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Human-Lion conflict around Nairobi National Park: Lion (Panthera leo melanochaita, Hamilton Smith, 1842) Population Structure, Landscape Use and Diet, in a Semi-Fenced Park

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Impact of Climate Variability on Feeding Ecology of a Lion (*Panthera leo melanochaita*) Population under Urban Pressure in Nairobi National Park, Kenya

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Abstract

The aim of our study was to analyze the effects of climate variability and associated rainfall on the feeding ecology of lions in Nairobi National Park (NNP). We conducted carcass counts and collected scats to determine lion diets based on microscopic analysis of hair morphology, by DNA-metabarcoding.

Our results show that the lions of Nairobi National Park (NNP) have a mixed diet. They feed on large (< 200 kg), medium-sized (50-200 kg) and small-sized prey (5-50 kg), supplemented with very small prey (<5 kg). During and after three months of heavy rainfall more very small prey items were found in the lions' diet. Prey composition varied significantly between the dry and the wet season (also influenced by climate variability), showing different foraging strategies in different seasons.

Our findings validate the application of hair morphology and DNA-metabarcoding in a lion feeding study. We recommend further study of the role of very small prey in lions' diets by analyzing DNA from lion scats.

Keywords
Panthera leo, carcasses, Scats, DNA, Diet, Prey size

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4.1 Introduction

The free ranging lion *(Panthera leo leo)* populations in Africa are locally and regionally threatened as a result of habitat encroachment, a decline in prey populations and by conflicts with human communities (Bauer & Van der Merwe 2004; Craigie et al. 2010; Henschel et al. 2010; Riggio et al. 2013). The most important driving forces in this process are human population growth and economic development (McKee et al. 2004; Craigie et al. 2010; Stuart et al. 2010).

Male and female lions require a mean daily uptake of 10.4 and 7.5 kg of fresh meat respectively (Schaller 1972). They are considered to be opportunistic hunters and they can travel long distances (some 20 km per day) in search of prey and are therefore expected to encounter the full range of potential prey species occurring in their habitat (Hayward & Kerley 2005; Tuqa et al. 2014). However, prey abundance and density is subject to temporal changes (e.g. seasonal changes in rainfall, migration of prey species) and therefore will, differ within a lion's range (Hayward et al. 2007; Hayward & Kerley 2005). Other factors are: prey species characteristics (e.g. prey body mass, age, sex); temporal and spatial distribution; defense or anti-predatory tactics; morphological (e.g. sable horns); ecological (e.g. occurring at low density) and behavioral (e.g. the large herd size and increased vigilance of eland) characteristics; and preferred weight range and preference (Sunquist & Sunquist 1989; Hayward & Kerley 2005).

Different authors suggest different lion preferences and weight ranges, depending on region and species presence in that geographical area. Hayward & Kerley (2005), for example, conducted an analysis of 32 studies over 48 different spatial locations on the distribution of lions and showed that prey species within a weight range of 190–550 kg are preferred. The most preferred weight of prey is 350 kg and the mean mass of all preferred species was 201 kg (Hayward & Kerley 2005). Overall, gemsbok (*Oryx gazella*), African buffalo (*Syncerus caffer)*, wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*) and zebra (*Equus quagga*) were reported as the five most significantly preferred prey species in the analysis by Hayward & Kerley 2005. Being opportunistic feeders, lions regularly feed on medium-sized (50-200 kg) and large prey (>200 kg) (Bauer *et al.* 2008).

The dispersion of prey in a protected area is regulated by rainfall (Sogbohossou et al. 2011; Tumenta et al. 2013). Tuqa (2015) reported wildebeest and zebra as the most preferred species in Amboseli National Park. The Amboseli study analyzed prey preference before and after a period of drought, which resulted in mass mortality among wildebeest and zebra, forcing the lions to shift prey selection towards smaller prey species (such as impala and

warthog) and larger prey species (giraffe and African buffalo), in addition to livestock (Tuqa et al. 2014). After the drought, lions shifted back to medium-sized prey such as zebra and wildebeest, confirming the preference for these species (Tuqa et al. 2014). This largely coincides with the findings of Schaller 1972.

Nairobi National Park (NNP) is experiencing the impact of climate change and other human related changes (Owino et al. 2011). As a result, the human communities around the park are rapidly changing their strategies to cope with changes in their environment, shifting from pastoralism to urban livelihoods (Nkedianye et al. 2009). These changes have a direct impact on the lion's habitat and the feeding ecology of lions.

The role of large and medium-sized mammals in the lion's diet is well studied (Hayward & Kerley 2005; Bauer et al. 2008). However, it has been observed that occasionally very small prey species (body mass <5 kg), such as rodents or small birds, are also part of a lion's diet (Sogbohossou et al. 2011; Davidson et al. 2013). There are very few studies on the contribution of very small mammals and birds to the diet of lions. The detection of very small prey is more difficult with traditional methods of diet assessment, such as carcass counts and analysis of prey hair morphology in scats.

The use of DNA extracted from lion scats for diet studies of carnivores is an emerging field of research. In our study, we used a combination of carcass counts, microscopic analysis of prey hair morphology in scats and DNA techniques to detect the full range of prey in the lions' diet. This methodology was selected in order to fill a gap in research and determine the contribution of very small prey species to lions' diet.

Our aim is to assess the effects of climate variability and rainfall on the feeding ecology of lions. We hypothesize that NNP does not have sufficient wild prey all year round to meet the energetic demands of lions. Consequently, we suggest that lions in NNP need to supplement their diet with very small prey. The following research questions will be addressed: (i) What is the diet composition of lions in time and space? (ii) What is the prey choice of lions in time and space? (iii) What is the effect of climate variability and associated rainfall on lion diet? (iv) What are the trends in prey carcasses biomass in in time and space? (v) What is the added value of the meta DNA barcoding method compared to the diet methods based on the scat analysis and carcass counting?"

4.2 Materials and methods

4.2.1 Study area

Nairobi National Park (NNP) is located to the south-west of Nairobi City, Kenya (Owino et al. 2011) (Fig. 4.1). The park was established in 1946 with an area of 117 km^2 (Owino et al. 2011; Lesilau et al. 2018). It is situated between latitudes 1° 20′-1° 26 S and longitudes 36° 50′-36° 58′E (Ogutu et al. 2013) within an altitude ranging between 1533 m to 1760 m above sea level (Rudnai 1974; Owino et al. 2011). It has a long wet season from March to May with a mean of 150 mm of rainfall and a short wet season from November to December with a mean of 90 mm of rainfall; the annual temperature range is between 13.6°C and 25.3°C (Deshmukh 1985).

