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Dietary spectrum in Himalayan wolves: comparative analysis of prey choice in conspecifics across high-elevation rangelands of Asia

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Abstract

The Himalayan wolf is one of the most basal among wolf lineages in the world today. It inhabits mostly the high elevations, northwards from the Himalayas (1500–5000 m) in the Asian region. We conducted a meta-analysis to understand the dietary habits of Himalayan wolves and wolves of the high rangelands of Asia from seven countries (n = 22). We found 39 different prey items reported across the distribution of the Himalayan wolf from a total of 2331 scats (average of 105.95 ± 20.10 scats per study). Comparison of the relative frequency of occurrence of different prey species shows that domestic prey consumption (48.21 ± 5.61%) across the zones or continent was similar to wild prey consumption (42.94 ± 5.25%). Small wild prey species constituted approximately (24.53 ± 3.77%) of the total wolf diet. Wolves of the Asian Highlands consumed relatively more large prey (40.01 ± 5.42%) than small prey (25.19 ± 3.85%) or medium-sized prey (23.17 ± 3.78%). Wolves consumed a larger proportion of domestic (54.92 ± 5.94%) than wild prey (36.13 ± 6.12%) in areas that had regular livestock grazing and vice versa. East, west and central Himalayan and Central Asian wolves consumed mostly large wild and domestic prey. On the contrary, wolves in the Qinghai–Tibetan Plateau, Inner Mongolia and the Karakoram consumed a relatively higher proportion of smaller-sized prey and livestock. Overall, wolves utilized mostly domestic livestock and marmots (Ivlev's index, 0.22–0.77). High localized utilization of Przewalski's horse (*Equus ferus przewalkskii*, 0.94) was recorded, whereas Goral (*N. goral*) and Pika (*Ochotona* spp) were particularly underutilized (−0.99 and −0.92) in wolf diet. A landscape or trans-boundary approach is advocated to restore natural large wild prey, for such a relic lineage species and reduce human-wolf conflicts.

Introduction

Wolves (*Canis lupus*) are a charismatic species that have been extensively studied across the Americas and Europe (Mech & Boitani, 2010). Their role as an ecosystem regulator through trophic cascades has been well documented (Ripple *et al.*, 2001; Ripple & Beschta, 2004; Halofsky & Ripple, 2008). Wolves were once hunted to near extinction; however, over a period of time, increased public awareness toward the species has help garnering strong legal protection, favorable media coverage and furthered ecological research (Mech, 1995; Ripple & Beschta, 2007; Chapron, Andren & Liberg, 2008; Imbert *et al.*, 2016). Yet, persecution remains as one of the biggest obstacles to wolf recovery around the world (Newsome *et al.*, 2016), including the Himalayan wolf.

The Himalayan wolf is a subspecies of the gray wolf (*Canis lupus*), found in the cold and hypoxic high-altitude ecosystems of the Himalayas and the Tibetan Plateau, extending into China, Manchuria and Mongolia (Zhang *et al.*, 2014). Their unique ancient lineage was highlighted recently via several taxonomic and evolutionary studies. However, there is limited understanding of its ecology, behavior and habitat requirements primarily due to its cryptic nature and the unforgiving landscape that it inhabits (Sharma, 2001; Aggarwal *et al.*, 2007; Werhahn *et al.*, 2017).

The high-altitude rangelands of Asia are harsh grounds, interspersed with transhumant pastoralist. Wolves here have survived through a history of human interference (Bagchi & Mishra, 2006; Namgail, Fox & Bhatnagar, 2007). They forage on domestic livestock, small prey and even garbage. Therefore, wolves are often considered to be no less than a marauder of livestock and have been consequently persecuted despite legal protection. The Himalayan wolf or highland wolf, also known as the Woolly wolf or Tibetan wolf also shares its range with another apex predator, the endangered snow leopard (*Panthera uncia*). Depredation by these sympatric species has led to increased conflicts and perhaps reduced their acceptance by the local people (Suryawanshi *et al.*, 2013).

Many studies on the feeding ecology of wolves have focused on the geographical variability, its trophic ecology and prey selection (Okarma, 1995; Meriggi & Lovari, 1996; Capitani *et al.*, 2004; Mech & Boitani, 2010; Newsome *et al.*, 2016). However, information on wolf diet is limited from the Asian region. Newsome *et al.* (2016) reviewed only five out of 177 studies on diet from this region and found these wolves to mostly rely on small prey, rodents and domestic livestock. On the contrary, in North America and Eurasia including the Arctic, wolves frequently fed on medium- to large-sized prey. One of the main reasons for such difference cited by Ripple *et al.* (2015) is that, in Central Asia for example, the expansion of wool production for international export has reduced many large herbivore habitats. Livestock competition has also created a significant threat to large herbivores in India, China and Mongolia with consequent impacts on their predators like wolves (Ripple *et al.*, 2015).

The current review aims to bridge the information gap on diet and feeding ecology of Himalayan wolves. This study will inform better on diets of wolves from the Asian high-elevation rangelands and complement existing knowledge on the species. In Asia, wild prey densities are low in many areas where wolves occur. We hypothesized that Himalayan wolves mostly predated on domestic prey in areas with historical grazing practices. Alternatively, in undisturbed natural areas, wolves should utilize more wild prey. We conducted a meta-analysis with the following objectives:

- To understand wolf prey choice with respect to the Tibetan/Himalayan wolves of Asia in particular,
- To investigate the levels of domestic and wild prey share in difference sub-regions within their habitat range and
- To understand the determinants of dietary choice in such regions with respect to prey characteristics and environmental variables.

