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RESEARCH

# Dietary patterns of three sympatric carnivores- insights from a resource-scarce landscape of nubra, Trans-Himalaya

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## Abstract
Diet is an important factor that provides valuable information on resource partitioning among carnivores and helps in understanding the dynamics of coexistence and competition between species. We investigated the food habits and dietary partitioning among three sympatric carnivores viz., snow leopard *Panthera uncia*, Tibetan wolf *Canis lupus chanco*, and red fox *Vulpes vulpes* through analysis of their scats in the Karakoram Wildlife Sanctuary (WS) in Nubra, Trans-Himalaya. Both morphological and DNA-based identification was used to establish species identity of the field-collected scats followed by micro-histological examination of prey hairs in 350 scats. Snow leopard diet was majorly contributed by wild ungulates (48.34%) including blue sheep *Pseudois nayaur*, ibex *Capra ibex siberica* and Ladakh urial *Ovis vignei vignei*, and livestock (42.81%) in terms of biomass contribution with frequent consumption of *Myricaria sp*, while the Tibetan wolf predominantly relied on livestock (67.2%) to fulfill its dietary requirement. The diet of red fox mostly included small mammals (56.78%) and livestock carrions (28.31%) along with significant consumption of plant matter. Wolves showed a wider (0.51) dietary niche breadth compared to snow leopards (0.47) and red foxes (0.30), and showed high dietary overlap (0.72) with snow leopards. Comparable niche breadth and dietary overlap between snow leopard and Tibetan wolf may be a result of limited wild prey or differential use of resources at spatial and temporal scales which requires further investigation. Notable contribution of livestock in the carnivore diet unfolds a serious concern that may lead to aggravated carnivore-human interactions and increased risk of disease transmission to carnivores. We therefore recommend a comprehensive study on multi-dimensional niche parameters of predator-prey interactions along with strengthening conservation efforts to improve wild prey populations and their habitats in the region.

**Keywords** Coexistence · Livestock · Niche breadth · Sympatric carnivores · Trans-Himalaya

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## Introduction

Sympatric species exhibit niche differentiation and resource partitioning to minimize competition (Schoener 1974; Vogel et al. 2019; Wang et al. 2024). Diet is a fundamental aspect of the species ecological niche and profoundly helps shape species communities, especially at higher trophic levels, such as carnivores. Feeding patterns among carnivores reflect essential biotic interactions and summarize the trophic relationships within a community. Mammalian carnivores, including both apex- and mesopredators play a pivotal role in ecosystem dynamics by regulating prey populations and shaping biotic community structures (Wallach et al. 2010; Dickman et al. 2019). In mountainous ecosystems with limited resources and variable environmental conditions, the equation becomes complex, as both abiotic and biotic factors equally affect resource use

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by carnivores (Bagchi et al. 2020; Hutchinson et al. 2022). Given the threats to which the mountainous ecosystems are exposed, including declining prey abundance, habitat loss and fragmentation, and increasing interaction with humans (Schaller et al. 1998; Courchamp et al. 2018), assessing feeding patterns among sympatric carnivores becomes crucial for understanding resource partitioning and the dynamics of coexistence or competition between species to ensure species conservation in the long term.

In the Trans-Himalayan region, carnivore dietary patterns are shaped by complex interactions among predator guilds, the abundance of wild prey, and the availability of domestic livestock (Mishra et al. 2003; Bagchi et al. 2004; Mishra et al. 2004; Suryawanshi et al. 2017; Patel et al. 2024). This high-altitude landscape, with low primary productivity, limited wild prey species diversity and abundance, imposes dietary restrictions on carnivores owing to fewer foraging opportunities, thus resulting in dependency on livestock (Namgail et al. 2007; Ahmed et al. 2018; Maheswari and Sathyakumar 2019; Bagchi et al. 2020; Shrotriya et al. 2022). For instance, the two large predators snow leopard and Tibetan wolf inhabiting the region compete for the same prey base (including livestock) (Mishra et al. 2003). This leads to a significant overlap in their diet (Jumabay-Uulu et al. 2014). Furthermore, resource sharing between sympatric species and overall community structure is influenced by the body size of carnivores (Monterroso et al. 2020), because large predators typically exert dominance over the best available resources compared with small predators (Linnell and Strand 2000). This creates an additional resource opportunity for mesocarnivores through carrion scavenging (Maheshwari et al. 2012). Similar to other parts of the Trans-Himalayas, Ladakh represents a typical cold desert characterized by a combination of Arctic and desert climates and poor diversity and abundance of wild prey species (Namgail 2009; Pfister 2004). The Tibetan wolf (*Canis lupus*) and snow leopard (*Panthera uncia*) serve as the major apex carnivores that occur in this landscape (Mishra et al. 1997; Watts et al. 2019), whereas the red fox (*Vulpes vulpes*), an opportunistic generalist shares the habitat of these apex predators as a subordinate predator (Reshamwala et al. 2018; Shrotriya et al. 2022).

To improve our understanding of how these sympatric carnivores partition the available food resources in the region, we conducted this study to investigate their feeding ecology in the Karakoram Wildlife Sanctuary in Nubra, Ladakh. We hypothesize that in this resource-limited Trans-Himalayan landscape of Nubra, the dietary overlap between snow leopards and Tibetan wolves will be high, resulting in insignificant dietary partitioning between the two species. Additionally, we assume that the red fox being a subordinate and opportunistic feeder will exhibit more dietary flexibility by consuming a wide range of food resources. With this background, we aimed to address three research objectives through this study viz., i) to examine the feeding habits of three sympatric predators in an area with a limited wild prey, (ii) to assess niche breadth and dietary overlap among these three predators, and (iii) to evaluate the relative importance of wild and domestic prey in their diets. This study aims to contribute to a broader understanding of carnivore feeding ecology and to inform appropriate strategies in the resource-scarce environments of Nubra Ladakh for better conservation and management of mammalian carnivores in the region.

## Materials and methods

### Study area

Nubra Valley (34°15–35°31′N and 76°55′–78°05′E) situated in the northernmost region of the Leh district within the Union Territory of Ladakh, falls within the Trans-Himalayan biogeographic zone (1 A) of India. The area is drained by the Shayok River with the Nubra River as its primary tributary. The Shayok River continues its course westward and eventually converges with the Indus River before flowing into Pakistan. The Nubra Valley is encompassed by the Ladakh mountain range in the south and the Karakoram Range in the north, with a significant part permanently underneath glaciers. The valley (Fig. 1), with an area of approximately 15,000 km$^2$, was designated as a protected area in 1987 as the Karakoram (Nubra Shayok) WS. The sanctuary spans elevations from 2,700 to 7,000 m above the mean sea level. The region has a cold arid climate, characterized by erratic and scanty precipitation, averaging less than 80 mm per annum. The area is covered with thickets of sea buckthorn shrubs and extensive plantations of willows and poplar trees. This region also harbors a diverse array of wild fauna, including elusive species such as the snow leopard, lynx (*Lynx lynx*), Tibetan wolf, and various mountain ungulates including ibex, blue sheep, and Ladakh urial. The Karakoram WS represents a human-dominated landscape majorly agro-pastoralist communities engaged in livestock rearing and agricultural activities.

