Diet of four sympatric carnivores in Savé Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog (*Lycaon pictus*)

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Most populations of wild dogs (*Lycaon pictus*) are declining across southern and southeastern Africa, and in the Savé Valley Conservancy (SVC) the decline appears to be associated with declining populations of prey and increasing numbers of competitors. Identifying the threats to this wild dog population is currently needed to determine the most appropriate conservation actions. We studied the diet composition, breadth and overlap among four sympatric carnivores in SVC: African wild dog, spotted hyaena (*Crocuta crocuta*), lion (*Panthera leo*) and leopard (*Panthera pardus*), using faecal analysis. We found remains of 16 mammalian prey species, ranging from small to large mammals (2–525 kg). The four carnivores had many prey species in common (>70% diet overlap), with impala (*Aepyceros melampus*) consistently the most frequent. The frequency of occurrence of impala, however, was highest in the diets of wild dogs (74%), and wild dogs were found to have the narrowest standardized dietary niche breadth (0.087). The diets also varied significantly in the contribution of different prey-size categories, with large prey (>100 kg) contributing most to the diets of lions and hyaenas, and small prey (<5 kg) to the diet of leopards. With impala populations in decline, competition for prey can explain the observed decline in the less competitive and more specialized wild dog, whose main food resource is shared with a rapidly increasing population of spotted hyaenas and lions in the SVC.

Key words: African wild dog, diet, competition, carnivores, faecal analysis.

INTRODUCTION

Conservancies such as the Savé Valley Conservancy in southern Africa are important in protecting a wide diversity of natural habitats, permitting the reintroduction and effective conservation of a number of wildlife species of conservation concern (Lindsey *et al.* 2009). Due to conflict with human activities, populations of large carnivores in southern Africa in particular, have been largely restricted to conservation estates that are large enough and ecologically intact to accommodate them (Vucetich & Creel 1999). However, the clumping of predators within these restricted spaces is bound to increase interspecific competition among carnivores at high density, potentially leading to local extinctions. Moreover, habitat loss and the restriction of suitable habitats to protected areas can enhance the effects of other critical factors such as diseases (Creel 2001) and human persecution (Woodroffe & Ginsberg 1998). In the Savé Valley Conservancy, created more than two decades ago, populations of some carnivores are on the increase, while prey populations decline, with apparent negative effects on the local population of endangered wild dogs (R.G. Groom, unpubl.). This study seeks to understand the relationships among carnivores in SVC, with regards to their dietary needs, and the population trends of carnivores as well as of their main prey.

Knowledge of a carnivore's diet is important to assess its role in the ecosystem, including the level of competition with other carnivores and impacts on prey populations (Klare *et al.* 2011). Dietary analyses have been vital in the development of many carnivore management plans, especially when economically important or endangered

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carnivores were involved (Klare *et al.* 2011). Among the various techniques used to study the feeding ecology of carnivores (*e.g.* Mills 1992; Pole *et al.* 2004; Davies-Mostert *et al.* 2010), the identification of prey remains in faeces has been widely used (Reynolds & Aebischer 1991) to determine the feeding behaviour of many carnivores in Africa, such as the African wild dog, lion, leopard, spotted hyaena and African golden cat (*Caracal aurata*) (Henschel & Skinner 1990; Sillero-Zubiri & Gottelli 1995; Hart *et al.* 1996; Kruger *et al.* 1999; Breuer 2005).

Dietary studies have contributed to recognize both interference and exploitation competition as important mechanisms shaping ecological relationships among large carnivores (Kruuk 1972; Caro & Stoner 2003). In many situations carnivores have been adversely influenced by other members of the guild, typically the smaller-sized predator (Karanth & Sunquist 1995; Palomares *et al.* 1996; Creel & Creel 1996: Breuer 2005; Hayward & Kerley 2008). The relatively small size of wild dogs makes them particularly vulnerable to competition with spotted hyaenas and lions (Fanshawe & Fitzgibbon 1993; Mills & Gorman 1997), through direct predation of wild dog pups, interference competition at kills, exclusion from areas of high prey density (Mills & Gorman 1997; Creel *et al.* 2004), and diminished prey populations when there is dietary overlap (Jones & Barmuta 1998).

