

Distributional congruence of mammalian herbivores in the Trans-Himalayan Mountains

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Abstract Large-scale distribution and diversity patterns of mammalian herbivores, especially less charismatic species in alpine environments remain little understood. We studied distributional congruence of mammalian herbivores in the Trans-Himalayan region of Ladakh to see if the distributions of less prominent and smaller herbivores can be determined from those of larger and more prominent herbivores like ungulates. Using a similarity index, we assessed shared distributions of species in 20×20 km² grid-cells in an area of about 80,000 km². We used the Unweighted Pair-Group Method with Arithmetic Average (UPGMA) to classify mammalian herbivores into groups with similar distributions. We then used the G-test of independence to look for statistical significance of the groups obtained. We identified six groups of mammalian herbivores with distributions more similar than expected at random. The largest group was composed of nine species whereas the other large group comprised six species. Canonical Correspondence Analysis (CCA), used to relate the groups with environmental features, showed that the largest group occurred in higher and flatter areas, while the other large group occurred in lower and steeper areas. Large herbivores like ungulates can be used as surrogate for less prominent small herbivores while identifying areas for latter's protection in the inaccessible mountainous regions of the Trans-Himalaya [*Current Zoology* 59 (1): 116–124, 2013].

Keywords Mountain ungulates, rodents, lagomorphs, UPGMA, biogeography, Trans-Himalaya

Information on species distribution and diversity patterns is crucial for understanding the ecological and evolutionary determinants of spatial heterogeneity in biodiversity (Ricklefs and Schluter, 1993). Species either diverge or converge in their response to environmental gradients, forming geographical groups with similar distributions (Gómez-González et al., 2004). Spatial congruence of species distributions has been studied in several taxa (Gómez-González et al., 2004, Marquez et al., 1997; Oertli et al., 2005), but it remains poorly understood in mammalian herbivores. Given that mammalian herbivores are important, both aesthetically and economically, and their populations are declining rapidly (Gordon et al., 2004), there is an urgent need to understand their distribution and diversity patterns for identifying areas for their protection.

Distributional associations of related species have been studied with probabilistic approaches using similarity indices (Armenteras et al., 2003; Real et al., 2008; Real and Vargas, 1996). They have been investigated to evaluate the suitability of some taxa as surrogate for others while prioritizing conservation areas with limited time and resources (Balmford and Long, 1995; Toranza

and Arim, 2010; Warman et al., 2004; Williams and Gaston, 1994). Such studies are suitable for assessing biodiversity, especially in areas that are difficult to survey due to harsh environmental conditions (Badgley, 2010). Although several studies on distributional associations of discrete taxa such as reptiles and birds were carried out (Pawar et al., 2007), distributional congruence amongst sub-groups within a taxon such as mammal has rarely been explored.

Ladakh is a remote mountainous region, bounded by the world's highest mountain ranges: Karakoram on the north and the Greater Himalaya on the south. It represents a transition zone between the open plains of the Tibetan Plateau in the east and the rugged mountains of Hindu Kush Mountains in the west. Despite the low primary productivity (Namgail et al., 2012), it supports 20 species of wild mammalian herbivores, representing 6 families and 11 genera (Fox et al., 1991; Pfister, 2004). These include several endangered ungulates, rodents and lagomorphs (Namgail, 2009; Pfister, 2004). Most of these animals are Palearctic in origin, a trend also observed in the region's avifauna (Namgail and Yom-Tov, 2009).

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Few studies carried out on the wild ungulates of Ladakh suggest that species like the Tibetan argali *Ovis ammon hodgsoni* and the Tibetan gazelle *Procapra picticaudata* prefer open and rolling areas (Namgail et al., 2004; Namgail et al., 2008), while species like the Asiatic ibex *Capra ibex sibirica* and blue sheep *Pseudois nayaur* occur in rugged areas (Namgail, 2006). As far as the diet is concerned, limited information only on the Caprinae suggest that the Tibetan argali and blue sheep consume a higher proportion of graminoids, while the Ladakh urial *Ovis vignei vignei* and Asiatic ibex incorporate a higher proportion of non-graminoids in their diets (Johnsingh et al., 1999; Mishra et al., 2004; Van Den Tempel and De Vrij, 2006). Habitat use and dietary affinities of the small herbivores such as rodents and lagomorphs in the region are not known.

