The lion's share: implications of carnivore diet for threatened herbivores in Tsavo, Kenya

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Abstract Predation can have cascading, regulatory effects across ecological communities. Knowledge of the diet of predators can therefore provide important information regarding their ecology and conservation, as well as their impacts on prey populations. Using scats collected during 2019–2023 and estimates of prey abundance from aerial surveys, we characterized prey consumption and preferences of the Vulnerable African lion *Panthera leo* population in Tsavo, Kenya. Biomass models applied to prey frequencies in scats revealed that > 85% of lion diet comprised large ungulates weighing > 150 kg. The Critically Endangered hirola *Beatragus hunteri* and Endangered Grevy's zebra *Equus grevyi* (species that were introduced in Tsavo as part of ex situ conservation programmes in the 1960s) were amongst the seven prey species, of 16 detected, that were preferred by lions. Our results potentially indicate a disproportionate impact of lion predation on the small hirola and Grevy's zebra populations. Preferential predation, coupled with high availability of alternative prey, may trap the small populations of hirola and Grevy's zebra within a predator pit. Our findings provide a better understanding of lion diet, optimal foraging and the potential effects predators can have on threatened and rare prey species in an important conservation landscape. Based on our findings, we recommend an observational study of the predation ecology of lions and other predators in this system, to provide information on age- and sex-specific predation rates on hirola and Grevy's zebra for a population viability analysis, to support the management of these two threatened and rare herbivores in Tsavo.

Muhtasari Uwindaji unaweza kuwa na athari mbaya, za udhibiti katika jamii za ikolojia. Uelewa wa chakula cha wanyama wanaowinda wanyama kwa hiyo unaweza kutoa taarifa muhimu kuhusu ikolojia na uhifadhi wao, pamoja na athari zao kwa makundi ya wanyama wanaowinda. Kwa kutumia kinyesi cha simba kilichokusanywa kati ya mwaka wa 2019 na 2023, na makadirio ya wingi wa mawindo kutokana na utafiti, tumelinganisha ulaji wa mawindo na upendeleo wa simba wa kiafrika *Panthera leo* aliyeathiriwa na uchache wa idadi yake katika Tsavo, Kenya. Modeli ya biomasi zilizotumika kwa kinyesi cha mara kwa mara cha mawindo zilifichua kuwa zaidi ya asilimia 85 ya mlo wa simba ulijumilisha kiwango kikubwa cha mamalia wenye kwato na uzani unaozidi kilogramu 150. Wakati mamalia wakubwa wenye kwato wakipendelewa pia kama mawindo kwa wepesi wa kupatikana kwao, tulipata upendeleo wa simba kwa swara aliye hatarini zaidi hirola *Beatragus hunteri* na pundamilia aliye hatarini pia Grevy's zebra *Equus grevyi* ambaye ni speshi walioletwa Tsavo kama mpango wa uhifadhi kwa kuwatoa makao halisi (ex situ) miaka ya sitini. Matokeo yetu yana uwezekano wa kuonyesha athari isiyo na uwiano ya uwindaji wa simba kwa hirola na Grevy's zebra ambao idadi yao ni chache lakini muhimu. Uwindaje wa kupendelea pamoja na upatikanaji wa juu wa mawindo mbadala, huenda kuwafanya hirola na pundamilia kwa jina Grevy kuwa lishe mnyama mwindanji. Haya matokea ya utafiti ni hatua inayoelekea katika kuelewa bora lishe ya simba, na uwezo wa athari kwa speshi za mawindo adimu na waliohatarini zaidi katika mandhari yenye kuhitaji uhifadhi zaidi. Kutokana na matokeo yetu, tunapendekeza uchunguzi wa kina kwa ikolojia ya uwindaji wa simba na wanyama wengine wanaowinda katika huu mfumo ili kutoa habari zaidi kuhusu umri na jinsia haswaa ya viwango vya uwindaji wa hirola na pundamilia wa Grevy; muhimu kwa uchanganuzi wa uwezekano wa idadi na usimamizi wa wanyama hawa wawili walio hatarini na nadra katika Tsavo.

