Trophic interaction and livestock dependence of snow leopard and sympatric carnivores in Tianshan, Northwest China.

Hua Zhong
Eco-Bridge Continental
Luciano Atzeni
University of Oxford
Fengjiao Li
Eco-Bridge Continental
Yixuan Liu
Eco-Bridge Continental
Ruifen Wang
Eastern Tianshan State Forestry Administration of Xinjiang Uygur Autonomous Region
Abduzaire Alemiti
Eastern Tianshan State Forestry Administration of Xinjiang Uygur Autonomous Region
Kun Shi
kunshi@bjfu.edu.cn

Eco-Bridge Continental

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Abstract

Diets of carnivores provide insights into predator-prey relationship and intra-guild competition, and contribute to drafting fruitful conservation strategies. However, few high-resolution dietary dataset of carnivores exist in Central Asia, hindering deep understanding of their coexistence in grazing landscape. Here, we present detailed trophic interaction among four carnivores in Tianshan Mountains of Northwest China deriving from 179 fecal samples.

Using DNA metabarcoding, we identified 20 prey items across 5 orders. High dietary overlap (O_{jk} = 0.995) was found between snow leopard (*Panthera uncia*) and wolf (*Canis lupus*), which mainly preyed on large mammals (*%PR* = 85%, 91%). Red fox (*Vulpes vulpes*) mainly consumed large and small mammals (%PR = 43%, 31%). Significant differences ($P < 0.001$, $P < 0.05$) and lower dietary overlaps (O_{jk} = 0.761, 0.756) were observed between red fox and snow leopard/wolf.

Wild animals such as ibex (*Capra sibirica*) were detected in the diet of dog (*Canis lupus familiaris*), indicating wildlife depredation. High dietary overlaps were observed between dog and snow leopard/wolf (O_{jk} = 0.989, 0.999). These results suggest that dog compete with wild predators for prey resources and underline the need to further study their potential disturbance to natural ecosystems. All carnivores consumed livestock (*%PR* = 14 ~ 27%). Corrals reinforcement and husbandry practice improvement are necessary to prevent potential economic losses and retaliatory killing.

Our results suggest that dietary partitioning and livestock subsidies facilitate carnivore coexistence in Tianshan and have implications for developing effective conservation intervention to promote human-carnivore coexistence in Central Asia.

Introduction

Mammalian carnivores are ecologically important because they exert strong top-down regulation on herbivores and prevent them from over-exploiting vegetation (Terborgh et al., 2001; Ryall & Fahrig 2006; Ripple & Beschta 2012), thereby maintaining the structural and functional stability of terrestrial ecosystem and regional biodiversity (Roemer et al., 2009; Estes et al., 2011). However, habitat degradation, fragmentation, or shrinkage of prey populations has led to the continuous decline of populations of global carnivores over the past two centuries (Ceballos & Ehrlich 2002; Ripple et al., 2014). Excessive hunting, grazing, deforestation, urban construction and other anthropogenic activities seriously reduce the ecological fitness of carnivores and potentially increase intra-guild competition (Miller & Schmitz 2019).

Among all factors affecting carnivores, prey is the factor that could have the strongest influence on them (Santos et al., 2019; Davis et al., 2021). Exploring the dietary composition of carnivores in human-dominated landscape provides information related to trophic interaction and intra-guild competition (Cusack et al., 2017), and contributes to drafting effective conservation strategies (Sousa *et al.*,). Nevertheless, Microhistology (the microscopic examination of hair characteristics such as cuticle scales, medullary types, thickness of cortex and medulla etc.) has been predominant in classical carnivores dietary studies (Janecka et al., 2020), which may strongly bias the results (Akrim et al., 2018). The development of molecular biology techniques in recent decades such as High-throughput sequencing and DNA Metabarcoding has advanced the research of trophic ecology in recent years (Thuo et al., 2019).

The threatened snow leopard (*Panthera uncia*) is an apex predator found in mountainous ecosystems of Central Asia, coexisting with other wild predators such as wolf, lynx (*Lynx lynx*), red fox etc. Models predict a net reduction between 8 and 23% of currently identified snow leopard range (~ 2.2 million km^2) by 2070, based on occurrence records from 1983 to 2015 (Li et al., 2016). Such large-scale changes will likely cause reductions and distribution shifts of snow leopard, their prey, and biodiversity (Li et al., 2016). Tianshan, the eastern edge of TianShan-Pamir-HinduKush-Karakoram mountain ranges, has been predicted to function as refugia for snow leopard as projected to be climatically stable habitat of them (Li et al., 2016). As pivotal distribution range of snow leopard, Tianshan still remains poorly studied in terms of dietary study of carnivores, hindering deep understanding of its food-web structure and predator-prey relationship.

