KOEDOE - African Protected Area Conservation and Science
ISSN: (Online) 2071-0771, (Print) 0075-6458

Longitudinal dietary resilience of lion (*Panthera leo*) in a semi-arid fenced reserve of South Africa

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Dates:
Received: 22 Jan. 2025
Accepted: 25 Sept. 2025
Published: 15 Dec. 2025

How to cite this article:
Le Brun, R., Naude, V.N., Tambling, C.J., Ferreira, S.M., Lottring, C., & Radloff, F.G.T., 2025, 'Longitudinal dietary resilience of lion (*Panthera leo*) in a semi-arid fenced reserve of South Africa', Koedoe 67(1), a1850. https://doi.org/10.4102/koedoe.v67i1.1850

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Understanding the dietary composition of large carnivores and how these relate to the availability of suitable habitat and prey is crucial to population management, especially in fenced reserves. This study aimed to determine the current diet of the lion (*Panthera leo*) in the Karoo National Park and to establish whether prey preference has changed over the 12 years post-introduction. Global positioning system-collar-based kill-site cluster investigations and scat analyses were used to determine contemporary lion diet, while multinomial logistic regressions were used to investigate longitudinal changes in prey preference by comparing a decade of historical kill and aerial census records. Lion (n = 8) collar fixes identified 358 (12%) 'potential' kill-site clusters across 2945 discernible clusters over 15 months (i.e. 2021/2022). The subsequent in-field investigation of 227 (63%) 'potential' kill sites yielded 144 (63%) and 103 (45%) independent lion kill and scat samples, respectively. While these two methods offered different sampling advantages, both provided sufficient data to show lion preference for greater kudu (*Tragelaphus strepsiceros*), common eland (*Tragelaphus oryx*) and red hartebeest (*Alcelaphus buselaphus caama*). Other prey species included gemsbok (*Oryx gazella*), springbuck (*Antidorcas marsupialis*), common duiker (*Sylvicapra grimmia*) and mountain zebra (*Equus zebra*). Historical carcass records (n = 1035, $\bar{x}$ = 89.6 ± 13.8 Standard Error [SE] per annum), since the reintroduction of lions in 2010, indicate no significant change in dietary composition over time (X^2 = 1.98, df = 5, p = 0.85), when controlling for lion population size, despite post-introduction acclimation with substantial inter-annual variability in rainfall and prey availability.

Conservation implications: Understanding dietary changes in response to systemic disturbances is crucial to ensuring that lions are ethically and sustainably managed for their ecological efficacy in fenced metapopulations. With no significant change in hunting behaviour, management concerns are unlikely to be driven by reduced prey suitability or availability.

Keywords: aerial census; cluster analysis; carcass records; GPS telemetry; Karoo National Park; kill records; predator -prey dynamics; scat analysis.

Introduction

African lions (*Panthera leo*) function as sentinel species for terrestrial biodiversity conservation (Loveridge et al. 2009) and, as apex predators, play a critical role in ecosystemic functionality (Sargent et al. 2022). However, African lions are considered 'vulnerable' under the International Union for the Conservation of Nature (IUCN Red List; Nicholson et al. 2024), inhabiting an estimated 6% of their historical range (Sargent et al. 2022), where only the southernmost states (i.e. Botswana, Namibia, South Africa and Zimbabwe) are not experiencing population declines (Bauer et al. 2015). Approximately 500 lions were subsequently reintroduced to at least 45 different reserves throughout South Africa since 1958 (Miller et al. 2013), which grew to a population of > 750 lions across 59 reserves by 2018 (Kettles & Slotow 2009; Selier et al. 2024). While some have argued that these small and isolated populations are of minimal conservation value because of the potential reduction of genetic diversity (Slotow & Hunter 2009), more recent assessments have illustrated the species-level value of effectively conserving these otherwise fragmented populations (Selier et al. 2024). Continued growth in South Africa and regional lion population stability is thus largely because of coordinated reintroductions and metapopulation management across relatively small (i.e. < 1000 km^2), fenced and well-funded reserves (Bauer et al. 2015; Selier et al. 2024). This approach accepts that the population exists in discontinuous units that have variable demographics with limited dispersal (Olivier, Van Aarde & Ferreira 2009). By employing best practices to artificially induce demographic variability and mimic dispersal-driven connectivity through translocations (Miller et al. 2013), as guided by the social dynamics of lions (Miller et al. 2013), this managed metapopulation has become one of the largest lion conservation units in Africa (Selier et al. 2024).

As part of the growing metapopulation framework, lions were reintroduced into the Karoo National Park (KrNP) near Beaufort West in the Western Cape province of South Africa in 2010 (Spies 2017). Concern has, however, been expressed that the predatory role of these lions has not been adequately restored, and that consequent social constraints and pressures have been observed (Bissett et al. 2021). Managing lions in small reserves is operationally complex, requiring responsive monitoring and recovery protocols (Miller et al. 2013) as these populations are highly vulnerable to environmental fluctuations and anthropogenic pressures (Becker et al. 2022). This is typically because of the reduced buffering effect of relatively small population sizes and the isolation of reserves (Miller et al. 2013). In some cases, such as that of KrNP, these effects are further exacerbated by the arid and resource-poor environment in which the reintroductions occur (Castley et al. 2002). Another major challenge in managing lions in small areas is the lack of natural regulation of population sizes (Miller et al. 2013), which may carry consequences for predator–prey dynamics (Owen-Smith & Mills 2008; Slotow & Hunter 2009; Tambling & Du Toit 2005). There is also a comparative lack of established knowledge regarding lions in semi-arid regions such as KrNP (Beukes et al. 2017; Davidson et al. 2013; Stander 1992).