Nairobi National Park has three distinct vegetation zones: (i) semi-evergreen forest patches (*Croton macrostachys* and *Olea Africana*) with open grass glades (Foster & Coe 1968); (ii) an open grass savannah with monocods like *Pennisetum meszzianum* and *Themeda triandra* and trees like *Balanites spp.* and *Acacia melifera*; and (iii) riverine vegetation dominated by *Acacia xanthophloea Acacia mellifera* (Rudnai 1974). Dwarf woody plants are a result of controlled burning by park management (Foster & Coe 1968).

As a result of its locality, the park was semi-fenced in 1955 (Steinhart 1994). A chain-link fence with galvanized wire was erected along 36.3 km (56.1%) of the park's 64.7 km perimeter. The fenced is powered by electricity (6 Kv) and runs from the East via the northern boundary to the West in order to separate wildlife from the Nairobi metropolis (Foster & Coe 1968; Reid et al. 2008). The park's southern boundary is beyond the Mbagathi River and provides open access to the Athi-Kaputiei Plains (AKP) with an area of rangeland of 2200 km^2 (Reid et al. 2008).

The park is home to four species of the so-called Big Five: lion (*Panthera leo)*, leopard *(Panthera pardus),* African buffalo *(Syncerus caffer caffer)*, and eastern black rhinoceros (*Diceros bicornis*). The blue wildebeest (*Connochaetus taurinus),* Burchell's zebra (*Equus quagga burchelli)* and associated smaller ungulates such as Grant gazelle (*Gazella granti)*, Thompson's gazelle (*Eudorcas thomsoni)* and warthog (*Phacochoerus africanus*) tend to range into community land during the wet season (Gichohi 1996). Other resident ungulate species include: White rhinoceros (*Ceratotherium simum),* Common eland *(Tragelaphus oryx)*; hartebeest *(Alcephalus buselaphus*); giraffe *(Giraffa Camelopardalis)*; impala (*Aepyceros melampus),* waterbuck (*Kobus ellipsiprymnus),* Bohor reedbuck *(Redunca redunca)* and Common reedbuck *(Redunca arundinum)* (Owino et al. 2011). The park is an important bird

area with a high diversity of bird species (see http://www.naturekenya.org/content/important-bird-areas).

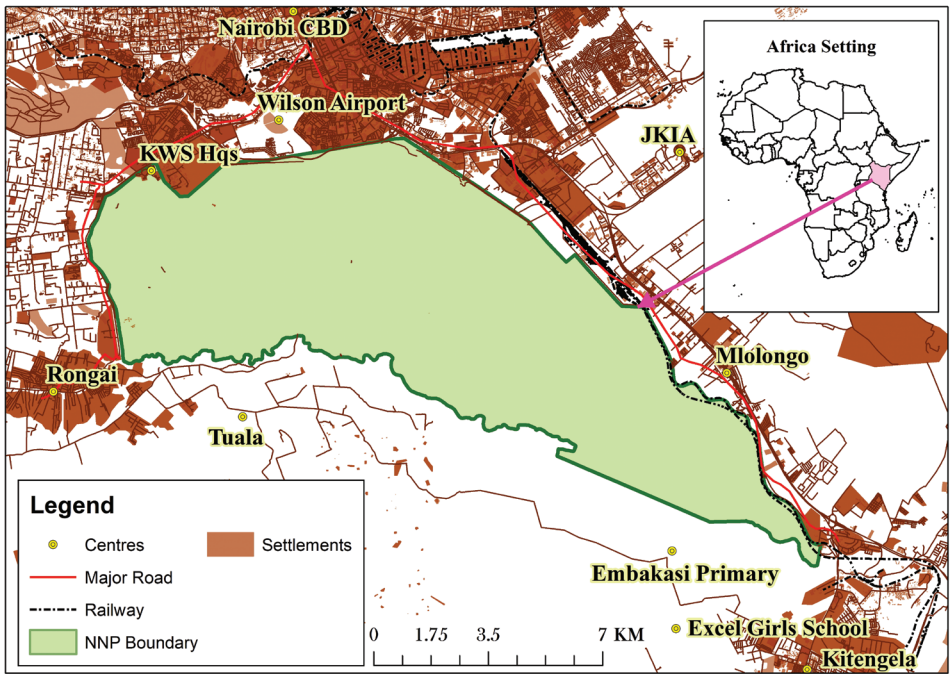


Figure 4.1
Map situating different habitat types within Nairobi National Park. Vegetation data provided by the KWS GIS and Biodiversity Office (2011). (Designed in Arcmap 10.3.1 (ESRI Software, USA))

4.2.2 Data collection

4.2.2.1 Prey hair in lion scats

Prey hairs in carnivore scat are usually unspoiled (Ramakrishnan et al. 1999). Lions live in family units and prides at the apex of their social organization (Stander 199; Bauer et al. 2003; Elliot 2017). Each adult member of a pride marks their territory using scats, urine and scents (Schaller 1972). As a result, scats from lions are commonly found throughout NNP. The scats were searched for at previously sighted lion resting sites, around prey carcasses killed by lions, along the roads while driving, and at opportunistic encounters with lions (Bisceglia et al. 2008; Tuqa 2015). Lion scats have a number of distinguishable features; they can be blackish, pungent smelling, segmented appearance, turning white when dry due to bones (Stuart & Stuart 2000). The

scats identified in the field were collected before sun drying and stored in a labelled zip-lock bags in a secure enclosure in order to prevent the samples from curious baboons, following Tuqa (2015). We recorded the GPS locations (including date and time) of the scats and later air-dried them. Lions do not necessarily feed on one prey at a time. For example, we observed (12 October 2015) a lion feeding on a hartebeest and a Thomson gazelle simultaneously, in which case hairs from both species would be present in the scat. Microscopic hair identification was prepared according to the procedure used by Reynold & Aebischer (1991) and Ramakrishnan, Coss & Pelkey (1999). We made a Prey Reference Hair Collection (PRHC) from fresh prey carcasses in NNP by collecting hair specimens from stuffed animals in the Natural History Museum, Naturalis in Leiden, The Netherlands, and from livestock encountered around the NNP. Prey hair items were identified using hair structure (cuticle scales) and color and by comparing them with previously prepared PRHC morphology (Corbett 1989). Prey weight categorization was adapted according to Bauer et al. (2008) into large (>200 kg), medium (50-200 kg) and small (5-50 kg).

