Prey preferences and dietary overlap amongst Africa's large predators

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Africa supports Earth's richest assemblage of large predators, which coexist despite a high degree of dietary overlap. This study used reviews of the prey preferences of African wild dog *Lycaon pictus,* cheetah *Acinonyx jubatus,* leopard *Panthera pardus,* lion *P. leo,* and spotted hyaena *Crocuta crocuta* to investigate the degree of dietary overlap and dietary niche breadth amongst the guild. Wild dogs and cheetahs exhibited the greatest dietary overlap and smallest dietary niche breadth, while lions exhibited the least dietary overlap and, with leopards, had the broadest dietary niche breadth. Increased extinction risk within the guild was related to lower dietary niche breadth. The behavioural and morphological specializations of the two most threatened predators (wild dogs and cheetahs) limit the prey available to them, and increases the potential for dietary competition. Conversely, the large body mass and group hunting strategy of lions and the predatory flexibility of leopards and spotted hyaenas minimizes the effects of dietary overlap, assuring a more secure status. This study intimates reasons why cheetahs and African wild dogs are naturally less common than lions, leopards and spotted hyaenas in unmodified landscapes. The methods used can be applied to all adequately studied faunal guilds and could highlight previously undetected competitors.

Key words: conservation ecology, exploitation competition, extinction, optimal foraging, prey preferences, predation, threatening processes, top-down/bottom-up limitation.

INTRODUCTION

Both interference and exploitation competition have long been recognized as important in shaping the ecological relationships of large carnivores (Kruuk 1972; Schaller 1972); however, carnivore populations are generally limited by their food supply (Macdonald 1983). Competition theory suggests that species that differ sufficiently in body mass do not compete (Hutchinson 1959; Wilson 1975). Larger predators are thought to utilize food unavailable to smaller predators *via* a competitive advantage, which can be enhanced or diminished by prey size distribution and carrying capacity (Wilson 1975). Furthermore, where appropriately sized prey is not limited, selective predation is thought to facilitate large carnivore coexistence (Karanth & Sunquist 1995).

The morphological partitioning of body masses of the five large African predators should reduce dietary overlap (and therefore competition); however, group-hunting strategies within the guild may confound this prediction. Habitat partitioning and partitioning of prey in the Serengeti are thought to minimize the extent of exploitative competition to minor levels (Bertram 1979), but elsewhere the extent of competition is unknown (Sunquist & Sunquist 1997). Yet interspecific competition is more intense among large carnivores than smaller ones because prey are difficult to capture and represent a large quantity of food, which is worth stealing and defending (Xiaoming *et al.* 2004). Similarly, the significant, positive linear relationship between predator density and the biomass of their preferred prey (van Orsdol *et al.* 1985; Fuller *et al.* 1992; Laurenson 1995; Stander *et al.* 1997; Hayward *et al.* 2007d) highlights that food is a limiting factor to population growth and hence, exploitative competition theoretically occurs. Furthermore, the smallest of Africa's large predators are considered to be threatened by competition and predation from the largest (Laurenson 1995; Creel & Creel 1996; Carbone *et al.* 1997; Mills & Gorman 1997; Gorman *et al.* 1998; Vucetich & Creel 1999; Durant 2000), which weigh up to an order of magnitude more. Finally, all large African carnivores face similar levels of human persecution

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(Smuts 1978; Creel *et al.* 2001), yet some are inherently rarer than others (Vucetich & Creel 1999). All this suggests that dietary overlap and food limitation occur and may be a threatening process.

Lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) are considered the most intense competitors (Mills & Harvey 2001), killing similar prey at similar times of the day when in sympatry (Mills & Biggs 1993; Hayward 2006; Hayward & Hayward 2007). They consistently show a high level of aggression toward one another, even when no food is present (Kruuk 1972; Mills 1984), although there is no evidence that this competition limits population sizes.

In the riverbeds of the Kalahari, leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*) share springbok (*Antidorcas marsupialis*) as their major prey species (Mills 1984). Cheetahs select adults while leopards take more subadults, which partition the prey community. Cheetahs also suffer from interactions with lions *via* direct intraguild predation (Caro 1994; Laurenson 1994; Laurenson 1995; Laurenson *et al.* 1995), which leads to a negative relationship between recruitment and lion density (Durant *et al.* 2004; Hayward *et al.* 2007b) and causes cheetahs to find refuges from competition and predation (Durant 1998). Kleptoparasitism, disease and human interference are also threats to cheetahs inside protected areas; however, habitat loss and direct exploitation are threats outside (Mills & Biggs 1993; Caro 1994; Marker-Kraus & Kraus 1997).

African wild dogs (*Lycaon pictus*) that survived human persecution during the mid-20th Century (Bere 1956; Attwell 1959) were subsequently threatened by habitat loss, human-caused mortality, disease and interference competition with lions and spotted hyaenas (Fanshawe *et al.* 1991; Creel & Creel 1996; Gorman *et al.* 1998; Vucetich & Creel 1999; Woodroffe & Ginsberg 1999). While large African predators suffered similar levels of human persecution, ecological factors limit wild dog populations to smaller sizes than sympatric members of the guild (Creel *et al.* 2001). The impacts of competition on wild dogs occur *via* direct predation, interference competition at kills, diminished prey populations, and exclusion from areas of high prey density (Mills & Gorman 1997; Creel *et al.* 2004). While larger packs are better able to defend themselves and their kills from lions and hyaenas (Fuller & Kat 1990), optimal foraging by larger packs is likely to lead to larger prey being taken (Hayward *et al.* 2006c), increasing the threat of exploitative competition to wild dogs.

