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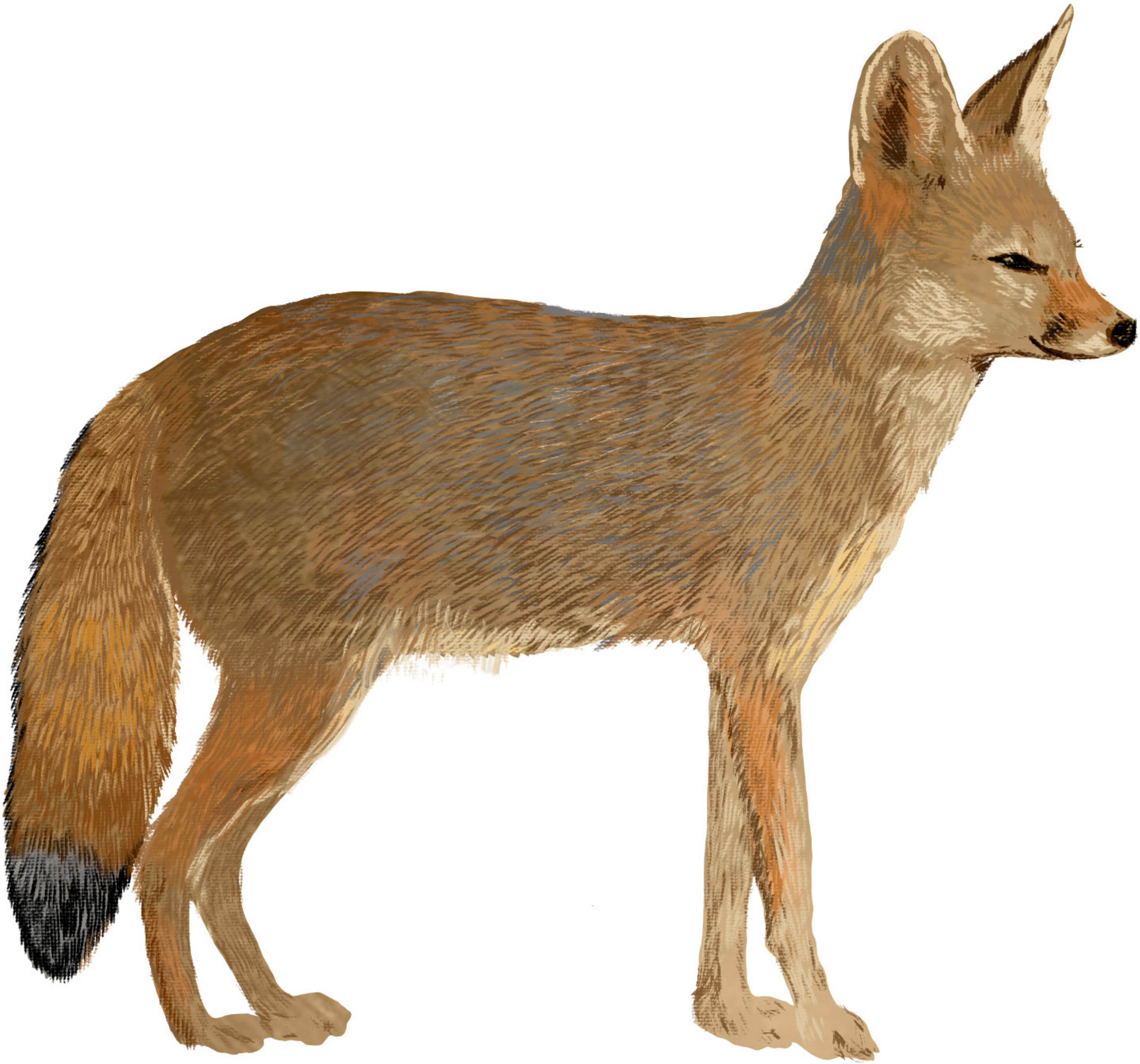

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ARTICLE

Feeding dynamics of sympatric large carnivores in an anthropogenic landscape of the Indian Terai

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Abstract: An important challenge for large carnivore conservation is negative human-wildlife interaction. Livestock depredation by carnivores is one important aspect of this negative interaction. Hence, it is critical to understand the extent of livestock depredation by large carnivores through their diet profiles and feeding habits for managing and strategizing conservation measures. We investigated the food habits and dietary patterns of two large sympatric carnivores, the Tiger *Panthera tigris* and the Leopard *Panthera pardus* based on scat samples collected in wildlife corridors outside protected areas (PAs) in the Indo-Nepal transboundary and Corbett landscape in Uttarakhand, India. The frequency of occurrence of prey items in the scat samples was used to estimate the relative prey biomass and number of preys consumed by the Tigers and Leopards using a generalised biomass model. Scat analysis revealed the presence of mainly wild prey species, encompassing 12 species in tiger scat and 14 species in Leopard scat. The results show that Tigers and Leopards primarily depend on medium-sized prey, with relative prey biomass consumption of 53% and 60%, respectively. Tigers preyed most frequently on Wild Boar *Sus scrofa*, followed by Spotted Deer *Axis axis*, and Leopards preyed mostly on Spotted Deer, followed by Wild Boar. The relative biomass of livestock species in Tiger and Leopard diets is 14.2% and 15.7%, respectively. Dietary overlap between Tiger and Leopard was high, with the Leopard exhibiting a broader dietary niche breadth than the Tiger. Augmenting wild prey population through habitat improvement and protection outside PAs can significantly limit human-large carnivore conflict by decreasing livestock contribution in their diet. Studies on dietary habits need to expand to wildlife corridors and outside PAs in human-dominated landscapes to understand the ecological dynamics of human-wildlife negative interaction for future conservation strategies.

