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RESEARCH PAPER

Diet composition of Asiatic lions in protected areas and multi-use land matrix

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Abstract. Comparative studies on the diet of large felids in protected areas (PAs) and surrounding multi-use landscapes are important for their conservation. The Asiatic lion is an endangered felid distributed in Gir PA and the surrounding multi-use land matrix. Based on scat analyses, we assessed the dietary composition of Asiatic lions. The frequency of occurrence (FOO), biomass consumption model, dietary niche breadth and dietary overlap index was used to quantify diet. The Asiatic lion ate more wild prey (74%) than domestic livestock (26%) in the Gir PA. In contrast, lion diets comprised 51% wild prey and 42% domestic livestock in the multi-use land matrix. Sambar contributed most (38%) to the diet in PAs, while blue bull most (29%) in the multi-use land matrix. However, diet diversity and niche breadth were similar between these two areas. The dietary overlap in the lions' diet between these two areas was 0.52. The results suggest that large-size wild ungulates are the main prey species in Gir PA, while in the surrounding multi-use land matrix, both large wild ungulates and domestic livestock are the main prey. The present study may help future lion conservation management decisions.

Key words: conservation, diet, Gir, landscape, ungulate prey, scat

Introduction

Because of their predatory behaviour and requirements for substantial land areas, large carnivores act as indicator species in a variety of ecosystems (Atkins et al. 2019); their effective management enhances the conservation of co-occurring biodiversity (Karanth 2003). Large predators can affect the structure and function of natural communities through direct (predation) and indirect effects (shift in the ecological aspects of prey and subordinate members of the carnivore guild) (Laundré et al. 2001, Ripple et al. 2014). Large carnivores also provide ecosystem services for humans directly or indirectly (Gilbert et al. 2017, Braczkowski et al. 2018). Despite their ecological significance and importance for human well-being, large carnivore populations worldwide have been reduced owing to a decline in required resources, such as habitat and large ungulate prey (Ripple et al. 2014, Jacobson et al. 2016). Scientifically assessing the resource requirements of large carnivores is a fundamental aspect of their conservation and management (Miquelle et al. 1996).

Food is a crucial resource requirement of large carnivores due to their specialised needs for large

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prey (Karanth et al. 2004, Hayward et al. 2007). Assessing dietary composition can shed light on critical ecological processes such as population dynamics, prey preference, dietary competition and impact on prey population dynamics (Creel et al. 2001, Fuller & Sievert 2001, Sinclair et al. 2003). Large mammalian ungulates are essential food resources for large carnivores worldwide (Hayward & Kerley 2005, Hayward et al. 2006). However, due to anthropogenic driven habitat loss and other factors, the populations of large mammalian ungulates have declined globally, especially in multi-use landscapes (Ripple et al. 2014). While domestic prey such as livestock may become more critical outside of protected areas (PAs) (Valeix et al. 2012). Predation by large carnivores upon domestic livestock may lead to negative interactions between humans and large carnivores (Inskip & Zimmermann 2009, Puri et al. 2020). Therefore, scientific data on the diets of large carnivores inside and outside PAs could help in devising strategies to conserve and manage large carnivores at a landscape level.

The endangered Asiatic lion (*Panthera leo persica*, hereafter lion) is a large carnivore restricted to the Saurashtra region of the Gujarat state in western India. An increase in the lion population has primarily been driven by the success of lions within the Gir National Park, Gir Wildlife Sanctuary, Paniya Wildlife Sanctuary and Mitiyala Wildlife Sanctuary – collectively referred to as the Gir Protected Area. Moreover, with the support of local people and continuous conservation and management efforts, this big cat's population and geographic range have significantly increased over the last six decades in Gujarat (Singh & Gibson 2011, Singh 2017b, Singh & Nala 2018, Gujarat Forest Department 2020). The spill-over of the lion population from Gir PA is into the surrounding multi-use land matrix, which consists of forest patches, pasture (*Gauchers*), wasteland, panchayat land, linear infrastructures, and human settlements (Singh 2017b, Singh & Nala 2018, Gujarat Forest Department 2020). Gir PAs (consisting of four protected areas – Gir National Park, Gir Wildlife Sanctuary, Paniya Wildlife Sanctuary, Mitiyala Wildlife Sanctuary), Girnar Wildlife Sanctuary, and surrounding areas have different ecological settings, with contrasting prey composition and abundance. For instance, the density of spotted deer (*Axis axis*) and sambar (*Rusa unicolor*) in Gir PA and Girnar Wildlife Sanctuary is high compared to the surrounding multi-use land matrix, which has a high blue bull (*Boselaphus tragocamelus*) density (Ram et al. 2021). Such differences in prey composition and abundance could affect prey encounter rates, prey catchability, and, consequently, lion diet composition. Thus, studying the diet of lions in the PAs and multi-use land matrix may help understand how lions adjust their diet with changes in prey composition and abundance.