We constructed a Prey Reference Hair Collection (PRHC) from fresh prey carcasses in NNP and from collected specimens in the collection of the Naturalis Biodiversity Centre (Leiden, The Netherlands) and from livestock encountered around the NNP.

4.2.2.2 Rainfall

We acquired Wilson Airport Meteorological station rainfall data from the Kenya Meteorological Department (KMD, 2012, 2014-2016). We considered the high altitude of NNP and high rainfall and chose 30.0 mm of rainfall per month to be the cut-off point for the transition between the dry and the wet season.

4.2.2.3 Prey DNA in lion scat

We only applied DNA (deoxyribonucleic acid) analysis of scat during the heavy rainfall year of 2015 to confirm the findings of hair morphology in the scats and carcasses. A sub-sample of the ten fresh scat samples collected in July – September 2015 from NNP was taken and preserved in a sterile DNA-free Eppendorf with 99.7% ethanol. The remaining scats was collected as described by Tuqa (2015) for prey hair analysis. The composition of lion diets was further determined using a recently developed method based on next-generation sequencing (Shezad et al. 2012).

We took samples from the center of the fresh lion scat using plastic gloves and a sterilized surgical blade and preserved them in a DNA-free Eppendorf tube containing 1.8 ml of 99.7% ethanol to minimize the collection of scats

with DNA degraded by ultraviolet light, or the collection of overabundant epithelial cells from the predator's intestinal tract. The tubes were labelled and stored in the dark at room temperature. The rest of the scats were collected and secured in labelled zip-lock bags for hair morphological and other remnants analysis.

We successfully extracted prey DNA from lion scats at the Leiden University molecular laboratory following previously optimized protocols (Bertola et al. 2011, 2016) using the Qiagen QIAamp DNA stool mini kit (Qiagen Inc., Valencia, California, USA). Controls were included to check for contamination during the extraction process.

4.2.2.4 Prey carcasses

We conducted prey carcass counts by searching for lions and prey carcasses. In addition, we collected ranger reports and reports from tour guides of sightings of fresh prey carcasses during 2012, 2014-2016. Finally, we counted carcasses during opportunistic encounters. The carcasses were inspected by the principal author who examined them for lion feeding signs and traces (e.g. claw marks and scats) in order to identify them as a lion feed, as described in Bauer et al. (2008). We excluded those carcasses showing no signs of lion feeding from the analysis. We recorded the Global Positioning System (GPS) coordinates of the carcasses (Garmin GPS), prey species, season (wet/dry) and condition of the carcass (fresh/old) in a pre-structured form.

4.2.3 Data analysis and statistics

4.2.3.1 Prey hair in the scats

We expressed occurrence of each prey hair item in each of the scat samples as presence or absence within the scats. We obtained the percentage frequency of occurrence by dividing the total prey hair items of a particular species by the overall number of prey hair items for all species and multiplied by 100%. The presence of bones, skull fragments, feathers, beaks, claws, jaws and teeth fragments of very small prey <5 kg (e.g. mice and birds) were determined only to genus or family level.

4.2.3.2 Rainfall

When analyzing the results of the prey hair analysis, we took into account rainfall data during the three months prior to scat collection. We carried out all statistical tests using the software R version 3.3.2 (R Foundation, Vienna, Austria). We used a significance level of $p < 0.05$ for all the tests.

4.2.3.3 DNA- Meta-barcoding

To amplify vertebrate prey DNA without any a priori knowledge of dietary composition, we conducted a polymerase chain reaction (PCR) with the highly conserved universal primer binding sites 12SV5F/12SV5R for all vertebrates with blocking primer for lion (Riaz et al. 2011; Shezad et al. 2012). This method has successfully been implemented with other felid species (Shezad et al. 2012, 2015). A PCR of the control, as well as a control PCR reaction were included to rule out contamination. We checked all PCR reactions on the Bioanalyzer (Agilent Genomics) and they were subsequently equimolarly (concentration 19.0 ng/μl) pooled for sequencing. We generated data using paired-end sequencing (Run length 125bp) on an Illumina HiSeq 2500 and subsequent quality control, as implemented by Baseclear (Leiden, The Netherlands). This includes Illumina Chastity filtering, removing reads containing the PhiX control signal and removing read containing partial adapters, while maintaining a minimum read length of 50 bp. We de-multiplexed all samples based on a unique combination of eight base pair tags attached to both the F and the R primers (tags were designed so that all the tags differ from each other by >2bp).

After quality control, sequence data were analyzed using a pipeline hosted at Naturalis Biodiversity Center. Sequence read were filtered, clustered and BLASTed using scripts implemented in the galaxy platform (Giardine et al. 2005). We used the Uchime de novo tool from the Usearch package to remove chimeric sequences from an amplicon set (Edgar 2010). We clustered rea above 100nt with CD-HIT-EST at 100% similarity and removed any clusters smaller than 10 reads (Fu et al. 2012). We used representative sequences from the clusters for BLAST search identification against a local copy of GenBank. Only 100% matches were selected (Camacho et al. 2009).

We performed a chimera check (as implemented in Galaxy – chimera removal). We chose these stringent options to reduce the noise and chances of false positives. The resulting list of identified prey species was further analyzed by excluding all hits that were represented by <3% of clustered reads. We compared the composition of the prey hair item identified from scats and prey carcasses counted with DNA scats results of the same season.

4.2.3.4 Prey carcasses

We first determined the total number of kills per prey species (Druce et al. 2004). We then split the prey species carcass data into seasons based on the monthly amount of rainfall (wet/dry). We used 30 mm of rainfall per month as a cut-off point between the wet and dry season. The percentage frequencies of prey species carcasses were calculated seasonally, based on the cumulative number of carcasses of each season, and biomass was multiplied

by ¾ of individual female weight, as in Hayward & Kerley (2005), to obtain the total carcass biomass for the dry and wet seasons. We excluded livestock carcasses from biomass analysis.

4.2.3.5 Comparison on data collection techniques

We compared the composition of the diets based on prey hair items identified from scats and from prey carcass counts, with diets based on DNA analysis of scats during the same (wet) season to determine the prey species presence and absent between the three methods.