The primary aim of this study was to determine which members of Africa's large predator guild potentially compete for food. We then investigate how this is related to their conservation status. We predict that lions and spotted hyaenas would exhibit the greatest degree of dietary overlap, as they are considered the fiercest of competitors in the guild (Mills & Harvey 2001). We also predict that subordinate members of the guild would suffer higher levels of potential dietary overlap as they have similar preferred prey and preferred prey weight range (Sinclair *et al.* 2003; Radloff & du Toit 2004). It would be attractive to extend this analysis to other large carnivores from other continents; however, the lack of a common prey base would make subsequent niche breadth analyses impossible. We stress from the outset that this is a correlative, rather than manipulative, study and issues of causation may be problematic, hence we focus on the *potential* for exploitation competition to occur.

Behavioural and morphological adaptations to preferentially prey on a species have occurred on an evolutionary timescale. While evolution acts on individuals, mechanisms to minimize factors shaping evolution (competition, predation, etc.) are manifested as adaptations of species, rather than populations. Furthermore, prey vulnerability to one particular predator is not related to the presence of sympatric predators, rather to behavioural and morphological adaptations of both predator and prey. Hence, we have investigated the dietary overlap (and therefore the *potential* for exploitation competition) from the perspective of the species rather than individual populations. We reiterate that it is only *via* manipulative experimentation that the true nature of competition within guilds will be revealed.

METHODS

Numerous resource states (niche axes) can be used to investigate competition among species (Krebs 1989); however, food appears to be the most obvious for sympatric predators. We reviewed all published work on the prey and prey preferences of African wild dogs (Hayward *et al.* 2006c), cheetahs (Hayward *et al.* 2006b), leopards (Hayward *et al.* 2006a), lions (Hayward & Kerley 2005) and spotted hyaenas (Hayward 2006), which provided data with which to estimate the potential for dietary overlap (and hence *potential* competition) between these species. The location and timing of studies used to determine prey preferences of Africa's large predators and the number of kills recorded in each are presented as Appendix 1; however, each occurs in savanna biomes where these predators and their prey evolved in sympatry.

These studies determined preference using Jacobs' index (Jacobs 1974):

$$D = \frac{r-p}{r+p-2rp},$$

where r is the proportion of a predator's total kills of a certain prey species at a site and P is the proportional abundance of that prey species. A Jacobs' index value was calculated for each prey species that has been recorded frequently occurring in sympatry with the five large predators at each site. Hence, these reviews investigated the species-specific diet of each predator, rather than the site- or population-specific diet.

In this study, the standardized (+1 to ensure non-negative values) mean of these Jacobs' index values for each prey species of each predator were then used as an index of prey preference and are referred to as 'preferred prey'. The mean of the relative percentage of kills of each prey species at each site was then calculated from the reviews and are referred to as 'actual prey' (Table 1). Both of these data sources (preferred and actual) were used to calculate dietary niche overlap (% and Pianka's index) and Levin's niche breadth (Krebs 1989). Friedman's non-parametric ANOVA was used to test for differences in the ranks of dietary overlap of each predator. The species pair with the greatest overlap were each ranked 1, and so on down to the pair with the least overlap.

The niche breadth values were then plotted against the estimated total number of extant individuals of each species and a categorical variable of the IUCN status of each species and analysed using Spearman's rank order correlation (Zar 1996). The endangered African wild dog (McNutt *et al.* 2004) was given an extinction status value of 1, the vulnerable cheetah (Cat Specialist Group 2004a) and lion (Bauer *et al.* 2004) as 2, the lower risk but conservation-dependent spotted hyaena (Hyaena Specialist Group & IUCN 2004) as 3, and the leopard, which is of least concern (Cat Specialist Group 2004b) was categorized as 4 (Table 2). Cheetahs (2.0) were given a higher risk of extinction within the vulnerable category than lion (2.5) based on its smaller population size, relative rarity, continued decline and longer time listed as vulnerable to extinction (Bauer *et al.* 2004; Cat Specialist Group 2004a). We consider these conservation status categories as good proxies for use in this analysis as they correlate strongly with estimated number of individuals of each species surviving (Spearman's $R = 1$) and period of listing at current threat level ($R = -0.78$) based on IUCN (2004) species evaluation reports. Because we use Spearman's rank order correlation, the results will not vary with minor variation in the rank of lions, as long as they are considered more threatened than hyaenas and less threatened than cheetahs, as this test functions by ranking each data point (Zar 1996).

RESULTS

African wild dogs and cheetahs exhibited the greatest dietary overlap on their actual diets (73.5%), followed by cheetahs and leopards (68.7%), wild dogs and leopards (65.7%), and lions and spotted hyaenas (59.9%). Based on actual diet, lions exhibited the least amount of overlap with wild dogs (31.6%), leopards (39.1%) and cheetahs (42.5%; Table 2).