Earlier scientific studies (Meena et al. 2011, Zehra 2014, Chaudhary et al. 2020) on lion diets concentrated only on Gir PAs, and there is a lack of information regarding prey consumption by lions in the multi-use land matrix and its comparison with PAs. Therefore, we aimed to compare lion diet composition in PAs and multi-use land matrix to assess lion: a) diet composition and biomass consumption, and b) diet diversity and diet niche breadth. Carbone et al. (1999), while reviewing the diet of large carnivores, found that large carnivore species above the weight of 21 kg feed mainly on vertebrate prey up to 45% of their body weight. The average weight of Asiatic lions ranges from 116 to 140 kg (Vasavada et al. 2022), and based on the prediction of Carbone et al. (1999), we hypothesised that the Asiatic lion would consume two large prey species; sambar (130 kg) and blue bull (180 kg), in Gir PA more than other prey species, such as spotted deer (45 kg), wild pig (*Sus scrofa*) (32 kg), and four-horned antelope (*Tetracerus quardicornis*) (12 kg). While in the surrounding multi-use land matrix, the lion was predicted to primarily consume blue bull and domestic cattle (150 kg). Further, the multi-use land matrix lacks richness and abundance of wild prey due to anthropogenic disturbance in comparison with protected areas. Therefore, large carnivores may have to feed on a greater variety of food items in the multi-use land matrix to meet their resource requirements. Therefore, we hypothesised that lion diet diversity would be higher in the multi-use land matrix.

Study Area

The study was carried out in protected areas (PAs) and surrounding multi-use land matrix (approximately 2,155 km^2), collectively known as the Asiatic Lion Landscape (Fig. 1). The landscape includes five protected areas (Gir National Park, Gir Wildlife Sanctuary, Paniya Wildlife Sanctuary, Mitiyala Wildlife Sanctuary and Girnar Wildlife Sanctuary) and other forest classes which have a residential or regularly visiting population of lions. The multi-use land matrix consists of several large and small protected forests, reserved forests (including reserved and unreserved grasslands, locally known as *vidis*), unclassed forests, agricultural land, wasteland, panchayat land, *Gauchers*, other pasture lands,