### Trail sampling and scat analysis

We collected carnivore scat samples during trial sampling carried out for nearly two years from February 2021 to December 2022. The sampling involved repeated monitoring (2–6) of the marked trials ($n=14$) laid in the study area. Scat samples were also collected opportunistically during the reconnaissance and follow-up surveys across

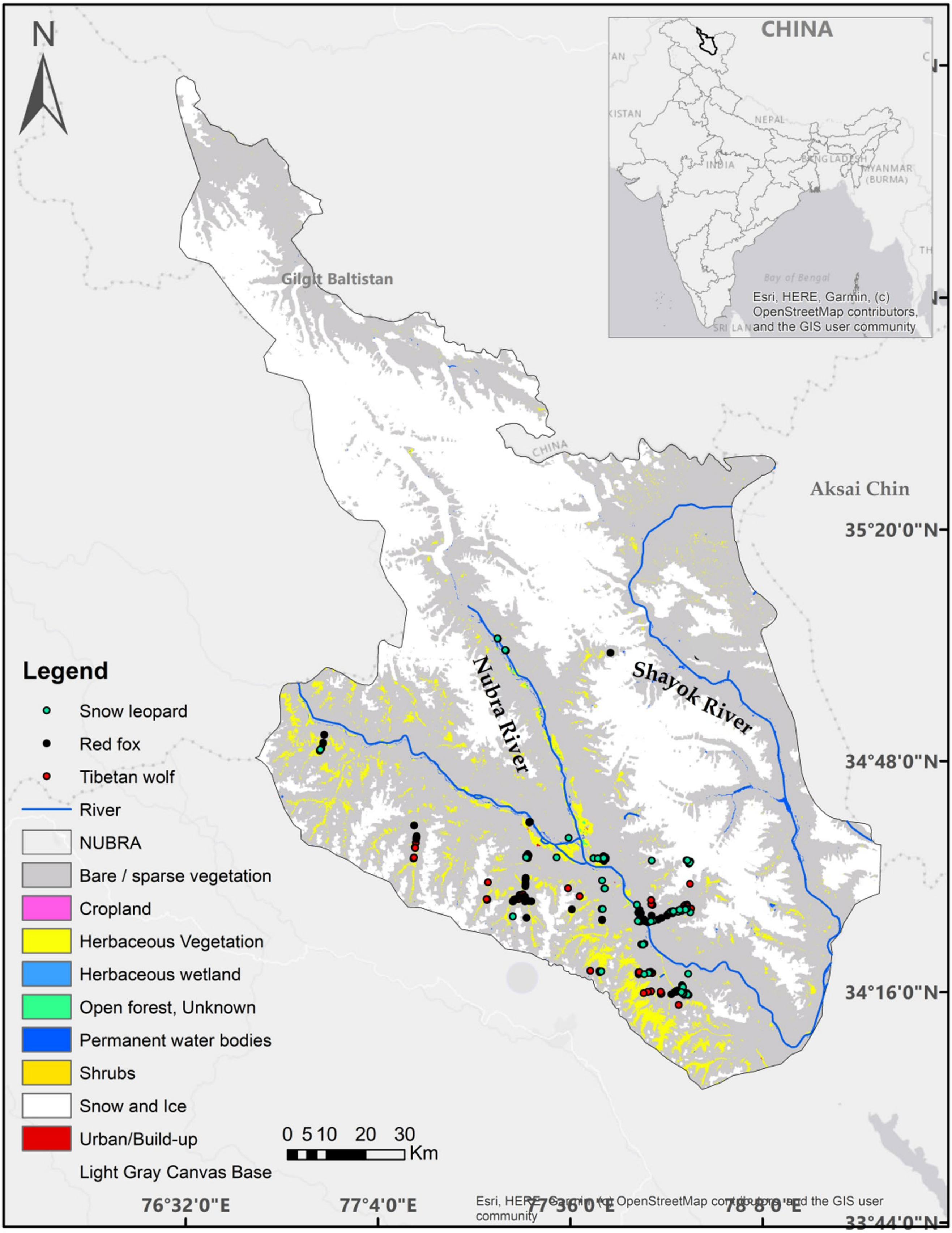


**Fig. 1** Land-use land cover map of the study area overlaid with sampling points and two important rivers; Shayok and Nubra River

the Nubra Valley. Scats were collected in paper bags and sterile collection vials and tagged with information, such as place, date, sample ID, GPS coordinates, and other habitat related parameters. Initially the collected scats (Fig. 2) were identified and assigned to different carnivore species (snow leopard, Tibetan wolf, red fox) based on their morphological characteristics including shape, size, substratum, and other associated signs such as tracks and scrapes (Devkota et al. 2013; Ahmed et al. 2018). Furthermore, we conducted DNA-based verification of ambiguous scat samples using a carnivore-specific primer targeting the 148-bp mitochondrial cytochrome b gene. We extracted DNA from scat samples using the QIAamp® Fast DNA Stool Mini Kit (QIAGEN, Hilden, Germany) complying with the manufacturer's protocol. We amplified the cytochrome b gene using the same primer pair and PCR assay conditions as those defined by Farrell et al. (2000). The following primers were used Forward5 -TATTCTTTATCTGCCTATACATRCACG-3´; Reverse5´ AAACTGCAGCCCCTCAGA ATGATATTTGTCCTCA-3 (Farrell et al. 2000). Based on morphological and DNA analyses, we identified a total of 350 scats, among which 94 belonged to snow leopard, 82 to Tibetan wolf and 174 to the red fox.

## Laboratory method

After assigning scats to carnivore species, we used the standard micro-histological examination of prey hairs in scats to assess carnivore diet (Vogel et al. 2019). The scats were washed with tap water through a fine sieve (mesh size = 0.5 mm) to remove the soil and other impurities. Washed scats with non-digestible food remains, such as hair, teeth, bones, feathers, seeds, and plant materials were oven dried in paper bags at 60 °C for 48 h. To select prey hairs for examination, we scattered the oven-dried scat samples on a lab enamel tray, and used the modified point-frame method (Ciucci et al. 2015) to randomly select 40–50 hairs closest to each intersection in the gridded tray (Fig. 3). Selected hair were transferred to glass petri dishes and kept in 90% ethanol overnight, followed by xylene treatment for 4–5 h. The hair samples were mounted on glass slides using glycerol mountant and examined for medullary patterns under the microscope (Bahuguna et al. 2010; Wegge et al. 2012). Photographs of the hair structure observed through the microscope were compared with previously prepared reference slides of hair specimens of potential prey species (both wild and domestic) (Fig. 4) in the area (Koppikar and Sabnis 1976; Reynolds and Aebischer 1991).

## Statistical analysis

Prior to data analysis, the adequacy of the sample size required to determine the food habits of each carnivore was assessed by randomizing the scat IDs for each carnivore. The cumulative number of species identified in each scat was then plotted against the total number of scats analyzed for each carnivore species. The minimum number of scats required to determine a carnivore's diet was therefore evaluated by marking the point where the plot reaches asymptote, with no further addition of new prey species to the diet.

