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Sympatric snow leopards and Tibetan wolves: coexistence of large carnivores with human-driven potential competition

Anna Bocci[1,2] · Sandro Lovari[1,2,3] · Muhammad Zafar Khan[4] · Emiliano Mori[1]

Abstract The snow leopard *Panthera uncia* coexists with the wolf *Canis lupus* throughout most of its distribution range. We analysed the food habits of snow leopards and wolves in their sympatric range in the Karakoram mountains of Pakistan. A total of 131 genotyped scats ($N = 74$, snow leopard; $N = 57$, Tibetan wolf) were collected during the cold periods (i.e. winter and spring) of 2011 and 2012 in the Hushey valley. Large mammals, i.e. livestock and ibex, accounted for 84.8 and 83.1% of the diet (relative frequency) of the snow leopard and the wolf, respectively. Domestic prey was the staple of the diet of both snow leopards (66.6%) and wolves (75.1%). Ibex *Capra ibex*, the only wild ungulate in our study area, contributed 18.2 and 16.9% of relative frequencies in the diets of the snow leopard and the wolf, respectively. In winter, the snow leopard heavily relied on domestic sheep (43.3%) for food, whereas the wolf preyed mainly on domestic goats (43.4%). Differently from other study areas, both snow leopards and wolves showed no apparent prey preference (Jacobs index: snow leopard min. − 0.098, max. 0.102; Tibetan wolf min. − 0.120, max. 0.03). In human depauperate areas, with livestock and only a few wild prey, should competitive interactions arise, two main scenarios could be expected, with either predator as a winner. In both cases, the best solution could primarily impinge on habitat restoration, so that a balance could be found between these predators, who have already coexisted for thousands of years.

Keywords *Panthera uncia* · *Canis lupus filchneri* · Competition · Large-carnivore coexistence · Siberian ibex

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Introduction

Large carnivore species can occur in simpatry throughout the world because of prey partitioning, body size differences, different activity rhythms or habitat use (Palomares et al. 1996; Lovari et al. 2015; Sugimoto et al. 2016), which limit inter-specific competition (Palomares and Caro 1999; Donadio and Buskirk 2006). When they compete, it is apparently through interference, where usually the smaller species experiences negative effects on its population dynamics (for reviews on competition among carnivores: Palomares and Caro 1999; Donadio and Buskirk 2006). Although there is a wealth of studies showing interference competition among carnivores, exploitative competition has not been documented so far in this order (but see Watts and Holekamp 2008). Information is limited on the role of the snow leopard *Panthera uncia* within its ecosystem, as well as its ecological relationships with the carnivore guild of wolf *Canis lupus*, brown bear *Ursus arctos* lynx *Lynx lynx* and common leopard *Panthera pardus* (Schaller 2016). These large carnivores may use the same prey

species, and competition for resource exploitation could arise between them, although relevant evidence of effects at the population level has been lacking so far. The potential for competition is greater where the local resource spectrum is poor (Stephens and Krebs 1986; Peiman and Robinson 2010, for a review); thus, studies in such areas should be especially important for conservation purposes.

The snow leopard and the Tibetan grey wolf *Canis lupus filchneri* are key predators of the Himalayan rangelands (Fox et al. 1991; Mishra 1997). The former is globally listed as 'vulnerable' in the IUCN Red List of Threatened Species (IUCN Red List: http://www.iucnredlist.org/details/22732/0 - Accessed on 26th October 2017), whereas the latter is common throughout Central Asia (IUCN Red List: "least concern": http://www.iucnredlist.org/details/3746/0 - Accessed on 10th April 2017), even locally considered as a pest (Lescureux 2006). As to Pakistan, the Tibetan grey wolf has been listed as 'endangered' in the red list of Pakistan Mammals (Sheikh and Molur 2004). Information on food habits is a crucial first step to understand ecological features and to predict predator influence on prey communities (Shrestha 2008; Anwar et al. 2011).

