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RESEARCH ARTICLE

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Seasonal variation in prey preference, diet partitioning and niche breadth in a rich large carnivore guild

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Abstract

Large carnivore community structure is affected by direct and indirect interactions between intra-guild members. Co-existence between different species within a carnivore guild may occur through diet, habitat or temporal partitioning. Since carnivore species are highly dependent on availability and accessibility of prey, diet partitioning is potentially one of the most important mechanisms in allowing carnivores to co-exist. Intra-guild interactions may vary over time as carnivore prey preference and diet overlap can change due to seasonal changes in resource availability. We conducted scat analysis to compare the seasonal changes in prey preference, diet partitioning and niche breadth of four large carnivore species, namely leopard *Panthera pardus*, spotted hyena *Crocuta crocuta*, brown hyena *Parahyaena brunnea* and wild dog *Lycaon pictus* in central Tuli, Botswana. Large carnivores in central Tuli display a high dietary overlap, with spotted hyena and brown hyena displaying almost complete dietary overlap and the other carnivore species displaying slightly lower but still significant dietary overlap. Dietary niche breadth for both hyena species was high possibly due to their flexible foraging strategies, including scavenging, while leopard and wild dog showed a relatively low niche breadth, suggesting a more specialised diet. High dietary overlap in central Tuli is possibly explained by the high abundance of prey species in the area thereby reducing competition pressure between carnivore species. Our research highlights the need to assess the influence of diet partitioning in structuring large carnivore communities across multiple study sites, by demonstrating that in prey rich environments, the need for diet partitioning by carnivores to avoid competition may be limited.

KEYWORDS
competition, diet, large carnivores, niche partitioning, scat analysis

Résumé

Dans le cadre de l'étude, la structure des communautés de grands carnivores est affectée par les interactions directes et indirectes entre les membres d'une même guilde. La cohabitation entre différentes espèces au sein d'une guilde de carnivores peut se faire par le biais du régime alimentaire, de l'habitat ou du cloisonnement temporel. Les espèces de carnivores étant très dépendantes de la disponibilité et de l'accessibilité des proies, la répartition du régime alimentaire est potentiellement l'un des mécanismes les plus importants permettant aux carnivores de coexister. Les interactions au sein de la guilde peuvent varier dans le temps, car les préférences des carnivores en matière de proies et le chevauchement des régimes alimentaires peuvent changer en fonction des variations saisonnières de la disponibilité des ressources. Nous avons procédé à une analyse des excréments pour comparer les changements saisonniers dans la préférence des proies, la répartition du régime alimentaire et l'étendue de la niche de quatre grandes espèces de carnivores, à savoir le léopard Panthera pardus, la hyène tachetée Crocuta crocuta, la hyène brune Parahyaena brunnea et le chien sauvage Lycaon pictus dans le centre de Tuli, au Botswana. Les grands carnivores du centre de Tuli présentent un chevauchement alimentaire élevé, la hyène tachetée et la hyène brune présentant un chevauchement alimentaire presque complet, tandis que les autres espèces de carnivores présentent un chevauchement alimentaire légèrement inférieur mais néanmoins significatif. Les deux espèces de hyènes avaient une niche alimentaire très étendue, probablement en raison de leurs stratégies de recherche de nourriture flexibles, y compris la récupération des déchets, tandis que le léopard et le chien sauvage avaient une niche relativement faible, ce qui suggère un régime alimentaire plus spécialisé. Le chevauchement alimentaire élevé dans le Tuli central s'explique probablement par la grande abondance des espèces de proies dans la région, ce qui réduit la pression de la concurrence entre les espèces de carnivores. Nos recherches soulignent la nécessité d'évaluer l'influence du partage du régime alimentaire dans la structuration des communautés de grands carnivores sur plusieurs sites d'étude, en faisant la démonstration que dans les environnements riches en proies, le besoin de partage du régime alimentaire par les carnivores pour éviter la compétition peut être limité.

1 | INTRODUCTION

The structure of large carnivore communities is affected by direct and indirect interactions between intra-guild members (Hayward & Kerley, 2008; Linnell & Strand, 2000; Prigioni et al., 2008). Through competition, either via exploitation (direct use of a limited resource) or interference (whereby individuals of a subordinate species is harassed, kleptoparasitized or killed by individuals of a dominant carnivore species), it is predicted that subordinate species in rich large carnivore communities will occur in low densities or ultimately be excluded when they lack a distinct niche (Beaudrot et al., 2013; Helland et al., 2008; Karanth et al., 2017; Tilman, 1982).

In large carnivore communities, co-existence may occur through several mechanisms, among others diet, habitat or temporal partitioning (Barrientos & Virgós, 2006; Di Bitetti et al., 2010; Helland et al., 2008; Schoener, 1974; Vissia et al., 2021). While dominant carnivore species can suppress subordinate carnivore species (Creel & Creel, 1996; Durant, 2000; Mills, 1982), dominant carnivore species can also facilitate these subordinate carnivore species by providing scavenging opportunities and access to otherwise inaccessible food sources (Mills & Maude, 2005; Stein et al., 2013; Yarnell et al., 2013).