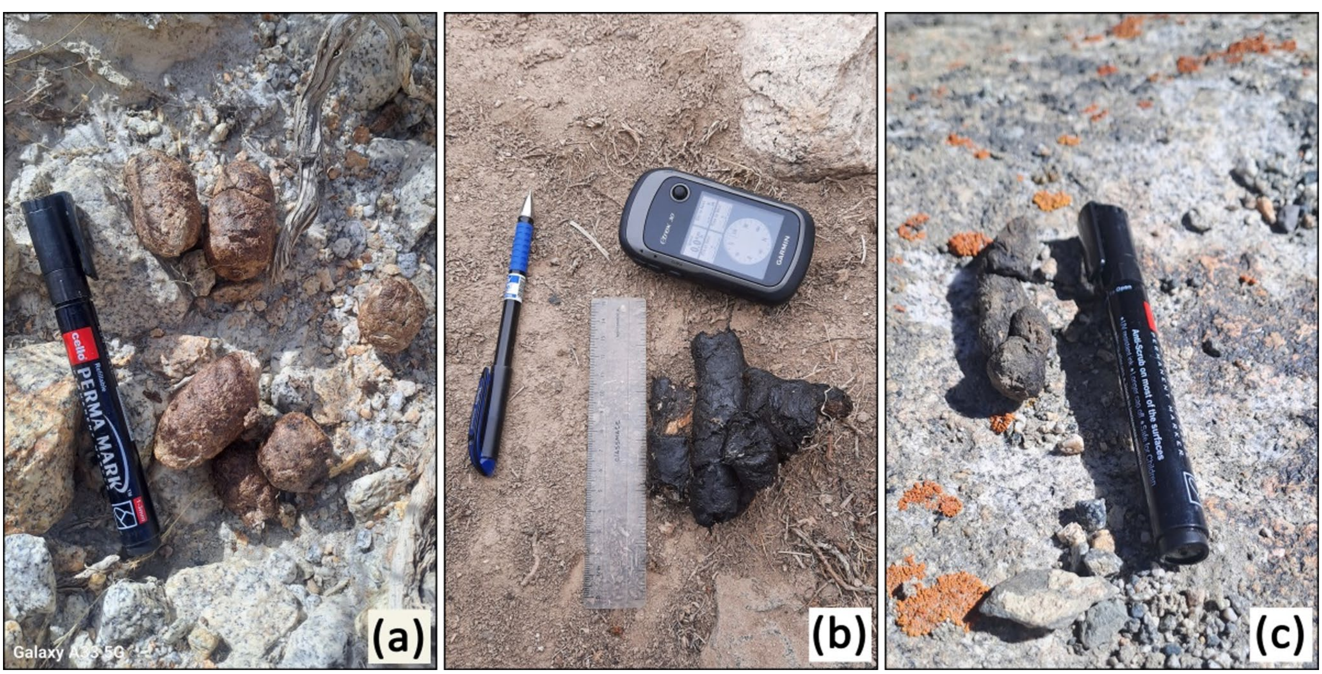


**Fig. 2** Scat samples of (**a**) snow leopard, (**b**) Tibetan wolf, and (**c**) red fox. Photo credits: Chamba Wangmo

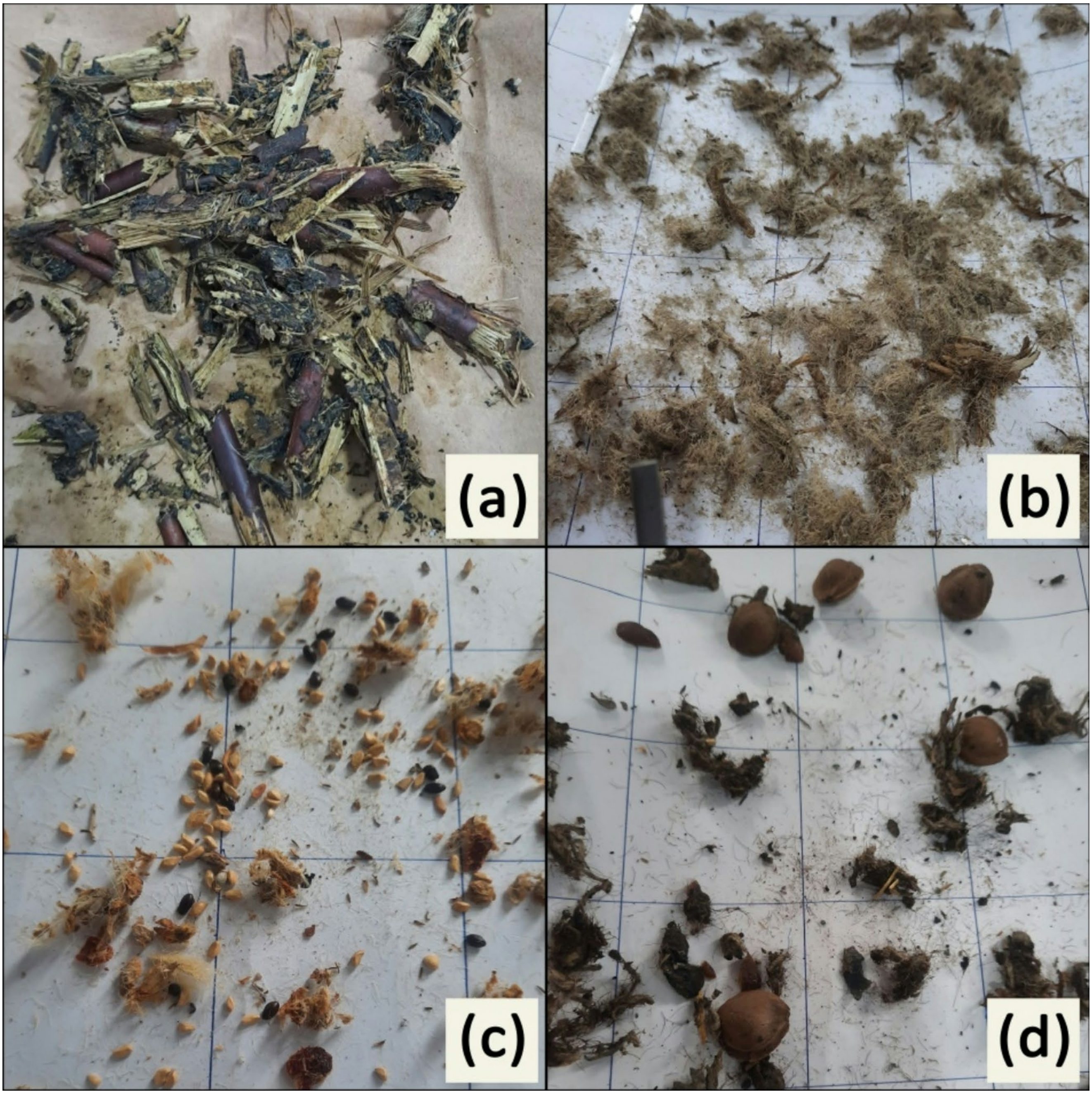


**Fig. 3** Pictures showing (**a** and **b**) Myricaria species in the snow leopard scat, (**c**) wild berry seeds and (**d**) apricot seeds in the red fox scat

To quantify the carnivore diet, we estimated both the percent frequency of occurrence, per cent relative occurrence, and relative biomass of prey species in scats (Vanak and Gompper 2009). Frequency of occurrence (FO) is the measure of the proportion of scats that contains a specific prey item, calculated by dividing number of scats containing prey item by number of total samples as

$$FO = \left(\frac{sx}{N}\right) * 100$$

Where sx is the number of scat samples containing each prey type and $N$ is the total number of scats.