Based on what Africa's large predators prefer to prey on, African wild dogs and cheetahs still exhibited the greatest percentage potential dietary overlap (72.2%), followed by cheetahs and leopards (67.7%), wild dogs and leopards (66.6%), and lions and spotted hyaenas (63.4%). Lions exhibited the least amount of overlap of preferred prey with wild dogs (41.0%), cheetahs (43.7%) and leopards (48.3%).

There were significant differences between Africa's predators over what they actually prey on based on Pianka's niche overlap (Friedman's ANOVA $\chi^2_4 = 13.20$, $P = 0.01$) with wild dogs exhibiting most overlap (mean rank = 4), followed by cheetahs (4.75), leopards (5), spotted hyaenas (5.5) and lions (8). There were also significant differences in Pianka's niche overlap in what Africa's predators prefer to prey on (Friedman's ANOVA $\chi^2_4 = 10.53$, $P = 0.03$) with wild dogs exhibiting most overlap (mean rank = 3.5), followed by spotted hyaenas (4.75), cheetahs (5.25), leopards (6.75) and finally lions (7.25; Fig. 1). Wild dogs and cheetahs had the greatest overlap based on Pianka's index, with leopards and lions having the least (Fig. 1; Table 2).

Lions had the broadest actual dietary niche breadth (Levin's niche breadth = 14.36), followed by leopards (10.53), spotted hyaenas (9.09),

Table 1. Main actual and significantly preferred prey of Africa's large predator guild (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006a; Hayward *et al.* 2006b; Hayward *et al.* 2006c) showing mean percentage of kills and Jacobs' index from all studies ± 1 S.E.

	African wild dog	Cheetah	Leopard	Lion	Spotted hyaena
Main prey at sites where they occur (actual) (% ± 1 S.E.)	Thomson's gazelle, *Gazella thomsoni* (62 ± 9%)	Thomson's gazelle (53 ± 9%)	Impala (48 ± 6%)	Springbok (29 ± 15%)	Gemsbok (64 ± 9%)
	Impala, *Aepyceros melampus* (42 ± 6%)	Impala (32 ± 5%)	Thomson's gazelle (33 ± 10%)	Kob, *Kobus kob* (28 ± 14%)	Impala (28 ± 8%)
	Kudu, *Tragelaphus strepsiceros* (24 ± 4%)	Springbok, *Antidorcas marsupialis* (30 ± 15%)	Nyala (19 ± 9%)	Blue wildebeest, *Connochaetes taurinus* (26 ± 4%)	Thomson's gazelle (21 ± 10%)
	Nyala, *T. angasi* (12 ± 8%)	Grant's gazelle, *G. granti* (15 ± 5%)	Springbok (17 ± 16%)	Gemsbok, *Oryx gazelle* (23 ± 12%)	Blue wildebeest (27 ± 7%)
			Common duiker (11 ± 3%)	Buffalo, *Syncerus caffer* (20 ± 4%)	Nyala (15 ± 10%)
Significantly preferred prey species (preferred) (Jacobs' index value)	Kudu (0.35 ± 0.10)	Blesbok, *Damaliscus dorcas phillipsi* (0.62 ± 0.07)	Impala (0.36 ± 0.08)	Gemsbok (0.70 ± 0.06)	No significantly preferred prey species
	Thompson's gazelle (0.68 ± 0.13)	Impala (0.11 ± 0.08)	Bushbuck (0.45 ± 0.12)	Buffalo (0.32 ± 0.10)	
	Impala (0.25 ± 0.09)	Thompson's gazelle (0.50 ± 0.10)	Common duiker (0.42 ± 0.11)	Zebra, *Equus burchelli* (0.16 ± 0.07)	
	Bushbuck, *T. scriptus* (0.36 ± 0.15)	Grant's gazelle (0.59 ± 0.10)		Giraffe, *Giraffa camelopardalis* (0.24 ± 0.10)	
		Springbok (0.14 ± 0.11)			
Preferred prey weight range	16–32 and 12–140 kg	23–56 kg	10–40 kg	190–550 kg	56–182 kg
Total number of species used to assess prey preferences	45	58	111	42	30
Total sites used to assess prey preferences	18	23	33	32	15

Table 2. IUCN status category of each predator (see text) and the rank of the degree of preferred (P) and actual (A) dietary niche overlap (% and Pianka's index) and Levin's dietary niche breadth. The overlap, dietary niche breadth and level of endangerment are ranked from highest (rank = 1) to lowest (5).

	African wild dog		Cheetah		Lion		Spotted hyaena		Leopard	
Estimated number of individuals surviving today (IUCN 2004)	3000–5500		7500–10 000		23 000		27 000–47 000		>50 000	
IUCN conservation concern status (IUCN 2004)	Endangered		Vulnerable		Vulnerable		Conservation dependent		Least	
IUCN status rank	1		2.0		2.5		3		4	
	P	A	P	A	P	A	P	A	P	A
% overlap	2	2	1	1	5	5	2	3	4	3
Pianka's overlap	1	1	3	1	5	5	2	4	4	3
Dietary niche breadth	5	5	4	4	2	1	3	3	1	2

cheetahs (8.36) and African wild dogs (5.72; Fig. 2). Leopards have the broadest dietary niche breadth of preferred prey (Levin's niche breadth = 25.93) followed by lions (23.08), spotted hyaenas (21.83), cheetahs (18.43) and African wild dogs (15.08; Fig. 2).