Since carnivore species are highly dependent on the abundance and distribution of prey species, diet partitioning or overlap is potentially one of the important mechanisms that allows for co-existence among guild members (Schoener, 1983; Shao et al., 2021). Dietary niche partitioning among sympatric carnivores is demonstrated in studies conducted worldwide and among different carnivore guilds. For example, Arjo et al. (2002) concluded that dietary niche partitioning facilitated co-existence of wolves *Canis lupus* and coyotes *Canis latrans* in Montana (USA), while a study in Michigan (USA) concluded that, despite relatively high dietary overlap, coyotes avoided competitive exclusion by wolves by selecting small and more varied prey Petroelje et al. (2021). However, other studies demonstrated minimal dietary niche partitioning among sympatric carnivores. For example, diet overlap in a predator guild composed of tiger *Panthera tigris*, leopard *Panthera pardus* and dhole *Cuon alpinus* (Andheria et al., 2007; Ramesh et al., 2012; Wang & MacDonald, 2009) and of African wild dogs *Lycaon pictus*, cheetahs *Acinonyx jubatus*, lions *Panthera leo* and leopards (Vogel et al., 2019) was high and there was potential for strong intra-guild competition. These contradicting conclusions underline the importance of assessing carnivore diet partitioning in rich carnivore communities to reveal possible intra-guild competition.

Intra-guild competition varies over time when prey preference and diet overlap change due to external conditions, such as rainfall conditions, extreme environmental events and disease outbreaks, influencing resource availability (Owen-Smith, 2008; Vanak et al., 2013). In periods of relative prey scarcity in terms of abundance during the dry season, dietary overlap between carnivores tends to increase (Krebs, 1978; Pyke et al., 1977; Vanak et al., 2013), while during the wet season prey is more abundant (Pereira et al., 2014) and dietary overlap might decrease. While studies have assessed diet overlap in African carnivore guilds (Du Preez et al., 2017; Hayward & Kerley, 2008), possible effects of season on prey preference and diet overlap in large carnivores are not studied to date.

Niche breadth refers to the diversity of food items used and is considered to be important in evaluating the level of dietary specialisation in a species (Carvalho & Cardoso, 2020; Segurado et al., 2011). Species with small niche breadths are relatively specialised, and species with broad niches are considered more generalist species (Amundsen et al., 1996; Bridcut & Giller, 1995; Smith et al., 2011). Spotted hyena *Crocuta crocuta* and brown hyena *Parahyaena brunnea* are considered to be generalist species with a large niche breadth due to their scavenging nature (Binder & Van Valkenburgh, 2000; Green et al., 2018; Owens & Owens, 1978), whereas leopard also display generalist dietary patterns (Hayward, Henschel, et al., 2006; Vogel et al., 2019). Contrary, wild dogs *Lycaon pictus* have a narrower niche breadth and are seen as specialists (Hayward & Kerley, 2008; Vogel et al., 2019). Similar to niche overlap, we expect seasonal differences in niche breadth between large carnivores. During the wet season, niche breadth is expected to be wider as prey is more abundant (Allen et al., 2020), and calves are relatively vulnerable to predators.

Africa supports Earth's richest large carnivore guilds that may experience intense intra-guild competition between the different carnivore species. Here, we compared the seasonal changes in diet of four large carnivore species, namely leopard, spotted hyena, brown hyena and wild dog in central Tuli, Botswana. We determined diet overlap and niche breadth amongst these members of the local large carnivore guild. We predicted that leopard, brown hyena, spotted hyena and wild dog would have a low degree of dietary overlap to facilitate co-existence, and that diet overlap would be higher and niche breadth smaller during the dry season than during the wet season.

2 | METHODS

2.1 | Study area

The study area was located in the Central Tuli Game Reserve, an approximately 600 km^2 protected area in South East Botswana (Figure 1). It is comprises of privately owned properties of which most host ecotourism lodges or private holiday houses and a few properties have livestock with no fences between the individual properties.

The dominant flora is riverine woodlands with large bands of large fever berry trees (*Croton megalobotrys*) and mopane (Mopane-Combretum) shrub savanna. Most precipitation falls during the wet summer months, spanning from November to April, with 350 mm average annual total rainfall. The carnivore guild consists of lion, leopard, spotted hyena, brown hyena, wild dog, aardwolf *Proteles cristata*, black-backed jackal *Canis mesomelas*, bat-eared fox *Otocyon megalotis*, African wildcat *Felis sylvestris lybica*, African civet *Civettictis civetta*, honey badger *Mellivora capensis* and small-spotted genet *Genetta genetta* all being present in central Tuli.