The percent relative occurrence (RO) of prey items is more indicative of the relevance of each prey item in the diet.

$$RO = \left(\frac{px}{T}\right) * 100$$

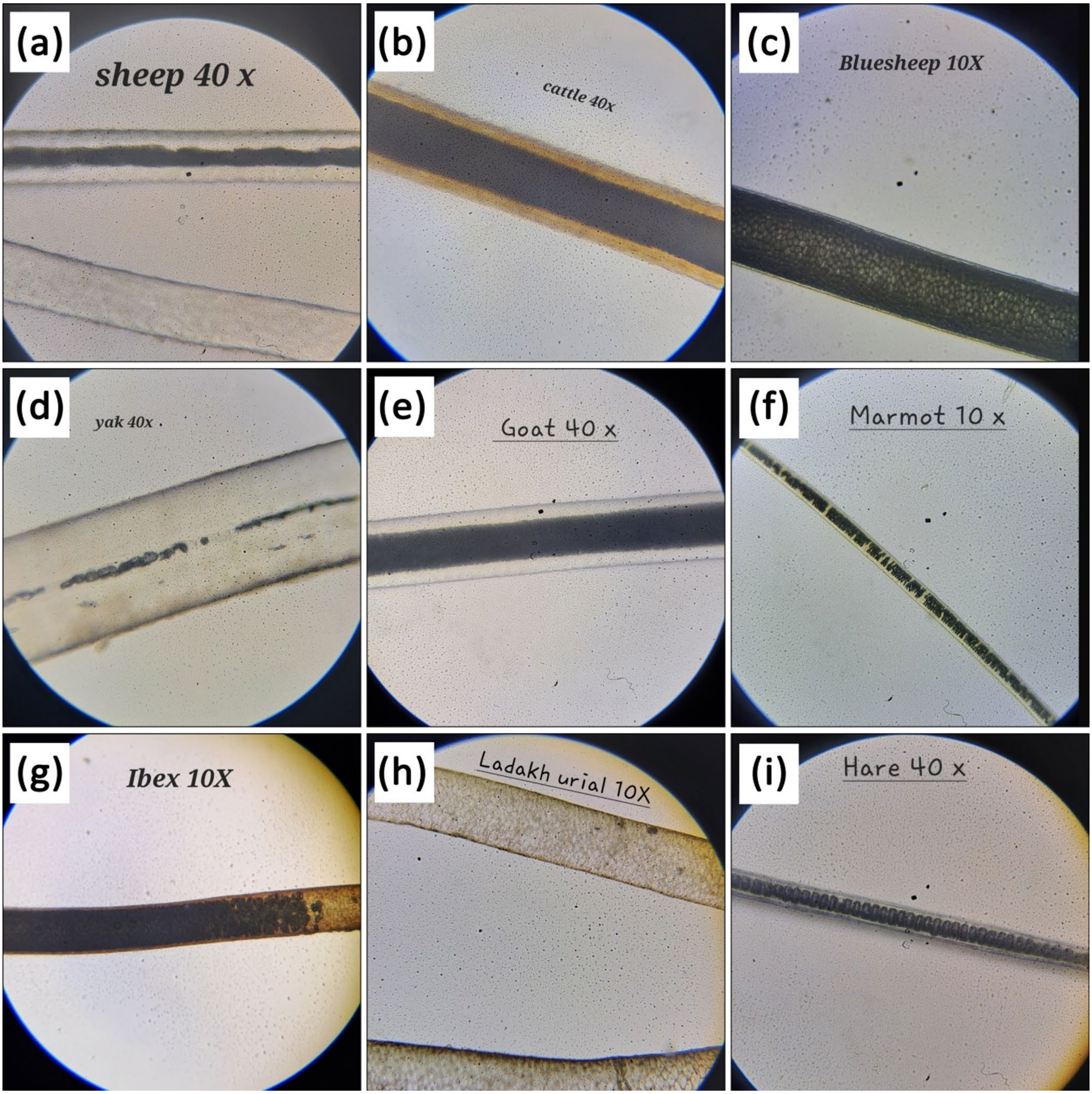


**Fig. 4** Medullary patterns of different prey species for reference (**a**) Sheep (**b**) Cattle (**c**) Blue sheep (**d**) Domestic yak (**e**) Goat (**f**) Marmot (**g**) Ibex (**h**) Ladakh urial (**i**) Hare

Where px is the number of prey items x, and T is the total number of occurrences of all prey items in all scat samples.

We calculated the total biomass consumption by snow leopards using the correction factor equation ($Y=1.980+0.035X$) developed by Ackerman et al. (1984) for Cougars. Similarly we used $Y=6.76+0.013X$ (Maurya et al. 2012)$d=50.439+0.008X$ (Weaver 1993), equations for assessing the biomass consumption by red fox and wolves, where Y is the biomass of prey consumed (kg) to produce a scat, and X is the average body weight of the prey species (kg). The average weight of the prey species was obtained from the published literature (Chundawat and Rawat 1994; Anwar et al. 2011). We assessed the relative biomass consumed by dividing the species-specific biomass by the total biomass consumed. Further, we estimated the dietary overlap among carnivore species using the Pianka's niche overlap index (Pianka 1974; Bahuguna et al. 2010), calculated using the following formula:

$$DO = \frac{\sum PijPik}{\sqrt{\sum P^2ij \sum P^2ik}}$$

Here, $P_{ij}$ is the proportion of prey category *i* in the diet of predator *j* and *ik* is the proportion of prey category *i* in the diet of predator *k*. The values ranged from 0 (no overlap) to 1 (complete overlap). We also assessed the diet specialization of carnivore species by estimating their trophic niche breadth using the Levin's Index (Levins 1968);

$$B = \frac{1}{(\sum pi^2)}$$

Where pi is the relative frequency of ingested food item by predator *p* and Levin's standardized index ($B_{sta}$) (Krebs 1999), $B_{sta}=(B-1)/(B_{max}-1)$, where B is Levin's index (Levins 1968), and $B_{max}$ is the total number of prey categories. The $B_{sta}$ values range between 0 (minimum breadth) and 1 (maximum breadth). All statistical analyses were performed using MS Excel and Programme R ver. 4.2.2 (R Core Team 2013).

## Results

### Adequacy of sample size

The diet stabilization curve plotted for the three sympatric carnivore species showed that our sample size was adequate to generate precise and reliable information on the feeding patterns of our study species (Fig. 5). The results revealed that a minimum of 45, 38, and 95 scat samples were required to determine the food habits of snow leopards, Tibetan wolves, and red foxes in our study area, respectively.