Several studies in the last decade also shed some light on the distribution of larger herbivores in the region (Bagchi et al., 2004; Mishra et al., 2004, Namgail et al., 2007, Namgail et al., 2009; Namgail et al., 2010), but the distribution and diversity patterns of smaller herbivores like pikas *Ochotona* spp. and voles *Alticola* spp. remain virtually unknown (Bagchi et al., 2006). This is unfortunate as the population of these small herbivores are declining in Ladakh and other Trans-Himalayan areas due to systematic eradication in the name of pest control management (Holzner and Kriechbaum, 2001). Their protection is stymied by lack of information on their status and distribution. Furthermore, because of their sheer size these small herbivores are difficult to survey and monitor, especially in mountainous regions of the Trans-Himalaya.

Recognizing this, we investigated whether we can infer the distributions of these neglected and difficult-to-detect small herbivores from those of the larger and charismatic herbivores. To this end, we identified groups of mammalian herbivores in Ladakh with similar distributions, and determined the climatic and other physical factors that influence such grouping.

1 Materials and Methods

1.1 Study area

Ladakh (32° to 36°N and 75° to 80°E) encompasses an area of about 80,000 km². Altitude in the region ranges from 2,800 to 7,600 m above sea level; this gradient provides a variety of habitats for a wide range of mammalian herbivores. Trans-Himalaya was formed as a result of the collision between the Indian and Eurasian plates about 35 million years ago (Dewey et al., 1988). The associated orogenesis gave rise to the Greater Hi-

malaya, which made the climate of the land beyond progressively drier (Ramstein et al., 1997). Subsequently, a predominantly endemic assemblage of herbivores developed in the region, as several species especially of the family Bovidae underwent adaptive radiations by evolving ecological and phenotypic diversities, occupying the newly created mountainous niches (Ropiquet and Hassanin, 2005).

Ladakh has three mountain ranges: Zangskar, Ladakh and Karakoram that run almost parallel to one another and a network of streams drain these ranges. The soil is sandy or sandy-loam, and are generally characterized by poor in organic matter and nitrogen content (Murti, 2001). There is no forest cover, and the vegetation is desert-like, consisting of low shrubs and herbs (Rawat and Adhikari, 2005). Some trees like poplar *Populus* spp. and willow *Salix* spp. grow along river-valleys (Namgail et al., 2012). The rangelands of the region are also characterised by low graminoid biomass (Mishra, 2001).

1.2 Data collection

We collected presence-absence data on 20 species of mammalian herbivores (Table 1) from 39 randomly selected grid-cells (20 × 20 km²; Fig. 1), which spanned entire Ladakh, and represented each landscape type: rugged terrain as well as open plains. Although we surveyed 75 grid-cells, the remaining 36 were not included in the analysis as we could not survey them thoroughly. It was difficult to establish the absence especially of small herbivores such as pikas *Ochotona* spp. and voles *Alticola* spp. in these grid-cells.

Although we collected information opportunistically on species presence-absence from the grid-cells over a period of seven years beginning in early 2000, intensive surveys were carried out between May 2006 and June 2008. During these surveys, species' presence-absence in the grid-cells was determined by walking on mountain trails, and from vantage points (Namgail, 2006). Sixty-five percent of the data used in the study were gathered during these surveys. In addition to direct observations, we recorded the occurrence of fresh body parts such as horns of ungulates as presence of a species in a grid-cell (de Vrij and van den Tempel, 2006). Presence of fossorial herbivores such as marmots and pikas was also determined by locating their active burrows.

Occurrence of large herbivores was also determined by interviewing wildlife officials and researchers working in various grid-cells. Apart from these, we used data from published sources (e.g., Chundawat and Qureshi, 1991; Fox et al., 1991; Mallon, 1991; Pfister, 2004).