Keywords: Dietary profile, human-wildlife interaction, leopard, tiger, wildlife corridor.

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Author contributions: All authors contributed to the study conception and design. VR and GV did sample collection and fieldwork. Material preparation and data analysis were performed by VR. RB and SAH contributed to the intellectual review and supervision of the study. This study was supervised by RB, SAH and PMD. PMD acquired the necessary permissions and provided field support from the Uttarakhand Forest Department. The project under which this study was conducted was supervised by PMD. The first draft of the manuscript was written by VR and reviewed by GV. All authors reviewed the final draft and commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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INTRODUCTION

Large carnivores are wide-ranging species inhabiting variable habitats and serving as flagship species for biodiversity conservation (Harihar et al. 2011). Although energy restrictions limit their population sizes in the wild, large predators significantly influence the organisation of communities through trophic cascades (Lamichhane et al. 2019). Predation is a phenomenon that connects trophic levels and is essential to many ecological and evolutionary processes (Fryxell et al. 2007). When sympatric species share a trophic level, niche differentiation and resource partitioning are evident (Schoener 1986). Differential use of food resources is an essential mode of resource partitioning in ecological communities (Karanth & Sunquist 2000) in addition to prey size (Gittleman 1985), activity patterns (Fedriani et al. 1999), space use patterns, and habitat use preference (Palomares et al. 1996; Shameer et al. 2021). Understanding the patterns of dietary niche overlap of sympatric carnivores is crucial for devising adequate conservation measures.

India harbours more than 75% of the world's wild Tiger population, with a population growth of 6.1% from 2006 to 2022 (Qureshi et al. 2023). The Tiger is distributed across India along with its co-predators Leopard and Dhole *Cuon alpinus* (Ramesh et al. 2012; Qureshi et al. 2023). These three large carnivores inhabit forests and coexist across various landscapes through spatio-temporal & dietary partitioning (Karanth & Sunquist 1995; Andheria et al. 2007; Ramesh et al. 2012; Selvan et al. 2013; Lamichhane et al. 2019; Mohan et al. 2021; Shameer et al. 2021). The distribution of the Dhole in the Indian Terai has declined extensively due to persecution in the past and is now restricted to a few protected areas (PAs) (Qureshi et al. 2023), including Nandhaur Wildlife Sanctuary, and adjoining wildlife corridors in the Terai of Uttarakhand (Ranjan & Dhakate 2021).

The dietary profile of animals can be studied easily with the most widely used non-invasive method of scat or faecal analysis (Ackerman et al. 1984; Karanth & Sunquist 1995; Klare et al. 2011). This method is very effective for large carnivores (Karanth & Sunquist 1995; Chakrabarti et al. 2016; Biswas et al. 2023). The dietary habits of the tiger and leopard have been studied extensively in India mainly in PAs (Andheria et al. 2007; Majumder 2011; Athreya et al. 2013; Basak et al. 2018; Biswas et al. 2023). Limited studies are available on the diet of the two species outside PAs in India, such as food habits and characteristics of livestock predation in human-dominated landscapes (Puri et al. 2020; Mohan et al. 2021; Dahya et al. 2023).

In tropical forests, the relative densities of various size classes of prey can vary naturally and due to human activity, affecting or influencing the community structures of large carnivores (Karanth & Sunquist 1995). The abundance and availability of prey species are critical to the sympatry of large carnivores (Andheria et al. 2007). Prey abundance does not necessarily affect prey selection (Bagchi et al. 2003; Lovari et al. 2015). The high density of wild prey limits or reduces livestock depredation and negative human-wildlife interactions (Basak et al. 2018; Upadhyaya et al. 2018; Puri et al. 2020). Sometimes, the human-large carnivore conflict scenarios are exaggerated due to political and social attributes of a specific region (Dickman 2010; Dickman et al. 2013; Nyhus 2016). Thus, the diet profile of large carnivores will also reveal the nature of conflict situations.

Our study focused on the feeding habits and dietary overlap of Tigers and Leopards in a multi-use landscape outside the PAs encompassing the critical wildlife corridors in the Terai-Bhabar region of northern India at the foothills of the Himalaya, a critical Tiger conservation landscape (Sanderson et al. 2006). We also explored the dependence of the large carnivores on livestock for food in areas outside PAs, where wild prey population is low and anthropogenic disturbances are high.

