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Himalayan wolf foraging ecology and the importance of wild prey

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ABSTRACT

Carnivore predation on livestock and game species leads to human-carnivore conflict. Thus, understanding the foraging ecology of threatened carnivores is important for conservation planning. We explore the summer diet of the Himalayan wolf, and of sympatric carnivores, based on the analysis of 257 field collected and genetically confirmed scat samples collected across three study areas in the Himalayas of Nepal (Humla, Dolpa, and Kanchenjunga Conservation Area) and two study areas on the Tibetan Plateau of China (Zhaqing and Namsai Township). We compared the prey species consumed to the relative availability of wild and domestic prey species. Himalayan wolves tend to select wild over domestic prey, smaller (e.g. Tibetan gazelle, *Procapra picticaudata*) over larger sized wild ungulates (e.g. White-lipped deer, *Cervus albirostris*), and plains-dwelling (Tibetan gazelle) over cliff-dwelling ungulates (naur, *Pseudois nayaur*). Tibetan gazelle was consistently selected for by the Himalayan wolf and smaller mammals such as Himalayan marmot (*Marmota himalayana*), woolly hare (*Lepus oiostolus*) and pikas (*Ochotona* spp.) are important supplementary food resources. Himalayan wolves avoided livestock which showed a seasonal high abundance, that exceeded many-fold the abundance of wild prey species during the summer study period. Given this seasonally high livestock abundance, depredation by Himalayan wolves is inevitable and a major conservation concern. Habitat encroachment and depletion of wild prey populations are important drivers of this conflict. But we found that livestock was avoided when wild prey was available, a finding that can direct conservation. We conclude that the protection of Himalayan wolves, and other sympatric carnivores can be enhanced by a) securing healthy wild prey populations (ungulates and small mammals) through setting aside wildlife habitat refuges, and b) more sustainable livestock herding including reduced livestock loads and improved herding practices and protection.

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1. Introduction

Wolves (*Canis lupus*), like other large carnivores, come into conflict with humans. At the root of human-wolf conflict is the wolf's predatory habit, and therefore competition with humans over livestock and game (Naughton-Treves et al., 2003; Newsome et al., 2016). This requires conservation management strategies that foster coexistence with an increasing human population (Treves and Karanth, 2003). Any such strategies must be multifactorial, delivering healthy wildlife populations and habitats, and sustainably managed livestock loads, pastureland use, and livestock protection, and requires a good understanding of carnivore foraging ecology. After centuries of wholesale wolf eradication grey wolf populations are recovering in North America and Europe, partly motivated by the perceived benefits of their ecological services (Newsome et al., 2016; Ripple et al., 2014, 2013; Ripple and Beschta, 2012).

Himalayan wolves are a genetically distinct wolf lineage unique to the Asian high altitudes of the Himalayas and the Tibetan Plateau (Werhahn et al., 2018a); habitats which are recognised as a biodiversity hotspot (Lamoreux et al., 2006; Olson and Dinerstein, 1998; Pimm et al., 2014; Watson et al., 2016). The Himalayan wolf is increasingly being recognised as a taxon in need of protection (Werhahn et al., 2017a) but little remains known of its ecology or populations status. Evidence of its phylogenetic uniqueness is mounting (Aggarwal et al., 2007; Sharma et al., 2004; Shrotryia et al., 2012; Werhahn et al., 2017b, 2018a, 2019). The Himalayan wolf's taxonomic classification is pending but recently recommended as *Canis lupus chanco* until full genomes verify the existing evidences which all indicate species eligibility (Álvares et al., 2019; Werhahn et al., 2017b, 2018a, 2019). Besides these wolves, snow leopards (*Panthera uncia*) and red foxes (*Vulpes vulpes*) are important carnivores in these high-altitude ecosystems (Jnawali et al., 2011). Snow leopards and wolves are reported to be the main depredation conflict causing carnivores (Chetri et al., 2017; Kusi et al., 2019; Suryawanshi et al., 2014) but only snow leopards receive scientific and conservation attention (Devkota et al., 2013; Lyngdoh and et al., 2014; McCarthy and Mallon, 2016; Oli, 1993). And the red fox is a smaller mesopredator less studied in the region (Hoffmann and Sillero-Zubiri, 2016).

We focus our investigation on the Himalayan wolf's foraging ecology across the Himalayan range of Nepal and on the Tibetan Plateau in Sanjiangyuan National Nature Reserve in Qinghai, China. We then compare the diet of wolf and snow leopard to shed light on the depredation conflict which is similarly reported for the two species but receives differing attitudes by local people (Kusi et al., 2019). We further include the red fox, a little studied mesopredator in this region (Hoffmann and Sillero-Zubiri, 2016), to understand dietary niche partitioning among these three important Himalayan carnivores. We hypothesize that the wolves and snow leopards share diets high in ungulate content with a high dietary niche overlap where the relative amounts of livestock and wild prey consumed reflect their respective abundance in the landscape. Whereas the red fox is hypothesized to forage mainly on smaller wild mammal species with little livestock consumed.