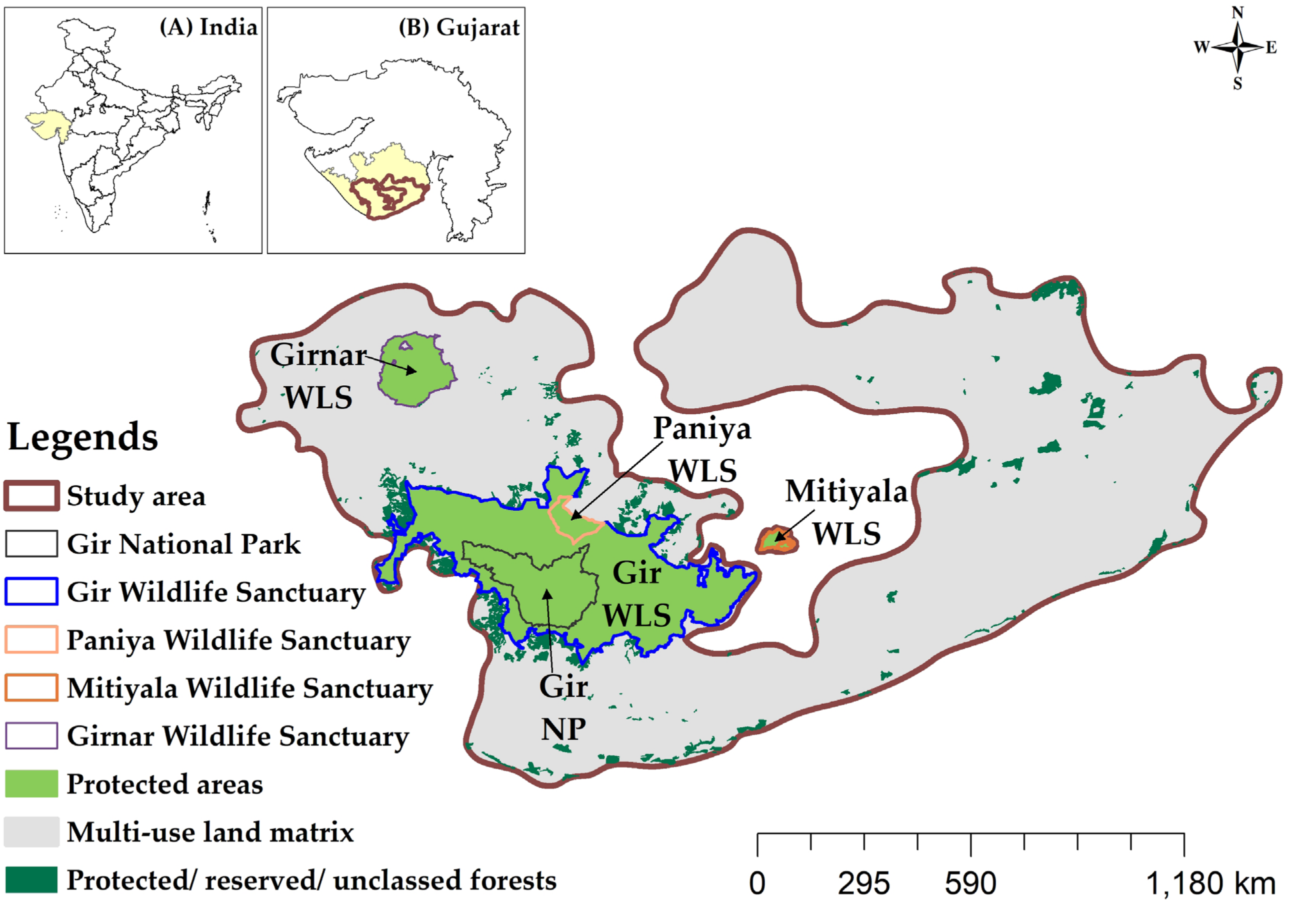

Fig. 1. Map of study area indicating sample collection sites including protected areas and multi-use land matrix in the Asiatic Lion Landscape. Map insets indicate the location of Gujarat in India (A) and the study area in the Asiatic Lion Landscape in Gujarat (B).

industrial areas and human settlements. Dominated by undulating terrain, the landscape consists of hills, including Gir, Girnar, Mitiyala and Palitana. In addition, the study area contains rivers such as the Shetrunji, Raval, Ardak, Bhuvatirth Machhundri, Hiran, Shingoda, Shigvada, Dataradi, Ozat, Safaraa, Gagadiya, Kalubhar that flow in different directions and debouch into the Arabian Sea.

The landscape is typical of the semi-arid Gujarat-Rajputana zone (Rodgers & Panwar 1988). There are three seasons based on temperature (summer: March-June, monsoon: July-October, winter: November-February). The aridity index ranges between 20-40% (Jadav 2010). The mean annual rainfall is approximately 600 mm (Farooqui et al. 2013) (past 25 years (1996-2020); the average annual rainfall in Gir PAs is 976.50 mm (Vasavada et al. 2022)). The mean maximum and minimum temperatures are 34 °C and 19 °C, respectively (Gundalia & Dholakia 2013). The natural ecosystem in the landscape includes thorn-scrub forests, grasslands, dry deciduous and riverine forests, mangroves, and coastal forests (Kalubarme 2014, Mehta 2015, Singh 2017a, Vasavada et al. 2022).

