

The Lion King and the Hyaena Queen: large carnivore interactions and coexistence

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ABSTRACT

Interactions among species, which range from competition to facilitation, have profound effects on ecosystem functioning. Large carnivores are of particular importance in shaping community structure since they are at the top of the food chain, and many efforts are made to conserve such keystone species. Despite this, the mechanisms of carnivore interactions are far from understood, yet they are key to enabling or hindering their coexistence and hence are highly relevant for their conservation. The goal of this review is thus to provide detailed information on the extents of competition and facilitation between large carnivores and their impact in shaping their life histories. Here, we use the example of spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) and provide a comprehensive knowledge of their interactions based on meta-analyses from available literature (148 publications). Despite their strong potential for both exploitation and interference competition (range and diet overlap, intraguild predation and kleptoparasitism), we underline some mechanisms facilitating their coexistence (different prey-age selection and scavenging opportunities). We stress the fact that prey abundance is key to their coexistence and that hyaenas forming very large groups in rich ecosystems could have a negative impact on lions. We show that the coexistence of spotted hyaenas and lions is a complex balance between competition and facilitation, and that prey availability within the ecosystem determines which predator is dominant. However, there are still many gaps in our knowledge such as the spatio-temporal dynamics of their interactions. As both species' survival becomes increasingly dependent on protected areas, where their densities can be high, it is critical to understand their interactions to inform both reintroduction programs and protected area management.

Key words: *Crocuta crocuta*, facilitation, interspecific competition, intraguild predation, kleptoparasitism, scavenging, *Panthera leo*, predator.

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I. INTRODUCTION

(1) Coexistence and conservation of large predators

Interactions among species have profound effects on natural population dynamics and community structure (Estes & Palmisano, 1974; Menge & Sutherland, 1987; Paine, Wootton & Boersma, 1990; Bengtsson, Fagerström & Rydin, 1994). This is particularly true for large mammalian carnivores, many of which act as keystone species in the top-down control of terrestrial ecosystems (for review see Estes *et al.*, 2011). As such, their removal is thought to release other predator populations with consequences at other trophic levels (Terborgh, 1992; McLaren & Peterson, 1994; Palomares *et al.*, 1998; Berger & Gese, 2007). Despite the increasing interest in trophic interactions, few studies have documented the interactions of top carnivores, partly because few systems host a diversity of them, and hence little is known about the consequences of a shift of dominance among top carnivore species.

These charismatic predator species are also flagships for conservation and produce significant tourism income, especially in Africa (Dalerum *et al.*, 2008). The safekeeping of viable large carnivore populations is essential to ecosystem equilibrium, but this cannot be ensured without understanding how they affect each other.

Interactions between species range from facilitation to direct predation, through competition. Facilitation occurs when interactions between organisms benefit at least one of them and cause harm to neither (Bertness & Callaway, 1994). For instance, McNaughton (1976) showed that Thomson's gazelles (*Eudorcas thomsonii*) prefer to feed in areas already grazed by wildebeests (*Connochaetes taurinus*) as these areas produce young green regrowth which is not found in ungrazed areas. Gazelles take advantage of this growth stimulated by the grazing, and so benefit from the wildebeest. Despite their importance in ecological processes, these positive interactions have been far less studied than negative ones.

On the other hand, competition can be defined in a stricter sense as interactions between individuals that lead to reduced fitness (Wiens, 1989). However, this competition *sensu stricto* is very difficult to demonstrate in field studies. Competitive interactions are usually divided into exploitation and interference competition. Exploitation competition refers to indirect negative effects where one species uses resources that are then no longer available to others (Vance, 1984). It is likely to

occur when food is limiting and diet overlap is high, which is often the case for carnivores (Crooks & Vuren, 1995; Fedriani *et al.*, 2000; Azevedo *et al.*, 2006; Hayward & Kerley, 2008). Interference competition on the other hand, is the direct negative effect resulting from one species preventing the other from obtaining resources (Vance, 1984). These range from interspecific territoriality (Durant, 1998, 2000*a,b*), kleptoparasitism (Cooper, 1991; Creel & Creel, 1996) and ultimately intraguild predation which constitutes an extreme case of interference competition and affects many species (Palomares & Caro, 1999; Donadio & Buskirk, 2006). Most theoretical and empirical studies have focused on exploitation competition, despite the omnipresence of interference competition. Competition can have profound effects on populations, resulting in behavioural responses, changes in space and habitat use, reductions in population size and even local extinction (Creel & Creel, 1996; Durant, 1998, 2000*a,b*, 2004; Vucetich & Creel, 1999; Creel, 2001; Kamler *et al.*, 2003; Ripple & Beschta, 2004; Fortin *et al.*, 2005; Hayward & Kerley, 2008).

However, competing species can live sympatrically, and it has been suggested that resource partitioning can promote coexistence. In such cases, the realized ecological niche of the competitors differs from each other. A competitively inferior species can escape competition by using different areas, finding empty patches (spatial avoidance, e.g. Durant, 2000*a*) or using the same patch but at different times (temporal avoidance, e.g. Hayward & Slotow, 2009). This leads to a reduction in interspecific competition and thus facilitates coexistence (Durant, 2000*a*; Broekhuis *et al.*, 2013). In most cases, the situation is complex as coexistence simultaneously generates costs and benefits for both species. For example, spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) in Africa both prey on medium- to large-sized herbivores, kleptoparasitise from each other and scavenge from each other's kills (Kruuk, 1972; Schaller, 1972; Switalski, 2003; Hayward & Kerley, 2005; Hayward, 2006; Atwood & Gese, 2008).

The African savanna presents a unique opportunity to study coexistence among large carnivores as it is one of the few remaining ecosystems with complete guilds of both predators and prey. As the largest and most abundant large carnivores, spotted hyaenas (hereafter hyaenas) and lions have profound effects on smaller carnivores such as African wild dogs (*Lycan pictus*) and cheetahs (*Acinonyx jubatus*, Creel & Creel, 1996; Durant, 2000*a,b*) and prey population dynamics (Erlinge *et al.*, 1984; Sinclair, 1985; Sinclair, Dublin &

Borner, 1985; Sinclair & Arcese, 1995). Even though their potential for competition is high (Hayward, 2006), hyaena and lion distributions overlap extensively, with lions sharing nearly 95% of their range with hyaenas (Fig. 1). This overlap is likely to increase, as they are both increasingly restricted to protected areas (PAs) due to human encroachment, and the resulting habitat and prey losses (Packer, 1990; Castley *et al.*, 2002; Kissui & Packer, 2004). Within some of these PAs, predator densities are increasing locally (especially in small fenced reserves, Hayward *et al.*, 2007a), as is competition for food and space thus increasing the impact of potential competition on their long-term viability (Riggio *et al.*, 2012).

However, there is a paucity of literature on the mechanisms by which lions and hyaenas coexist. Many detailed studies have been conducted on each species separately, while to our knowledge there has been only one comprehensive study of lions and hyaenas across their range (Watts & Holekamp, 2008).

In order to take our understanding of the mechanisms by which predators coexist further, we reviewed the available literature on lions and hyaenas searching for critical parameters relating to their cohabitation. We used a meta-analysis to identify the parameters affecting the extent of competition and/or facilitation between these two species.

We start with a short description of hyaena and lion life histories based on available data for their densities and different population parameters (group size, adult sex ratio, foraging group size). We then evaluate their diets and overlap across their range to measure the potential for exploitation competition. We review the evidence for potential direct competition such as kleptoparasitism and predation. We also investigate mechanisms (prey-age selection, scavenging opportunities) that could facilitate their coexistence. Finally, we stress the fact that there are still many gaps in our knowledge and that more research is necessary to understand more fully coexistence between lions and hyaenas in particular, and among large predators in general.