Increasingly threatened predators have smaller preferred dietary niche breadths than secure predators, based on correlations between niche breadth and IUCN status and extant population size (Spearman's rank order correlation $R = 0.900$, $n = 5$, $P = 0.037$ for both; Fig. 3). A similar relationship exists for the actual dietary niche breadth of each predator and their conservation status/extant population size, although this is not significant ($R = 0.700$, $n = 5$, $P = 0.188$; Fig. 3).

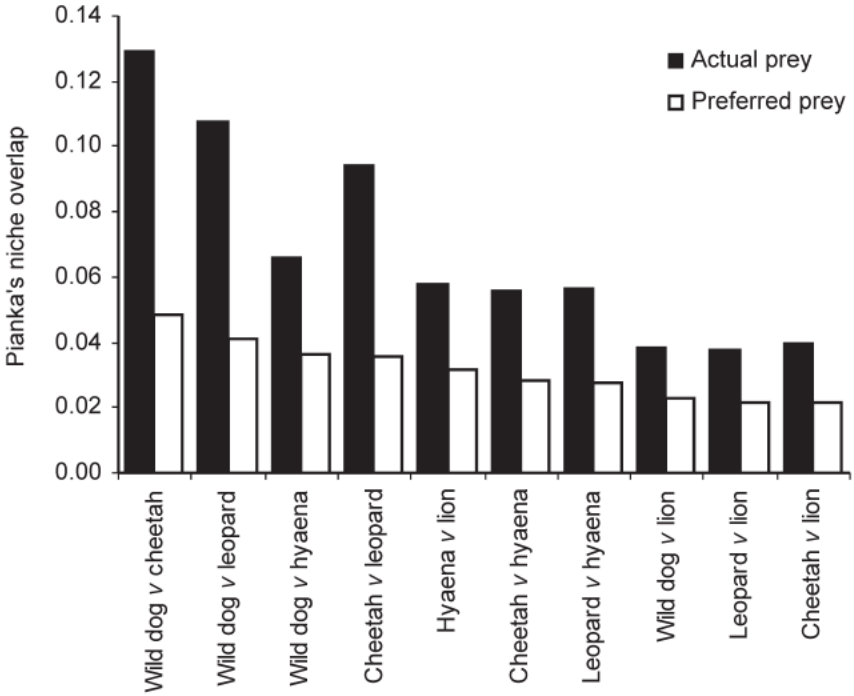

Fig. 1. Pianka's dietary niche overlap amongst Africa's large predator guild.

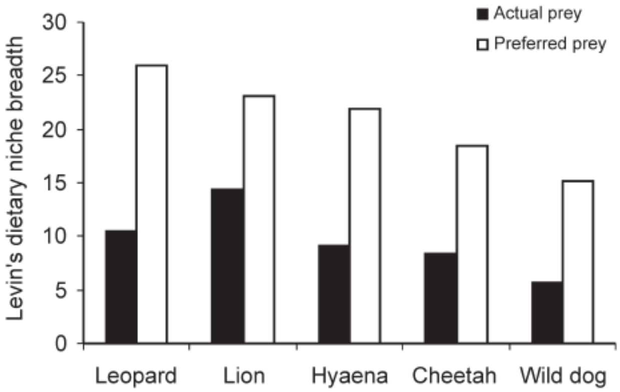

Fig. 2. Levin's niche breadth measure for Africa's large predator guild.

DISCUSSION

These results suggest that Africa's large predators have evolved amidst a battle for food and modern changes to prey dynamics are now affecting the conservation status of the most specialized. The predators with the smallest preferred dietary niche breadth have the fewest remaining members and are the most threatened (Fig. 3). These also suffer from the greatest degree of preferred and actual diet overlap (Fig. 1). Resource use overlap does not necessarily provide evidence of exploitative competition unless food is a limiting factor (Wiens 1989; Macdonald & Thom 2001; Melero *et al.* 2008). The density of each of Africa's large predators exhibits significant, positive linear relationships with the biomass of their preferred prey (van Orsdol *et al.* 1985; Fuller *et al.* 1992; Laurenson 1995; Stander *et al.* 1997; Hayward *et al.* 2007d) indicating that food must be a limiting resource for each species. Thus the relationship between dietary niche breadth and surviving population size/risk of extinction in large African predators is compelling and provides theoretical reasons for their inherent rarity in areas protected from other threatening processes (Vucetich & Creel 1999).