Keywords African lion, carnivore conservation, Grevy's zebra, hirola, predation ecology, predator–prey relationships, ungulate conservation

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Introduction

The charisma of carnivores and their connection with the human psyche, coupled with their important functional roles in ecosystems, often make carnivores suitable flagship species for conservation (Gittleman et al., 2001; Dalerum et al., 2008; Ducarme et al., 2013; Ripple et al., 2014). The tiger *Panthera tigris*, lion *Panthera leo*, grey wolf *Canis lupus* and cheetah *Acinonyx jubatus* have been the face of projects focused on habitat conservation, ecosystem revival and conservation introductions (Bangs & Fritts, 1996; Jhala et al., 2019; Packer, 2019; Jhala et al., 2021). Although such conservation policies currently aim to restore carnivores through protection and/or augmentation, carnivore recovery can lead to increased conflicts with people (e.g. with brown bears *Ursus arctos* in the Pyrenees mountains; Piedallu et al., 2016) and reduction of threatened prey species (e.g. predation of bighorn sheep *Ovis canadensis* by pumas *Puma concolor*; Johnson et al., 2012). The depletion of threatened or rare prey through predation is particularly important in systems where predators have abundant primary prey. As a result of this, predator densities in such systems can remain high and are not restricted by the availability of rare or secondary prey. Such high predator densities can, however, result in high predation on rare prey, trapping them in a predator pit that can lead to further population declines (Allee et al., 1949; Messier, 1994; Sinclair et al., 1998; Schmidt, 2004; Johnson et al., 2012). Because of such layered effects mediated by carnivores, knowledge of their ecology and behaviour remains key for effective management of ecosystems (Boitani & Powell, 2012).

Lions are iconic for their connection to human culture and their apex position in ecosystems, often making them symbols of conservation (Roemer et al., 2009). However, lions are also one of the top species involved in conflict, severely threatening human lives and livelihoods (Ray et al., 2005). Direct persecution and detrimental habitat alteration have reduced their numbers by > 75% since 1970, with a range contraction of > 90% (Ripple et al., 2014; Loveridge et al., 2022). The Tsavo Conservation Area (hereafter Tsavo) in south-east Kenya is a semi-arid, drought-prone landscape that hosts one of the largest populations of lions in East Africa (Henschel et al., 2020). This landscape is also an important connection between two major African biomes: mesic grassland savannah to the south and semi-arid bush savannah to the north (Henschel et al., 2020). Nearly 450 lions live in the Tsavo landscape (covering both East and West Tsavo National Parks; Elliot et al., 2021), yet lion ecology has been understudied in this landscape (barring mane growth, Kays & Patterson, 2002, and the human-eating tendencies of two infamous male lions, DeSantis & Patterson, 2017). This contrasts with other well-studied East African lion populations in Serengeti and Ngorongoro (Packer et al., 2019).

Tsavo is also home to one of the last remaining populations of the Critically Endangered hirola *Beatragus hunteri*. The hirola is restricted to a small area of its natural range on the Kenyan–Somali border, but was introduced to Tsavo East National Park in 1962 and 1996 as insurance against extinction in its natural range (Probert et al., 2014). The hirola population in Tsavo has remained small, and such small herbivore populations can be prone to the detrimental effects of predator mediated apparent competition when primary prey is abundant (Johnson et al., 2012). The Endangered Grevy's zebra *Equus grevyi* was also introduced to Tsavo, in 1964 and 1977, but the population has also remained small (Githiru, 2017). Multiple factors can impede recovery of introduced herbivores, and predation is a plausible cause for the lack of population growth in these two species of conservation concern in Tsavo (Evans, 2011; Probert et al., 2014).

To examine the ecology of this important population of lions and their potential predation impacts on the hirola and Grevy's zebra, we present information on lion diet and preferences in Tsavo, determined from scat analysis using biomass models. Our findings have important implications for predation ecology of threatened herbivores in an important conservation landscape.

Study area

We conducted the study in the southern part of Tsavo East National Park, south of the Galana River in Kenya (Fig. 1). Our study area spans > 4,065 km² and is bordered by Tsavo West National Park to the west, Taita ranches and settlements to the south and south-west, and Galana and Kulalu ranches to the east (Lala et al., 2021). Our study area has a high density of lions and herbivores compared to elsewhere in Tsavo (Elliot et al., 2021), as the Galana River to the north forms a natural barrier for animal movement. It is a semi-arid landscape with a dry season from January to early March and a cool season from June to October. Annual temperature is 20–30 °C and annual precipitation 200–700 mm (Lala et al., 2021).