Wild ungulates are the main prey of the snow leopard (Lovari et al. 2013a; Lyngdoh et al. 2014), e.g. Siberian ibex *Capra ibex sibirica* (Anwar et al. 2011), bharal *Pseudois nayaur* and Himalayan tahr *Hemitragus jemlahicus* (Oli et al. 1993; Lovari et al. 2013b). Similarly, wild ungulates build up also the largest proportion of the wolves' diet in Central Asia (Schaller 1977; Blumestein 1993; Newsome et al. 2016). Where these two predators coexist, if the wild ungulate community is rich, their diet differentiates, with wolves preying on plain dwellers (e.g. gazelle *Gazella* spp., kiang *Equus kiang* and Marco Polo sheep *Ovis ammon polii*) and snow leopards selecting cliff-dwelling species (e.g. bharal: Chetri et al. 2017). By contrast, where species richness is low, diet overlap may increase (e.g. Kyrgyzstan: Jumabay-Uulu et al. 2013; NW China: Wang et al. 2014). In areas with high livestock densities, the percentage of domestic ungulates in the snow leopard diet may increase up to 70% (Bagchi and Mishra 2006; Anwar et al. 2011). Livestock is also frequently found in the wolf diet, ranging from 38 to 65% in northern Pakistan (Schaller 1977; Khan 2012). In one area of Nepal (Jackson 1996) and in one of northern Pakistan (Khan 2012; Khan et al. 2017), where both snow leopards and wolves live, most herders suspected snow leopards as responsible for livestock depredations, whereas in Ladakh, India, the wolf was considered responsible for most killings (Namgail et al. 2007). The high mountains of northern Pakistan host a declining population of snow leopards (Ud Din et al. 2016). In this region, wolf packs are also present, although the density of wild ungulates is very low (Schaller 1977; Blumestein 1993; Khan 2012). Thus, a high dietary overlap between these large carnivores would be expected. Should resource competition

arise between these carnivores, the more generalist species (i.e. the wolf, Newsome et al. 2016) could outcompete the more specialised one (i.e. the snow leopard, Sharma et al. 2015; Lovari and Mishra 2016).

Our study objectives were to (i) investigate the food habits of the snow leopard and the Tibetan wolf in an area with a poor wild prey spectrum, in Northern Pakistan; (ii) estimate niche breadth, prey selection and diet overlap of these predators and (iii) assess the relative importance of wild and domestic prey in the diet of both predators.

Materials and methods

Study area

Our study was conducted in the largest protected area in Pakistan, the Central Karakoram National Park (hereafter, CKNP; about 10,557 km^2, with the annexed buffer zone). This national park contains some of the world's largest glaciers and the greatest concentration of high mountains on earth, ranging from 2000 to over 8000 m.a.s.l., including K2. As to its climate, the CKNP area can be considered a transition zone between the arid climates of western Asia and the semi-humid sub-tropics of southern Asia. The whole region is characterised by relatively dry summers, with an average annual precipitation of less than 300 mm in low-lying areas (Clemens and Nusser 1997), because of mountains limiting monsoon movements to the west and heavy winter snowfalls at the highest altitudes (WWF-Pakistan 2008). Five altitudinal ecological layers are recognised (Champion et al. 1965): Alpine dry steppe (2600–3000 m.a.s.l.), dominated by mugwort *Artemisia* spp. and juniper *Juniperus* spp.; sub-alpine scrub zone (3000–3500 m.a.s.l.), with birch forests *Betula utilis*, juniper *Juniperus* spp., wild rose *Rosa canina* and *Hippophae rhamnoides*; Alpine grasslands (3500–4200 m.a.s.l.); sub-nival (4200–5000 m.a.s.l.) and nival zones (over 5000 m a.s.l.), where only *Salix denticulata* and *Mertensia tibetica* may be found.