African wild dogs in unmodified areas are at least an order of magnitude scarcer than lions or

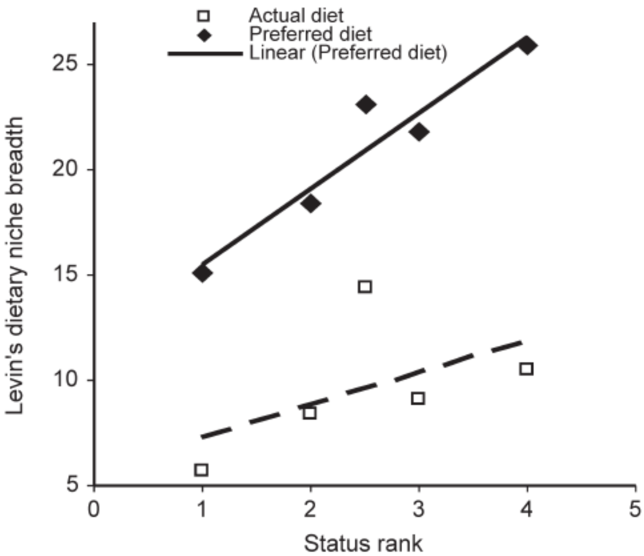

Fig. 3. Increasingly threatened predators have smaller preferred (R = 0.900, P = 0.037) and actual (R = 0.700, P = 0.188) dietary niche breadths when their IUCN conservation status is plotted against their niche breadth. 1 = endangered (African wild dog), 2 = vulnerable (2.0 for cheetah and 2.5 for lion), 3 = lower risk – conservation dependent (spotted hyaena); and 4 = least concern (leopard). Exactly the same relationship exists when estimated surviving population size of each species is plotted against niche breadth (R = 0.900; P = 0.037).

hyaenas (Creel & Creel 2002). The current theory for this natural scarcity is that interference competition and intraguild predation by lions and spotted hyaenas forces wild dogs to exist at low densities (Creel *et al.* 2001). Two lines of evidence are used to support this. Firstly, there is a significant negative correlation throughout Africa between wild dog density and that of lions and spotted hyaenas (Creel & Creel 1996) that has been linked to intraguild predation and consequent spatial avoidance (Mills & Gorman 1997; Creel & Creel 2002). Secondly, long-term data from the Serengeti shows that wild dogs were most abundant in the 1960s and 1970s when lion and hyaena density was low, and wild dogs declined to extinction when lion and hyaena densities doubled in the proceeding two decades (Creel *et al.* 2001).

Yet these two trends can be similarly explained by changes in prey dynamics. Firstly, lions and hyaenas optimally forage on prey much larger than that preferred by wild dogs, but also opportunistically forage on smaller species (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006c) and, given the relationships between predator density and prey biomass, when the preferred prey of these species increases in abundance so will the predators (van Orsdol *et al.* 1985; Fuller *et al.* 1992; Hayward *et al.* 2007d). Secondly, the extinction of the Serengeti wild dog population may be reinterpreted in light of this new evidence suggesting food limitation may have been a factor. An increase in wildebeest and zebra density (Borner *et al.* 1987; Ottichilo *et al.* 2000) – lions' and hyaenas' preferred prey species or size (Hayward & Kerley 2005; Hayward 2006); led to a corresponding increase in these two predators – wild dog's competitors; and corresponded with a decline in Thomson's gazelle (Borner *et al.* 1987; Ottichilo *et al.* 2000) – wild dog's preferred prey (Hayward *et al.* 2006c). The increasingly abundant wildebeest and zebra are above the preferred prey weight range of wild dogs (Hayward *et al.* 2006c) and would therefore have been preyed on inefficiently or suboptimally by wild dogs – a species whose energetic requirements demand optimal foraging (Gorman *et al.* 1998). The decline of the preferred prey species of the wild dogs placed them under increasing pressure and they ultimately went locally extinct. The energetic limitations of the wild dog means that sub-optimal foraging threatens the persistence of populations and exacerbates pack size limitations (Courchamp & Macdonald 2001).

Wild dogs are considered endangered by habitat fragmentation, human persecution, and interference competition with larger carnivores (Woodroffe & Ginsberg 1997). Food limitation, and potential exploitative competition, may now be added to that list, particularly in conservation areas that are free from habitat alteration and human persecution but where management strategies have led to unnaturally high population densities of all predators which reduce the availability of competition refuges.

This paper presents relationships, not causation. In practice, it is difficult to show that competition affects the population dynamics of a species (Creel *et al.* 2001) and only manipulative experimentation is likely to determine the causes of the inherent relative rarity of some large predators. The value of this study is that predictive hypotheses can be developed that can subsequently be tested (Table 3). Cheetahs and wild dogs are predicted to decline in numerical abundance *via* exploitation and interference competition with the increase or introduction of dominant competitors. They will also increase their use of suboptimal prey until such time as their numbers equilibrate to the new, reduced carrying capacity. They will show similar, but smaller and more specific changes to increases or introductions of other subordinate competitors. Although intense competitors, there is no evidence that lions and hyaenas limit each other's population abundance and so there is no predicted response. Leopards prefer and take prey smaller than that of other guild members and this, coupled with their use of denser habitats and adaptability, suggests they will be largely unaffected by variation in competitor levels. The rationale behind these predictions is that dietary overlap is likely to increase during periods of relative prey scarcity at individual sites (Pyke *et al.* 1977; Krebs 1978), even though strong directional selection resulting from interspecific competition produces adaptations most suited for resources that are used most exclusively by individual species (Schoener 1982). *Post-hoc* manipulative experiments are possible using data from the large number of sequential predator reintroductions occurring in southern Africa (Hayward *et al.* 2007a; Hayward *et al.* 2007b).