Wild dogs reoccupied the SVC during the early 1990s after being locally extirpated due to persecution by cattle ranchers (Pole 1999). This particular wild dog population can provide insights into the influence of inter-specific competition as densities of competing carnivores (specifically lions and spotted hyaenas) were exceptionally low when wild dogs first re-colonized the area (Pole 1999), and have now increased considerably in recent years. In this study we explore the species' diet composition and overlap, to investigate the extent to which wild dogs, spotted hyaenas, leopards and lions share the pool of prey in the SVC and the potential for exploitation competition. Complementarily, we analysed data from ongoing monitoring initiatives in SVC to update the status and trends of populations of prey and carnivores. Finally we discuss the implications of our results for the conservation of wild dogs in this conservancy.

METHODS

Study area

Savé Valley Conservancy is a privately-owned area of approximately 3490 km^2 in the semi-arid southeast region of Zimbabwe (20°05′S; 32°00′E) (Romanach & Lindsey 2008). Elevation varies from 480 to 620 m, with a gently undulating topography and scattered rocky outcrops. The climate is characterized by a single wet season from November to March, and a long dry season from April to October. Mean annual rainfall varies, within the region and between years, between 300–500 mm (du Toit 1994). The conservancy is bordered primarily by high-density communal land (11 to 82 people per km^2), and some commercial land to the south and east (A. Pole, pers. comm.). Subsistence farmers settled an area of 1051 km^2 during the land reform programme in 2001, restricting the wildlife area in the conservancy to 2439 km^2. In addition to the loss of habitat, the last decade has seen very high levels of poaching in the conservancy (Lindsey *et al.* 2011).

Sample collection

Faecal samples were collected along roads and trails, which all carnivores favour for faecal deposition. Samples were collected in intervals of five or more days, to ensure independence of samples (Davies-Mostert *et al.* 2010). Locations of samples, dates of collection and age of the samples were recorded. Samples were visually categorized into fresh (<1 day old), recent (around 1–5 days old) and old (more than 5 days old) (Breuer 2005). Faeces of the same age were only collected if they were at least 5 km apart (Hart *et al.* 1996). Samples were placed in paper bags with an identity number and stored in a cool, dry place. The identification of the faeces by experts was based on shape, colour, diameter, odour and associated field sign such as tracks and den sites (Breuer 2005). For example hyaena faeces are white when they are dry due to the high bone content constituting their meals, wild dog faeces have a strong smell, lion faeces are segmented with a diameter of at least 40 mm while leopard faeces are smaller than that of adult lion with a diameter of 20–30 mm. Faeces of doubtful identity were excluded from the analysis.

Processing and analysis of faecal samples

Faecal samples were sun-dried for up to four days. Samples were then ground in a mortar, and washed in a 1 mm sieve using hot water, to separate hair, bones, hoof fragments, teeth and other prey components from other organic material. The separated hair was then sun dried and placed in marked envelopes. Samples of hair were then placed in glass Petri dishes, washed in acetone, dehydrated in 100% ethanol, and dried on filter paper (Ramakrishnan *et al.* 1999). Prey identification was based on microscopic characteristics of hairs from observations of scale patterns and cross sections. A reference collection was build up from hair samples collected from known prey species killed by hunters in the SVC, collected from all the parts of the pelage of the prey species. Scale patterns were examined by using hair imprints made in gelatin as described by Keogh (1983). Cross-sections of hair strands were made by adapting the plastic tubing method of Douglas (1989).