Our study area was located in the easternmost valley of the park, the Hushey valley (76 20′ E to 35° 27′ N), covering over 4000 km^2 (map surface, actual size being over three times greater because of altitudinal development; Fig. 1), from 3000 to 5000 m.a.s.l., with a main N-S orientation. The valley is split into four main sub-valleys: Aling, Musherbrum, Ghandogoro and K6 (WWF-Pakistan 2008; Khan et al. 2014). The persistence of snow (December–May, i.e. winter and spring, hereafter 'cold period') and the frequent landslides on the only connecting road isolate the area for long periods. Livestock and subsistence agriculture are the main resources of the local population (c. 1200 humans, in 150 households). Livestock is composed of goats (500–600 individuals), sheep (c. 700), donkeys (c. 20), cattle (c. 200) and domestic yaks (c.
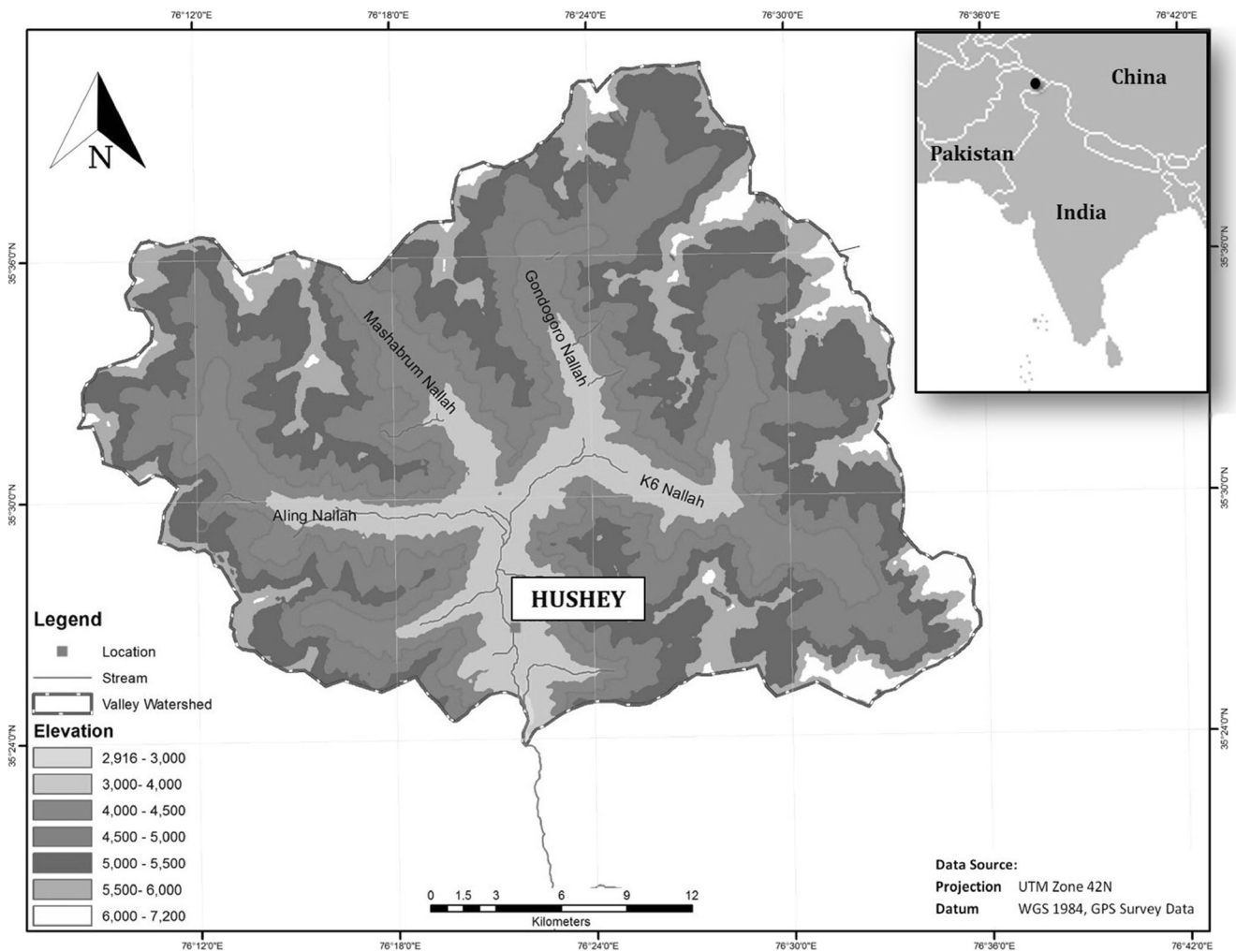
Fig. 1 Location of the study area (WWF-Pakistan 2008)

30). The Siberian ibex is the only wild ungulate in this area. Official counts of ibex contemporary to our study indicated about 370 individuals (Khan et al. 2014). Besides the snow leopard and the Tibetan wolf, the red fox *Vulpes vulpes* and the corsac fox *Vulpes corsac* are also present.

The Himalayan snowcock *Tetraogallus himalayensis*, the chukar partridge *Alectoris chukar* and the Royle's pika *Ochotona roylei* are also relatively abundant.

Data collection and diet analysis

Carnivore scats were collected monthly, along fixed trails evenly distributed through the four valleys of our study area (Fig. 1), for a total of nearly 35 km, during spring (March–May) and winter (December–February) 2011–2012. A thorough, conservative selection of scats was made in the field on the basis of different features (e.g. smell, position, size, contents and presence of tracks) to reduce the risk of collecting scats of other species (cf. Lovari et al. 2009). Furthermore, approximately 1 cm^3 of each fresh scat was preserved in a vial

with silica gel for later DNA analyses. Upon genetic validation (Jan E. Janečka, Duquesne University, USA, unpublished), we confirmed 90.5% of scats as belonging to the wolf ($N = 63$), while 93.7% were confirmed as belonging to the snow leopard ($N = 79$). We proceeded with diet analyses (131 scats: snow leopard, SL: $N = 74$; wolf, W: $N = 57$). Scats were sun-dried and then preserved in polyethylene bags, labelled with date, GPS coordinates and altitude. All the plastic bags were frozen ($-30 \degree$ C) until the start of the diet analysis (Reynolds and Aebischer 1991).