Much of the landscape is open and shrubby grasslands, with a mosaic of riparian habitats along the rivers. In addition to the hirola and Grevy's zebra, common herbivores include the savannah elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, plains zebra *Equus quagga* and Cape buffalo *Syncerus caffer*. The lion, cheetah, leopard *Panthera pardus*, African wild dog *Lycaon pictus* and spotted hyena *Crocuta crocuta* are common carnivores. A list of the mammalian and avian species of Tsavo can be found in Lack et al. (1980), Lepage (2004) and Tóth et al. (2014). Tsavo is a keystone habitat that with Amboseli National Park forms the Tsavo–Amboseli ecosystem.

Methods

Scat collection and processing

We opportunistically collected 74 whole lion scats during November 2019–February 2023, with the majority of the scats collected during the dry season (Fig. 1). All scats were georeferenced in the field, and were identified based on their size and the presence of lion tracks and scrapes.

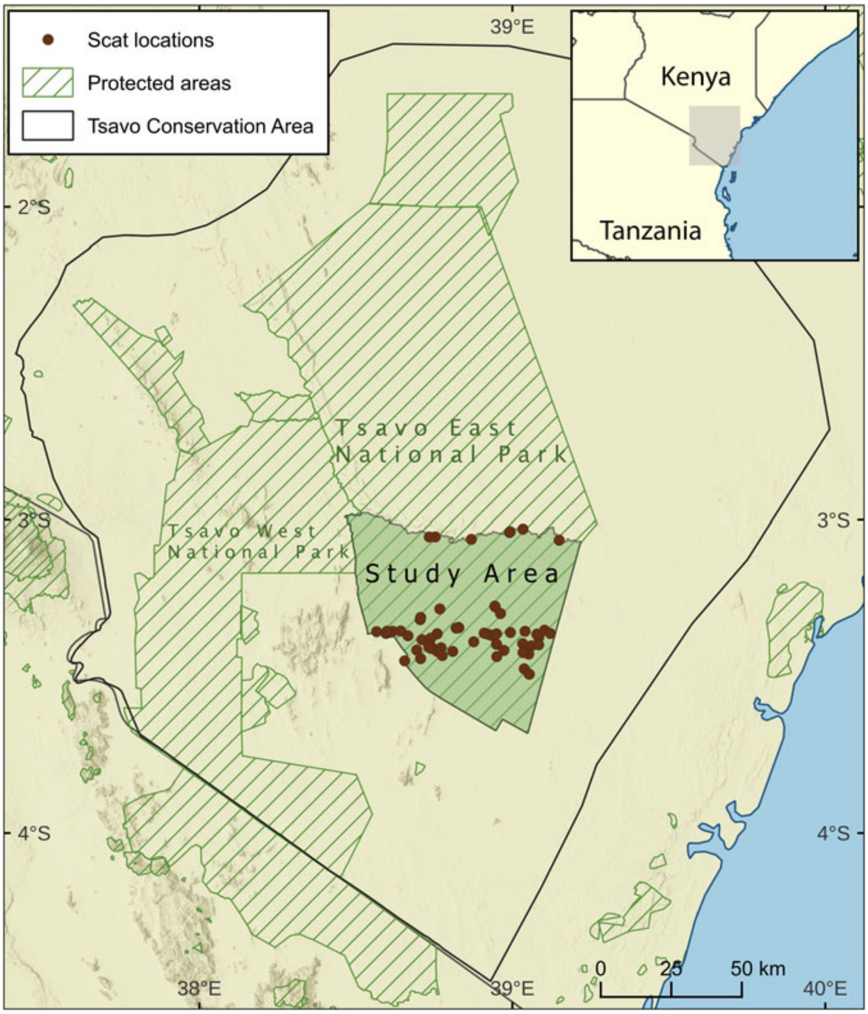

Fig. 1 The location of Tsavo Conservation Area in southern Kenya, with the locations of the 74 lion scats collected in the southern part of Tsavo East National Park, south of the Galana River during 2019–2023.