(2) Life history of two large predators

Spotted hyaenas and lions are the biggest and most abundant large predators in Africa (Cardillo *et al.*, 2004). Being at the top of the food chain, they share some of their characteristics but are different in many ways. Spotted hyaenas are the largest member (45–60 kg) of the Hyaenidae family. Their estimated total population is between 27000 and 47000 individuals with several populations exceeding 1000 mostly in East and southern Africa (Honer, Holekamp & Mills, 2013). They have a wide distribution south of the Sahara desert with the exception of tropical rainforests in West and Central Africa (Fig. 1). They live in matriarchal societies with a strict hierarchy (among each sex, with females dominant over males) unique among carnivores. Groups, or clans, are characterised by fission–fusion dynamics, forming foraging groups (hunting or looking for food to scavenge) which are variable in composition and size (Kruuk, 1972). Clans

are highly territorial when prey resources are stable but boundaries between clan territories can fade when prey are nomadic or migrant (Kruuk, 1972; Mills, 1990; Hofer & East, 1993a,b). Hyaenas are predominantly crepuscular and nocturnal, but can also be active during the day during the cold winter months (Kruuk, 1972; Mills, 1990; Hayward & Slotow, 2009; Cozzi *et al.*, 2012).

Hyaenas are efficient hunters, killing up to 95% of their prey (Cooper, Holekamp & Smale, 1999). Their hunting success averages 33% (Holekamp *et al.*, 1997) and can reach 92% depending on prey species (Kruuk, 1972; Mills, 1990). Hyaenas are cursorial predators, relying on their endurance to take down their prey after chases of up to several kilometres (Kruuk, 1972; Mills, 1990). Their preferred prey body mass range is 56–182 kg (Hayward, 2006). They are highly flexible in their foraging strategies and will readily scavenge from carcasses left by other predators (Kruuk, 1972; Cooper, 1991; Creel & Creel, 1996; Honer *et al.*, 2002; Watts & Holekamp, 2009). Moreover, large groups are capable of stealing carcasses from other predators including lions while they are still present (e.g. Kruuk, 1972; Cooper, 1991; Creel & Creel, 1996; Honer *et al.*, 2002). Long-term changes in prey populations have been shown to trigger functional responses and changes in foraging behaviour (e.g. Honer *et al.*, 2002). In the Ngorongoro Crater, hyaenas respond to changes in prey guild composition by switching to species easier to hunt and increasing kleptoparasitism from lions (Honer *et al.*, 2002). When anthropogenic food resources are available, hyaenas may change their foraging behaviour to use those additional resources (Kolowski & Holekamp, 2008). Hyaenas may influence sympatric carnivores and prey species, whose populations are suspected to be affected, and sometimes limited, by hyaena predation (Kruuk, 1972; Vucetich & Creel, 1999; Durant, 2000a; Creel, 2001). Hyaenas are therefore a key species in most African ecosystems.

Lions are the second biggest member of the Felidae family. Their population is currently estimated at between 32000 and 35000 individuals (Riggio *et al.*, 2012). Bauer (2008) with the IUCN SSC Cat Specialist Group estimated that 42% of major lion populations are declining, particularly those outside PAs. Lions are a dimorphic species, with males weighing 150–225 kg and females 122–192 kg (Sunquist & Sunquist, 2009). They have a wide habitat tolerance but are not found in dense lowland forests, and are now largely constrained to PAs (Riggio *et al.*, 2012, Fig. 1). Lions are the most social of the felids and live in fission–fusion groups, the foundation of which is a group of related females and their offspring (Packer, Scheel & Pusey, 1990). Male lions are transient to the pride and often form single-sex coalitions of related males during sub-adulthood and adulthood (Schaller, 1972). Lions display male-biased dispersal, but some females (around one-third) do disperse (Pusey & Packer, 1987). Lions are mostly sedentary but some populations follow migratory movements of their prey (Schaller, 1972). Each pride defends its own territory from neighbouring prides. Lions usually hunt at night, resting during the day (Schaller,

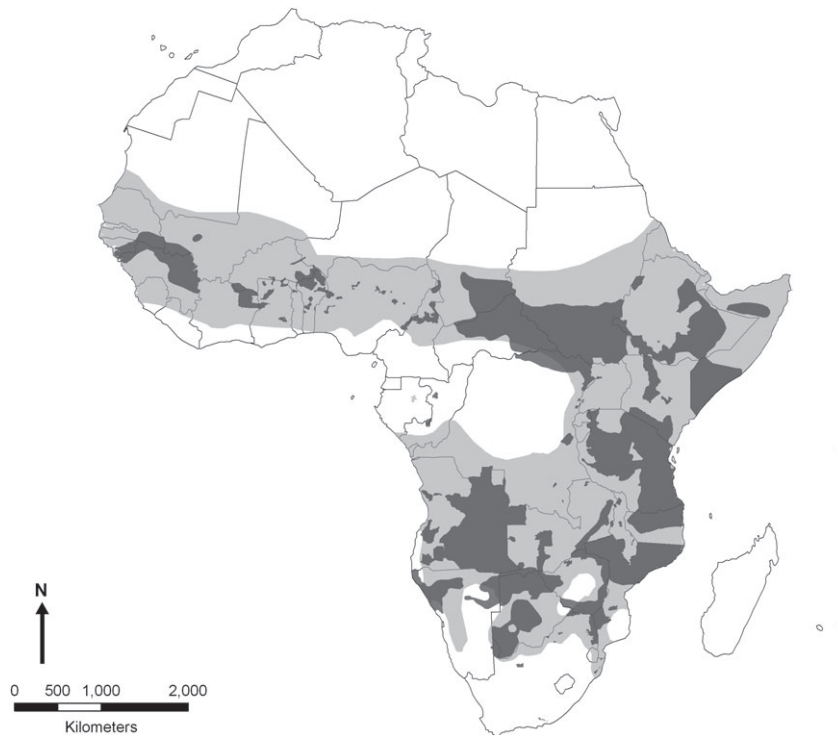


Fig. 1. Distribution map of spotted hyaena (light grey) and lion (dark grey). Most lion populations are nowadays restricted to protected areas. Total overlap in distribution represents 94.9% of the lion range. Data from the IUCN database. (The population of Indian lions is omitted from this map but not from calculation of range overlap).

1972; Sunquist & Sunquist, 2009). Lions hunt predominantly medium- to large-sized ungulates (Hayward & Kerley, 2005). They ambush their prey from cover and manage to run them down over short distances (a few to a hundred meters, Loarie, Tambling & Asner, 2013). In the Serengeti, 30% of stalks are successful when several individuals hunt together, but this reduces to 17–19% when hunting alone (Schaller, 1972). Their preferred prey body mass range is 190–550 kg (Hayward & Kerley, 2005). Lions readily scavenge and it is relatively easy for them to chase cheetahs or wild dogs from their kill, but fights with spotted hyaenas at carcasses can be lethal for both species. Because of the rapidly growing human population, lions are in increasingly close proximity with humans and are renowned livestock killers, fostering intense conflict with populations living alongside them. Retaliatory killing is one of the main causes of death in some areas and can cause population decline (Frank, Woodroffe & Ogada, 2005; Woodroffe & Frank, 2005; Kissui, 2008; Chardonnet *et al.*, 2010; Funston, 2011). On the other hand, lions have a high economic value for game viewing and trophy hunting (Loveridge *et al.*, 2010b; Lindsey *et al.*, 2012).

Coexistence between lions and hyaenas is thus a complex balance of competition and facilitations. Figure 2 summarizes our current understanding of their interactions. The goal of this review is to provide detailed information on the extents of these two mechanisms and their impact in shaping the life histories of both carnivores.

II. MATERIALS AND METHODS

(1) Data collection

We gathered data on hyaenas, lions and their prey across Africa from a total of 148 publications (Table 1; see online supporting information Appendix S1 for a full list of references used). These studies were conducted in 42 locations, 41 of which were within PAs, either National Park (NP) or Game Reserve (GR) encompassing 22 study sites in southern Africa (15 NPs, 6 GRs and 1 unprotected area), 10 in East Africa (seven NPs and three GRs), 5 NPs in central Africa and 5 NPs in western Africa. In terms of habitat, 10 of these locations are open (grassland, desert), 18 are mixed (open tree savannah, bushland) and 14 are closed (woodland). PA size averaged $7957 \pm 1636.0 \text{ km}^2$ (mean \pm S.E.) ranging from 91 to 49770 km^2 and annual rainfall ranged from 17 to 1551 mm ($681.3 \pm 48.6 \text{ mm}$). For two locations (Ngorongoro NP and Katavi GR), we found detailed information for two different time periods, thus both were included to give 44 final datasets.