We report on these carnivores' estimated summer diet and relate what they consumed to the relative abundance estimates of the respective prey species in the habitats. We thereby deliver insights into important prey species for the Himalayan wolf, reveal prey selection and avoidance, including characterisation of livestock depredation in the high-altitude habitats, and thus draw conservation inferences.

2. Methods

2.1. Study areas

We collected data in three study areas in the Himalayas of Nepal and two study areas in Sanjiangyuan National Nature Reserve of the Tibetan Plateau of Qinghai, China (Fig. 1 and Table 1). Humla and Dolpa are situated within the arid zones of the Nepalese Himalayas and comprise alpine grasslands and alpine steppe habitats, while Kanchenjunga Conservation Area (KCA) is situated within the Inner Valleys of the eastern Himalayas (Miehe et al., 2016). Zhaqing and Namsai Township (Zadoi County, Yushu Prefecture, Qinghai) are situated on the Tibetan Plateau. Carnivore species in these high-altitude habitats include the Himalayan wolf, snow leopard, red fox, Tibetan fox (*V. ferrilata*), Pallas's cat (*Otocolobus manul*), Eurasian lynx (*Lynx lynx*), brown bear (*Ursus arctos*), and domestic dog (*Canis familiaris*). Wild prey species observed in the study areas include kiang (*Equus kiang*), naur, Tibetan gazelle, Tibetan argali (*Ovis ammon hodgsoni*), white-lipped deer *(Cervus albirostris)*, and the smaller Himalayan marmot, woolly hare, several species of pika (*Ochotona* spp.), and rodents. Livestock species kept in the study areas were yak (*Bos grunniens*), jhoppa (yak-cow hybrid, *Bos grunniens-Bos taurus*), horse (*Equus ferus caballus*), goat (*Capra hircus*), and occasionally sheep (*Ovis aries*) (Fig. 2). Livestock is usually brought up to the summer pasture lands from May to September. The herding regime varies according to species: Yaks and their hybrids are usually kept in small (5–10 animals) to larger (10–100 animals) herds with a herder loosely present in the vicinity. Smaller stock like goats and sheep are usually kept in larger herds of 25–100 (but up to 300) animals and are generally much closer herded and guarded compared to yaks. Horses, mostly used as a means of transport, are left unguarded in the pasture lands for multiple months at a time in small groups of 2–6 animals.

2.2. Sample collection and preparation

We opportunistically collected samples across the Nepalese Himalayas and the Tibetan Plateau that were then genetically tested for species identification. This led to a total of 257 included scat samples collected during the summer season, 240 samples from the Nepalese Himalayas and 17 from the Tibetan Plateau (Table 2). In Nepal we collected scats also from other