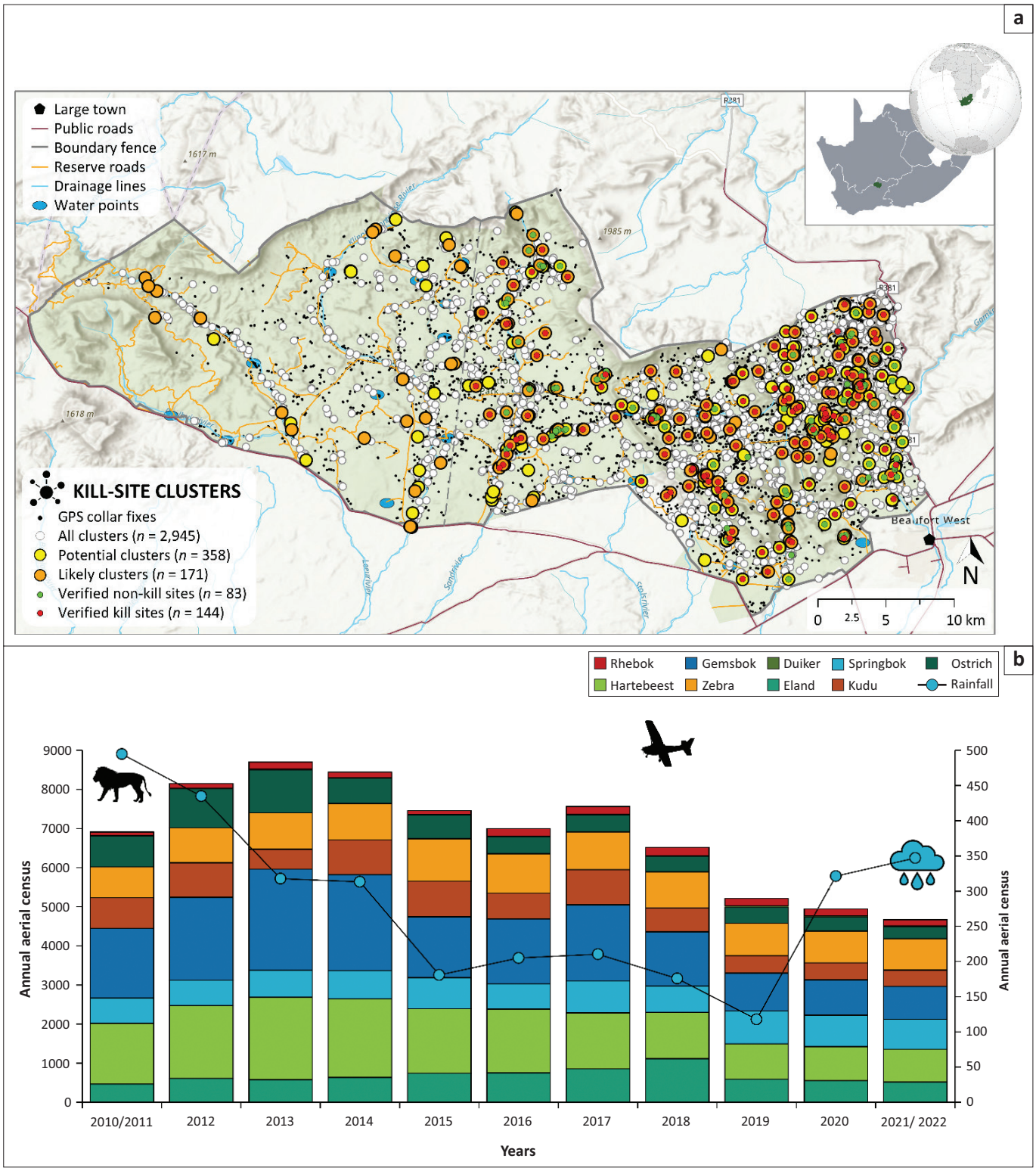
In larger reserves, less impacted by disturbance, lion populations are generally self-regulated through social dynamics (Miller et al. 2013), though ~63% of the variability in lion density across Africa is explained by bottom-up factors (e.g. density of preferred prey species; Hayward et al. 2007). In contrast, smaller and isolated reserves host relatively small prides with fewer rivals, where reduced competition among dominant males can inflate their tenure from 2 to 10 years (Miller et al. 2013). Subsequent reductions in male conflict-related mortalities and infanticide may lead to rapid overpopulation, requiring more regular interventions (Lehmann et al. 2008; McEvoy, Ferreira & Parker 2021; Miller et al. 2013). In contrast to the 40% – 59% cub survival in larger reserves (Funston 2011; Lehmann et al. 2008), lion cub survival in these small reserves is ~87%, with limited dispersal opportunities for subadults (Miller et al. 2013). As a result, fenced reserve lion population sizes often approach or exceed their estimated carrying capacities (Power 2002), where unfenced populations or those occurring in larger fenced reserves require less management intervention (Packer et al. 2013). An unsustainable increase in lion numbers may, in turn, also constrain prey populations (Tambling & Du Toit 2005). Disrupted prey dynamics (McEvoy et al. 2021; Miller et al. 2013), leading to low prey suitability and availability (Lehmann et al. 2008; Power 2002) within reserves, could result in lions seeking prey outside the fenced boundaries (Oriol-Cotterill et al. 2015; Slotow & Hunter 2009; Tambling & Du Toit 2005). Further social pressures may force young dispersing male lions, or less dominant prides, into less suitable or peripheral habitats within the landscape (Lehmann et al. 2008; Miller et al. 2013) or even outside protected area boundaries in search of prey (Loveridge et al. 2009). Understanding how changes in dietary profiles in response to predator–prey demographics impact lion population dynamics (Owen-Smith & Mills 2008) can directly inform management decisions (Becker et al. 2013). Although lion dietary composition and preferences have been comprehensively reviewed (Hayward & Kerley 2005; Miller et al. 2013; Power 2002), there has been limited representation from semi-arid environments (Beukes et al. 2017; Davidson et al. 2013; Stander 1992). Within the KrNP, it is unclear what the dietary profile of lions is, if preferences may have changed over time, and whether present dietary constraints provide motivation for lions to search for prey beyond the boundaries of the park.

Understanding dietary changes in response to systemic change (e.g. rainfall, as well as prey abundance and guild composition) is crucial to ensuring that lions are effectively managed in fenced metapopulation reserves. This study aims to determine the current diet of lions in the KrNP and to establish whether prey preference has changed post-introduction. Global positioning system-collar-based kill-site cluster investigations and scat analyses were used to determine contemporary lion diet over 15 months (i.e. 2021/2022). Multinomial logistic regressions were then used to investigate longitudinal changes in prey preference by comparing a decade of historical kill and aerial census records (i.e. 2010–2022). We discuss our findings in the context of prey availability within KrNP, among broader ongoing management challenges faced by these relatively small, fenced metapopulation reserves.

Research methods and design

Study system

Karoo National Park borders the town of Beaufort West in the Western Cape province of South Africa (32°10′S–32°23′S, 22°15′E – 22°35′E; Figure 1a) and covers 883 km2 (Spies 2017). This study focused on the eastern portion (i.e. approximately half) of the park because of accessibility and logistical constraints but provided a representative sample of the reserve's four broad landscape types, and this was also the area that the majority of lions utilised during the time of the study. The KrNP is situated in the semi-arid Nama-Karoo and along the Nuweveld Mountain range (Kraaij & Milton 2006). Characteristic mountains within the park form part of the Great Escarpment, where a substantial contrast in elevation (820 masl – 1620 masl; Spies 2017) drives a warm steppe climate in the southern lowland sections of the park along a relief rainfall gradient to a cool steppe along the northern escarpment (Spies 2017). The KrNP receives predominantly (60% – 75%) summer rainfall (i.e. 175 mm – 406 mm per annum along a west-east gradient), with a mean maximum summer temperature exceeding 32°C and cold-dry mean minimum winter temperature below 3.5°C (Rubin, Palmer & Tyson 2001). Over the 12-year study period, the rainfall averaged 289 [118–495] mm per annum (Figure 1b), where the period between 2015 and 2019 was particularly dry, resulting in a drought with an average of only 178 [118–210] mm of rain per annum over 5 years (Moeletsi et al. 2022).