Table 1 Mammalian herbivores in the Ladakh Trans-Himalaya and their abbreviations used in the figures and tables

Order/Family	Scientific name	Common name	Abbr.
Artiodactyla			
Bovidae	<i>Capra sibirica</i>	Asiatic ibex	Asi Ibx
	<i>Ovis ammon hodgsoni</i>	Tibetan argali	Tib Arg
	<i>Ovis vignei vignei</i>	Ladakh urial	Lad Uri
	<i>Pseudois nayaur</i>	Blue sheep	Blu She
	<i>Pantholops hodgsoni</i>	Tibetan antelope	Tib Ant
	<i>Procapra picticaudata</i>	Tibetan gazelle	Tib Gaz
	<i>Bos mutus</i>	Wild yak	Wil Yak
Perissodactyla			
Equidae	<i>Equus kiang</i>	Tibetan wild ass	Wil Ass
Rodentia			
Sciuridae	<i>Marmota caudata</i>	Long-tailed marmot	LoT Mar
	<i>Marmota bobak himalayana</i>	Himalayan marmot	Him Mar
Muridae	<i>Alticola roylei</i>	Royle's mountain vole	RoM Vol
	<i>Alticola argentatus</i>	Silvery mountain vole	SiM Vol
	<i>Alticola stoliczkanus</i>	Stoliczka's mountain vole	StM Vol
Lagomorpha			
Leporidae	<i>Lepus oiostolus</i>	Tibetan woolly hare	Wol Har
	<i>Lepus capensis</i>	Cape hare	Cap Har
Ochotonidae	<i>Ochotona curzoniae</i>	Plateau pika	Pla Pik
	<i>Ochotona ladacensis</i>	Ladakh pika	Lad Pik
	<i>Ochotona macrotis</i>	Large-eared pika	LaE Pik
	<i>Ochotona nubrica</i>	Nubra pika	Nub Pik
	<i>Ochotona roylei</i>	Royle's pika	Roy Pik

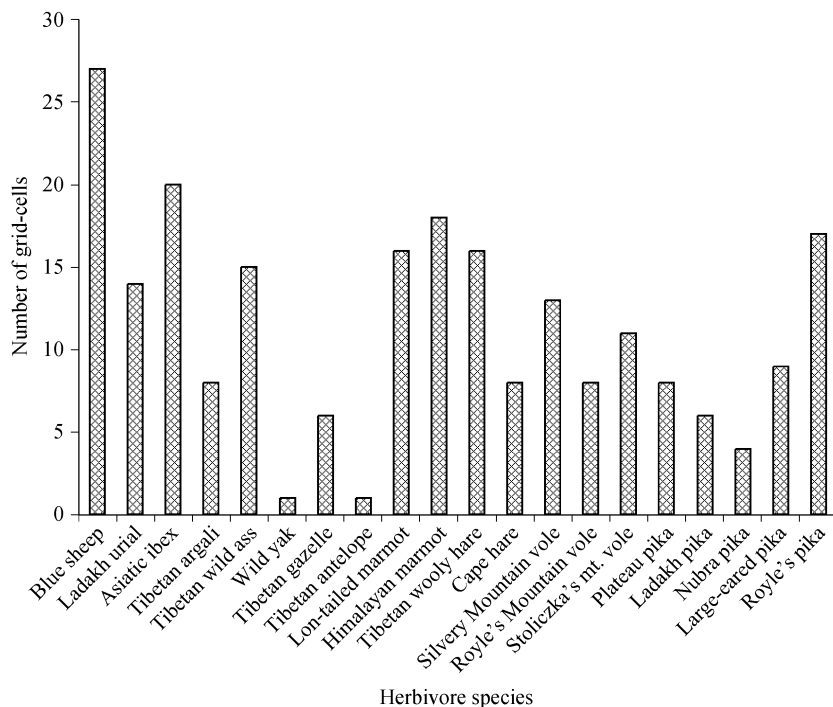


Fig. 1 Occupancy of 39 randomly selected grid-cells (20x20 km²) by mammalian herbivores in the Ladakh Trans-Himalaya

Such multiple sources of data, and the fact that we carried out long-term studies in some areas, ensured a thorough sampling from each grid-cell.