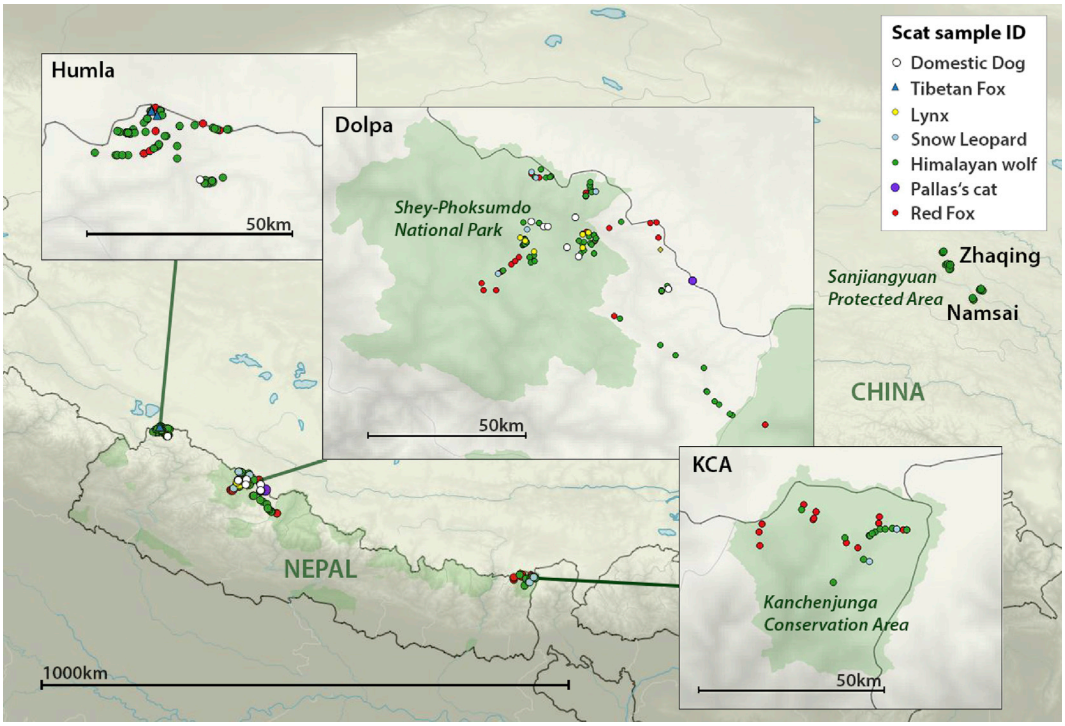

Fig. 1. Study areas in Nepal: Humla (currently situated outside the Nepalese national protected area system), Dolpa (within Shey-Phoksundo National Park), and KCA (a community managed Conservation Area). Study areas in China: Zhaqing and Namsai Townships in Sanjiangyuan National Nature Reserve, Tibetan Plateau of Qinghai Province.

carnivores such red fox, Tibetan fox, snow leopard, Eurasian lynx, domestic dog, and Pallas's cat (Fig. 2). Wolf samples were identified in the field according to scat appearance (size and form) and odour (wolf scats have a characteristic odour that aids identification). These were later verified by mtDNA analysis, as field misclassification can be high (Chetri et al., 2017; Jumabay-Uulu et al., 2014; Weiskopf et al., 2016). Genetic samples were swabbed from the surface of the tapering scat end and stored in an isohelix solution (for details refer to Werhahn et al. (2017b)). Diet samples were stored in paper envelopes and thoroughly sun-dried. They were then washed to dissolve the soluble remains by wrapping each sample individually in a stocking and rinsing it with water. This left only the insoluble scat contents such as hair, bones, soil, stones, vegetation and other solid fragments, which were thoroughly dried in preparation for microscopic analysis.

2.3. *Microscopic dietary analysis*

We built a hair reference collection for all potential domestic and wild prey species found across the study areas. We used a modified point-frame method (Ciucci et al., 2004) to randomly select 40 diet items (hair, bone, stones, etc.) per sample. We scattered each scat sample on a gridded tray and selected the item at each grid intersection with tweezers for identification. These hair items were fixed to a slide with nail polish and inspected under a microscope (Bresser Science TRM-301,40x-1000x) at 40x magnification. The hairs were assigned to consumed species based on cuticular cell arrangements, medullary patterns, relative lengths and overall appearance with our reference collection (supplementary material S2) and literature (Bahuguna et al., 2010; Ciucci et al., 2004; Klare et al., 2011; Oli, 1993; Teerink, 1991). Bone items, tissue fragments and larger plant material was stored in annotated plastic bags. For the microscopic analysis of the Nepalese samples we worked in a pair with two microscopes which allowed cross-verification in case of doubt. A systematic crosscheck whereby both observers scored the same samples ($n = 9$) resulted in a confidence of >90% overlap in assigning the hair in scats to the same species.

Vegetation included any kind of plant material and was commonly entire grass/sedge blades. Rodents, pikas (*Ochotona* spp.), and insectivores were pooled in a ‘small mammal’ category, whereas yak, cows and jhoppa were pooled in a ‘yak/cow’ category.

2.4. *Statistical analysis of diet data*

To determine the adequacy of overall sample size and sample size per study area we calculated the Brillouin's index (Brillouin, 2013) for each sample, ran a bootstrap resampling for 1000 samples, and then determined sample size at which an

Table 1
Study areas and details of distance transects and field observed wild prey species. Transects were spatially replicated with two transects per grid.

Study Area	Year	Month	Elevation (m)	Study area size (km^2)	No. of transects	Transect length (km)	Wild prey species observed
Humla (Nepal)	2015	Jul/Aug	4560 −5120	384	38	57	kiang, Tibetan gazelle, Tibetan argali, Himalayan marmot, naur, woolly hare
Dolpa (Nepal)	2016	May/Jun/ Jul	3850 −5540	1088	153	230	Tibetan argali, Himalayan marmot, naur, woolly hare
KCA (Nepal)	2016	Sept	3980 −5150	368	50	75	Himalayan marmot, naur, woolly hare
Namsai (China)	2017	Aug	4360-4770	175	12	18	Himalayan marmot, naur, woolly hare
Zhaqing (China)	2017	Aug	4380 −4800	452	31	47	white-lipped deer, Himalayan marmot, naur, Tibetan gazelle, woolly hare

Fig. 2. Carnivores and their prey considered in this study: A) Himalayan wolf, B) snow leopard, C) Eurasian lynx, D) red fox, E) Tibetan fox, F) domestic dog (Tibetan mastiff). Herbivore species found in the study areas: G) Naur, H) Tibetan argali, I) Tibetan gazelle, J) Kiang, K) Himalayan marmot, L) Plateau pika (*Ochotona curzoniae*), M) Woolly hare, N) White-lipped deer, O) domestic yak, P) domestic horse, Q) domestic goat (Photographs by GW). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Overview of genetically verified samples and species per study area.