Study Area

Our study area is part of the Terai Arc Landscape, which lies in the Terai-Bhabar topography at the foothills of the Himalaya (Semwal 2005). The study area is located between Corbett Tiger Reserve (CTR) and the Indo-Nepal border in the eastern and southern parts of the state of Uttarakhand, bordering the Indian state of Uttar Pradesh. The study area is divided into two blocks (Image 1). Block 1 constitutes the Kosi corridor with adjoining areas of CTR, Ramnagar Forest Division (FD), and Almora FD of Uttarakhand. Block 2 encompasses the Kilpura-Khatima-Surai (KKS) and Boom-Brahmadev (BB) corridors with adjoining forest habitats of the Terai East FD, Haldwani FD, and Champawat FD of Uttarakhand. The Kosi corridor connects CTR with the Ramnagar FD and Pawalgarh Conservation Reserve along the Kosi River east of CTR in Uttarakhand (Johnsingh 2006; Anwar et al. 2014). The KKS corridor connects Nandhaur Wildlife Sanctuary (NWS) in Uttarakhand with Pilibhit Tiger Reserve (PTR) in Uttar Pradesh and the Indo-Nepal border in the Khatima forest range of the Terai East FD. The BB corridor connects NWS to the Kanchanpur

FD in Nepal, a transboundary landscape that expands to Shuklaphanta National Park in Nepal (Semwal 2005; Qureshi et al. 2014).

The study area lies in Tiger Habitat Block (THB) II and III (Johnsingh et al. 2004) and tiger conservation landscape (Sanderson et al. 2006; WWF & RESOLVE 2015). The large mammalian species in the region are Asiatic Elephant *Elephas maximus*, Tiger, Leopard, Sloth Bear *Melursus ursinus*, Sambar Deer *Rusa unicolor*, Spotted Deer *Axis axis*, Wild Boar *Sus scrofa*, and Northern Red Muntjac *Muntiacus vaginalis*. The study area falls in the 2B Himalaya – western Himalaya and 7A Gangetic Plain – upper Gangetic Plain biogeographic provinces of India (Rodgers et al. 2000).

Livestock grazing is common in the study area because it lies outside the PAs in a multi-use mosaic landscape where reserved forests are interspersed with human settlements and fragmented due to linear infrastructures (Johnsingh et al. 2004; Chanchani et al. 2014). Two important pastoralist community in the study area are 'Bakarwal' and 'Van Gujjars'. The nomadic community of 'Bakarwal' migrates from the high-elevation Himalaya to lower elevations of the Terai-Bhabar during November to January with their large herds of sheep and goats camping for several days and months in the forest areas of the Himalayan foothills (Dangwal 2024). The 'Van Gujjars' is a pastoralist community residing in the study area's forests with large herds of Water Buffalos *Bubalus bubalis* and Cattle *Bos taurus* (Sharma et al. 2012; Dangwal 2024).

MATERIALS AND METHODS

Scat Sample Collection

Scat samples of Tigers and Leopards were collected opportunistically in the study area during camera trapping and vegetation surveys on wildlife trails and