Scats were washed with tap water in a fine-mesh sieve (0.5 mm), and indigestible remains of the hair, teeth, hooves, bones, feathers and claws were oven dried at 60 °C for 24 h. Fragments of plastic or other man-made materials were eliminated from our analyses. Prey species were identified by comparison with a reference collection of slides and photographs of the cuticle (*cuticula*) and the *medulla* of the hair of potential prey species (Teerink 1991; Oli 1993), at × 100–× 400 magnifications. Hairs were washed in warm water with detergent, rinsed in distilled water, dehydrated in 70% ethanol and dried

on filter paper. Twenty individual hairs were collected from each scat for identification. The hair was placed on a glass slide, on a layer of transparent nail polish, to observe the cuticle structure. After drying up the slide, the hair was removed and the cast was observed at the microscope (see above). The hair was longitudinally sectioned and wetted with cedar oil at the section level to observe the medullar pattern.

Data were tabulated as absolute (AF: number of occurrences of each food, when present/total number of scats × 100) and relative (RF: number of occurrences of each food, when present/total number of occurrences of all food items × 100) frequencies of occurrence of each prey species (Lucherini and Crema 1995). Seasonal differences in the absolute occurrences of main prey items in faecal samples were assessed through the G test. For each sample, the estimated relative volume of food ingested (estimated volume of each category/total number of scats × 100) was scored on a seven-point scale (absent, < 5, 6–25, 26–50, 51–75, 76–95, > 96%: Kruuk and Parish 1981). Relative frequencies and volumes were then plotted in a diagram (Kruuk 1989). The Levins' standardised index (B_{STA}) was used to assess the trophic niche breadth (Krebs 1999), $B_{sta} = (B-1)/(B_{max}-1)$, where B is the Levins' index (Levins 1968) and B_{max} is the total number of prey categories. B_{sta} varies between 0 (minimum breadth) and 1 (maximum breadth). The Pianka index (O_{jk}) was used to assess the trophic niche overlap (Pianka 1974). Eight food categories were identified: domestic sheep, domestic goat, Siberian ibex (hereafter, ibex), cattle, yak (and hybrids with cattle), small mammals, birds, plant material and other. Occasionally, canids—but not felids—may use fruits as food, whereas grass blades are used as roughage, but they go undigested through the stomach and the intestines of both dogs and cats (cf. Bothma 1966; Hoppe-Dominik 1988). Accordingly, we have used the category 'plant material' only for the analysis of absolute frequencies, where the addition of this category does not affect the quantitative evaluation of the others. Conversely, we eliminated this indigestible category from relative frequency, volume and trophic niche overlap analyses. As to fruits, there was none during the cold period, in our study area. We have preferred not to estimate the biomass consumed, because of the substantial biases which may affect this calculation (cf. Chakrabarti et al. 2016; Lumetsberger et al. 2017) with further uncertainties, which make biomass estimation misleading, i.e. it is usually impossible to know (i) whether a young/sub-adult/male/female has been preyed upon (body mass is normally quite different in different age classes and sexes, especially of polygynous ungulates); (ii) whether a predator scavenged from a carcass already partly eaten by other carnivores or from its own fresh kill and (iii) whether it fed alone on it or with conspecifics. The selection of ungulate species as prey of snow leopards and Tibetan wolves was estimated through the comparison of the percentage of occurrence of each ungulate in the scats (i.e. use) with the availability of the same ungulate species in the study area. Prey (ungulate) selection was assessed through the Jacobs index (Jacobs 1974; Lovari et al. 2015).

Results

The Brillouin diversity index (Hass 2009; Lovari et al. 2015) suggested that our sample was large enough to assess the seasonal diet of both species in both seasons, as no new food category was found after 21 and 12 scats (winter) and 18 and 21 scats (spring), respectively, for the snow leopard and the wolf (Fig. 2).

Diets of snow leopards and wolves differed significantly (SL: $N = 74$; W: $N = 57$; $G = 26.87$, degrees of freedom = 8, $P < 0.01$; Fig. 3), especially in winter (SL: $N = 37$; W: $N = 17$; $G = 34.22$, degrees of freedom = 6, $P \ll 0.01$; Table 1).

Domestic sheep comprised the staple in the diet of the snow leopard, whereas goats and sheep were eaten by wolves in comparable numbers (Table 1; Fig. 3). Plant material was present in 69.9% of faecal samples of the snow leopard (mainly *Myricaria rosea*), as well as in 48.5% of the wolves (Table 1; Fig. 3). The trophic niche showed the same breadth for both species, in both seasons (SL: winter = 0.50, spring = 0.49; W: winter = 0.47, spring = 0.50). The Pianka index suggested a great overlap of trophic niche between snow leopards and wolves during the whole period ($O_{jk} = 0.74$), as well as in winter ($O_{jk} = 0.67$) and in spring ($O_{jk} = 0.77$) respectively.