Species/Study area	Humla	Dolpa	KCA	Namsai	Zhaqing	Total
Himalayan wolf	69	77	13	9	8	176
Snow leopard[a]	0	5	3			8
Red fox	13	28	14			55
Eurasian lynx[b,a]	0	6	0			6
Pallas's cat[b,a]	0	1	0			1
Tibetan fox[c,a]	3	0	0			3
Domestic dog	1	7	0			8
TOTAL	**86**	**124**	**30**	**9**	**8**	257

[a] Sample size less than N = 10.
[b] Reported in Werhahn et al. (2018b).
[c] Genetic findings reported in Werhahn et al. (2016).

asymptote was reached for diet diversity in the plot of H_b versus increasing sample size according to the methods applied in Imbert et al. (2016). For the statistical analysis of the dietary data we used the following categories: naur, kiang, Tibetan gazelle, Tibetan argali, woolly hare, white-lipped deer, Himalayan marmot, small mammal, goat, yak/cow, horse, vegetation, stone, soil, and plastic. We calculated the Frequency of Occurrence (FoO) per food item and biomass of food consumed according to the recommendations of Klare et al. (2011). Both approaches have their advantages and limitations: FoO may over-represent small mammals as it does not reflect the relative proportion of items ingested, which can be better approximated through biomass models, while biomass models have limitations based on the study animals used for developing the models (Klare et al., 2011). For the biomass model calculation we used the relative frequency as equivalent of relative volume and used the later in the biomass calculation model developed for grey wolf based on feeding trials (Floyd et al., 1978; Weaver, 1993). To estimate food ingested per prey species we used the biomass calculation by Weaver (1993) Bio_{Wea}: $Y = 0.439 + 0.008X$, where Y = the biomass of prey consumed to produce a scat, and X = the average body weight of each prey species. This model is a refinement of the model developed by Floyd et al. (1978). For snow leopards we used the model by Ackerman et al. (1984). For red foxes we used the model coefficients used by Rühe et al. (2008). We calculated the dietary niche breadth with the Levins Index: $B = 1/(\sum pi^2)$, where pi is the relative frequency of ingested food item by predator p (Colwell and Futuyma, 1971; Levins, 1968). For the dietary niche overlap between the Himalayan wolf, red fox and snow leopard we used the Pianka Index (Pianka Index ranges from 0 to 1, from no overlap to complete overlap) (Loveridge and Macdonald, 2003; Pianka, 1975, 1973). We calculated the Jacobs Index for assessing prey selection versus avoidance based on the relative biomass eaten relative to the biomass availability of the same ungulate in the study area (Bocci et al., 2017). We then performed a bootstrap resampling with 1000 replicates to estimate mean and confidence interval for the Jacobs index, to check if '0 = no selection' falls within the confidence limits.

2.5. Abundance of wild and domestic prey

Prey abundance estimation of wild and domestic ungulate prey in the landscapes was conducted with distance sampling (Buckland, 2004). The distance samples were collected by visual detection while walking along two randomly placed 1.5 km long transects per grid with the two transects representing spatial replication. Transects were conducted in the morning and late afternoon to evening hours when generally herbivores are most active. Grid cell size in Nepal (Humla, Dolpa, and KCA) was 4 × 4km, while in China (Zhaqing and Namsai Township) it was 5 × 5km. Wherever possible we placed the distance sampling transects randomly in the grids through pre-assigned random starting points. Field logistics and landscape features (e.g. cliffs) did however at times constrain transect layout and forced us to situate them along more feasible features such as valley floors. These transect layout constraints occurred at random across the study areas and remain a possible source of bias in our estimates of ungulate densities. The distance sampling data were analysed with the package 'unmarked' in R (Chandler et al., 2011). For all assessed ungulate species we used the same model with a half-normal detection function. For each transect we also noted human pressure as represented by number of humans sighted and mean elevation.

Relative abundance of marmots across study areas was estimated by counting the number of burrows within a radius of 10 m (~314.2 m^2 of area) at the start, the midpoint and the end of the distance sampling transects, and the number of direct sightings along the entire transect. The counted burrows and direct sightings were summed into a relative marmot index per distance sampling transect which in turn was averaged per study area.

