BIODIVERSITY RESEARCH

Effects of herbivore species richness on the niche dynamics and distribution of blue sheep in the Trans-Himalaya

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ABSTRACT

Aim To understand the community structure of mountain ungulates by exploring their niche dynamics in response to sympatric species richness.

Location Ladakh and Spiti Regions of the Western Indian Trans-Himalaya.

Methods We used the blue sheep *Pseudois nayaur*, a relatively widely distributed mountain ungulate, as a model species to address the issue. We selected three discrete valleys in three protected areas with similar environmental features but varying wild ungulate species richness, and studied blue sheep's diet and habitat utilization in them. Habitat variables such as slope angle, distance to cliff and elevation at blue sheep locations were recorded to determine the habitat width of the species. Faecal pellets were collected and microhistological faecal analysis was carried out to determine the diet width of blue sheep in the three areas with different ungulate species richness. Blue sheep's niche width in terms of habitat and diet was determined using the Shannon's Index.

Results The habitat width of blue sheep had a negative relationship with the number of sympatric species. However, contrary to our expectation, there was a hump-shaped relationship between blue sheep's diet width and the sympatric species richness, with the diet width being narrower in areas of allopatry as well as in areas with high herbivore species richness, and the greatest in areas with moderate species richness.

Main conclusions We suspect that the narrow diet width in allopatry is out of choice, whereas it is out of necessity in areas with high herbivore species richness because of resource partitioning that enables coexistence. We suggest that interactions with sympatric species lead to niche adjustment of mountain ungulates, implying that competition may play a role in structuring Trans-Himalayan mountain ungulate assemblages. Given these results, we underscore the importance of including biotic interactions in species distribution models, which have often been neglected.

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INTRODUCTION

Theoretical and empirical studies in community ecology in the last four decades revolved around niche-related competitive interactions, and the principle of competitive exclusion gained almost an axiomatic status (Gause, 1934; Hutchinson, 1959; Schoener, 1983). The basic tenet of competitive exclusion is that *n* number of species cannot coexist on

fewer than *n* resources (Gause, 1934; Hutchinson, 1959). This implies that resource availability constrains the number of species occurring in an area (MacArthur, 1972), and thus there is a ceiling to species richness in ecological communities (Terborgh & Faaborg, 1980; Tonn *et al.*, 1990). Resource constraints allow the coexistence of only those species that show trade-offs in niche utilization in response to competition (Chase & Leibold, 2003). Therefore, species

may avoid or reduce competition by adjusting their respective niche widths in response to their co-inhabitants (Chase & Leibold, 2003).

Studies on niche-related resource partitioning have been conducted on several taxa (Thorman, 1982; Toft, 1985; Wheeler & Calver, 1996; Toda *et al.*, 1999; McDonald, 2002), but niche relationships are less understood in large herbivores such as ungulates, largely because of their low population densities and the difficulties associated with manipulating their populations. Most of the studies on wild ungulates have addressed resource partitioning in single assemblages (Jenkins & Wright, 1988; Putman, 1996; Voeten & Prins, 1999), but it is not known as to how the niche of a given species can vary across assemblages in response to the number of sympatric species. This information is crucial for predicting species distributions at a macroecological scale (Araújo & Luoto, 2007).

Owing to the presence of sympatric species sharing resources, animals in multi-species assemblages may use only a subset (i.e. realized niche) of all the resources available (i.e. fundamental niche) in an area (Hutchinson, 1957). Given this, species can be packed into assemblages as a result of either increasing the resource range, or narrowing the niche width of the constituent species (MacArthur, 1972). In low productive environments, since resources are scarce, niche adjustment is expected to be the predominant way of accommodating additional species. Thus, when a species becomes extinct from a community, niche space (habitat supplying resources for a species' survival) is expected to become vacant that can be either occupied by an invading species or exploited by the extant species, leading to readjustment in their niche widths.

Therefore, it is postulated that disappearance of large herbivore species from ecological communities leads to increase in the niche width of the extant species (Diamond, 1975; Ricklefs & Schluter, 1993). But in case of diet, loss of a potentially competing sympatric species of large herbivore may have an opposite effect on niche width of a given species, as it may narrow down its niche by including fewer but more nutritious plant species in its diet in the absence of competitors. Inversely, the species may widen its diet spectrum when a new species invades the assemblage, as it may need to include less nutritious plants in the diet because of resource constraint imposed by the invading species. Thus, food and habitat widths could have different relationships with the number of sympatric species in an assemblage.

