Biological Conservation 292 (2024) 110542

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Diet responses of two apex carnivores (lions and leopards) to wild prey depletion and livestock availability

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ARTICLE INFO

Keywords:
Livestock depredation
Human-carnivore conflict
Carnivore conservation
Cattle
Lion
Leopard

ABSTRACT

Prey-depletion is a significant threat facing carnivores globally, resulting in reduced population numbers, diet alterations, and increased livestock consumption, which increases human-carnivore conflict. We compared the diets of lions (*Panthera leo*) and leopards (*P. pardus*) in the prey-abundant Kruger National Park (KNP, South Africa), with that in the prey-depleted/livestock-abundant Limpopo National Park (LNP, Mozambique), using scat analyses. Lions and leopards had broader dietary niche breadths and consumed a greater proportion of smaller (previously suboptimal) prey in LNP relative to KNP. Downshifting in lion and leopard prey size consumption and the continued reliance on previously suboptimal prey may adversely affect carnivore fitness. Diet overlap between lions and leopards was low in both KNP and LNP, suggesting that even when prey is depleted, lions and leopards can partition food resources. Whilst consuming livestock in LNP, lions and leopards strongly avoided cattle (*Bos taurus*), even though they are the most abundant ungulate in LNP. This suggests that lions and leopards modulate their foraging behavior, so reducing human-carnivore conflict. Efforts to promote carnivore recovery and reduce human-carnivore conflict should focus on prey population restoration, particularly large prey.

1. Introduction

Carnivore populations are, in part, limited by prey availability, with carnivore densities positively correlating with the abundance of their preferred prey (e.g., van Orsdol et al., 1985; Rosenblatt et al., 2016). Large (> 21.5 kg) terrestrial carnivores are dependent on a vertebrate diet, primarily feeding on ungulates weighing between 10 and 1000 kg (Carbone et al., 2011). However, prey populations are declining globally, due to habitat loss, over-harvesting, and competition with livestock (Ripple et al., 2015), with much of the remaining habitat available for carnivores being prey-depleted (Wolf and Ripple, 2016). Whilst carnivores can persist (albeit at lower densities) in human-impacted, prey-depleted landscapes (Karanth and Sunquist, 1995; Woodroffe et al., 2007), prey depletion can result in increased competition between sympatric carnivores (Dorresteijn et al., 2015), due to reduced dietary partitioning (Creel et al., 2018; Smith et al., 2018; Manlick and Pauli, 2020). Since dietary partitioning is a crucial mechanism for competition reduction (Donadio and Buskirk, 2006), understanding the impact of prey depletion on carnivore diets is of direct conservation relevance.

Optimal foraging theory predicts that when preferred prey are depleted, carnivores will increase the consumption of previously suboptimal prey (Pyke et al., 1977) and increase the number of species they prey upon (Svanbäck and Bolnick, 2007), resulting in dietary niche expansions. Dietary niche expansions in response to prey depletion have been recorded in various North American carnivore species (Moss et al., 2016; Manlick and Pauli, 2020). Relative to small prey, large prey are more vulnerable to human impacts due to their diet requirements, long life histories and high human-value, and are usually the first to experience population declines under human pressure (Ripple et al., 2015). Carnivores may therefore be forced to increase their consumption of smaller prey in human-impacted systems due to large prey depletion (Creel et al., 2018).

Alternatively, reduced prey availability may force carnivores to hunt fewer prey species, compressing their diet breadths to what is available. In Zambia's Kafue National Park, for instance, the loss of large prey resulted in dietary niche compression and increased diet overlap for the

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https://doi.org/10.1016/j.biocon.2024.110542
Received 3 August 2023; Received in revised form 20 December 2023; Accepted 5 March 2024

large carnivore guild (Creel et al., 2018). Similarly, various North American carnivores exhibit dietary niche compressions due to prey depletion (Smith et al., 2018). Although diet flexibility apparently bodes well for carnivore conservation, changes in prey selection and hunting strategies may result in reduced energy gains when hunting previously suboptimal prey and negatively affect fitness (Gorman et al., 1998; Vinks et al., 2021).

Livestock depredation patterns are partly influenced by wild prey and livestock availability, carnivore prey-size preferences, and the perceived fear of humans (Khorozyan et al., 2015; Everatt et al., 2023). Whilst some studies have shown livestock preference among carnivores (Yirga et al., 2013; Loveridge et al., 2017), possibly due to livestock having limited morphological and behavioral defenses against predation compared with wild prey (Ogada et al., 2003), carnivores generally prefer wild prey over livestock (Khorozyan et al., 2015). Livestock depredation often results in persecution and retaliatory killings of carnivores (Ontiri et al., 2019). Thus, carnivores may be able to perceive the danger of hunting livestock and modulate their foraging behavior to reduce human-carnivore conflict (Everatt et al., 2023), resulting in livestock avoidance (Valeix et al., 2012; Tumenta et al., 2013; Yirga et al., 2013; Everatt et al., 2023). Prey depletion, however, may force carnivores to increase the consumption of livestock (Khorozyan et al., 2015). Given that human-carnivore conflict and persecution are key threats jeopardizing the global survival of carnivores (Ripple et al., 2014), it is imperative to understand the importance of livestock in carnivore diets in prey-depleted systems, to inform human-carnivore conflict mitigation programs.