Materials and methods

Collating data on Himalayan wolves from Asia

Data on Himalayan wolf diets across high-altitude rangelands from Asia were collected through published sources using a keyword search in Google scholar. Keywords, Tibetan wolf diet, Himalayan wolf diet, Mongolian wolf diet, *Canis lupus chanco*, *Canis lupus laniger* and wolves from Central Asia were used. Available literature was also reviewed from Newsome *et al.,* (2016). A detailed list of the literature used is provided in Tables 1 & 2, Supplementary Material, Annex 2-3. The study was also supplemented with unpublished literature and field-collected scats (n = 118) from the Spiti region where diet information was missing. (Supplementary material, Annex 1). We also tabulated data on grazing pressure in terms as limited or regular grazing based on the studies found.

Prey potential zones and diet representation as relative frequency of occurrence (RFO)

Data were tabulated as (1) absolute frequency of occurrence, that is, FOO (number of occurrences of each prey item in scats/total number of scats *100) and (2) relative frequency of occurrence, that is, RFO (number of occurrences of each prey item in scats/total number of occurrences of all prey items *100). We used RFOs of all studies for overall comparisons. RFOs represented as percentages avoid the ambiguity of over-representation and standardize the prey item occurrences. To estimate biomass consumed per unit scat, we used the correction factors provided for wolves (Weaver, 1993; Wachter *et al.*, 2012). Weaver, (1993) used a regression-based correction factor to address biomass consumed by wolves based on body weights of prey which was later refined by Wachter *et al.* (2012), for cheetah and simultaneously for wolves through an exponential equation that is more realistic in ecological terms. However, we used both for comparative purposes. The weight of prey used for biomass calculation was 3/4th of the female weight of prey (Hayward *et al.*, 2006; Lyngdoh *et al.*, 2014).

We divided the data on wolf diet into seven zones based on the wild prey uniqueness and physiography (Schaller, Junrang & Mingjiang, 1988; Lyngdoh *et al.*, 2014). Zone 1, the north-west and Afghanistan areas encompass, that is, the Karakoram and Pamirs (KA). Zone 2 included western Himalayas and parts of India, that is, Ladakh and Himalayan parts (WH). Zone 3, comprises of the Central Himalayan region, that is, mostly the Dolpa and Nepalese Himalayas (CH). Zone 4, encompasses the eastern Himalayan region (Sikkim and Bhutan Himalayas- EH). Zone 5, includes the Central Asian region which includes the Tien Shan and surrounding rangelands (CA) while zone 6, encompasses the Mongolian region (IM) and zone 7, comprises of the Qinghai–Tibetan Plateau region (QTP). These regions are known to have a unique prey base, distinct from each other (Schaller, 1988; Bagchi & Mishra, 2006; Jumabay-Uulu *et al.*, 2014; Lyngdoh *et al.*, 2014; Chetri, Odden & Wegge, 2017). In Zone 2–4, blue sheep and Ibex are dominant prey, while in Zone 5, Argali is known to occur widely. In zone 6, the Mongolian region, the presence of red and roe deer is also known to drive snow leopard diet (Nakazawa *et al.*, 2008). Zone 7, QTP region consists mostly of small wild and domestic prey (Yan *et al.*, 2006; Van Duyne *et al.*, 2009; Zhang *et al.*, 2014). Thus, these zones differ in their major prey species diversity and abundance. These zones also differ physio-geographically and are well separated from each other (Fig. 1).

Prey choice and Niche overlaps

To analyze prey utilization and selection by wolves, Ivlev's selectivity index (IVI) was used using the formula, D = (ri-pi)/(ri + pi) where, ri is the proportion of species i among the total kills at a site and pi is the proportion of species i in the available prey community. We used availability data of prey abundance (n = 19, Table 3, Supplementary material, Annex –