3. Results

Collected scats were correctly field assigned to the genetically verified carnivore species in 76% of scats from Dolpa, in 82% of scats from Humla, and in 64% of scats from KCA. The samples incorrectly assigned in the field were between wolf, snow leopard, red fox and Tibetan fox. Our overall sample size of 176 wolf samples was large enough to draw dietary diversity inferences from our data given the minimum sample size across all study areas as indicated by the Brillouin Index being 96 samples. The sample size was also sufficient for the Nepalese study sites (i.e. a minimum of 68 required for Dolpa, 68 for

Humla, and 9 for KCA) but sample size for the two sites in Qinghai (minimum of 49 needed for Namsai, and 81 for Zhaqing) was not sufficient for robust statistical analysis and hence the results for Namsai and Zhaqing are to be considered as preliminary trends. An overview of the genetic identification of species producing each scat is given in Table 2, while dietary results are reported in Tables 3 and 4. Plant parts from the genus *Myricaria* ssp. were found in three wolf scats resulting in a FoO of 1.88 for the wolf scats.

Himalayan wolf individuals sampled in Qinghai China had the widest dietary niche breadth (Levins Index = 5.65; N = 17), followed by wolves in Nepal (Levins Index 5.12; N = 159), snow leopards (Levins Index = 3.25; N = 8, but note the sample size <10) and the meso-predatory red fox with a more narrow dietary niche (Levins Index = 1.86; N = 55). The red fox scats contained mainly marmots, woolly hare and small mammals.

Pianka Index for dietary niche overlap between carnivores in Nepal was 0.19 for the Himalayan wolf and the red fox, and 0.81 for the Himalayan wolf and the snow leopard.

The Jacobs Index indicates a tendency for the Himalayan wolf to select wild prey over livestock, and to select for the smaller plain dwelling Tibetan gazelle, a trend supported in the study areas and the mean over all study areas (Fig. 3 and Supplementary Material Table S1). Livestock was very abundant in all study areas during the summer and exceeded the biomass of wild prey several fold (Supplementary Material Table S1). However, the average Jacobs index and 95% confidence interval for 1000 bootstrap resamples was −0.17 ± 0.01, hence indicating a slight negative bias in our Jacobs Index data. This may be a result of the large livestock numbers in the landscape, which were generally avoided, and thereby leading to larger negative Jacobs indices, when compared to the values found for wild prey.

4. Discussion

Our study confirms our hypothesis of a high dietary niche overlap between Himalayan wolves and snow leopards, whereas red foxes tend to feed on smaller wild prey species. Contradictory to our hypothesis of wolves feeding on livestock and wild prey relative to their abundance in the landscape, we find that Himalayan wolves tend to select for wild ungulates and avoid livestock.

Specifically, across our study areas we found a tendency of the Himalayan wolf to 1) select wild prey over livestock, even though the seasonal relative biomass of livestock exceeded that of wild prey several fold, and to 2) select for the small plains-dwelling Tibetan gazelle (13.2–15 kg, Jacobs Index = 0.94), followed by the larger plains-dwelling kiang (250–400 kg, Jacobs Index = 0.64), whereas the selection for the cliff-dwelling naur (35–75 kg, Jacobs Index = −0.06) was positive in the Nepalese study sites but negative in the study areas on the Tibetan Plateau which however only indicate a preliminary trend due to the low sample size in Namsai and Zhaqing. This trend may possibly be driven by the higher availability of Tibetan gazelle in the latter study areas (Fig. 3). The Tibetan gazelle is a comparably small wild ungulate found across the Tibetan plateau (IUCN SSC Antelope Specialist Group, 2016) with its distribution range approximately corresponding to that for the Himalayan wolf (Werhahn et al., 2018a). The Holarctic grey wolf shows a comparable tendency towards smaller sized ungulate prey species (e.g. roe deer *Capreolus capreolus* (10–25 kg) selected in Europe (Hosseini-Zavarei et al., 2013; Marucco et al., 2008; Reig and Jedrzejewska, 1988; Rigg and Gorman, 2004), and white-tailed deer *Odocoileus virginianus* (40–125 kg) in North America (Fuller, 1989)). Marmots are an important summer food source of the Himalayan wolf (Table 4) and similarly other smaller mammals such as woolly hare, pikas, and rodents may be important year-round sources.

Where Tibetan gazelle are absent or rare, other wild prey are selected, e.g. kiang and naur in Humla, and naur in Dolpa. The cliff dwelling Tibetan argali was present at low numbers and only occasionally sighted in Humla and Dolpa (Kusi et al., 2018; Werhahn et al., 2015), but never found in the wolf scats. Similarly, white-lipped deer, despite being locally abundant in the two Tibetan study areas, was not represented in the Himalayan wolves' diet. Indeed, grey wolf pack size is likely correlated with local prey size (Fuller, 1989; Jędrzejewski et al., 2002). The observed Himalayan wolf packs (mean five animals - Werhahn et al., 2017a) are smaller than grey wolf packs (6–12 animals, Sillero-Zubiri et al., 2004), possibly reflecting relatively small prey size.