### Dietary spectrum of carnivores

Scat analysis revealed the occurrence of six wild prey species (blue sheep, Ladakh urial, ibex, hare (*Lepus spp.*), pika (*Ochotona spp.*) and Himalayan marmot in the diet of carnivores in the region. Among the domestic prey species, snow leopard consumed the maximum number ($n=7$) which includes goat, sheep, domestic yak, cattle, Dzo/Dzomo, donkey and horse, while wolf consumed six species excluding donkey, while red fox scavenged on all domestic prey species except the horse. Wild ungulates contributed significantly (Fig.6a) to the diet of snow leopards, both in terms of frequency of occurrence (58.49%), relative occurrence (35.24%), and relative biomass consumption (48.34%). Among livestock, snow leopards consumed seven species of domestic prey contributing 42.81%to its total biomass consumption (Table 1). Plant remains from the genus *Myricaria sp.* were also consumed frequently by the snow leopard occurring in 37.23% of the analyzed scats. Livestock contributed significantly (Fig.6b) to the diet of wolves, both in terms of the frequency of occurrence (80.45%), relative occurrence (50.8%), and relative biomass consumption (67.2%). Among the wild ungulates, wolves mostly preyed on blue sheep, ibex, and Ladakh urial contributing 23.93% to their total biomass consumption (Table 2). On the contrary, red foxes mainly fed on small mammals in terms of frequency of occurrence (58.3%), relative occurrence (36.84%), and relative biomass consumption (56.78%). Livestock carrions constituted 14.18% while plant material such as fruits and seeds contributed 32.11% to the red fox diet in terms of their relative occurrence (Fig. 6c). The majority of the seeds in red fox scats were of wild berries such as wild rose berry (*Rosa sp.*) and sea buckthorn (*Hippophae rhamnoides*), followed by apricot (*Prunus armeniaca*). We also detected the presence of bird feathers in the scats accounting to 1.45% relative occurrence in the red fox diet (Table 3).

### Dietary niche breadth and overlap

The Tibetan wolf (0.51) and snow leopard (0.47) showed a comparable niche breadth contrary to the narrower niche breadth shown by the red fox (0.30) (Fig. 7). Snow leopard and the Tibetan wolf also showed a significant dietary overlap (0.72), which was quite high compared to that with the red fox (with Tibetan wolf = 0.31) and (with snow leopard = 0.30), respectively.

## Discussion

### Carnivore dietary habits

Our study generates information on the understudied carnivore intraguild interactions in the resource-scarce landscape of the Nubra, Trans-Himalaya. Based on the analysis of their scats, we identified a broad dietary spectrum constituting of six wild prey species and several domestic species contributing significantly to the carnivore diet. Our results were consistent with studies conducted in similar landscapes where these carnivores were known to feed on a diversity of prey species including wild as well as domestic ungulates (Devkota et al. 2013; Ahmed et al. 2018; Shrestha et al. 2018).Carnivore predation on prey species is known to depends on several factors, including prey abundance, distribution, and weight, as well as the spatio-temporal interactions between prey and predators (Allen et al. 2021). The significant contribution of wild ungulates to the snow leopard diet validates its dependence on wild prey species

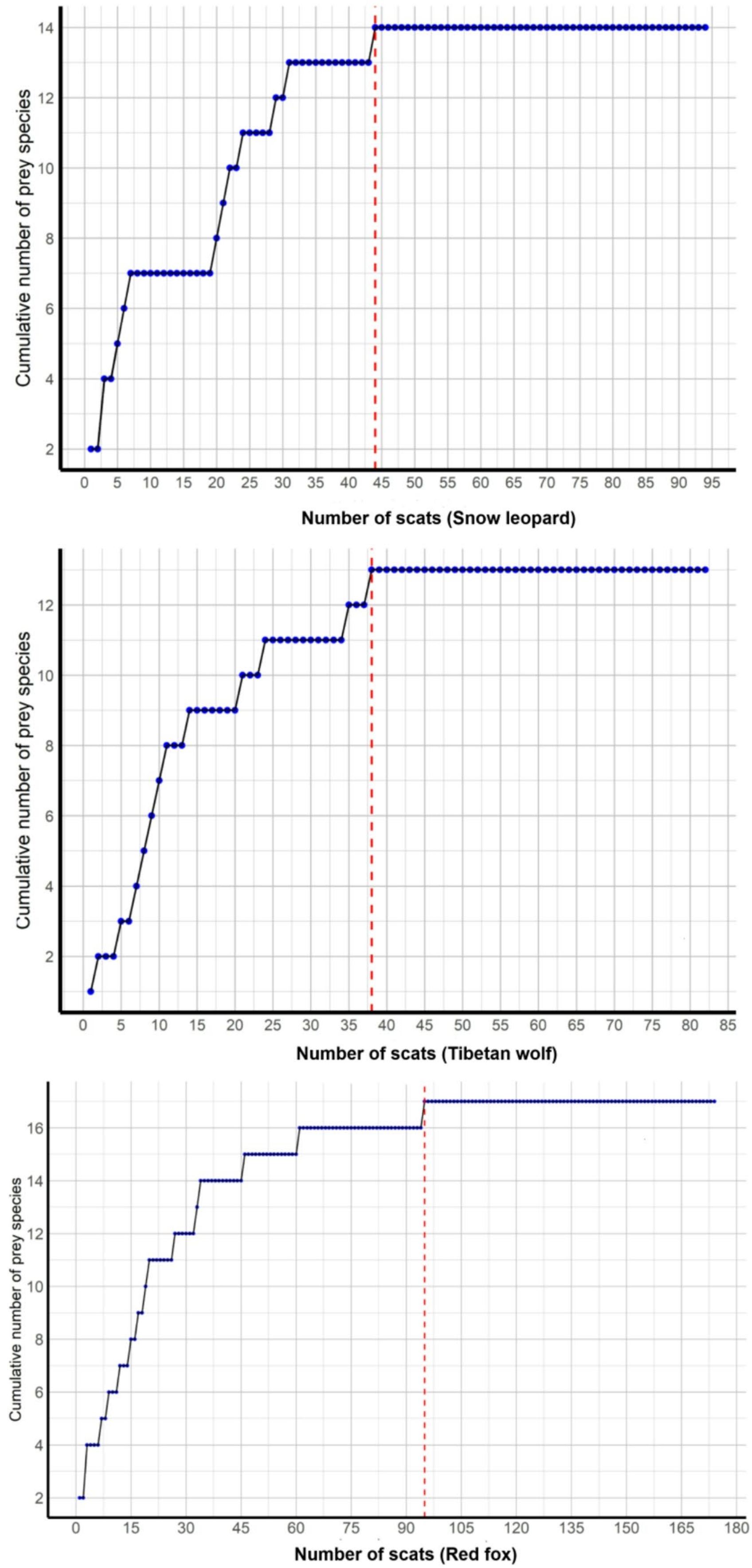


**Fig. 5** Diet stabilization curve and sample size adequacy for assessing food habits of carnivore species in Nubra valley s (**a**) Snow leopard (**b**) Tibetan wolf and (**c**) Red fox