Note: Indicated are national public roads (dark red lines) surrounding the fenced reserve boundary (grey lines), as well as roads (orange lines), drainage channels (blue lines) and water points (blue ovals) within the reserve. Lion GPS collar fixes (black dots) were clustered (white circles, n = 2,945), from which characteristic potential (yellow circles, n = 358) and likely (orange circles, n = 171) clusters were verified in-field as non-kill (green circles, n = 80) and confirmed kill (red circles, n = 145) sites. Annual aerial census counts of prey are indicated (by stacked bar colours), alongside mean annual rainfall (connected black lines and blue circles). Annual lion population sizes are indicated numerically above the stacked plots.

GPS, global positioning system.

FIGURE 1: Study area: (a) map indicating global positioning system-collar-based lion kill site cluster verification between March 2021 and May 2022 and (b) annual aerial census of prey species, rainfall and lion population size between 2010 and 2022 for the Karoo National Park of South Africa.

Nama-Karoo covers the majority of the park, but a relatively small portion of the Grassland Biome persists on top of the Nuweveld Mountain plateau (Kraaij & Milton 2006; Spies 2017). Structurally, the vegetation is characterised by low-lying shrubs, sparse trees and grass cover on the slopes and open plains, with thicker riparian vegetation and trees along drainage lines and riverbed valleys (Bezuidenhout et al. 2024). The park hosts 58 mammal species (Spies 2017),

with plains game typical of the Karoo (Figure 1b), including gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus caama*), springbok (*Antidorcas marsupialis*), cape mountain zebra (*Equus zebra zebra*), greater kudu (*Tragelaphus strepsiceros*), common eland (*Tragelaphus oryx*), ostrich (*Struthio camelus*), grey rhebok (*Pelea capreolus*) and plains zebra (*Equus quagga*). Less common, but present are Chacma baboon (*Papio ursinus*), Cape porcupine (*Hystrix africaeaustralis*), klipspringer (*Oreotragus oreotragus*), mountain reedbuck (*Redunca fulvorufula*) and warthog (*Phacochoerus africanus*). To avoid ambiguity across the study period, we note that KrNP currently supports only Cape mountain zebra (Equus zebra zebra); plains and/or Burchell's zebra (E. quagga burchellii) linked to the former Quagga Project were removed in 2015, and historical carcass entries recorded as 'zebra sp.' reflect undifferentiated records.

Data collection

Prey aerial census

Prey species composition and relative abundance (i.e. as derived from total counts) were derived from a mandated annual aerial census record between 2010 and 2022 (Table 1-A1) provided by SANParks (Bissett et al. 2021). Aerial transects of 400 m (i.e. 200 m strips on either side of the helicopter) are flown east-west across the entire park over 5 days, with contours flown along the higher mountain ranges with steeper terrain. Total prey counts were consistently conducted by a regional ecologist and several rangers from ~200 ft at ~80 km/hr along the predefined transects. All animals seen were identified and counted, where herds were flushed and/or circled if required to ensure a robust count. All counts and associated global positioning system (GPS) records were digitised in-flight (Colibri Software, Wolfville, Canada). No corrections were made to the data; however, the 2011 count, considered erroneous by park authorities, was replaced with the average between the 2010 and 2012 counts. In the coronavirus disease 2019 (COVID-19) pandemic year of 2020, no prey census was conducted, and values used in the analyses for that year are similarly the average between the 2019 and 2021 count values for each species (Figure 1b).

Historic carcass records

Since the reintroduction of lions to KrNP in November 2010, park management has ensured that at least one member of each lion pride is fitted with a Very High Frequency (VHF) and Satellite Transceiver (ST)-enabled collar (African Wildlife Tracking, Pretoria, South Africa). This approach is used to provide multiple daily location points (i.e. 4-h fix-rate), allowing for known individuals and their associated prides to be observed on a regular basis (i.e. weekly) and facilitating rapid localisation and routine monitoring of individuals. KrNP rangers have since maintained an opportunistic record of lion prey using GPS fix 'clusters' to manually identify potential kill sites (Tambling et al. 2012). Clusters were manually identified by rangers in a subjective manner by considering plotted location points that were close to each other (i.e. ≤ 2 km between three sequential fixes). These clusters were followed up on by routine field ranger patrols if accessible and logistically feasible, where the prey species was identified and recorded if the carcass was located (Tambling et al. 2012). A concentration of two or more consecutive GPS fixes within a 100-m radius was considered a cluster point (Tambling et al. 2012). The clusters were identified by rangers manually in a subjective manner by visual observation of plotted location points, which were then visited, especially when easily accessible from roads, and prey remains were identified when found. It was conducted as part of routine operations, and there was variation in effort and success between years. The identified kills from clusters were augmented with opportunistic observations of lion kills and were recorded in a 'carcass register'. The carcass register was summarised in the monthly ranger reports, which were further scrutinised, and the necessary data extracted. For the purposes of this study, the kill records of November and December 2010 were pooled with those of 2011, as lions were only present in the last 2 months of 2010.

Contemporary kill-site global positioning system clusters

The contemporary diet (March 2021–May 2022) of lions was also studied using the GPS cluster analyses approach, but in a much more intensive and rigorous way than in the preceding decade. All the clusters obtained from the location data of eight collared lions between March 2021 and May 2022 were considered in a systematic way, and clusters were prioritised for investigation based on the following criteria. Global positioning system location clusters were identified as ≥ 2 consecutive fixes with each pair < 100 m apart, collected on collars scheduled hourly at night (and hourly or thrice daily by day); the 100 m cut-off exceeds the trialled GPS error (≤ 82 m) to ensure proximity reflects true stationing rather than error (Author). Firstly, we investigated the ratio of distance moved in the 24 h before the cluster formation against the distance moved in the 24 h after moving away from the cluster (i.e. R24), with a higher ratio depicting movement (e.g. searching for food) prior to a cluster and resting (e.g. sleeping after feeding) following a cluster (Tambling et al. 2012). Secondly, we prioritised clusters where lions had remained at the location for a longer period, increasing the likelihood of there being a feeding event (Tambling et al. 2012). Thirdly, we prioritised clusters that start during the night compared to those that start during the day because of lions hunting more at night (Tambling et al. 2012).