Goats are an appropriately sized prey for wolves, but they were intensively tended by herders. Goats were avoided across the study areas with the exception of Dolpa. Their representation in the wolf diet in Dolpa might be related to the limited wild ungulate community there, with a low density of naur and the biomass of wild prey dwarfed by that of livestock (41.7 times the biomass of livestock vs. wild ungulates). Our results show that yaks and yak-cow hybrids are frequently consumed by the wolves in all study areas, and indeed were ubiquitously present at high densities. Yaks are less rigorously tended than goats. A herdsman generally accompanies yaks, but the herd disperses over a large area while calves are seasonally abundant. Liu and Jiang (2003) studied wolf diet in Qinghai Tibet and found that yak, hare and small rodents are the important prey species of these (presumed Himalayan) wolves in the summer, and yak, sheep and hare in the winter. The authors found few seasonal differences in the wolves' diet and concluded that livestock remains in the wolves' scats can largely be attributed to scavenging on the grounds that few livestock went missing during the study period. Doubtless carcasses were available to the wolves in the harsh high-altitude conditions of our study sites, but the proportion of scavenged food to fresh kills cannot be discerned by scat analysis. The yak remains in red fox scats surely originate from scavenged carcasses. Insofar as our study reports on Himalayan wolf diet only during the summer months, when livestock predation is most intense (Kusi et al., 2019), future studies of seasonal variations in the wolf's diet will be informative.

The dietary niche overlap that we report between snow leopard and Himalayan wolf (Pianka Index = 0.81) was relatively high and comparable to observations of these sympatric carnivores in Kyrgyzstan (Pianka Index = 0.91) (Jumabay-Uulu et al.,

Table 3

Carnivore summer diet across the three study areas in Nepal for Himalayan wolf (HW), snow leopard (SL), and red fox (RF). Relative proportions eaten (%) (RPE), relative biomass eaten (%) RBE, and relative number of prey individuals eaten (%) (RNPE). Please note that sample sizes lower than N = 10 are flagged with * and need to be considered as preliminary trends.

	Dolpa HW (N = 77)			Dolpa SL (N = 5) *			Dolpa RF (N = 28)			Humla HW (N = 69)			Humla RF (N = 14)			KCA HW (N = 13)			KCA SL (N = 3) *			KCA RF (N = 14)		
	RPE	RBE	RNPE	RPE	RBE	RNPE	RPE	RBE	RNPE	RPE	RBE	RNPE	RPE	RBE	RNPE	RPE	RBE	RNPE	RPE	RBE	RNPE	RPE	RBE	RNPERN
Yak/Cow	**34.7**	**66.2**	**2.3**	**2.5**	**11.1**	0.2	0.7	33.3	0.5	**8.0**	**17.3**	1.0				**32.5**	**63.5**	**1.0**	0	0	0	0.4	**6.0**	0.3
Horse	3.8	10.1	0.2	0	0	0	0	0	0	0	0	0	0	0	0	2.5	6.7	0.1	**40.0**	**96.9**	1.3			
Goat	4.1	2.2	0.7	0	0	0	2.7	14.5	1.9	0	0	0	0	0	0	0	0	0	0	0	0	0.5	1.1	0.4
Kiang										**18.9**	**52.9**	**1.7**	0	0	0									
Naur	**15.4**	**11.0**	1.7	**16.7**	**28.0**	**2.1**	**2.8**	**29.9**	**1.9**	6.5	5.2	1.0	**6.0**	**57.6**	**4.3**	**35.0**	**25.7**	**1.7**	**0.8**	**0.6**	0.04	**23.4**	**91.8**	**17.1**
Tibetan gazelle	0.7	0.3	0.2							1.6	0.8	0.6							0	0	0			
Marmot	**21.2**	**8.5**	**10.8**	**62.1**	**59.1**	**36.8**	**7.0**	**18.8**	**10.1**	**50.2**	**22.8**	**36.5**	**16.7**	**40.3**	**25.0**	2.3	0.9	0.5	1.3	0.5	0	**0.2**	**0.2**	**0.3**
Small mammals	3.3	1.2	**82.9**	2.1	1.8	**60.9**	**77.3**	**2.9**	**84.7**	1.6	0.7	**58.2**	**62.3**	**2.1**	**70.7**	**8.5**	**3.1**	**96.7**	**7.5**	**2.5**	**98.7**	**71.3**	1.0	**82.0**
Hare	1.1	0.4	1.2	0	0	0	0.6	0.7	0.9	0.7	0.3	1.2	0	0	0	0	0	0	0	0	0	0	0	0

Study areas in China: Namsai and Zhaqing for the Himalayan wolf (HW) scat samples.