Animal husbandry has been a important source of income for local people living across TianShan for thousands of years (Wang et al., 2014a). While snow leopard are thought to prefer wild prey, they often consume livestock (Wegge et al., 2012; Chetri et al., 2017; Bagchi *et al.*, 2019). Economic losses caused by livestock depredation could promote negative attitudes towards large carnivores and lead to retaliatory killing (Hussain 2003). This poses challenges for the wildlife manager to taking into account the livelihood of local people while promoting the restoration of carnivore population and habitats (Chen et al., 2016b; Wang et al., 2019). Revealing the extent of carnivores dependency on livestock is therefore the cornerstone to mitigate conflict (Hacker et al., 2021).

In TianShan, snow leopard not only coexist with wild predators, but also with the domesticated free-ranging dog in TianShan (Smith et al., 2010). As predators in natural habitat, stray dogs have been observed to compete with native carnivores through exclusion (interference competition) and prey on natural prey (Glen et al., 2006). Unearthing wild/domestic prey consumption of stray dog contribute to reveal its potential ecological impacts on wild predators in natural habitat.

The aim of this study is to first use the DNA metabarcoding and Next Generation Sequencing to investigate the detailed molecular dietary composition of carnivores living in eastern Tianshan. By assessing the livestock depredation of wild predators, wildlife depredation of stray dogs, and comparing dietary composition of carnivores, we hope to provide solid scientific basis for developing management strategies needed to conserve biodiversity and mitigate human-wildlife conflict in this region.

Methods

1.1 Field investigation

Tianshan, recognized as one of the seven major mountain systems globally, is situated in the central region of Eurasia, spanning latitudes 39°27'36" to 45°22'12" North and longitudes 73°55'12" to 95°04'48" East. Our research was conducted within the Eastern Tianshan division of the State Forestry Administration (Fig. 1). Between September 2021 and June 2023, we engaged in camera-trapping surveys in this area. To deploy cameras, transects were established, and animal scats were collected as and when feasible, based on the ease of access to different locations. For each scat sample, the tip was collected and preserved in a 50ml centrifuge tube, which included 30ml of silica beads to ensure dryness, following the method described by (Wasser et al., 1997). These scat samples were kept in shaded, cool conditions before being stored at a temperature of -20°C.

1.2 Laboratory analysis

Following the homogenization process and DNA extraction, we utilized primer 16S (Xiong et al., 2016) (Appendix S1: Table S1) to ascertain the origin of the scat. Subsequently, the tagged universal primer 12SV5 (Tiayyba et al., 2011) (Appendix S1: Table S1) was employed for amplifying the food DNA and identifying prey species. To inhibit the amplification of predator DNA, we employed blocking oligos (Hege & Simon 2008; Vestheim et al., 2011; Shao et al., 2019) (Appendix S1: Table S2). The PCR products were then purified, combined, and sequenced using NovaSeq6000 (Illumina Inc., San Diego, CA, USA). The sequenced reads obtained were filtered and processed using QIIME 2 (2022.02) (Bolyen et al., 2019), and then allocated to their respective samples based on the tag. Identification of prey species was conducted via BLAST (Altschul 2012), drawing on the local species inventory, references from "A Guide to the Mammals of China" (Smith et al., 2010), "A Field Guide to the Birds of China" (Mackinnon & Phillipps 2000), and the IUCN Red List. Comprehensive laboratory methods are detailed in Appendix S1.

1.3 Statistical analysis

1.3.1 Dietary metrics

Dietary data were summarized across samples using prey MOTU (Molecular Operational Taxonomic Unit) and two metrics commonly used in molecular dietary data analysis (Lovari et al., 2009): For a specific predator, (1) Occurrence Frequency (*%FO*) indicates how common a prey MOTU is in its diet, while (2) weighted Relative Proportion (*%PR*) indicates how important a prey MOTU is (Pompanon et al., 2012). The *%FO* and *%PR* of each prey MOTU in each carnivore's diet were calculated as:

$$\%FO_i = \left(\frac{1}{S} \sum_{k=1}^{s} I_{i,k} \right) \times 100\%$$

and

$$\%PR_i = \left(\frac{1}{S} \sum_{k=1}^{s} \frac{I_{i,k}}{\sum_{i=1}^{n} I_{i,k}} \right) \times 100\%$$

where *S* is the total number of samples, *n* is the total number of prey MOTUs, $I_{i,k}$ indicates the occurrence of prey MOTU *i* in sample *k* ($I_{i,k}$ = 1 if prey MOTU *i* is present in sample *k*, and $I_{i,k}$ = 0 if not) (Pompanon et al., 2012).

1.3.2 Dietary diversity

We used the Shannon index (*H*) and Peilou's evenness (*J*) (Shannon & Weaver 1949) to assess the dietary diversity and dietary evenness of each carnivore. For a specific predator, Shannon index and Peilou's evenness were calculated as:

$$H = -\sum_{i=1}^{n} (p_i \times ln(p_i))$$

and

$$J = \frac{H}{ln(n)}$$

Where p_i is the relative proportion (%PR) of the prey MOTU *i*, and *n* is the total number of prey MOTUs.