Cheetahs are most threatened by habitat loss, which reduces the availability of suitable prey and subsequently hunting success, and increases cub mortality and interference competition (Marker & Penzhorn 1998; Frame 1999). Interactions with larger predators also threaten cheetahs in the Serengeti (Laurenson 1995); however, the influ-

Table 3. Predicted predatory behavioural and functional responses of members of Africa's large predator guild to population increases and competitor additions. Dominant predators are lion and spotted hyaenas. We predict the opposite responses to those described below to population declines and species removals.

Species	Competitors added or increasing	Predicted behavioural response	Predicted functional response
Wild dog	Dominant competitors	Decreasing preference for main prey species and increase in number of prey species killed	Decrease in population size *via* both interference and exploitation competition
	Cheetah	Decreasing preference for main prey species weighing less than 56 kg. A slight increase in preference for larger prey	Minor decrease in population size *via* exploitation competition
Cheetah	Dominant competitors	Decreasing preference for main prey species and an increase in prey outside the 23–56 kg range, although this is tempered by the morphological limitations of the cheetah	Minor decrease in population size *via* exploitation competition
Leopard	All other members of the guild	Little discernible change	Little discernible change
Lions and hyaenas	All other members of the guild	Little discernible change	Little discernible change

ence of lion predation on cheetah cubs is far less influential in other environments (Broomhall 2001) and is likely to be a natural ecological process (Mills 2005). Food limitation, possibly *via* dietary competition with wild dogs, may now also be considered.

Wild dogs and cheetahs are the two most threatened of Africa's large carnivore guild based on the reasons for their IUCN listings. Their relatively large body mass facilitates obligate predation on large vertebrates (Carbone *et al.* 1999); however, their morphological and behavioural specializations (Hayward *et al.* 2006b; Hayward *et al.* 2006c) have resulted in a narrowed dietary niche breadth (than expected based on body mass) which exacerbates competition for food. The similar diurnal activity pattern exhibited by these two competitors intensifies the potential for competition between them.

Lions are largely incompatible with the large-scale, extensive agricultural practices existing today and direct persecution from humans has led to their virtual restriction to conservation areas (Bauer *et al.* 2002; Ogada *et al.* 2003). Their large group sizes and overt nature make them relatively easy to be exterminated by humans. The threat of human persecution, rather than food limitation, has brought about the decline in lions. Lions have the least dietary overlap as they fill a largely vacant niche at the upper end of Africa's predator guild (Hayward & Kerley 2005). These results also confirm local patterns of predation in observed in individual ecosystems (Sinclair *et al.* 2003).

Spotted hyaenas also suffer from human persecution and prey loss but, like leopard, they are nocturnal (Hayward & Hayward 2007), more secretive and therefore interact with humans less frequently. Both spotted hyaenas and lions have very rich and varied diets (Hayward & Kerley 2005; Hayward 2006) and competition does not appear to affect them (Table 2).

Cheetahs and wild dogs overlap in prey species more intensely than Africa's two dominant predators (Figs 1 & 2). That the cheetah is less threatened than the wild dog is probably because wild dogs exists at the very edge of their physiological capabilities, where even a minor reduction of energy intake leads to impossibly excessive energy outputs necessary in hunting to satisfy its high metabolic requirements (Gorman *et al.* 1998). This suggests that the species lacks the resilience to cope with a reduction in available food resources caused by high dietary overlap with other members of the guild, and its population sizes are limited accordingly.

While exploitative competition is likely to be evident in structuring the large African carnivore community (Durant 2000), the effects may have been concealed from previous researchers by more obvious interference interactions at individual sites (*e.g.* Laurenson 1995; Mills & Gorman 1997). This may have occurred because of the low densities that wild dogs and cheetahs exist at where they are sympatric, the infrequency of such sympatry, and the far more obvious impact on each from dominant competitors. We also suggest there has been an overemphasis on interference competition because it may be more evident and may be ultimately caused by food limitation. Cheetah cub mortality is dependent on the mother's vigilance and anti-predator behaviour (Laurenson 1994); however, when the mother is forced to spend excessive time foraging (due to exploitation competition) then she will have less time available to protect her cubs. Similarly, wild dogs that have to forage for longer can ill afford additional pup guards.

Indeed, if interference competition were the primary factor affecting the population dynamics of Africa's large predator guild, then it is hard to imagine how cheetahs and wild dogs will persist under the continuing threat from lions and hyaenas given the likely stochastic and genetic problems that will affect their small populations. It is also hard to imagine how such a lop-sided interaction evolved and remains so influential today, given interference competition has affected these species for over a million years. Thus, exploitation competition is a more likely population determinant for all guild members. Essentially, this analysis illustrates that both bottom-up and top-down forces limit the populations of each member of Africa's large carnivore guild, whereas previous research has focused on top-down factors only.