	Namsai – HW (N = 8)*			Zhaqing – HW (N = 9)*		
	RPE	RBE	RNPE	RPE	RBE	RNPE
Yak/Cow	**16.1**	**29**	0.6	**15.6**	**92.9**	22.7
Horse	0	0	0	0	0	0
Goat	0	0	0	0	0	0
Kiang						
Naur	0.3	0.5	0.04	0	0	0
Tibetan gazelle	12.8	**23**	**7.6**	4.1	1.4	5.9
Marmot	**25.3**	**45.5**	**32.3**	**33.8**	**5.6**	49.1
Small mammals	0.8	1.5	**58.6**	**15.3**	0.1	22.3
Hare	0.3	0.5	0.9	0	0	0

Table 4
Frequency of Occurrence per food item in % as found in the summer diet. Himalayan wolf results are shown pooled and separate for the Nepalese study areas, while the results are pooled for the other species and the study areas in China. Please note that sample sizes lower than N = 10 are flagged with * and need to be considered as preliminary trends.

Row Labels	Yak/ Cow	Horse	Goat	Kiang	Naur	Tibetan gazelle	Marmot	Small mammal	Hare	Vegetation	Bird	Insect	Soil	Stone	Plastic	Unknown
Himalayan wolf (Dolpa)	57	3.90	11.7	0	24.7	1.3	36.4	9.1	1.3	65.0	2.6	0.00	10.4	27.3	0.00	24.7
Himalayan wolf (Humla)	14.3	0.00	0	20.0	10.0	5.7	64.3	7.1	1.4	68.6	0.00	4.3	14.2	21.4	1.4	11.4
Himalayan wolf (KCA)	46.2	15.4	0.00	0.00	76.9	0.00	23.1	30.8	0.00	69.2	0.00	0.00	15.4	23.1	0.00	7.7
Himalayan wolf (Nepal)	**37.5**	**3.13**	**5.6**	**9.38**	**22.5**	**3.1**	**47.5**	**10.0**	**1.3**	**66.9**	**1.3**	**1.9**	**12.5**	**24.4**	**0.62**	**17.5**
Snow leopard*	**12.5**	**25**			**25**		**50**	**25**		**62.5**	**12.5**		**12.5**	**37.5**		**25**
Tibetan fox*								**100.00**	**33.33**	**66.67**				**33.33**		**33.33**
Red fox*	**5.17**		**5.17**		**18.97**		**20.69**	**93.10**	**5.17**	**50.00**	**18.97**	**24.14**	**8.62**	**8.62**	**3.45**	**17.24**
Pallas's cat*,[a]								**present**	**present**	**present**				**present**		
Eurasian lynx*,[a]			**33.33**				**16.67**	**66.67**						**33.33**		
Domestic dog*	**50.00**		**12.50**		**12.50**	**12.50**	**25.00**					**12.50**	**12.50**	**25.00**	**12.50**	**12.50**
Himalayan wolf (China)	**76.47**					**5.88**				**70.59**		**35.29**	**47.06**	**17.65**	**23.53**	**52.94**

[a] Published in Werhahn et al. (2018b).

2014), or in the Pamir mountains (Pianka Index = 0.87) (Wang et al., 2014). The red fox on the other hand had a comparably narrow dietary niche mainly foraging on smaller mammals and less overlap with the wolves. Our results for snow leopard diet are however only indicative due to small sample size but complement the findings of Chetri et al. (2017), Jumabay-Uulu et al. (2014), Shrestha et al. (2018), and Weiskopf et al. (2016).

Vegetation is a frequent component of carnivore diet as it provides fibres to help digestion, cleans the digestive tracts of parasites and hair, and can provide supplemental nutrients (Mech and Boitani, 2003; Rigg and Gorman, 2004; Wang et al., 2014). We frequently found grass/sedge vegetation in the wolf scats and found the small twigs of false tamarisk *Myricaria* sp. plants in three wolf scats. False tamarisk has also been detected repeatedly in snow leopard scats in other studies (Bocci et al., 2017; Chetri et al., 2017; Devkota et al., 2013; Wang et al., 2014). It may be relevant that local human communities use this plant to treat stomach-ache, uterine bleeding and food poisoning (Kala, 2006; Lama et al., 2001).