The mountainous rangelands of the Indian Trans-Himalaya support a relatively diverse assemblage of eight wild ungulates (Fox *et al.*, 1991), including four Caprinae species that represent 40% of this taxon found in the Himalayan region. But their populations are fragmented, and there is a spatial variation in the species richness, with local assemblages representing smaller subsets of the regional species pool. The causes of this variation and the factors that influence the organization of herbivore assemblages in this region are poorly understood, although excessive livestock grazing has been implicated as one of the causes (Mishra *et al.*, 2004).

Using the blue sheep *Pseudois nayaur*, a relatively widely distributed animal, as a model species, we explored how the niche of a wild ungulate varies in response to sympatric species richness. For this, we studied its habitat and diet in areas where it occurs allopatrically and contrasted them with areas where it occurs sympatrically with one: Ladakh urial *Ovis vignei vignei* and two Caprinae species: Asiatic ibex *Capra ibex siberica* and Ladakh urial. These sympatric species are comparable with blue sheep in morphology (Van den Tempel & De Vrij, 2006) as well as behaviour (Schaller, 1977), and thus have similar ecological requirements (Mallon, 1991; Namgail, 2006b). We further explored the relationship by including additional information from the literature on blue sheep's diet from other Trans-Himalayan ungulate assemblages with more than three sympatric species.

We predicted (1) an inverse relationship between blue sheep's habitat width and the number of co-occurring species and (2) a positive relationship between its diet width and the number of co-occurring species.

METHODS

Study area and species

The Western Indian Trans-Himalaya (31°36′–34°40′ N and 75°40′–79°30′ E) is classified as a cold desert. The moisture-laden monsoon clouds hardly reach this region because of the rain-shadow effect of the Himalayan range. The magnitude of precipitation, mostly in the form of snow during winter, is therefore minimal, with the mean annual precipitation rarely crossing 100 mm. The temperature ranges from −30 °C in peak winter (December–January) to +35 °C in summer (June–August). Vegetation is characterized by dry alpine steppe (Champion & Seth, 1968), and the plant cover rarely crosses 30% except in meadows around water bodies such as lakes and rivers (Rawat & Adhikari, 2005). There are only few tree species, including poplar *Populus* spp. and willow *Salix* spp., which are confined to the river valleys. The most common vegetation includes *Caragana* spp., *Artemisia* spp., *Lonicera* sp. and *Acantholimon* sp. Some of the common herbs include *Potentilla* spp., *Oxytropis* spp., *Astragalus* spp. and *Dracocephalum* sp.

The three study sites where blue sheep occurs allopatrically and with varying number of sympatric species are as follows: (1) Rongolong (32°20′ N, 78°02′ E) in the Kibber Wildlife Sanctuary (hereafter Kibber) is located south of Ladakh and is administratively a part of Himachal Pradesh; (2) Puyul valley (33°43′ N, 77°47′ E) of the proposed Gya-Miru Wildlife Sanctuary (hereafter Gya-Miru); and (3) Rumchung valley (34°08′ N, 77°24′ E) of the Hemis National Park (hereafter Hemis) are administratively a part of Ladakh, Jammu and Kashmir. Reconnaissance surveys were carried out in these protected areas prior to the study to find out valleys with the desired number of ungulate species but with

almost similar environmental features. Thus, our study site in Kibber had only one species: blue sheep and Gya-Miru had two species: blue sheep and Ladakh urial, whereas Hemis supported three species: blue sheep, Ladakh urial and Asiatic ibex. There are also small populations of the Himalayan marmot *Marmota bobak* in these areas, except in Kibber, where it has not been observed for several years (Mishra, 2001).