(2) Predator population data

We extracted all available data on hyaena and lion densities (27 study sites for hyaenas, 40 for lions), adult and total hyaena clan/lion pride size (adult clan size, $N = 10$; total clan size, $N = 8$; adult pride size, $N = 12$; total pride size,

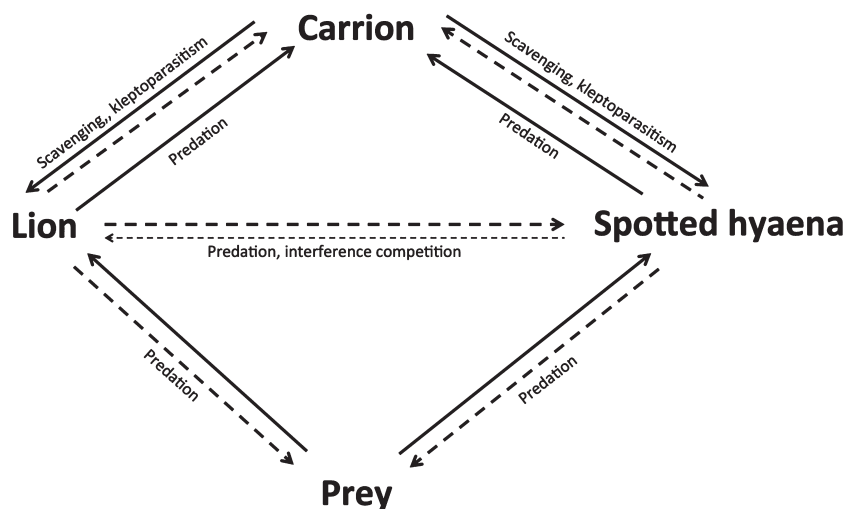


Fig. 2. Diagram of the interactions between lions and hyaenas. Solid arrows represent positive effects and dashed arrows represent negative effects. Thicker lines indicate stronger effects. From the point of view of the spotted hyaenas, lions have a negative impact on live prey and both a positive (predation) and negative (scavenging) effect on the availability of carrion. Lions also have a direct negative effect on hyaenas through intraguild predation. Live prey and carrion availability both have a positive effect on hyaenas through predation and scavenging. Lions thus have a positive effect on hyaenas by providing scavenging and kleptoparasitism opportunities. The situation is symmetrical from the point of view of lions except that there is barely any mortality directly due to hyaenas.

Table 1. Data on locations, predators and prey extracted from the publications listed in Appendix S1

	Parameters	Notes
Location	Name Level of protection Area (km ²) Habitat type Annual rainfall (mm)	National Park or Game Reserve Closed, mixed or open
Predators		
Both species	Total density (individuals/km ²) Clan or pride total size Clan/pride size in adults Foraging group size Home range size (km ²) Diet (% of each prey species) Extent of scavenging and kleptoparasitism Activity pattern Habitat selection Causes of death	Includes data on age selection
Hyaena	Feeding group size	
Lion	Adult male:female sex ratio	
Prey	Total density (prey/km ²) and biomass (kg/km ²) Very small prey density and biomass Small prey density and biomass Medium prey density and biomass Large prey density and biomass Very large prey density and biomass	Body mass < 20 kg Body mass 20–120 kg Body mass 120–400 kg Body mass 400–600 kg Body mass >600 kg

$N = 15$), foraging group size (hyaena, $N = 13$; lion, $N = 20$) and home range (HR) size (hyaena, $N = 15$; lion, $N = 10$). For lions total pride size included all individuals while adult pride size includes only adult females and large cubs. For hyaenas, adult clan size includes only adults and sub-adults.

(3) Prey density and biomass

We also extracted data on ungulates, i.e. prey densities at each site. We use total prey densities as the sum of densities of all species (hippopotamus, ostriches and apes were not included). We also calculated densities of different prey size classes when

publications provided densities by prey species. We calculated prey biomass (75% of adult female body mass to take calves and sub-adults into account, Hayward & Kerley, 2005) based on unit weights from Coe, Cumming & Phillipson (1976) and Wilson & Mittermeir (2011). Missing data from some publications were obtained from other works conducted in the same location and during the same time frame.

(4) Diet estimation

For sites where diet was recorded for several lion prides, hyaena clans or at different periods, we pooled the data to obtain diet composition for each site. The complete data set provided 59 diet compositions in 13 different sites for hyaenas and 78 diet compositions in 31 different sites for lions. Diet estimation for hyaenas was balanced between scats ($N = 26$) and feeding observations ($N = 33$) but was skewed toward direct observations for lions (74 versus 4 estimations based on scat data). Prey were also assigned to size classes based on 75% of their female adult body mass and diet based on prey classes was also computed for each site. These diets were used to calculate diet overlap and breadth for each study site. Overall diet composition was calculated as the average of the proportion of each species in the diet across all sites (the sum of all proportions can thus exceed 1). We then pooled the raw data without any distinction by location to estimate the proportion of each prey item in each predator diet and used this to calculate the overall diet breadth and overlap for hyaenas and lions. Species occurring in very low proportions in the diets such as porcupine (family Hystricidae), ostrich (*Struthio camelus*), rodents or birds, as well as predator species were grouped into a class named ‘other’ for these analyses.

We used the Levin’s index (Smith, 1982) $1 / \sum_i (p_i)^2$ where p_i is the proportion of prey item i in the carnivore diet to define niche breadth for lions and hyaenas. We then used Pianka’s niche overlap indices (Pianka, 1973) for species j $\alpha_{jk} = \sum_i p_{ij}p_{ik} / \sqrt{\sum_i p_{ij}^2 \sum_i p_{ik}^2}$ and species k $\alpha_{kj} = \sum_i p_{ij}p_{ik} / \sqrt{\sum_i p_{ij}^2 \sum_i p_{ik}^2}$ where p_{ij} and p_{ik} are the proportion of food item i in species j and k diets, respectively. This definition generates a different α value for each species providing their niche breadths differ. We also used Pianka’s ‘multiplicative measure of overlap’ (Pianka, 1973) that provides a single value for a given pair of species (i.e. niche breadths are considered the same) $\alpha_{jk} = \alpha_{kj} = \sum_i p_{ij}p_{ik} / \sqrt{\sum_i p_{ij}^2 \times \sum_i p_{ik}^2}$ and the percentage overlap defined as $(\sum_i \min(p_{ij}, p_{ik})) \times 100$ (Krebs, 1989) to estimate diet overlap between the two species. We calculated Levin’s index for 14 sites for hyaenas and 33 sites for lions, and were able to calculate niche overlap for 11 sites (i.e. where diet composition for both species, and prey availability were known). We did not investigate prey preferences.

(5) Kleptoparasitism and scavenging intensity

Fourteen studies provided details on the kleptoparasitism and scavenging intensity between hyaenas and lions. We

extracted the percentage of kills from one species at which the other one was present, the percentage of kills lost to the other species and the percentage of food (in terms of biomass) obtained from and lost to the other species. Kills were attributed to a given species either when the hunt and/or kill was directly observed or when predation marks on the carcasses allowed identification of the killer. We also extracted the percentage of carcasses (killed or scavenged) at which the two species were seen feeding irrespective of the killer species.

(6) Statistical analysis

We estimated range overlap between the two species using spatial data from the IUCN database (Bauer, Nowell & Packer, 2013; Honer *et al.*, 2013). We calculated the total area of overlap and the proportion of overlapping area for each species. We used Pearson and Spearman correlation tests and linear models to investigate statistical relationships between the variables of our dataset.

All statistical analyses were performed in R 3.0.2 (R Core Team, 2013). Results are presented as means with standard errors (S.E.).

III. PREDATOR POPULATION CHARACTERISTICS AND DIET

(1) Predator populations

Hyaena density ranged from 0.005 to 1.8 individuals/km² (0.39 ± 0.10 , $N = 27$ studies). Total clan size and adult clan size ranged from 3.8 to 60.1 (30.84 ± 7.39 , $N = 10$) and from 1.2 to 34.7 (14.97 ± 4.27 , $N = 8$), respectively. Lion density ranged from 0.0015 to 0.40 individuals/km² (0.112 ± 0.02 , $N = 40$). Prides averaged 13.45 ± 1.67 individuals (range = 5–21.5, $N = 12$) and 5.57 ± 0.56 adult females and large cubs (2–9.1, $N = 15$). Total prey density varied by more than 130-fold, ranging from 0.7 to 97.4 prey/km² (22.98 ± 3.95 , $N = 32$) and biomass by more than 180 times from 95.3 to 17508.7 kg/km² (4159.6 ± 733.87 , $N = 31$).