1.3.3 Body-size-based dietary differences and overlaps

According to the body size of the prey (Jones et al., 2009), we divided all MOTUs into the following category: the large ungulates from Artiodactyla were classified as "Large mammals", hare (*Lepus tolai*), marmot (*Marmota baibacina*) and Eurasian red squirrel (*Sciurus vulgaris*) were classified as "Medium-sized mammals", other small rodents and insectivores from Rodentia and Eulipotyphla such as Large-eared vole (*Alticola macrotis*) and Siberian shrew (*Crocidura sibirica*) were classified as "Small mammals", Himalayan Snowcock (*Tetraogallus himalayensis*) and Chukar were classified as "Large birds".

Then we first determined dietary difference between pairs of carnivore species using Chi-square test with a significance level of 0.05, and secondly quantified the dietary overlap between pairs of carnivore species using Pianka's index (O_{jk}) (Pianka & Pianka 1976), which varies from 0 (no overlap) to 1 (complete overlap). O_{jk} was calculated as follows:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where O_{jk} is Pianka's overlap between species *j* and *k*, p_{ij} is the relative proportion (%PR) of the category prey *i* of the total prey used by species *j*, p_{ik} is the relative proportion (%PR) of the category prey *i* of the total prey used by species *k*, and *n* equals 4, the total number of prey category.

1.3.4 Livestock/wildlife depredation

To determine the importance of domestic/wild prey in each carnivore's diet, we classified sheep (*Ovis aries*), goat (*Capra hircus*), cattle (*Bos taurus*) into " Domestic prey ", and wild species into " Wild prey", and calculated the Relative Proportion of domestic/wild prey.

Results

A total of 179 scats were collected in eastern Tianshan from 2021 to 2023, of which 156 were identified to the species level. The majority of the scats collected were from snow leopards, totaling 91 samples. This was followed by 31 from red foxes, 17 from dogs, and 7 from wolves. Scats from lynx (n = 2), stone marten (*Martes foina*) (n = 3) and Eurasian badger (*Meles meles*) (n = 2) were excluded from the analysis due to small sample size. After processing the raw data from high-throughput sequencing, we obtained a total of 15.08 gigabases (G) of clean data across four libraries for further analysis. This led to the identification of 20 Molecular Operational Taxonomic Units (MOTUs), comprising 18 mammalian MOTUs and 2 bird MOTUs, which span across 2 classes and 5 orders.

2.1 Detailed dietary composition

Seven food MOTUs were identified in the diet of snow leopard, with an average of 1.5 MOTUs per sample. Ibex was found to be the primary prey of snow leopard (*%FO* = 49%, *%PR* = 31%) (Fig. 2). Five food MOTUs were found in wolf´s diet, averaging 1.6 MOTUs per sample. Ibex was also the main prey of wolf (*%FO* = 57%, *%PR* = 36%) (Fig. 2). There were seven food MOTUs in the dog´s diet, with an average of 1.5 MOTUs per sample, and Ibex and elk were the main prey (*%FO* = 47%, *%PR* = 31%) (Fig. 2). We found 15 food MOTUs in the diet of red fox, averaging 2.1 MOTUs per sample. Chukar was the primary prey of red fox (*%FO* = 35%, *%PR* = 17%) (Fig. 2). Detailed MOTU Table are in Appendix S1 (Table S3).

2.2 Dietary diversity

Red fox displayed the highest dietary diversity (H = 2.30), followed by dog (H = 1.55), wolf (H = 1.43) and snow leopard (H = 1.32) (Table 1). Wolf had the highest dietary evenness (J = 0.89), followed by red fox (J = 0.85), dog (J = 0.80) and snow leopard (J = 0.68) (Table 1).

Table 1
Dietary diversity of different carnivore species

Species	Snow leopard	Wolf	Dog	Red fox
Shannon Index (H)	1.32	1.43	1.55	2.30
Peilou's evenness (J)	0.68	0.89	0.80	0.85

2.3 Livestock/wildlife depredation

We found that all carnivores consumed less domestic prey and more wild prey. Among four predators, wolf consumed more domestic prey (*%PR* = 27%) than snow leopard, dog, red fox (*%PR* = 19%, 19%, 14%). Red fox consumed slightly more wild prey (*%PR* = 86%) than other carnivores (*%PR* = 81%, 81%, 73%) (Fig. 3).

2.4 Body-size-based differences and overlaps

Snow leopard, wolf and dog mainly consumed large mammals (*%PR* = 85%, 91%, 92%). Diet of red fox was more balanced, mostly consuming large mammals (*%PR* = 43%), followed by small mammals (*%PR* = 31%) and large birds (*%PR* = 19%) (Fig. 4).

