RESEARCH ARTICLE

Feeding ecology of the large carnivore guild in Madikwe Game Reserve, South Africa

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Southern Africa has a diverse large carnivore guild. When this large carnivore guild is confined to fenced protected areas, the degree of intraguild competition may increase. Dietary overlap is a notable point of competition and can have considerable effects on lower trophic levels. We considered the prey preferences, dietary overlap, and dietary niche breadth of the large carnivore guild in Madikwe Game Reserve through direct observations and scat analysis, over one year of sampling. These data were analysed using the Jacobs' index for prey preference, the Pianka's index for dietary overlap and Levin's index for dietary niche breadth. Leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*) had a high degree of dietary overlap and were specialized in their diet selection. Lions (*Panthera leo*), brown (*Parahyaena brunnea*) and spotted hyaenas (*Crocuta crocuta*) also showed a high degree of dietary overlap and had broad diets. Our results show similarities to those of open systems, suggesting that large carnivore diet selection may not be negatively affected when they are confined by fences. We recommend further investigations into the variables which may affect site-specific carnivore diet selection.

Keywords: carnivore diet, prey species, fenced protected areas.

INTRODUCTION

Southern Africa has one of the most diverse large carnivore communities in the world (Ripple *et al*., 2014). To coexist, carnivores have developed the ability to occupy different niches in terms of habitat use, unique behaviour and/or diet (Durant, 1998). Ways in which carnivores may relieve competition are to become specialized in their dietary selections, through adjusting their dietary niche breadth (Briers-Louw & Leslie, 2020). In addition, to coexist carnivores may adjust their dietary niche breadth, either through a broadening or a narrowing of their niche breadth (Briers-Louw & Leslie, 2020). Carnivores may also select prey based on the energetic benefits obtained from the prey item or they may select prey based on the diversity and abundance of prey species (Hayward *et al*., 2006).

Selection of certain prey species to maximize energetic intake may result in increased pressure on certain prey species (Carbone, Teacher & Rowcliffe, 2007). For example, species such as lions (*Panthera leo*) usually select medium and large prey, whereas cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*) and African wild dogs (*Lycaon pictus*) select mostly medium-sized prey species (Hayward, Henschel, O'Brien, Hofmeyer, Balme & Kerley, 2006; Hayward, Hofmeyr, *et al*., 2006; Lehmann, Funston, Owen & Slotow, 2009; Vogel *et al*., 2019). When multiple carnivore species predate on certain prey groups it can negatively affect these prey populations. Significantly, continued pressure on a specific prey

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species can result in the removal of a species due to over-consumption (Fritz, Loreau, Chamaille-Jammes, Valeix & Clobert, 2011).

Carnivores can have significant impacts on lower trophic levels which may be amplified within fenced areas, where carnivores often occur at higher densities than they typically would in open landscapes (Creel *et al*., 2013; Lindsey *et al*., 2017; Lindsey, 2008; van der Waal & Dekker, 2000; Edwards *et al*., 2019). Therefore, understanding their site-specific prey preferences is essential for ensuring sustainability within a fenced protected area (Hayward & Kerley, 2009).

Data on carnivore diets can be obtained through direct and indirect methods (Clements, Tambling, Hayward & Kerley, 2014). Both approaches have limitations in the quantification of the proportion at which species occur in diets. Direct methods such as visual observations are biased towards larger prey items and rely on constant monitoring of the target species which is often not logistically possible (Rapson & Bernard, 2007). Indirect methods, such as scat sampling, overestimate the contribution of small mammals in diet (van Dijk *et al*., 2007) and cannot distinguish between hunted, kleptoparasitism, or scavenged prey items (Comley *et al*., 2020).

Despite biases in sampling methods, the information provided from dietary studies is vital for monitoring how carnivores utilize prey species. An understanding of how carnivores coexist through resource partitioning can provide insights into the mechanisms within these areas of increased interspecific competition. Where there is high interspecific competition, subordinate carnivores may become more specialized (Ferretti *et al*., 2020). By contrast, apex predators may experience less competition and are able to utilize a wider variety of the available resources (Ferretti *et al*., 2020). However, optimal foraging theory predicts that in more abundant environments, species will become more specialized to optimize energetic intake from the available resources (Pyke, 1984). Despite fenced protected areas typically having high diversity and abundance of carnivore species, these areas of increased competition may result in specialization due to competition and less so due to energetic benefits (Ferretti *et al*., 2020).