Diet composition

We used *relative frequency of occurrence* to interpret dietary composition in terms of the importance of each food item to the overall diet (Loveridge & MacDonald 2003). This was calculated as (r/R), which is the number of times a food item was encountered in the whole sample (r) as a percentage of the total occurrence of all prey species (R). In order to compare the composition of the diets of different carnivores we applied contingency tables and χ^2-tests (all analyses conducted with R). We compared the contribution of the main prey species to each carnivore's diet, and the contributions of each prey category as defined by body size, namely: large prey (>100 kg), medium-sized prey (25–100 kg), small prey (5–25 kg) and very small prey (0–5 kg).

Dietary overlap and breadth

Diet overlap was calculated using Pianka's (1973) index

$$Oab = (\Sigma n\ PiaPib)/(\Sigma nPia^2 \Sigma nPib^2)^{1/2} ,$$

where: O*ab* is diet overlap between species *a* and *b;* P*ia* is the relative frequency of the item *i* found in the diet of species *a*; P*ib* is the relative frequency of *i* found in the faeces of species *b*; and *n* is the total number of prey species in carnivore diet. The index ranges from 0 (no overlap) to 1 (complete overlap). Overlap is generally considered to be biologically significant when the value exceeds 0.60 (Navia *et al.* 2007).

Breadth of diet was calculated using Levins' index in its standardized form as follows

$$B_i = 1/(\Sigma P_i^2) \text{ and } BA = (B - 1) / (n - 1) ,$$

where B_i = the Levins' measure of niche breath, P_i = proportion of occurrence of each prey species in carnivore diet; BA = Levins' standardized niche breath and n = number of prey species in carnivore diet (Levins 1968). Levins' index of niche breadth (B_i) ranges from 1 to n, whereas Levins' standardized niche breadth (BA) ranges from 0 to 1 (Navia *et al.* 2007). Low values indicate diets dominated by few prey items (specialist predators) while higher values indicate generalist diets.

Prey aerial census

Data on prey have been collected annually since 2004 to monitor population trends in the conservancy. A Cessna 206 aircraft was used to conduct all the aerial surveys following methods by Bothma *et al.* (1990). The survey team consisted of a pilot, a scribe and four observers divided into teams of two to count on the right and left-hand sides of the aircraft, within a strip width of 375 m (determined by fixing a streamer to the strut of the aircraft, calibrated to markers on the ground, and flying at 300 feet). A Global Positioning System (GPS) connected to a laptop computer was used to collect real-time data during the ecological aerial survey.

Carnivore spoor counts

The Lowveld Wild Dog project carries out annual counts of large carnivore footprints along transects following standardized methodology based on Stander (1998) and Davidson & Romanach (2007), using road transects that represent a fair coverage of the area. For every 6 to 1 km^2 of sampled area, 1 km of transect was surveyed, creating a penetration density (expressed as a ratio of kilometres of transect surveyed to total sample area) of between 1:6 and 1:7. Each transect was driven at a speed of between 10 and 20 km/h with one tracker sitting on the front of the vehicle scanning for spoor. Transects ranged between 12.6 km and 29.4 km in length, with a mean transect length of 20.6 km. Spoor density (the number of individual animal's spoor per 100 km) was used to estimate animal density per 100 km, as shown by Stander (1998), that spoor density is a close estimation of the true animal density.

RESULTS

Diet composition

A total of 238 faecal samples was collected and analysed: 72 from wild dogs, 78 from hyaenas,

Table 1. Frequency of occurrence of prey species in the carnivores' diets.