4.3 Results

4.3.1 Prey diversity in lion scats

We collected 425 scats during 2012, 2014-2016 and 35 (8.4%) doubtful scats were excluded from analysis, either because they did not contain hair to match the PRHC, or because they were suspected to be from other carnivores. In 21 scats, bones, skull fragments, feathers, pieces of horn, beaks, claws, grass, jaws and teeth were found (Fig. 4.2a and b). After discarding doubtful scats, we were left with 390 scats. Of the remaining 390 scats, 298 were collected in the dry season and 92 scats in the wet seasons during 2012, 2014-2016. The dry season scats contained 265 prey hair items and the wet season scats contained 111 prey hair items based prey hair morphology and scale pattern from lion scats (Fig. 4.2c). There is a significant difference in the expected equal prey hair items between the dry season scats and the wet season scats ($\chi^2 = 64.7$, df = 1, p-value = 0.001). There are 20 different prey species hair items from the lion scats. Three wild large prey species, five medium-sized species, seven small species and five very small prey species were found, with a significant difference between prey biomass category found in the prey hair items (Table 4.1; $\chi^2 = 104.5$, df = 3, p-value < 0.001). In 102 scats we identified more than one prey species, with the highest being four different prey species in one scat.

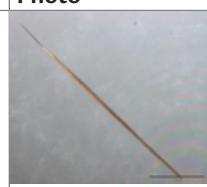
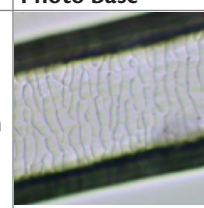
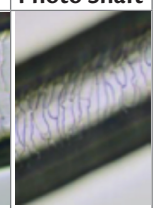
Species	Morphology	Photo	Scale Pattern	Photo Base	Photo Shaft
Impala	Reddish Brown (Raw Sienna) over entire length with black tip (0.8 mm)		**Base & Shaft**: regular waved mosaic, 2-3 scales across width, scale margin smooth. **Tip**: slightly irregular, scale margin smooth to ripple.		

Figure 4.2
(a) small prey carcass remains from lion scats; (b) Lioness feeding on a marabou stork (*Leptoptilos crumenifer*); (c) prey hair morphology and scale pattern from scats

The main species found in the scats during the dry season was zebra (23%), followed by African buffalo (14%), hartebeest (10%), rodents (9%) and wildebeest (7%). Results for the wet season were similar, with zebra (27%), African buffalo (11%), warthog (9%), hartebeest (9%) and impala (8%) (Table 4.1). During 2012 and 2014-2016, the result shows large prey contribute 31% of the prey hair items, medium size prey is 52%, small size prey is 17% and very small prey is 0% (Fig. 4.4c)

Table 4.1
Frequency and percentage of occurrence of different wildlife prey hair items in the scats of NNP lions (data are cumulative during 2012, 2014-2016, by season).

Class weight	Species	No. of prey hair items in the scats	Total in dry (Jul-Sept)	Total wet (Feb-Apr)	Dry season (%)	Wet season (%)
Large	Buffalo	48	36	12	14	11
	Eland	13	10	3	4	3
	Giraffe	9	5	4	2	4
Medium	Hartebeest	37	27	10	10	9
	Ostrich	12	7	5	3	5
	Waterbuck	10	5	5	2	5
	Wildebeest	23	18	5	7	5
	Zebra	91	61	30	23	27
Small	Bushbuck	4	2	2	1	2
	Bushpig	1	0	1	0	1
	Grant's gazelle	21	16	5	6	5
	Impala	28	19	9	7	8
	Reed Buck	1	0	1	0	1
	Thompson's gazelle	15	12	3	5	3
	Warthog	25	15	10	6	9
Very small	Bird	7	6	1	2	1
	Hare	1	0	1	0	1
	Rodent	28	25	3	9	3
	Snakelike	1	1	0	0	0
	Lizard	1	1	0	0	0
		376	265	111	100	100

4.3.2 Climate variability effects

The amount of rainfall of three months prior to data collection had a direct positive impact on the presence of very small prey in the lions' diet. As rainfall increased, the contribution of prey hair items of large ($r^2 = 0.5$) and medium (r^2 0.03) prey decreased, while the proportion of the small ($r^2 = 0.24$) and very small ($r^2 = 0.04$) prey hairs increased (Fig. 4.3)

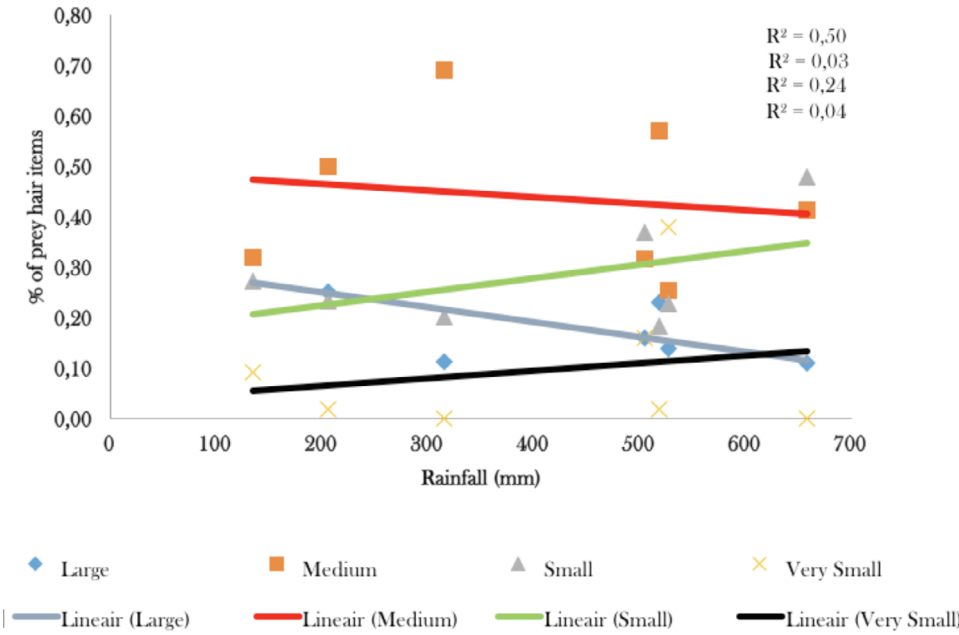


Figure 4.3

The El-Nino rainfall impact on lion diet, based on prey hair items in the lion scats. Rainfall is based on cumulative rainfall for three months prior to data collection months. Large (L), Medium (M), Small (S) and Very Small (V) prey size.

4.3.3 Meta-barcoding results

We used DNA to confirm the effects of rainfall on the diet already established from hair morphology in the scats. From the ten samples, we obtained a total of 546,768 reads, which were accepted after FastQC (version 0.10.0) quality control. We retained 97% of all reads after a chimera check. After removing clusters that represented <3% of all clustered reads, BLAST identification resulted in a list of two to six species per sample. Multiple clusters had identical BLAST identification.