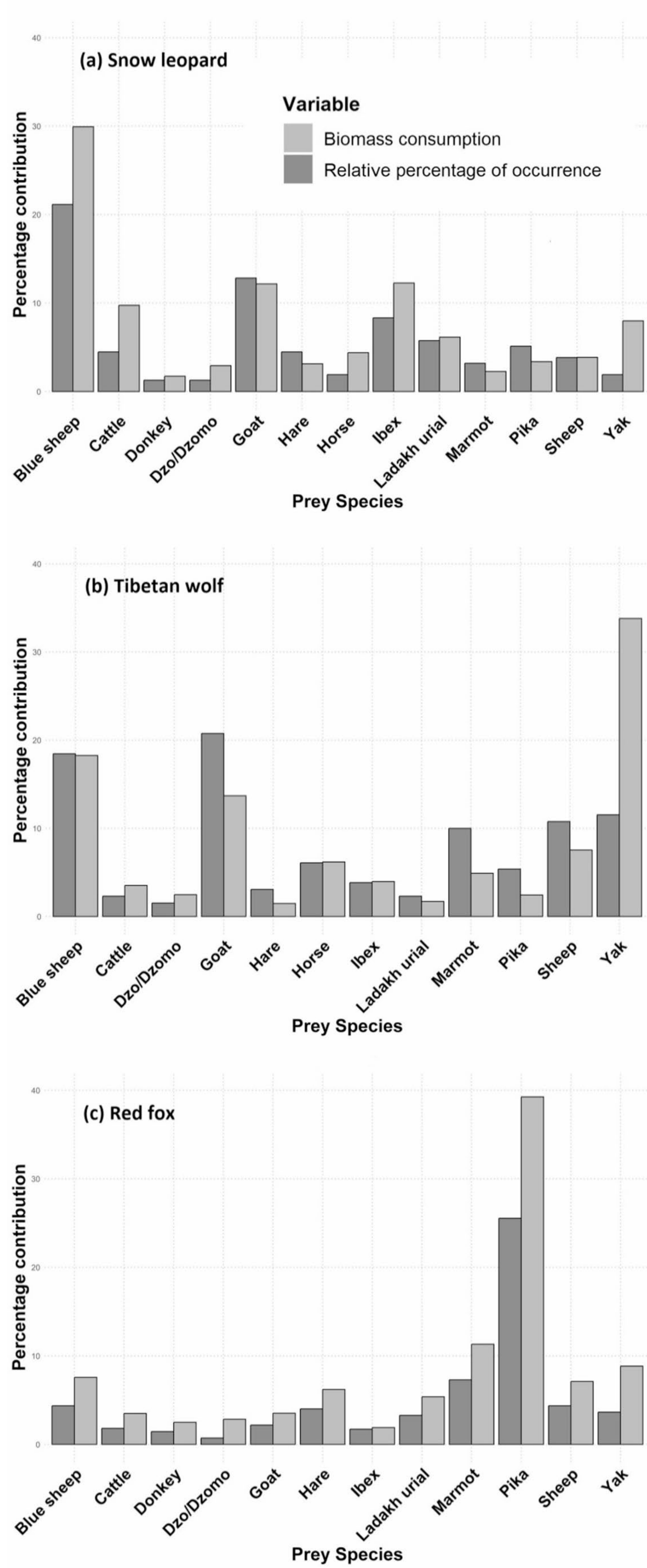


**Fig. 6** Contribution of different prey categories in the diet of snow leopard (**a**) wolf (**b**) and red fox (**c**) in the Nubra valley, Ladakh

**Table 1** Dietary composition of snow Leopard in Trans-Himalaya, Nubra valley, Ladakh

| Prey Species | Frequency of occurrence | Percent of occurrence | Assumed Weight (X) | Biomass per scat (Y) | Nos. in scats (C) | Biomass consumed (D) | Percentage consumption (E) |
|---|---|---|---|---|---|---|---|
| Blue sheep | 35.1 | 21.15 | 65 | 4.25 | 33 | 140.41 | 29.93 |
| Ladakh urial | 9.57 | 5.76 | 35 | 3.2 | 9 | 28.84 | 6.145 |
| Ibex | 13.82 | 8.33 | 70 | 4.43 | 13 | 57.59 | 12.27 |
| Goat | 21.27 | 12.82 | 25 | 2.85 | 20 | 57.1 | 12.17 |
| Sheep | 6.38 | 3.84 | 30 | 3.03 | 6 | 18.18 | 3.87 |
| Dzo/Dzomo | 2.127 | 1.28 | 140 | 6.88 | 2 | 13.76 | 2.93 |
| Donkey | 3.191 | 1.28 | 60 | 4.08 | 2 | 8.16 | 1.73 |
| Horse | 2.12 | 1.28 | 140 | 6.88 | 3 | 20.64 | 4.39 |
| Cattle | 7.44 | 4.48 | 130 | 6.53 | 7 | 45.71 | 9.74 |
| Domestic yak | 3.19 | 1.92 | 300 | 12.48 | 3 | 37.44 | 7.98 |
| Himalayan marmot | 5.31 | 3.2 | 4.5 | 2.13 | 5 | 10.68 | 2.27 |
| Hare | 7.44 | 4.48 | 3.5 | 2.1 | 7 | 14.71 | 3.13 |
| Pika | 8.51 | 5.12 | 0.2 | 1.98 | 8 | 15.89 | 3.38 |
| Plants and vegetation | 37.23 | 22.43 | - | - | 35 | - | - |
| Unidentified remains | 3.19 | 1.92 | - | - | 3 | - | - |

**Table 2** Dietary composition of Tibetan Wolf in the Trans-Himalaya, Nubra valley, Ladakh

| Prey Species | Frequency of occurrence | Percent of occurrence | Assumed Weight (X) | Biomass per scat (B) | Nos. in scats (C) | Biomass consumed (D) | Percentage consumption (E) |
|---|---|---|---|---|---|---|---|
| Blue sheep | 29.26 | 18.46 | 65 | 0.95 | 24 | 23.01 | 18.26 |
| Ladakh urial | 3.65 | 2.3 | 35 | 0.71 | 3 | 2.15 | 1.71 |
| Ibex | 6.09 | 3.84 | 70 | 0.99 | 5 | 4.99 | 3.96 |
| Goat | 32.92 | 20.76 | 25 | 0.639 | 27 | 17.25 | 13.69 |
| Sheep | 17.07 | 10.76 | 30 | 0.97 | 14 | 9.5 | 7.54 |
| Dzo/Dzomo | 2.43 | 1.53 | 140 | 1.55 | 2 | 3.11 | 2.47 |
| Horse | 6.09 | 3.84 | 140 | 1.55 | 5 | 7.79 | 6.18 |
| Cattle | 3.65 | 2.3 | 130 | 1.47 | 3 | 4.43 | 3.52 |
| Domestic yak | 18.29 | 11.53 | 300 | 2.83 | 15 | 42.58 | 33.8 |
| Himalayan marmot | 15.85 | 10 | 4.5 | 0.47 | 13 | 6.175 | 4.9 |
| Hare | 4.87 | 3.07 | 3.5 | 0.46 | 4 | 1.86 | 1.48 |
| Pika | 8.53 | 5.38 | 0.2 | 0.44 | 7 | 3.08 | 2.44 |
| Plants and Vegetation | 3.65 | 2.3 | - | - | 3 | - | - |
| Unidentified remains | 3.65 | 2.3 | - | - | 3 | - | - |
| Birds | 2.43 | 1.53 | - | - | 2 | - | - |

particularly blue sheep and ibex as depicted in other studies as well (Namgail 2009; Suryawanshi et al. 2017; Shrotriya et al. 2022). Despite being a specialist predator with strong preference for steep terrain and medium-sized wild herbivores (Lovari and Mishra 2016; Sharma et al. 2015), the contribution of livestock to the snow leopard diet indicates its adaptation and dietary plasticity to overcome low wild prey densities by switching to easily accessible abundant livestock (Wang et al. 2014).