The blue sheep is a sturdy animal with strong muscular legs that help it in climbing steep cliffs, which are used as a refuge against predators (Namgail *et al.*, 2004). It grazes on open alpine pastures within an altitudinal range of 3500–5500 m, but keeps closer to precipitous cliffs to avoid predation. The animal exhibits an altitudinal migration by coming down to lower elevations during winter, when upper reaches get covered with heavy snow (Namgail, 2006b). It has been reported to feed largely on graminoids such as *Carex/Kobresia* and *Stipa* during summer (Harris & Miller, 1995; Mishra *et al.*, 2004). Blue sheep is distributed all across the Tibetan plateau and its marginal mountains, although the population is fragmented and the density varies across its distributional range (Schaller, 1998). There is an estimated population of *c.* 11,000 individuals in Ladakh, which makes it the most abundant wild ungulate in the region (Fox *et al.*, 1991; Namgail, 2009).

Field methods

Habitat

Data were collected between May 2005 and August 2007. Blue sheep herds were located from trails and vantage points (Namgail *et al.*, 2004). We searched the mountain slopes with 8 × 40 binoculars. Scan sampling was the primary method for animal observations. Whenever a group of animals was located, its size and subsequently the habitat variables: slope angle, distance to cliff and elevation at its location, were recorded. Individuals were considered to be solitary or belong to different groups when they stood 50 m away from another group. Although we also gathered information on physical variables such as slope aspect and slope position, only the aforementioned variables were used to estimate the habitat-niche width of the animal; a model selection procedure (the Akaike information criterion) identified these as the most important variables in the blue sheep habitat selection (Namgail, 2006a). An altitudinal gradient provides different habitats for plants, and thus the vegetation diversity and abundance vary along such a gradient in Ladakh (T. Namgail, unpublished data), whereas distance to cliff provides a gradient in plant biomass (more vegetation away from cliffs) as well as in predation risk, as the animal uses cliffs as escape terrain (Namgail *et al.*, 2004). Since differences in availability of habitat in the three areas could confound the influence of ungulate species richness on blue sheep's niche dynamics, we recorded the available habitats in different areas to control for it.

Diet

Blue sheep's summer diet information for Kibber was available from Mishra *et al.* (2004). For the other two areas, we conducted microhistological faecal analysis. We also used additional information from Harris & Miller (1995) on blue sheep's microhistological faecal analysis-based diet in Yeniu-gou, China, with six sympatric species to further explore the relationship between diet width and species richness. Although Mishra *et al.* (2004) quantified feeding signs on vegetation after observing animals feeding in the field, given that the animals could be observed at close quarters, we believe that the diet information from the two studies are comparable. Despite the fact that faecal analysis is the most suitable method for assessing diet composition of Trans-Himalayan herbivores (Shrestha & Wegge, 2006), initially we also did direct observations on feeding animals to make the results comparable, but given the workload in the field: estimating habitat use, availability and plant species richness and biomass during two seasons in different study areas, we found it less practical in this large-scale study. Therefore, one of us handled the laboratory work, while another carried out the field work. For microhistological analysis, fresh faecal pellets were collected from the field. To prevent assigning pellets mistakenly to a different species than the one intended to, we collected them from bedding sites by waiting for the animals to get up and move away. A group of *c.* 50 pellets was collected from each herd of blue sheep. Subsequently, five pellets were randomly drawn from each group to form one sample for the respective herd. Thus, there were 11 samples from Gya-Miru and nine from Hemis.

These samples were air-dried and stored in paper bags before boiling in water for *c.* 1 h and soaking overnight. They were then crushed in the laboratory, the inner tissue separated from the epidermis and cuticle by mixing a 5-g subsample with water for 1 min in a Waring blender and the mixture strained over a plankton sieve following the procedure described by de Jong *et al.* (2004). The residue was then washed again with tap water, transferred into a Petri-dish and allowed to settle. Using a Pasteur pipette, 10 random grab samples of the residue were then taken, and each droplet was put on a glass slide, spread out evenly and covered with a 2.4-cm cover slip.

We prepared separate reference slides for plants collected from the field. For this, small pieces of plant parts were cleaned in household bleach overnight, washed in water and fragments of epidermis were then stripped off and mounted in glycerol (de Jong *et al.*, 2004). Photomicrographs of epidermal material on a set of these reference slides were used to identify the fragments of cuticles observed in samples of the animal faeces. At least 100 cuticle or epidermal fragments were identified in each sample. To quantify the composition of the faecal material, the area of epidermal fragments was measured at a magnification of 100-X using a grid of small squares (each representing 0.01 mm^2) in the microscope eyepiece. The abundance of each species was calculated as a percentage of the total area of the fragments measured (Putman, 1984; Alipayo *et al.*, 1992; Homolka & Heroldova, 1992).