We encountered lion DNA in all ten samples and this data was used as an internal control to check the identity of the scat samples. In one case, 63% of the reads were attributed to leopard. Leopard was also found in three other samples, albeit in a lower percentage. We identified serval DNA in three samples. The reads of leopard were interpreted as errors and not taken into account, although it cannot be excluded that lions eat leopards. We excluded the reads without other species from further analysis. The reads of other prey animals in the scats with leopard reads were still used for the analysis. So we analyzed 10 lion scat samples in total. We also found human DNA

in three samples. In two samples, BLAST returned tiger as a hit, which we attribute to damage in the DNA, resulting in a sequence change (1 bp) that resembles a tiger sequence. All other identified species are likely to be true prey species for the lion: blue wildebeest, zebra, suni (*Neotragus moschatus*), African buffalo, common eland, shoat and mole rat (*Tachyoryctes sp* as the only representative of a very small prey species.) (Fig. 4.4a, b and Table 4.2). With the exception of the DNA of tiger, leopard, human and serval cat, we had identified all other species either through carcasses or hair morphology. The aforementioned reads were not included in the statistical analysis, while a possible cross contamination was indicated by negative controls. We mention these findings here to highlight the diversity of prey composition that can be detected based on DNA analyses.

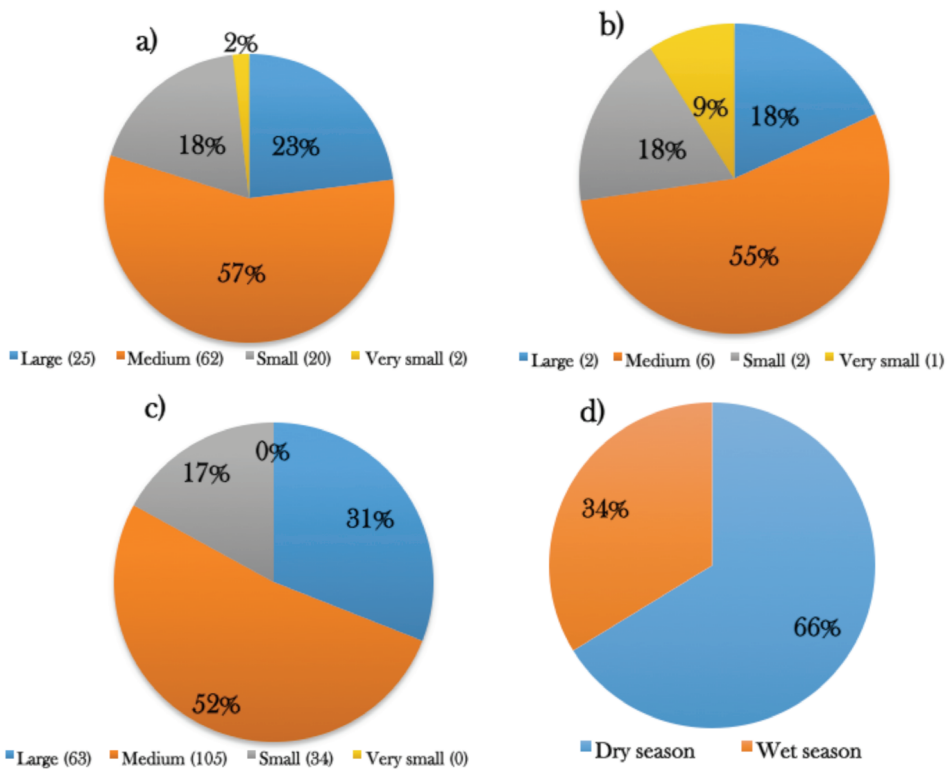


Figure 4.4

(a) Prey size proportions based on hairs from lions' scats of July – September 2015; (b) DNA-metabarcoding results of ten scats samples collected in NNP in July – September 2015 (excluding livestock and carnivores); c) Frequency of prey sizes occurrence in the park based on carcass surveys during 2012 and 2014-2016 (Large 200 kg, medium 50–200 kg, small <5–50 kg and very small < 5 kg, based on Bauer et al. 2008); d) Seasonal average of wild species biomass (kg) carcasses from 2012, 2014-2016 in NNP, based on average male and female weight, following Hayward & Kerley (2005).

Table 4.2
DNA, prey weight classification, counts and percentage in DNA analysis from ten scat samples

Weight class	Scientific names	Species	Count	Percentage
Large (>200 kg)	*Syncerus caffer*	African buffalo	1	9.1
	Tragelaphus oryx	Common eland	1	9.1
Medium (50-200 kg)	*Connochaetes taurinus*	Blue Wildebeest	4	36.4
	Equus burchellii	Zebra	2	18.2
Small (<5-50 kg)	*Neotragus moschatus*	Suni	2	18.2
Very Small (< 5 kg)	*Tachyoryctes sp*	Mole rat	1	9.1

4.3.4 Prey carcass diversity and biomass

A total of 234 carcasses of 14 wild prey species, three livestock prey species and four unknown prey species were recorded during 2012, 2014-2016. We excluded 28 livestock carcasses and four unidentified carcasses from the analysis, since livestock are not legally found in the park and carcasses could be as a result of unherded or stray livestock killed by lions, except when comparing DNA-metabarcording with hair and carcasses in the sample of July-September 2015. Of the 202 remaining carcasses, 148 carcasses were found during the dry season and 54 carcasses during the wet season (Fig. 4.4a; $\chi^2 = 43.7$, df = 1, p-value <0.001). Our average detection rate is 40 carcasses (62%) in the dry season and 25 in the wet season (38%). The average wild prey carcass biomass amounted to 8,356 kg/km^2 (66%) in the dry season and 4,259 kg/km^2 (34%) in the wet season (Fig. 4.4d). There is a significant 68% decline in carcass biomass (kg) from dry season to wet season (Fig. 4.4d, Table 4.3; t = 2.42, df = 15, p-value < 0.031). The six main prey species killed by lion amount to 55% of all carcasses in the dry season. In the wet season, the six main prey species amount to 25% of the total carcass biomass (Table 4.3). The overall average frequency of carcasses per body size class for the dry season are: large 21%; medium 35%; and small 11%. For the wet season, the contribution of large is 10%, medium 17% and small 6%, as shown in Fig. 4.4. A Chi-square test reveals a significant difference prey size class distribution between the wet and the dry season ($\chi^2 = 64.5$, df = 3, p-value < 0.001). We also found a significant negative correlation between log-monthly precipitation and log-number of prey species carcasses found in the park using Pearson correlation test: ($r^2 = -0.66$, p-value<0.004; Fig. 4.5).

