than in more mesic savannas. Whereas in the latter the largest and numerically dominant carnivores contributed the major share of animals killed across a wide size range (Owen-Smith & Mills, 2008a; Sinclair *et al.*, 2003), this is more equitably shared by the predator community in arid areas. Additionally, high rates of food loss by smaller carnivores (e.g. in the Ngorongoro Crater) where lions stole much food from spotted hyaenas (Kruuk, 1972), has not been recorded in the arid Kalahari. The relationship between the lion and the brown hyaena in the arid Kalahari is also an unusual example of a smaller carnivore deriving considerable benefit from a larger one.

Clearly arid regions are important habitat for large carnivores. Their flexibility to adapt foraging behaviour and the varied nature of the relationships between the species are aspects of functional biodiversity that need to be conserved. Because of the extent to which arid regions cover Africa, more attention should be given to research and conservation in these areas. As has been pointed out by Durant *et al.* (2014), the restoration of desert ecosystems will not only benefit biodiversity, it may also help to mitigate against global climate change if it leads to increasing aridity.

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