Since the difference in plant species richness between the areas is likely to affect the relationship between blue sheep niche width and ungulate species richness, we accounted for this parameter by estimating it in the three areas. The information on plant species richness for Kibber was obtained from Mishra (2001), whereas for Gya-Miru and Hemis, a transect was laid on an altitudinal gradient at every 200 m alternately on either side of the valley, starting at the valley mouth. These transects were laid in the main valleys as well as in the side valleys. Each transect was then divided into 50-m segments, and a 2×2 m plot was sampled at every 50-m intercept. The adequacy of the plot size was ascertained by examining the species accumulation curves, which reached an asymptote at 2×2 m. We also estimated aboveground biomass from these transects. Plants in these plots were identified in the field using a plant field guide (Polunin & Stainton, 1990). The unidentified ones were collected and later identified at the Wildlife Institute of India.

Statistical analyses

Blue sheep's niche width in terms of habitat and diet was determined using the Shannon–Wiener Index (Magurran, 1988). This index varies from 0 for minimum resource items to *c.* 5 for niche spectrum with maximum resource items, taking into account the number or abundance of each item. We assigned different resource units (e.g. 50 m in case of distance to cliff) into discrete categories to determine the niche (habitat) width, whereas for the diet width, each plant species formed a discrete category. The class intervals for the physical variables were as follows: altitude (interval 100 m; range 4000–5300 m), slope angle (5°; 0–65°) and distance to cliff (50 m; 0–600 m). Bootstrap resamplings were used to construct 95% confidence intervals to estimate the variability in the measure associated with sampling errors. The differences in the niche width (both diet and habitat) of blue sheep between the areas with differing species richness were tested for significance using a special *t*-test with the Shannon–Wiener indices as $t = \frac{H'_1 - H'_2}{\left[\text{var}(H'_1) + \text{var}(H'_2)\right]^{1/2}}$, where H'_1 is the niche (habitat or diet) width of the species in one area and H'_2 is its niche width in another area (Poole, 1974).

We pooled the habitat data of 2005 and 2006 from Kibber as there was no inter-annual variation in habitat use (Hotelling's $T^2 = 5.60, F = 1.81\ P < 0.15$ for summer & $T^2 = 8.65, F = 2.58$

$P < 0.08$ for winter). In addition to the changes in niche width, there might also be niche shifts, utilizing different resource units in different areas as well as seasons. To assess this possible flexibility, we checked for significant differences in habitat use between areas as well as seasons with analysis of covariance (ANCOVA), using availability as covariate (Zar, 1984).

RESULTS

A total of 71 observations on blue sheep habitat use during summer and 42 during winter were made in Kibber. The mean group size of the animal in this area during summer was 18, whereas that during winter was 15 (Table 1). In Gya-Miru, 46 observations were made during summer and 86 during winter. A total of 74 observations during summer and 28 during winter were made in Hemis. Median group size between seasons (winter = 15, summer = 14) or between areas was not significantly different, and the average group size of blue sheep was thus 13.7.

Habitat

During summer, blue sheep had the widest habitat width in Kibber ($H' = 3.06$), where it occurs allopatrically, and had the narrowest ($H' = 2.76$) in Hemis, where it shared resources with two sympatric species. This trend remained similar in winter (Fig. 1). The animal's niche width, in terms of habitat, thus declined with increase in the number of sympatric species in the assemblage (Fig. 1). This decline was significant during summer as well as during winter, adjudged by the differences in the niche width of the animal from the three areas using *t*-tests (Table 2).

Table 1 Mean and range of group size of blue sheep *Pseudois nayaur* in the study sites in the Indian Trans-Himalaya.