The region has one of the highest concentrations of apex predators, i.e. Asiatic lion and Indian leopard *Panthera pardus fusca* in India (Singh 2007, Singh & Gibson 2011). The other carnivores that are present are the striped hyena (*Hyaena hyaena*), Indian golden jackal (*Canis aureus*), jungle cat (*Felis chaus*), Indian fox (*Vulpes benghalensis*), honey badger (*Mellivora capensis*), rusty-spotted cat (*Prionailurus rubiginosus*), ruddy mongoose (*Herpestes smithii*), Indian grey mongoose (*Herpestes edwardsii*) and small Indian civet (*Viverricula indica*). The native wild prey base includes spotted deer, blue bull, sambar, wild pig, hanuman langur, Indian gazelle, four-horned antelope, blackbuck, and Indian peafowl (*Pavo cristatus*). Apex predators also frequently hunt domestic livestock (domestic cattle *Bos indicus*, domestic buffalo *Bubalus bubalis*) (Singh & Gibson 2011, Vasavada et al. 2022).

Material and Methods

Sample collection

Due to their nocturnal activity, cryptic behaviour and long-range movements, large carnivores are hard to monitor directly (Mills 1992). Therefore, scat analysis has been a widely used as a cost-effective method to study the dietary composition of large carnivores (Mukherjee et al. 1994). We collected lion scat from the study area by walking trails, forest roads, agriculture fields and village roads where scats are often found (Samarasinghe et al. 2022). Lion scats were identified from their morphological features and associated clues, such as pug and scrape marks (Banerjee et al. 2012). We excluded the scats of unidentified origin from the collection. Once encountered, scats were placed in a zip-lock bag while fresh scats collected during the survey were sun-dried to avoid fungal growth and transferred to Sasan-Gir Wildlife Rescue Centre for further examination. Dried scats were washed in lukewarm water under a thin sieve to remove impurities and segregate prey hair and other body parts, such as bones, nails, and skin, and dehydrated in 70% ethanol solution (Zehra 2014). Identifying prey species from hair requires a reference slide of prey species. Reference slides from the repository at Sasan-Gir Wildlife Rescue Centre were used for the comparison. We used the medullary pattern of prey hair to identify the species consumed (Mukherjee et al. 1994). From 2017 to 2021, 884 scat samples of lions (443 from inside the PAs, 441 from the multi-use land matrix) were collected (Table 1). Mukherjee et al. (1994) standardised the scat required to assess lion diet in Gir and found that 50 scat samples are required to assess lion food habits. In this aspect, the sample size in this study was far larger than the recommended size.

Data analysis

We used frequency of occurrence (FOO), defined as the count of occurrence divided by scat sample, and per cent occurrence (PO), the number of occurrences of prey items divided by the total number of prey items across all prey species, to quantify diet composition (Klare et al. 2011). Since FOO and PO are biased towards small prey species, we calculated biomass consumed by the lion using generalised models of biomass consumption developed for tropical felids by Chakrabarti et al. (2016). Finally, we calculated Relative Biomass Consumed (RBC) by dividing the prey biomass consumed of particular prey species by the total biomass consumed.

We assessed diet diversity in PAs and multi-use land matrix using the Shannon-Weiner diversity index (Shannon & Weaver 1949). The dietary niche breadth of the diet was calculated using standardised Levin's index (Levins 1968), which ranges between 0-1, where 0 indicates a specialised diet and 1 a generalised diet. We also assessed the dietary overlap in the diet of lions between PAs and the surrounding multi-use land matrix using the Pianka niche overlap index (Pianka 1973), which ranges from 0-1, where 0 indicates no similarity in diet and 1 indicates total overlap in the diet.

Table 1. Season and area-wise collection of scats during the study.

Year	Season	No. of scats: Protected areas	No. of scats: Surrounding multi-use land matrix
2017	Summer	45	45
	Winter	46	44
2018	Summer	44	44
	Winter	44	44
2019	Summer	44	44
	Winter	44	44
2020	Summer	44	44
	Winter	44	44
2021	Summer	44	44
	Winter	44	44
Total number of scats		443	441

Results

Dietary composition

Lions consumed 12 and 11 prey species in PAs and multi-use land matrix, respectively. In PAs, the largest contribution (PO) was of sambar (35%), followed by spotted deer (19%), domestic buffalo (13%), domestic cattle (13%), blue bull (8%), wild pig (6%), hanuman langur (3%), Indian hare (2%), Indian peafowl (2%), Indian porcupine (0.61%), Indian gazelle (0.20%) and domestic goat (0.20%) (Table 2). Wild prey contributed 74% to the diet, while domestic livestock (buffalo, cattle, goats) contributed 26% to the diet.