Across their range, both predator densities were positively correlated with prey biomass (Pearson’s correlation, hyaena: $\rho = 0.75$, $P < 0.001$, $N = 21$; lion: $\rho = 0.57$, $P = 0.001$, $N = 20$, Fig. 3A) in accordance with previous results (Van Orsdol, Hanby & Bygott, 1985; Hayward, O’Brien & Kerley, 2007c). Hyaena clans were bigger in areas with higher prey biomass ($\rho = 0.80$, $P = 0.005$, $N = 9$) but interestingly lion pride size was not correlated to any prey abundance parameter. Clan size increased with hyaena density ($\rho = 0.83$, $P = 0.031$, $N = 9$) indicating that at higher density hyaenas form larger groups rather than more groups.

The average foraging group size for hyaenas was 2.6 ± 0.28 (1.3–4.8, $N = 13$). Hyaenas are reported usually to forage alone (75% of the time) for small prey items, but to form large groups to hunt big prey (Holekamp *et al.*, 1997). However, they fed in groups averaging 7.73 ± 1.48 individuals (3.4–16.7, $N = 9$). These group sizes were neither

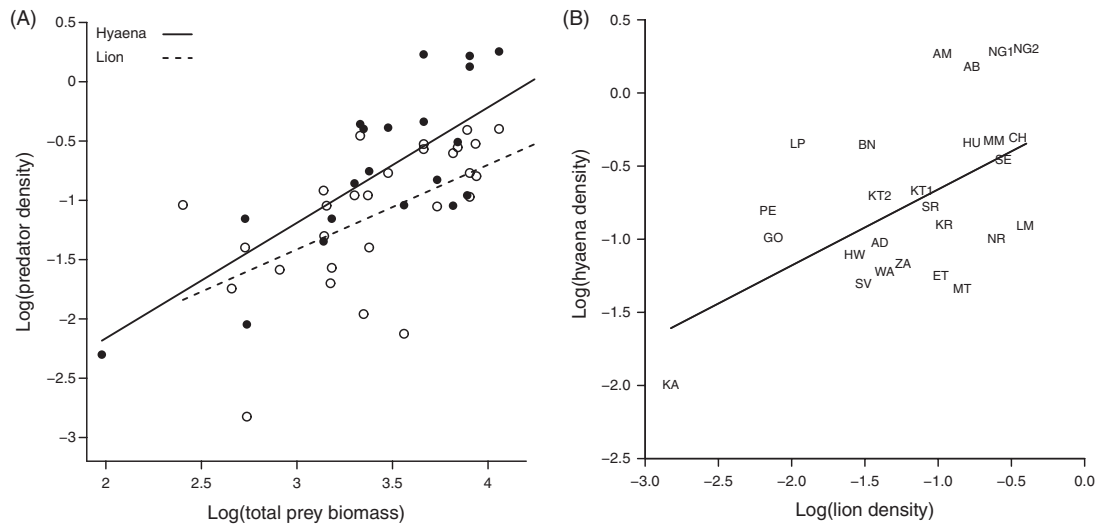


Fig. 3. (A) Spotted hyaena (solid symbols and line) and lion (open symbols, dashed line) densities *versus* total prey biomass (excluding hippos and ostriches). $\text{Log}(\text{hyaena density}) = -4.11 + 0.97 \times \log(\text{prey biomass})$; $\log(\text{lion density}) = -3.55 + 0.71 \times \log(\text{prey biomass})$. (B) Spotted hyaena density *versus* lion density. Letters represent location codes defined in Appendix S1. $\text{Log}(\text{hyaena density}) = -4.11 + 0.97 \times \log(\text{lion density})$.

correlated with clan size nor with prey abundance. Lions foraged in groups ranging from 1.5 to 5.23 individuals (3.54 ± 0.28 , $N = 20$). Similar to hyaenas, foraging group size in lions was not correlated with pride size or prey abundance. The adult sex ratio of lions averaged 0.43 ± 0.04 males per female (0.18–0.90, $N = 15$).

Lion home range (HR) size obtained by minimum convex polygons (MCPs) and Kernels isopleths averaged $209.33 \pm 113.19 \text{ km}^2$ and ranged from 29.5 to 1112.5 km^2 ($N = 10$). Hyaena HRs averaged $178 \pm 79.19 \text{ km}^2$ ($N = 15$) ranging from 24.5 to 1095 km^2 . For both carnivores, HR size was inversely correlated with prey abundance (lion–total prey density $\rho = -0.79$, $P = 0.007$, $N = 9$; hyaena–total prey biomass $\rho = -0.83$, $P < 0.001$, $N = 13$). This result is in accordance with data from Loveridge *et al.* (2009) showing that lion HR size decreased as prey biomass increased. Hayward *et al.* (2009) also showed that lion territory sizes were correlated with preferred prey availability. In addition, hyaena HR size was inversely correlated with their density ($\rho = -0.86$, $P < 0.001$, $N = 14$) and clan size ($\rho = -0.77$, $P = 0.01$, $N = 10$) and lion HR size was negatively correlated with lion density ($\rho = -0.71$, $P = 0.017$, $N = 10$) but was independent of pride size ($\rho = -0.47$, $P = 0.35$, $N = 6$).

Hyaena:lion ratio, calculated for 26 locations as the ratio between hyaena and lion densities, averaged 5.68 ± 1.59 hyaenas per lion (range 0.28–36.36). This ratio was not correlated with any of the parameters studied.

(2) Predator diets

Hyaena diet was composed of 33 food items (Table 2); their main prey were gemsbok (*Oryx gazella*, 41.3%), springbok (*Antidorcas marsupialis*, 29.8%), wildebeest (*Connochaetes taurinus*, 28.3%), impala (*Aepyceros melampus*, 22.7%) and zebra (*Equus quagga*, 17.5%) where they were present. Lions fed on 35

food items and their main prey were wildebeest (24.6%), buffalo (*Syncerus caffer*, 21.9%), kob (*Kobus kob*, 20.2%), roan (*Hippotragus equinus*, 15.4%) and hartebeest (*Alcelaphus bucelaphus*, 15.0%) where present (see Table 2).

There were no significant differences between lion and hyaena diets in term of prey size classes eaten (Freidman $\chi^2 = 9.1429$, d.f. = 5, $P = 0.104$), in accordance with findings of Hayward (2006). Both predators mostly prey on medium-sized ungulates (45.1% of lion diet and 41.5% of hyaena diet, Table 3). However, lions appeared to include more large prey in their diet than hyaenas (20.1% for lions, 7.9% for hyaenas). Similar resource partitioning trends were reported by Hayward & Kerley (2005) and Hayward (2006). Proportions of very large prey and ‘other’ types of prey also appeared higher in the hyaena diet (14 and 13.2%, respectively, *versus* 7.6 and 6.2% in lions).

The proportion of medium-sized prey consumed by both predators increased with the ratio of this prey type within the prey population showing that both species favour the most abundant and rewarding prey (hyaenas: $\rho = 0.62$, $P = 0.023$, lions: $\rho = 0.62$, $P = 0.004$). Lions consumed less large- and very-large-sized prey as the ratio of medium-sized prey increased (large prey $\rho = -0.62$, $P = 0.004$; very large prey $\rho = -0.74$, $P = 0.004$) showing a tendency to prefer medium-sized prey as also suggested by Hayward (2006).