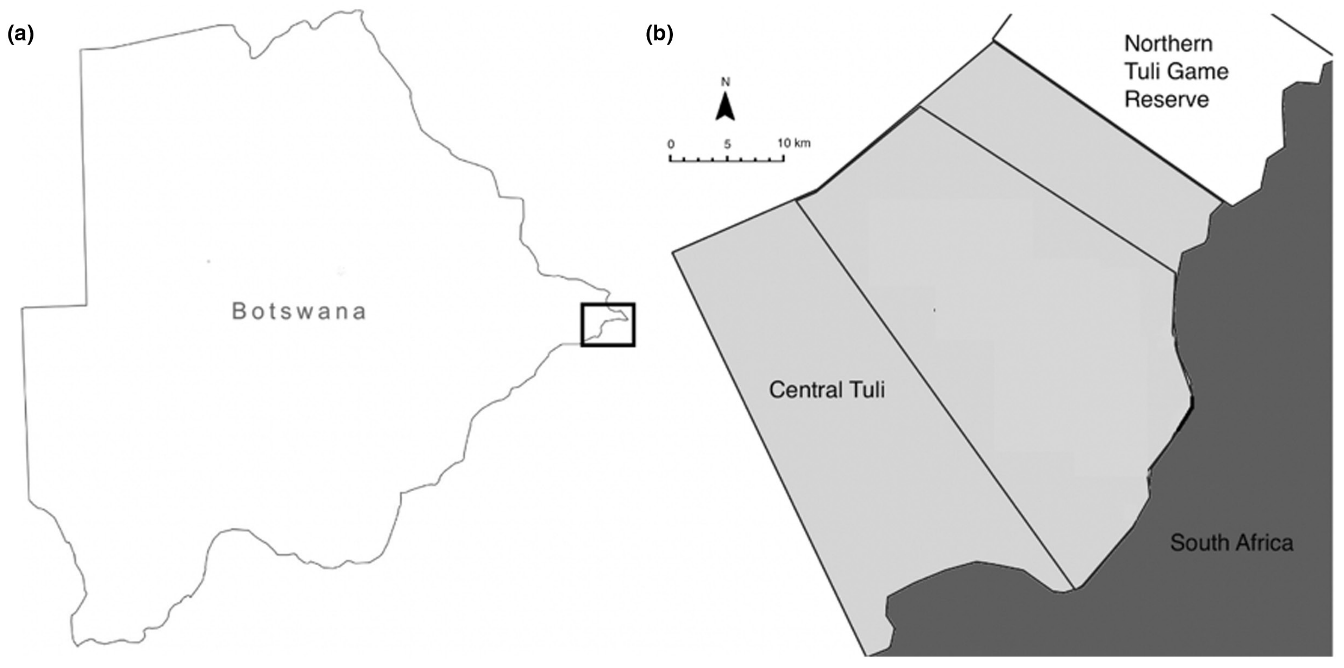

FIGURE 1 Map of (a) Botswana and (b) Central Tuli (pale grey) including the location of the survey area (delineated area).

2.2 | Sampling design and field methods

A commonly used method to assess carnivore diets is scat analysis, which is a non-invasive (Marucco et al., 2008), relatively simple and inexpensive method (Klare et al., 2011; Walsh, 2015). A 200 km^2 area was delineated in Central Tuli where scat samples were collected for the four-carnivore species. Carnivore faeces were collected in both the dry and wet season, during the period from February 2018 to November 2020. A total of 228 samples were collected (leopard $n = 58$, spotted hyena $n = 60$, brown hyena $n = 74$, wild dog $n = 27$, lion $n = 9$). Scat samples were collected opportunistically, near latrines, waterbodies and sighting sites. To avoid overrepresentation of a prey species in the carnivores' diets, only one scat was collected when scats were found at the same location at the same day. Due to the limited number of lion scats found, lion was excluded from the analyses.

The collected carnivore scats were air-dried, washed and analysed by creating scale imprints of hairs from each scat sample (Faure et al., 2019; Mills & Maude, 2005). A total of 30 representative hairs were extracted from each sample comprising of hairs of different size, thickness, colour, length and shape. Imprints were made on microscope slides by placing the hairs in a thin layer of clear nail polish and removing the hairs once the nail polish was dry (De Marinis & Agnelli, 1993; Faure et al., 2019). Imprints were then photographed through the microscope for identification purposes and compared to published hair reference collections (Beveridge & van den Hoogen, 2013; Seiler, 2010) and one created in the study area by opportunistically collecting hair from kill sites.

2.3 | Relative abundance

Camera traps were used to gather data on relative abundances of carnivores and herbivores. This method is non-invasive and allows for reliable density estimates through animals "captured" on camera (Rowcliffe et al., 2008). A total of 27 fixed Bushell E3 cameras were placed in strategic locations, such as roads, game trails and latrines. Individuals from the same herbivore species caught on camera traps within 15 min were regarded as the same individuals. Carnivore densities were estimated by identifying individuals based on their unique coat patterns, using spatially explicit capture-recapture modelling (Vissia et al., 2021; Vissia et al., 2022). The relative abundance of herbivores was calculated by taking the total number of detections per species divided by the total number of detections of all species (Springer et al., 2012).

2.4 | Data analysis

To determine prey preference for each carnivore species the Jacob's index was used (Jacobs, 1974):

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

where r is the proportion of a predator's total kills of a certain prey species at a site and p is the proportional abundance of that prey species (Hayward & Kerley, 2008). Values can range from −1 (maximum avoidance) to +1 (maximum preference) (Hayward et al., 2006).

Furthermore, carnivores that utilise only a small portion of available prey species are considered to have narrow niche breadths, while carnivores who utilise many different prey species have a broad niche breadth. Carnivore niche breadth was calculated by using the weighted version of Levin's measure (Hurlbert, 1978):

$$B' = \frac{1}{\sum_i^R p_i^2}$$

where B' is dietary niche breadth, p_i is proportion of diet that consists of species i and R is total number of prey species in the carnivore's diet (Smith, 1982). Broader dietary niche breadth is indicated by a higher B' while a small dietary niche breadth is indicated by a low B'.