The aim of our study was to determine the diet, prey preference, level of dietary overlap and dietary niche breadth of the large carnivore guild (brown hyaenas, *Parahyaena brunnea*, spotted hyaenas, *Crocuta crocuta*, leopards, cheetahs, African wild dogs and lions) in Madikwe Game Reserve, South Africa. We predicted that the carnivores which occurred at lower densities (leopards, cheetahs and wild dogs) would show greater dietary specialization than those carnivores which occurred at higher densities (lions and both brown and spotted hyaenas).

MATERIAL AND METHODS

Study site

Madikwe Game Reserve (Madikwe hereafter) is situated in the North-West province of South Africa (24.7604°S, 26.2777°E). Madikwe is state run and consists of 750 km^2 of fenced arid savanna (Szott, Pretorius & Ganswindt, 2020). Madikwe averages 750 mm of rainfall annually (Szott *et al*., 2020). Madikwe has a variety of habitat types and supports a diverse mammal community. The large carnivore guild in Madikwe at the time of the study consisted of 91 brown hyaenas, 82 spotted hyaenas, 33 lions, 24 leopards, 12 African wild dogs and three cheetahs (H.P. Nel, pers. comm.; Honiball, 2021).

Direct observations

Direct observations of kills were recorded opportunistically from January 2019 until June 2020. Madikwe has 33 safari lodges and supports over 100 eco-tourist guides (Szott *et al*., 2020). The researchers, eco-tourist guides, and North-West Parks Board staff recorded kills observed in Madikwe. Each observation recorded included a GPS location, date, time, species of predator and prey, number of predators and prey where relevant, age of predator and prey, sex of predator and prey and any additional comments deemed necessary by the observer. Observations were then logged on a central database for later analysis. Duplicate recordings were noted and removed.

Scat analysis

Fresh scat samples were collected opportunistically from May 2019 until June 2020. The majority of the scat samples came from the dry season (May–August) due to the difficulty of accessing certain parts of the reserve during the wet season. Therefore, seasonal analysis was not possible. Scats were identified per target species and a sample was collected. The date of collection, scat age, location, and species were recorded with each sample. Only samples where the species could confidently be identified were collected. Scat identification was based on scat size, diameter, shape and, when available, the presence of species tracks (Bothma & le Riche, 1994). Scat freshness was determined by visual observations of moisture in the sample and by the age of tracks around the sample. Only samples with no evidence of deterioration were used (<2 weeks old). Samples were air-dried, then placed in a thick stocking and washed in hot water to remove all digested matter, leaving only hairs, plant matter, feathers and bone fragments. The stocking ensured minimal loss of identifiable material such as hair or bone fragments (Klare, Kamler & MacDonald, 2011). After the samples were washed, they were air-dried for further analysis.

Mukherjee, Goyal & Chellam (1994) determined that a minimum of 15 hair samples were needed to identify all species within a scat sample. Therefore, to ensure complete coverage of all present species, 30 hair samples were randomly removed from each scat sample for analysis. Hair samples were mounted on microscope slides using a thin layer of clear nail polish (Klare *et al.*, 2011). We ensured all ranges of hair types were represented in the 30 hair samples, based on colour, length, and thickness (Keogh, 1985). Hairs were removed from the slide after the nail polish was dry, leaving only the cuticular scale pattern. Scale patterns were then analysed microscopically, under ×10 magnification. These scale prints were compared to Keogh (1983 & 1985) and to a supplementary reference library of 14 species opportunistically collected within Madikwe. Additionally, bones, feathers, fish scales, plant matter, and anthropogenic substances were also visually identified and recorded. Hair samples were classified to the lowest taxonomic level.