(3) Predator effects on each other

Hyaena and lion densities were positively correlated ($\rho = 0.56$, $P = 0.003$, $N = 26$, Fig. 3B) suggesting that competition does not lead to mutual exclusion at the population level. Lion and hyaena densities are therefore mainly driven by abundance of their prey rather than that of their main competitor. Hyaena HR size decreased as lion density increased ($\rho = -0.77$, $P = 0.01$, $N = 10$). Hyaena

Table 2. Diet composition in prey species for lions and hyaenas. Proportions are averaged for all ecosystems with available data

Prey species	Lion			Hyaena		
	%	Range (%)	<i>N</i>	%	Range (%)	<i>N</i>
Baboon	3.2 ± 1.6	0.1–6.7	4	0.8	0.7–0.8	2
<i>Papio anubis</i>						
Blesbok	9.9 ± 6.4	3.5–16.3	2	—	—	—
<i>Damaliscus pygargus phillipsi</i>						
Buffalo	21.9 ± 3.5	0.1–61.7	23	7.3 ± 2.6	0.1–23.5	11
<i>Syncerus caffer</i>						
Bushbuck	5.8 ± 1.8	0.0–21.1	15	8.4 ± 7.3	0.3–30.4	4
<i>Tragelaphus sylvaticus</i>						
Bushpig	1.8 ± 1.1	0.0–4.9	4	1.9 ± 1.1	0.4–4.2	3
<i>Potamochoerus larvatus</i>						
Duiker	2.5 ± 1.1	0.1–11.5	11	3.0 ± 1.3	0.2–7.4	6
<i>Sylvicapra grimmia</i>						
Eland	2.7 ± 0.5	0.5–5.9	17	2.5 ± 2.2	0.3–7.0	3
<i>Taurotragus oryx</i>						
Elephant	11.2 ± 5.8	2.2–34.0	5	6.3 ± 5.4	0.1–22.3	4
<i>Loxodonta africana</i>						
Gazelles	3.1	3.1	1	9.9 ± 4.0	4.9–17.9	3
<i>Nanger granti</i> & <i>Eudorcas thomsonii</i>						
Gemsbok	9.4 ± 7.5	1.1–32.0	4	41.3 ± 19.5	8.8–76.1	3
<i>Oryx gazella</i>						
Giraffe	7.2 ± 2.0	0.4–21.4	13	8.9 ± 5.8	0.6–31.6	5
<i>Giraffa camelopardalis</i>						
Grant gazelle	0.8 ± 0.2	0.2–1.3	4	0.4 ± 0.1	0.3–0.5	2
<i>Nanger granti</i>						
Grysbuck	—	—	—	0.1	0.1	1
<i>Raphicerus sharpei</i>						
Hartebeest	15.0 ± 5.1	0.6–81.3	15	1.3 ± 1.1	0.0–4.7	4
<i>Alcelaphus buselaphus</i>						
Hippo	3.5 ± 2.3	0.1–10.2	4	0.1	0.1	2
<i>Hippopotamus amphibius</i>						
Impala	11.4 ± 2.9	0.4–43.5	18	22.7 ± 7.1	0.9–57.4	8
<i>Aepyceros melampus</i>						
Kob	20.2 ± 5.0	2.1–37.7	7	—	—	—
<i>Kobus kob</i>						
Klipspringer	—	—	—	0.8 ± 0.2	0.6–1.0	2
<i>Oreotragus oreotragus</i>						
Kudu	11.6 ± 2.2	0.4–33.9	17	5.2 ± 1.7	0.6–12.9	7
<i>Traelophus strepsiceros</i>						
Lechwe	0.5	0.5	1	—	—	—
<i>Tragelaphus leche</i>						
Nyala	8.3 ± 8.0	0.1–24.3	3	6.8 ± 6.2	0.6–13.0	2
<i>Tragelaphus angasii</i>						
Oribi	1.3 ± 1.5	0.8–1.8	2	—	—	—
<i>Ourebia ourebi</i>						
Puku	1.2	1.2	1	—	—	—
<i>Kobus vardonii</i>						
Reedbuck	4.4 ± 3.3	0.3–36.8	11	2.1 ± 1.1	1.0–3.2	2
<i>Redunca arundinum</i>						
Rhino	0.3 ± 0.2	0.2–0.5	2	0.4	0.4	1
<i>Diceros bicornis</i> & <i>Ceratotherium simum</i>						
Roan	15.4 ± 4.5	0.3–35.0	8	0.4 ± 0	0.4	2
<i>Hippotragus equinus</i>						
Sable	2.1 ± 1.0	0.8–5.1	4	1.4 ± 1.2	0.2–2.5	2
<i>Hippotragus niger</i>						
Springbok	12.8 ± 8.3	0.8–36.2	4	29.8 ± 23.5	2.5–76.6	3
<i>Antidorcas marsupialis</i>						
Steenbok	0.5 ± 0.4	0.0–1.3	3	1.8 ± 0.5	0.3–3.1	6
<i>Raphicerus campestris</i>						
Suni	—	—	—	14.4	14.4	1

Table 2. Continued

Prey species	Lion			Hyaena		
	%	Range (%)	<i>N</i>	%	Range (%)	<i>N</i>
<i>Neotragus moschatus</i>						
Thomson gazelle	13.3 ± 6.7	0.4–22.6	3	10.4 ± 5.5	1.3–20.2	3
<i>Eudorcas thomsonii</i>						
Topi	5.6 ± 3.8	0.9–17.0	4	5.8 ± 3.0	2.8–8.8	2
<i>Damaliscus korrigum</i>						
Tsessebe	0.7 ± 0.2	0.1–1.3	5	4.5 ± 4.1	0.4–8.6	2
<i>Damaliscus lunatus</i>						
Warthog	11.6 ± 2.0	1.1–35.5	25	5.1 ± 2.4	0.1–17.2	7
<i>Phacochoerus africanus</i>						
Waterbuck	5.5 ± 0.9	0.1 + 14.9	22	2.9 ± 1.1	0.0–8.6	8
<i>Kobus ellipsiprymnus</i>						
Wildebeest	24.6 ± 3.8	2.6–60.6	19	28.3 ± 8.0	3.7–76.9	10
<i>Connochaetes taurinus</i>						
Zebra	11.6 ± 1.7	1.0–37.5	23	17.5 ± 5.1	1.5–63.5	12
<i>Equus quagga</i>						
Other	6.2 ± 1.6	0.2–26.9	17	12.2 ± 3.3	0.7–37.8	12

N is number of studies reporting a given prey to be eaten by the predator. Bold italic numbers indicate main prey species.

Table 3. Diet composition in prey size classes for lions and hyaenas. Proportions are averaged for all ecosystems with available data

Prey class	Lion		Hyaena	
	%	Range (%)	%	Range (%)
Very small	2.8 ± 0.1	0.6–12.3	5.6 ± 1.3	0.8–14.4
Small	29.4 ± 6.6	2.7–62.3	31.8 ± 2.5	3.5–67.9
Medium	45.1 ± 6.2	3.3–90.1	41.5 ± 8.6	4.7–89.4
Large	20.1 ± 1.9	2.8–61.7	7.9 ± 0.1	1.4–23.5
Very large	7.6 ± 0.4	1.3–21.9	14.0 ± 0.8	2.7–31.6
Other	6.2 ± 0.2	1.1–26.9	13.2 ± 1.7	1.9–37.8

foraging group size decreased with increasing adult pride size ($\rho = -0.95$, $P = 0.004$, $N = 6$).

Prey abundance appears to be key to understanding the mechanisms of coexistence between hyaenas and lions, although not in a simple way. The more prey available, the more these predators are able to coexist, i.e. competition pressure decreases with increasing prey abundance. However, increasing prey abundance leads to an increase in both predators' densities, thus possibly increasing interference competition, as they are more likely to encounter each other. Further, as prey availability increases so does hyaena clan size while their HR decreases. All these combine to enable hyaenas to sustain competition with lions effectively: as they form bigger clans, more clan members share a smaller territory and can be recruited rapidly in conflict situations. Therefore, as prey abundance increases, hyaenas are more able to protect their kills or aggressively to take over lion kills.

We expected a positive correlation between lion pride size and hyaena foraging group size, since both predators in larger groups would be better able to defend their kills or chase the other species from theirs. However, despite a low sample size ($N = 6$), we found a negative correlation between

these two variables (Fig. 4) which is somewhat surprising. It is interesting to note that pride size does not seem to be related to prey abundance. However, pride size might be more related to local (e.g. within HRs) prey availability rather than the global one over the entire PA (Hanby & Bygott, 1995; Mosser *et al.*, 2009). In addition, pride members do not spend all of their time together and sometimes split into different groups that hunt independently (Schaller, 1972). Increasing prey abundance could lead to the formation of larger clans in hyaenas thereby increasing the risk of lions losing their kills and decreasing their chances of stealing hyaena kills. In this case, it would be beneficial for lions to form smaller prides, making them less conspicuous when on the move, and tackling smaller prey which can be quickly consumed, and hence reducing the time spent at carcasses. If this is true, it would demonstrate that competition with hyenas impacts lion group-forming patterns as suggested by Cooper (1991).