Prey	Wild dog (*n* = 72) Frequency of occurrence (%)	Hyaena (*n* = 78) Frequency of occurrence (%)	Leopard (*n* = 67) Frequency of occurrence (%)	Lion (*n* = 21) Frequency of occurrence (%)
Impala (*Aepyceros melampus*)	73.6	46.2	40.3	42.9
Kudu (*Tragelaphus strepsiceros*)	12.5	19.2	7.5	9.5
Waterbuck (*Kobus ellipsiprymnus*)	4.2	2.6	4.5	9.5
Duiker (*Sylvicapra grimmia*)	1.4	5.1	1.5	0.0
Warthog (*Phacochoerus africanus*)	2.8	0.0	1.5	4.8
Wildebeest (*Connochaetes taurinus*)	1.4	6.4	6.0	0.0
Baboon (*Papiocynocephalus anubis*)	1.4	2.6	14.9	4.8
Sable (*Hippotragus niger*)	1.4	6.4	6.0	9.5
Bushpig (*Potamochoerus larvatus*)	1.4	2.6	0.0	0.0
Bushbuck (*Tragelaphus scriptus*)	1.4	6.4	0.0	0.0
Buffalo (*Syncerus caffer*)	0.0	2.6	4.5	9.5
Eland (*Taurotragus oryx*)	0.0	1.3	4.5	0.0
Scrub hare (*Lepus saxatilis*)	0.0	0.0	4.5	0.0
Monkey (*Cercopithecus aethiops*)	0.0	0.0	3.0	0.0
Civet (*Civettictis civetta*)	0.0	0.0	3.0	0.0
Zebra (*Equus quagga*)	0.0	0.0	0.0	9.5

67 from leopards and 21 from lions. Analysis of faecal samples revealed a total of 16 mammalian prey species in the diet of the four carnivores, 10 in wild dog faeces, 11 in spotted hyaena's, 13 in leopard's and eight in lion's. Impala was the prey species most frequently recorded in the faeces of all four carnivores (Table 1), but its frequency of occurrence was highest in the wild dog diet. The larger prey items present in the samples were zebra (*Equus burchelli*) and buffalo (*Syncerus caffer*), and these constituted a greater part of the lion diet (Table 1). The contribution of prey species, based on their frequency of occurrence, was significantly different (χ^2 = 183.6528, d.f. = 45, P < 0.05) among the diets of the four carnivores; significant differences were detected in the contribution of impala, warthog (*Phacochoerus africanus*), baboon (*Papio ursinus*), bushbuck (*Tragelaphus scriptus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), scrub-hare (*Lepus saxatilis*), monkey (*Chlorocebus pygerythrus*), civet (*Civettictis civetta*), and zebra (*Equus burchellii*). The frequency of occurrence of impala was significantly different between wild dogs and the other three species: (χ^2 = 16.3333, d.f. = 1, P < 0.05) with hyaena; (χ^2 = 23.5822, d.f. = 1, P < 0.05) with leopard and (χ^2 = 19.792, d.f. = 1, P < 0.05) with lion.

There was a significant variation in the consumption of prey of different size category by the four carnivores (χ^2 = 63.3, d.f. = 9, P < 0.05). Medium-sized prey (25.1–100 kg) was the most frequent in the diets of the four carnivores, and predation upon impala explained the higher frequency of occurrence of medium-sized prey in the diet of wild dogs, compared with the other three carnivores (Fig. 1). Large prey (>100 kg) was most frequent in the lion faeces (47.6%), than in any of the other predators, and its frequency of occurrence was significantly higher than in the wild dog (χ^2 = 18.9, d.f. = 1, P < 0.05) and leopard's diet (χ^2 = 5.3, d.f. = 1, P = 0.02) but not significantly different to the hyaena's diet (χ^2 = 2.0, d.f. = 1, P = 0.15). The leopard was the only predator with a diet component that included prey weighing up to 5 kg, making up 7.5% of its diet (Fig. 1).

The diets of all the four carnivores overlapped significantly (O*ab* > 0.60). There was an almost complete overlap (0.9) between the diets of wild dogs and spotted hyaenas, but the higher dietary specialization in wild dog diet was evidenced by the low standardized niche breadth (0.09); spotted hyaena, leopard and lion in that order showed more generalized diets (Table 2).