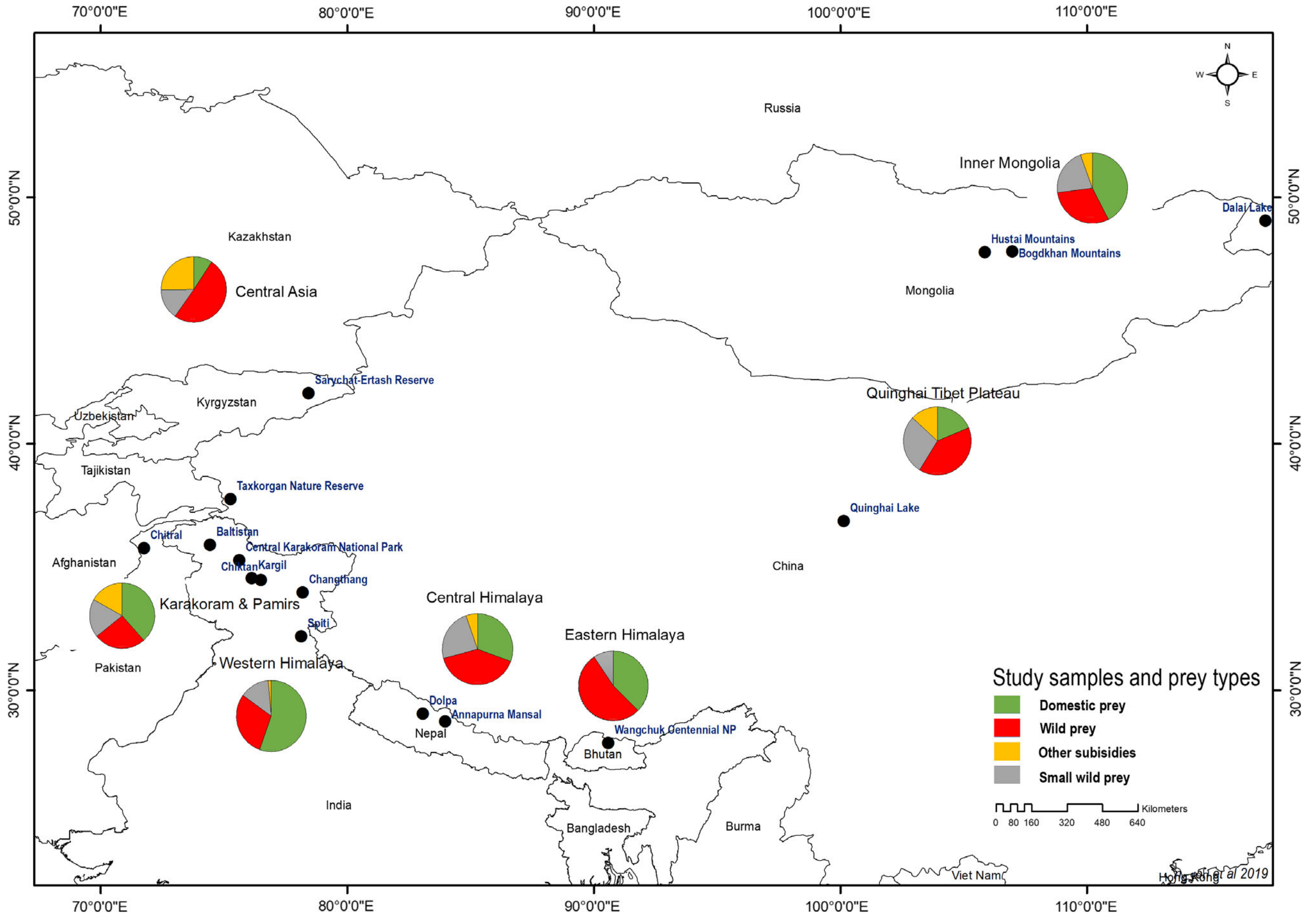

Figure 1 Area-wise percentage frequency of occurrence of prey items in the diet of wolves.

4) from published literature from similar study on snow leopard for comparability and compatibility from Lyngdoh *et al.*, 2014. Prey availability data for Red deer (*Cervus elaphus*) and Przewalski's Horse (*Equus ferus przewalskii*) were obtained from Burbaitė & Csányi, (2010) and King *et al.,* (2015), respectively. Estimates of Tibetan wild ass (*Equus kiang*), Tibetan Gazelle (*P picticaudata*) and Goral were used from Bhatnagar *et al.,* (2006); Duckworth & MacKinnon, (2008) and Leslie, (2010), respectively. The utilization preference of prey species is presented along a gradient of −1 to +1 such that the values range from +1 (maximum use) to −1(maximum avoidance). We excluded various prey types such as garbage, invertebrates, plant or vegetative matter and insect as they could not be quantified in terms of biomass.

We used Pianka's index to examine the degree of dietary niche overlap between each zone (Pianka, 1966). RFO of prey species items in scats from these zones identified were used in null model simulations of Pianka's dietary niche breadth, with relaxed and zero states retained. RFOs were tabulated for each species and zones in program Ecosim (Lyngdoh *et al.*, 2014). The Observed Index was calculated for the data, whereas the Mean and Variance of Simulated Index were calculated for the set of simulated matrices (n = 1000 simulations). Ecosim uses randomization algorithms that generate a simulated matrix. A probability test was computed to compare the observed mean niche overlap index with the overlap from the simulated matrix. We also calculated species richness between the zones using Ecosim (Acquired Intelligence Inc. Kesey-Bear, Pinyon Publishing 2011).

Determinants of wolf diet in high-altitude rangelands

To assess what factors would influence wolf diet across the zones, for prey species identified, we extracted information on the species latitudinal and longitudinal extent based on IUCN red list and available literature (Supplementary Material, Annexe 2–4). Size, height, length, home range, group size, elevation range, habitat and prey species behavior (nocturnal or diurnal) were considered as predictor variables. Prey items such as plant and insects, as well as the vegetative matter, were excluded from this analysis. Variables such as height and longitudinal extent were highly correlated with length and latitudinal extent, respectively and were excluded from the model set of predictors. Eight of ten variables were subjected to a general linear model (GLM) with main effects only with frequency of occurrence (FOO) as the dependent variable. Best-fit models were chosen from possible of 256 (2^8 variables) candidate models through an automated model selection and multi-model inference with the GLMs using *glmulti* package in R (Calcagno & de Mazancourt, 2010). Top models that described wolf prey choice were ranked as per + Δ2 within the least AICc value. The importance value for a particular predictor or its relative importance was estimated by the sum of the weights/probabilities from the models in which the variable appeared.

We used non-metric dimensional scaling (NMDS) with six environmental variables and ANOSIM with Bray–Curtis similarity index in PAST software (Hammer, Harper, & Ryan, 2001). FOO, latitudinal extent, longitudinal extent, weight, length and home range were variables considered in order to determine dietary patterns across 7 zones and different prey species.