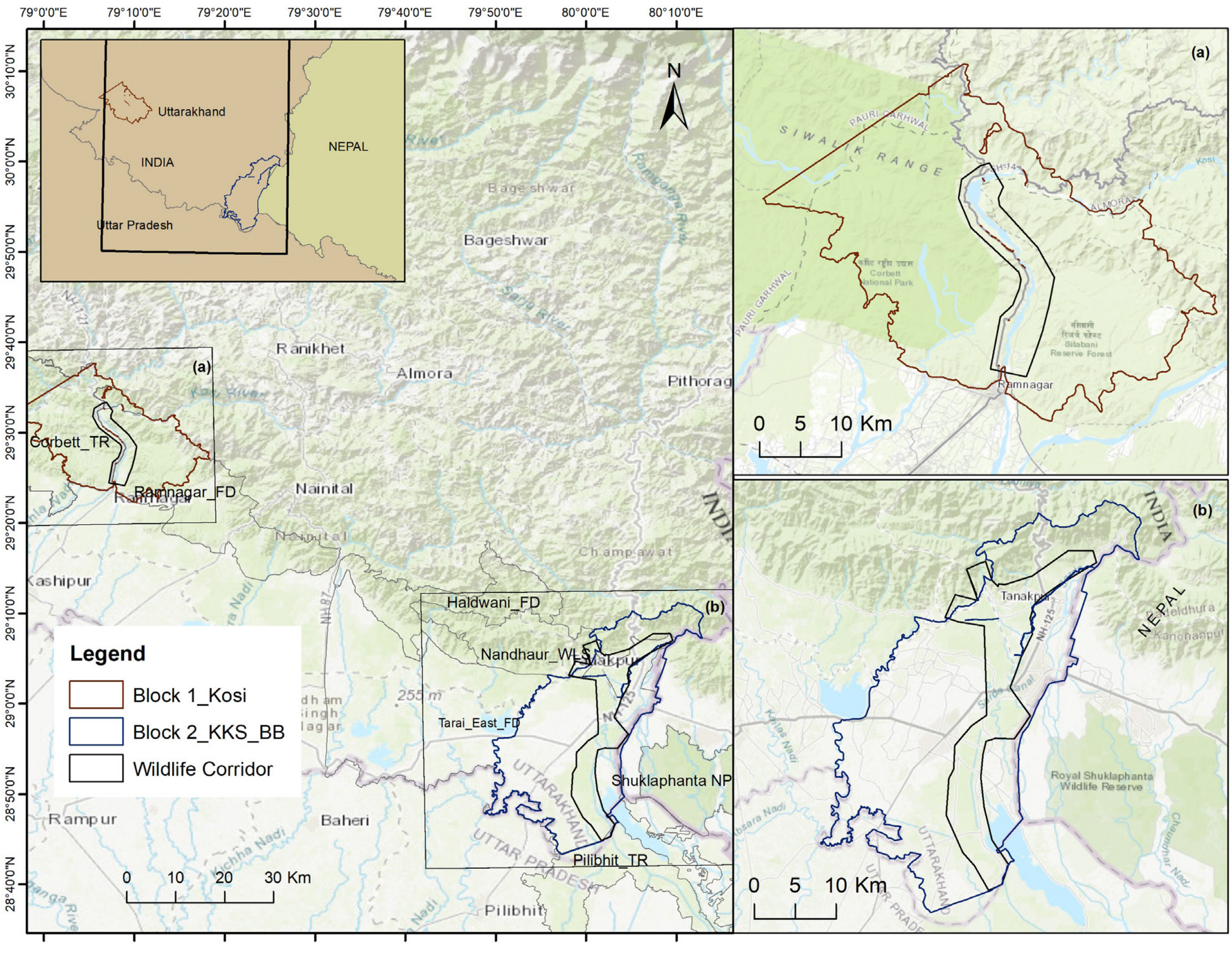

Image 1. Study area map with the two study blocks comprising of wildlife corridors: a—Block 1 with Kosi corridor connecting Corbett Tiger Reserve to Ramnagar forest division | b—Block 2 with Kilpura-Khatima-Surai (KKS) and Boom-Brahmadev (BB) corridor in Indo-Nepal transboundary landscape.

forest roads. We collected scat in the summer season from March–June and in winter season from October–February. Scat collection was not possible during the monsoon season as forest areas were not accessible.

Tigers, Leopards, and other carnivores deposit scat on forest roads and wildlife trails as part of the communication mechanism (Smith et al. 1989; Karanth & Sunquist 1995; Andheria et al. 2007). The samples were collected from October 2019 to December 2021, stored in plastic zip lock bags, and predator species were identified based on ancillary signs and methods described in earlier studies based on visual and indirect signs (Karanth & Sunquist 1995; Andheria et al. 2007; Harihar et al. 2011; Lovari et al. 2015; Basak et al. 2018). Tiger scat has been observed to be less coiled with a more considerable distance between two successive constrictions (Johnsingh 1983; Mohan et al. 2021). The scat samples which were not identified for species based on ancillary signs were not analysed. After collection, the remaining scat samples were removed from the track to avoid repetitive sampling. We avoided collecting scat in village areas or metalled roads in forest habitats to avoid misidentification of species due to lack of indirect signs of species.

Sample processing and prey species identification

A substantial part of each sample was put in nylon stockings, a knot was tied and then soaked in water for 24 hours (Klare et al. 2011). After soaking, it was washed in running water in a sieve of <1 mm to remove debris and dirt (Ramesh et al. 2009; Upadhyaya et al. 2018). Then it was sun-dried for 72 hours (Andheria et al. 2007) before separating 20 random hairs per sample for identification of prey based on its general appearance, colour, relative length, width, cortex pigmentation, and medullary structures under a microscope (Mukherjee et al. 1994; Bahuguna et al. 2010; Dharaiya & Soni 2012).

Data analysis

We did not perform an analysis of vegetation, which we found in some scat samples of both species. We calculated the frequency of occurrence of each prey item in the scat samples, denoted as A, and expressed as a per cent of scat samples in which a particular prey item was found (Andheria et al. 2007). We calculated the corrected frequency of occurrence based on the number of prey items per scat; if two items were present in one scat, it was calculated as 1/2; if three items were present, then 1/3, and so on (Karanth & Sunquist 1995). However, when the body size of prey varies significantly, the frequency of occurrence can be misleading (Floyd et al. 1978; Ackerman et al. 1984). The non-linear models developed for the leopard (Lumetsberger et al. 2017) and the Tiger (Fàbregas et al. 2017) show better accuracy than linear models in assessment of biomass and number of prey consumed. The linear model is biased for tropical large carnivores and significantly underestimates the consumption of medium-sized prey (Chakrabarti et al. 2016). We used the nonlinear asymptotic generalised model developed by Chakrabarti et al. (2016) for carnivores in India based on the following formula:

$$Y_c = 0.033–0.025exp^{-4.284\,(X|Z)}$$

Y_c is biomass consumed per collectable scat/predator weight, X is the live weight of prey, and Z is the average live weight of predator. Y_c is used as a correction factor for estimating the relative prey biomass consumed by multiplying Y_c by the observed frequency of occurrence (A). The generalised biomass model is better suited for our study, where we want to assess the contribution of livestock to the food habits of Tigers and Leopards since this model does not overestimate large prey (Chakrabarti et al. 2016; Upadhyaya et al. 2018).

Our calculations are based on values for the average body weight of prey (Table 1), Tiger (140 kg) and Leopard (65 kg) (Harihar et al. 2011; Ahmed & Khan 2022). The relative prey biomass (D) and relative numbers of prey consumed (E) were calculated as per the equation below (expressed in percentage) described by Andheria et al. (2007).

$$D = \frac{A * Y}{\Sigma(A * Y)} * 100$$

$$E = \frac{D/X}{\Sigma(D/X)} * 100$$

To assess the dietary overlap between the Tigers and Leopards, we used the Pianka index (Pianka 1973) based on the frequency of occurrence, which ranges from 0 for no overlap to 1 for complete overlap.

$$Pianka\ index = \frac{\Sigma P_{ij} * P_{ik}}{\sqrt{\Sigma(P_{ij}^2 * \Sigma P_{ik}^2)}}$$