Species accumulation curves were created for each carnivores' prey species from direct observations and for scat analysis separately (Appendix 1). Accumulation curves were used to determine if all prey species had been detected by each method, indicated by the curve reaching an asymptote. Species accumulation curves were produced using the R package 'vegan' (Oksanen, Blanchet & Kindt, 2003). The species accumulation curve for the direct observations of lion diet reached an asymptote, showing sufficient direct observations were recorded to determine the diet of lions over one year (Appendix 1). Scat analysis of leopard diet showed a near asymptote despite high confidence intervals. Although the remaining species did not reach an asymptote, the data produced remain valuable.

Categories such as small mammals (<10 kg), birds, bones, arthropods, plant matter, anthropogenic substances and fish were not included in the analysis for prey preference due to the lack of availability data for these groups or inapplicability of the substance to the analysis (*e.g.* anthropogenic substances, arthropods, fish, and birds), as is typical of dietary studies for large carnivores.

Prey species abundance estimates

Prey species population abundance estimates were obtained from annual triplicate aerial counts conducted by Madikwe (North-West Parks and Tourism Board, unpubl. data). Twenty-four species were available as potential prey (Appendix 2). From the available prey species, we determined the available biomass (kg). Prey biomass was calculated using the adult female weight of each species (Cumming & Cumming, 2003).

Prey preference

Prey species were represented as the proportional occurrence in scats and direct observations, respectively. To confront the biases within both methods we used the species biomass consumed as opposed to the frequency of occurrence to determine prey preference (Klare *et al.*, 2011). Using the frequency of occurrence method further increases the biases towards the contribution smaller species make towards diet (Klare *et al.*, 2011). Klare *et al.*, (2011) tested the various methods in analysing dietary data and found the biomass approach to be the most reliable. To calculate biomass consumed by each carnivore group, we calculated the annual intake (kg) of each carnivore species from Carbone, Teacher & Rowcliffe (2007). As daily intake or energetic requirements of brown hyaenas are not available, we used an estimation of 3 kg from Bere & Nutsa (2021) to calculate annual intake (kg). The percentage each prey species represented for each method in the diets of the respective carnivores was then converted into the consumed biomass (using female weight (kg) and the annual intake (kg) of each carnivore) (Periquet *et al.*, 2015). The utilization of prey biomass provides a more holistic approach to determining the prey preference of carnivores (Clements *et al.*, 2014).

Biomass data were then analysed using the package 'selectapref' in R (Richardson, 2017). We used Ivlev's index which was corrected using the

Jacobs' index (Jacobs, 1974). The Jacobs' index minimizes biases in preference estimations (Jacobs, 1974).

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

where r is the proportion of prey species consumed and p is the proportional availability of the prey species killed (Jacobs, 1974). A resultant value between '– 1' and '1' is produced for each prey species, a value of '1' indicating preference, and '– 1' indicating avoidance (Jacobs, 1974).

Dietary niche overlap

Niche overlap was calculated separately for direct observations and for scat. Niche dietary overlap between the six study species was calculated with the R package 'spaa' (Zhang, 2013) using the Pianka's index (Pianka, 1973).

$$Q_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} {p_{ij}}^2 \sum_{i}^{n} {p_{ik}}^2}}$$

where pi is the frequency of occurrence of prey item i in the diet of species j and k (Pianka, 1973). This resulted in a value ranging from '0' to '1', where '0' indicates no overlap and '1' indicates a strong overlap, 95% confidence intervals were also calculated using 999 bootstrap intervals.

Niche dietary breadth

Niche breadth was calculated for each method respectively, using the R package 'spaa' (Zhang, 2013). We used the Levin's index to determine to dietary niche breadth ($\hat{B}$) for each carnivore species.

$$\hat{B} = \frac{Y^2}{\sum N_j^2}$$

where Y is the total number of species sampled and N_j is the number of individuals using prey species j. The resultant values range from zero to the number of prey species, which is in this case 24. Higher values indicate broader niche breadth, while lower values indicate specialization. Niche breadth was not calculated for the direct observations of spotted hyaena and brown hyaena as the observations were insufficient.