Table 4.3

Seasonal wild species carcasses, contribution of each species from 2012, 2014-2016 in NNP on ¾ weight of female adult, based on Hayward & Kerley (2007).

Classes	Species	No of carcasses during study period			Seasonal averages of carcasses and biomass				Seasonal percentages (%)	
		Dry season carcasses	Wet season carcasses	Body Mass (kg) per species	Dry season average	Wet season average	Dry season Biomass	Wet season Biomass	Dry season	Wet season
Large	Bu	25(16.9%)	6(10.7%)	432	6	2	2592	864	31.0%	20.3%
	El	11(7.4%)	5(9.3%)	345	3	2	1035	690	12.4%	16.2%
	Gi	11(7.4%)	5(9.3%)	550	3	2	1650	1100	19.7%	25.8%
Medium	Os	2(1.4%)	2(3.7%)	70	1	1	70	70	0.8%	1.6%
	Wb	0(0%)	1(1.9%)	188	0	0	0	188	0.0%	4.4%
	Ha	13(8.8%)	6(11.1%)	95	3	2	285	190	3.4%	4.5%
	Wbz	13(8.8%)	3(5.6%)	135	3	1	405	135	4.8%	3.2%
	Ze	49(33.1%)	16(29.6%)	175	12	5	2100	875	25.1%	20.5%
Small	Im	8(5.4%)	3(5.6%)	30	2	1	60	30	0.7%	0.7%
	Gg	3(2%)	0(0%)	38	1	0	38	0	0.5%	0.0%
	Po	0(0%)	1(1.9%)	12	0	0	0	12	0.0%	0.3%
	Rb	2(1.4%)	0(0%)	16	1	0	16	0	0.2%	0.0%
	Tg	5(3.4%)	1(1.9%)	15	1	0	15	15	0.2%	0.4%
	Wa	6(4.1%)	5(9.3)	45	2	2	90	90	1.1%	2.1%
	Total	148	54	2146	38	18	8356	4259	100	100

Buffalo (Bu), Eland (El), Giraffe (Gi), Grants Gazelle (Gg), Hartebeest (Ha), Impala (Im), Ostrich (Os), Thompson's Gazelle (Tg), Warthog (Wa), Waterbuck (Wb), Wildebeest (Wbz), Zebra (Ze), and Porcupine (Po) and Bushbuck (Bb)

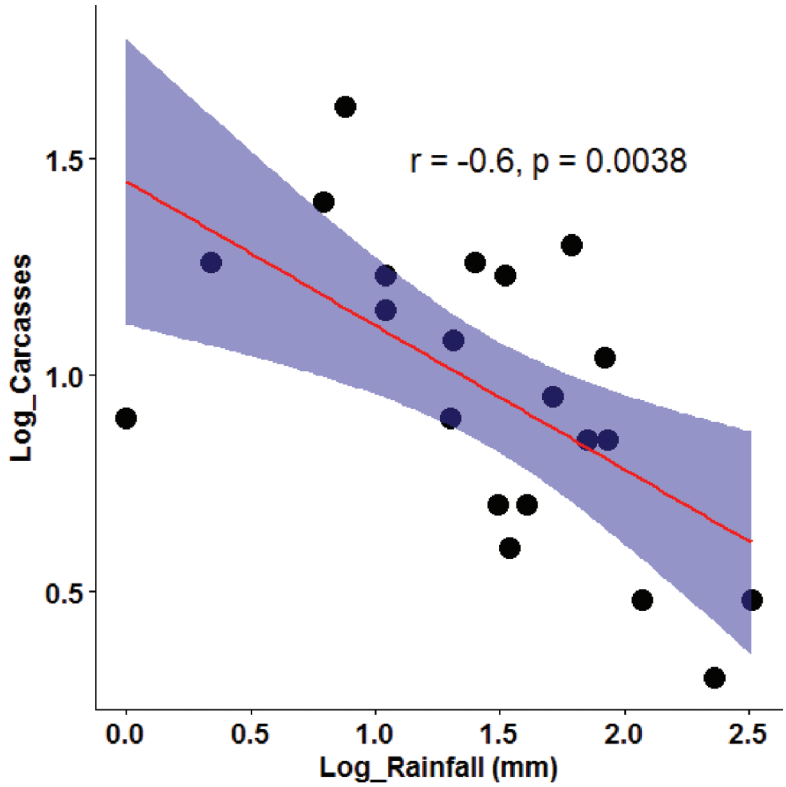


Figure 4.5
Correlation between the log-number of prey carcasses and log-maount of rainfall in NNP during 2012 and 2014-2017.

4.3.5 DNA-metabarcoding analysis versus scat and carcass sampling

A comparison between the three sampling techniques shows that African buffalo, eland, zebra and wildebeest were found in the analysis of the carcasses, prey hair items morphology and in the DNA analysis of the same (wet) season (Table S1). Suni and Rodents were only present in DNA analysis and not in carcasses and prey hair analysis of the same (wet) season. For all techniques combined and throughout the study period, few very small prey such as birds, hare, rodents and some scales most likely to originate from snakes or lizards were only found in the scats. We observed a lion killing and feeding on a marabou stork (*Leptoptilos crumeniferus)* (Figs. 4.2a and b, Table S1).

4.4 Discussion

4.4.1 Diet composition

NNP lions have a mixed diet, consisting of a wide range of prey size classes. With the exception of very large prey, such as rhinoceros and hippopotamus, lions in NNP feed on very small prey to large prey (Figs. 4.2, 4.4 and Table 4.2). The long stay of wild prey in the community land would result into one lion roaming longer in the community by following migrating pay and intensity of human-lion conflict. Thus lion would have developed preference to livestock. Secondly, lion would put more pressure on non-migrating wild prey and cause "predator dip". Predator dip is a situation why a population of certain declined due to over depredation. The dominant presence of large-medium prey, supplemented by small-medium prey and fewer very small prey, confirm the findings of other studies (Hayward & Kerley 2005; Bauer et al. 2010).

The increased presence of bird feathers in lion scat during the dry season could possibly be attributed to the increased number of herbivore carcasses in the park, and consequently the higher availability, and possibly catchability, of scavenging birds such as vultures at such carcass sites (Fig. 4.2; Table 4.1).

