

**Geography of mammalian herbivores in the Indian
Trans-Himalaya: patterns and processes**

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Thesis

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To my family and friends for their love and patience,
to the people of Ladakh for their respect for nature, and
to the wildlife of Ladakh for their beauty and grace.

*'The land is so barren and the passes are so high that only the best friends or the fiercest enemies
would want to visit us'*

A Ladakhi saying



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Preface

Ecology is one of the youngest and least settled branches of biology. Earnest analytical investigations in ecology started only in the 1960's with Robert MacArthur working on the Lotka-Volterra's model. Several ecologists including MacArthur were startled by the uneven distributional pattern of biodiversity on earth. This pattern, although described by naturalists long before ecology as a science was conceived, remains to be understood thoroughly. Early ecologists adopted a reductionist approach to look at biodiversity pattern on the planet. But that changed in the last couple of decades with ecologists adopting a more pluralistic and macro-ecological approach. This thesis is a step into that direction.

It became apparent in the last few decades that species distributional patterns are dynamic and depend on the configuration of resources in the environment. Species colonize areas, exploit resources and expand their populations, provided the resources are abundant and their birth rates exceed death rates. Thus, animal distributional ranges change through space and time. If we look at this dynamicity in the animal kingdom, nothing can beat the rate at which man's distribution changed in the early phases of human history. For instance, Europeans invaded the Polynesian islands, depleted resources and left for other archipelagoes within a decade. But human distribution became more static once we resorted to agriculture, which enabled production of surplus food in a particular area.

The settled life and mass production of food also allowed us to indulge in recreational activities. Consequently, human needs and aspirations have sky-rocketed. Today, when we think about the Hutchinsonian niche hypervolume, no species befit this more than we do. The list of our resource requirements is growing exponentially with technological developments, because it is associated not only with survival but also with vanity. So today when we ask what is the single most important factor determining human distribution, for some lanky and scrawny models walking down the fashion-ramps of Paris, it definitely will not be food, but cosmetics like lipsticks, mascara, nail-polish, so on and so forth. These can be produced in one corner of the world and get transported to another within a short time, thereby precluding the need to redistribute human population according to the availability of these resources.

Non-human animal distribution however remains fluid even today, depending on availability of food, water and shelter. Their distributions thus depend on the presence of these resources, and given the resource state and biological factors of an area, we can predict their distribution in that area. But things get complicated and murky once one asks how animal assemblages are formed and maintained through time. Here one simultaneously need to deal with distribution of more than one species, and the niche space of an animal gets additional dimensions such as sympatric competitors, predators and parasites feeding on them. Moreover, we need to integrate the evolutionary history of the constituent species of an assemblage.

Therefore, environmental factors, evolutionary history, dispersal, competition, facilitation, predation and parasitism are some of the most important factors determining the formation and maintenance of animal assemblages. Nevertheless, given that some species survive in foreign terrain, once introduced there, environmental factors seem less important, suggesting that geographical barriers or competitors had stopped them from advancing into those areas. Furthermore, when we talk of the biotic environment of a species, herbivores form a unique taxon whose distribution is limited not only by food resources but also by predators at higher trophic levels, thereby further complicating the issue. So what are the most important biotic and abiotic factors that determine the formation and maintenance of herbivore assemblages? I plunged headlong into a venture four years ago with this very question in mind. I chose the mountainous rangelands of

the Indian Trans-Himalaya to address this question, and at the end of the project, I have emerged with scores of new questions while trying to find an answer. Furthermore, I flash out banners with answers like it depends on the taxon under investigation, spatial and temporal scales. In any case, if I managed to spark an interest amongst ecologists on the fascinating assemblage of mammalian herbivores in the Trans-Himalaya, and thereby stimulate further research, I would have accomplished an important goal.

Abstract

Namgail, T. (2009). Geography of mammalian herbivores in the Indian Trans-Himalaya: patterns and processes.