RESULTS

The large carnivores in Madikwe consumed 19 of the 24 available prey species (Appendix 2). Species which were not consumed by the large carnivore guild in Madikwe occurred in low densities, *e.g.* eland (*Tragelaphus oryx*), tsessebe (*Damaliscus lunatus*), and mountain reedbuck (*Redunca fulvorufula*). Leopards had a more specialized diet in comparison to the other species, despite unique prey items found in scats such as fish, millipedes, marula (*Sclerocarya birrea*) seeds and bird feathers. Wild dogs also appeared to consume millipedes. We found that cheetahs, brown hyaenas and spotted hyaenas consumed anthropogenic substances such as plastic, despite these items providing no nutritional value. Furthermore, a nearly completely intact piece of kitchen cloth was found in a brown hyaena scat.

Prey preference

Impala (*Aepyceros melampus)*, one of the most abundant herbivores in Madikwe, were a preferred prey item for leopards, wild dogs, cheetahs and brown hyaenas (Fig. 1). We show that the large carnivore guild did not only select for the most abundant prey but had also developed preferences for prey species with lower densities. Steenbok (*Raphicerus campestris*) were preferred by all carnivores except lions. Leopards only avoided species which they were observed to have scavenged – giraffe (*Giraffa camelopardalis*) and elephant (*Loxodonta africana*) (both known to have died of natural causes) but showed a level of preference for all other prey items detected from both methods (Fig. 1).

Niche dietary overlap

From the scat analysis, we found that African wild dogs had the lowest potential for niche dietary overlap in the guild (Appendix 3). Leopards overlapped with all other large carnivores. Brown hyaenas displayed a strong overlap (51–80%) with spotted hyaenas, lions and cheetahs. From both methods, we recorded a strong dietary overlap between cheetahs and wild dogs, and cheetahs and lions. Wild dogs and lions and wild dogs and brown hyaenas only showed a medium level of overlap (20–50%) from both methods (Appendix 3).

Niche dietary breadth

Based on direct observations, lions had the broadest dietary niche despite consuming the same number of species as cheetahs (seven), because lions consumed their prey species in more even proportions (Table 1). Brown hyaenas,