Ungulates (livestock and ibex) made up 85.8 and 82.8% in relative volume of the snow leopards and the wolves, respectively (Table 1; Fig. 4). Small mammals and birds were not present in the wolf's diet and only rarely in the snow leopard's (Table 1; Fig. 4). In winter, sheep was the category with the greatest total volume in the diet for the snow leopard, while goats had the highest volume in that of the wolf (Fig. 4). In spring, sheep showed the greatest volume in the diet for both carnivores, even if much more was consumed by wolves (Fig. 4).

During the cold period, ungulates were eaten proportionally to their local availability by both snow leopards and Tibetan wolves (Table 2).

Discussion

An unexpected result of our study was the apparent lack of any selection, positive or negative, in the use of ungulate prey species by both predators. This is in contrast with the data provided by Jumabay-Uulu et al. (2013) and Chetri et al. (2017) who found a different selectivity, with the wolf concentrating on ungulates of undulating terrain and the snow leopard selecting cliff-dwelling ones. This difference could be due to the different composition of local prey spectra,
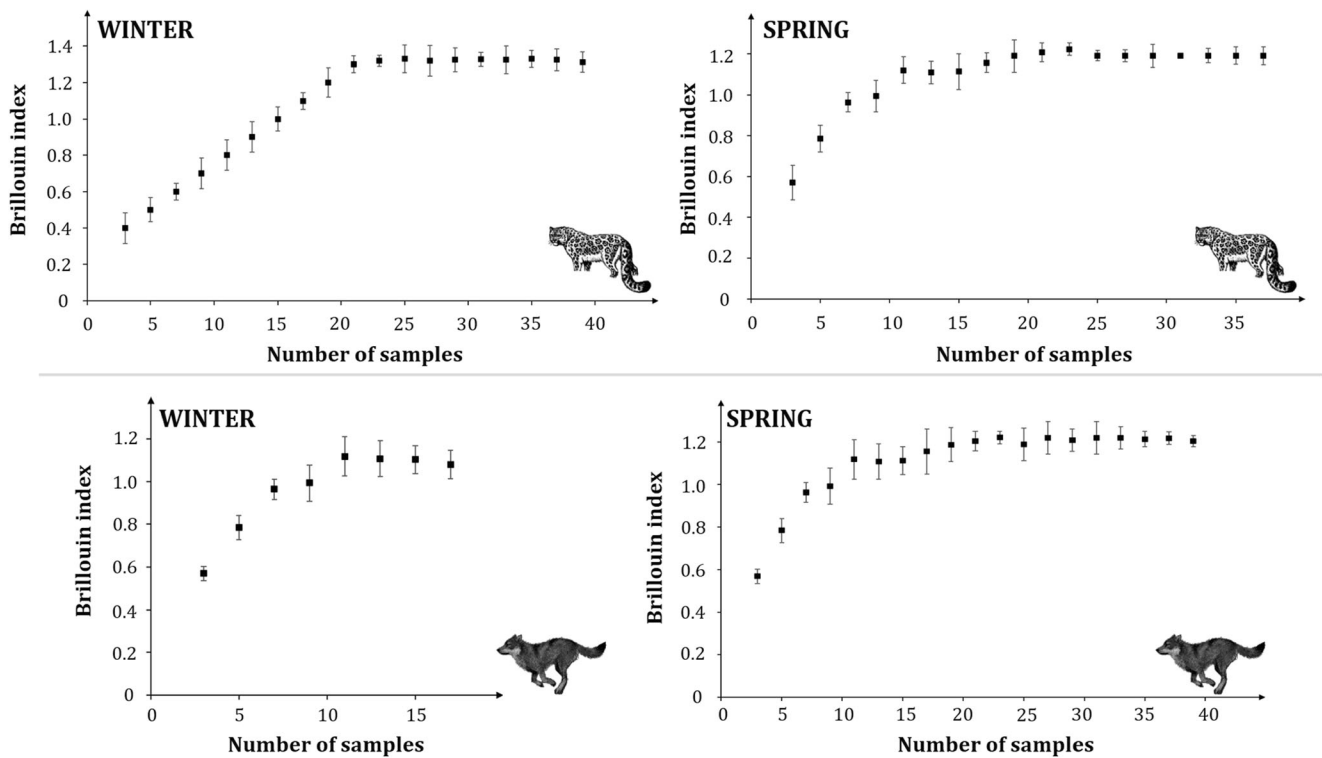
Fig. 2 Brillouin diversity index for the snow leopard (above) and the Tibetan wolf (below), for winter (left) and spring (right)