African lions (*Panthera leo*) and leopards (*P. pardus*) serve as useful model species to explore the impact of wild prey depletion and livestock availability on carnivore diet responses, due to their differing ecological traits and adaptability. Globally, lions and leopards are classed as vulnerable (Bauer et al., 2016; Stein et al., 2020) and are limited by exploitative and interference competition with humans (Everatt et al., 2019b; Rogan et al., 2022). Lions are Africa's largest carnivore (120–225 kg) and are competitively dominant over leopards (20–90 kg; Mills and Harvey, 2001). Lions hunt cooperatively (Mills and Harvey, 2001) and prefer prey weighing between 92 and 632 kg (Clements et al., 2014). Leopards are solitary, but with highly adaptable hunting strategies, and have the broadest diet breadth of Africa's large carnivores (Mills and Harvey, 2001). Leopards prefer prey weighing between 1 and 45 kg (Clements et al., 2014). Due to their different prey preferences, competition for food between lions and leopards is likely limited when prey is abundant (Hayward and Kerley, 2008).

Here we assessed carnivore diet responses to prey depletion and livestock availability, by comparing lion and leopard diets in the prey-abundant Kruger National Park (KNP) and the prey-depleted/livestock-abundant Limpopo National Park (LNP; Lindsey et al., 2017). Using prey size as a proxy for foraging profitability, we hypothesized that lions and leopards will consume larger, non-domesticated prey in KNP relative to LNP. We expected that lions and leopards would either: (1) expand, or (2) compress their dietary niche breadths in LNP relative to KNP; or due to their differing hunting strategies and dietary flexibility, (3) respond differently to each other with lions compressing and leopards expanding their diet breadths in LNP relative to KNP. We hypothesized that there would be a greater degree of dietary niche overlap in LNP relative to KNP. Regarding livestock (cattle (*Bos taurus*)) use in LNP, we hypothesized that lions and leopards would either: (1) prefer; or (2) avoid livestock.

2. Methods

2.1. Study area

The study focused on the northern half (north of Olifants River) of South Africa's KNP (19,485 km^2), and the adjacent LNP (11,233 km^2; Fig. S1) in Mozambique within the Greater Limpopo Transfrontier Conservation Area. The climate is warm, dry tropical, receiving variable rainfall, between 400 and 530 mm/year (Gandiwa et al., 2016). Geologically, Granite and Karoo Basalt dominate in the west and east of KNP, respectively (Schutte, 1986). Rhyolite volcanic rock and a red sand mantle are dominant in the north and south of LNP, respectively (DINAC, 2003). Vegetation across the region is classified as mixed savanna and grasslands, with riverine forest in low-lying areas (Gertenbach, 1983; Stalmans et al., 2004).

KNP is well-developed for conservation and ecotourism, with extensive infrastructure (e.g., roads and accommodation) and staff, and no local communities or livestock residing in the park (Everatt et al., 2019b). Wildlife populations in KNP are considered near carrying capacity (Lindsey et al., 2017), barring rhino (*Ceratotherium simum* and *Diceros bicornis*), that are depleted by poaching (Ferreira and Dziba, 2023). LNP is poorly developed for ecotourism, with approximately 30,000 people residing in the park (Milgroom and Spierenburg, 2008), together with approximately 36,000 cattle, and 8000 sheep (*Ovis aries*) and goats (*Capra hircus*; Grossmann et al., 2014), and packs of domestic dogs (*Canis lupus familiaris*; Andresen et al., 2014). Human activities in LNP include subsistence crop and livestock farming, and illegal bushmeat hunting, logging, charcoal production, and lion, rhino, and elephant (*Loxodonta africana*) poaching (Grossmann et al., 2014; Everatt et al., 2019a). Wildlife populations in LNP are well below carrying capacity (Lindsey et al., 2017), due to Mozambique's civil war (1977–1992) decimating the region's wildlife (Hatton et al., 2001), decades of poaching (Baghai et al., 2018) and insufficient conservation funding (Lindsey et al., 2017). There are approximately 1600 (Ferreira and Funston, 2010) and 22 (Everatt et al., 2019a) lions, and 2000 (Maputla et al., 2013) and 66 (Everatt unpublished) leopards in KNP and LNP, respectively.

2.2. Scat collection

Lion and leopard scats were collected between 2014 and 2015 in LNP, and in 2015 in KNP, following procedures per MacKay et al. (2008). Scats were collected across the landscape by walking a trained detection dog (Conservation Canines) for 10–20 km in the early morning, where scenting was optimal. Care was taken to ensure an even sampling effort across road-accessible regions of northern KNP and LNP, and no area was sampled more than once to minimize pseudo-replication (Fig. S1). Scats were identified in the field based on their physical features (color, size, segmentation, etc.) and deposition characteristics. We then genetically tested the identity of the scat donor using single nucleotide polymorphisms (see Supplementary Material for DNA extraction and genotyping procedures), thereby ensuring that our diet descriptions were for the focal carnivores. Scat locations were recorded using a Cyber tracker V3.440 (www.cybertracker.org/), and sampled scats were double-wrapped in air-tight, plastic bags with silica in the inner bag for storage.