We relied on the ecological knowledge of experienced field personnel from the Wildlife Research and Training Institute, and Kenya Wildlife Service rangers, who are familiar with the area. We only analysed scats that could be unambiguously identified as those of lions.

Each collected scat was sun dried before being washed through fine mesh (1–3 mm) sieves. We separated prey hairs from other remains such as bones, hooves and teeth, and randomly selected 20 prey hairs from each washed sample. Each hair was mounted on a slide with a drop of DPX mountant and a coverslip, and examined under a compound microscope at × 400 magnification. We cross-referenced the cortex and medulla patterns, and the thickness and proportion of the medullary layer in each hair with a key for mammalian prey hair from the area (Perrin & Campbell, 1980) and with a digital hair library at the Kenya Wildlife Service (Evans, 2011), facilitating identification of each prey hair to species. The reference library at the Kenya Wildlife Service (compiled using hairs collected from the Kenya Wildlife Service animal orphanage and from known predation events) was required as Perrin & Cambell's (1980) key did not include all prey species occurring in the study area. From each scat sample of 20 randomly selected hairs, we determined the number belonging to a particular prey species, and converted it into a proportion or scat equivalence (Chakrabarti et al., 2016), where:

Scat equivalence of prey species A in sample i = number of hair/s of species A in sample i / 20

We added the scat equivalence for each prey species across all 74 scats to obtain the whole scat equivalence for that species (Chakrabarti et al., 2016). We used the whole scat equivalence to compute biomass consumption for each prey species instead of the more commonly used frequency of occurrence because it provides a more accurate representation of consumption (Chakrabarti et al., 2016).

Prey consumption

We calculated the total biomass consumption of each prey species found in the scats using a lion specific biomass model (Chakrabarti et al., 2016): $y = 4.105 - 3.116\ exp^{-0.032x}$,

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where x is the mean prey weight and y is the prey biomass consumed per scat. The biomass consumed per scat for each prey species was then multiplied with its whole scat equivalence to estimate total biomass consumption of that particular prey in our collected samples. For prey weights, we used 75% of the mean adult female body weight, following Schaller (1972) and Hayward & Kerley (2005), because it accounts for the weights of juveniles and subadults in the population and is a better representation of the mean weight of a prey population available to a predator. Prey weights were obtained from Stewart (1963), Sachs (1967), Myers et al. (2008), Pinto (2018) and Hayward & Kerley (2005). To examine the importance of each prey species in lion diet, we calculated the relative biomass consumed for each prey as a per cent of total consumption.

Prey selection

We used recent herbivore aerial census data from Tsavo (Waweru et al., 2021) to estimate study site specific abundance/individuals observed for lion prey species. We apportioned herbivore sightings to our study area by clipping all sightings by the boundary of the study area. Although post hoc, this delineation ensured that prey consumption, based on scats, and prey availability were matched geographically. We subsequently calculated the relative abundance of each prey species as an index of availability, in which the abundance of each prey species was converted as a per cent of the total abundance of all prey species occurring in the lion scats in our study area. We could not include dikdik (*Madoqua* sp.) and fringe-eared oryx *Oryx beisa callotis* in this prey selection analysis because of the lack of sightings in our study area during the aerial census. Our analysis indicates that consumption of these two species by lions was low in Tsavo, and hence we are confident that their exclusion did not significantly alter the prey selection indices. We also excluded elephants from this part of our analysis as we found elephant hair in only one scat. From the relative biomass consumed and relative prey density, we computed Jacobs' selectivity index for each prey species occurring in the lion scats, using the *dietR* package (Borstein, 2020) in *R 4.2.1* (R Core Team, 2021). Jacob's selectivity index (D) ranges from +1 to −1, indicating maximum preference and maximum avoidance respectively, and a value close to 0 indicates random selection of a prey species (Jacobs, 1974).

Results

The cumulative species occurrence plot indicated our sampling was adequate to characterize lion diet in Tsavo East as no new species were detected after 20 scats (Fig. 2). We identified 16 prey species from the scats; African elephant being the largest and dikdik being the smallest (Table 1).