Carnivore and prey populations

The analysis of encounter rates of carnivore spoors indicated that lions and spotted hyaenas continue to increase in Savé Valley Conservancy (Fig. 2). In 2010 there were an estimated 148 lions in the conservancy, representing a density of 5.8 lions/100 km^2 and about 209 spotted hyaenas with a density of 8.2 hyaenas/100 km^2. The wild dog

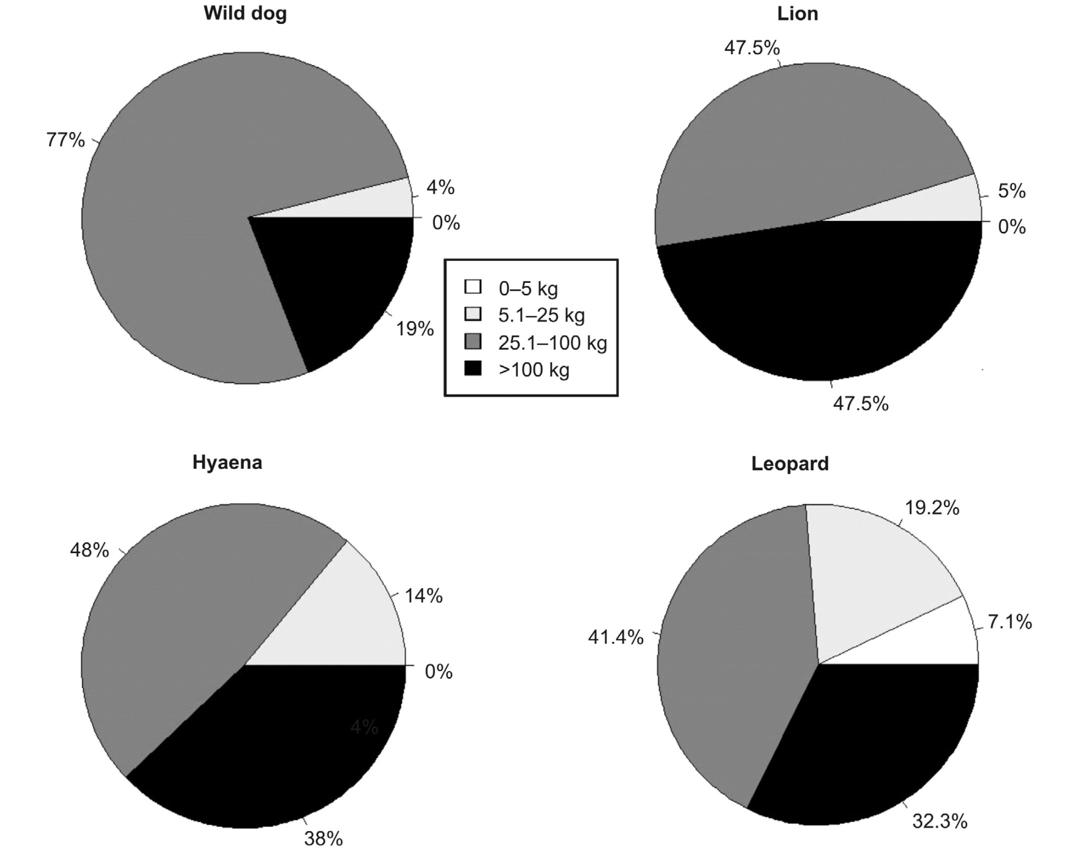

Fig. 1. Relative frequency of prey size categories in the diet of the four carnivores in the Savé Valley Conservancy.

population initially increased, between 1999 and 2004, but started to decline slowly thereafter; by 2010 there were only 64 wild dogs (adults and yearlings) in the SVC (Fig. 2), all restricted to the northern part of the conservancy. The most marked drop in abundance coincided with an increment in lion and hyaena numbers. Over the recent years wild dog densities remained low but stabilized.