Lastly, to reveal dietary overlap between different carnivore species, the Pianka's index was used (Pianka & Pianka, 1976):

$$O_{jk} = \frac{\sum (p_{ij} \times p_{ik})}{\sqrt{\sum \left(p_{ij}^2\right) \times \sum \left(p_{ik}^2\right)}}$$

where p_{ij} is the proportion of prey i on the diet of carnivore j; and p_{ik} the proportion of prey i on the diet of carnivore k. The Pianka's index (O_{jk}) ranges between 0 (no overlap) and 1 (complete overlap). In addition, the EcoSimR package (Gotelli & Ellison, 2013), which includes algorithms and metrics for niche overlap, was used. The analysis reveals whether the estimated niche overlap calculated among all unique pairs of carnivore species, is more or less than would be expected if species used resource categories independently of one another.

The collected data from the scat analysis and prey abundances was separated by season. All calculations mentioned above were conducted for both seasons, as well as for all data merged. A detrended correspondence analysis is presented to illustrate the seasonal differences in ordination of carnivores' diets, for both seasons and prey species. Statistical analyses were conducted to further research the differences between diets. A Kruskal-Wallis test was used to test differences of body mass of prey preferences between carnivores. Two separate linear regression models were used to analyse the Jacob's index scores, for two separate independent variables considered to influence predation, herd size and body mass of prey. Body mass (kg) per prey species (average female and male) and the categories for herd sizes in which the prey species generally occur (one individual, two pairs, three small family groups, four small herds, i.e., <50 individuals, five big herds, i.e. >50 individuals) were obtained from Smithers (2012).Three generalised linear models with a logarithmic link function and gamma distribution were conducted to analyse the percentage of prey in the carnivores' diet, using herd size, body mass and prey availability as independent variables.

3 | RESULTS

3.1 | Prey abundances

The calculated herbivore abundances, used to estimate prey availability, showed large differences between species (Table 1). Impala was captured the most on camera, representing 36% of the total prey abundance. Followed by zebra (28%) and elephant (18%).

The detrended correspondence analysis illustrated that the diets of almost all carnivore species differed considerably between the wet and dry season (Figure 2). While the spotted hyena's diet seemed to differ the most between seasons, leopard and brown hyena diet similarly differed considerably between the wet and dry season as well. Wild dog diet did not differ considerably between seasons.

3.2 | Diet preference

The Jacob's index scores for the different carnivore species can be found in Table 2 and Figure 3. The table includes all prey species found in the scats, whereas the figure shows an overview of wild prey species for which the availability is considered valid, i.e., which are considered to have no bias when captured by camera traps. Waterbuck was the most preferred prey species for all carnivore species while duiker was preferred for all carnivore species except wild dog. Kudu was preferred by spotted hyena and wild dog while leopard and brown hyena displayed no clear preference. Zebra and impala, the most abundant prey species, were avoided or preyed on according to availability by all carnivores but made up the largest share of all carnivore species diets (Table 2 and Figure 3).

TABLE 1 Number of individuals captured on camera and relative abundance per prey species

Species	Individuals	Relative abundance
Aardvark	20	0.12
Baboon	660	3.92
Bat-eared-fox	22	0.13
Cow	32	0.19
Dog	8	0.05
Duiker	110	0.65
Eland	580	3.44
Elephant	2968	17.61
Impala	5993	35.55
Klipspringer	60	0.36
Rock Hyrax	7	0.04
Kudu	595	3.53
Springhare	154	0.91
Warthog	103	0.61
Waterbuck	60	0.36
Wildebeest	688	4.08
Zebra	4797	28.4

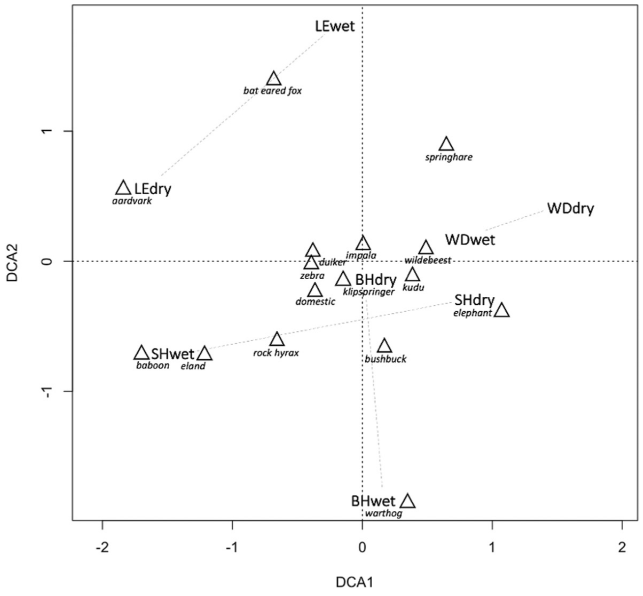

FIGURE 2 Detrended correspondence analysis of the four studied carnivore species' diets (BH, brown hyena; LE, leopard; SH, spotted hyena; WD, wild dog) in the wet season (from December to April) and dry season (from May to October). Triangles represent different prey species, to which carnivore species are graphically closer when a larger proportion of prey is found in their diet. The distance between each carnivore species (illustrated by the dashed lines) at dry and wet season shows the difference in diets between seasons.