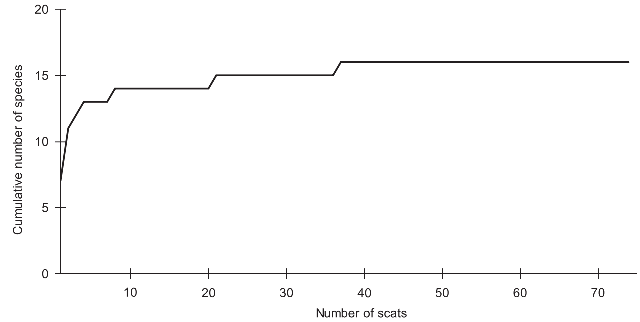

FIG. 2 Calculation of sampling adequacy for the 74 lion scats collected in Tsavo East National Park, Kenya (Fig. 1), during 2019–2023 for the characterization of diet, with no additional prey identified with the analysis of > 20 scats.

The majority of lion diet comprised of herbivores that weigh > 150 kg, with zebra, giraffe, Cape buffalo and waterbuck *Kobus ellipsiprymnus* accounting for > 70% of biomass intake. Small antelopes, such as gerenuk *Litocranius walleri* and Grant's gazelle *Nanger granti* were rarely consumed (2% of the total biomass intake). Approximately 5% of the diet comprised the Endangered Grevy's zebra and Critically Endangered hirola.

Based on prey availability, seven of the 16 species detected were preferred by lions (Grevy's zebra, hirola, waterbuck, warthog *Phacochoerus africanus*, Cape buffalo, gerenuk and giraffe), and five species were avoided (Grant's gazelle, hartebeest *Alcelaphus buselaphus*, plains zebra, impala *Aepyceros melampus* and lesser kudu *Tragelaphus imberbis*). The eland *Tragelaphus oryx* was consumed according to its availability (Table 1, Fig. 3).

Discussion

Comprehensive characterization of diet is critical for understanding animal ecology and is of particular importance for apex carnivores as their predation can have cascading implications for the entire ecosystem. We investigated diet and prey selection of lions south of the Galana River in Tsavo East National Park, Kenya, using scat analysis through a lion-specific biomass conversion model and estimation of prey abundance. Earlier studies of lion diet have either relied on direct observations or frequency of occurrence of prey remains in scats (Hayward & Kerley, 2005), which have the limitations of overestimating large and small prey, respectively (Chakrabarti et al., 2016). Biomass conversion models account for differential prey digestibility and hence provide a more accurate representation of carnivore diet from scats (Ackerman et al., 1984; Chakrabarti et al., 2016).

Our findings reveal that lions in this area include a wide size range of mammalian prey species in their diet, from the dikdik to the African savannah elephant, but they typically rely on large ungulates (Fig. 4). Our findings also reflect

Table 1 The 16 prey species detected in 74 lion *Panthera leo* scats collected in Tsavo East National Park during 2019–2023, with their body weight (75% of mean adult female body weight), whole scat equivalence (WSE; see text for details), biomass consumed per scat (y; see text for details), total biomass consumed (WSE * y), relative biomass consumed (per cent of total consumption), total abundance (total number of individuals of a species observed within our study area), and relative abundance (per cent of the total abundance of all prey species). Species are sorted by relative biomass consumed, and those in bold indicate preferred prey items, with a threshold of preference/avoidance set at $D \pm 0.3$ (see Fig. 3 for details). Dikdik and fringe-eared oryx could not be included in the prey preference analysis as a population estimate for the species is not available, and the elephant was excluded as hair was found in only one lion scat.