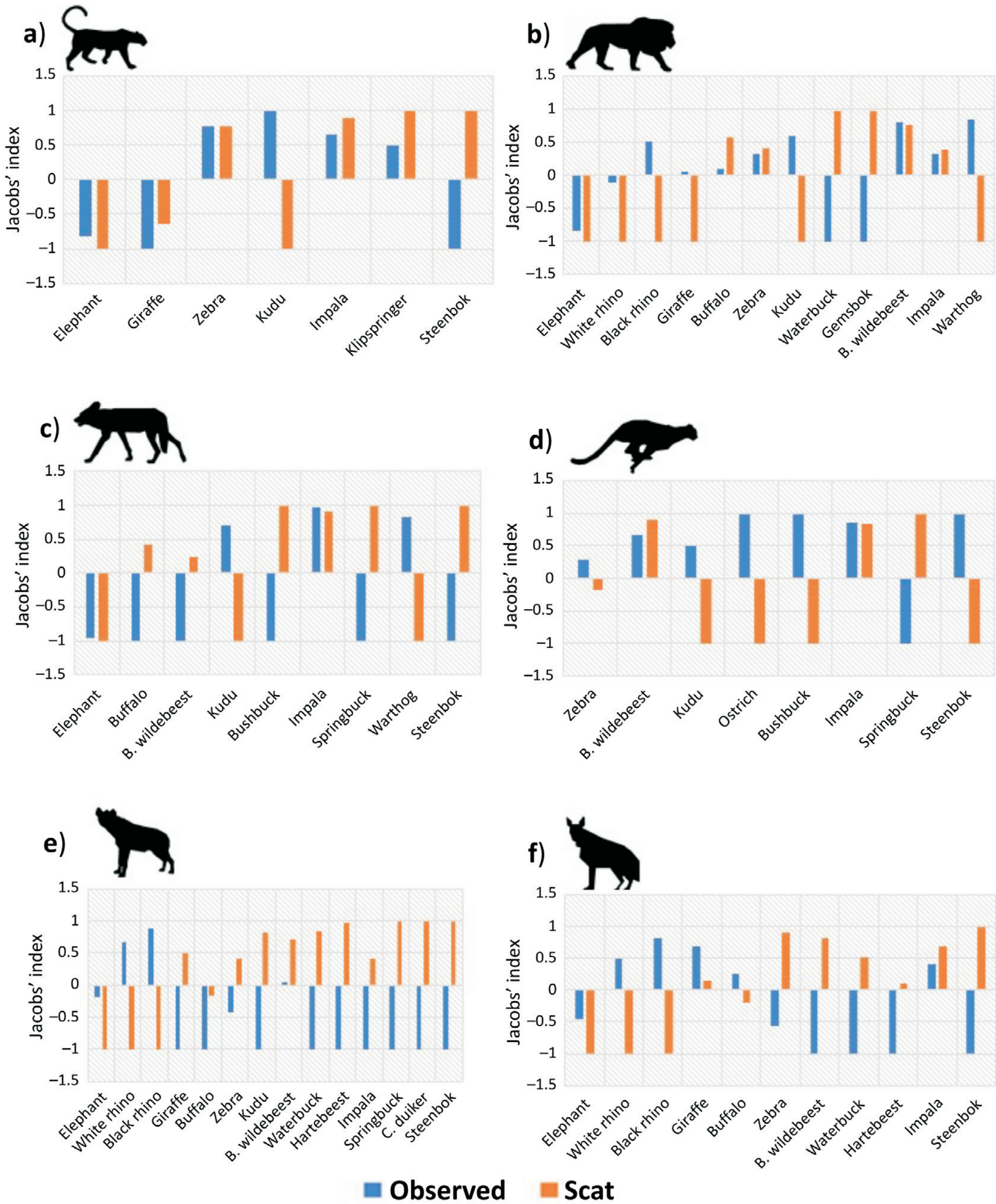

Fig. 1. Prey preferences as indicated by the Jacobs' index, whereby '1' indicates complete preference and '–1' indicates complete avoidance of a prey species.

cheetahs and spotted hyaenas had increasingly specialized diets, respectively. However, the observations of the two hyaena species were strictly scavenging events. Leopards and wild dogs were the most specialized, preying mainly on impala, even though a variety of other species were also consumed (Table 1). Based on the scat analysis, spotted hyaenas, lions and brown hyaenas had the broadest diet of the large carnivore guild in Madikwe (Table 1).

Table 1. The number of species each carnivore consumed as determined by direct observations and scat analysis. The 24 available prey species and their respective Levin's index values for dietary niche breadth (higher values indicate wider niche breadth) are also shown.

		Number of records	Species consumed (n/24)	Levin's index
Leopard	Observed	17	5	2.43
	Scat	11	6	2.33
Cheetah	Observed	26	7	4.23
	Scat	12	5	2.88
Wild dog	Observed	26	4	1.38
	Scat	14	5	2.93
Lion	Observed	92	7	5.85
	Scat	20	6	5.01
Spotted hyaena	Observed	20	5	2.82
	Scat	38	11	6.66
Brown hyaena	Observed	29	7	5,27
	Scat	29	8	4.23

DISCUSSION

Understanding the diet of large carnivores in fenced protected areas is vital for the management of these confined areas. Our results show how large carnivores adjust their diet, prey preference and niche breadth to occupy different dietary niches. Although there is strong overlap in the diets within the large carnivore guild, species occurring at higher densities in Madikwe, such as the lions and spotted hyaenas, appeared to be more generalist species. In contrast to studies in different fenced protected areas (Hayward & Kerley, 2009), leopards in Madikwe had one of the most specialized diets among the large carnivore guild. This specialization of dietary niche breadth has also been recorded in leopards in Majete Game Reserve, Malawi (Briers-Louw & Leslie, 2020). These findings demonstrate that leopards may adjust their dietary niche breadth in fenced areas in response to site-specific variables, as is the case in some open systems (Mann *et al.*, 2019).