3.3 | Dietary niche breadth

Spotted hyena and brown hyena displayed the broadest dietary niche breadth. Comparatively, wild dog and leopard had narrower niche breadth. For all carnivore species, except wild dog, niche breadth was wider during the wet season compared to the dry season (Figure 4).

3.4 | Dietary overlap

Spotted hyena and brown hyena exhibited a near complete dietary overlap as did leopard and brown hyena. Leopard and spotted hyena, leopard and wild dog, spotted hyena and wild dog and brown hyena and wild dog all synergistically experienced slightly lower but still significant dietary overlap with each other (Figure 5).

TABLE 2 Carnivore species, prey species, associated Jacob's index values, number of scats per carnivore containing that prey species (*n*), availability in percentage of that prey species, proportion of prey in predator's diet, body mass (kg) per prey species (average female and male) (Smithers, 2012) and categories for herd sizes used: One individual, two pairs, three small family groups, four small herds (<50 individuals), five big herds (>50 individuals) (Smithers, 2012)

Carnivore species	Prey species	Jacob's index	*N*	Availability (%)	Prey (%)	Body mass (kg)	Herd size
Leopard 	Aardvark	0.79	1	0.16	1.37	53	1
	Baboon	−1.00	0				
	Bat eared fox	0.88	2	0.18	2.74	3.6	2
	Bushbuck	1.00	1	0.00	1.37	35	1
	Cow	−1.00	0				
	Dog	−1.00	0				
	Donkey	1.00	3	0.00	4.11	280	
	Duiker	0.52	2	0.88	2.74	19.7	1
	Eland	−1.00	0				
	Elephant	−1.00	0				
	Goat	−1.00	0				
	Impala	−0.03	34	48.15	46.58	47.7	5
	Klipspringer	−1.00	0				
	Kudu	0.07	4	4.78	5.48	193.5	3
	Rock Hyrax	0.92	1	0.06	1.37	3.55	4
	Sheep	−1.00	0				
	Springhare	0.05	1	1.24	1.37	3.1	3
	Warthog	−1.00	0				
	Waterbuck	0.90	6	0.48	8.22	225	4
	Wildebeest	−0.35	2	5.53	2.74	222	4
	Zebra	−0.38	16	38.54	21.92	290	3
Spotted hyena 	Aardvark	−1.00	0				
	Baboon	−0.58	1	4.00	1.11	25.25	5
	Bat eared fox	−1.00	0				
	Bushbuck	1.00	4	0.00	4.44	35	1
	Cow	0.71	1	0.19	1.11	910	
	Dog	0.92	1	0.05	1.11	40	
	Donkey	1.00	2	0.00	2.22	280	
	Duiker	0.54	2	0.67	2.22	19.7	1
	Eland	−0.53	1	3.52	1.11	560	1
	Elephant	0.90	1	17.99	1.11	1000	4
	Goat	−1.00	0				
	Impala	−0.17	26	36.33	28.89	47.7	5
	Klipspringer	−1.00	0				
	Kudu	0.66	14	3.61	15.56	193.5	3
	Rock Hyrax	0.93	1	0.04	1.11	3.55	4
	Sheep	−1.00	0				
	Springhare	−1.00	0				
	Warthog	−1.00	0				
	Waterbuck	0.95	12	0.36	13.33	225	4
	Wildebeest	0.24	6	4.17	6.67	222	4
	Zebra	−0.24	18	29.08	20.00	290	3

TABLE 2 (Continued)

Carnivore species	Prey species	Jacob's index	*N*	Availability (%)	Prey (%)	Body mass (kg)	Herd size
Brown hyena	Aardvark	−1.00	0				
	Baboon	−1.00	0				
	Bat eared fox	−1.00	0				
	Bushbuck	1.00	5	0.00	4.42	35	1
	Cow	−1.00	0				
	Dog	−1.00	0				
	Donkey	1.00	5	0.00	4.42	280	
	Duiker	0.34	2	0.88	1.77	19.7	1
	Eland	−1.00	0				
	Elephant	−1.00	0				
	Goat	−1.00	0				
	Impala	−0.25	40	47.69	35.40	47.7	5
	Klipspringer	0.30	1	0.48	0.88	11.9	2
	Kudu	0.32	10	4.73	8.85	193.5	3
	Rock Hyrax	0.96	3	0.06	2.65	3.55	4
	Sheep	1.00	1	0.00	0.88	87.5	
	Springhare	−0.16	1	1.23	0.88	3.1	3
	Warthog	0.04	1	0.82	0.88	82.50	3
	Waterbuck	0.93	14	0.48	12.39	225	4
	Wildebeest	0.14	8	5.47	7.08	222	4
	Zebra	−0.44	22	38.17	19.47	290	3
Wild dog	Aardvark	−1.00	0				
	Baboon	−1.00	0				
	Bat eared fox	−1.00	0				
	Bushbuck	1.00	2	0.00	4.26	35	1
	Cow	−1.00	0				
	Dog	−1.00	0				
	Donkey	−1.00	0				
	Duiker	−1.00	0				
	Eland	−1.00	0				
	Elephant	−1.00	0				
	Goat	1.00	1	0.00	2.13	80	
	Impala	−0.03	21	48.78	44.68	47.7	5
	Klipspringer	−1.00	0				
	Kudu	0.55	9	4.84	19.15	193.5	3
	Rock Hyrax	−1.00	0				
	Sheep	−1.00	0				
	Springhare	0.25	1	1.25	2.13	3.1	2
	Warthog	−1.00	0				
	Waterbuck	0.90	5	0.49	10.64	225	4
	Wildebeest	0.29	5	5.60	10.64	222	4
	Zebra	−0.65	3	39.04	6.38	290	3

Note: Prey species not found in carnivore scat samples were not reported in the table as these species were all avoided with a Jacobs index of −1.