The loss of mammalian herbivores from grazing ecosystems has become a major concern, and efforts to stem such losses are stymied by lack of information on the proximate and ultimate factors influencing their distributions and diversity patterns. This research investigated the distribution, species-richness patterns and underlying mechanisms in mammalian herbivores of the Trans-Himalayan region of Ladakh, India. It adopted a multi-spatial approach to understand these issues in the little-known herbivore assemblage of the region. Since vegetation is the most important factor that determines the distribution of herbivores, first I researched the distribution and abundance patterns of vascular plants along an altitudinal gradient at different spatial scales. Both plant species-richness and aboveground biomass showed a hump-shaped relationship with altitude. Such a relationship in case of species-richness is expected, but it is contrary to my expectation of a negative linear relationship, in case of abundance. I relate this unexpected pattern to the limited precipitation and pervasive livestock grazing at lower altitudes in this dry alpine environment. I then investigated the biogeography of mammalian herbivores, and found that they form geographical groups on the basis of their evolutionary histories. Subsequently, I assessed the niche relationship between Asiatic ibex *Capra ibex siberica* and blue sheep *Pseudois nayaur*, the most common large herbivores in Ladakh, to see whether local level processes like competition generate spatial pattern of herbivore species-richness. The results showed that blue sheep constrains the distribution of ibex, which implies that competition amongst native species does play a role in structuring large herbivore assemblages in the region. Recognising the lack of information on large herbivores' niche variation across assemblages, I also studied blue sheep's niche width in relation to herbivore species-richness. It became apparent that the species' niche varies across assemblages with different number of sympatric species, which could negatively influence the animal's reproductive performance and population. Finally, I asked if the distributional range of the endangered Ladakh urial *Ovis vignei vignei* is constrained by the abundant blue sheep, and found that these two species associate randomly at large geographical scales, but co-occur at the landscape level as a result of local habitat-level resource partitioning. These results contribute towards understanding the mechanisms responsible for the formation and maintenance of large herbivore assemblages in the Trans-Himalaya and other mountainous regions of the world.

Key words: Large herbivores, mammalian herbivores, mountain ungulates, biogeography, chorotype, species richness, diversity, biome, ecotone, Ladakh urial, blue sheep, Asiatic ibex, marmot, hare, pika, vole, vascular plants, altitudinal gradient

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Every research project ends with lot of memories, and this is the section to revive them all, and express gratitude to those who made them memorable. Four years ago, I set out on a quest of understanding herbivore diversity in the Trans-Himalaya. The journey was rather tortuous that needed assistance at every turn. Here I thank all those who helped me, making the journey smooth and enjoyable. While carrying out this research, I had the privilege of meeting some of the brightest and dynamic people I have ever known. Constraint of space would not allow me to list them all. Some of them contributed immensely, and here I make a humble effort to express my gratitude to them in words.

My research carrier started in 1997, when I worked on insects pests of poplar trees under the supervision of Prof. P.K. Tewari at the Panjab University, Chandigarh. I thank her for getting me interested in research. Then I shifted my focus on bigger animals: large mammals. I was fortunate to get an opportunity to work with Dr. Joe Fox in Norway. Joe you gave me a break when I needed one desperately. You led me through murky waters, and gave fresh impetus that enabled me to do a Ph.D. Yours is one of those contributions that words would be too feeble to express gratitude for. Thank you so much in any case. Dr. Yash Veer Bhatnagar is another person that played a crucial role in my early research carrier. Yash Veer, I still remember the time when you gifted me a copy of the 'Mountain Monarchs', which I cherish to this day. The 'earthwatch days' in Ladakh were absolute fun. Thanks so much for all your support, guidance and encouragement over the years.

The discourse for a PhD started with a trip to Wageningen in 2001. No, it was neither the tulips nor the windmills, not even the cheese that brought me to the Netherlands, but the erudite insight of Prof. Herbert Prins that brought me here. Herbert, things didn't start the way we wanted, but start it did, and I consider myself lucky to get this opportunity to work with you and the group. Yours has been a contribution as big as the Himalaya, so the word of gratitude has to be equally big, and I don't know if exists in the lexicon. You taught me how to turn a question on its head and look on the other side of the picture. I am glad that you guided me away from the species chauvinist approach. Moreover, your intellectual insight, expert guidance and humour made this journey far easier than expected. I cherish our conversations on the mountain trails and at campsites over tea. Thanks for being a constant source of inspiration.