2.3. Prey density estimates

Relative abundance data on wild prey and livestock (species between 16 and 750 kg) were obtained from Everatt et al. (2023). Here, transects driven at <20 km/h with a minimum of two observers, were conducted in the early morning and late afternoon, when animals were most active. At each observation, the species, number of individuals, and location (using a Cyber tracker V3.440 program) were recorded. Given that Everatt et al. (2023) focused on lion diet, some potential leopard prey species (e.g., klipspringer *Oreotragus oreotragus*) were not surveyed.

2.4. Physical sorting

Of the 109 and 192, and 208 and 148 scats identified in field as lions and leopard from LNP and KNP, respectively, we randomly selected 82 scats from each predator from each national park. However, following genetic identification of scat donors, our sample size was reduced to 58 and 48 lion samples from KNP and LNP respectively, and 60 leopard samples for both KNP and LNP. We soaked samples in a 5 % formalin solution for 24 h to soften them and kill parasites. We then rinsed samples under running water in a sieve, retaining solid remains (hair, bones, etc.). This material was then oven-dried at 50 °C for 24–48 h (Van de Ven et al., 2013). We macroscopically examined bone fragments and hooves from the scat samples (Van de Ven et al., 2013) and randomly subjected 10 hairs from each scat sample to microscopic hair scale imprint identification (Perrin and Campbell, 1980). We mounted hairs on slides with transparent nail varnish and removed them once the varnish dried to obtain a hair scale imprint (Perrin and Campbell, 1980). After training with known samples, we microscopically examined imprints with a light microscope at 400× magnification and compared the imprints with a reference collection available at the Centre for African Conservation Ecology at Nelson Mandela University, and other published material (Perrin and Campbell, 1980; Keogh, 1983; Buys and Keogh, 1984; Keogh, 1985; Wade et al., 2018).

2.5. *Statistical analyses*

Statistical analyses were performed using R software (R Core Team, 2021), applying a significance value of 0.05 throughout.

2.5.1. *Sampling efficiency*

To test for adequate sampling in terms of the number of scats sampled, we generated species accumulation curves (Foggo et al., 2003) for each predator at each site, using the package “vegan” (Oksanen et al., 2013). Adequate sampling was achieved when the number of prey species identified in the scats reached an asymptote (Oksanen et al., 2013). We used segmented regression models, in the package “segmented” (Muggeo, 2008), to calculate breakpoints, to determine where species accumulation curves reached asymptotes.

2.5.2. *Diet composition*

We analyzed diet composition on two levels. Firstly, we calculated the frequency of occurrence of each prey species recorded in the diets of lions and leopards, expressed as the percentage of scats in which the prey species was sampled. However, since this approach overestimates the importance of small prey, we calculated a corrected frequency of occurrence to account for more than one prey item recorded in a single scat. We estimated the corrected frequency of occurrence as the proportion of each prey species relative to the number of different species in each scat, such that if 4 prey species were recorded in a scat, each species counted as 0.25 (Karanth and Sunquist, 1995).

Secondly, we calculated the biomass consumed per scat using a generalized biomass model (Chakrabarti et al., 2016), as:

$$\mathrm{Y} = 0.033 - 0.025 exp^{-4.284(\mathrm{X}/\mathrm{Z})}$$

where Y is the prey biomass consumed per scat, X is the average prey weight, and Z is the average predator weight. This generalized biomass model was derived from feeding trials of various carnivores, including lions and leopards, and is more accurate than linear models for estimating biomass consumed (Chakrabarti et al., 2016). We assigned prey and predator masses based on three quarters of mean adult female body mass (Hayward and Kerley, 2005), using published prey masses (Teye and Sunkwa, 2010; Stuart and Stuart, 2015). We assumed that all prey species where prey mass was <2 kg were entirely consumed (Chakrabarti et al., 2016), and therefore only applied the above equation to prey species weighing ≥ 2 kg.

2.5.3. *Wild prey size classes*

To test the prediction of downshifting prey size use, we grouped wild prey species (excluding birds) into size classes (following Mbizah et al., 2012), namely very small (< 5 kg), small (5–25 kg), medium (25–100 kg), and large (> 100 kg). We used two-proportion Z-tests with continuity corrections to compare the percentage biomass consumed in each class within lion and leopard diets across sites.

2.5.4. *Dietary niche breaths and overlap*

We calculated Levins’ index, as standardized by Hurlbert (1978), to compare the dietary niche breadths of lions and leopards from KNP and LNP as:

$$\mathrm{BA} = \frac{\left(\frac{1}{\sum \mathrm{P}_i^2}\right) - 1}{\mathrm{n} - 1}$$

where P_i is the frequency of occurrence of prey item i in the diet of predator P, and n is the number of prey species consumed by the predator. BA ranges from 0 to 1, with low and high values indicating narrow and broad dietary niche breadths, respectively (Hurlbert, 1978).