Using these criteria, we separated the clusters that were likely to be a kill into those where we were more confident (i.e. 'likely clusters') and those that we were less confident ('potential clusters'). A 'potential cluster' was defined as a cluster that had an R24 ratio of ≥ 3 and a duration time of ≥ 8 h and was formed during the night. A 'likely' cluster was considered as a cluster that had an R24 ≥ 10 and a duration time ≥ 12 h and was formed during the night. All likely clusters were visited, and some additional potential clusters if either the R24 or duration was high (i.e. either the R24 ratio was ≥ 10 or the duration time was ≥ 12 h or if the cluster was relatively

easy to access (i.e. en route to another kill site and/or close to road access). Clusters occurring outside of these parameters were largely excluded from investigations (Figure 1a).

The first GPS location point of an identified cluster was used as the start of the search pattern for searching for prey remains. The respective GPS points that made up the cluster were loaded onto a handheld GPS unit (Garmin E-Trex, Garmin International, Olathe, KS, US), with their corresponding point name, to facilitate locating the identified clusters in the field. The clusters were visited on an average of 33.5 [1–126] days after the cluster formation, with 56% visited within 30 days of formation. The GPS points were deemed relevant and worth visiting if they were more recent than 60 days, or if they were a highly likely cluster that was older than 60 days (i.e. this was during the initial period of the study when some of the cluster sites were older and had not been visited before the study). Cluster locations were tracked by road, as far as possible, and then on foot. The area around the identified location point of a cluster was exhaustively searched in a spiralling pattern, irrespective of time taken, within a 100 m radius, for evidence of prey remains (Tambling et al. 2012).

A feeding event site was confirmed if either a carcass or parts thereof (e.g. rumen content, hair, bone, jaw, horn or blood) were found, or evidence of lion activity, such as irregular soil disturbance and trampled vegetation as a result of a struggle or feeding frenzy, was evident (Davidson et al. 2013). Available evidence was used to classify prey, where possible, to species, age and sex (Tambling et al. 2012).

Scat sampling

Lion scat was identified (Beukes et al. 2017) and collected opportunistically during the kill site visitation process. Species identified from scat may therefore have been killed at the collection site or originate from a previous feeding event. Scat analysis focuses on the undigested remains of prey items, allowing for the identification of prey species consumed (Tambling et al. 2012). Samples underwent overnight hot water immersion to soften and isolate the undigested hair, bone, teeth or hoof material (Rühe, Ksinsik & Kiffner 2008), before being washed of soluble material using a 2-mm sieve and dried for laboratory analyses. A random subsample of ≥ 10 hairs was taken from the remaining undigested parts of each scat sample before being cleaned with 90% ethanol, air dried and set in paraffin wax. Medullary cross-sections of each hair sample were then mounted for conventional light microscopy, and cuticle patterns examined by creating hair scale imprints in nail varnish (Beukes et al. 2017). Prepared slides were then compared to a reference library of hair cross sections and scale imprints developed for the available prey species within KrNP. Scats collected within close proximity (i.e. < 200 m) to the remains of large prey species potentially contained hair from the consumed carcass. To reduce the probability of such bias, scats that contained remains of species similar to the prey item fed on at the collection site were removed from further analyses.

Statistical analyses

Sampling adequacy

The Brillouin Index (*Hb*) is recommended to measure the adequacy of a collection (Pielou 1975). We applied this index across data types (i.e. kill-site clusters and scat sampling) to assess whether the number of samples and records collected were adequate to confidently interpret lion diet (i.e. within the 15-month sampling window [2021/2022] for contemporary diet determined by kill-site clusters and scat sampling or per year between 2010 and 2020 for longitudinal trends in diet as determined by aerial census and carcass records) as Equation 1:

$$Hb = \frac{\ln N! \sum \ln n_i!}{N} \quad \text{[Eqn 1]}$$

where *Hb* represents the cumulative diversity of prey in the collection, N is the total number of individuals in the specific sample and n_i is the number of individuals belonging specifically to the ith species (Brillouin 1956). Cumulative diversity was calculated by bootstrapping 10 000 random samples in increments of three and plotted against the total number of samples collected. Sampling effort was deemed adequate if the cumulative diversity curve reached an asymptote and the incremental change declined to <1% (Briers-Louw & Leslie 2020).

Contemporary lion diet

Kill-site clusters and scat sampling were used as complementary approaches to determining contemporary lion diet relative to aerial census-derived prey abundance within the 15-month sampling window between March 2021 and May 2022. The frequency with which identified prey species occurred within each sampling type (i.e. kill-clusters and scat samples) provided independent assessments. The lion scat analysis provides an approximation of the overall diet, including smaller prey, while the cluster analyses allow for a robust appraisal of large prey use, which is comparable to the historic kill database recorded for lions. These proportions were then considered together to generate a robust contemporary diet profile for lions in the KrNP.

Proportional representation of each prey species could then be compared to the relative proportional availability of each species from the aerial census to determine contemporary prey preferences (Hayward & Kerley 2005), using the Jacobs' Index (*D*) (Equation 2):

$$D = \frac{r - p}{r + p - 2rp} \quad \text{[Eqn 2]}$$

where r is the proportional contribution of a species in the total lion sample and p is the proportional availability of that specific species. The lion kill-cluster and scat sampling data provided r, while p was derived from the aerial game census. The Jacobs' Index quantifies prey preference when different relative abundances of prey are compared, where resulting scores range between +1 and –1, with zero indicating no selection, +1 indicating maximum preference, and –1

indicating maximum avoidance (Jacobs 1974). Values between –0.2 and 0.2 indicate that the species was consumed as would be expected and in proportion to relative availability (Hayward et al. 2011).

The combined (i.e. kill-clusters and scat samples) frequencies of prey occurrence in lion diet were then converted into relative biomass indices (RBIs) to determine the estimated total biomass contribution of each identified prey species to lion diet in the KrNP (Radloff & Du Toit 2004; Tambling et al. 2012). Relative biomass indices were calculated using the average adult female body weight for each prey species obtained from Skinner and Chimimba (2005), multiplied by the proportional contribution of each prey species identified to the overall lion diet.

Longitudinal trends in lion diet

We quantified three annual diet metrics from carcass records and aerial census data: (1) the dietary profile, defined as the composition of kills by prey species (i.e. each carcass assigned to one species); (2) prey preference, calculated per species and year using Jacobs' index D (i.e. use vs. availability; –1 to +1) from carcass use and aerial-census availability, then classified for analysis as avoided (≤ –0.2), neutral (–0.2 to 0.2) or preferred (≥ 0.2) and (3) the relative biomass contribution (RBC; i.e. the proportion of edible biomass attributable to each species per year). To test for temporal differences, we fitted multinomial logistic regressions (*nnet*::multinom; Venables & Ripley 2002) separately for each metric, with 'year' as a factor (2010–2022); annual lion population size was included as a covariate to control for changing population context. We evaluated overall effects using Type III likelihood-ratio tests (*car*: Anova; Fox & Weisberg 2011), obtained estimated marginal species probabilities (or preference-class probabilities) by year and conducted Tukey-adjusted pairwise contrasts among years using least-squares means/estimated marginal means (*lsmeans*/*emmeans*) (Lenth 2016). We visualised marginal effects by year using the *effects* package (Fox & Hong 2010). For context, we note that multinomial models are a standard approach for multi-category diet outcomes in carnivores, with Jacobs' index thresholds (±0.2) widely used to interpret prey preference, and that alternative compositional models (e.g. Dirichlet-multinomial) yield similar inferences. All analyses were conducted in R v4.2.1. (R Core Team 2022).