4.1. Selection of wild prey over livestock

Our data indicate that the Himalayan wolf selects wild prey species over livestock during the summer period despite the seasonally overwhelming abundance of yaks and goats in the study areas (see also Chetri et al. (2019). Similarly, studies from different regions around the globe find indications that grey wolves prefer wild to domestic prey (Meriggi and Lovari, 1996; Rigg and Gorman, 2004; Wang et al., 2014). A review of wolf dietary studies over 15 years in southern Europe shows that wild ungulates are preferred by grey wolves over livestock and that the presence of multiple wild prey species can reduce livestock depredation (Meriggi and Lovari, 1996). The review also emphasised the importance of effective livestock protection and grazing management in reducing predation on livestock (Meriggi and Lovari, 1996). Other studies have concluded that where wild prey is available only a minority of wolf packs kill livestock (Jedrzejewski et al., 2003; Muhly et al., 2003; Treves et al., 2003, 2001). The results from southern Europe suggest that grey wolves switch their diets away from domestic species if more wild ungulates are available (Newsome et al., 2016). In line with optimal foraging theory, all ungulates are sufficiently profitable to wolves, making encounter rate a critical determinant of prey selectivity (Huggard, 1993). Depleted prey populations are an important driver for wolves to turn to livestock. Consequently maintaining and restoring wild ungulate populations should be a key priority for Himalayan wolf as for grey wolf conservation (Ripple et al., 2014).

4.2. Recommendations for conservation: importance of intact wild prey populations

Wild ungulate populations worldwide face many threats including habitat destruction and encroachment, unsustainable human hunting activity, competition with livestock, and disease transmission by livestock (Karimov et al., 2018; Newsome et al., 2016; Ripple et al., 2015). In our study areas in the Himalayas and the Tibetan Plateau we observed habitat encroachment, competition with large numbers of livestock, and illegal poaching as immediate concerns for the wild herbivore populations. Wild prey has to compete with the encroaching livestock and as a consequence may move to other areas (Karimov et al., 2018). The observed densities of naur in our Nepalese study areas (0.8–3.1 naur/km^2) were lower than the 6.6–10.2 naur/km^2 in the Annapurna Conservation Area documented by Oli (1994). The naur is a widely distributed wild ungulate across our study region (Harris, 2014) and presents an important wild ungulate prey for the Himalayan wolf and the sympatric snow leopard (Chetri et al., 2017). The kiang in Nepal is restricted to few trans-Himalayan habitats in Humla and Mustang (Jnawali et al., 2011). And similarly, the Tibetan gazelle in Nepal is restricted to a few individuals in the trans-

Fig. 3. Prey in the wolf diet (relative biomass in %), prey abundance in the landscape (relative biomass in %), and the Jacobs Index for prey selection during the summer (−1 indicates prey avoidance and +1 indicates prey selection) per study area and mean with SD. For more details see Supplementary Material Table S1. Please note that the wolf scat sample sizes used for the analysis for Namsai (N = 9) and Zhaqing (N = 8) were less than 10 and therefore are only to be considered preliminary trends.

Himalayan habitats of Humla and Mustang (Jnawali et al., 2011; Werhahn et al., 2015) though this species appears more common on the Tibetan Plateau habitats of China (IUCN SSC Antelope Specialist Group, 2016). While Tibetan gazelles to date are not reported from Dolpa, this species was found in a wolf scat from Dolpa, collected from alpine steppes very close to the Tibetan plateau habitats in the neighbouring Tibetan Autonomous Region (TAR) of China. Based on the far roaming nature of wolves, it is possible that the wolf killed a Tibetan gazelle on the Chinese side while depositing the scat on the Nepalese side (a possibility that underlines the importance of transboundary conservation).

Conservation priorities should be improving wild ungulate populations in these high altitude ecosystems by a) protection of favourable wild herbivore habitat refuges (Lyngdoh and et al., 2014), b) sustainable management of pastureland use, livestock numbers and improving livestock protection, and c) combating illegal poaching of ungulates and carnivores.

Further, the vulnerability of livestock in the high-altitude habitats of the Himalayas and the Tibetan Plateau may be reduced by more rigorous presence of herders. And the night protection of corralled herds may be improved by a combined use of fladry (Musiani et al., 2003), and electric, audio and visual deterrents (Newsome et al., 2016). The safeguarding of smaller prey species (hare, marmot, pika) is another priority for the conservation of Himalayan wolves and indeed snow leopard, foxes and Eurasian lynx, based on the importance of these small mammals in diet of the studied carnivores.

5. Conclusion

Successful protection of large carnivores requires protecting entire ecosystems (Estes et al., 2011). Understanding their feeding behaviour is an important element of planning the conservation of Himalayan wolves, because of their dependence and impact on both wild and domestic prey, and the associated conflict with people. Our study suggests that predation on livestock increases where wild prey is scarce. It emerges that the restoration and maintenance of healthy wild prey populations, in combination with effective livestock protection, are fundamental for the conservation of Himalayan carnivores.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00780.

Conflicts of interest

The authors have no conflict of interest.

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