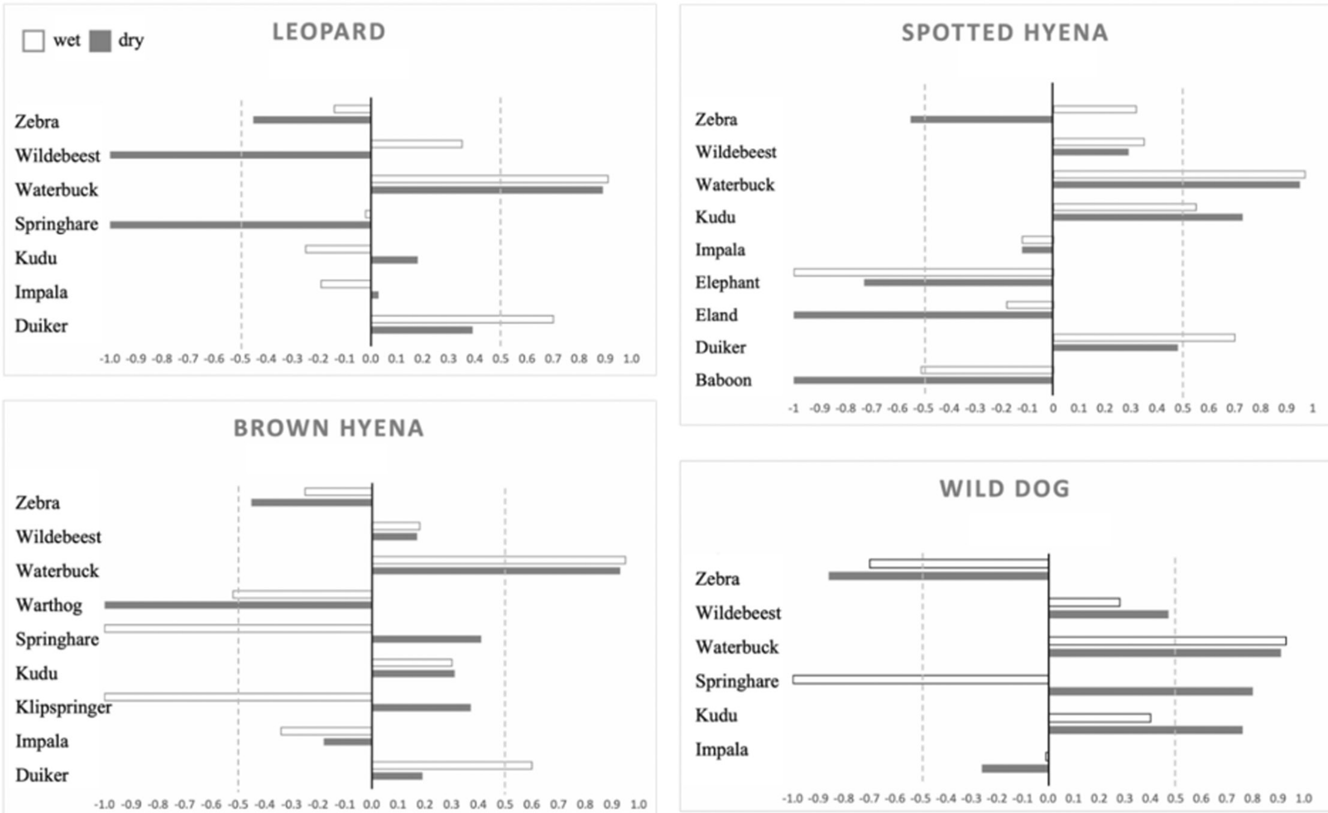

FIGURE 3 Leopard, spotted hyena, brown hyena and wild dog preferences. Species with bars that exceed 0.5 are considered preferred; species with bars lower than −0.5 are considered avoided. 0 means a species is consumed according to availability (Jacobs, 1974).

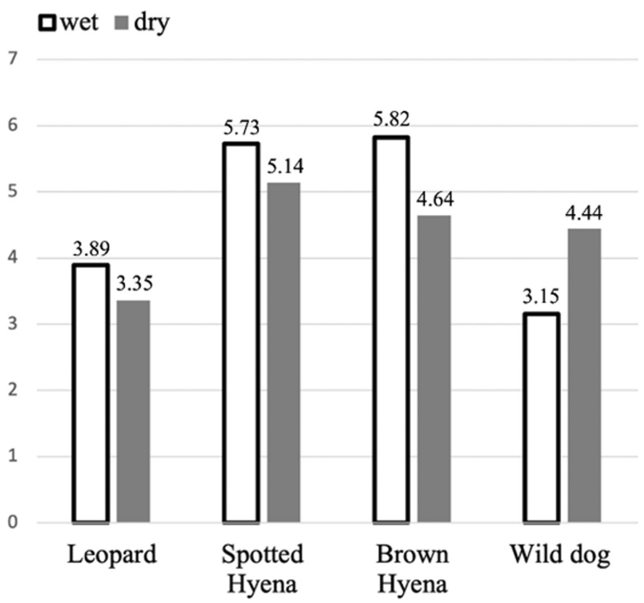

FIGURE 4 Levin's niche breadth index scores for all carnivores, for wet and dry seasons.