We calculated the Pianka index (Pianka, 1973) for the degree of diet overlap for lions and leopards in KNP and LNP, as:

$$\mathrm{Ojk} = \frac{\sum \mathrm{P}_{\mathrm{ij}}\mathrm{P}_{\mathrm{ik}}}{\sqrt{\sum \mathrm{P}^2\mathrm{ij} \sum \mathrm{P}^2\mathrm{jk}}}$$

where P_i represents the frequency of occurrence of a particular prey species in the diets of predators j and k. Ojk ranges from 0 to 1, with 0 indicating no overlap, and 1 indicating complete overlap (Pianka, 1973).

We then performed G-tests, using the package “AMR” (Berends et al., 2022), to determine if BA differs within species across sites, and if Ojk differs between the two sites.

2.5.5. *Prey preferences*

We calculated prey preferences for lions and leopards in KNP and LNP as Jacobs’ index (Jacobs, 1974), as:

$$\mathrm{JI} = \frac{\mathrm{r} - \mathrm{p}}{\mathrm{r} + \mathrm{p} - 2\mathrm{rp}}$$

where r is the frequency of occurrence each prey species comprises of the predator’s diet, and p is the relative abundance of the prey species. JI ranges between - 1 and +1, with - 1 indicating complete avoidance and +1 indicating complete preference (Jacobs, 1974). We investigated cattle preference/avoidance by lions and leopards. We only estimated JI values for wildlife species where r and p data were available at both sites.

3. Results

Prey identifications were made for all scats analyzed for each site. Based on segmented models, adequate sampling was achieved at 41 and 44 lion, and 55 and 49 leopard samples from KNP and LNP, respectively (Fig. S2; Table A1). In all data sets, the analyzed sample sizes exceeded these values.

3.1. *Diet composition*

Lion diets in KNP and LNP consisted mainly of buffalo (*Syncerus caffer*) and wildebeest (*Connochaetes taurinus*; Table 1). Lions consumed a greater proportion of impala and warthog (*Phacochoerus africanus*), and a lower proportion of buffalo and wildebeest in LNP relative to KNP, respectively (Table 1). Cattle and goats were recorded in LNP lion diets, but not KNP (Table 1). Lions consumed 17 and 16 wild prey species in KNP and LNP, respectively, and 2 livestock species in LNP (Table 1).

Leopard diets consisted mainly of impala and warthog in KNP, and of impala, nyala (*Tragelaphus angasii*), and duiker (*Sylvicapra grimmia*) in LNP (Table 1). Consumption of impala and warthog declined in LNP relative to KNP, and buffalo, zebra and wildebeest were absent from their diet in LNP (Table 1). Goats, cattle, and domestic dogs were

Table 1

Corrected frequency of occurrence (CFO, %) and relative biomass consumed (B, %), expressed as percentage biomass consumed per species relative to total biomass consumed, for lion and leopard prey species in the Kruger and Limpopo national parks. Prey body mass (X, kg) from literature (see text) and prey mass consumed per scat (Y, kg) derived from generalized biomass model (see text). Relative prey abundances (p, %) from each site from Everatt et al. (2023). Wild prey ranked for each carnivore based on their mass. Domestic prey (*) placed at the end of the prey species list for each carnivore.