Higher pairwise dietary overlaps were observed between snow leopard and wolf, snow leopard and dog, wolf and dog (O_{jk} = 0.995, 0.989, 0.999). Lower pairwise dietary overlaps were observed between red fox and other three large predators (O_{jk} = 0.761, 0.756, 0.763) (Table 2).

Table 2
Pianka's dietary overlap (O_{jk}) index values between carnivore species

Species	Snow leopard	Wolf	Dog	Red fox
Snow leopard	/	0.995	0.989	0.761
Wolf	/	/	0.999	0.756
Dog	/	/	/	0.763

Additionally, Chi-square test shows that diet of red fox was significantly different from that of snow leopard, wolf and dog ($P < 0.05$), while no statistical differences ($P > 0.05$) were found between diets of snow leopard and wolf, snow leopard and dog, wolf and dog. Detailed hypothesis testing results are in Appendix S1 (Table S4).

Discussion

Traditional dietary analysis of microscopic examination can yield distorted food-web relationships due to its biased coverage and low taxonomic accuracy (Pringle & Hutchinson 2020). Next-generation sequencing (NGS) and DNA metabarcoding can greatly increase the understanding of predator–prey dynamics and the human-wildlife conflict, but remains underused for carnivores such as the threatened snow leopard (Hacker et al., 2021). Our study is the first to use the NGS and metabarcoding approach to reconstruct complex food webs with fine-scale trophic interspecific relationships in the human-dominated landscapes of Central Asia.

Trophic competition between large carnivores

In this study, we found that the diets of snow leopard and wolf are consistent with previous molecular dietary studies that large carnivores can be more specialized in preying on large ungulates (Wasim et al., 2012; Lanszki et al., 2019; Shao et al., 2021a). The difference of the body size of prey is related to the energy profitability of predation and prey availability (Marquard-Petersen & Ulf 1998). Due to the large size and high metabolic demand of endotherms, large carnivores such as snow leopard and wolf usually expend a large amount of energy in one hunt (Ripple et al., 2014). Therefore, large mammals providing high energy profitability are often the best food choices for large predators (Prokopenko et al., 2023).

Despite ecological theory predicts that sympatric carnivores should avoid excessive interspecific competition through niche differentiation (Lovari et al., 2015), high dietary overlap between snow leopard and wolf in this study suggests that they do not base their coexistence on dietary partitioning, and substantial interspecies competition of prey resource can exist between them. Similar-sized predators can prey on similar prey species, thus their diets could be similar (Lovari et al. 2013). In this case, spatial-temporal avoidance might play a key role in the coexistence of these two large carnivores, or that preferred local food resources (wild and domestic ungulates) are abundant. As opportunistic, ambush predators, snow leopard are reported to typically prefer steep and rugged terrain (Jackson & Ahlborn 1989), while wolf are cursorial predators highly adapted to chase their prey over long distances (Husseman et al., 2003). It could be hypothesized that difference in hunting strategies and trophic competotion avoidance might lead to different habitat selection, and subsequent spatial separation facilitate co-existence of the two apex predators (Shrotriya et al., 2022).

Animal husbandry accounts for a large proportion of livelihood in grazing landscape like eastern Tianshan, and it is common for local herdsmen keeping dogs to guard their homes, or to assist grazing activities. Roaming between human settlements and wildlife habitats, free-ranging dogs are likely to compete with wild predators (Glen et al., 2006). In our study, wild species such as ibex, elk, wild boar (*Sus scrofa*), hare, were detected in the diet of dog, and dog consumed more wild prey than other three carnivores. Furthermore, large dietary overlaps between stray dog and snow leopard/wolf demonstrated that they compete against wild predators for food resources. If the population of free-ranging dogs is not controlled in the future, it may continue to grow and may disturb the population of local wildlife, not only through competition (wild carnivores) and predation (wild herbivores), but also through potential pathogens and diseases transmission (rabies and canine distemper virus etc) (Gompper 2014). Therefore, we call attention to the potential ecological impacts of free-range dogs in natural ecosystems, underlining the need of better management to address the unexpected roles (predators, competitors, and prey of wildlife) of the livestock guardians.

Dietary partitioning of mesocarnivore

Our finding that the primary food of red fox being large mammals supported previous study that red fox, a mesocarnivore species with scavenging behaviour, might consume carcasses of large ungulates left by large carnivores (Helldin & Danielsson 2007). In this case, the proportion of large mammals in the diet of red fox can be high. Red fox is a worldwide distributed species, and its large population are based on diverse food resources. In this study, we detected most 15 food MOTUs in the diet of red fox, 8 of which were small rodents and small insectivores that were not detected in diets of other carnivores. This leads to higher dietary diversity (*H* = 2.30) in the diet of red fox, re-comfirming that red fox, as a mesocarnivore species, could have more generalized food habits and can prey on varieties of small mammals (Shao et al., 2021b). Lower dietary overlaps between red fox and snow leopard/wolf suggest that there was obvious dietary partitioning between red fox and the other two large carnivores.