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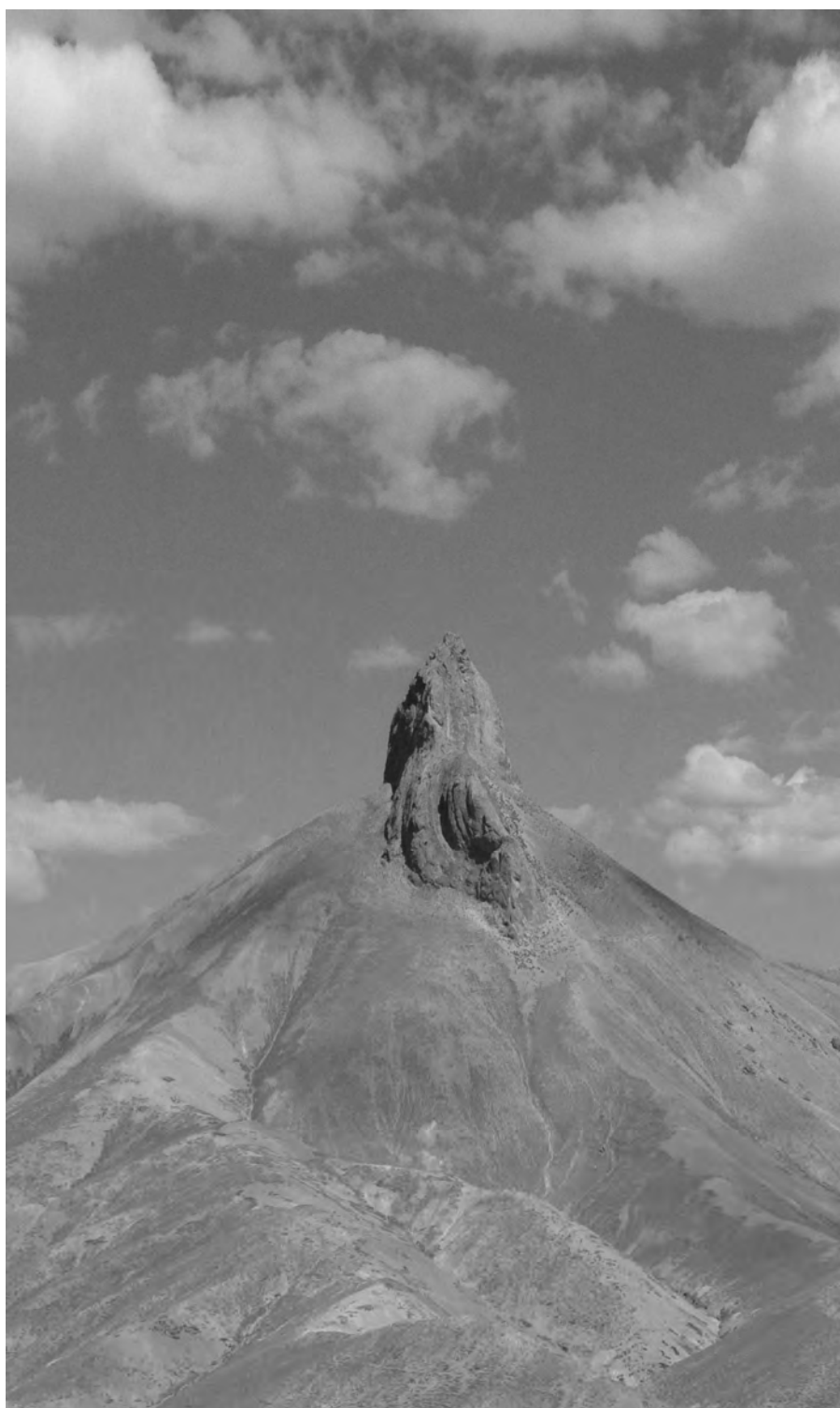
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Tsewang Namgail
Wageningen, 2009



CHAPTER 1

Herbivore species-richness: introduction

Tsewang Namgail

"Be thankful for problems. If they were less difficult, someone with less ability might have your job"

Anonymous

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Chapter 1

Introduction

Biodiversity on earth is uneven with some biogeographic units harbouring more species than others, a pattern observed long ago by naturalists (Hooker, 1853; Sclater, 1858; Wallace, 1876). The most prominent of this discrepancy in species richness being exemplified by the latitudinal gradient in species diversity with more species in the tropics and less in the temperate and polar regions (Pianka, 1966; Rohde, 1992). Within these broad geographical zones, some biomes support more and some less number of species. Therefore, one obvious question is what determines such spatial pattern of species diversity. To answer such questions, studies have been conducted on different taxa at several spatial and temporal scales. These studies have indicated that factors such as competition (Tilman, 1994), habitat diversity (Shmida & Wilson, 1985; Tews et al., 2004), time-for-speciation or evolutionary time (Stephens & Wiens, 2003), area (Prins & Olff, 1998; Losos & Schluter, 2000), spatial scaling of resource use by species (Ritchie & Olff, 1999), climatic oscillations (Dynesius & Jansson, 2000), geometric constraints (Colwell & Lees, 2000), optimal precipitation/soil fertility (Olff et al., 2002) and several other parameters (Pianka, 1983) may influence species richness across the planet.