Ethical considerations

The collaring of lion forms part of the carnivore lion management programme of SANParks (Spies 2017). Permission was granted by SANParks (Permit Number: RADL-F/2021-04) to access the GPS information collected from fitted collars. Additional data were collected following all ethical standards for research without direct contact with human or animal subjects.

Results

Sampling adequacy

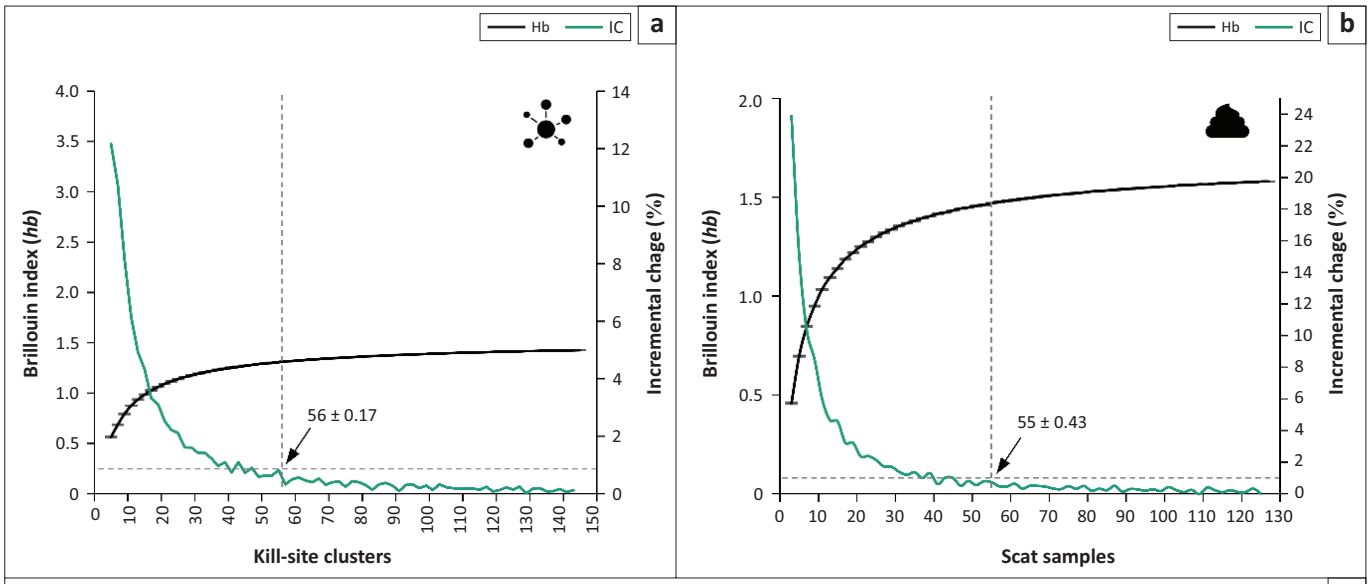
Sampling effort was deemed more than sufficient for both verified kill-sites (n = 144; Figure 2a) and the scat collection (n = 103; Figure 2b), with 56 ± 0.17 clusters and 55 ± 0.43 scat samples calculated as being the minimum sampling threshold required for the robust determination of contemporary lion diet. While most carcass record years were deemed adequate for longitudinal dietary trend analyses (Figure 2c), the 2010/2011 (i.e. 59 of 59 ± 0.15 required) and 2018 (i.e. 58 of 61 ± 0.20 required) were only just adequate; carcass records from 2012 (i.e. 37 of 67 ± 0.06 required) to 2020 (i.e. 43 of 64 ± 0.14 required) had to be removed from further analyses.

Contemporary lion diet

At the time of the study, the lion population in KrNP was estimated at ~11 individuals, comprising two males and nine females, of which eight were collared (i.e. both males and six females), with equal and unrestricted access to the entire reserve. During the 15-month study period (i.e. March 2021–May 2022), lion collar fixes presented 358 (12%) 'potential' kill-site clusters across 2945 discernible clusters, of which 171 were considered 'highly likely' kill sites. Subsequent in-field investigation of these 'highly likely' and some 'potential' kill sites clusters (n = 227, 63%) yielded 144 and 103 independent lion kill and scat samples, respectively.

At the 144 locations where lion prey remains were found (Figure 1a), the three most commonly identified prey species were greater kudu (n = 32, 22%), common eland (n = 31, 21%) and red hartebeest (n = 31, 21%), accounting for 64% of the carcasses found during the study period (Figure 3a). These were followed by gemsbok (n = 17, 12%), zebra (pooled species, n = 10%) and ostrich (n = 4, 3%). The less frequent and largely individual cases of chacma baboon, cape porcupine and warthog comprised ~4% of the diet profile. The prey species of 19 kill sites visited could not be identified to species level and were removed from further analysis. Eland were the greatest biomass contributors to lion diet at 25%, followed by hartebeest and kudu at 23% and 24% each, then gemsbok (16%), Cape mountain zebra (8%) and ostrich (1%).

Ten of the 103 lion scats collected were omitted from these analyses as the prey identified in these scat samples matched that of the corresponding kill site to preserve the independence of the scat dataset and to avoid event-level pseudoreplication and ascertainment. An additional two samples were omitted as the samples were unidentifiable, thus reducing the sample size to 91, from which 100 prey items were identified. Scat analyses of contemporary lion diet in KrNP identified 13 prey species, comprising 12 ungulates and a rodent (Figure 3b). Large prey species (> 50 kg) were consumed most often, making up 64% of the identified prey items. The six most frequently consumed large prey species were eland (17%), red hartebeest (15%), gemsbok (13%) and kudu (12%), with Cape mountain zebra (6%) and warthog (1%) being recorded less frequently. Small mammals (< 50 kg) with the highest dietary frequency were springbok (16%) and common duiker (10%), followed by porcupine (4%) and grey rhebok (3%), while klipspringer, mountain reedbuck and hare (Lepus spp.) were only identified once. Scat analyses indicated that large prey collectively accounted for 94% of the lion biomass



c

	2010/2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021/2022
Carcass records	59	37	147	116	77	168	99	58	89	43	91
Minimum threshold	59 ± 0.15	67 ± 0.06	44 ± 0.56	46 ± 0.29	54 ± 0.18	37 ± 0.45	52 ± 0.26	61+ 0.20	53+ 0.29	64± 0.14	48± 0.27

Note: Prey species rarefaction curve (Hb; mean and 95% confidence intervals; black) based on the Brillouin Index and sequential proportion of incremental change (IC; %; green) in lion kill-site cluster and scat samples. The dashed lines (grey) indicate the adequate sampling threshold, as the randomised sequential proportion of incremental change in prey species composition declines to < 1%. The table shows the number of carcass records and associated minimal sampling thresholds (red = insufficient; yellow; marginal but acceptable) per year.