Carnivore	Prey		X (kg)	*Y* (kg)	Kruger National Park			Limpopo National Park		
					p	CFO	B	*p*	CFO	B
Lion (125 kg)	Birds	–	–	–	–	–	–	–	1	–
	Vervet monkey	*Chlorocebus pygerythrus*	3.5	1.35	–	0.9	0.6	–	–	–
	Steenbok	*Raphicerus campestris*	8	1.75	–	0.9	0.8	–	2	1
	Porcupine	*Hystrix africaeaustrlis*	10	1.91	–	–	–	–	2	1
	Duiker	*Sylvicapra grimmia*	16	2.34	0.7	2	1	1.9	4	3
	Bushbuck	*Tragelaphus scriptus*	22.5	2.68	0.2	2	1	0.3	2	2
	Impala	*Aepyceros melampus*	30	3.01	42.9	9	7	29.1	10	9
	Southern reedbuck	*Redunca arundinum*	32	3.08	0.2	2	1	–	–	–
	Warthog	*Phacochoerus africanus*	45	3.46	1.3	5	5	0.6	9	10
	Nyala	*Tragelaphus angasii*	47	3.50	2.3	–	2	3.9	4	4
	Tsessebe	*Damaliscus lunatus*	90	3.98	0.9	2	2	–	2	2
	Kudu	*Tragelaphus strepsiceros*	135	4.09	2.7	5	6	3.6	6	7
	Wildebeest	*Connochaetes taurinus*	135	4.09	4.0	16	16	0.3	6	7
	Zebra	*Equus quagga*	175	4.12	8.9	7	7	1.5	8	9
	Sable antelope	*Hippotragus niger*	180	4.12	–	2	2	0.8	–	–
	Waterbuck	*Kobus ellipsiprymnus*	188	4.12	4.2	5	6	3.4	4	5
	Eland	*Tragelaphus oryx*	345	4.13	0.2	4	4	0.1	3	5
	Buffalo	*Syncerus caffer*	432	4.13	28.3	33	35	17.5	25	28
	Giraffe	*Giraffa camelopardus*	550	4.13	2.9	5	6	0.3	2	2
	Goat*	*Capra hircus*	25	2.80	–	–	–	–	2	2
	Cattle*	*Bos taurus*	410	4.13	–	–	–	36.6	4	5
Leopard (51 kg)	Birds	–	–	–	–	2	–	–	0.8	–
	Woodland dormouse	*Graphiurus murinus*	0.2	0.2	–	–	–	–	0.8	0.2
	Pygmy mouse	*Mus minutoides*	0.2	0.2	–	–	–	–	2	0.4
	Multi-mammate mouse	*Mastomys c.f. coucha*	0.5	0.5	–	–	–	–	0.8	0.6
	Small-spotted genet	*Genetta genetta*	1	1	–	–	–	–	0.8	1
	Giant rat	*Cricetomys gambianus*	1	1	–	0.8	2	–	–	–
	Cape hare	*Lepus capensis*	2	0.61	–	0.8	0.7	–	0.8	0.7
	Scrub hare	*Lepus saxatilis*	2	0.61	–	0.8	0.7	–	0.8	0.7
	Rock hyrax	*Procavia capensis*	2	0.61	–	3	1	–	2	2
	Bat-eared fox	*Otocyon megalotis*	3	0.69	–	–	–	–	0.8	0.8
	Vervet monkey	*Chlorocebus pygerythrus*	3.5	0.73	–	0.8	0.8	–	2	2
	Steenbok	*Raphicerus campestris*	8	1.03	–	5	3	–	3	2
	Porcupine	*Hystrix africaeaustrlis*	10	1.13	–	3	2	–	3	3
	Klipspringer	*Oreotragus oreotragus*	10	1.13	–	3	2	–	–	–
	Duiker	*Sylvicapra grimmia*	16	1.35	0.7	7	6	1.9	12	11
	Baboon	*Papio ursinus*	21.5	1.47	–	2	2	–	5	5
	Bushbuck	*Tragelaphus scriptus*	22.5	1.49	0.2	5	5	0.3	7	7
	Mountain reedbuck	*Redunca fulvorufula*	23	1.50	–	2	2	–	2	2
	Grey rhebuck	*Pelea capreolus*	25	1.53	–	2	2	–	–	–
	Impala	*Aepyceros melampus*	30	1.58	42.9	33	34	29.1	29	32
	Warthog	*Phacochoerus africanus*	45	1.65	1.3	10	9	0.6	7	8
	Nyala	*Tragelaphus angasii*	47	1.66	2.3	5	7	3.9	7	8
	Spotted hyena	*Crocuta crocuta*	60	1.68	–	–	–	–	2	2
	Kudu	*Tragelaphus strepsiceros*	135	1.68	2.7	3	4	3.6	2	2
	Wildebeest	*Connochaetes taurinus*	135	1.68	4.0	3	4	0.3	–	–
	Zebra	*Equus quagga*	175	1.68	8.9	5	5	1.5	–	–
	Waterbuck	*Kobus ellipsiprymnus*	188	1.68	4.2	2	4	3.4	2	2
	Eland	*Tragelaphus oryx*	345	1.68	0.2	1	2	0.1	–	–
	Buffalo	*Syncerus caffer*	432	1.68	4.13	3	4			
	Domestic dog*	*Canis lupus familiaris*	20	1.45	–	–	–	–	3	3
	Goat*	*Capra hircus*	25	1.53	–	–	–	–	3	4
	Cattle*	*Bos taurus*	410	1.68	–	–	–	36.6	3	4

recorded in LNP leopard diets, but not KNP (Table 1). Leopards consumed 23 and 22 wild prey species in KNP and LNP, respectively, and 3 domestic species in LNP (Table 1).

3.2. Size class consumed

Lion diets in KNP and LNP consisted mainly of large (KNP: 80 %, LNP: 67 %) and medium (KNP: 16 %, LNP: 26 %) prey. They supplemented their diet with small prey in KNP (3 %) and LNP (7 %) and very small prey in KNP (0.6 %), based on relative biomass consumed (Fig. 1). As predicted, lions showed a significantly lower consumption of large prey ($Z_1 = 8.18$, $p = 0.004$), a significantly greater consumption of medium-sized prey ($Z_1 = 5.12$, $p = 0.02$) and a non-significantly greater proportion of small prey ($Z_1 = 2.13$, $p = 0.14$) in LNP relative to KNP (Fig. 1).

Leopard diets consisted mainly of medium (KNP: 50 %, LNP: 55 %) and small (KNP: 24 %, LNP: 33 %) prey, followed by large (KNP: 22 %, LNP: 4 %) and very small (KNP: 4 %, LNP: 8 %) prey, based on relative biomass consumed (Fig. 1). Leopards consumed significantly less large prey ($Z_1 = 9.58$, $p = 0.002$) and insignificantly more medium ($Z_1 = 0.24$, $p = 0.63$), small ($Z_1 = 1.25$, $p = 0.26$) and very small ($Z_1 = 0.48$, $p = 0.49$) prey in LNP relative to KNP (Fig. 1), as predicted.