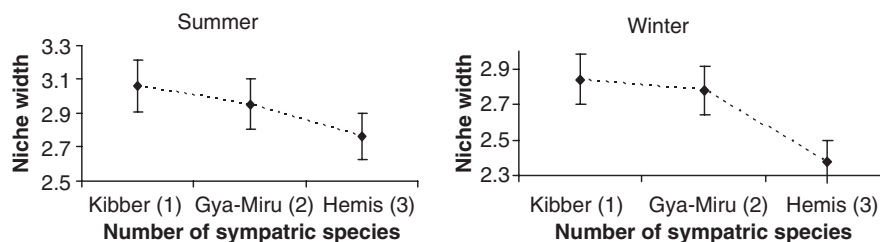| Place	Season	*n*	Group size (mean)	Group size (range)
Hemis	Summer	74	11.7	1–34
	Winter	28	8.0	1–23
Gya-Miru	Summer	46	13.6	1–53
	Winter	86	16.2	1–48
Kibber	Summer	71	17.6	1–68
	Winter	42	15.0	3–48

Figure 1 The relationship between blue sheep's habitat-niche width (Shannon–Wiener indices with 95% confidence intervals) and the number of sympatric species (in parentheses) in the Indian Trans-Himalaya.

Table 2 Differences in habitat width of blue sheep *Pseudois nayaur* in Kibber (allopatric), Gya-Miru (with one sympatric species) and Hemis (with two sympatric species) in the Indian Trans-Himalaya.

	Summer		Winter	
Area pair	*t*-Value	*P*-value	*t*-value	*P*-value
Kibber and Gya-Miru	1.546	0.123	1.077	0.282
Kibber and Hemis	3.66	< 0.001	2.495	0.013
Gya-Miru and Hemis	1.621	0.106	3.664	< 0.001

Table 3 Summary of ANCOVAs carried out on habitat use by blue sheep during two seasons (summer and winter) in three Trans-Himalayan sites with different species richness with available habitat as covariate.

Variable*	Effect	*F*	d.f.	*P*-value
Distance	Species	20.01	2	< 0.001
	Season	23.26	1	< 0.001
	Species × Season	1.75	2	0.174
	Available	0.02	1	0.885
Slope	Species	8.47	2	< 0.001
	Season	0.38	1	0.539
	Species × Season	4.56	2	0.011
	Available	2.17	1	0.141
Elevation	Species	36.15	2	< 0.001
	Season	18.55	1	< 0.001
	Species × Season	6.33	2	< 0.001
	Available	3.93	1	0.048

*Distance to cliff (m), Slope angle (deg.) and Elevation (m).

The distance of blue sheep locations from the nearest cliffs differed significantly between areas with different species richness (ANCOVA, $F = 20.01$, $P < 0.001$) as well as seasons ($F = 23.26$, $P < 0.001$; Table 3). For instance, the mean distance to cliff for blue sheep sightings during summer in Kibber was 144 m, whereas that in Gya-Miru and Hemis were 114 and 46 m respectively (Table 4). The species also differed in the slope angle of locations between the areas ($F = 8.47$, $P < 0.001$), but not between seasons ($F = 0.38$, $P = 0.539$). Nevertheless, there was a significant interaction between species richness and season, with the animal using steeper areas (mean = 34°) during summer and flatter areas

(mean = 31°) during winter in Kibber and Gya-Miru and vice versa in Hemis ($F = 4.56$, $P < 0.01$; Table 4).

Blue sheep also differed significantly in its use of the altitudinal gradient between the areas ($F = 36.15$, $P < 0.001$) as well as between seasons ($F = 18.55$, $P < 0.001$). There was also an interaction effect ($F = 6.33$, $P < 0.001$), as the animal used higher areas (mean = 4523 m) during summer and lower areas (mean = 4385 m) during winter in Kibber, where it occurs allopatrically, and in Gya-Miru with one sympatric species, whereas this seasonal trend was opposite in Hemis with two sympatric species (Table 4). But for this variable, there is an effect of the available habitat on these differences ($F = 3.93$, $P = 0.048$; Table 3).
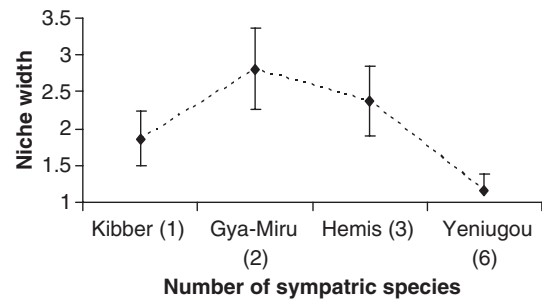

Figure 2 Relationship between blue sheep's diet-niche width (Shannon–Wiener indices with 95% confidence intervals) and the number of sympatric species (in parentheses) in the Trans-Himalaya (data source for Yeniugou: Harris & Miller, 1995).