When comparing data from large open areas such as Hwange National Park, Zimbabwe, to our results, lion prey preferences remained with larger species such as buffalo (*Syncerus caffer*) (Davidson *et al.*, 2013). Our results for African wild dogs in Madikwe also align with those of studies from the Okavango Delta, Botswana, whereby wild dogs preyed predominantly on impala (Tshimologo *et al.*, 2021).

Brown hyaenas showed a broad diet selection and a high degree of overlap with the large carnivore species. As brown hyaenas are predominantly scavengers, we expected a strong dietary overlap with other large carnivores (Mills & Mills, 1978; Faure, Holmes, Watson & Hill, 2019). Across both methods, brown hyaenas and spotted hyaenas showed very strong dietary overlap with each other. Hayward (2006) reviewed spotted hyaena diet in southern Africa and found that spotted hyaenas have a broad dietary breadth. This finding was supported by Comley *et al.* (2020) in Selati Game Reserve, South Africa, and Periquet *et al.* (2015) in Hwange National Park. Our results further confirm that spotted hyaenas have a broad diet, showing a degree of preference for the majority of the species detected in their diet within Madikwe. Spotted hyaenas in Etosha National Park, Namibia, showed varied prey size selections and these were dependant on hunting group size (Trinkel, 2010). Although we did not investigate the effects of group size on prey selection in spotted hyaena, this should be considered in future. Spotted and brown hyaenas were the only species to show a preference for megaherbivores. The occurrence of megaherbivores in their diets, however, was a result of poaching incidents of black and white rhinoceroses (*Diceros bicornis* and *Ceratotherium simum*), and the natural deaths of elephants (T. Honiball, pers. obs., 2020). This scenario is becoming a more common occurrence across southern Africa as the poaching of rhinoceroses, in particular, continues to increase (Ferreira, Phab & Knight, 2014).

Carnivore species occurring at lower densities such as wild dogs and cheetahs often become more specialized in their diet to avoid competition (Durant, 1998; Lindsey, du Toit & Mills, 2004; Hayward, Hofmeyr, *et al.*, 2006; Hayward *et al.*, 2006). However, a high abundance and diversity of prey can lessen the pressures of dietary overlap (Periquet *et al*., 2015). We show that large carnivores in Madikwe do not only select prey which are abundant, but that they also display preference towards less abundant prey species.

CONCLUSION

Improper management of large carnivores in fenced reserves can result in extreme pressure on lower trophic levels (Fritz *et al*., 2011). Understanding the pressure carnivores place on ungulates can allow managers to pre-empt and avoid potential losses at lower trophic levels. Because prey availability acts as a limiting source for predators (Hayward & Kerley, 2009; Fritz *et al*., 2011), having large numbers of dominant predators may limit subordinate predators by changing the prey community structure considerably in fenced reserves (Hayward & Kerley, 2009). The similarities between the diets of large carnivores in natural landscapes and that of Madikwe could suggest that large carnivore diet is more dependent on factors such as prey availability than on being confined to a fenced protected area. Therefore, understanding the site-specific prey selection of carnivores is vital for managing these enclosed protected areas.

A diverse carnivore guild is a positive attribute of a healthy ecosystem. However, when limiting movement through fences, we need to understand the effects that these carnivores may have on their localized ecosystem. Although our sample sizes for both direct observations and scat analysis were small, we believe our study contributes to understanding large carnivore diets in small, protected areas. We recommend further studies on the feeding ecology of large carnivores in fenced protected areas to further understand their ecological role in these systems. Such research is particularly important considering the continued growth of the human population across Africa and the associated pressure that will be placed on protected areas.