Despite such research efforts, hitherto there is no consensus on the primary mechanisms (Hawkins et al., 2003). It, however, became apparent that species assembly patterns hinge on the spatial scale of investigation, as different factors play important roles at different scales (Levin, 2000; Willis & Whittaker, 2002; Chase & Leibold, 2003; Rahbek, 2005). For example, climatic and historical factors play a major role in determining species richness at continental scales (Whittaker et al., 2001), while interspecific competition and habitat structure become more important at local and regional scales (Huston, 1999; Amarasekare, 2003; Tews et al., 2004). Thus, space has been considered to be pivotal to many ecological processes.

The studies on spatial pattern of biodiversity are however biased towards birds, fish, insects and plants, and remains little known for large herbivores (but see Prins & Olff, 1998; Olff et al., 2002; Klop & Prins, 2008; Cromsigt et al., 2009a; Cromsigt et al., 2009b). Large herbivores are represented by a wide variety of taxa, and occupy a range of ecosystems across the planet. They influence the structure and functioning of ecosystems by altering the dynamics of plant communities (Naeem & Li, 1997; Augustine & McNaughton, 1998; Ritchie & Olff, 1999). Large herbivores also constitute important prey of large carnivores, thereby maintaining species diversity at higher trophic levels. Thus, large herbivores play an important role in ecosystem functioning, which provides compelling reasons to study diversity patterns of large herbivores that will help in maintaining their diversity in grazing ecosystems.

In understanding species-richness pattern of an area, the primary question that needs to be answered is, do local assemblages represent smaller subsets of the regional species pool? If so, what processes determine such non-random distribution of co-occurrences? Why do some areas contain more species than others do? Are there specific determinants of these patterns? Early ecologists had come to the conclusion that species diversity of a region reflected its age (Pianka, 1983), and they did not clearly distinguish between regional and local diversity, but more recently ecologists partitioned the regional from the local diversity (Ricklefs & Schluter, 1993), and took on diversity as an ecological problem that they could solve by resorting to insights from population biology. However, to understand the species diversity at a global scale, ecologists need to abandon the parochial view of local determinism and recognise that ecology, evolution, geography and history are different facets of a single set of processes and the patterns they generate (Brown, 1985).

Introduction

MacArthur (1972) proposed a simple model to explain species richness D_s as a function of resource availability and niche relationships among species: $D_s = Dr/Du(1 + Ca)$, where Dr represents the diversity of resources, Du the niche width of each species, C describes the number of potential competitors in niche space, and a is the mean competitive coefficient or mean niche overlap. This model predicts that assemblages differ in species richness in three different ways, (1) an area with greater resource diversity (larger Dr) can maintain more niches and therefore contain higher number of

species (Fig. 1b), (2) assemblages where species exploit smaller portions of the total niche space (smaller Du) contain more species (Fig. 1c), and (3) greater overlap of niches (larger a) facilitates co-existence of more species (Fig. 1d). This model can serve as a useful starting point in understanding species richness in local and regional assemblages of large herbivores

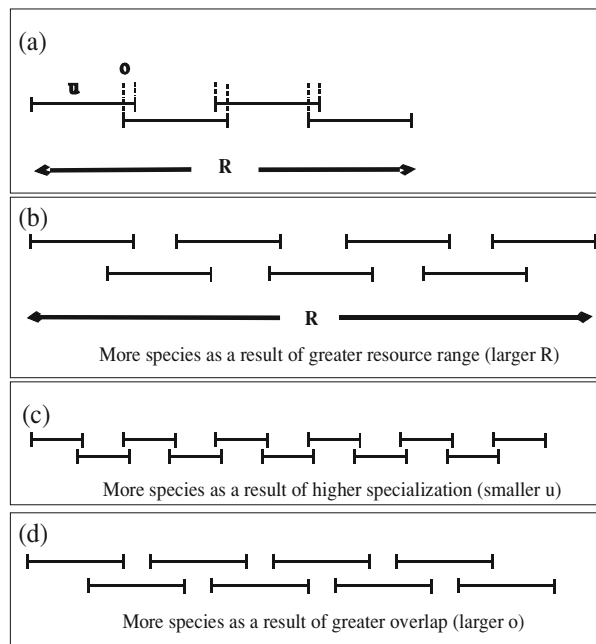


Fig. 1. A simple model of species richness, (a) each species uses a portion u of the available resources (R), overlapping with adjacent species by an

amount a . More species may occur in one assemblage than another because (b) a greater range of resources is present (larger R); because (c) species are specialized (smaller average u); (d) greater overlap in resource use among species (larger average a), (Figure adopted from MacArthur, 1972).