FIGURE 2: Sampling adequacy tests indicated for (a) kill sites clusters and (b) scat samples between March 2021 and May 2022, as well as (c) annual carcass records between 2010 and 2022 for the Karoo National Park of South Africa.

consumed in KrNP, with eland, gemsbok, hartebeest and kudu collectively contributing 86% during the study period. Although small prey comprised 36% of the dietary profile, small mammals only contributed 6% to the biomass consumed by lions, with springbok being the largest contributor (4%).

Aerial census data from 2021 to 2022 indicate that gemsbok, hartebeest and Cape mountain zebra were the most abundant species throughout the KrNP, constituting 68% of the available large prey, followed by eland, kudu and ostrich (Figure 1b). Nevertheless, when combining such relative abundance data with kill-site cluster (Figure 3c) and scat analyses (Figure 3d), kudu, eland and common duiker (*Sylvicapra grimmia*) were among those most preferred by lions in the KrNP. In contrast, both kill-site cluster (Figure 3c) and scat analyses (Figure 3d) suggest that zebra, rhebok, ostrich and gemsbok are consumed less often than expected, given their relative abundance in KrNP.

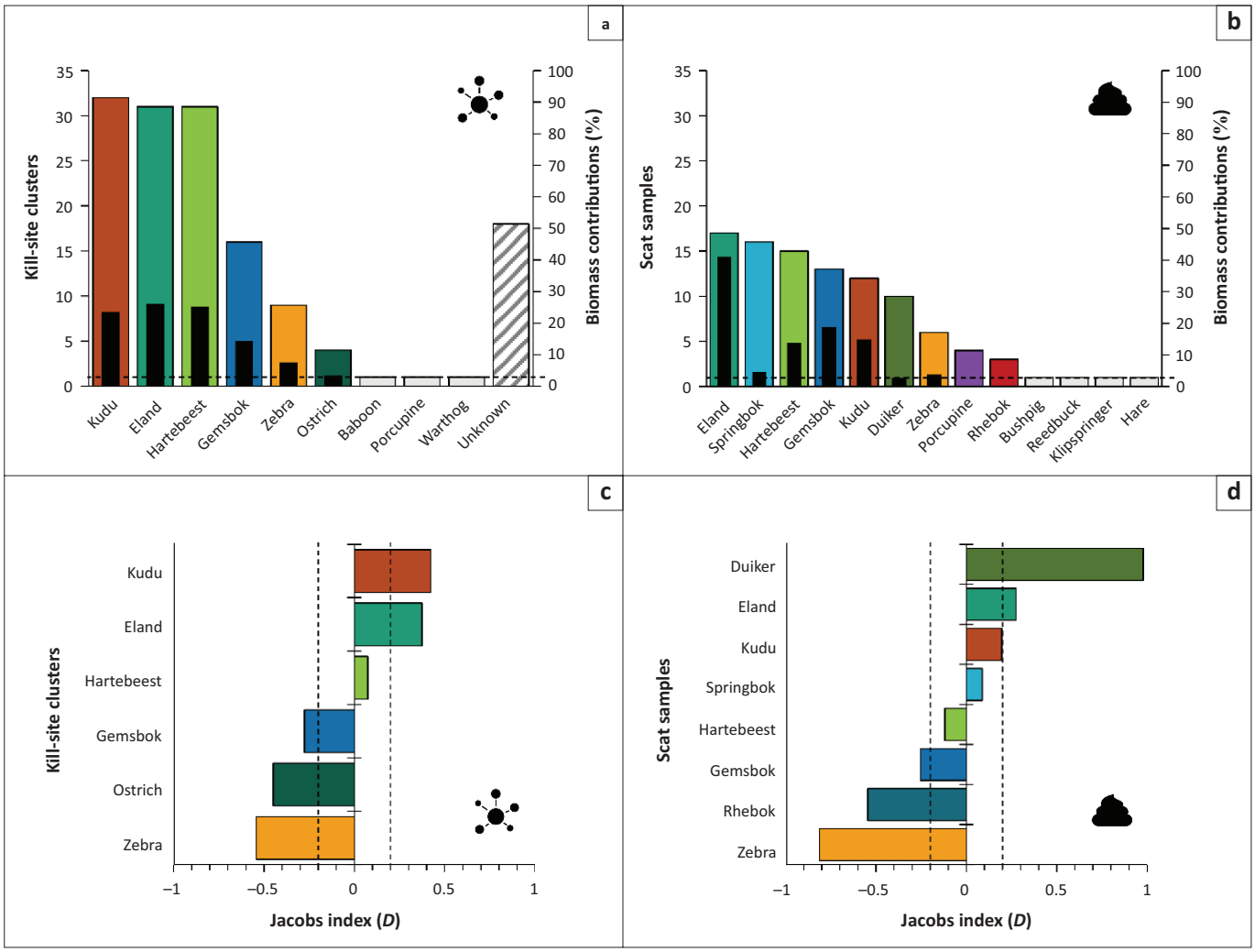
Longitudinal trends in lion diet

Estimated lion population sizes in KrNP have varied since their reintroduction in November 2010 (i.e. $\bar{x}$ = 15.5 ± 2.01 [7–26] individuals per annum; Figure 1b). However, carcass records (n = 1.035; Figure 4a) maintained by field rangers (i.e. $\bar{x}$ = 89.6 ± 2.01 [37–168] recorded kills per annum) indicate no significant ($x^2 = 1.98$, $df = 5$, $p = 0.85$) change in lion dietary composition over the 12-year study period (2010–2022) after controlling for inter-annual changes in population size (Figure 4b). Consistent with the composition result, prey preference classes and RBCs showed no inter-annual effect under the same multinomial framework (Type III LR tests).

Discussion

In small reserves, managers often assess whether changes in prey availability or composition could signal emerging challenges. In KrNP, diet remained consistent through the study period, with kudu and eland consistently important prey, suggesting no diet-related signal of change. Hartebeest and gemsbok were important secondary prey items, with hartebeest being more preferred and used in slightly greater proportions. Scat analysis revealed that springbok and duiker were the major small prey items consumed, but from a biomass perspective, these species contributed less than large antelope.