Similarly, the Tibetan wolf also exhibits greater biological flexibility in the use of local food resources (Newsome et al. 2016) which is depicted by significant contribution of livestock primarily domestic yak, goat, sheep and horses in its diet. The pack hunting strategy of wolves and the least guarding of the domestic yak and horses also encourage livestock depredation by wolves (Wang et al. 2014; Ahmed et al. 2018). This interaction is further facilitated by wolves' preference for high-altitude open pastures during summers (Fox and Chundawat 1995) and their movement to lower elevations during colder seasons, a strategy that coincides with the movement patterns of livestock herders in this landscape. Although, we did not assess the seasonal variation in dietary patterns of wolves due to inadequate sample size with respect to different seasons, the presence of livestock in the diet shows strong association with the year-round availability of livestock across the wide altitudinal range. Our results

**Table 3** Dietary composition of red Fox in Trans-Himalaya, Nubra valley, Ladakh

| Prey Species | Frequency of occurrence | Percent of occurrence | Relative Assumed Weight (X) | Biomass per scat (B) | Nos. in scats (C) | Biomass consumed (D) | Relative biomass Consumption (E) |
|---|---|---|---|---|---|---|---|
| Blue sheep | 6.89 | 4.37 | 65 | 7.6 | 12 | 91.26 | 7.57 |
| Ladakh urial | 5.17 | 3.28 | 35 | 7.21 | 9 | 64.93 | 5.38 |
| Ibex | 1.72 | 1.09 | 70 | 7.67 | 3 | 23.01 | 1.9 |
| Goat | 3.44 | 2.18 | 25 | 7.08 | 6 | 42.51 | 3.526 |
| Sheep | 6.89 | 4.37 | 30 | 7.15 | 12 | 85.8 | 7.11 |
| Dzo/Dzomo | 1.149 | 0.72 | 140 | 8.58 | 4 | 34.32 | 2.84 |
| Donkey | 2.29 | 1.45 | 60 | 7.54 | 4 | 30.16 | 2.5 |
| Cattle | 2.87 | 1.82 | 130 | 8.45 | 5 | 42.25 | 3.5 |
| Domestic yak | 5.74 | 3.64 | 300 | 10.66 | 10 | 106.6 | 8.843 |
| Himalayan marmot | 11.49 | 7.29 | 4.5 | 6.81 | 20 | 136.37 | 11.31 |
| Hare | 6.32 | 4.01 | 3.5 | 6.8 | 11 | 74.86 | 6.21 |
| Pika | 40.22 | 25.54 | 0.2 | 6.76 | 70 | 473.38 | 39.26 |
| Birds | 2.29 | 1.45 | - | - | 4 | - | - |
| Fruit and Seed | 50.57 | 32.11 | - | - | 88 | - | - |
| Plant and vegetation | 8.04 | 5.1 | - | - | 14 | - | - |
| Insects | 2.29 | 1.45 | - | - | 4 | - | - |

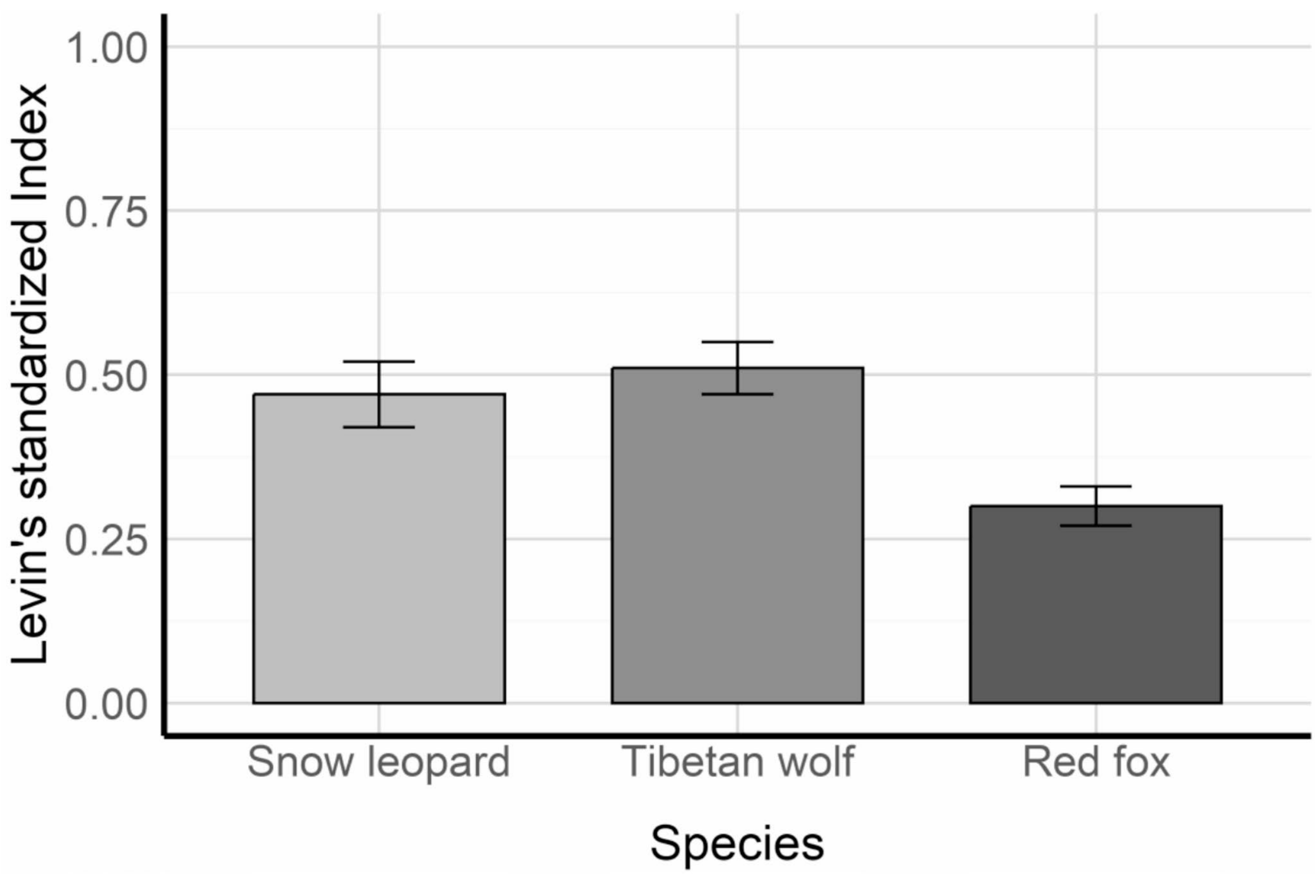


**Fig. 7** Levin's standardized index for dietary niche breadth of three species: Snow leopard, Tibetan wolf, and Red fox

corroborate with the findings of previous studies conducted in Ladakh (Ahmed et al. 2018; Maheshwari and Sathyakumar 2019; Shrotriya et al. 2022) and across the mountainous areas of Asia (Wegge et al. 2012; Jumabay-Uulu et al. 2014; Bocci et al. 2017; Chetri et al. 2017) which also report livestock as a major component of the wolves' diet. Moreover, livestock depredation by wolves has emerged as a major concern in the region, depicted though the presence of snare traps laid specifically for wolves by the local herders.