Results

We found 22 studies (Supplementary materials – Table S1, Figs S1-S3, Annex 2) on Himalayan/Tibetan/Mongolian and Central Asian (Holarctic) wolves. There were 39 different prey items reported (Fig. 2) across the distribution of the Himalayan wolf from 2331 scats with 105.95 ± 20.71 scats per study. The mean RFO in scats of wolves for large prey was 40.01 ± 5.42%, medium prey was 23.17 ± 3.78% and small prey (including domestic) was 25.19 ± 3.85% (Fig. 3). The northernmost study that reported on wolf diet was from Dalaihu Nature Reserve, Mongolia, while the southernmost was from Wangchuck Centennial National Park, Bhutan. The western and easternmost studies that reported on wolf diets were from Chitral, Pakistan and Saihanwula Nature Reserve, Inner Mongolia, PRC. Wolves consumed domestic prey (54.92 ± 5.94%) in higher proportion in heavily grazed areas than in areas in with limited grazing (36.13 ± 6.12%). Similarly, in sites with only limited or no grazing pressures from livestock, wolves utilized more wild prey (56.62 ± 9.39%) than its domestic counterpart (32.88 ± 9.28%).

Consumption patterns and overlaps

A comparison of RFO of various prey species showed that domestic prey consumption across the zones or continent was

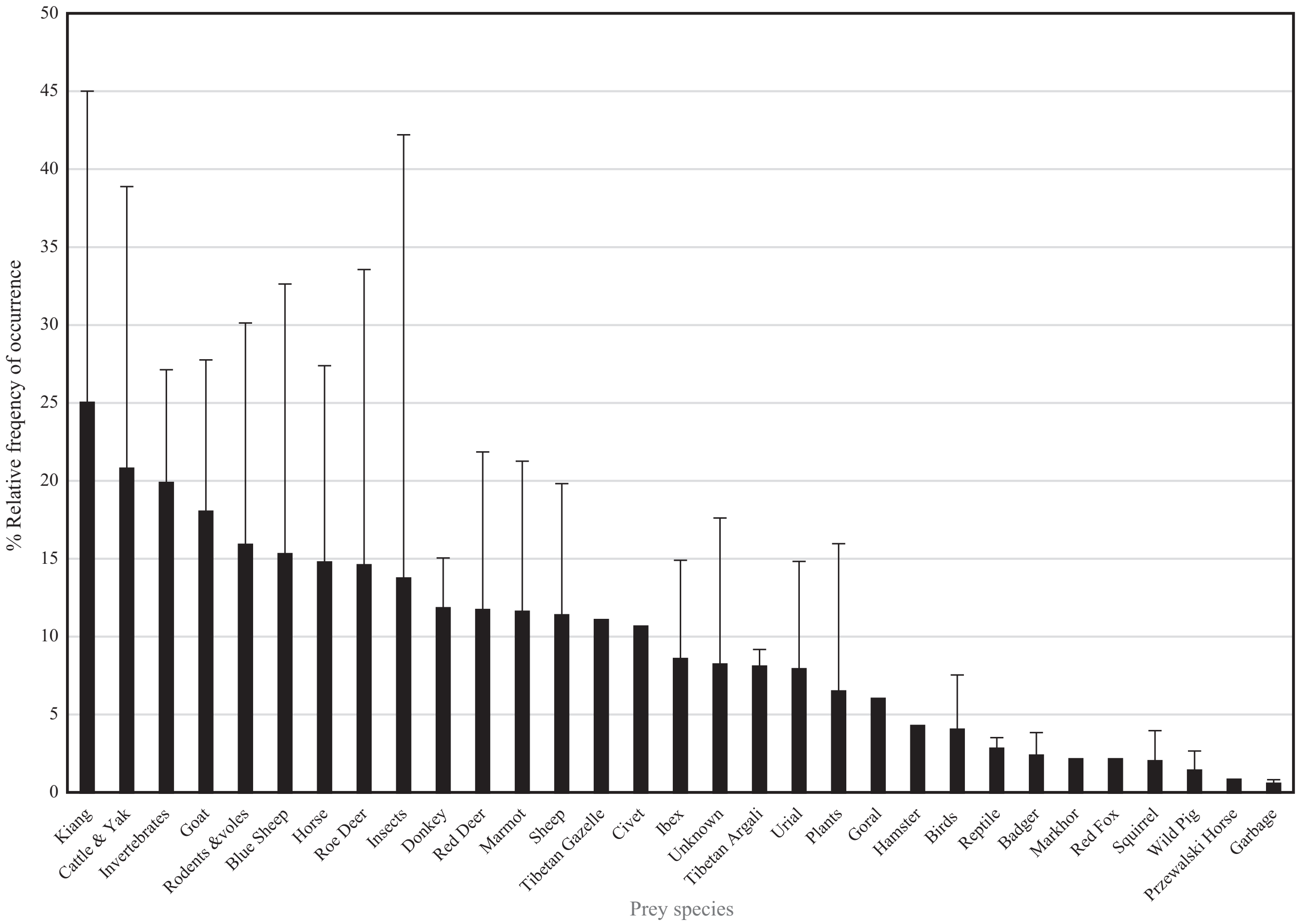

Figure 2 Dietary spectrum for collated data across 22 studies. Graphs indicate the percentage mean relative frequency of occurrence with a standard deviation of prey in wolf diet.