livestock included. The ungulate assemblies in the studies of Jumabay-Uulu et al. (2013) and Chetri et al. (2017) were comparatively rich (8 prey species, in the former; 12 prey species, in the latter) compared to our study area (5 prey species). In our study, options for selection were less, due to the depauperate prey community because of human actions, which could explain why domestic ungulates were heavily used, while they were avoided in the other studies. This may support the expectation that predation on livestock increases when the wild ungulate community is depleted (e.g. Meriggi and Lovari 1996, for the wolf in South Europe, whereas results are unclear as to the snow leopard: Suryawanshi et al. 2013; Johansson et al. 2015; Sharma et al. 2015; cf. Lovari et al. 2013a, for a review). Predation by snow leopards and wolves on livestock was high in our study area compared to

reports from other studies (Chundawat and Rawat 1994; Wang et al. 2014; Chetri et al. 2017), possibly because of the low availability of wild ungulates and the absence of alternative prey, e.g. marmots *Marmota himalayana* and *Marmota baibacina* (Khatoon 2010; Anwar et al. 2011; Lovari et al. 2013a; Lyngdoh et al. 2014). In Hushey valley, in the cold period, domestic livestock comprised 53.4 and 65.6% of the volume in the diet of the snow leopard and the wolf, respectively. The higher frequency of ibex in the diet of the former, with respect to that of the latter, could be due to the fact that ibex and leopards share the same terrain, whereas wolves seldom move into the steep terrain inhabited by ibex (Jumabay-Uulu et al. 2013).

In the cold period, both the snow leopard (Nawaz 2009) and the wolf (Mech 1970) descend to lower altitudes (<

Fig. 3 Absolute frequencies of food categories in snow leopard and wolf diets during the cold period
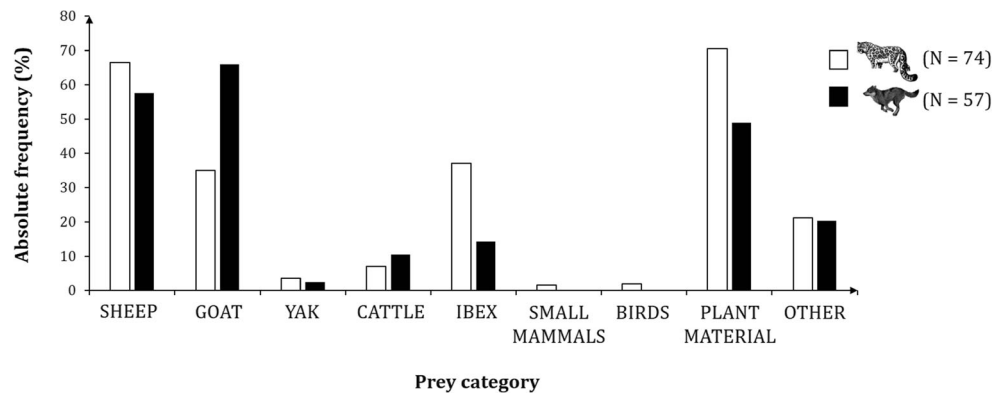
Table 1 Diet composition (AF, absolute frequency; RF, relative frequency: V, estimated volume) of snow leopard and Tibetan wolf, estimated through analyses of prey species remains in scats