P_{ij} is the percentage of prey items i of predator j; P_{ik} is the percentage of prey items i of predator k

D_c and E_c denote the relative prey biomass and relative number of preys consumed using the Y_c correction factor based on the generalised biomass model, respectively. The D_c and E_c of Tigers and Leopards were statistically compared using the Kruskal-Wallis test statistic to understand the difference in diet profiles of the two large sympatric carnivores. We used Kruskal-Wallis as it is a non-parametric test, which does not assume that underlying data has a normal distribution (Xia 2020). We categorised the prey size into three classes based on their body weight: (i) large (above 50

Table 1. Frequency of occurrence (A) of different prey items, percent occurrence of each prey species (Po), live weight of prey (X), the number of scats with each type of prey (No.), Relative biomass consumed (D_c) and Relative number of prey consumed (E_c).

Prey species	X (kg)	Tiger						Leopard					
		No.	A (%)	Po	Y_c	D_c (%)	E_c (%)	No.	A (%)	Po	Y_c	D_c (%)	E_c (%)
Sambar Deer	185	23	15.9	14.29	0.033	19.54	4.91	8	9.0	7.08	0.033	10.83	1.60
Nilgai	184	12	8.5	7.45	0.033	10.38	2.62	5	5.6	4.42	0.033	6.77	1.01
Spotted Deer	50	32	20.4	19.88	0.028	20.95	19.49	17	17.4	15.04	0.032	20.39	11.18
Northern Red Muntjac	25	18	11.4	11.18	0.021	9.03	16.79	17	15.2	15.04	0.028	15.61	17.12
Wild Boar	35	36	24.0	22.36	0.024	21.82	29.00	18	16.3	15.93	0.031	18.14	14.21
Indian Hog Deer	25	4	1.6	2.48	0.021	1.26	2.34	5	4.5	4.42	0.028	4.62	5.07
Porcupine	8	8	3.2	4.97	0.013	1.58	9.18	5	3.4	4.42	0.018	2.24	7.69
Langur	10	4	1.7	2.48	0.015	0.94	4.35	8	5.1	7.08	0.020	3.70	10.15
Indian Hare	4	2	0.7	1.24	0.011	0.29	3.38	7	3.9	6.19	0.014	1.98	13.57
Cattle	175	14	7.8	8.70	0.033	9.50	2.52	6	6.2	5.31	0.033	7.44	1.17
Water Buffalo	250	4	3.0	2.48	0.033	3.70	0.69	2	1.1	1.77	0.033	1.35	0.15
Domestic goat	10	4	1.9	2.48	0.015	1.01	4.72	8	7.9	7.08	0.020	5.76	15.80
Domestic sheep	25	0	0	0	0.021	0	0	1	1.1	0.88	0.028	1.16	1.27
Bird (Unknown)	0	0	0	0		0	0	6	3.4	5.31		0	0

kg; Sambar Deer, Nilgai *Boselaphus tragocamelus*, cattle *Bos taurus*, Water Buffalo *Bubalus bubalis*; (ii) medium (20–50 kg; Spotted Deer, Northern Red Muntjac, Wild Boar, Indian Hog Deer *Axis porcinus*, Domestic Sheep *Ovis aries*); and (iii) small (below 20 kg; domestic goat *Capra hircus*, porcupine, langur, Indian Hare *Lepus nigricollis*) to understand the food habits and diet profiles of the two sympatric large carnivores (Harihar et al. 2011). The diet niche breadth of Tigers and Leopards was estimated using the Levins index (Levins 1968), standardised to a scale of 0–1 (Hurlbert 1978) based on the frequency of occurrence of different prey species. The standardised scale considers the proportional abundance of each resource state (Hurlbert 1978). The statistical tests were performed in PAST 4.03 and other analysis related to scat were performed in Microsoft Excel application. The map was prepared in ArcGIS 10.7, and graphs were prepared in PAST 4.03 and Ms-Excel.

RESULTS

From October 2019 to December 2021, we collected and analysed 116 Tiger and 89 Leopard scat samples in our study area. Our sample size was adequate for dietary profile investigation of Tigers and Leopards as the graph reached asymptote position for the number of preys detected with increasing number of samples (Figure 1).

Scat samples of tigers contained 12 prey species, with 64.7% of all consisting of one prey species, 31.9% of two species and 3.4% of three species. Tigers preyed most frequently upon Wild Boar (24%), followed by Spotted Deer (20.4%) (Table 1), and cattle (7.8%) constituted the most frequent prey amongst all livestock species. Three livestock species were observed in tiger scat, i.e., cattle, Water Buffalo (3%), and domestic goat (1.9%). All 12 prey items were observed in scat collected during the winter season. Scat collected in the summer contained 10 species except goat and Water Buffalo, and a higher contribution of cattle remains (14%) than in the winter (8%).

Scat samples of leopards contained 14 prey species, with 73% of all samples consisting of one species and 27% of two species. Leopards preyed most frequently upon Spotted Deer (17.4%), followed by Wild Boar (16.3%). Four livestock species were observed in Leopard scat, namely domestic goat (7.9%), cattle (6.2%), Water Buffalo (1%), and domestic sheep (1%). Unidentified remains like feather and beaks of birds (3.4%) were also found in leopard scat samples (Table 1). All 14 prey items were observed in leopard scat collected during the winter season and 10 prey species in scat collected during the summer except langur, Cattle, Water Buffalo, and sheep. The contribution of Wild Boar remains was higher in summer (23%) than in winter (14%).