Mountain zebra was surprisingly under-utilised, given that they occurred in similar numbers to other large and preferred prey species, which may be indicative of anti-predatory behaviour (Courbin et al. 2016). Mountain zebra may exhibit distinct anti-predator strategies compared to plains zebra, potentially benefiting from their use of rugged terrain,



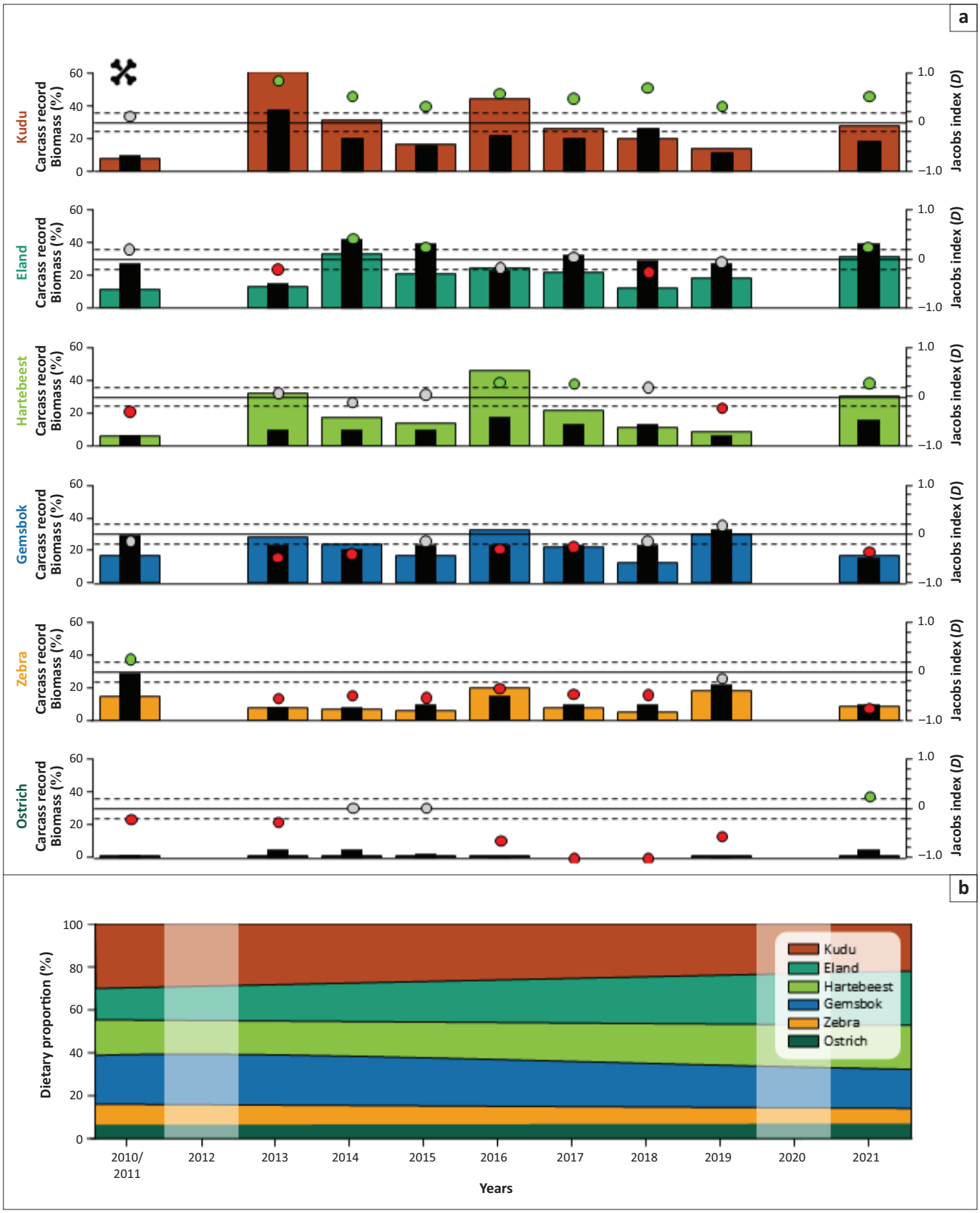
Note: Lion prey profiles are indicated by species (coloured bars) and biomass contribution (black bars), calculated using the mass of an adult female for each species. Less common prey species representing ≤ 1% (dashed horizontal line) contribution are noted but greyed out. Indicated also by species (coloured bars) are prey preferences, where D values of 0, > 0.2 and < -0.2 correspond with randomised indifference, preference and avoidance, respectively.

FIGURE 3: Contemporary lion diet profiles and relative biomass contributions as determined from (a) kill-site cluster and (b) scat sampling, where prey preference is also indicated for (a) kill-site cluster and (b) scat sampling between March 2021 and May 2022 for the Karoo National Park of South Africa.

increased vigilance or group behaviour, which could reduce predation risk (Davidson et al. 2013; Hayward & Kerley 2005). Their apparent lower preference by predators in areas like Mountain Zebra National Park highlights a knowledge gap in species-specific predator–prey dynamics that warrants further investigation.

Preferred lion prey mass is between 92 kg and 632 kg, with a mean around 350 kg (Hayward & Kerley 2005). Few potential prey species in KrNP were ≥ 350 kg, with eland being the only exception (Skinner & Chimimba 2005; Spies 2017). In the arid Kalahari, Beukes et al. (2017) found that collectively, gemsbok, wildebeest, hartebeest and eland contributed 92% of total biomass consumed and that less than 4% of the total biomass consumed by lions was small prey, similar to the trends observed in this study. Eland were the most preferred prey species in the Kalahari (Beukes et al. 2017) and Addo Elephant National Park (i.e. semi-arid thicket biome; Hayward et al. 2007), but in the Karoo, kudu were the most preferred. Eland were preferred across all years but were highly sought after in 2014 and 2015. The historic data showed that from 2010 to 2020, kudu contributed 27% and eland 19% to the overall large prey diet. However, the detailed interrogation of diet during 2021–2022 found that eland made up 26% of the species consumed and 40% of the biomass intake, whereas 24% of the species consumed was kudu, which contributed 19% to the biomass intake. Furthermore, lions are known to have a diverse diet, feeding on a wide range of prey, including small species (Beukes et al. 2017), which generally do not contribute to the majority of prey biomass consumed. Small prey consumed likely act as important 'top-ups' between predation events of larger prey (Barnardo et al. 2020). However, knowing which large prey species are preferred and utilised is essential to managing a sufficient prey base for any lion population, particularly in such small and fenced reserves (Owen–Smith & Mills 2008).

Kudu may have been a preferred prey species in KrNP because it restricts itself to dense areas (Gray et al. 2007), which are relatively scarce in this open semi-arid system (Letsoalo et al. 2023). The areas with a greater woody component provide reduced visibility and thus could be more beneficial for the lions to hunt in, as they can better



Note: Longitudinal lion prey profiles are indicated as the number of carcasses found per species (coloured bars) and the proportional biomass contribution of each kill (black bars), calculated using the mass of an adult female for each species. Indicated also by species (coloured bars) are prey preferences (circles), where D values of > 0.2 denote prey preference (green) and < -0.2 denote avoidance (red).