Although Hayward & Kerley's (2005) diet analysis shows zebra to be the predated species in the majority of African lions, our analysis confirms the findings of Davidson et al. (2013) that zebras are consumed regardless of season due to abundance (Ogutu et al. 2013) based on carcasses and prey hair items from NNP (Table S2). In the 1970s, Rudnai (1979) found that wildebeest was the most abundant prey in the park. The difference in these findings on few carcasses of wildebeest can probably be explained by a strong decline of the wildebeest population in NNP recent decades, as previously suggested by Owino et al. (2011) and Ogutu et al. (2013).

NNP lions also predate on giraffes as evidence in carcasses count and hair morphology (Table S2). Predation on giraffe in NNP, could be partly due to the grouping behaviour of juvenile giraffes. We observed that, during the dry season, baby and juvenile giraffes mostly remain in the NNP's forest ecotone, while the adults browse in the forest and valleys. This provides lions with an opportunity to predate on the giraffe juveniles. In Lake Nakuru National Park, Kenya, a skewed age structure of Rotchild giraffe has resulted due to juvenile removal by lions (Muller 2018).

Despite African buffalo being least predated by lions in the wet season, this study confirms findings by Rudnai (1974), who found that they are the most predated species in the dry season, based on the carcasses and prey

hair items from scats (Table S2). This contradicts the findings of Hayward & Kerley (2005) and Davidson (2013), which suggested that African buffalo was most predated species regardless of the season. Hayward & Kerley (2005) stated that buffalo are weaker in the dry season and more vulnerable to depredation during drought.

Spatial-temporal fluctuation of herbivores in the park has a significant impact on the lions' diet (Tumenta et al. 2013; Tuqa et al. 2014). In the dry season, wild prey biomass is considerably higher in NNP when wild prey concentrates around the available water sources and man-made dams in the park, compared to the wet season when they migrate out of the park into AKP (Gichohi 1996; Owino et al. 2011; Ogutu et al. 2013). During the dry season, the constraints of low forage quality, drinking requirements and presence of ambushing predators increases the vigilance of prey (Valeix et al. 2009).

Although we rarely observed some of the species, such as, bushbuck, porcupine, hare and bushpig carcasses, in the park, prey hair analysis revealed that they are available species in the park and form part of lion diet, based on hair morphology from the lion scat data during the wet season (Table S2). It is possible that the carcass count method is not suitable for these rare and cryptic species. With the seasonal decline of large and medium prey density in the park (Owino et al. 2011), small and very small prey become more common food for lions in NNP as evidence in prey hair item (Table S2).

4.4.2 Climate variability effects

We found a direct relationship between rainfall and lion diet in terms of prey size composition (Fig. 4.3). With increasing rainfall, the consumption of large and medium prey declined, while small and very small prey increased (Figs. 4.3 and 4.5). Decline in herbivore density during the wet season carcasses (Fig. 4.4c and d) allows for the growth of vegetation and it favors rodent density and other very small prey (Tian et al. 2015). We found a significant relationship between the amount of very small prey hair items and bones with a cumulative amount of rainfall in the three months prior to data collection (Fig. 4.3). The contribution of small prey (18%) and very small prey (<5 kg, 9%) in the lions' scats collected in NNP during 2015-2016 (Fig. 4.4b), confirms the diverse feeding ecology and opportunistic nature of lions (Table 4.1). Although the majority of prey hair items were found between cumulative rainfall of 400-500 mm, the data suggest the frequency of very small prey hair items in the scats is positively related to rainfall (Fig. 4.3).

A research project in China, conducted during 2005-2012 in Xi'an, found that a period covering three months' rainfall prior to sampling has an in-

fluence on rodent populations (Tian et al. 2015). Leirs et al. (1994) suggested that new vegetation growth stimulates rodent breeding. Rainfall and increased cloud cover enhance the activity of rodents and decreases the activity level and detectability of rodent predators which enhances their chances of survival (Lahaye et al. 2004; Wróbel & Bogdziewicz 2015). It is possible that the NNP lions hunt small and very small prey species when they encounter them by chance, as a possible 'snack', and they may also opportunistically take dead rodents, reptiles and birds killed, e.g. on the park roads as a result of dense traffic in the park. The main author observed a lion stalking, killing and consuming a marabou stork (*Leptoptilos crumeniferus)* in NNP on 21 January 2017 (Fig. 4.2a). We suggest that the high contribution of very small prey (< 5 kg) to the diet of NNP lions is partly due to the effects of extreme climate variability, which caused prolonged rainfall during 2015-2016.

Herbivores have a spatial-temporal impact on the ecosystem (Schippers et al. 2014) and modify vegetation composition and structure (DeWalt et al. 2003). The congregation of herbivores during the dry season in NNP (Gichohi 2003) changes the land cover and may affect the activity of rodents. As rodents move from cover to cover, they are exposed to risks of being killed by e.g. snakes, birds or traffic in the park. This may explain why there is an increase in hair, bones and feathers in NNP lion scats in the dry season (Fig. 4.3).

4.4.3 DNA-metabarcoding

We also found a broad spectrum of prey species with DNA-metabarcoding (Fig. 4.2c and Table 4.4). The fact that DNA-metabarcoding only identified mammals (Table 4.2) may be the result of a bias of the primers and sample size (ten samples from 2015), which are known to perform poorly for reptiles and potentially also for birds. Even when lowering the threshold and including even those clusters with very low numbers of reads, we encounter bird species in the DNA. However, we have chosen not to include these results as they may potentially represent false positives.

In the second analysis of the same set of samples, including a blocking primer to reduce the representation of lion DNA, four more species were identified after processing the samples: black-backed jackal (*Canis mesomelas*) (this may not be part of the lion's diet and can possibly be attributed to marking over the lion sample or scavenging of the lion kill, although this cannot be excluded), African pygmy mouse (*Mus minutoides*), chicken (*Gallus gallus*) and pig (*Sus scrofa*). Presence of leopard and serval cat in the DNA may be the result of territorial marking of a previously deposited lion sample.

Despite three cases of lions attacking humans in NNP reported to KWS during 2012-2017 (Ombati 2017), there was no human hair in any of the lion scats collected from the park. Human DNA found by DNA-metabarcoding is likely a result of sample processing in the lab. We assumed that the absence of human hair in the lion scats is due to the relatively low number of human attack cases in the park and few scat samples for DNA analysis. Therefore, our study cannot confirm that humans are part of the lions' diet or the existence of a man-eating lion in NNP.