For assessing the relationship between environmental/climatic variables and species distributional data, we recorded mean altitude and slope angle from each grid-cell. Climatic variables (average annual temperature and precipitation) at 1 km² resolution were obtained from the WorldClim database (Hijmans et al., 2005). Although there are uncertainties associated with this dataset, especially from the mountainous regions (Hijmans et al., 2005), hitherto this is the only large scale climatic data available for Ladakh. We used Normalised Difference in Vegetation Index (NDVI) as a proxy variable for primary productivity in the grid-cells; mammalian species richness has been related to variability in NDVI (Oindo and Skidmore, 2002). NDVI image of 1×1 km spatial resolution was obtained from the National Oceanic and Atmospheric Administration (NOAA) - Advanced Very High Resolution Radiometer (AVHRR) sensor.

1.3 Statistical analysis

To classify species according to their distributions, we used the similarity index of Baroni-Urbani and Buser (1976) to each pair of species *x* and *y* as

$$B = \frac{\sqrt{C \cdot D + C}}{\sqrt{C \cdot D + A + B + C}} \quad \text{Eqn. 1}$$

where *A* is the number of grid-cells where only species *x* is present, *B* is where only species *y* is present, *C* is where both are present, and *D* is where both are absent. This similarity coefficient ranges from 0 (no species with common distribution) to 1 (all species have similar distributions). Although there is an array of similarity indices available (Wolda, 1981), we chose Baroni-Urbani & Buser’s index because this allows co-absences to be considered in a pair-wise comparison. A confirmatory analysis with the more commonly used Jaccard’s index gave similar results.

The significance of the similarity coefficients, organised in a matrix (species × species), were assessed by using the probability table in Baroni-Urbani and Buser (1976). This similarity matrix (0 to 1 values) was then transformed into a matrix of significant similarities in which we replaced the similarity values with ‘+’ (distributions significantly more similar than expected at random), ‘-’ (significantly dissimilar) and ‘0’ signs (not significantly different from expected, indicating random associations; see Table 2).

A dendrogram was then obtained by applying the Unweighted Pair-Group Method using Arithmetic Average (UPGMA) to the matrix of above described significant similarities (‘+’, ‘-’ and ‘0’s). Subsequently, we tested for the significance of groups separated by each fork in the dendrogram with a G-test of independence,

Table 2 Matrix of significant similarities between the distributions of mammalian herbivores in Ladakh

Species	LoT Mar	Asi Ibx	LaE Pik	Nub Pik	Cap Har	Lad Uri	Wil Yak	Roy Pik	RoM Vol	Tib Gaz	SiM Vol	Wol Har	Him Mar	Wil Ass	Lad Pik	Pla Pik	StM Vol	Tib Arg	Blu She
Tib Ant	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LoT Mar		+	-	-	+	+	-	+	+	-	-	-	-	-	-	-	-	-	0
Asi Ibx			-	0	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-
LaE Pik				+	+	+	+	0	+	-	+	+	+	+	-	-	0	-	0
Nub Pik					+	+	-	-	-	+	-	-	-	-	-	-	-	-	-
Cap Har						+	-	0	-	0	-	-	-	-	-	-	-	-	-
Lad Uri							-	+	-	0	-	-	-	-	-	-	-	-	-
Wil Yak								-	-	-	-	-	-	-	-	-	0	+	-
Roy Pik									+	+	+	+	+	+	+	+	+	0	+
RoM Vol										-	+	+	+	+	-	+	-	-	+
Tib Gaz											+	+	+	+	+	+	+	+	-
SiM Vol												+	+	+	+	+	+	+	+
Wol Har													+	+	+	+	+	+	+
Him Mar														+	+	+	+	+	+
Wil Ass															+	+	+	+	+
Lad Pik																+	+	+	+
Pla Pik																	+	+	+
StM Vol																		+	+
Tib Arg																			+

A submatrix from this table corresponding to each fork in the dendrogram (Fig. 2) was used to test for significant segregation between various groups obtained by the cluster analysis. For instance, the submatrix in the box corresponds to group I and II in the dendrogram (Fig. 2). The submatrix was divided into three sets: *A* and *B* (corresponding to two groups at a fork) to measure the homogeneity within a group and *AxB* (corresponding to the intersection between the two groups) to measure the differences between the two groups. See table 1 for species abbreviations. ‘+’ is similarity more than expected, ‘-’ similarity less than expected and ‘0’ as expected at random.

beginning with the groups that were most similar (McCoy et al., 1986). We took a sub-matrix, corresponding to two groups separated by a fork, from the matrix of significant similarities (Table 2), and divided it into three sets: *A*, *B* and *AxB*. *A* and *B* correspond to each of the clusters separated by the fork, and *AxB* corresponds to the intersection of the two groups.