Conflict with human activities largely restricts large carnivores to conservation estate, which must be large and ecologically intact to accommodate them (Vucetich & Creel 1999). The clumping of so many competing predators into restricted spaces, however, may increase the likelihood of interspecific competition by creating artificially high population densities and may inevitably lead to further extinctions. Active management to reduce interspecific competition may be necessary for Africa's large predator guild as space becomes more restricted. Varying the prey species assemblage to favour the preferred prey of more threatened predators may be one mechanism to do this (Hayward *et al.* 2007c).

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Appendix 1. Location and timing of studies used to determine prey preferences of Africa's large predators, the number of kills recorded in each and the information source. Kills were recorded using all available techniques for all study species including scat analysis, incidental observations of carcasses and kills, and continuous follows.

Species	Country	Site	Years/Period	No. kills	Source
Cheetah					
	Kenya	Nairobi National Park	1966	53	Eaton (1974)
			1966–1967	13	Foster & McLaughlin (1968)
			1967–1969	183	McLaughlin (1970)
	Namibia	Etosha National Park	1975–1978	63	Berry (1981)
	South Africa	Hluhluwe-Umfolozi Park	Early 1980s	144	Whateley & Brooks (1985)
		Kalahari Gemsbok National Park	1974–1988	229	Mills (1990)
		Klaserie Private Nature Reserve	1979–1981	27	Kruger (1988)
		Kruger National Park	1956–65 South	458	Pienaar (1969)
			1956–65 Central	417	As above
			1956–65 North	222	As above
			1987–1990	68	Broomhall (2001)
			Early 1990s	61	Mills & Biggs (1993)
		Kwandwe Game Reserve	2003	127	Bissett (2004)
			2004	94	As above
		Madikwe Game Reserve	1996–1998	56	Hayward *et al.* (2006b)
		Phinda Resource Reserve	1992–1996	325	Hunter (1998)
		Pilanesberg National Park	1997	16	Hofmeyr & van Dyk (1998)
		Shamwari Game Reserve	2003	29	Hayward *et al.* (2006b)
			2004	65	As above
			2005	33	As above
		Timbavati Game Reserve	1964–1966	47	Hirst (1969)
	Tanzania	Serengeti National Park	Late 1950s	Only % shown	Wright (1960)
			1965–1966	23	Kruuk & Turner (1967)
			1966–1967	138	Schaller (1968)
			1970s	443	Frame (1986) in Caro (1994)
			Late 1980s	417	Caro (1994)
	Zambia	Kafue National Park	1960–1963	33	Mitchell *et al.* (1965)
	Zimbabwe	Wankie (Hwange) National Park	1969–1973	39	Wilson (1975)
Leopard					
	Kenya	Lakapia Ranches	1989–1995	57	Mizutani (1999)
	Namibia	Kaudom National Park	1990s	131	Stander *et al.* (1997)
	South Africa	Hluhluwe-Umfolozi Park	Early 1980s	64	Whateley & Brooks (1985)
		Kalahari Gemsbok National Park	1974–1988	80	Mills (1990)
			1976–1992	80	Bothma *et al* (1997)
			1976–1983	20	Bothma & le Riche (1984)
		Klaserie Private Nature Reserve	1979–1981	95	Kruger (1988)
		Kruger National Park	1956–65 South	1881	Pienaar (1969)
			1956–65 Central	1808	As above
			1956–65 North	1798	As above
			1973–1975 Sabie River	151	Bailey (1993)
			1973–1975	91	As above
		Nwaswitchaka River	Early 1990s	63	Mills & Biggs (1993)
		Madikwe Game Reserve	1996–1998	26	Hayward *et al.* (2006a)
		Phinda Game Reserve	1992–1998	228	As above
			2002–2005	187	As above
		Shamwari Game Reserve	2004	28	As above
		Timbavati Game Reserve	1964	20	Hirst (1969)
			1965	86	As above
			1966	46	As above
			1967	16	As above
		Waterberg – Melk River	1986–7	60	Grimbeek (1992)
		Waterberg – Naboomspruit	1986–7	18	As above

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Appendix 1 (*continued*)