3.5 | Herd size, body mass and availability of prey

Body mass of preferred prey did not differ among predators (Kruskal-Wallis test, $X^2 = 3.80$, $n = 323$, df = 4, $p > 0.05$). Hence, the carnivores were pooled for further statistical analyses. Two linear regression models were used to predict the Jacob index scores with herd size (factor) (Table 2) and body mass of prey (kg) as explanatory variables. We found significant differences in Jacob's index between the classes of herd size of consumed prey (F (50, 4) = 8.751, $p < 0.001$; $R^2 = 0.4118$). No significant correlation was found between Jacob index scores and body mass of consumed prey (F (53, 1) = 0.538, $p > 0.05$).

Three generalised linear models were used to predict the proportion of prey in a predator's diet with herd size (as factor), body mass of prey (kg) and the availability of prey as explanatory variables. The proportion of prey in the predators' diets differed significantly between the classes of herd size of consumed prey (df = 4, $n = 64$, $p < 0.001$). No significant correlation was found between the proportion of prey in predator's diet and the body mass of consumed prey (df = 63, $n = 64$, $p > 0.05$). Finally, availability of prey significantly contributed to the prediction of proportion of prey in the predators' diet (df = 63, $n = 64$, $p < 0.001$).

When considering the Jacob index scores, large carnivores seem to prefer herbivore species that live solitarily, in pairs or small herds (Figure 6). However, herbivores found in large herds were more found in the diets of these carnivores (Figure 6). Herbivores that live solitarily or in small group may be less available, which increases the Jacob's index scores through low availability scores. When considering availability, there is a linear relationship between the proportion of prey found in the carnivores' diets and their availability,

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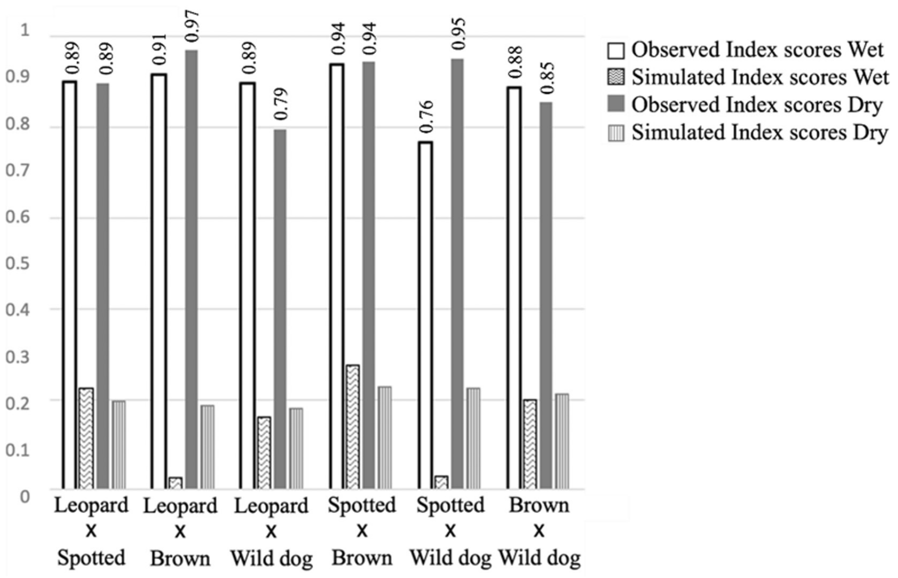

FIGURE 5 Observed Pianka's niche index scores and mean of simulated index scores for all carnivore pairs, for wet and dry seasons. Observed indexes were calculated for each season, revealing the percentage of diet overlap between each pair of carnivore species. Simulation index scores were calculated based on 1000 random generated diets, to compare with actual indexes.

confirming the importance of prey availability in determining carnivores' diet.

4 | DISCUSSION

Using scats, we studied diet partitioning, prey selection, niche breadth and possible seasonal variation for four large carnivore species, namely leopard, spotted hyena, brown hyena and wild dog. Previous research by Vissia and van Langevelde (2021) in central Tuli, Botswana concluded that temporal and spatial overlap between the four large carnivore species was high and consequently diet partitioning between large carnivores might be vital in facilitating co-existence.

Contrary to our expectations, diet overlap between the different carnivore species was high, with spotted hyena and brown hyena displaying most diet overlap and wild dog and leopard displaying slightly lower but still high diet overlap (at least 80% for all species). Spotted hyena predominantly hunt in central Tuli and might provide scavenging opportunities for brown hyena, explaining high diet overlap between both hyena species. Similarly, leopard and wild dog may provide scavenging opportunities for both brown and spotted hyena hereby explaining the high dietary overlap between all carnivore species (Balme et al., 2019; Carbone et al., 1997; van der Meer et al., 2011; Vissia et al., 2021).