The Wild Boar had the highest prey biomass contribution to the Tiger's diet with 21.82%, while Spotted Deer had the highest prey biomass contribution

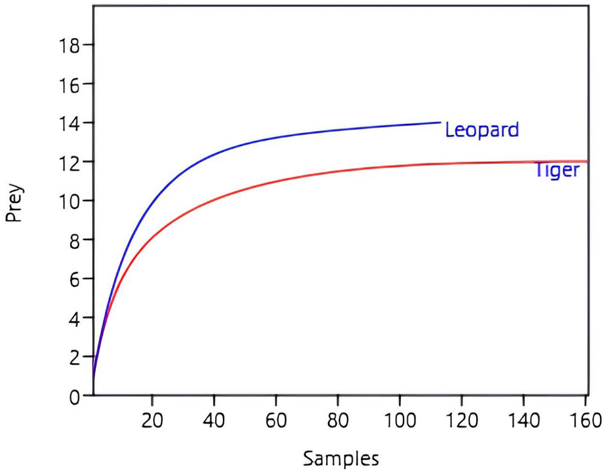

Figure 1. Graph showing number of preys in scat samples of Tiger and Leopard analysed for the study.

to the Leopard's diet with 20.39%. The cattle relative biomass contribution is the maximum among livestock species for both Tigers and Leopards. Overall, for all prey items, the diet composition showed no significant difference between relative prey biomass consumption (p = 0.53, χ^2 = 0.378) and relative number of preys consumed (p = 0.85, χ^2 = 0.032) by Tiger and Leopard.

Tiger and Leopard diets consist predominantly of medium-sized prey (Figure 2). Large prey constitutes 43.1%, medium prey ~53%, and small prey ~3.8% of biomass consumption in the Tiger diet profile. The leopard relative prey biomass consumption is highest for medium-sized prey (~60%), followed by large (26.4%) and small (13.7%) prey. The contribution of smaller prey is considerably higher in the diet of Leopards than of Tigers. Tiger relative prey biomass consumption primarily depends on wild prey (~85.8%), and around 14.2% on livestock. Relative prey biomass consumption of Leopards has a slightly higher share of livestock (~15.7%) than of Tigers (~14.2%). The relative number of medium-sized prey (67.6%) consumed by Tigers is substantially higher than that of large (10.8%) and small (21.6%) prey (Figure 2). However, the relative number of medium (48.9%) and small (47.2%) sized prey consumed by Leopards is equivalent but considerably higher than large prey (~3.9%) (Figure 2).

The relative prey biomass contribution of Wild Boar, Spotted Deer, and Sambar Deer is significant in the Tiger's diet. At the same time, Leopard food habits show a significant dependence on Spotted Deer, Wild Boar, and Northern Red Muntjak for biomass consumption (Figure 2). The dietary overlap between Tiger and Leopard in the study area is approximately 93% (Pianka Index = 0.928). The dietary niche breadth of Tiger and Leopard using the Levins index is 6.51 & 9.11, respectively, and the standardised diet niche breadth is 0.5 & 0.62 for Tiger and Leopard, respectively (Figure 3).

DISCUSSION

In the present conservation paradigm of large carnivores, it is essential to understand the feeding habits and prey-predator dynamics outside protected areas (Kshettry et al. 2018; Puri et al. 2020; Mohan et al. 2021; Dahya et al. 2023). Our study fills this gap in our understanding of the dietary habits of sympatric large carnivore species outside PAs in wildlife corridors of the Terai landscape of India. It is of paramount importance to understand the dependence on livestock, resource sharing, and diversity of food resources of sympatric large carnivores to address human-wildlife conflict in the landscape (Chakrabarti et al. 2016; Fàbregas et al. 2017; Lumetsberger et al. 2017; Puri et al. 2020; Dahya et al. 2023). Our results highlight that Tigers and Leopards prey largely on wild species, but they also indicate a substantial contribution of livestock to their diets, likely due to the lower abundance of wild species in wildlife corridors.

The higher dietary contribution of wild prey highlights that both Tiger and Leopard prefer wild prey over livestock. The lower share of livestock species in Tiger and Leopard diet even when the grazing is high can be attributed to the presence of a herder accompanying livestock herds, and the collection of a few scat samples from the inner areas of forest habitats with minimal disturbances. The contribution of livestock species is substantially lower in comparison to wild prey, still higher than inside PAs in the Terai landscape (Harihar et al. 2011; Basak et al. 2018; Upadhyaya et al. 2018). Studies in the mosaic landscape of PAs and non-PAs in the Terai Arc landscape also show a significant difference in livestock contribution in the diet of Tigers inside PAs and outside PAs (Harihar et al. 2011; Lamichhane et al. 2019; Biswas et al. 2023). Livestock depredation entails the loss of human property, and hence has a more pronounced effect on the conservation of large carnivores and human-wildlife negative interactions (Dickman et al. 2013; Nyhus 2016).

The number of stray cattle in forest habitats has increased in recent years due to government policies (Vivek Ranjan, pers. obs.; Governor of Himachal Pradesh 2014), which have an aggravated negative effect on large carnivore prey availability and feeding habits (Baker et al.