higher (48.21%) than the wild prey consumption (42.94%). Small wild prey species constituted approximately 24.53% of the wolf diet (Fig. 1). Wolves also relied on subsidies such as garbage or insects (mean = 11.61% ± 3.93). Although diet did not vary significantly across the seven zones, wolves chose their prey differentially between prey types (ANOVA $_{2\ \text{factor}}$, d.f. = 3, 18; P_{prey} = 0.0006; P_{zones} = 0.92). Among all zones, the highest average consumption of wild prey was reported from the Central Asian region (80.84 ± 8.34%), followed by western Himalayan zone (34.13 ± 11.12%), while the lowest was from the eastern Himalayan zone (22.66 ± 20.52%). Similarly, the average domestic prey intake was highest for the western Himalayan zone (64.18 ± 8.06%) and lowest for the Central Asian zone (14.70 ± 8.34%). Small prey was the highest consumed component in the QTP region (47.06 ± 10.94%). Other subsidies like plants and invertebrate prey were highest for the Central Asian zone (40.19 ± 2.29%, Figs 1 and 4).

Diet overlaps (diet similarity) across zones was 29.86% (± 2.04). Simulated indices were estimated to be 19.33% (± 0.04). Observed mean niche overlap was significantly greater than expected by chance ($0.99 \leq P \leq 0.003$). The standardized effect size was 3.88. The observed variance was not statistically different from the null model ($0.21 \leq P \geq 0.78$). The highest overlap was between eastern Himalayan and western Himalayan zone (61%). The lowest overlap was between eastern Himalayan and inner Mongolian zone (0.05%). ANOSIM showed that there were no significant differences in the dietary patterns of the wolves across the study areas ($P = 0.09$, mean rank between = 1182, mean rank within = 1129).

Determinants of Prey Choice and Regional patterns

Out of 256 candidate models (Supplementary Material, Table S4-S5, Annex 6), the best-fit model showed that the *'home range'* ($t = 2.91$, $P < 0.05$) and '*length'* were the best predictors of prey consumption, 'FOO' (*AICc = 201.33, p = 0.005,* $R^2_{adj} = 0.25$*)*. Across all possible models (taking their relative weights into consideration), multi-model inference estimated variable '*home range'* was a consistent predictor (92.34%, $P = 0.002$, Fig. 4), followed by longitudinal extent ('*longex*' = 48.78%, $P = 0.03$) and '*length'* (36.77%, $P = 0.06$, Supplementary Information Table S4-S5, Fig. S1, Annex 6-7). Wolves preferred large and ubiquitous prey as explained by 'home range' and 'longitudinal extent', which were important contributors to the diet choice among various studies.

Ordination (NMDS) revealed 97.8% and 11.4% of the information on the first axis and second axis, respectively, with 0.029 stress (Fig. 5). The latitudinal and longitudinal extent showed a strong positive relationship with both the axis, while the home range showed a negative correlation. Length, weight and size of prey showed a negative relation with *axis 1* and positive with *axis 2*. The zones, that is, Eastern Himalaya, Central Asia, Western Himalaya and Central Himalayan areas aligned positively toward large wild and domestic prey. On the other hand, wolf diet from the regions of Qinghai–Tibetan Plateau, Inner Mongolia and the Karakoram showed affinities for mostly smaller-sized prey and livestock, as they were closer to groups of species that had large latitudinal and longitudinal extents.

Overall prey preferences

Wolves of the high rangelands of Asia utilized domestic livestock more than wild prey. *Equus ferus przewalskii* (IVI: 0.94 ± 0.42, Fig. 6) was utilized the most with respect to its availability, followed by *E.f.cabbalus* (IVI: 0.85 ± 0.30) and *Bos* spp (IVI: 0.69 ± 0.14). Among the wild species, *Cervus elaphus* (IVI: 0.22 ± 0.34) and *Marmorata* spp (IVI: 0.33 ± 0.22) were also utilized positively. Wolves of the Asian Highlands underutilized Naemorhedus *goral* (−0.99 ± 0.41), *Ochotona* spp (IVI: −0.87 ± 0.27) and wild prey (Table 1, Fig. 6).

Discussion

Our study observed that Himalayan wolves, like other Highland wolves of Asia, significantly utilized domestic prey. This result is consistent with the conclusions of earlier studies as well (Hovens & Tungalaktuja, 2005; Newsome *et al.*, 2016). The differences in broad prey type (wild, domestic, small wild prey and other subsidies) consumed across the Himalayan wolf range and other non-Himalayan wolf ranges (Central Asia) were not significant. This could be attributed to a high quantity of domestic prey overlaps in the wolf diet across these rangelands. However, wolves still utilized wild prey in larger quantity in some areas where livestock grazing occurred in limitation. Our results indicate that wolf populations may be facing extreme threat due to extensive dependence on domestic prey and consequent livestock depredation related conflicts in much of its range. These regions are mostly low in productivity and highly overstocked. As conflict levels are difficult to ascertain from scatological analysis alone future investigations of such aspects may provide a more in-depth perspective.