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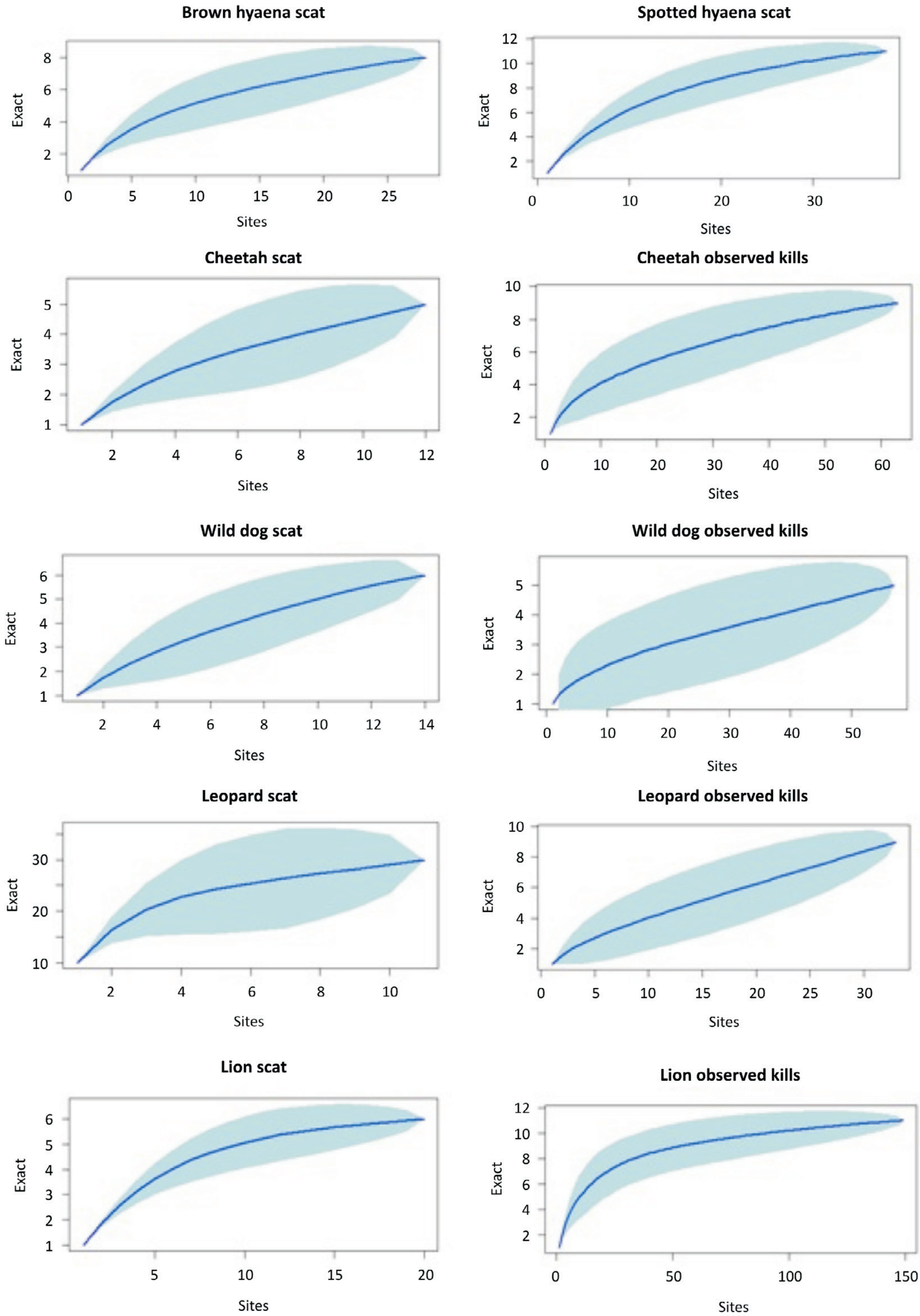
Appendix 1. Species accumulation curves for direct observations and scat analysis of prey species for six large carnivores.



Appendix 2. Weight class and occurrence of available prey species in Madikwe Game Reserve. 'x' indicates the presence of the prey species.