Overall, it appears that if prey abundance is reduced – despite predator densities, and hence their encounter rates, decreasing – competition pressure is likely to increase and local competitive exclusion may occur. We tested these hypotheses using published data on the intensity of competition between the two species. We expected diet overlap, kleptoparasitism and direct killing to increase with decreasing prey abundance.

IV. THE POTENTIAL FOR COMPETITION BETWEEN HYAENAS AND LIONS

(1) Dietary breadth and overlap

Dietary breadth (Levin's index) was higher for hyaenas (Table 4). This is in accordance with their catholic diet and opportunistic feeding behaviour. Pianka's index was

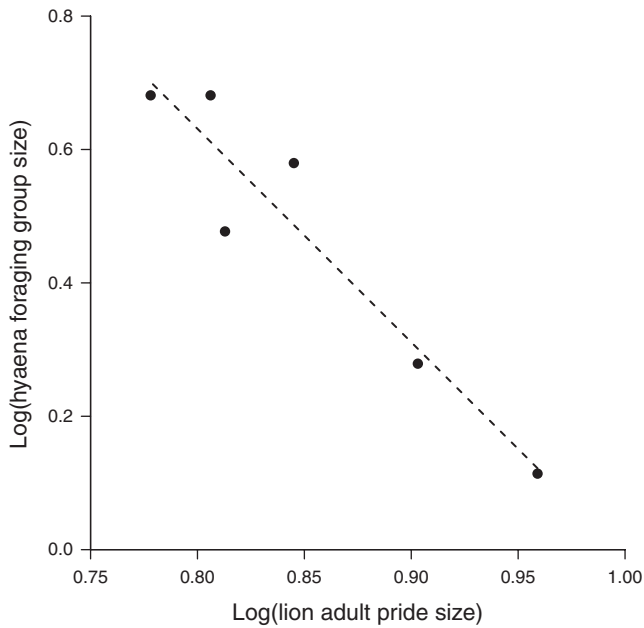


Fig. 4. Hyaena foraging group size *versus* lion adult pride size.

Table 4. Dietary breadth (Levin's index) and overlap (Pianka's index) for lions and hyaenas

Species	Levin's index	Pianka's index	% overlap
Hyaena	7.94	0.92	—
Lion	7.06	0.82	—
Both	—	0.43	68.5

also higher for hyaenas indicating that they proportionally share more of their prey with lions than *vice versa* (Table 4). The overall percentage of diet overlap between these two predators was high (over 68%), confirming the value of 68.8% preferred prey species overlap reported by Hayward (2006). This suggests that there is strong potential for exploitation competition between lions and hyaenas.

(2) Kleptoparasitism

From 13 studies conducted in 10 locations in Southern Africa, it is clear that kleptoparasitism occurs in both directions. It is however impossible to determine to what extent this activity contributes to predator diets. Hyaenas appear to lose more of their kills (70%) to lions than *vice versa* (35%, Wilcoxon test, $W = 27$, $P = 0.015$, Table 5). Despite this, hyaenas do not lose more food to lions in term of food biomass than they gain from them (11.7 *versus* 11.6%, $W = 14$, $P > 0.05$, Table 5), neither do lions to hyaenas (16.7 *versus* 22.4%, $W = 5$, $P > 0.05$, Table 5). Somewhat surprisingly, both predators obtain a similar amount of food from the other (12 *versus* 22.4%, $W = 5.5$, $P > 0.05$, Table 5). Hyaenas most probably compensate for the loss of their kills by obtaining more food from lions by scavenging their leftovers. Hyaenas are well equipped to acquire nutrients from carcasses due to

Table 5. Kleptoparasitism between hyaenas and lions. Total percentage of food loss takes both killed and scavenged carcasses into account

	Hyaena	Lion
% of total food loss	11.7 ± 1.3 (0.6–24) $N = 6$	16.7 ± 2.2 (0.6–30) $N = 3$
% of kills at which the other species is present	23 ± 1.4 (20–25.9) $N = 2$	55.9 $N = 1$
% of kills lost when the other species is present	69.7 ± 2.2 (35.7–100) $N = 5$	34.6 ± 1.9 (0–57.1) $N = 6$
% of kills made by the species where the other one was present	64.9 ± 12.3 (41.5–92.3) $N = 3$	7.3 $N = 1$
% of food obtained from the other species (kleptoparasitism and scavenging)	11.6 ± 1.18 (4.5–20) $N = 5$	22.4 ± 1.8 (5.6–35.8) $N = 4$

their very efficient digestive system and strong jaws, allowing them to make use of skin, bones and dry meat where lions cannot (Kruuk, 1972).

Kleptoparasitism success has been suggested to depend on the ratio of hyaenas to lionesses and large cubs at a kill and/or the presence of adult male lions. This implies that lion foraging group size should have an impact on hyaenas. Only two studies (Cooper, 1991 in Savuti, Botswana; Honer *et al.*, 2002 in Ngorongoro Crater, Tanzania) examined the ratio of lionesses to hyaenas at kills; both concluded that larger groups of hyaenas have a higher chance of displacing lions from kills or retaining their own kills. Cooper (1991) showed that to take over a kill, hyaenas had to outnumber lions by a factor of 4. This ratio is linked to clan and pride sizes, and hyaena foraging group sizes, as well as territory sizes. Indeed, the larger the clan and the smaller the territory, the easier and quicker it is for hyaenas to recruit clan members and therefore to access/defend a kill. In Etosha NP, where hyaenas were scattered over large territories, they were unable to steal kills from lions and to defend their own kills (Trinkel & Kastberger, 2005).

Three studies report the effect of the presence of an adult male lion on the outcome of encounters at carcasses. They all conclude that if at least one male lion is present, hyaenas will almost always lose their kill and never access a lion kill. In the Ngorongoro Crater, Honer *et al.* (2005) reported that when a male lion was present at a carcass, hyaenas never attempted to acquire it before the male left. Cooper (1991) showed that in the Savuti region, when hyaenas were chased away by a male lion they usually left the scene, whereas if only lionesses and cubs were present, they remained in the vicinity of the carcass. Elliott & McTaggart-Cowan (1978) report that male lions never abandoned their kills to hyaenas whereas lionesses sometimes did. Furthermore, prides with males obtain between 10 and 40% of their food from hyaenas compared with 7% for a pride of

females. Hyenas seem to fear male lions to a much greater extent than lionesses, perhaps because male lions are a higher cause of hyaena mortality than lionesses (see Section IV.3).

However, we were not able to detect any pattern suggesting an effect of lion group size (clan, pride, foraging group) or adult sex ratio in lions on kleptoparasitism intensity. This might be due to the very limited number of locations where values for these parameters were available ($N < 6$). Based on these results, it appears that no species is consistently dominant in food-related interactions, with the outcome of such interactions rather depending on the ecosystem in which they occur. If an adult male lion is present, then hyenas are subordinate. However, if the lion group is composed only of lionesses and sub-adults, then the numerically dominant species wins the encounter. In some areas, one species may benefit more from the other (Kruuk, 1972; Schaller, 1972; Cooper, 1991; Honer *et al.*, 2002), while in others, neither has a clear advantage (Mills, 1990).

(3) Intraguild predation

Lions were seen to kill hyenas in 10 studies (six locations, Table 6). Seven of them report lions, particularly adult males, as a primary cause of mortality for both adult and juvenile hyenas (Kruuk, 1972; Watts & Holekamp, 2008, 2009). Most predation events on adult hyenas occur at kills during fights with lions. There is little information on hyenas killing lions, although a cub was killed in the Serengeti (Schaller, 1972) and an old lioness in Hwange NP (Loveridge *et al.*, 2010a). Lionesses are also sometimes severely injured in fights with hyenas. Although we did not find any correlation between the intensity of direct killing of hyenas by lions and prey abundance (prey total density: $\rho = -0.31$, $P = 0.56$, prey total biomass: $\rho = 0$, $P = 1$), this could be due to the very limited sample size (six locations).