In the multi-use land matrix, blue bulls showed the largest contribution (25%) to the lion's diet, followed by domestic cattle (24%), domestic buffalo (17%), wild pigs (15%), sambar (4%), Indian hare (3%), spotted deer (3%), Indian gazelle (2%), domestic goats (2%), Indian peafowl (0.65%), and domestic sheep (0.22%) (Table 2). Wild prey contributed 51% of the lions' diet, while livestock (cattle, buffalo, goat, sheep) contributed 42%. The remaining 7% of samples were not identifiable.

Biomass consumption

In PAs, sambar contributed most to the biomass of the diet (38%), followed by spotted deer (18%), domestic buffalo (15%), and domestic cattle (14%) (Fig. 2). Wild ungulates made up 69% of the total biomass consumed by lions. In contrast, domestic livestock comprised 29% of the total biomass consumed in protected areas.

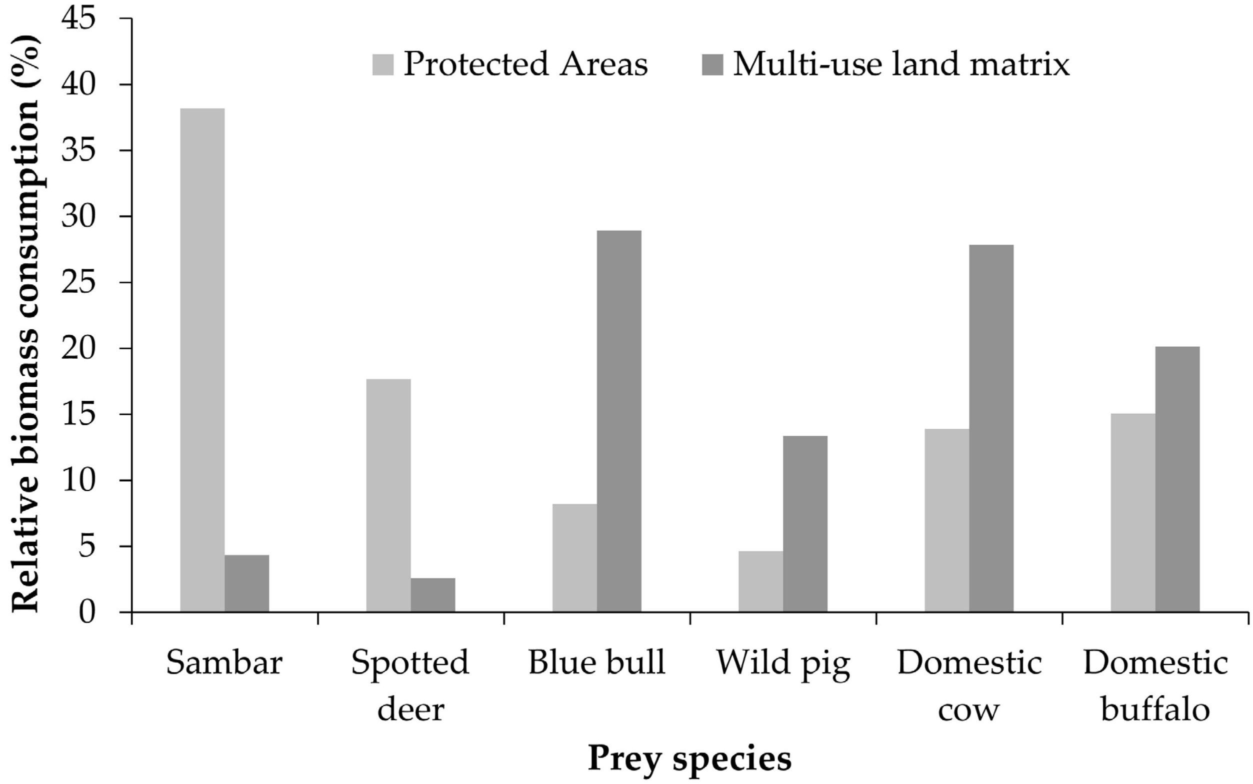

Fig. 2. The relative contribution of wild prey species and domestic livestock in protected areas and multi-use land matrix.