FIGURE 4: Longitudinal trends in lion diet, indicating (a) annual diet profiles, relative biomass contributions and prey preference are (b) modelled as dietary proportion effects between March 2021 and May 2022 for the Karoo National Park of South Africa.

conceal themselves and stalk more readily (Elliot 1977). Eland are generally not considered a preferred prey species within southern Africa, presumably because of anti-predator benefits provided by their scarcity (Hayward et al. 2011). However, in the Kalahari (Beukes et al. 2017), as well as in Madikwe and Pilanesberg Game Reserves, eland was a preferred prey species for lions (Louw et al. 2012). In this study, eland was also preferred but less so when compared to kudu, and considering 94% of their diet consists of browse (Watson & Owen-Smith 2000), they spend the majority of their time in areas with greater cover and thus better stalking potential for lions (Elliot 1977). Furthermore, eland are versatile in their habitat selection and can inhabit mountainous areas (Skinner & Chimimba 2005), like parts of the KrNP. Multiple studies have shown that landscape curvature can aid in a successful hunt (Elliot 1977; Hopcraft, Sinclair & Packer 2005), and it can thus be expected that these mountainous landscapes could aid lions in prey capture because of the cover provided by the broken drainage patterns and the difficulty of the terrain underfoot that might hinder prey flight (Wheatley et al. 2021).

Conversely, gemsbok and Cape mountain zebra were not preferred, though both species feed significantly more on grass than kudu and eland (Cain et al. 2017). In KrNP, the grass is largely associated with the lower plateau regions, which are more open with less wood and shrub, except in the riverbeds, which are generally narrow strips of riverine woodland (Bezuidenhout et al. 2024). This lack of cover could account for the non-preference of these species (Hopcraft et al. 2005). That zebra were not selected as prey, except in 2010–2011, differs from many studies in which zebra contribute between 4% and 19% towards the overall dietary composition or in some cases are the greatest contributors to the lion diet (Barnardo et al. 2020; Briers-Louw & Leslie 2020; Davidson et al. 2013), potentially suggesting some form of anti-predatory behaviour (Courbin et al. 2016).

Kill-cluster investigations from GPS-collared predators provide precise, spatially explicit data on prey selection and hunting behaviour, but are labour-intensive and biased towards larger or persistent kills (Knopff et al. 2009). Scat-based diet sampling, including DNA metabarcoding, captures a broader dietary spectrum over time, including small or fully consumed prey, though it lacks spatial context and may be biased by digestibility (Deagle et al. 2019). Using both methods in parallel offers complementary strengths, improving dietary accuracy and reducing method-specific biases (Beukes et al. 2017). Additional tools–camera traps, stable isotope analysis and accelerometers–provide further insights but vary in resolution, cost and prey specificity (Newsome et al. 2010; Wang, Smith & Wilmers 2015).

Gemsbok, zebra and ostrich appear to be avoided, relative to their abundance, including hartebeest and eland, for some years. Taken together, this suggests that despite fluctuations in prey availability and lion abundance over time, there is substantial long-term lion dietary resilience in KrNP. The lion's dietary profile is generally well studied and defined in literature (Hayward & Kerley 2005); however, comparative evidence from arid and semi-arid regions, such as the KrNP, remains crucial, but limited (Beukes et al. 2017). Interestingly, the few studies conducted in semi-arid regions where zebra were present, they do contribute to the overall lion diet (Davidson et al. 2013; Stander 1992), and in some cases, such as in a study using mortality records for Etosha National Park in Namibia, zebra contributed 55% to the overall diet (Berry 1981). However, Stander (1992) found that zebra contributed <10% to the lion diet in the same reserve, while Davidson et al. (2013) report similar contributions and non-preference for zebra in Hwange National Park of Zimbabwe. The contemporary and longitudinal components of this study arguably provide the most robust account of lion diet in a semi-arid system to date, supporting that zebra contributed only 8% to KrNP lion diet and was also not preferred as the fifth greatest overall contributor. It should be noted, however, that few studies have specifically assessed mountain versus the comparatively well-studied plains zebra contributions to the lion diet (Hrabar & Kerley 2013), meriting further investigation.

Conclusion

The lions in KrNP showed their hunting flexibility, using at least three large herbivores with ease (i.e. kudu, eland and red hartebeest) with a preference for kudu and eland that predominantly browse (Gray et al. 2007; Watson & Owen-Smith 2000). KrNP lions also showed long-term consistency in their diet despite changing conditions and the challenges of this semi-arid landscape. Taken together, this longitudinal dietary resilience suggests that prey suitability and availability are unlikely to constrain lion foraging within the park. However, the preference for kudu and eland might be because of the tendency of these species to occupy and feed in denser areas with more cover (Bezuidenhout 2024; Watson & Owen-Smith 2000) that presumably promote more successful hunts. If so, kudu and eland might be key to lion persistence, where these species may require additional monitoring and management as preferred lion prey. The importance of lion hunting habitat, apart from prey abundance, appears to be important in this landscape, and an investigation into the availability versus catchability of prey within the KrNP would further enhance our understanding of lion feeding ecology within this rather unique semi-arid and mountainous landscape.

Acknowledgements

The authors acknowledge the following people: Mr Armond Nel, Dr Chalene Bisset and Mr Brian Courtenay.

Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

Robert Le Brun, Vincent N. Naude, Craig J. Tambling, Sam M. Ferreira, Cairestine Lottring, Frans G.T. Radloff contributed

equally to the conceptualisation, writing and editing of the manuscript and share first authorship. All authors contributed to the article, discussed the results and approved the final version for submission and publication.

Funding information

This research received no specific grant but was supported by the SATIB Trust and the Cape Peninsula University of Technology.

Data availability

All data that support the findings of this study are available on reasonable request from the corresponding author, Robert Le Brun.

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Appendix 1

TABLE 1-A1: Aerial census counts between 2010 and 2022 for the Karoo National Park of South Africa.

Prey species	2010–2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021–2022
Eland	471	609	583	637	744	755	857	1116	589	553	516
Red hartebeest	1550	1863	2105	2008	1650	1630	1429	1183	906	873	840
Kudu	781	884	512	888	909	662	897	609	443	429	414
Gemsbok	1783	2119	2582	2457	1555	1659	1948	1387	970	907	843
Zebra	788.5	891	929	932	1088	1005	970	921	830	818	805
Ostrich	789.5	1000	1109	645	607	437	439	403	418	366	313
Total	**6163**	**7366**	**7820**	**7567**	**6553**	**6148**	**6540**	**5619**	**4156**	**3943.5**	**3731**

Note: Indicated are total counts of lion prey species and overall, per annum, where data for 2011 and 2021 are interpolated as the mean between adjoining survey years.