(4) Spatial and temporal overlap

Both species overlap in distribution to a wide extent. Lions share 94.9% of their overall distribution range with hyenas, while hyenas only share 33.6% of their distribution with lions (Fig. 1).

Hyenas are generalists in their habitat requirements; they do not need vegetation as cover while hunting. They are therefore likely to use any habitat where prey are most abundant. On the contrary, the hunting tactics of lions require some degree of concealment: hunting success increases in taller grass (Funston, Mills & Biggs, 2001) and when the terrain facilitates concealment (Schaller, 1972; Elliott, Cowan & Holling, 1977; Van Orsdol, 1984; Davidson *et al.*, 2012). In addition, lions appear to favour habitats where prey are more easily caught rather than where they are more abundant (Hopcraft, Sinclair & Packer, 2005). Optimal habitat for lions seems to be open woodland with thick bush and grass complexes that provide shade for resting and cover for ambushing prey (Sunquist & Sunquist, 2009). Davidson *et al.* (2012) showed that within their HR, lions

select for bush grassland and open areas around waterholes, both characterised by high prey density. However, in their study on cheetah, Broekhuis *et al.* (2013) showed that lions and hyenas select for mixed woodland and grassland while avoiding swamps in Moremi GR, Botswana. Mills & Biggs (1993) also noted that in Kruger NP, South Africa, both hyenas and lions favour thickets with high concentrations of impalas. A more recent study (Schuette *et al.*, 2013) showed that patterns of occupancy of mixed-use landscapes in Kenya were very similar between lions and hyenas. For instance, they both favoured habitat close to water and highest occupancies were found in the PA. Thus both species may prefer the same habitat, most probably where prey are most abundant, thus increasing their probability of encounter.

Both predators are reported to be mainly nocturnal and crepuscular (Kruuk, 1972; Schaller, 1972; Mills, 1990; Kolowski *et al.*, 2007). Both can also be active during cool winter days. In the Okavango Delta, Botswana, Cozzi *et al.* (2012) showed that 60 and 68% of the activity budget of lions and hyenas, respectively, was at night, thus restricting possible temporal partitioning. These results are comparable to those of Hayward & Slotow (2009) showing an overlap in activity period of more than 80% between hyenas and lions. However, Schuette *et al.* (2013) showed that even though both were predominantly nocturnal, their activity peaks differed slightly. Hyenas were more likely to be active during a couple of hours after sunset and before sunrise, while lions were more active during the middle of the night.

To date, there is no study using telemetry data on both species simultaneously to allow evaluation of spatio-temporal avoidance. It is possible that, depending on prey and predator population parameters such as density, group size or lion adult sex ratio, hyenas avoid (risk of kleptoparasitism and predation) or follow (kleptoparasitism and scavenging opportunities) lions.

V. CONDITIONS FOR FACILITATION

(1) Resource partitioning in prey size

Hyenas are much smaller than lions, and although they hunt in groups, we expected that both predators would select prey of different body size, at least to some extent (Kissui & Packer, 2004; Hayward & Kerley, 2005; Donadio & Buskirk, 2006; Hayward, 2006). The main prey for lions and hyenas are medium-sized herbivores (Tables 2 and 3) and when their ratio in the prey population (number of medium-sized prey/number of total prey) increases, hyenas and lions both increase the proportion of medium-sized ungulates in their diet. However, hyenas seem to make more use of small and very large prey than do lions, even though this tendency is not statistically significant (Table 3).

We expected dietary breadth to decrease with increasing prey abundance as the availability of preferred prey would increase. Niches should also increasingly differ with increasing prey abundance. In addition, we expected diet

Table 6. Main causes of death of hyaenas

Location	Sample size (number of deaths recorded)	% death caused by lions	Other cause of deaths	Lions as a leading cause of mortality?	Time frame	References
Chobe NP	13	53	NA	Yes	1986–1988	Cooper (1991)
Etosha NP	NA	71	NA	Yes	2000–2001	Trinkel & Kastberger (2005)
Kalahari NP	50	12	24% rabies	No	1972–1980	Mills (1990)
	35 adults	9	12% humans			
	15 juveniles	13	3% rabies 20% rabies			
Kruger NP	6	66.7	NA	Yes	1982–1984	Henschel & Skinner (1991)
Masai Mara GR	5	60	30% humans	Yes	1979–1983	Frank (1986)
	73	27	18% humans	Yes	1988–2006	Watts & Holekamp (2009)
	24 adults	15	10% humans	NA		
	49 juveniles	15	15% hyaenas 15% starvation 10% disease 5% humans	NA		
	16	69	31% humans	Yes	1979–1992	Frank, Holekamp & Smale (1995)
	13 adults	69	31% humans	Yes		
	3 juveniles	67	33% humans	Yes		
Serengeti NP	NA	10.2	18.2% hyaenas 15.9% starvation	No	1987–1992	Hofer & East (1995)
	28	46.4	17.9% dis- ease/starvation 14.3% hyaenas 7.2% humans	Yes	1964–1969	Kruuk (1972)
	18 adults	44.4		Yes		
	10 juveniles	50		Yes		
	NA	10 individuals killed		NA	1966–1969	Schaller (1972)

NA, not available.

overlap to be lower in areas rich in prey, due to resource partitioning with hyaenas switching to small and very small prey, leaving medium prey to lions.

Hyaena dietary breadth seems to be independent of prey abundance. However, lion dietary breadth decreases significantly with increasing total prey biomass ($\rho = -0.51$, $P = 0.017$, $N = 22$) and with total prey density. In addition, we found that Pianka's index for hyaenas decreases significantly with increasing small prey biomass (Spearman correlation, $\rho = -0.76$, $P = 0.025$, $N = 10$) and small prey biomass ratio in the prey community ($\rho = -0.67$, $P = 0.039$, $N = 10$). Percentage overlap also decreased with increasing small prey density ratio in the ecosystem ($\rho = -0.68$, $P = 0.035$, $N = 10$) as does the overall Pianka's index ($\rho = -0.61$, $P = 0.037$, $N = 10$). All these results suggest that increasing availability of small prey in an ecosystem allows hyaenas to reduce their niche overlap with lions.

For medium-, large- and very-large-sized prey, juveniles are much smaller than adults and easier to kill, providing another opportunity for niche partitioning between hyaenas and lions. We found that the proportion of juveniles in the hyaena diet was significantly higher than in the lion diet

Table 7. Proportion of adults and juveniles in the diets of hyaenas and lions

Species	Proportion of adults in the diet	Proportion of juveniles in the diet
Hyaena	0.66 ($N = 2232$)	0.34 ($N = 1134$)
Lion	0.77 ($N = 4119$)	0.23 ($N = 1221$)

($\chi^2 = 98.75$, d.f. = 1, $P < 0.0001$, Table 7), in agreement with results of Mills (1984a) in the Kalahari desert, Kruuk (1972) in the much richer Serengeti ecosystem and Mills & Biggs (1993) in Kruger NP. By preying on different age classes within the same prey species, lions and hyaenas will reduce their niche overlap.

(2) Scavenging opportunities and food gains from the other species

Here, we define scavenging as a species consuming food left by another species, with no actual fight or confrontation. This food is thus cost free for the finder. It is very difficult

to quantify scavenging benefits from another species as this would require knowledge of all kills made by those two species over a certain period of time, the amount of food left and all the carcasses at which they fed. Both hyaenas and lions are efficient scavengers that potentially benefit from the other's leftovers. However, hyaenas probably gain more from such scavenging opportunities as they can use elements such as bones and skin that lions cannot; lions require meat remaining in a carcass for it to be profitable.

Scavenging appears to be more beneficial to hyaenas, making up 5% of their diet in the Ngorongoro Crater (Kruuk, 1972; Palomares & Caro, 1999), 36.3% in the Kalahari (Mills, 1984a) and as much as 80% in the Timbavati GR (Bearder, 1977). For lions, between 1 and 42% of their food is scavenged, most of it coming from hyaenas (Schaller, 1972; Elliott & McTaggart-Cowan, 1978; Hanby, Bygott & Packer, 1995). Once again, there is a difference between the sexes: lionesses appear to scavenge less (~7% of their food) than males (up to 40%, Elliott & McTaggart-Cowan, 1978; Sunquist & Sunquist, 2009).