Niche theory and herbivore diversity

Although large herbivore diversity on a continental/global scale may be determined by climatic factors (Olf et al., 2002), biotic interactions (Prins & Olf, 1998) and habitat features (Ben-Shahar & Skinner, 1988) become more important at local and regional scales. Facilitation and competition are important biotic factors potentially governing herbivore species richness (Arsenault & Owen-Smith, 2002). The former may enhance species richness in communities in high productive areas in the Tropical systems (Huisman & Olf, 1998), but perhaps is less important in structuring herbivore assemblages in less productive ecosystems where competition tends to be the dominant form of interaction (Mishra et al., 2002; Mishra et al., 2004; Namgail et al., 2007b). However, large herbivores in these ecosystems may avoid strong competition by diverging in their diet and/or habitat use (see Namgail et al., 2004), as these are the most important resource dimensions along which species segregate in order to coexist

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(Schoener, 1974). Thus, biotic factors are more important in the more productive tropical ecosystems, while the physical environment plays a significant role in the development and maintenance of communities in less productive ecosystems toward the poles (MacArthur, 1972).

A plethora of studies on niche separation between large herbivores have been carried out (e.g., Jenkins & Wright, 1988; Voeten & Prins, 1999; Namgail et al., 2004). Nonetheless, the most crucial factors determining assembly patterns remain elusive. Most of the previous studies were conducted in single assemblages, and it is not known as to how the niche of a species can vary across herbivore assemblages with varying number of sympatric species. Based on niche theory, one might expect the habitat-niche width of a species to decline with the number of sympatric species during summer (Fig. 2), and the diet-niche width to increase with species richness due to availability of a greater range of plant species in high altitude drier environments during this growth season. In contrast, both diet and habitat widths are expected to decline with number of sympatric species in an assemblage during winter due to plant senescence and snow cover (Fig. 2).

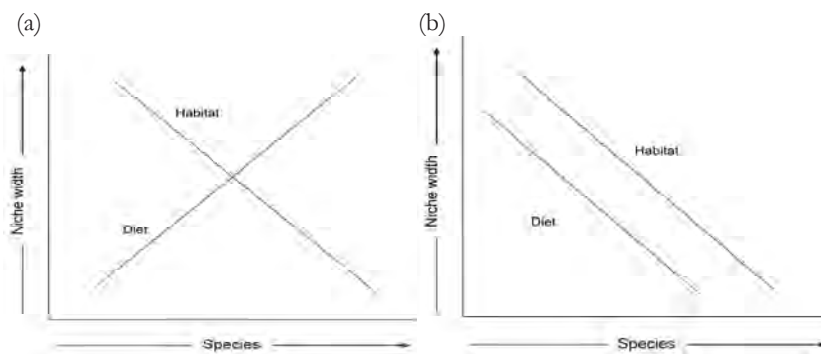


Fig. 2. A conceptual model of the expected relationship between niche (diet and habitat) width and sympatric herbivore species-richness during summer (a) and winter (b).

Herbivore diversity, at local scale, is a function of the number of niches (Rosenzweig, 1995), and competitive interactions amongst sympatric species promote local species richness through modifying niche relations (Amarasekare, 2003). This implies that energetic constraints set a limit to the number of species that an area can support (MacArthur, 1972; Olff & Ritchie, 1998; Ritchie & Olff, 1999). Such limitations allow the coexistence of only those species, which exhibit trade-offs in resource use in response to competition (Chase & Leibold, 2003; Dayan & Simberloff, 2005). In other words, co-occurring species are superior in exploiting alternative resources (Pianka, 1983), and divergence along any one niche dimension promotes species coexistence and thus richness in a community (MacArthur & Levins, 1967; Kneitel & Chase, 2004).

The overarching role of competition in structuring ecological communities has, however, been disputed in the recent years, especially in the wake of differential responses of species to environmental gradients (Wiens, 1977; Strong et al., 1984; Putman, 1996). It has been suggested that abiotic factors play an equally important role in organising ecological communities (Dunson & Travis, 1991). In any case, recognising the importance of both biotic and abiotic factors in organising species assemblages, contemporary ecologists have adopted a more pluralistic view (Schoener, 1986; Dunson & Travis, 1991).