4.4.4 DNA-metabarcoding versus prey hair analysis and carcass counts

Our results show that DNA-metabarcoding is a complementary method for the analysis of lion diets, when compared with prey hair analysis from scats and carcass counts, despite overestimating the larger prey size during carcass counts (Fig. 4.4), and underestimating smaller species in lion scats because of the small body mass and low amounts (or absence, in case of reptiles) of hairs from small species present.

A major advantage of microscopic analysis of prey hair and DNA-metabarcoding is therefore that it also allows for the identification of smaller prey species, which are not detected through carcass counts or microscopic analysis of hair morphology in lion scats (Biswas & Sankar 2002; Bagchi et al. 2003; Ogara et al. 2010).

Ackerman et al. (1984) stated that large prey has more flesh with fat and thus, lions feeding on more meat alone, rather than skin, bone and hooves, produce more liquid scats which dry quickly, and these would probably not be collected during field studies or may have few hairs. Our analysis of scats from the same season shows more very small prey in the DNA analysis (9%) compared to the diets based on prey hair items (2%). We recommend the application of DNA to assess the role of very small prey in lions' diet.

Despite well-known limitations, such as DNA-amplification bias, this technique shows great promise for obtaining additional insights into dietary composition of species (Yoccoz 2012; Pompanon et al. 2012; Bohmann et al. 2014; Mumma et al. 2015).

Application of DNA technique on lion scats has added value of detecting more species in the lion diet compared to carcass count and microscopic hair morphology analysis. We recommend the application of DNA to assess the role of very small prey in lions' diet.

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Supporting Information

Table S1

Proportion of prey hair items found in lion scats, carcasses and DNA-metabarcoding based on results of ten scat samples collected in NNP in July – September 2015. The shaded boxes with grey colour represents the species with highest proportion in scats, carcasses and DNA.

Size	Species	Hair	Proportion	Carcasses	Proportion	DNA	Proportion DNA
Large	Buffalo	21	0.17	11	0.16	1	0.09
	Giraffe	0	0.00	5	0.07	0	0.00
	Eland	4	0.03	3	0.04	1	0.09
Medium	Cow	1	0.01	1	0.01	0	0.00
	Hartebeest	17	0.14	4	0.06	0	0.00
	Ostrich	5	0.04	0	0.00	0	0.00
	Waterbuck	5	0.04	0	0.00	0	0.00
	Wildebeest	11	0.09	6	0.09	4	0.36
	Zebra	24	0.20	25	0.37	2	0.18
Small	Impala	4	0.03	1	0.01	0	0.00
	Pig	1	0.01	0	0.00	0	0.00
	Shoats	12	0.10	3	0.04	0	0.00
	Thompson's gazelle	3	0.02	3	0.04	0	0.00
	Warthog	6	0.05	2	0.03	0	0.00
	Bushbuck	1	0.01	0	0.00	0	0.00
	Reedbuck	0	0.00	2	0.03	0	0.00
	Grant's gazelle	6	0.05	2	0.03	0	0.00
	Suni	0	0.00	0	0.00	2	0.18
Very Small	Bird	1	0.01	0	0.00	0	0.00
	Rodent	0	0.00	0	0.00	1	0.09
	Snakelike	1	0.01	0	0.00	0	0.00

Table S2

Comparison on seasonal prey carcasses, prey hair items and their proportion based on the data collected during 2012 and 2014-2017 at NNP. The shaded boxes with grey represent, the species with the highest representation per seasons.

Category	Species	Total number prey carcasses for the study period, per season and their proportion						Total number of prey hair items for the study period, per season and their proportion					
		Carcasses	Proportion of whole period	Dry	Proportion of prey carcasses in dry season	Wet	Proportion of prey carcasses in wet season	No. of prey hair	Proportion of whole period	No. dry season scats	Proportion of prey hair in dry season	No. of prey hair wet	Proportion of prey hair in wet season
Large	Bu	31	0.15	25	0.17	6	0.11	48	0.13	36	0.14	12	0.11
	El	16	0.08	11	0.07	5	0.09	13	0.03	10	0.04	3	0.03
	Gi	16	0.08	11	0.07	5	0.09	9	0.02	5	0.02	4	0.04
Medium	Wb	1	0.00	0	0.00	1	0.02	10	0.03	5	0.02	5	0.05
	Wbz	16	0.08	13	0.09	3	0.06	23	0.06	18	0.07	5	0.05
	Ze	65	0.32	49	0.33	16	0.30	91	0.24	61	0.23	30	0.27
	Ha	19	0.09	13	0.09	6	0.11	37	0.10	27	0.10	10	0.09
	Os	4	0.02	2	0.01	2	0.04	12	0.03	7	0.03	5	0.05
Small	Gg	3	0.01	3	0.02		0.00	21	0.06	16	0.06	5	0.05
	Im	11	0.05	8	0.05	3	0.06	28	0.07	19	0.07	9	0.08
	Bb	0	0.00	0	0.00	0	0.00	4	0.01	2	0.01	2	0.02
	Bp	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	1	0.01
	Po	1	0.00	0	0.00	1	0.02	0	0.00	0	0.00		0.00
	Rb	2	0.01	2	0.01	0	0.00	1	0.00	0	0.00	1	0.01
	Tg	6	0.03	5	0.03	1	0.02	15	0.04	12	0.05	3	0.03
	Wa	11	0.05	6	0.04	5	0.09	25	0.07	15	0.06	10	0.09
Very Small	Ro	0	0.00	0	0.00	0	0.00	28	0.07	25	0.09	3	0.03
	Sn	0	0.00	0	0.00	0	0.00	1	0.00	1	0.00		0.00
	Hr	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	1	0.01
	Li	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	1	0.01
	Bi	0	0.00	0	0.00	0	0.00	7	0.02	6	0.02	1	0.01
		202	1.00	148	1.00	54	1.00	376	1.00	265	1.00	111	1.00

Buffalo (Bu), Eland (El), Giraffe (Gi), Waterbuck (Wb), Wildebeest (Wbz), Zebra (Ze), Hartebeest (Ha), Impala (Imp), Ostrich (Os), Grant gazelle (Gg) Bushbuck (Bb), Bushpig (Bp), Porcupine (Po), Thomsons gazelle (Tg), Warthog (Wa), Snake (Sn), Hare (Hr), Lizard (Li), Bird (Bi), Rodents (Ro) and Reedbuck (Rb)