Inferior predators (often in smaller body sizes) are likely to avoid superior predators (in bigger body sizes) spatially and/or temporally (Ramesh et al., 2012; Sunarto et al., 2015; Bu et al., 2016), as larger predators try to eliminate competition of small predators by predation or killing of individuals (Palomares & Caro 1999; Jose et al., 2000; Hass 2009). Our result agrees with the finding that prey diversity is one of the ways that red fox reduce the pressure of inter-specific competition, allowing red fox to coexist with sympatric large predators by exploiting a broader trophic niche (Shrotriya et al., 2022).

Conservation implications

Promoting the harmonious coexistence between human societies and carnivores populations in protected areas has always been an important but difficult challenge.

In this study, we found that all carnivores depended on livestock (%PR = 14% ~ 27%), despite the degrees of livestock dependence were generally lower than their counterparts in a previous carnivores dietary analysis in an adjacent region (relative proportion from 29–39%) (Wang et al., 2014b). We also found that goats were more frequently preyed upon than other livestock, and wolf consumed livestock more frequently than other carnivores. This result is consistent with previous studies that found wolf was the species that causes most conflicts with local residents (Chen et al., 2016a).

With livestock depredation by wild carnivores has been being a key factor triggering retaliatory killings (Janeiro-Otero et al., 2020), our result emphasizes the the potential possibility of human-wildlife conflict escalation in eastern TianShan. The large food requirement of large carnivores and the wide distribution of livestock in wildlife habitat make it common of livestock depredation by large carnivores, resultant conflict hinders local perception towards carnivore and effectiveness of conservation intervention worldwide (Janeiro-Otero et al., 2020). Without effective management, subsequent retaliatory killings could undermine populations of wild carnivores, especially endangered carnivores species such as snow leopard. To prevent economic losses caused by livestock predation, escalation of conflicts and potential resurgence of retaliatory killing, we suggest improving animal husbandry practices through measures such as predator proof livestock corrals (Maheshwari & Sathyakumar 2020). At the same time, conservation implications that disseminate the ecological significance of carnivore communities is also needed to foster continuous widespread positive attitudes towards them.

In this study, we revealed trophic interaction among carnivores in eastern Tianshan by constructing detailed dietary composition. Meanwhile, we quantified the livestock dependence of wild carnivores and wildlife consumption of stray dogs. These results suggest that dietary partitioning and availability of domestic animals facilitate the coexistence of carnivores and provide baseline ecological data and implications for the sustainable conservation supporting human-carnivore coexistence in Central Asia.

Declarations

Competing Interests

The authors declare no conflict of interest. All the data is original to the study and hasn't been used in other works that are published, in press, submitted, or soon to be submitted elsewhere.

Ethics Statement

This research has been examined and approved by the Ethic and Animal Welfare Committee of Eco-Bridge Continental, and complies with the principles of animal protection, animal welfare and ethics. All sampling methods (molecular scatology) used in this study were noninvasive and would not present any harm to the endangered species or any other wildlife in the study area.

Author Contribution

All authors conceived the conception and designed methodology. Hua Zhong and Luciano Atzeni led in drafting and revising the manuscript. Hua Zhong and Fengjiao Li led the laboratorial analyse. All authors made contributions to acquisition of data. All authors agreed to be accountable for all aspects of the work and gave final approval for publication.

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Data Availability

Data in this study (raw data and metadata used to generate tables, figures, plots) are not yet provided, these data will be permanently archived in Dryad repository if the paper is accepted for publication. All methods or protocols utilized to generate the data have been cited in the manuscript or supporting information. This study includes no novel code, computer software or derived data products.