If most of the ‘+s’ are in *A* or *B*, and most of the ‘-s’ and ‘0s’ are in *AxB*, then the groups compared are con-

sidered separate geographical groups. When ‘-’ predominated in *AxB*, segregation is strong, whereas if ‘+’ predominated in *AxB*, segregation is weak. The resulting parameters are *GW* for weak segregation and *GS* for strong segregation. We considered species to be in a group if *DW* (measure of homogeneity) for that group is positive and either *GW* or *GS* are statistically significant (Table 3). See Appendix 1 and McCoy, Bell and Walters (1986) for detail on the derivation of these parameters.

Table 3 Significant segregation of species’ distributions indicated by the forks in the dendrogram obtained by UPGMA (Fig. 2)

Groups obtained by UPGMA			Aggregation		Segregation			
Group <i>A</i>	Group <i>B</i>	Similarity Coeff.	<i>DW</i> (<i>A</i> x <i>A</i>)	<i>DW</i> (<i>B</i> x <i>B</i>)	Weak		Strong	
					<i>GW</i>	<i>P</i>	<i>GS</i>	<i>P</i>
Wol Har-Him Mar	Wil Ass	0.917	0.00	0.00	1.05	NS	0.00	NS
SiM Vol	Wol Har-Wil Ass	0.885	-0.71	0.00	1.59	NS	0.00	NS
Lad Pik-Pla Pik	StM Vole-Tib Arg	0.764	0.00	0.00	2.09	NS	0.00	NS
SiM Vol-Wil Ass	Lad Pik-Tib Arg	0.723	0.00	0.00	6.05	NS	0.00	NS
Nub Pik-Cap Har	Lad Uri	0.685	0.00	-0.71	1.05	NS	0.00	NS
SiM Vol-Tib Arg	Blu She	0.614	0.00	-0.71	1.76	NS	0.00	NS
LaE Pik	Nub Pik-Lad Uri	0.539	-0.71	0.00	1.59	NS	0.00	NS
Tib Gaz	SiM Vole-Blu She	0.495	0.63	0.08	19.54	**	0.00	NS
LoT Mar-Asi Ibx	LaE Pik-Lad Uri	0.436	0.31	0.31	1.24	NS	0.00	NS
Roy Pik-RoM Vol	Tib Gaz-Blu She	0.412	0.18	0.15	23.41	***	2.64	NS
Wil Yak	Roy Pik-Blu She	0.170	0.07	0.52	3.50	NS	15.19	***
LoT Mar-Lad Uri	Wil Yak-Blu She	0.152	0.27	0.30	17.32	NS	27.12	**
Tib Ant	LoT Mar-Blu She	0.000	0.00	0.03	0.00	NS	56.86	***

***P* < 0.05; *** *P* < 0.005; NS: Non-significant.

DW (*A* x *A*) and *DW* (*B* x *B*) indicate internal homogeneity (i.e., they measure as to what extent the similarities higher than expected (+) tend to be in sets *A* and *B*, but not in set *AxB*; the values range from -1 to +1; see Appendix 1 for greater detail), while *GW* and *GS* are the parameters of a G-test of independence used to test the significance of the segregations (*GW*= weak, *GS* = strong) between two groups compared. See Table 1 for species abbreviations.

1.3.1 Ordination method We used the Canonical Correspondence Analysis (CCA) to relate the geographical groups with environmental variables. The analysis was carried out using the CANOCO software (Ter Braak, 1986).

2 Results

The 20 mammalian herbivores comprised eight ungulates, seven lagomorphs and five rodents (Table 1). Fifty percent of the species were present in more than 10 grid-cells sampled. Blue sheep was the most common mammalian herbivore occurring in more than 25 grid-cells, followed by the Asiatic ibex and Himalayan marmot *Marmota bobak* (Fig. 1). Many species formed groups with distributions significantly more similar than expected at random (Fig. 2).