In turn, the populations of the three main wild dog prey (impala, kudu and waterbuck) continued decreasing steadily. For example, the population of impala dropped from 34 978 in 2004 to 17 959 in 2010, a 49% decrease in seven years (Fig. 3). The population of kudu (*Tragelaphus strepsiceros*) decreased from 4679 in 2004 to 1170 in 2010, a decrease of 75% in seven years (Fig. 4).

DISCUSSION

In the Savé Valley Conservancy, wild dogs were taking prey that weigh between 11 and 165 kg, but specialized in medium-sized ungulates weighing between 25 and 100 kg. This supports earlier findings by Creel & Creel (1996) in Selous, where wild

Table 2. Diet overlap and niche breadth of the four carnivores in the Savé Valley Conservancy

	Diet overlap				Niche breadth	Standardized niche breadth
	Wild dog	Hyaena	Leopard	Lion		
Wild dog	–				1.78 (n = 10)	0.09
Hyaena	0.95	–			3.73 (n = 11)	0.27
Leopard	0.91	0.91	–		4.81 (n = 13)	0.32
Lion	0.92	0.91	0.92	–	4.28 (n = 8)	0.47

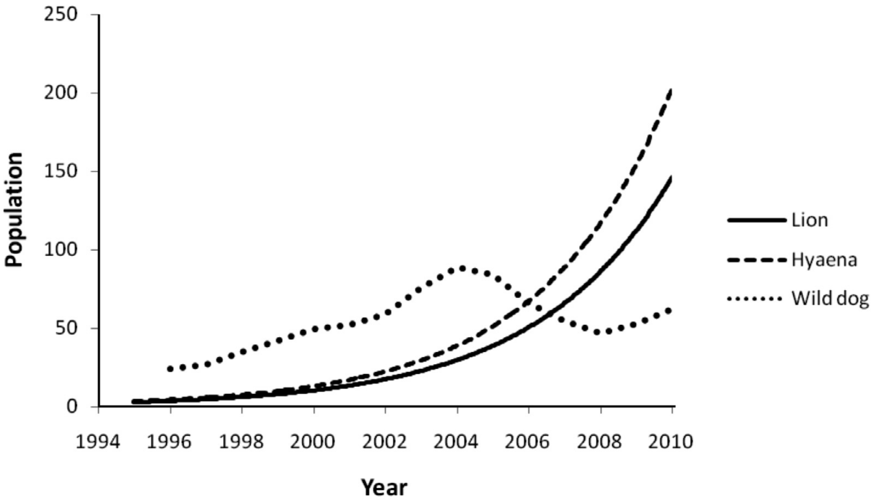

Fig. 2. Population estimates of wild dogs, spotted hyaenas and lions in Savé Valley Conservancy, expanding the results presented by Pole (1999) and Davidson & Romanach (2008, unpubl.).

dog groups take prey that weigh between two and 200 kg but specialize on medium-sized ungulates (15–100 kg). In southern Africa wild dogs prey on a variety of species and, like in this study area, the most abundant prey usually is the principal prey species (Kruger *et al.* 1999; Hayward *et al.* 2006; Davies-Mostert *et al.* 2010). In SVC impala was the species more commonly preyed upon by wild dogs and the most abundant. The relative proportions of impala in the diet of wild dogs have been shown to vary from an estimated 37% (Creel & Creel 2002) to 89% (Reich 1981); compared with 74% in this study.

We assessed diet overlap and niche breadth on the bases of the relative frequency of occurrence of prey remains in faeces, a method which weighs the presence of small and large food items equally, underestimating the importance of large prey (Klare *et al.* 2011). To convert prey remains into relative biomass consumed, requires measuring the volume or weight of each prey remain, and to know conversion factors for each prey and predator (Reynolds & Aebischer 1991; Weaver 1993; Marker *et al.* 2003). In this case calculating biomass consumption is problematic, because these carnivores prey upon animals of different age and sex classes, and also from carcasses. Scavenging spotted hyaenas, for example, do not consume much fur and this food source may be underestimated (Jones & Barmuta 1998), and wild dogs