Species	Weight (kg)	WSE	y (kg/scat)	Biomass consumed (kg)	Relative biomass consumed (%)	Abundance	Relative abundance (%)
Cape buffalo *Syncerus caffer*	432	23.10	4.11	94.83	33.47	722	9.04
Waterbuck *Kobus ellipsiprymnus*	188	12.10	4.10	49.58	17.50	68	0.85
Giraffe *Giraffa camelopardalis*	550	9.40	4.11	38.59	13.62	535	6.70
Plains zebra *Equus quagga*	175	8.80	4.09	36.02	12.72	3,273	40.99
Warthog *Phacochoerus africanus*	45	4.40	3.37	14.82	5.23	72	0.90
Eland *Tragelaphus oryx*	345	3.25	4.11	13.34	4.71	636	7.97
Grevy's zebra *Equus grevyi*	190	1.90	4.10	7.79	2.75	14	0.18
Hirola *Beatragus hunteri*	90	1.70	3.93	6.68	2.36	74	0.93
Impala *Aepyceros melampus*	30	1.90	2.91	5.53	1.95	558	6.99
Hartebeest *Alcelaphus buselaphus*	95	1.15	3.96	4.55	1.61	1,093	13.69
Fringe-eared oryx *Oryx beisa callotis*	158	1.05	4.09	4.29	1.51		
Gerenuk *Litocranius walleri*	44	1.25	3.34	4.18	1.48	47	0.59
African elephant *Loxodonta africana*	1600	0.30	4.11	1.23	0.44		
Grant's gazelle *Nanger granti*	38	0.30	3.18	0.95	0.34	847	10.61
Lesser kudu *Tragelaphus imberbis*	99	0.15	3.97	0.60	0.21	46	0.58
Dikdik *Madoqua kirkii*	4	0.25	1.36	0.34	0.12		

similar patterns in lion diet across the species' global range (Hayward & Kerley, 2005), as well as in the adjacent population in Amboseli (Courtois, 2015). Lions in Tsavo seem to consume large and dangerous prey species such as Cape buffalo and giraffe, substantially (Table 1). Although lions often hunt alone (Packer, 1986; Packer et al., 1990), killing large and dangerous prey may require cooperation. When lions hunt as a group, the simplest tactics of cooperation, which include either similarity in actions or synchrony, or a combination of both, can be sufficient to hunt such prey (Boesch & Boesch, 1989; Palmer et al., 2023). Complex co-operative hunting that requires coordination and collaboration has been documented only in Etosha National Park in

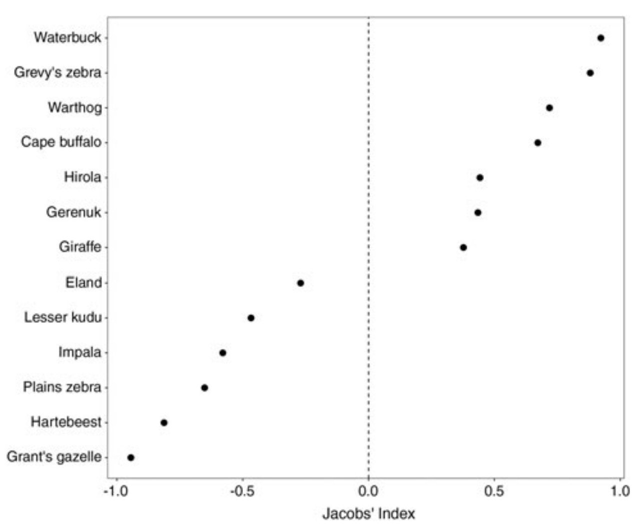

Fig. 3 Jacobs' selectivity indices (D) for prey species (excluding dikdik, elephant, and fringe-eared oryx) occurring in 74 lion scats from Tsavo East National Park, Kenya, collected during 2019–2023. Values < -0.3 indicate avoidance and values > 0.3 preference for the corresponding prey species, and values ±0.3 indicate that the corresponding species were predated randomly or in proportion to their availability. Waterbuck, Grevy's zebra, warthog, Cape buffalo and hirola were the most preferred prey items.

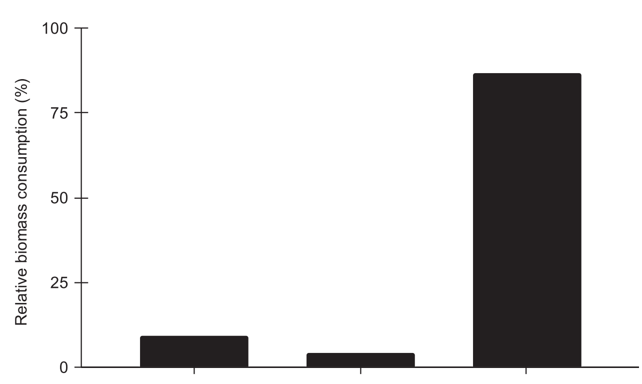

Fig. 4 Relative biomass consumption of lion prey (Table 1) segregated into weight categories (small, < 50 kg; medium, 50–150 kg; large, > 150 kg). Large prey comprise the majority (> 75%) of lion diet. Prey weight is 75% of mean adult female body weight, following Schaller (1972) and Hayward & Kerley (2005).