2008; Harihar et al. 2011; Pimenta et al. 2017). Moreover, the depredation of these stray livestock is not reported or recorded by the Forest Department. The maximum share of cattle in the diet of Tiger and Leopard amongst the livestock species can be attributed to its higher population than other livestock species and easier to hunt than Water Buffalo which is similar in other studies (Harihar et al. 2011; Lamichhane et al. 2019; Puri et al. 2020; Biswas et al. 2023). The Water Buffalo has also been observed in two Leopard scat samples from study block 2, which may be attributed to the Water Buffalo calf depredation or buffalo carcass. Carcass dumping was not observed in the Kosi corridor area; however, infrequent carcass dumping was observed in study block 2 areas. The presence of cattle and large livestock species in the forest habitats significantly affects the distribution of wild prey, especially large wild prey like Sambar Deer, which are more sensitive to (Gaynor et al. 2018; Upadhyaya et al. 2018; Habib et al. 2021). This also explains the higher dependence on medium-sized prey in the current study area.

The high dietary overlap of 93% between Tigers and Leopards in the current study area is consistent with findings in earlier studies from the Indian subcontinent (Wang & Macdonald 2009; Harihar et al. 2011; Mondal et al. 2012; Lamichhane et al. 2019). The high dietary overlap also indicates that these sympatric species do not base their coexistence on diet partitioning based on prey type, however, apparent partitioning may occur in prey selection based on body size, age class, and sex of the species (Ramesh et al. 2012; Lovari et al. 2015). The notions of optimal foraging theory preferring larger prey are invalid when the availability of prey is an important limiting factor other than ecological energetics, which supports hunting of prey with equivalent body size/weight and convenience of hunting, which optimises energy use (Gittleman 1985; Chakrabarti et al. 2016; Basak et al. 2018; Upadhyaya et al. 2018). The equivalence of relative number of medium and small prey consumed by leopards can be attributed to their agility and ability to climb trees easily for hunting smaller prey such as porcupines, Indian Hare, and langurs. The Tiger is a top predator, and its increasing population density affects the food habits of its co-predators inhabiting the same habitat by shifting their prey preference, selection of sex, age classes of prey, and hunting time (Andheria

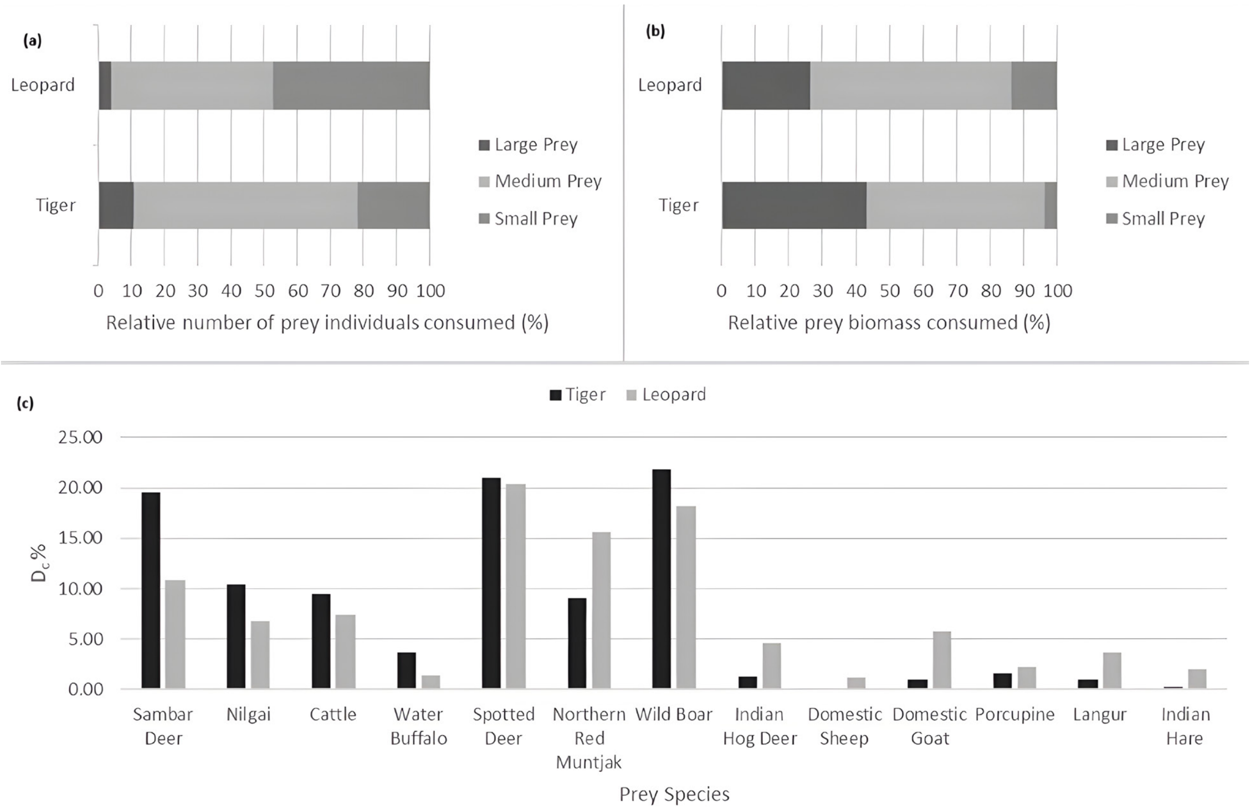

Figure 2. Diet profile of tiger and leopard in the study area: a—Relative prey biomass consumed (D_c) by the two sympatric large carnivores using a generalised biomass model for three categories of prey based on body size | b—Relative number of prey consumed (E_c) by two large carnivore species using a generalised biomass model | c—Contribution of different prey species in the prey biomass consumed by two sympatric carnivores. (Large prey >50 kg, Medium prey 20–50 kg, Small prey <20 kg)