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Figures

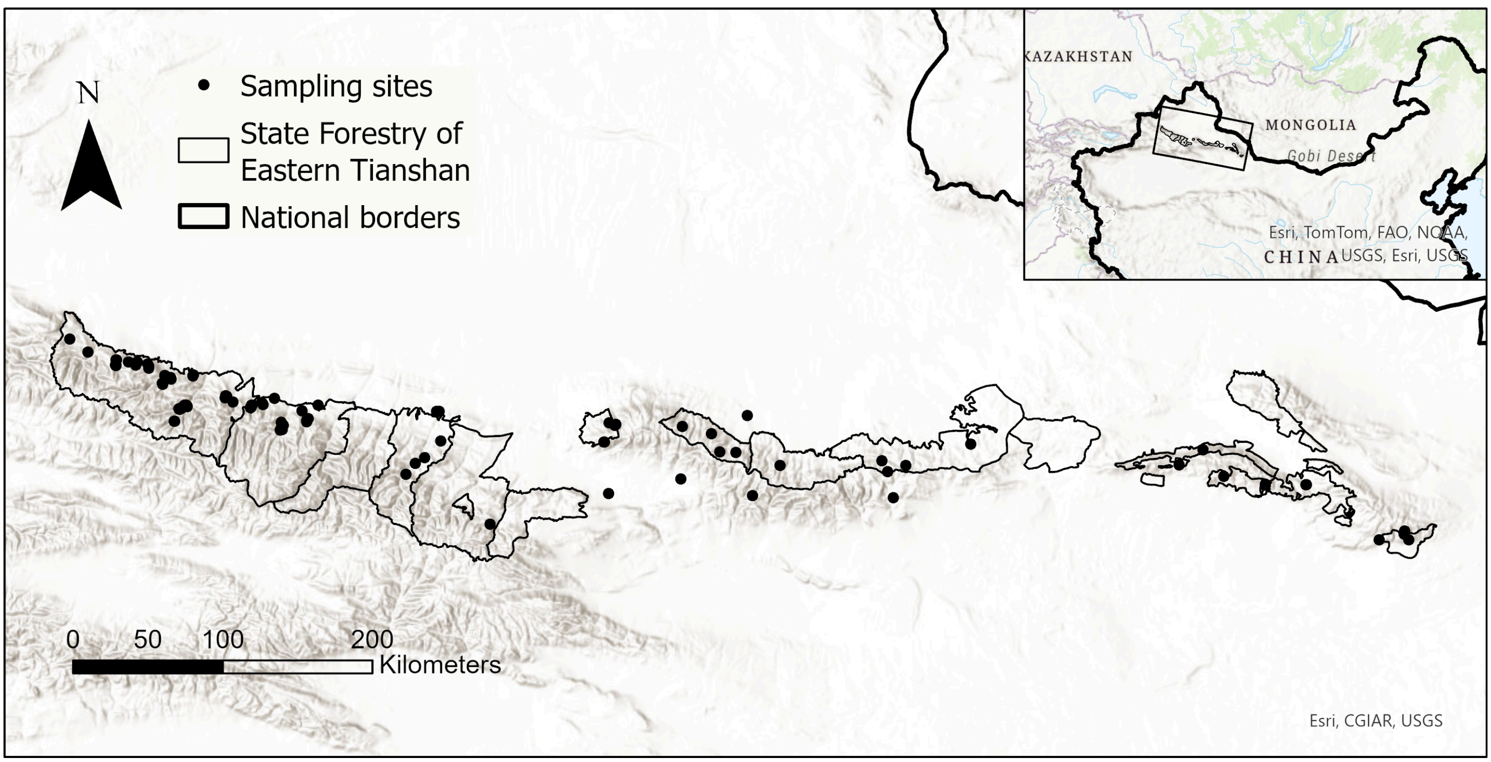

Figure 1

Map of the study area and sampling sites

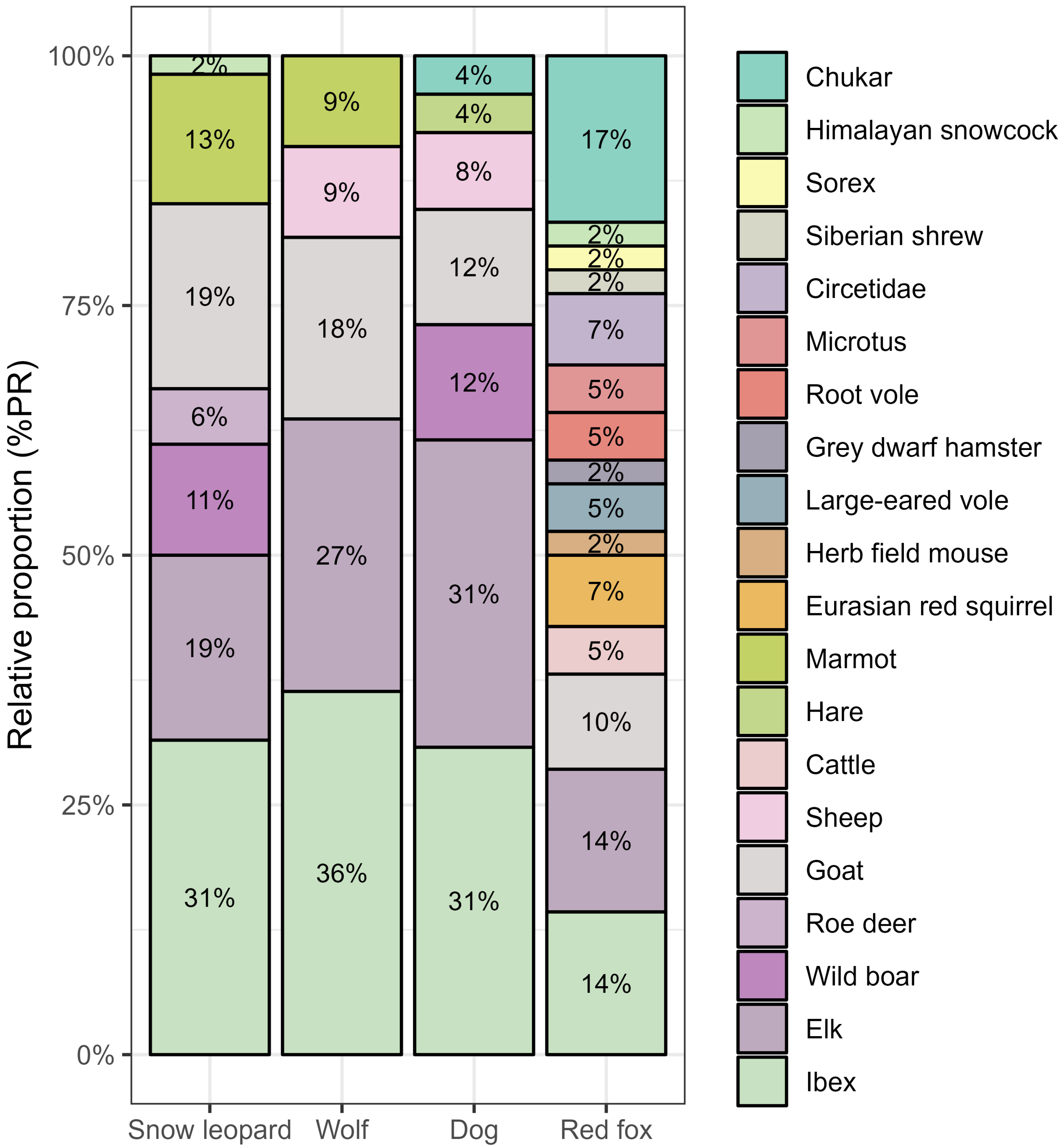