|	Winter						Spring						Total					
	Snow leopard			Tibetan wolf			Snow leopard			Tibetan wolf			Snow leopard			Tibetan wolf		
	AF (%)	RF (%)	V (%)	AF (%)	RF (%)	V (%)	AF (%)	RF (%)	V (%)	AF (%)	RF (%)	V (%)	AF (%)	RF (%)	V (%)	AF (%)	RF (%)	V (%)
Sheep	70.3	43.3	35.4	35.3	25.9	25.1	55.6	28.3	28.9	78.6	38.5	47.6	62.9	37.4	34.9	56.9	32.7	38.2
Goat	35.1	23.7	21.2	70.6	43.4	47.5	30.6	22.6	23.9	52.4	27.2	27.5	32.9	19.8	16.6	61.5	36.8	23.3
Yak	2.7	2.3	2.6	5.9	3.1	0.9	2.8	2.1	2.5	0.0	0.0	0.0	2.7	3.1	0.6	2.9	1.4	0.9
Cattle	5.4	2.4	2.7	11.8	6.2	3.1	5.6	4.2	0.8	7.1	3.0	0.7	5.5	6.3	1.3	9.5	4.2	3.2
Siberian ibex	27.0	18.4	17.7	11.8	6.2	13.5	47.2	22.8	26.7	28.6	18.2	17.3	37.1	18.2	32.4	20.2	16.9	17.2
Small mammals	0.0	0.0	0.0	0.0	0.0	0.0	2.8	2.1	2.6	0.0	0.0	0.0	1.4	1.4	1.3	0.0	0.0	0.0
Birds	2.7	1.2	3.9	0.0	0.0	0.0	2.8	2.1	0.8	0.0	0.0	0.0	2.7	3.1	1.6	0.0	0.0	0.0
Other	18.9	8.7	16.5	23.5	15.2	9.9	33.3	15.8	13.8	30.9	13.1	6.9	26.1	10.7	11.3	27.3	8.0	17.2
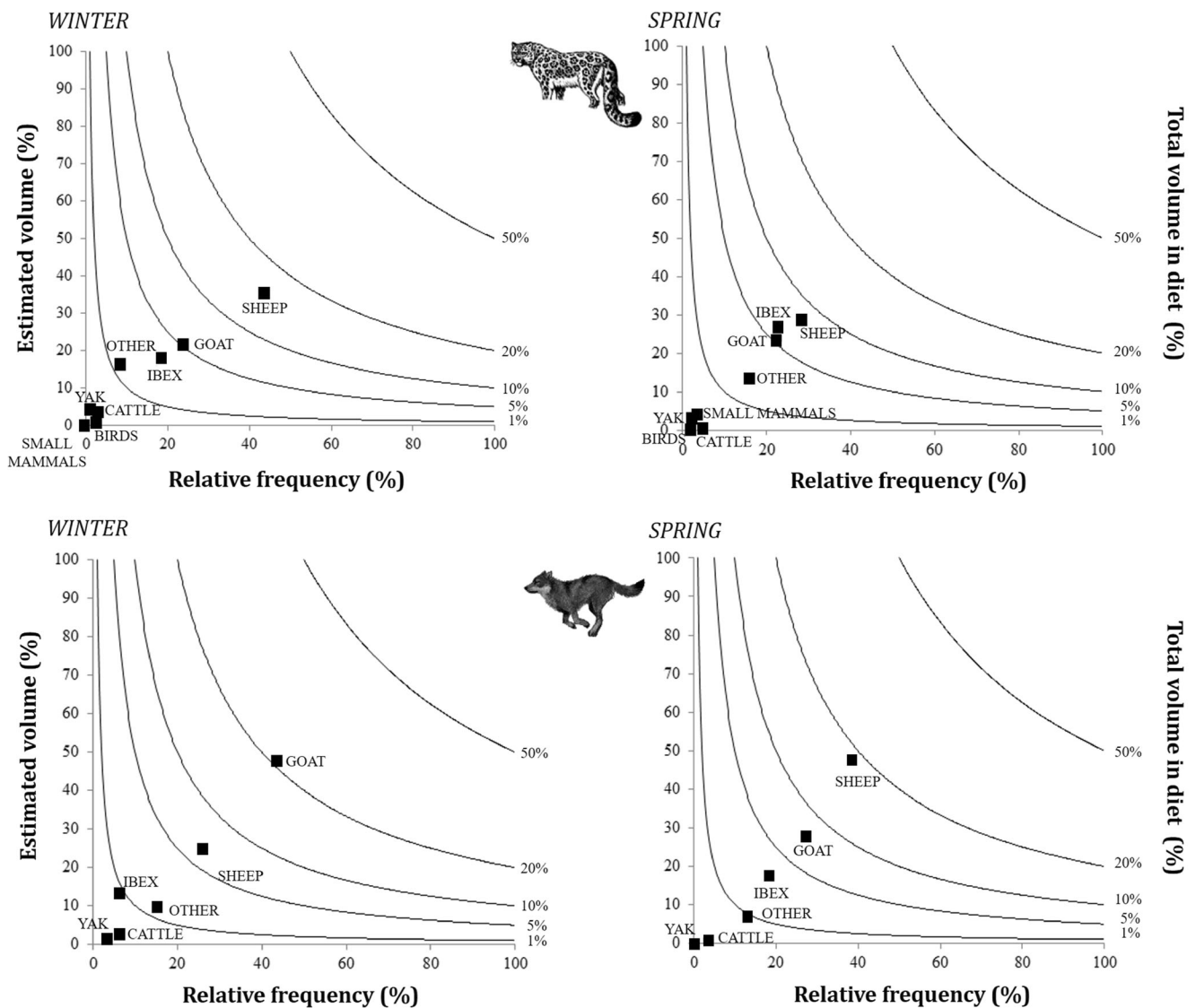
Fig. 4 Diet of the snow leopard and of the Tibetan wolf in winter (left) and spring (right). Isopleths connect points of equal relative volume

Table 2 Jacobs index (from − 1, total avoidance, to + 1, max. selection) of selection for ungulates in the diet of snow leopards (SL) and wolves (W); Occ, occurrence of each ungulate species on the total number of scats containing ungulate remains

Ungulate species	Occ_{SL} (%)	Occ_W (%)	Availability	Jacobs index	
				SL	W
Sheep	44.96	37.31	38.89	− 0.0018	+ 0.0006
Goat	23.40	41.11	27.78	+ 0.0035	− 0.0060
Yak	1.95	2.04	1.67	− 0.0980	− 0.1204
Cattle	3.88	6.35	11.11	+ 0.1015	+ 0.0385
Siberian ibex	25.81	13.19	20.56	− 0.0052	+ 0.0145