As species with small niche breadths are relatively specialised and species with broad niches are considered more generalist species (Carvalho & Cardoso, 2020; Segurado et al., 2011), we conclude that in central Tuli spotted hyena and brown hyena can be considered more generalist species displaying the largest niche breadth, while leopard and wild dog are more specialist species displaying the smallest niche breadth. The larger dietary niche breadth for both hyena species compared to leopard and wild dog suggest that hyena have a more flexible and generalist foraging strategy, which may be attributed to facultative scavenging in spotted hyena and obligate scavenging in brown hyena (Hayward, 2006; Pienaar, 1969). In contrast, leopard and wild dog generally do not scavenge (Schaller, 1972; Bailey, 1993). Unfortunately, we could not test the fraction of scavenging as scat analysis cannot accurately distinguish between predation and scavenging.

Although we found relatively small niche breadth of leopard, leopard over the whole range in sub-Saharan Africa has the broadest diet of the large carnivore species, with 92 prey species recorded (Mills & Harvey, 2001). Leopards are known to be able to subsist for relatively short periods on invertebrates or small vertebrates in areas where large vertebrate prey is absent (Hayward, Henschel, et al., 2006), but our study suggests that in a prey-rich environment, leopard maximises prey acquisition, resulting in a low dietary niche breadth. Similarly, we found wild dog had relatively small niche breadth. Wild dog energetic requirements demand for optimal foraging, due to the high energetic cost of hunting by this species (Gorman et al., 1998). As prey species outside the preferred prey weight range (Hayward et al., 2006) are inefficiently preyed on, these tend to be avoided as a strategy to reduce possible negative population effects.

Despite high levels of diet overlap and broad niche breadths, the large carnivore community in central Tuli with four large species is possibly explained by the high abundance of prey species in the area as competition between different species with high dietary overlap may not occur when resources are not limited (Schoener, 1983). Next to camera traps, we implemented distance sampling and found high abundances of the main prey species, namely impala ($42.2 \pm 10.5\,km^{-2}$) and zebra ($12.2 \pm 3.7\,km^{-2}$) (Vissia unpublished results). These abundances are high compared to other areas where these prey species co-exist with the four-carnivore species of this study (Braczkowski et al., 2022; Rija & Hassan, 2011; Shorrocks et al., 2008). The high prey density of our study area may also explain the fact that we found no differences in diet overlap and niche breadth between seasons.

Central Tuli hosts a rich large carnivore guild despite high levels of dietary overlap between all species. We hypothesize that

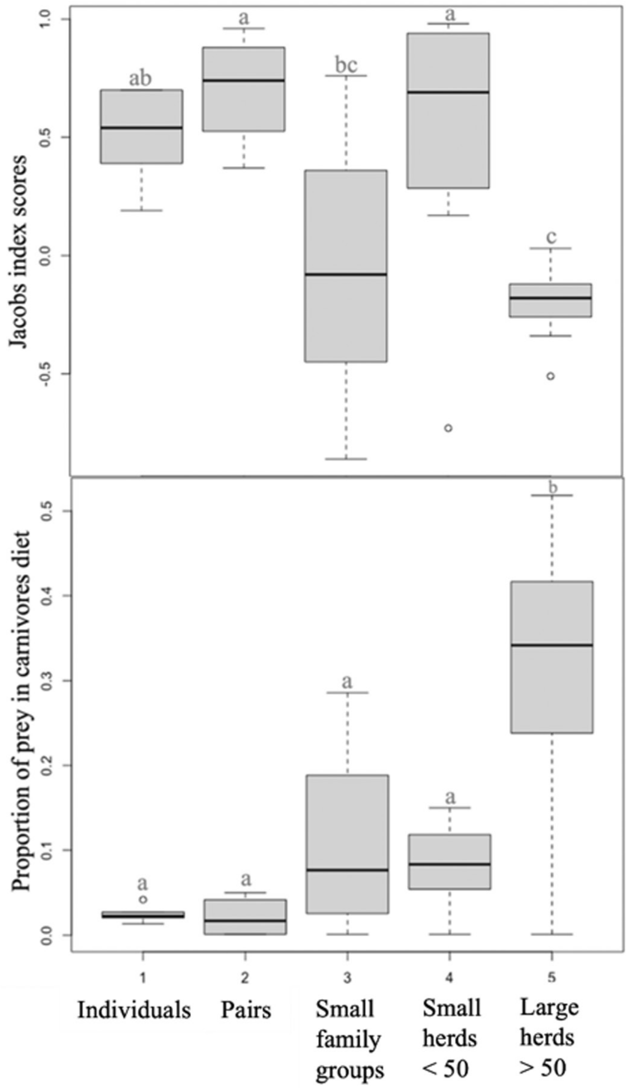

FIGURE 6 Jacob index scores of each herd size category of prey for all carnivores. Values of Jacobs' index scores between −1 and 0 show avoidance of the prey, while between 0 and 1 show preference. Carnivores preferred solitary herbivores, in pairs and small herds as prey, while avoiding large herds. Proportion of prey in all carnivores' diets (between 0 and 1) show that, when taking availability into account, most available prey is most consumed.

adequate availability of prey is allowing the high number of large carnivores in central Tuli to co-exist and more longitudinal research on prey abundance and carnivore diet is needed to test this hypothesis. Based on our results, we suggest that management and conservation practices to ensure and improve the abundance of prey species in the area will ensure the co-existence of these carnivore species.

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CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, upon reasonable request.

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