Table 2. Asiatic lion diet composition and biomass in PAs and multi-use land matrix. COO – Count of Occurrence, PO – Percent Occurrence, BC – Biomass Consumed, RBC – Relative Biomass Consumed.

Sr. No.	Prey species	Protected areas				Surrounding multi-use land matrix			
		COO	PO	BC	RBC	COO	PO	BC	RBC
1	Blue bull	36	7.38	158.81	8.21	112	24.30	494.08	28.93
2	Domestic cattle	61	12.50	269.09	13.91	108	23.43	476.43	27.84
3	Domestic buffalo	66	13.52	291.15	15.05	78	16.92	344.09	20.15
4	Wild pig	28	5.74	90.10	4.66	71	15.40	228.46	13.38
5	Sambar	169	34.63	739.51	38.20	17	3.69	74.39	4.36
6	Indian hare	10	2.05	7.21	0.37	12	2.60	8.65	0.51
7	Indian gazelle	1	0.20	2.65	0.14	9	1.95	23.89	1.40
8	Spotted deer	93	19.06	341.91	17.68	12	2.60	44.12	2.58
9	Domestic goat	1	0.20	1.54	0.08	7	1.52	10.78	0.63
10	Indian peafowl	9	1.84	7.30	0.38	3	0.65	2.43	0.14
11	Domestic sheep	0	0.00	0.00	0.00	1	0.22	1.54	0.09
12	Hanuman langur	11	2.25	21.01	1.09	0	0.00	0.00	0.00
13	Indian porcupine	3	0.61	4.50	0.23	0	0.00	0.00	0.00
14	No prey residue (Nil)	0	0.00	0.00	0.00	31	6.73	0.00	0.00

In the multi-use land matrix, blue bulls contributed the most to biomass consumption by lions (29%), followed by domestic cattle (28%), domestic buffalo (20%), and wild pigs (14%). Wild ungulates contributed 51% of all biomass consumed by lions, while domestic livestock comprised 49%.

Diet diversity and niche breadth

Our hypothesis regarding the diet diversity of lions was not supported since it remained relatively high between PAs (1.86) and multi-use land matrix (1.95). Dietary niche breadth between these two areas (PAs (0.33) *vs.* multi-use land matrix (0.39)) was also similar. However, the dietary overlap between these two areas was moderate (Pianka index value = 0.52), indicating a difference in more than half in the lions' diet similarity between PAs and multi-use land matrix.

Discussion

This study assessed the diet composition of lions from PAs and surrounding multi-use land matrix. Our first hypothesis regarding the consumption of large prey was supported, since the diet was dominated by large-sized prey (sambar, blue bull and domestic livestock) in both areas. The dominance of large-sized prey has been shown in earlier studies from Gir PAs (Meena et al. 2014, Zehra 2014, Chaudhary 2020) as well as from Africa (Scheel 1993, Hayward & Kerley 2005, Lehmann et al. 2008, Hayward et al. 2011, Davidson et al. 2013, Barnardo et al. 2020).

In PAs, the lions' diet is dominated by sambar in terms of FOO and RBC. The sambar is a large prey and provides a greater biomass reward than smaller prey species. Sambar also occur in small group sizes (mean group size: 2.15 individuals), which makes it less vigilant than species with large group sizes, such as spotted deer (mean group size: 8.6 individuals) (Ram et al. 2021) and, therefore, more susceptible to lion predation. Additionally, sambar has high temporal overlap with lions, which might increase their encounter rate (Chaudhary et al. 2020). Therefore, despite its low abundance (5,109 individuals) compared to spotted deer (75,316 individuals) (Ram et al. 2021), sambar dominated the diet in PAs. In contrast, sambar abundance is low in the multi-use land matrix (Ram et al. 2021), which might be the key reason for its low contribution to the diet of lions in that area.

The blue bull was another large prey species that lions did not consume as frequently as sambar in PAs, probably due to its comparatively low density in comparison with the multi-use landscape. Blue bull density in Gir PA is 2.52 individuals/km^2, whereas in the surrounding multi-use land matrix is up to 22 individuals/km^2 (Ram et al. 2021). The low density might result in a low encounter rate and fewer chances of predation in the PAs. In contrast, lions consumed the blue bull in greater numbers in the multi-use land matrix. Due to its open habitat and some scattered grasslands, the ecological conditions in this area are suitable for blue bulls, hence the greater density (Ram et al. 2021). Like sambar, the blue bull provides a high biomass in reward. Thus, the low availability of large-sized prey (sambar) possibly led the lions to feed on another large-sized abundant prey species (blue bull).