2.1 Geographical groups

Six geographical groups of mammalian herbivores were identified (Fig. 2). Group VI was the largest with nine species (see Table 1 for species abbreviations used in figures and tables), and included three rodents (Silvery mountain vole *Alticola argentatus*, Stoliczka’s mountain vole *Alticola stoliczkanus*, Himalayan marmot *Marmota bobak*), three lagomorphs (Tibetan woolly hare *Lepus oiostolus*, Ladakh pika *Ochotona ladacensis*, Plateau pika *Ochotona curzoniae*), and three ungulates (Tibetan wild ass *Equus kiang*, Tibetan argali and blue sheep. Distributions of the Tibetan antelope *Pantholops hodgsoni* (abbreviated as Tib Ant) and wild yak *Bos mutus* (Wil Yak) were significantly different from those of other species (Fig. 2).

Group II was strongly segregated from all other geo-

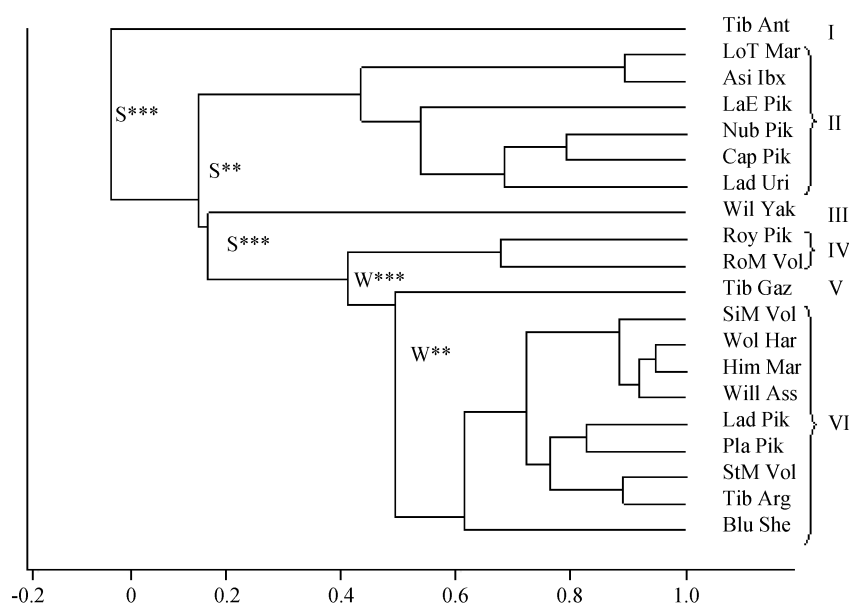


Fig. 2 Classification dendrogram of the mammalian herbivores with similar distributions in Ladakh

The scale on the x-axis represents the similarity coefficient. The roman numerals on the right indicate the group number described in the text (those in bold represent groups with single species); see Table 1 for species for abbreviations. S is strong and W is weak segregation amongst groups. ** $P < 0.01$; *** $P < 0.005$.

graphical groups (Table 3 & Fig. 2). It comprised one rodent (long-tailed marmot *Marmota caudata*), three lagomorphs (Large-eared pika *Ochotona macrotis*, Nubra pika *Ochotona nubrica*, Cape hare *Lepus capensis*) and two ungulates (Asiatic ibex and Ladakh urial; Fig. 2). Royle's pika *Ochotona roylei* and Royle's mountain vole *Alticola roylei* formed a separate group (group IV), but it was weakly segregated from other groups. Tibetan gazelle *Procapra picticaudata* (group V) also had a unique distribution.

2.2 Ordination of species

Environmental variables influenced the distributional patterns of mammalian herbivores (F -ratio = 4.57, $P = 0.002$). They explained 63% of the variation in species distributions. The first axis ordered species along a gradient of increasing slope angle and decreasing altitude, while the second axis ordered species along a gradient of decreasing precipitation. Asiatic ibex (abbreviated as Asi Ibx in the figures and tables) and long-tailed marmot (LoT Mar) occurred in lower and steeper parts, whereas Ladakh urial (Lad Uri), Nubra pika (Nub Pik) and Cape hare (Cap Har) occurred in lower and drier parts. Most of the other species occurred in flatter and higher areas (Fig. 3).