3000 m.a.s.l.) where they may meet with livestock, an easy prey compared to wild mountain ungulates (Anwar et al. 2011). A puzzling result of our work is the differential predation of these carnivorous species on livestock (sheep/goats), during the cold period. On winter–early spring, especially in case of poor snow cover, goats tend to graze/browse at higher altitudes or on ridges where snow has been swept away by blowing winds, whereas usually, sheep remain close to the village. One might assume that the group-living wolf tends to prey on livestock where the probability of being detected is the lowest (i.e. far from the villages, should the opportunity arise), whereas the solitary snow leopard could rely more on its stealthy behaviour not to be detected, even if close to human habitations. With snow melting, on spring, broken terrain tends to be more available and goats attend it more than in winter, thus escaping predation by the wolf, which could explain this predator's shift to sheep.

Alternative prey options such as small mammals and birds were absent in the diet of the wolf, whereas this category occurred in the snow leopard diet albeit rarely. In fact, smaller mammals may be used substantially by snow leopards when major prey species are not readily available (Chundawat and Rawat 1994). Plant material was more frequent in faecal samples of snow leopards than in those of wolves. As to the snow leopard, this category was mainly based on leaves and stems of the rosy false tamarisk *Myricaria rosea* (Dycotiledonae: Tamaricaceae), most likely as a way to clean the digestive tract, rather than as a food source (cf. Macdonald 1992; Lovari et al. 2013b).

The trophic niche breadths of these predators were comparable. A large diet overlap (up to 90%) has also been observed in another area, the Sarychat-Ertash, in Kyrgyzstan (Jumabay-Uulu et al. 2013), but not in the central Himalaya of Nepal (44%) where the ungulate community was particularly rich (Chetri et al. 2017). In the Hushey valley, the narrow niche breadth, the extensive overlap in diet and the apparent lack of prey selection would be expected to lead to food competition between these large carnivores. In fact, our data are limited to the colder months, when shortage of food is more likely to occur (Khan et al. 2014), thus enhancing potential competition.

Schaller (1977) outlined the vertical distribution of the main mammalian species in the north-west Himalaya, Karakoram and Hindu Kush. The snow leopard and the wolf have a widely overlapping altitudinal range, with the former between c. 1800 and 5000 m.a.s.l. and the latter from at least 1000 to over 5000 m.a.s.l. The greater biological flexibility of the wolf is confirmed, thus, both as to habitat type and to the use of local food resources (Mech 1970; Newsome et al. 2016). Conversely, the snow leopard appears to be much more of a 'specialist' species, strongly preferring open habitats and medium-sized wild herbivores (Sharma et al. 2015; Lovari and Mishra 2016). When an adaptable carnivore and a specialised one compete, most likely, the former will outcompete the latter (e.g. the red fox replacing the Arctic fox *Vulpes lagopus*: Tannerfeldt et al. 2002; for reviews on carnivore competition: Palomares and Caro 1999; Donadio and Buskirk 2006). A higher level of prey selection, with a minor risk of competition, should occur where the prey spectrum is rich (Butler et al. 2004; Wang et al. 2014). Conversely, where few prey species are observed and little or no prey selection occurs, interspecific competition is more likely to develop (cf. Stephens and Krebs 1986). In our study area, the outcome of a potential competition between the snow leopard and the wolf is difficult to predict. As the major food category is livestock, conflict with humans would drive consequences for both species more strongly than competition, as the availability of domestic prey is not limited in the same way as wild prey. Hence, most likely, competition for livestock would not escalate. Furthermore, in SW Asia, the coexistence of snow leopards and wolves is linked mainly to habitat type, with the leopard preferring cliffs and the wolf using less rugged, undulating terrain (Chetri et al. 2017). If herders start guarding livestock in a better way, the snow leopard could still prey on Siberian ibex, a cliff-dwelling species, whereas the wolf would be disadvantaged.

Overall, by contrast, current climatic changes have been suggested as detrimental to the survival of the snow leopard (Forrest et al. 2012; Lovari et al. 2013a; Aryal et al. 2016). In case of the development of competitive interactions, one could expect that this 'vulnerable' cold-adapted cat will be outcompeted by the 'least-concern' ecologically flexible wolf,

an unfortunate event which would make its conservation even more precarious.

In both cases, the best way out could be primarily local habitat restoration, i.e. reforestation, control over domestic sheep/goat distribution, reintroduction of local prey species and poaching control, so that a balance could be found between these predators, who have coexisted for at least 1.2–1.4 Ma (Turner and Anton 1997) thus showing their ability to coexist in the same area.

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