In resource-scarce areas with the lowest availability of wild prey species, snow leopards and wolves also consume small mammals to fulfil their dietary requirements (Chundawat and Rawat 1994; Shrotriya et al. 2022). A similar pattern was observed in the present study as we found alternative small prey species such as marmots, pika, and hares in both snow leopard and wolf diet. However, higher contribution of wild ungulates in the snow leopard diet compared to wolves seems evident due to snow leopards preference for the ibex and blue sheep as its primary prey since both use steep terrain and broken cliffs (McCarthy 2003), contrary to wolves that hardly move into the steep terrain (Jumabay-Uulu et al. 2014). Further, we also found the presence of plant material in the diet of both snow leopards and wolves; however its frequency was higher in the former. Frequent consumption of the genus *Myricaria sp.* by snow leopard and occurrence of grasses in wolf scats has also been reported in other studies (Chundawat and Rawat 1994; Wang et al. 2014; Bocci et al. 2017; Chetri et al. 2017). The likely reason suggested is the presence of fibres in such plant species, which aids in digestion and cleaning of the carnivores' digestive tract (Wang et al. 2014).

Although, the red fox scats revealed the occurrence of a wide range of prey items including small mammals, carrions, insects' remains and plant materials such as fruits and seeds, small mammals (marmot, pika, and hare) formed a significant portion of its diet. The contribution of livestock and wild ungulates could be attributed to its scavenging habits, as foxes feed on carcasses left by large-bodied predators or those that died naturally (Ghoshal et al. 2016; Ahmed et al. 2018). Among fruits and seeds, the red fox mostly consumed wild berries such as sea buckthorn and wild rose, demonstrating its omnivorous/frugivorous habit which goes in unison with the studies conducted on red fox across the Trans-Himalayas (Ghoshal et al. 2016; Reshamwala et al. 2018; Shrotriya et al. 2022). The frequent occurrence of sea buckthorn in the fox diet could be due to its high abundance and distribution in the Nubra Valley.

## Dietary partitioning among carnivores

Body size of carnivores has a strong influence on their prey selection, resource partitioning, and towards shaping the carnivore community in an ecosystem (Monterroso et al. 2020). As hypothesized we found a high dietary niche overlap between snow leopard and the Tibetan wolf due to the consumption of both domestic and wild prey by the two carnivore species. Our findings on the dietary overlap are similar to the findings from Sarychat-Ertash, Kyrgyzstan (up to 90%), and Pamir mountains (Pianka index 0.87 Jumabay-Uulu et al. 2014; Wang et al. 2014). In terrestrial ecosystems, the diversity and abundance of primary prey species shape the dietary partitioning among carnivorous guilds (Owen-Smith and Mills 2008). Ladakh- a cold and arid mountain ecosystem with generally less diversity and abundance of wild ungulates (Namgail 2009), thus facilitates weak dietary partitioning among sympatric carnivores compared to prey-rich areas. In circumstances where dietary partitioning is weak, predator guild coexistence may be expected to rely on other aspects of the niche scale including spatial and temporal partitioning, to avoid direct confrontations and reduce foraging competition (Schoener 1974; Justa and Lyngdoh 2023).

Although both the wolf (0.51) and snow leopard (0.47) depicted comparable trophic niche breadths, they exhibit variations in the consumption pattern of specific prey types. For instance snow leopard consumed blue sheep and ibex at higher frequencies than wolves. The differential spatial use of snow leopard and wolves likely explains their varying prey consumption, as each species frequently consumes prey associated with its preferred habitat (Jumabay-Uulu et al. 2014; Sharma et al. 2015; Chetri et al. 2017).

In contrast, red fox showed less overlap with both snow leopards (0.30) and wolves (0.33), indicating reliance on specific prey species. Although red fox fed on diverse food items, their weak dietary overlap with the two large sympatric carnivores and narrower tropic niche breadth could be explained by their omnivorous behaviour and intensive feeding on small mammals compared to other two predators. This niche differentiation supports the coexistence of carnivores in ecosystems, where differences in body size help partition resources and reduce direct competition. In an ecosystem, the coexistence of carnivores is known to be facilitated by differences in body size of predators, as it influences the prey selection by carnivores; large predators tend to hunt larger prey, while the mesopredators feed on small-sized prey (Monterroso et al. 2020). Such segregation was quite evident between large predators and the small mesopredator in our study. This was evident through significant consumption of large–medium size prey species by snow leopard and wolf, and reliance of red fox on small mammals. Furthermore, lower contribution of large-medium sized prey in the red fox diet indicates competitive interactions among carnivores where apex predators are likely to show more aggression towards subordinate predators on carrion sites due to limited resources (Ritchie and Johnson 2009).

## Conclusion

Our study highlights the feeding patterns and dietary partitioning among three sympatric carnivores in the Karakoram Wildlife Sanctuary, Nubra. Through field surveys and analysis of carnivore scats we identified significant dietary contributions by wild and domestic prey species in their diet highlighting a complex interplay between carnivores, prey species, and their environment. Our findings indicate that the two large-bodied predators, i.e. snow leopard and Tibetan wolf show a considerable dietary overlap probably due to limited resources in terms of availability and access to wild prey in the region as observed in similar landscapes (Jumabay-Uulu et al. 2014; Bocci et al. 2017; Chetri et al. 2017). However, red fox, a smaller-sized mesopredator exhibits limited dietary overlap with apex predators by shifting its diet to small mammals and plant material such as fruits and seeds (Shrotriya et al. 2022). Moreover, Tibetan wolf exhibited remarkable dietary flexibility with livestock contributing a significant portion of its diet, likely influenced by the year-round availability of livestock overlapping with the wolves' affinity for rangelands and pasturelands (Jumabay-Uulu et al. 2014). Despite being a specialist predator and driven by the availability of wild prey, the observed contribution of livestock to the snow leopard diet is likely due to its easy availability in the area compared to the sparsely distributed less abundant wild prey (Suryawanshi et al. 2017; Shrotriya et al. 2022). Our findings provide valuable insight towards understanding the predator-prey interaction in the Trans-Himalayan arid ecosystem of Nubra, thereby unfolding important concern over notable contribution of livestock in carnivore diet. Such dietary patterns may have serious implications thus driving carnivore-human interactions in the regions. Since, our data did not allow seasonal evaluation of carnivore dietary patterns, we could not elaborate on the pattern of livestock depredation by carnivores and the timings of their switching to domestic prey, if any. However, based on the reports from herders we identified incidence of livestock depredations mostly during the colder months of the year. We therefore recommend a comprehensive study on seasonal dietary patterns of carnivores in relation to livestock depredation, and evaluation of predator-prey relationships using multi-dimensional niche approach (involving space and time), to better understand the patterns of interaction, and inform conservation efforts to improve wild prey populations and their habitats in the region.

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**Data availability** The evidence and data supporting our findings can be provided on request from the corresponding author.

## Declarations

**Ethical approval** Not applicable.

**Clinical trial number** Not applicable.

**Competing interests** The authors declare no competing interests.

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