3.3. Dietary niche breadths and overlap

As predicted, both lions and leopards had broader dietary breadths in

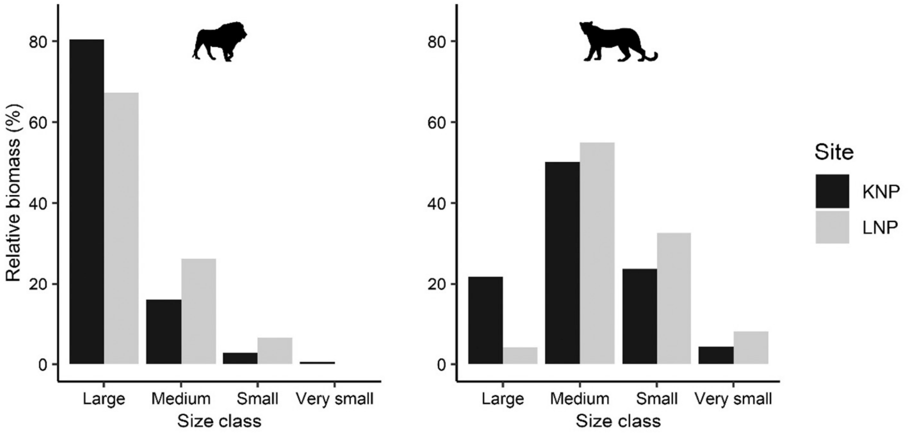

Fig. 1. Relative wild prey biomass consumed (%) in relation to size class (very small: < 5 kg, small: 5–25 kg, medium: 25–100 kg, large: > 100 kg) for lions (left column) and leopards (right column) in the Kruger (KNP) and Limpopo (LNP) national parks.

LNP (lions: $BA = 0.50$, leopards: $BA = 0.34$) relative to KNP (lions: $BA = 0.32$, leopards: $BA = 0.28$). This differed significantly for lions ($G_1 = 5.12$, $p = 0.045$), but not for leopards ($G_1 = 0.78$, $p = 0.38$). Lions and leopards showed a weak degree of diet overlap in LNP ($Ojk = 0.37$) with a non-significantly higher degree of diet overlap in KNP ($Ojk = 0.40$) relative to KNP ($G_1 = 0.12$, $p = 0.73$), contrary to predictions.

3.4. *Prey species preferences*

In KNP and LNP, lions strongly ($JI > 0.5$) preferred eland (*T. oryx*; KNP: $JI = 0.91$; LNP: $JI = 0.96$), bushbuck (*T. scriptus*; KNP: $JI = 0.78$; LNP: $JI = 0.76$), wildebeest (KNP: $JI = 0.62$; LNP: $JI = 0.91$), warthog (KNP: $JI = 0.60$; LNP: $JI = 0.90$), and giraffe (*Giraffa camelopardus*; $JI = 0.73$) and zebra ($JI = 0.71$) in LNP (Fig. 2). Lions strongly avoided ($JI < -0.5$) impala at both sites (KNP: $JI = -0.78$; LNP: $JI = -0.56$; Fig. 2). As predicted, lions strongly avoided cattle ($JI = -0.86$) in LNP (Fig. 2).

Leopards in KNP and LNP strongly preferred bushbuck (KNP: $JI = 0.92$; LNP: $JI = 0.92$), duiker (KNP: $JI = 0.81$; LNP: $JI = 0.71$) and warthog (KNP: $JI = 0.73$; LNP: $JI = 0.82$), whilst avoiding waterbuck (*Kobus ellipsiprymnus*; KNP: $JI = -0.47$; LNP: $JI = -0.40$), impala (KNP: $JI = -0.25$; LNP: $JI = -0.04$) at both sites, and kudu (*T. strepsiceros*; $JI = -0.42$) in KNP (Fig. 2). As predicted, leopards strongly avoided cattle