Overall, hyaenas obtain (from scavenging and kleptoparasitism) between 5 and 20% (Kruuk, 1972; Henschel & Skinner, 1990; Gasaway, Mossestad & Standers, 1991; Honer *et al.*, 2002) of their food from lions and lose between 0.6 and 24% of their food to lions (Kruuk, 1972; Cooper, 1991; Cooper *et al.*, 1999; Watts & Holekamp, 2008, Table 5). In Amboseli NP, Watts & Holekamp (2008) reported that hyaenas lose 0.2 kg/day of meat to lions, but gain slightly less than 0.3 kg/day, leading to a net benefit of 0.05 kg/day of meat. Thus, by coexisting with lions hyaenas gain only 1.5% of the 3.5 kg they have to ingest daily (Kruuk, 1972). However, in the Masai Mara, the same study reported that hyaenas have a net loss of 0.16 kg/day of meat to lions. Clearly, the dominance balance between competing species depends on the ecosystem involved, but overall the net loss or gain is minimal compared to their overall daily requirements.

VI. CONCLUSIONS

(1) Both hyaena and lion population densities are linked to that of their prey and thus are positively correlated with each other (Hayward *et al.*, 2007c). Their diets are very similar (Hayward, 2006) but there are suggestions that they may reduce their niche overlap, most probably by preying on different prey size (species or age classes). Figure 5 presents a summary of our findings. When prey abundance is high, large foraging groups of hyaenas could have a negative impact on lion pride size. Conversely, at low prey density, hyaena pressure on lion group size would be released allowing lions to form bigger groups and to outcompete hyaenas at carcasses, potentially leading to a reduced abundance of hyaenas. This situation is unlikely to happen in PAs where prey densities are usually stable, but may occur in other areas. However, in unprotected areas, lion densities are low due to conflict with humans (retaliatory killing) and trophy hunting (see Chardonnet *et al.*, 2010).

(2) While exploitation competition is likely to have an important role in shaping large carnivore communities (Loveridge *et al.*, 2007b), the impact of interference competition should not be neglected and more research is needed to better understand large carnivore guild functioning. For instance, there are few data published on their spatio-temporal use of their habitat. In addition, most studies were conducted in open areas, but interactions are likely to differ in closed savannas. For instance, it is much more difficult for predators to detect carcasses in dense habitat, potentially reducing the extent of kleptoparasitism in such areas (Hunter, Durant & Caro, 2007). Habitat heterogeneity in space and time has a crucial role in facilitating coexistence of hyaenas and lions, as it does for cheetahs, helping them to live sympatrically with hyaenas and lions (Mills, Broomhall & Du Toit, 2004; Hunter *et al.*, 2007; Broekhuis *et al.*, 2013). Further research is needed on their simultaneous resource use (food, space and time) to be able to identify the mechanisms behind their coexistence, and thus to increase our understanding of how both species can be maintained within small PAs.

(3) It is important to note that with populations within PAs (calculated using carnivore densities extracted from the literature) averaging 936 ± 232 hyaenas (10–5148) and 519 ± 136 lions (15–4095), any change in the competition balance could have dramatic effects. For instance, if prey abundance is reduced, prey guild composition is modified or the habitat is changed, this could lead to one species outcompeting the other, at worst resulting in local extinction. For instance, an increase in the small-prey community should favour hyaenas more than lions. In addition, hyaenas and lions can have strong effects on other sympatric carnivores. Increasing competition pressure with lions and hyaenas is thought to be responsible for the decrease in African wild dog (*Lycaon pictus*) populations inside PAs (Durant, 1998) and could be responsible for their local extinction (Creel & Creel, 1996; van der Meer *et al.*, 2011). A recent series of papers (Packer *et al.*, 2013a,b) argue that fencing is a solution for lion conservation. However, within small fenced areas, lion populations need to be actively managed to avoid high populations having a negative impact on prey communities (Miller *et al.*, 2013). In small fenced areas, it would be possible that strong lion populations would outcompete hyaenas and lead to their local decline and possibly extinction. Large PAs, where both predators and prey are free to roam over large distances seem to be extremely important for the conservation of these carnivores, particularly lions, and for the maintenance of their role in the food chain and ecosystem processes.

(4) Even though spotted hyaenas are classified as 'least concern' by the IUCN, their population is decreasing across their range (Honer *et al.*, 2013), including PAs, as is the lion population (Bauer *et al.*, 2013). A population genetics model predicted that large lion populations (50–100 prides) are necessary to conserve genetic diversity and avoid inbreeding (Bauer *et al.*, 2013); this condition is rarely met in the wild. Male dispersal is also important to maintain genetic diversity

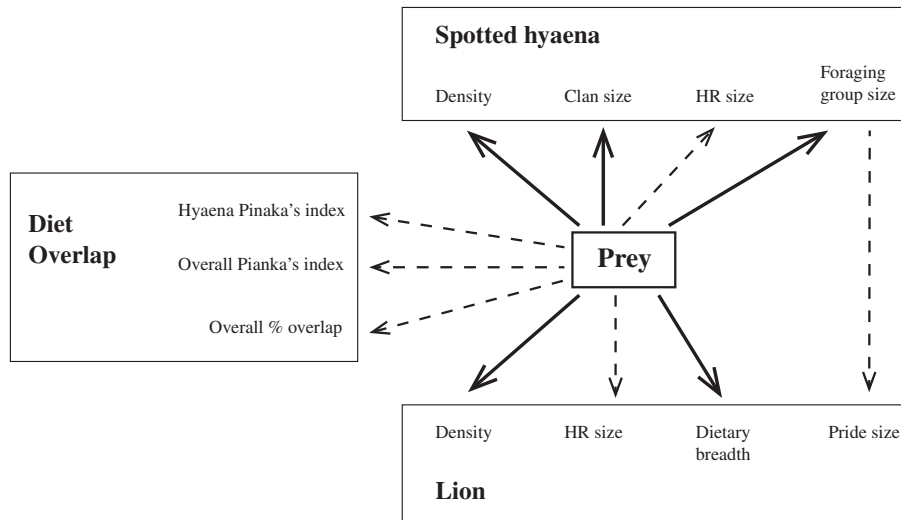


Fig. 5. Mechanisms of interactions between spotted hyaenas and lions showing the key role of prey. Solid arrows indicate positive impacts while dotted arrows reflect negative effects. HR, home range.

by connecting distant populations. Areas surrounding PAs can be sinks for these male lions (Björklund, 2003; Elliot *et al.*, 2014) and can affect the sex ratio of the whole lion population within the PA (Loveridge *et al.*, 2007*b*). We showed that the presence of an adult male at a kill always allows lions to outcompete hyaenas. If the adult sex ratio in the lion population changes, this might affect the competition balance and lions can either become the dominant or the subordinate species depending on other local conditions. Trophy hunting can induce such changes in lion populations (retaliatory killing, accidental snaring or trophy hunting, e.g. Packer *et al.*, 2009; Loveridge *et al.*, 2010*a*) and thus has the potential to disturb the equilibrium between lions and hyaenas.

(5) Large carnivores are iconic species, but because they naturally live at low densities are at increased risk of extinction (Gittleman *et al.*, 2001; Macdonald & Sillero-Zubiri, 2004). We therefore need a better understanding of their effects on each other to make decisions about their conservation. We show here that the relationship between hyaenas and lions is a complex balance of competition and facilitation. Some situations such as ecosystems poor in prey will tend to favour lions, while others favour hyaenas. In order to promote their coexistence, it is crucial to maintain a diverse and abundant prey base. This paper focuses on two large social carnivores, but it is important to note that other mechanisms may be relevant in solitary species such as cheetahs or cougars (*Puma concolor*) as well as in smaller species such as foxes (*Vulpes sp.*) or wild cats (*Felis sp.*). We hope that our work will promote new research projects investigating predator coexistence on a larger scale and that it will motivate the creation of conservation programs integrating all levels of interactions among species. In particular, there is a clear need to examine the spatio-temporal relationships between hyaenas and lions at different scales and investigate how these relationships

can influence whole-ecosystem functioning through trophic cascades.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. List of references used with country of origin, size of protected area (PA), ecological information, study period and area, and study subjects.

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