Prey consumption patterns: a comparison

The wolf is known to be a euryphagous animal that can feed on wild and domestic prey (Bibikov *et al.*, 1983). Existing studies have reported a range of values (25 to > 70%) of the percentage composition of domestic prey (RFO) in wolf diet (Figs 1–3). In the regions of Spiti (WH), Chiktan (WH) and Chitral (KA), wolf conflicts may be very high due to lack of wild prey and increasing anthropogenic threats such as overstocking (Bagchi & Mishra, 2006; Suryawanshi *et al.*, 2013). Many studies in trans-Himalaya have reported a low abundance of natural prey and poor livestock husbandry techniques resulting in depredation by large predators (Jackson & Ahlborn, 1989; Mishra, 1997; Anwar *et al.*, 2011; Subba, 2012; Boitani, Phillips, & Jhala, 2018). In certain cases, livestock depredation levels may be an outcome of individual pack traits as well (Kudatkin 1979 in "Wolves of the World," Mech & Boitani, 2010). On the other hand, Central Asian wolves may still have high wild prey available to consume. Historically, wolves have been known to feed on the saiga

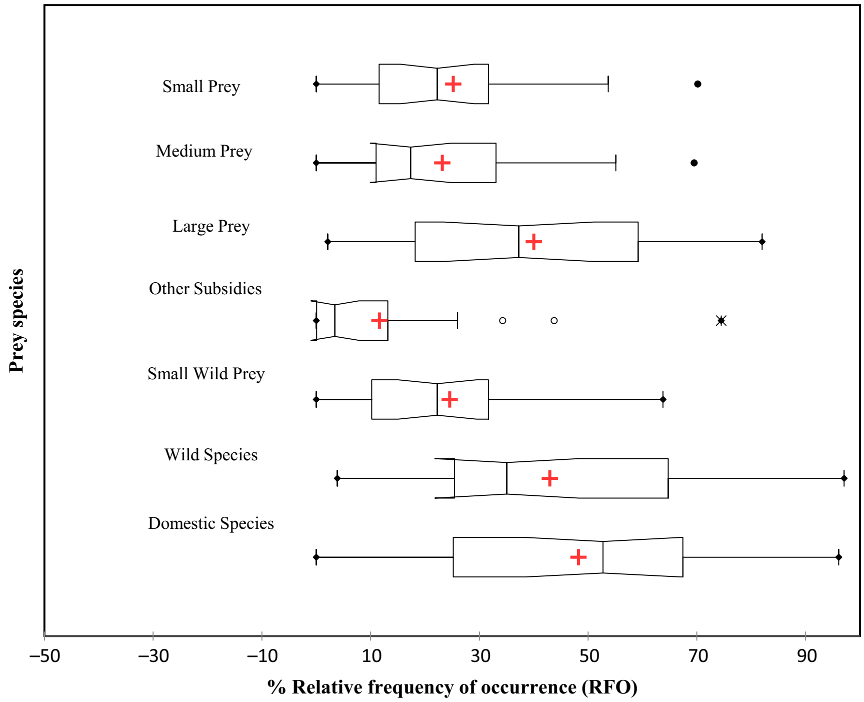

Figure 3 Box plot showing relative frequencies of overall prey type consumption by Wolves of Asian High rangelands. Red crosses denote mean of the point. Black dots indicate outliers. Lines indicate the range. Bounds indicate 1st and 3rd quartile range.

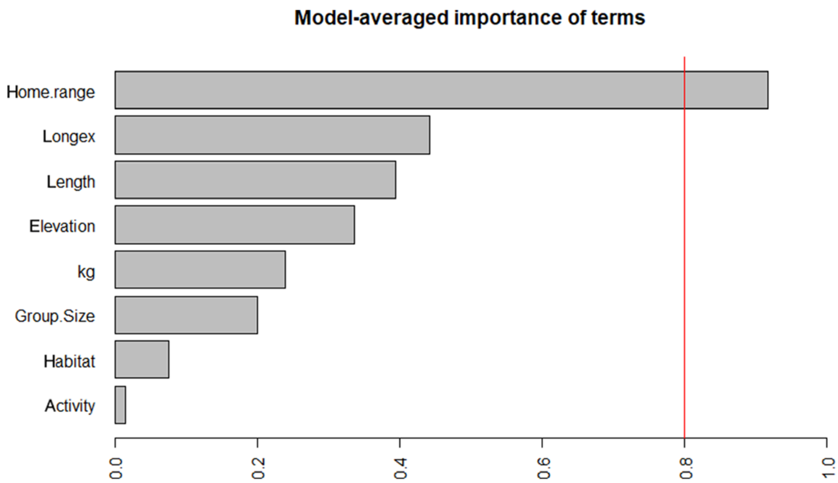

Figure 4 Multi-model inference showing relative weights of predictors. Home range and longitudinal extent (*longex*) of species were the most important contributors in the diet of Himalayan wolves.

antelope (*Saiga tartarica*), argali (*Ovis ammon*) and also roe deer (*Cervus elaphus*) in the Central Asian highlands, although we did not come across any study related to saiga consumption (Bibikov, 1973).