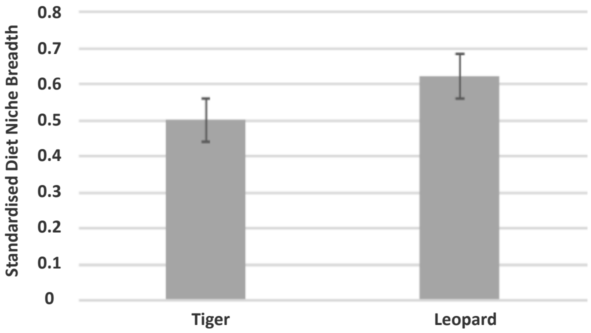

Figure 3. Standardised diet niche breadth of Tigers and Leopards in the study area with standard error using the Levins index.

et al. 2007; Harihar et al. 2011; Mondal et al. 2012; Shameer et al. 2021). It also explains the considerable difference in relative biomass and number of large prey consumption between Tiger (cumulative Dc = 43.1% and Ec = 10.8%) and leopard (cumulative Dc = 26.4% and Ec = 3.9%) in our study. This substantial difference in large prey relative consumption between Tiger and Leopard and the higher relative number of small prey in the Leopard diet indicates prey selection partitioning between the two sympatric species. The terrain of the habitat and prey behaviour also affect prey selection, causing spatiotemporal partitioning (Wang & Macdonald 2009).

The dietary specialisation of these two sympatric species is broad and suggests better adaptability to the existing environment and food availability. Both species exhibit a high dependence on medium body-size prey like Wild Boar and Spotted Deer, which could be attributed to their abundance in our study area. Similar trends and prey preferences have also been observed in other study areas of the Terai (Basak et al. 2018; Upadhyaya et al. 2018; Ahmed & Khan 2022). The broader dietary niche of Leopards observed in our study area indicates the generalist nature of prey selection and opportunistic feeding behaviour of Leopards (Puri et al. 2020; Mohan et al. 2021). Camera trap images obtained in the current study area have also shown evidence of poultry depredation by Leopards (Vivek Ranjan, unpub. data).

The absence of a wider variety of wild prey, high anthropogenic disturbance, and grazing pressure increase livestock depredation by large carnivores (Sankar et al. 2010; Basak et al. 2018). Our results show a higher livestock share in the Leopard diet with four livestock species compared to the Tiger diet with three species, which can be attributed to the varied habitat use patterns of these two sympatric predators. As the Tiger population density increases in the core forest habitats, the Leopard responds by spatially and temporally partitioning its habitat use, adapting to fringe habitats on the forest boundary, thereby increasing the chances of more frequent livestock depredation (Harihar et al. 2011; Bisht et al. 2019; Naha et al. 2020; Puri et al. 2022). Corbett Tiger Reserve (CTR), part of our study area, has the highest tiger population density among all the PAs in India (Bisht et al. 2019; Qureshi et al. 2023) and acts as a source population for the metapopulation of this landscape (Chanchani et al. 2014). The Tigers dispersing from the core habitats of CTR face a high risk of human-wildlife interactions outside PAs, mainly in the form of livestock depredation and human casualty in a few incidents (Bargali & Ahmed 2018; Bisht et al. 2019), as evident from compensation records of the Uttarakhand Forest Department (Uttarakhand Forest Department, unpub. data).

The seasonal migration of 'Bakarwal' disturbs the wild prey populations inhabiting those habitats and increases the probability of depredation by carnivores (Bisht et al. 2019; Qureshi et al. 2023), which is highlighted by the fact that all the scat samples of both the species with sheep hairs and all tiger scats with goat hairs were collected during winter. The large herds of Water Buffalo and cattle of 'Van Gujjars' negatively affects the wild prey population and disturbs the availability of pastures and foraging activity of wild prey species (Harihar et al. 2011). The livestock depredation of these pastoralist communities is also observed in the compensation records of the Uttarakhand Forest Department from the study area (Uttarakhand Forest Department, unpub. data).

Our study is based on a small sample size, but it highlights the importance of wild prey availability to contain conflict between people and large carnivores. Augmenting the wild prey population outside the PAs in wildlife corridors is vital to limit and reduce livestock depredation and improve habitat quality to accommodate wild prey populations in forest habitats. The wild prey population can be augmented by providing protection from hunting or poaching outside PAs. Additionally, improving habitat and heterogeneity in wildlife corridor areas and reducing anthropogenic disturbances are likely to provide a conducive environment for prey to naturally increase its population. The dietary profile of large carnivores of the study area provides information about the contribution of different prey species as food, which is crucial for understanding prey-predator dynamics in the landscape outside PAs. It will help develop a scientific management and mitigation plan for human-wildlife negative interaction and long-term conservation. More such studies with extensive sampling outside the PAs are needed to formulate long-term landscape conservation plans.

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