Figure 2

The relative proportion (*%PR*) of different prey MOTU of four carnivores

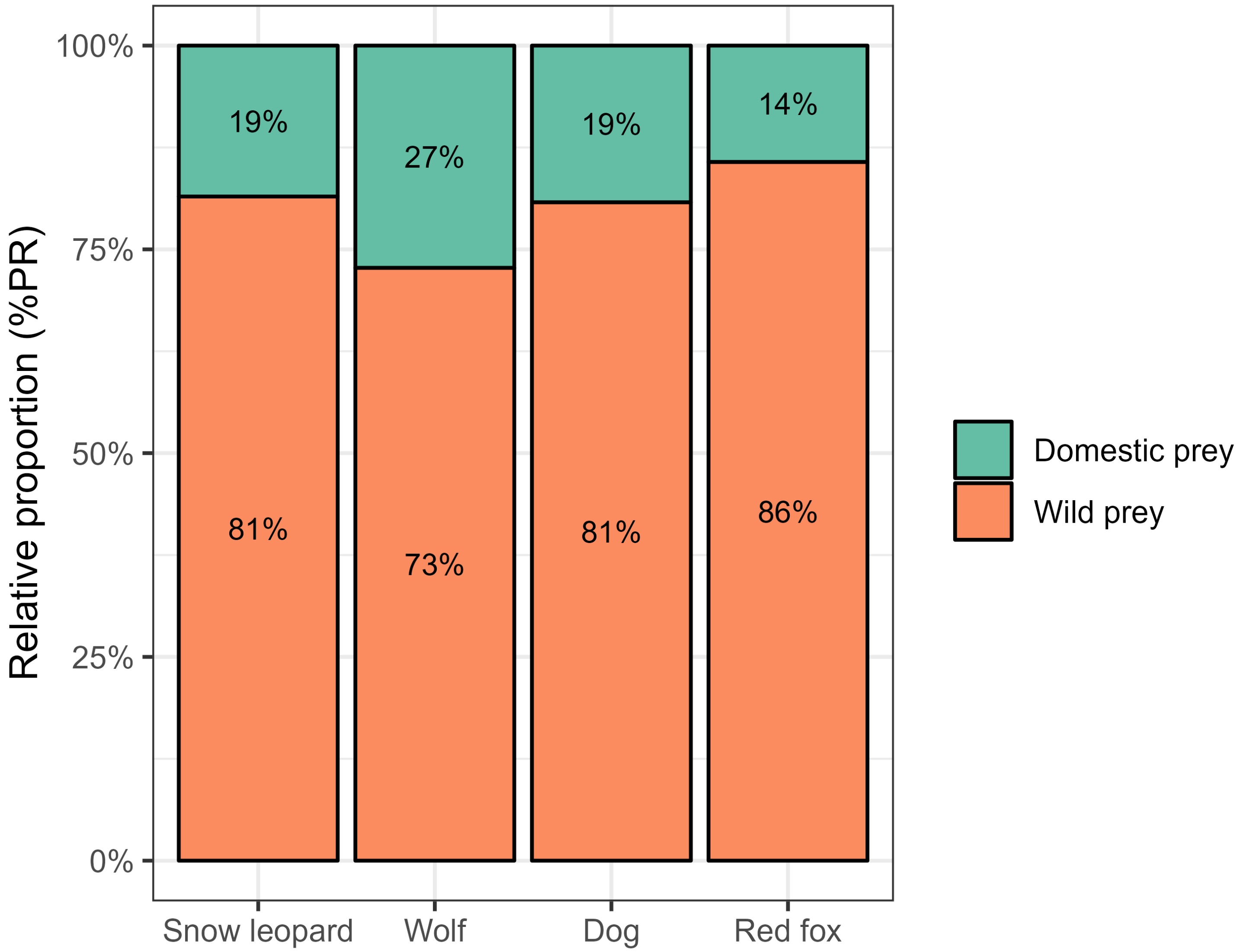

Figure 3

The relative proportion (*%PR*) of wild and domestic prey of four carnivores