Diet And human-Wolf conflict

Wolves are known to choose their prey based on wild prey abundance, vulnerability, pack stability, dispersal nature, habitat accessibility and husbandry regime in human-dominated landscapes (Imbert *et al.*, 2016). Patterns of wolf diet across these regions show that wolves consumed mostly large and domestic prey (40% and 48.21%, respectively). The adaptability of wolves in human-dominated landscapes and conflict perceptions in socio-cultural context may vary. For example, in the Spiti valley in India, despite high depredation levels of local livestock (66%), predominant socio-religious sentiments, indifference and awareness allow wolves to co-exist

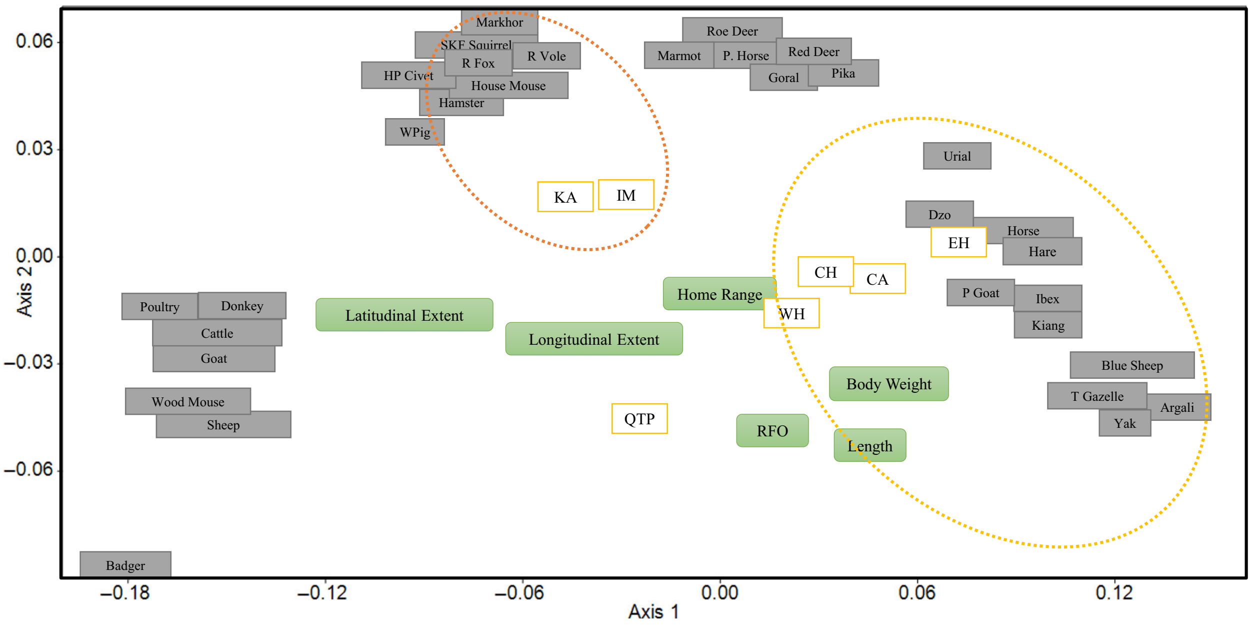

Figure 5 NMDS plot showing regional prey choices in various zones. Zones are indicated as KA – Karakoram and Pamirs, IM – Inner Mongolia, EH – Eastern Himalaya, CA – Central Asia, CH – Central Himalaya, WH – Western Himalaya, QTP – Qinghai–Tibetan Plateau. Environmental variables considered were the home range, body weight, length, RFO – Relative Frequency of Occurrence, longitudinal and latitudinal extent.

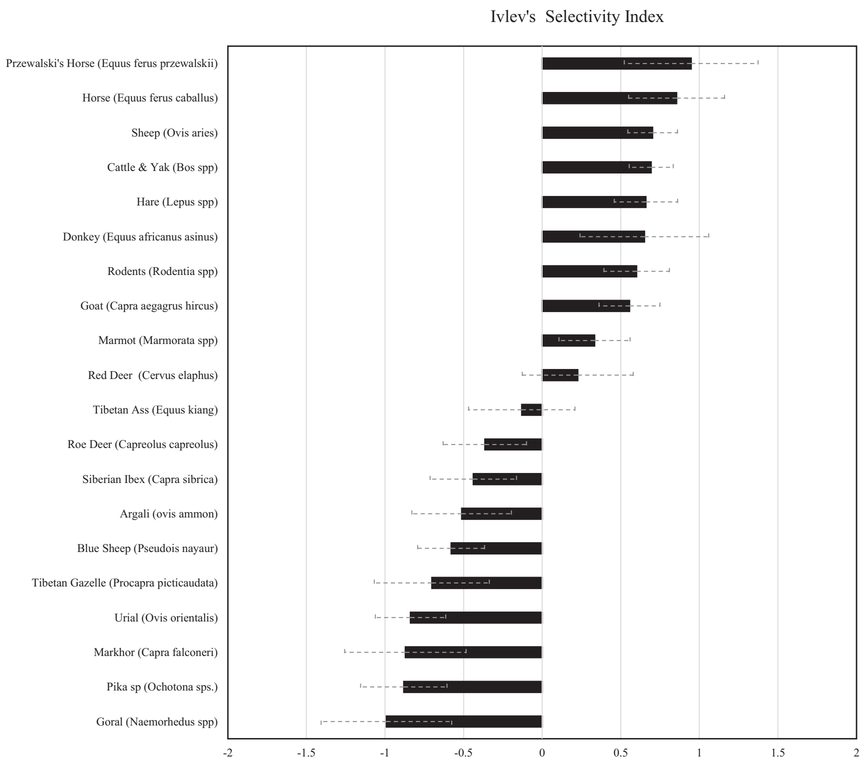

Figure 6 Ivlev's selectivity Index for various prey species.