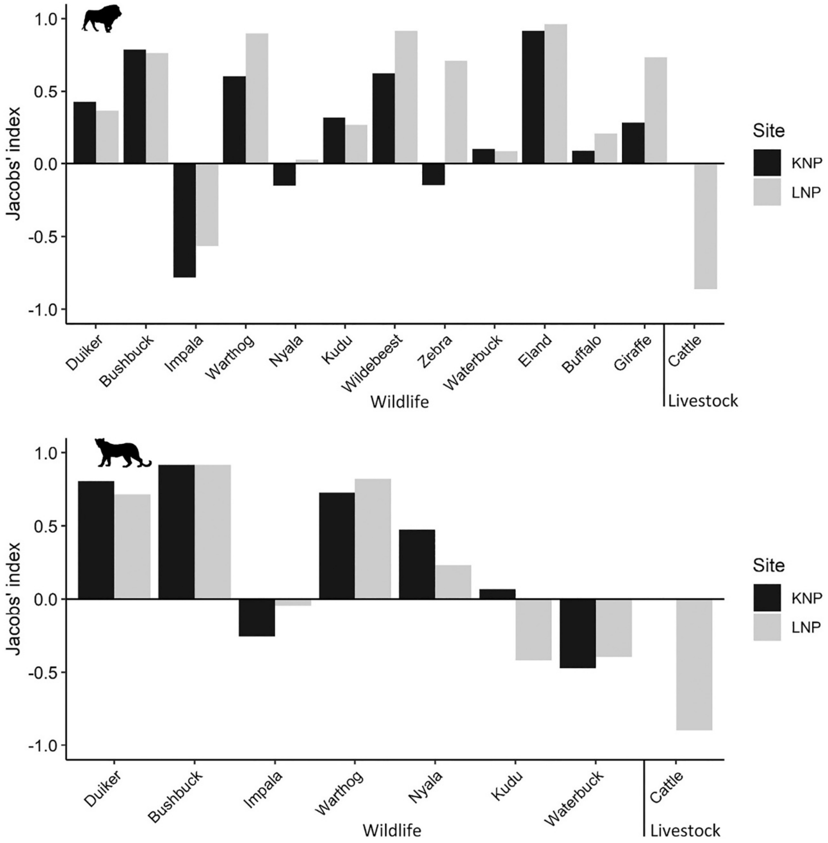

Fig. 2. Lion (top) and leopard (bottom) prey preferences (Jacobs' indices) in the Kruger (KNP) and Limpopo (LNP) national parks for prey species that were consumed at both sites and where availability data (see text) were available at both sites. Wild prey ordered from left to right based on ascending body mass, and livestock are grouped separately.

($JI = -0.90$) in LNP (Fig. 2).

4. Discussion

The combination of the prey-abundant KNP lying adjacent to the prey-depleted/livestock-invaded LNP, and the availability of diet samples for lions and leopards for both parks, allowed us to explore the effects of prey depletion and livestock intrusion on prey-use responses of these two apex carnivores. Prey depletion is a key threat facing carnivores, leading to declining populations (Bauer and de Iongh, 2005; Ripple et al., 2014), diet alterations (Moss et al., 2016; Creel et al., 2018; Smith et al., 2018; Manlick and Pauli, 2020; Everatt et al., 2023), and increased livestock consumption, which in turn increases human-carnivore conflict (Khorozyan et al., 2015). We show that lion and leopard diets differ in terms of composition and size class use, and that both carnivores avoided cattle.

Lions in KNP and LNP mainly consumed large prey, in agreement with previous studies (Hayward and Kerley, 2005; Clements et al., 2014), but supplemented their diets with smaller prey (Barnardo et al., 2020; Groen et al., 2023). Leopards in KNP and LNP mainly consumed small- and medium-sized prey, but readily consumed large prey, as seen elsewhere (Hayward et al., 2006; Clements et al., 2014). However, methods for describing carnivore diets are subject to different biases. For example, in our study area, Everatt et al. (2023) showed that lions consumed megaherbivores using GPS clustering (large prey bias; Tambling et al., 2012), which were not detected here with physical sorting (small prey bias; Spaulding et al., 2000). Conversely, we recorded small prey items in lion diets, missed by Everatt et al. (2023). This may necessitate an integrated approach to counteract biases associated with different carnivore diet description methods. This may be particularly pertinent for leopards, given their catholic prey selection (Hayward et al., 2006). Advances in molecular techniques for diet descriptions are increasingly effective in carnivore diet descriptions (Havmøller et al., 2021; Massey et al., 2021; Groen et al., 2023), and also allow for the confirmation of the scat donor. The latter is particularly pertinent given the inaccuracy of scat identifications in the field, as seen here and elsewhere (e.g., Morin et al., 2016), which may prejudice carnivore diet descriptions.

As predicted, both lions and leopards downshifted their prey size selection in LNP relative to KNP, based on relative prey biomass consumed, in support of previous studies (Creel et al., 2018; Everatt et al., 2023). Optimal foraging theory predicts that carnivores will increase their consumption of previously suboptimal prey when their preferred prey is depleted (Pyke et al., 1977), and large prey are usually the first to experience reduced populations because of human activity (Ripple et al., 2015). Although carnivores can survive on previously suboptimal prey (Woodroffe et al., 2007), the need to locate and kill more prey may have adverse energetic and fitness consequences (Gorman et al., 1998; Vinks et al., 2021). Experimental tests of the fitness consequences for hunting previously suboptimal prey are lacking but would provide mechanistic insights into how prey depletion affects carnivore populations.

The hypothesis that lions and leopards will have broader dietary niches in LNP relative to KNP was strongly and moderately supported for lions and leopards, respectively. Prey depletion has been attributed to leading to dietary niche expansions in various North American carnivores (Moss et al., 2016; Manlick and Pauli, 2020), but dietary niche compressions in Kafue National Park (Creel et al., 2018). Both lions and leopards in our study consumed more species in the prey-depleted LNP relative to the prey-abundant KNP, supporting the predictions of optimal foraging theory, that carnivores will increase the number of species they consume when preferred prey are depleted (Svanbäck and Bolnick, 2007).