Table 5 Differences in diet width of blue sheep *Pseudois nayaur* during summer in Kibber (allopatric), Gya-Miru (with one sympatric species), Hemis (with two) and Yeniugou (with six) in the Trans-Himalaya.

Area pair	*t*-Value	*P*-value
Gya-Miru and Kibber	2.95	< 0.01
Gya-Miru and Hemis	2.58	< 0.01
Kibber and Hemis	1.48	0.14
Yeniugou and Hemis	5.13	< 0.001
Yeniugou and Kibber	5.22	< 0.001
Yeniugou & Gya-Miru	8.38	< 0.001

Table 4 Mean (± SE) of the seasonal habitat use in relation to availability by blue sheep in Kibber (allopatric), Gya-Miru (with one sympatric species) and Hemis (with two) of the Indian Trans-Himalaya.

	Kibber			Gya-Miru			Hemis		
Variable*	Available	Summer	Winter	Available	Summer	Winter	Available	Summer	Winter
Distance	112.4 ± 13.1	144.01 ± 15.39	78.42 ± 13.3	238.5 ± 184.8	114.57 ± 16.09	60.29 ± 7.03	243.8 ± 199.0	45.58 ± 5.09	25.35 ± 3.83
Slope	17.7 ± 9.4	27.59 ± 1.74	26.78 ± 2.08	27.0 ± 8.12	34.13 ± 1.11	31.68 ± 1.11	26.02 ± 8.85	30.87 ± 1.44	39.14 ± 2.57
Elevation	4631.0 ± 02.8	4523.10 ± 30.89	4384.2 ± 40.4	4762.4 ± 351.8	4530.87 ± 50.30	4158.6 ± 50.21	4797.73 ± 271.77	4082.09 ± 37.38	4104.5 ± 39.35

*Distance to cliff (m), Slope angle (deg.) and Elevation (m).

Diet

Blue sheep's diet width had a hump-shaped relationship with the number of sympatric species. The animal had a narrower diet width in areas of allopatry and areas of high species richness, but wider niche width in areas with intermediate ungulate species richness (Fig. 2; Table 5). For instance, the diet width of blue sheep was narrower ($H' = 1.86$) in Kibber, where the animal occurred allopatrically; the widest in Gya-Miru ($H' = 2.81$) with one sympatric species; and again narrower ($H' = 2.36$) in Hemis with two sympatric species. Its diet width differed between Kibber and Gya-Miru ($t = 2.948$, $P = 0.004$), but not between Kibber and Hemis (Fig. 2). The diet width of the animal further narrowed down ($H' = 1.07$) in Yeniugou with six sympatric species, which was significantly different from blue sheep's diet width in Gya-Miru ($t = 8.30$, $P < 0.001$) and Hemis ($t = 5.13$, $P < 0.001$; Table 5).

Plant availability

There were 21 plant species in Gya-Miru, 17 in Hemis, 16 in Kibber and 20 in Yeniugou that are known to be an important constituent of the diets of mountain ungulates in the Trans-Himalaya. *Carex*, *Kobresia*, *Stipa*, *Festuca*, *Astragalus*, *Oxytropis*, *Leymus*, *Potentilla*, *Nepeta* and *Artemisia* were some of the most abundant genra in the study sites. The plant species richness did not differ between different areas ($P > 0.05$ for all paired t-tests). Data on aboveground biomass available from two sites show that the mean ($\pm$ SD) plant biomass in Gya-Miru was 6.31 ($\pm$ 3.7) g/m^2, whereas that in Hemis was 4.15 ($\pm$ 2.67) g/m^2, but the difference is statistically not significant ($t = 1.686$, $P = 0.10$).

DISCUSSION

This study has shown that blue sheep's niche width in terms of habitat declines as the number of sympatric species increases in an area, which is in line with our first prediction. Such a relationship is in concordance with niche trends observed in small mammal (Fox, 1981) and fish communities (Thorman, 1982). However, the animal's diet width, surprisingly, showed a hump-shaped relationship, with the widest diet width at intermediate species richness. For instance, blue sheep had a narrower diet width in Kibber, where it occurred allopatrically, and in Hemis with two sympatric species, but the widest diet width in Gya-Miru with one sympatric species. This trend was further strengthened when we included the diet data of blue sheep in Yeniugou with six sympatric species (Harris & Miller, 1995), where it had a diet width narrower than that in any of our study sites. This pattern is contradictory to our expectation under competition theory that as the number of sympatric species increases, the animal should widen its diet width, incorporating less nutritious plants in its diet because of forage constraint imposed by the sympatric species.