Table 1 Prey Size class and Ivlev's index of prey preference positive indicates utilized more than available and vice versa

Prey (*N*)	Scientific name	Prey size class	% Relative Frequency of Occurrence (RFO)	SD+1	Preference	SE
Kiang	*Equus kiang*	Large	25.00	20.02	-0.13	0.34
Cattle & Yak	*Bos spp*	Large	20.76	18.12	0.69	0.14
Invertebrates		Other subsidies	19.85	7.28		
Goat	*Capra aegagrus hircus*	Medium	18.00	9.76	0.56	0.19
Blue Sheep	*Pseudois nayaur*	Large	15.29	17.35	−0.58	0.21
Horse	*Equus ferus caballus*	Large	14.75	12.64	0.86	0.30
Roe Deer	*Capreolus capreolus*	Medium	14.57	18.99	−0.36	0.26
Insects		Other subsidies	13.71	28.50		
Donkey	*Equus africanus asinus*	Large	11.81	3.25	0.65	0.41
Red Deer	*Cervus elaphus*	Large	11.69	10.16	0.23	0.35
Marmot	*Marmorata spp*	Small	11.58	9.69	0.33	0.23
Sheep	*Ovis aries*	Medium	11.36	8.46	0.70	0.16
Tibetan Gazelle	*Procapra picticaudata*	Medium	11.05		−0.70	0.37
Civet		Small	10.63			
Rodents &voles	*Rodentia spp*	Small	9.40	7.52	0.60	0.21
Lepus spp	*Lepus spp*	Small	8.87	10.59	0.66	0.20
Ibex	*Capra sibrica*	Large	8.55	6.35	−0.44	0.27
Unknown		Other subsidies	8.20	9.41		
Tibetan Argali	*ovis ammon*	Large	8.06	1.12	−0.51	0.32
Urial	*Ovis orientalis*	Large	7.90	6.93	−0.84	0.22
Plants		Other subsidies	6.47	9.50		
Goral	*Naemorhedus goral*	Medium	6.00		−0.99	-0.42
Birds		Small	4.02	3.52		
Reptile		Small	2.79	0.73		
Badger		Small	2.35	1.49		
Markhor	*Capra falconeri*	Large	2.12		−0.87	0.39
Red Fox	*Vulpes spp*	Small	2.12			
Squirrel		Small	1.99	1.97		
Wild Pig	*Sus scrofa*	Large	1.40	1.27		
Przewalski Horse	*Equus ferus przewalskii*	Large	0.80		0.95	0.43
Garbage		Other subsidies	0.54	0.27		
Pika	*Ochotona spp*	Small	2.97	2.00	−0.88	0.27

(Rangarajan, 2005; Agarwala *et al.*, 2010). In Mongolia, since the herdsmen were aware of co-existing wolves, techniques such as close guarding of livestock caused wolves to switch back to wild prey predation (Van Duyne *et al.*, 2009). Likewise, in many parts of Central India, Kyrgyzstan and Mongolia, vigilant packs or individuals have been able to survive amidst human persecution and proximity.

Consequences of conflict due to prey un-availability can also hinder key conservation goals. For example, predation due to lack of prey by wolves on localized and threatened endangered animals such as Przewalski's horse in Mongolia is of critical concern. Therefore, it is essential to address prey restoration and livestock security to reduce conflict and achieve conservation goals (Bibikov *et al.*, 1983; Bhatnagar *et al.*, 2006; Suryawanshi *et al.*, 2017; Ghoshal *et al.*, 2018).

Characteristics of wolf prey in the Asian highlands

Energetic constraints of large carnivores make them prone to conflict as they need large prey (Carbone *et al.*, 1999). Our study observed that wolves preferred large and ubiquitous prey in general. This is also evident from the biomass consumed per scat, which showed higher returns from consuming large prey (50–200 kg, Fig. 2. Supplementary material, Annex 8). Twelve out of twenty-two studies showed that at least 50% of wolf diet consisted of domestic livestock. However, we also found seven studies that showed considerable wild prey utilization (56.62%) from sites that had limited domestic grazing pressures. Areas like Hustai, Wangchuk and Sarychat-Ertash where limited grazing pressures exists, natural wild prey can thrive. Interestingly, wolves in Chitral (Shabbir *et al.*, 2013) and Qinghai–Tibetan Plateau (Liu & Jiang, 2003) significantly utilized small prey (>40%). In the Qinghai–Tibetan Plateau, until 1989, prohibitory laws against hunting were non-existent (Jiang *et al.*, 2012). About 1.5 million wild animal skins, 271 742 wildfowl and 2.6 million tonnes of game meat were sold between 1965 and 1975 (Jiang *et al.*, 2012). As a result, large prey may have become scarce for wolves. This may have led to their increased dependence on domestic or smaller prey in the region (Liu & Jiang, 2003; Imbert *et al.*, 2016; Suryawanshi *et al.*, 2017).

Conclusions

Wolves are top predators and require large landscapes. As a generalist species, wolves also have wide-ranging ecological roles in such systems. It is important to recognize that in the long run, for the survival of such species; reduction in conflict with humans; habitat and prey restoration is crucial. In the case of the Himalayan wolf, a true Asian wolf and most basal lineage among all wolves, a trans-boundary strategy for prey and its protection or management in some areas to increase acceptance and conserve the species within its exclusive range is needed. Greater number studies on wolves with respect to its food web ecology; prey-predator dynamics and encouraging community participation for human-wolf conflict mitigation in such sensitive landscapes are advocated at policy and managerial levels.

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