		Leopard, *Panthera pardus*		Lion, *Panthera leo*		Cheetah, *Acinonyx jubatus*		African wild dog, *Lycaon pictus*		Spotted hyaena, *Crocuta crocuta*		Brown hyaena, *Parahyaena brunnea*	
	Female weight (kg)	Scat	Observed	Scat	Observed	Scat	Observed	Scat	Observed	Scat	Observed	Scat	Observed
Number of records:	–	11	17	20	92	12	27	14	26	38	20	29	20
African elephant, (1498) *Loxodonta africana*	2275		x		x				x		x		x
White rhino, *Ceratotherium simum*	1500				x						x		x
Black rhino, *Diceros bicornis*	850				x						x		x
Giraffe, (204) *Giraffa camelopardalis*	850	x	x		x					x		x	x
Buffalo, (813) *Syncerus caffer*	450			x	x			x		x		x	x
Eland, (8) *Tragelaphus oryx*	450												
Zebra, (2240) *Equus quagga*	302	x	x	x	x	x	x			x	x	x	x
Gemsbok, (30) *Oryx gazella*	225			x									
Blue wildebeest, (1453) *Connochaetes taurinus*	180			x	x	x	x	x		x	x	x	
Waterbuck, (108) *Kobus ellipsiprymnus*	175			x						x		x	
Kudu, (518) *Tragelaphus strepsiceros*	160				x		x		x	x			
Red hartebeest, (45) *Alcelaphus buselaphus caama*	136									x		x	
Tsessebe, (1) *Damaliscus lunatus*	126												
Ostrich, (8) *Struthio camelus*	100						x						

Continued on p. 164

Appendix 2 (continued)

	Female weight (kg)	Leopard, *Panthera pardus* Scat	Observed	Lion, *Panthera leo* Scat	Observed	Cheetah, *Acinonyx jubatus* Scat	Observed	African wild dog, *Lycaon pictus* Scat	Observed	Spotted hyaena, *Crocuta crocuta* Scat	Observed	Brown hyaena, *Parahyaena brunnea* Scat	Observed
Nyala (1) *Tragelaphus angasii*	62												
Impala, (4498) *Aepyceros melampus*	60	x	x	x	x	x	x	x	x	x		x	x
Warthog, (387) *Phacochoerus africanus*	57				x				x				
Springbuck, (15) *Antidorcas marsupialis*	39					x		x		x			
Bushbuck, (3) *Tragelaphus sylvaticus*	35						x	x					
Chacma baboon (12 troops) *Papio ursinus*	31,8												
Mountain reedbuck, (1) *Redunca fulvorufula*	28												
Common duiker, (12) *Sylvicapra grimmia*	20									x			
Klipspringer, (5) *Oreotragus oreotragus*	13,2	x	x										
Steenbok, (37) *Raphicerus campestris*	11	x					x	x		x		x	
Rodents	–	x						x				x	
Birds	–	x											
Fish	–	x											
Plant matter	–	x		x									
Bone fragments	–	x		x		x		x		x		x	
Arthropods	–	x						x					
Anthropogenic substances	–	x				x				x		x	

Appendix 3. Niche dietary overlap amongst the large carnivore guild in Madikwe Game Reserve from direct observations and scat analysis, including the upper (u) and lower (l) confidence intervals (c.i) for each relationship.

Species	Observations overlap	c.i (u/l)	Scat overlap	c.i (u/l)
Leopard/wild dog	0.915	0/0.995	0.604	0/0.971
Leopard/cheetah	0.870	0/0.980	0.510	0/1.00
Leopard/lion	0.407	0.128/0.874	0.544	0/0.935
Leopard/brown hyaena	0.333	0.195/0.791	0.728	0.066/0.989
Leopard/spotted hyaena	0.108	0/0.694	0.643	0.186/0.918
Wild dog/cheetah	0.793	0/0.980	0.712	0.138/0.981
Wild dog/lion	0.238	0.129/0.720	0.394	0/0.779
Wild dog/brown hyaena	0.260	0/0.794	0.493	0.075/0.944
Wild dog/spotted hyaena	0.038	0/0.815	0.384	0.149/0.742
Cheetah/lion	0.665	0.213/0.924	0.641	0/0.921
Cheetah/brown hyaena	0.209	0/0.588	0.816	0/0.981
Cheetah/spotted hyaena	0.066	0/0.493	0.683	0.308/0.917
Lion/brown hyaena	0.429	0.2180.910	0.881	0.639/0.985
Lion/spotted hyaena	0.412	0.344/0.908	0.799	0.298/0.950
Brown hyaena/spotted hyaena	0.894	0.145/0.994	0.901	0.512/0.985