Contrary to predictions, diet overlap between lions and leopards was marginally higher in the prey-abundant KNP relative to prey-depleted LNP. Increased diet overlap in prey-depleted systems have been recorded in other systems (Moss et al., 2016; Creel et al., 2018; Smith et al., 2018; Manlick and Pauli, 2020), suggesting an increased likelihood of competition occurring (MacNally, 1983). Diet overlap between lions and leopards is low in both sites (since overlap values of 0.6 are considered significant; Navia et al., 2007), a finding supported by some studies (Hayward and Kerley, 2008; Briers-Louw and Leslie, 2020), whilst others have found high degrees of overlap between lions and leopards (Mbizah et al., 2012; du Preez et al., 2017; Vogel et al., 2019). The low degree of overlap in both sites suggests that even under prey-depleted conditions, food resources are partitioned between lions and leopards, potentially reducing competition for food.

Lions and leopards strongly avoided cattle in accordance with predictions. Livestock depredation often results in persecution and retaliatory killings (Ontiri et al., 2019). Carnivores may be able to perceive these risks and may modulate their foraging behavior to reduce human-carnivore conflict (Everatt et al., 2023). Prey depletion may however, force carnivores to increase their consumption of livestock to compensate (Khorozyan et al., 2015), and downshifting prey size use as recorded here, is often accompanied by increased livestock use (Moss et al., 2016). Although both lions and leopards consumed cattle and goats in LNP, these accounted for <10 % of the biomass consumed by both carnivores (Table 1). Cattle and goats fall within the accessible weight ranges for lions and leopards (Clements et al., 2014), and yet livestock avoidances have previously been recorded in lions and leopards (Valeix et al., 2012; Tumenta et al., 2013; Yirga et al., 2013; Everatt et al., 2023). Furthermore, cattle are the most abundant ungulate in LNP (Grossmann et al., 2014). The avoidance for cattle recorded here by lions and leopards supports the notion that carnivores alter their foraging behavior to reduce human-carnivore conflict (Everatt et al., 2023).

4.1. Conservation implications

We used the prey-abundant/livestock-absent KNP as a baseline to compare diet alterations with the prey-depleted/livestock-abundant LNP. Since prey populations in KNP are approaching carrying capacity (Lindsey et al., 2017), KNP may serve as a robust baseline to compare carnivore diets in other dry-tropical, savanna systems that have experienced anthropogenic prey depletion. However, >80 % of Africa's protected savanna landscapes are deteriorating (Robson et al., 2022) and much of the remaining habitat suitable for large carnivores is prey-depleted (Wolf and Ripple, 2016). Given the clear dependence of prey availability on carnivore conservation (Carbone et al., 2011), there is a need for extensive prey restoration across carnivore ranges (Wolf and Ripple, 2016). Additionally, there is a grave risk that prey-depleted systems may be perceived as the norm (sensu "shifted baseline syndrome"; Pauly, 1995). Studies examining resource use of carnivores are urged to acknowledge historical prey abundances within the "shifted model" framework (Kerley and Monsarrat, 2022). Intact predator-prey systems are therefore important as a baseline for comparisons with anthropogenically-impacted systems, in addition to their role in conserving biodiversity. However, opportunities to conduct studies in systems that represent historical approximations for predator-prey densities are becoming increasingly limited. KNP may represent one of the few remaining systems in which studies of this nature can be conducted and is therefore of global importance.

5. Conclusion

The ability of lions and leopards to broaden their dietary niches in response to prey depletion, whilst avoiding livestock highlights their adaptability to prey depletion and their ability to perceive the risks of livestock depredation (Everatt et al., 2023). Although lions and leopards strongly avoided cattle, retaliatory killings of carnivores in response to depredation are common in LNP (Everatt et al., 2019a), jeopardizing their survival. Lions and leopards increased their utilization of smaller prey in LNP relative to KNP which may adversely affect fitness, through increased energy expenditure when hunting previously suboptimal prey. Efforts to reduce human-carnivore conflict and interspecific competition and promote carnivore population recovery in human-dominated landscapes should focus using human-fear of carnivores (Everatt et al., 2023) improving livestock husbandry practices (Ogada et al., 2003), and increasing prey populations, particularly large-sized prey (Creel et al., 2018).

Funding

Nelson Mandela University, Centre for African Conservation Ecology, National Geographic Big Cats Initiative. RF was funded by a postgraduate research scholarship at Nelson Mandela University and the Erasmus+ International Credit Mobility programme.

CRediT authorship contribution statement

Ryan E. Forbes: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Kristoffer T. Everatt:** Conceptualization, Investigation, Writing – review and editing, Supervision. **Göran Spong:** Supervision, Writing – review & editing. **Graham I.H. Kerley:** Conceptualization, Funding acquisition, Investigation, Supervision, Writing – review & editing.

Declaration of competing interest

None.

Data availability

Data are available from corresponding author on request.

All authors declare their permission to proceed with submission.

Acknowledgements

We thank South African National Parks, Kruger National Park, Administração Nacional das Áreas de Conservação de Moçambique and Parque Nacional de Limpopo for providing permits. We thank Leah Andresen and Jennifer Hartman of Conservation Canines for sample collection.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110542.

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