3 Discussion

Mammalian herbivores in Ladakh formed distinct geographical groups. Group II, comprising six species occurred in the steeper parts, while group VI comprising

nine species occurred in the higher and flatter areas; there are thus two biotic regions in Ladakh. Limited ecological information on the region's herbivores (see Namgail, 2009 and the relevant references therein) reveal that majority of the species within each of these groups have similar ecological requirements, which implies that the distributional congruence of herbivores in Ladakh is determined largely by their current ecology. The results of this study showed that several small herbivores share their distributions with the larger ungulates, suggesting that the easy-to-detect mammals like ungulates can be used as surrogate for the smaller herbivores such as pikas and rodents while identifying areas for the protection of these less prominent herbivores in the Trans-Himalaya.

Asiatic ibex and long-tailed marmot in Group II had similar distributions; CCA showed that they occurred in steeper and lower parts of Ladakh. Their distributions also overlap globally (IUCN, 2008). Limited ecological information suggests that Asiatic ibex uses rugged terrain as a predation escape strategy (Namgail, 2006), but the importance of this habitat type for the long-tailed marmot is less understood. It is possible that these burrowing rodents are using these areas, where they can dig easily into the colluvial debris fans. In any case, given the concordance in their distributions, it appears that the Asiatic ibex can be used as a surrogate for long-tailed marmot while identifying areas for latter's protection. Similarly, Nubra pika, cape hare and Ladakh urial in

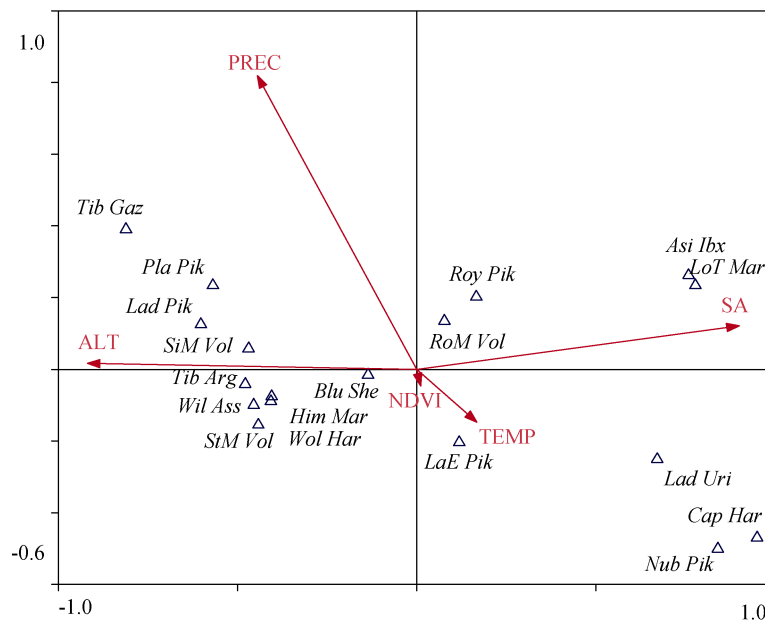


Fig. 3 First two axes of CCA ordination of the species and environmental variables

Altitude: ALT. Slope angle: SA. Temperature: TEMP. Precipitation: PREC and Normalized Difference in Vegetation Index: NDVI. See Table 1 for species identity.

Group II shared distributions, thus the Ladakh urial (ungulate) can be used as surrogate for these lagomorphs.

Tibetan woolly hare and Himalayan marmot in group VI shared distributions with the Asiatic wild ass more than the rest (Fig. 2). Globally, both these small mammals overlap in their distribution, largely in terms of altitude (Molur and Shreshtha, 2008). The CCA showed that these small herbivores and wild ass occur in higher and flatter areas. Thus high altitude and open areas seem to be important factors that determine their co-distribution, and it appears that prominent herbivores like the wild ass can be used as a surrogate for these small herbivores while identifying conservation areas. Furthermore, Stoliczka's mountain vole shared distribution with the Tibetan argali more than with other herbivores. Both these species are known to use habitats at higher altitudes close to snowline in alpine regions (Molur, 2008; Chundawat and Qureshi, 1999¹, Namgail et al., 2004).