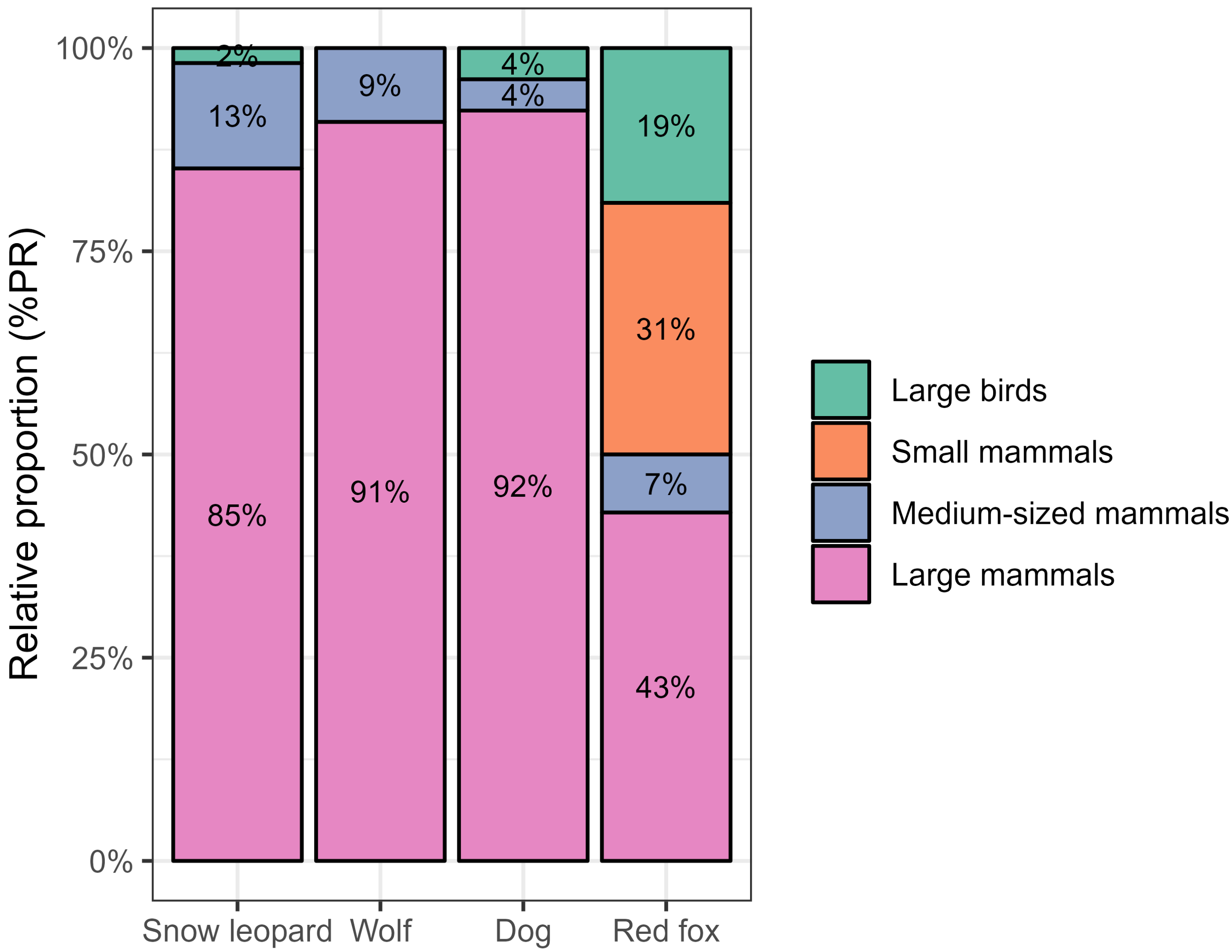

Figure 4

The relative proportion (*%PR*) of body-size-based category prey of four carnivores

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