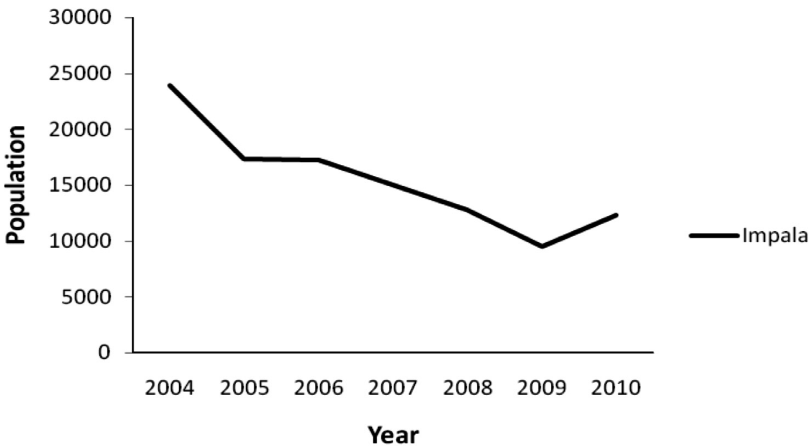

Fig. 3. Population estimates of impala in the Savé Valley Conservancy (source Joubert & Joubert 2010, unpubl., adjusted according to Bothma *et al.* 1990).

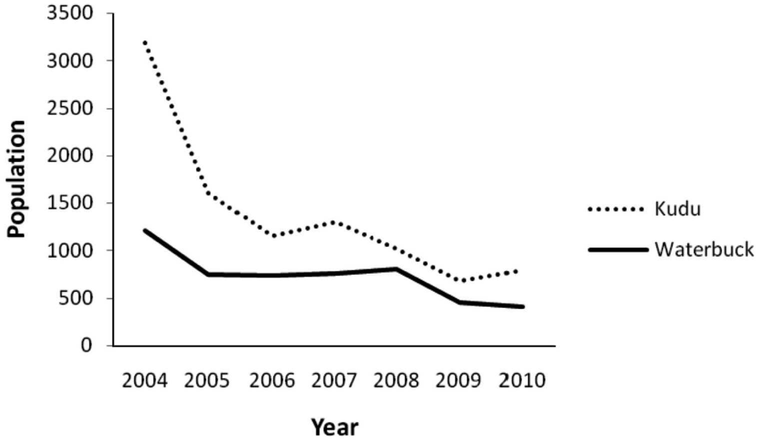

Fig. 4. Population estimates of kudu and waterbuck in the Savé Valley Conservancy (source Joubert & Joubert 2010, adjusted according to Bothma *et al.* 1990).

sharing a kill will consume different proportions of fur and flesh. As the presence of identifiable remains in faeces provides little information about actual biomass killed and consumed (Davies-Mostert *et al.* 2010), for this study we calculated and compared the contributions of prey of different sizes to the overall diet of each carnivore.

Prey size tends to increase with predator size from wild dog to lion (Radloff & Du Toit 2004), but in the SVC the larger predators (spotted hyaena, leopard and lion) also preyed on medium-sized and small prey, benefiting from increased dietary options. Larger populations of lion and spotted hyaena will therefore translate into a reduction in amount of food available to the wild dogs, due to competition for medium-sized prey and specifically impala. Indeed, the diets of wild dog and spotted hyaena are very similar everywhere they have been studied (Hayward *et al.* 2006), and the diets of lion and wild dogs are less similar but also overlap substantially (Creel & Creel 1998). Pole *et al.* (2004) and Buettner *et al.* (2007) also noted that wild dogs mainly take animals in poor condition, and so that both the condition and the numbers of prey could be limiting wild dog populations in the SVC.