Altitude and terrain ruggedness have also been identified as the most important variable that influenced niche partitioning of large herbivores in the region (Chundawat and Qureshi, 1999; Namgail et al., 2004; Namgail, 2006; Namgail et al., 2010), and elsewhere in

the Himalaya-Tibetan plateau region (Harris and Miller, 1995; Shrestha and Wegge, 2008). Thus, the co-distribution of small and large herbivores in Ladakh could be determined largely by active selection of habitats by these herbivores according to their adaptations. Although biogeographical analyses of mammals have been carried out (Badgley and Fox, 2000; Heikinheimo et al., 2007), this study to our knowledge is the first biogeographical analysis exclusively of mammalian herbivores including ungulates, and has important implications for a mechanistic understanding of their biogeography in the Trans-Himalaya and other alpine rangeland areas.

In summary, Ladakh is not a homogeneous geographical unit in terms of mammalian herbivore distribution, indicating that they are affected by non-random processes. The herbivore species form distinct geographical groups, which are determined largely by environmental variables like altitude, terrain type and precipitation. It seems that some of the larger ungulates can be used as surrogate species for the less charismatic small herbivores like rodents and lagomorphs in mountainous areas, where it becomes difficult to survey for these small herbivores.

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Appendix 1

We refer to $Pp(A \times A)$ as the number of '+' between each pair of species within set A divided by the total number of '+s', '-s' and '0s', possible for comparisons in set A (Carmona et al., 1999). So, $Pp(A \times A)$ is the proportion of '+s' in set A . $Psp(A \times A)$ is the number of species in set A that have at least one '+' divided by the total number of species for comparisons in set A , which represents the proportion of species in set A with at least one '+' (see McCoy, Bell and Walters, 1986 for more detail). We then compute $d1(A \times A)$ as follows: If the number of '+s' in A is zero, then $d1(A \times A) = 0$; otherwise,

$$d1(A \times A) = \frac{Pp(A \times A) \times Psp(A \times A)}{\sqrt{(Pp(A \times A))^2 + (Psp(A \times A))^2}} \quad \text{Eqn. 1}$$

We call $Pm(A \times A)$ and $Psm(A \times A)$ as the proportion of '-s' in set A and the proportion of species in set A with at least one '-', respectively, and these are computed in the same way as $Pp(A \times A)$ and $Psp(A \times A)$, but by taking into account the '-' in this case. We then define $d2(A \times A)$ in the following way: if the number of '-s' in set A is zero, then $d2(A \times A) = 0$; otherwise, we define $Pp(A \times B)$ and $Psp(A \times B)$ in a similar way as $Pp(A \times A)$ and $Psp(A \times A)$, but referred

$$d2(A \times A) = \frac{Pm(A \times A) \times Psm(A \times A)}{\sqrt{(Pm(A \times A))^2 + (Psm(A \times A))^2}} \quad \text{Eqn. 2}$$

to set $A \times B$. Then $d4$ is zero when the number of '+s' in $A \times B$ is zero; otherwise, We calculated $d1(B \times B)$, $d2(B \times B)$ and

$$d4(A \times A) = \frac{Pp(A \times B) \times Psp(A \times B)}{\sqrt{(Pp(A \times B))^2 + (Psp(A \times B))^2}} \quad \text{Eqn. 3}$$

$d4(B \times B)$ in the same way as calculated for $(A \times A)$ in the above equations, but computing the '+s' and '-s' in set B .

We then determined internal homogeneity in each of the groups divided by a fork as

$$DW(A \times A) = d1(A \times A) - d2(A \times A) - d4 \quad \text{Eqn. 4} \quad \text{and}$$

$$DW(B \times B) = d1(B \times B) - d2(B \times B) - d4 \quad \text{Eqn. 5}$$

where parameters $DW(A \times A)$ and $DW(B \times B)$ measure as to what extent the similarities higher than expected at random tend to be in sets A and B , respectively, but not in $A \times B$ (see McCoy et al., 1986), and therefore they are indicative of the internal homogeneity of each of the groups separated by a fork.