Namibia (Stander, 1992; Palmer et al., 2023) and recently in Gir National Park in India (Chakrabarti et al., 2023). Lions in Etosha cooperatively hunt large and dangerous herbivores such as giraffes (Stander, 1992), and cooperative hunting by lions in Gir involves killing livestock within human settlements, requiring individual lions to navigate threats from herders and other people. A substantial reliance on large and dangerous prey among Tsavo lions perhaps indicates that lions in this population employs cooperative hunting techniques, and observational studies are needed to examine this. Tsavo lions are also known to scavenge on elephant carcasses that become available as a result of drought or poaching (Morris et al., 2023). However, we found elephant hair in only one scat. This could be because our study did not coincide with a major drought event and/or because scavenging from a large carcass mainly involves consumption of flesh and organs rather than skin and hair, and is thus not detectable in scats without DNA analysis (Chakrabarti et al., 2016).

Although large ungulates such as the Cape buffalo and waterbuck were among the most consumed and preferred prey of Tsavo lions, we also found considerable consumption of small ungulates such as the warthog (Table 1). Warthogs comprised c. 5% of lion diet and were highly preferred. The warthog is a preferred prey species of the lion across its range as a result of its spatio-temporal sympatry with lions and its low evasion speed (Hayward & Kerley, 2005). Consumption of the threatened hirola and Grevy's zebra by lions in Tsavo was high, cumulatively accounting for c. 5% of their diet even though they comprised only c. 1% of the relative abundance of available prey. The introduced hirola population in Tsavo is of critical importance because of the relatively low numbers of this species in its natural range; the Tsavo population comprises nearly 15% of the species' global abundance (Probert et al., 2014; Waweru et al., 2021). The hirola population in Tsavo has remained small since its introduction, and its recovery is a management concern. Similarly, the Grevy's zebra population in Tsavo has remained small since its introduction. Little is known about the potential stressors that have kept these populations low (Jowers et al., 2020), although an earlier study of lion scats in Tsavo also reported relatively high predation of hirola (Evans, 2011).

Small prey populations can be disproportionately vulnerable to predation when primary prey is abundantly available. This is because a high primary prey density can sustain high, stable predator densities, which in turn can cause high and persistent offtake of the small, secondary prey population. A high predation pressure can reduce population growth and potentially trap the small prey population in a predator pit where the population size of the secondary prey species declines (Sinclair et al., 1998; Johnson et al., 2012; Ng'weno et al., 2019). Our analysis indicates that both the hirola and Grevy's zebra are consumed by lions relatively more than their proportional availability in Tsavo, perhaps because of abundant primary/alternative prey species that sustain high lion numbers. High predation can be detrimental to population recruitment and can potentially cause Allee effects or inverse-density dependent declines among these threatened and small herbivore populations (Allee et al., 1949; Messier, 1994; Sinclair et al., 1998; Schmidt, 2004; Johnson et al., 2012). Based on our diet analysis, we recommend a telemetry-based investigation of predation ecology of lions and other carnivores in this area, to examine age- and sex-class specific offtake of the hirola and Grevy's zebra. This will facilitate an accurate population viability analysis of these two threatened herbivores, and guide management decisions.

Author contributions Study conception and design: SC, FL, JKB; field and laboratory work: SN, GW, PIC, JK, FL; data analysis: EK, SC; writing: EK, SC, with inputs from JKB, FL, PO, RM, GW; funding acquisition: JKB, RM, SC; revision: all authors; project supervision: SC, JKB, FL, PO.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. Fieldwork was conducted as part of regular monitoring by the Wildlife Research & Training Institute and the Kenya Wildlife Service. The data involved no experimentation, collection or monitoring of live animals.

Data availability The scat analysis is in Table 1. Scat locations, which correspond to lion locations, have not been included because of their sensitive nature, and can be made available on reasonable request to the corresponding author. Prey abundance estimates are from published reports.

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