Interspecific competition and predation by larger carnivores has emerged as an important limiting factor for wild dogs and other endangered carnivores (Hayward *et al.* 2006; Caro & Stoner 2003). There is evidence that wild dogs do poorly where hyaenas and lions thrive (Creel & Creel 1996), and negative correlations have been recorded between the density of wild dogs and that of lions and spotted hyaenas (Creel & Creel 1996). On the other hand, there is no evidence to suggest that lions and hyaenas limit each other's abundance (Hayward & Kerley 2008), and in SVC lions, as expected, showed the least dietary overlap with other carnivores, filling a largely vacant niche at the upper end of Africa's predator guild (Hayward & Kerley 2005). It is therefore likely that wild dogs in the SVC are at risk of competition from the larger and more abundant lions and spotted hyaenas, and these interactions can have substantial impacts on population demography, including further declines if competition intensifies (Vucetich & Creel 1999). The decline of wild dogs in SVC post 2004 (Fig. 2) could be explained by density changes in response to ecological conditions, rising when competition is weak and dropping when competition is intense (Creel 2001). In SVC leopards were also taking smaller prey and using denser habitats, which suggests they will be largely unaffected by variations in the competitor's levels (Hayward & Kerley 2008).

Although a high degree of overlap does not necessarily mean that competition is taking place, it does provide indirect evidence for the likelihood of one species affecting another (MacNally 1983). It is believed that the wild dog 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 (Hayward & Kerley 2008). Klepto-parasitism by hyaenas can also have a substantial impact on small groups and declining populations of wild dogs (Gorman *et al.* 1998). While not directly observed in the SVC, spotted hyaenas could steal some of the wild dog kills, taking advantage of their supremacy in numbers, exacerbating the effects of decreasing prey by increasing the costs and risks of hunting (Gorman *et al.* 1998, van der Meer *et al.* 2011). Both lions and hyaenas could be limiting the wild dog populations through predation (Creel & Creel 1998), and pup predation by lion at den sites has been observed in the SVC. Finally, wild dogs in SVC were selecting habitats in a pattern consistent with prey availability during the 1990s, (Pole 1999), but in the presence of increasing numbers of lions and hyaenas, they may avoid areas of high prey density so as to avoid these predators (Mills & Gorman 1997; Creel & Creel 2002). Such a shift in habitat use can lead to additional problems in SVC, due to more frequent encounters with humans in the areas used by subsistence farmers (more than 30% of the conservancy). Here persecution and the risk of being caught in snare traps is greater, as well as the risk of contracting diseases from domestic dogs.

Conservation implications

Hayward & Kerley (2008) showed that predators with the smallest dietary niche breadth have the fewest remaining members and are the most threatened. In the wild dog, morphological and behavioural specializations have resulted in a dietary niche that is narrower than expected from its body mass (Hayward *et al.* 2006). This provides theoretical reasons for its inherent rarity in protected areas (Vucetich & Creel 1999), small population sizes, and high risk of extinction. Moreover, when food is a limiting factor, a high dietary overlap among sympatric carnivores can be evidence of exploitative competition, (Macdonald & Thom 2001; Melero *et al.* 2008). In SVC, a decrease in the population of impala would increase the effect of competition on the wild dog, and even pup survival – as wild dogs that have to forage for longer can ill afford additional pup guards (Courchamp *et al.* 2002).

The ultimate causes of wild dog population decline followed by stabilization are yet to be clearly defined in the SVC. Given the high diet overlap, low niche breadth and the eco-physiology of the wild dog, this population risks a continuous decline and even local extinction, if exploitation and interference competition increases with increasing populations of spotted hyaenas and lions. Relaxation of interspecific competition (Caro & Stoner 2003) is a promising solution in intensively managed wildlife areas, for example by regulating hyaena and lion numbers with trophy hunting. Managing the prey species assemblage is another possible mechanism, but the bottom line is that the future of the wild dog and other large carnivores relies on the establishment and maintenance of large protected areas, where natural processes are allowed to take place to maintain population viability of this endangered carnivore.

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