Species	Country	Site	Years/Period	No. kills	Source
	Tanzania	Serengeti National Park	Late 1950s	Only % shown	Wright (1960)
			1965–1966	55	Kruuk & Turner (1967)
			1968–1971	172	Schaller (1972)
			1972–1973	36	Bertram (1982)
	Zambia	Kafue National Park	1960–1963	96	Mitchell *et al.* (1965)
	Zimbabwe	Wankie (Hwange) National Park	1972–1973	54	Wilson (1975)
Lion					
	Botswana	Savuti, Chobe National Park	Wet season	49	Viljoen (1993)
			Dry season	67	As above
	Kenya	Nairobi National Park	1966	68	Foster & McLaughlin (1967)
			1967	61	As above
			1968–1972	375	Rudnai (1974)
		Masai-Mara Game Reserve	1973–1974	220	Saba *et al.* (1979)
	Namibia	Etosha National Park	1975–1978	110	Berry (1981)
			Unstated	232	Stander & Albon (1993)
	South Africa	Hluhluwe-Umfolozi Park	1965–1968	83	Steele (1970)
			Umfolozi	123	Whateley & Brooks (1985)
			Hluhluwe	102	As above
			1990s	1075	Maddock *et al.* (1996)
		Kalahari Gemsbok National Park	1971–1982	45	Eloff (1984)
			1974–1982	401	Mills (1984)
		Kruger National Park	1956–65 North	3189	Pienaar (1969)
			1956–65 South	3205	As above
			1956–65 Centr.	5792	As above
			1969	1155	Bryden (1976)
			1970	997	As above
			1971	830	As above
			Early 1990s	Only % shown	Mills & Biggs (1993)
			1990s	216	Harrington *et al.* (1999)
		Madjuma Game Reserve	1998	30	Power (2002)
			1999	55	As above
		Phinda Resource Reserve	1992–1996	397	Hunter (1998)
		Timbavati Game Reserve	1964	45	Hirst (1969)
			1965	174	As above
			1966	223	As above
			1967	97	As above
	Tanzania	Lake Manyara	1967–68	61	Makacha & Schaller (1969)
		Ngorongoro	1970–1972	94	Elliott & Cowan (1978)
		Selous	1974	77	Rodgers (1974)
			1993–2002	50	Creel & Creel (2002)
		Serengeti	1950s	Only % shown	Wright (1960)
			1965–1966	110	Kruuk & Turner (1967)
			1966–1969 Masai Pride	552	Schaller (1972)
			1966–1969 All	1007	As above
	Uganda	Queen Elizabeth (Ruwenzori) National Park	Ishashi Pride	35	Van Orsdol (1982; 1984)
			Mweya Pride	24	As above
	Zambia	Kafue National Park	1962–1964	410	Mitchell *et al.* (1965)
	Zimbabwe	Mana Pools National Park	1968–1969	17	Dunham (1992)
			1981–1984	38	As above
			1985–1989	57	As above
Spotted hyaena					
	Botswana	Moremi Game Reserve	1986–1988	93	Cooper (1990)
	Kenya	Aberdare National Park	1986–1987	311	Sillero-Zubiri & Gottelli (1992)
		Masai Mara National Reserve	1988–1995 Jan–Jun	355	Cooper *et al.* (1999)
			1988–1995 Jul–Sep	355	As above

Continued on p. 106

Appendix 1 (*continued*)

Species	Country	Site	Years/Period	No. kills	Source
			1988–1995 Oct–Dec	355	As above
	Namibia	Namib-Nauklauf Park	1976–1977	621	Tilson *et al.* (1980)
			1989	129	Skinner *et al.* (1992)
	Senegal	Niokolo Koba National Park	1995–1996	Only % shown	di Silvestre *et al.* (2000)
	South Africa	Addo Elephant National Park	2004	35	Hayward (2006)
		Hluhluwe-Umfolozi Park	1989	162	Skinner *et al.* (1992)
		Kalahari Gemsbok National Park	1974–1988	346	Mills (1990)
		Kruger National Park	1956–65	170	Pienaar (1969)
			1982–1984	24	Henschel & Skinner (1990)
			Early 1990s	27	Mills & Biggs (1993)
		Mkuze Game Reserve	1989	190	Skinner *et al.* (1992)
		Timbavati Game Reserve	1964	35	Hirst (1969)
			1965	24	As above
			1973–1975	749	Bearder (1977)
	Tanzania	Ngorongoro Crater	1965–1969	240	Kruuk (1972)
			1996–1999	82	Höner *et al.* (2002)
		Serengeti National Park	1965–1969	220	Kruuk (1972)
African wild dog					
	Kenya	Aitong	1989	29	Fuller *et al.* (1995)
	South Africa	Hluhluwe-Umfolozi Park	Early 1980s	85	Whateley & Brooks (1985)
			1992–1994	346	Krüger (1996)
		Kruger National Park	1956–65 South	1399	Pienaar (1969)
			1956–65 Central	422	As above
			1956–65 North	929	As above
			Early 1990s	52	Mills & Biggs (1993)
		Madikwe Game Reserve	1996	69	Hayward *et al.* (2006c)
			1997	76	Hayward *et al.* (2006c)
			1998	78	Hayward *et al.* (2006c)
		Pilanesberg National Park	1999–2001	137	van Dyk & Slotow (2003)
		Shambala Private Game Reserve	2002	56	Rhodes & Rhodes (2004)
		Shamwari Game Reserve	2004	58	Hayward *et al.* (2006c)
			2005	47	Hayward *et al.* (2006c)
		Timbavati Game Reserve	1964–1968	19	Hirst (1969)
	Tanzania	Ngorongoro Crater	1965–1966	50	Estes & Goddard (1967)
		Selous Game Reserve	1993–1999	180	Creel & Creel (2002)
		Serengeti National Park	Late 1950s	100%	Wright (1960)
			1965–1966	42	Kruuk & Turner (1967)
			1966–1969 Migration	131	Schaller (1972)
			1966–1969 Resident	66	As above
	Zambia	Kafue National Park	1960–1963	96	Mitchell *et al.* (1965)
	Zimbabwe	Wankie (Hwange) National Park	1972–1973	75	Wilson (1975)
		Savé Conservancy	1990s	430	Pole *et al.* (2004)

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