Spotted deer are another key prey species that contributed substantially to the diet of lions, and this observation is supported by earlier studies on Asiatic lions (Meena et al. 2011, Zehra et al. 2017). Spotted deer are among Gir PA's most abundant wild ungulate and exists at densities far higher (more than ten times) than sambar and blue bull (Ram et al. 2021). Furthermore, due to its broad habitat requirements, it has a wide distribution in PAs (Chaudhary et al. 2020). Its high density coupled with a wide distribution might result in a high encounter rate with lions, resulting in high predation rates. Spotted deer are a medium-sized prey species that can be tackled by solitary lions or small prides of 2-3 individuals.

We found that domestic livestock make a substantial contribution to the diet of lions in PAs. This high predation can be expected by the large body size of domestic species, which provides high rewards in terms of biomass (Hayward & Kerely 2005). However, the contribution of livestock to the diet has decreased significantly during the last four decades. Joslin (1973), in his doctoral work, found that domestic livestock contributed 75% to the diet of lions, while in the present study, it was 26%. Domestic livestock generally lack antipredator responses in comparison with native wild prey species and represent easy targets as prey (Eeden et al. 2018). The domestic livestock in PAs are kept in man-made corrals "*ness*" (a temporary settlement of the pastoralist community) and grazed during the day under the protection of 1-3 *maldharis* (pastoralists). However, cattle are sometimes left outside the corral, which makes them vulnerable to predation by lions. Furthermore, *maldharis* sometimes cannot detect lions during dawn and dusk, and the low light levels at these times provide an opportunity for lions to prey on livestock. However, there is no quantitative data regarding which ecological conditions lions kill livestock; hence further research is needed to support these observations.

Domestic livestock contributed nearly half of the lions' diet in the multi-use land matrix. This area also has a high abundance of feral cattle (locally known as *redhiyar*), which are not owned (Singh & Gibson 2011, Meena et al. 2014). Feral cattle are at more risk of predation due to their high abundance and absence of protection in the form of *ness* or *maldharis*. Thus, the high abundance of *redhiyar*, their feral habit, ease of capture and high biomass value result in high predation rates in the multi-use land matrix.

The diet diversity hypothesis was not supported since we did not detect a significant difference in diet diversity. After reviewing around 503 studies, Ferretti et al. (2020) found that large carnivores increase their diet diversity with an increase in prey richness. In our study area, prey richness is limited. In PAs, spotted deer, sambar, and blue bull are the primary prey species, while blue bull, feral cattle, and wild pig are major prey in the multi-use land matrix. In our study, therefore, lions have limited options to increase their dietary niche breadth and therefore show a specialised diet.

In conclusion, this study contributes to understanding the diet composition of Asiatic lions in different ecological settings. We found that wild ungulates are the key prey species in PAs, while blue bull, feral cattle, and wild pigs are important in the multi-use land matrix. Preying upon blue bulls and wild pigs in the multi-use land matrix might help limit the population sizes of these species, which benefits farmers since both species damage crops. Therefore, by acting as a biological controller of these species, lions provide an ecosystem service in the Asiatic Lion Landscape, Gujarat, India.

Conservation implications

Lions showed a high dependency on spotted deer and sambar in PAs, so monitoring these prey species is essential for future lion conservation and management. Identifying the ecological determinants of domestic livestock predation in PAs could help avoid human-wildlife conflicts. In the multi-use land matrix, monitoring, conservation and managing blue bull and wild pig populations are vital as they are the main prey species for the lions. Assessing the feral cattle population in the study area can also help the long-term conservation and management of lions since their population dynamics appear to play a crucial role in sustaining the Asiatic lion population.

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Author Contributions

Conceptualisation, methodology, formal analysis, data curation and writing – review and editing: M. Ram, L. Jhala, R. Chaudhary; investigation and analysis: L. Jhala, R. Chaudhary; resources: M. Ram, A. Sahu; writing – original draft preparation and visualisation: R. Chaudhary, M. Ram; supervision: M. Ram, A. Sahu, N. Srivastava. All authors have read and agreed to the published version of the manuscript.

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