We suggest that the narrow diet width of blue sheep in areas with greater number of sympatric species is out of necessity, as the forage intake of herbivores in low productive environments such as the Trans-Himalaya is constrained by availability of plants that are sparsely distributed and are also fed on by sympatric species. Thus, the animal narrows down its diet width, feeding on fewer but readily available plant species. On the contrary, the narrower diet width in allopatry is presumably out of choice, as the animal can choose the most nutritious plants from an array of plants available. In any case, it became apparent that the niche of herbivores in terms of habitat and diet has different dynamics in areas with different number of sympatric species in high-altitude grazing ecosystems in the Trans-Himalaya. Although there are marmots in these areas, given their largely localized distribution along moist areas such as stream banks with higher vegetation cover (Pfister, 2004), they would not have influenced the overall results of this study.

A caveat of this study is the lack of replication. But this was judged to be a minor disadvantage, as the field work in more areas in this observational study would have ensued more environmental (natural as well as artificial) heterogeneity amongst the study sites, thereby confounding the effect of sympatric species richness on blue sheep's niche width. However, we accounted for the differences in habitat availability that might also have an effect on blue sheep's niche utilization, because changes in the availability of habitat variables alter the competitive balance of the co-occurring species. Furthermore, the plant species richness was comparable in the three study areas as well as in Yeniugou. Although Mishra (2001) estimated plant species richness using a stratified random sampling method, given that over 2 years were spent in the area studying wildlife and rangeland, it is less likely that species richness was underestimated. To our knowledge, this is the first study looking at the relationship between niche width and herbivore species richness in wild ungulates at a regional scale, and has important implications for their management in grazing ecosystems.

Blue sheep is the most widely distributed mountain ungulate in the Ladakh region of the Indian Trans-Himalaya (Namgail, 2006b). This wide distribution of the animal could be related to its versatility in resource use according to availability determined by biotic factors as shown by this study, as well as abiotic factors such as terrain. For instance, although the animal is known to use steep cliffs as anti-predator habitat (Namgail *et al.*, 2004), it reportedly used boulders as escape terrain on the Tibetan plateau where availability of cliffs was low (Harris & Miller, 1995). Thus, blue sheep's wide distribution may be the result of its dietary and habitat flexibility, suggesting that compared with other Caprinae species, it may face fewer constraints to recolonize an area after local extinction.

To conclude, it became apparent that blue sheep's niche varies across areas with different number of sympatric species. Thus, biotic interactions seem to play a role in the distribution of mountain ungulates, which should be addressed further in other mountainous grazing ecosystems. Species distribution models often incorporate only the environmental variables and tend to neglect the biotic interactions (Araújo & Luoto, 2007), which perhaps leads to overestimation of distributional range

of species as animals cannot occupy all the suitable habitats because of competition with other sympatric species (Hutchinson, 1959). Therefore, our results underscore the role of interspecific interaction in species distributions and the importance of including this variable in species distribution models, perhaps by incorporating the diversity and abundance of sympatric species in the model.

Furthermore, the conventional contention that a large herbivore widens its niche width in areas with high species richness to avoid competition needs to be re-examined, especially in low productive environments like the Trans-Himalaya, where availability of resources is minimal because of low plant diversity and biomass, which further declines in winter as a result of plant senescence and snow cover. From a conservation point of view, it is obvious that given the tendency of the wild ungulates to change their niche widths in response to sympatric species, the mountain ungulates in the Ladakh Trans-Himalaya are probably at a disadvantage in the face of the recent increase in population of a variety of livestock in the region (Namgail *et al.*, 2007a). Although studies have been carried out at local scales to address this issue (Bagchi *et al.*, 2004; Mishra *et al.*, 2004; Namgail *et al.*, 2007b), there is no information at larger geographical scales, which is urgently needed because of the relationship between mechanisms underlying local and regional species richness (Ricklefs & Schluter, 1993).

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