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Food and habitat are the most important axes along which species segregate (Schoener, 1974). The differential use by species along these niche axes is associated with differences in body size among herbivores (Prins & Olff, 1998). Because larger herbivores eat diets of lower nutritional value, their nutritional requirement per unit body mass is lower than that of smaller herbivores (Hanley, 1982; Owen-Smith, 1988). On the other hand, smaller herbivores can forage selectively due to their narrower muzzles (Jarman, 1974; Drescher et al., 2006). Non-ruminants can consume relatively lower-quality bulk- forage, while ruminants are able to extract nutrients from intermediate-quality diets, due to their efficiency in digesting fibrous plants (Van Wieren, 1996). Such allometric relationships and physiological and/or morphological adaptations lead to differential use of diets (e.g., plant communities, plant species and plant parts) among large herbivores (Jarman, 1974).

This type of niche differentiation is possible in high-productivity environments, where range of resources (Dr in MacArthur's model) is larger, but is perhaps less important in areas of lower plant productivity and diversity (smaller Dr). In the latter situation, species may need to strike a balance between the need to maintain a sufficient intake rate for growth and reproduction, and the need to partition resources to enable coexistence with potentially competing species. In such systems, one can expect a relatively greater dietary overlap (ϕ in MacArthur's model) amongst herbivores; this is established by recent studies in the less productive ecosystem of Trans-Himalaya (Harris & Miller, 1995; Bagchi et al., 2004; Mishra et al., 2004). At the same time, high dietary overlap and resource limitation make competition an important interaction among species in areas with smaller Dr (De Boer & Prins, 1990), and this again is supported by recent studies focusing on livestock-wild herbivore relationships in the Trans-Himalaya (Mishra et al., 2002; Bagchi et al., 2004; Mishra et al., 2004).

Apart from the biotic environment, the physical habitat also influences the distribution of large herbivores as alluded to earlier (Ben-Shahar & Skinner, 1988). In fact broad-scale distributional patterns of large herbivores are determined mainly by abiotic factors, which act as constraints within which biotic mechanisms operate (Bailey et al., 1996). Therefore, differences in large herbivore distributions in response to heterogeneity in physical environment may also lead to resource partitioning, and facilitate coexistence of sympatric species. Physical environment become important especially in mountainous regions where the interaction between altitudinal gradients and topographic features enhances the landscape heterogeneity, which provide multiple niche axes for resource partitioning by large herbivores (Schaller, 1998; Geist, 1999). For example, large herbivores use different anti-predator habitats, which facilitate their co-existence in the same area (Lingle, 2002; Namgail et al., 2004). Thus, assemblages in areas with diverse habitats may contain a higher number of large herbivore species with different habitat requirements.

Meta-population theory and herbivore diversity

Animal populations are spatially structured, especially in patchy environments, where species have discrete populations in habitat islands. Under such scenarios, certain populations have better reproductive performance, and act as source populations that maintain metapopulation dynamics. Ever since its conception (Levins, 1969), metapopulation theory played a significant role in understanding population dynamics of animals. Metapopulation theory is especially relevant in understanding population dynamics at the edge of a species range, where populations of species tend to be more fragmented due to unsuitability of the environmental factors (Brown, 1984). Therefore, the presence-absence of a species in an area essentially reflects the balance between colonization and extinction (MacArthur & Wilson, 1967; Ricklefs, 1987; Huston, 1997).

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Environmental conditions generally closely correspond to a species' ecological requirements at the centre of its range (Brown, 1984). Towards the periphery of its range, the environmental suitability for a species is expected to decline. Thus, the probability of occurrence of a species (i.e., density) at regional scales is expected to decline from the centre of its range to the periphery due to decline in environmental suitability as well as its recolonization potential (MacArthur, 1972). Given this underlying spatial gradient in factors influencing species population density, different species in an assemblage, constrained by their respective biogeographic histories, perhaps respond differently to factors such as spatial heterogeneity and biotic relationships in any given area.

Early ecologists thought herbivore assemblages as interacting species without any reference to space (Tilman & Kareiva, 1997), but that changed once spatial ecology including the metapopulation theory developed (Hanski, 1998). Today, landscapes are viewed as patches of habitats where individual species persist through migration between different populations. Local species richness is often influenced by processes like immigration and emigration that operate at a regional scale (Hanski, 1998). These processes are the cornerstones of the metapopulation theory. The dispersal movement of animals ensures genetic exchange amongst populations, thereby maintaining genetic diversity in a species. Thus, for a given regional species-pool, the species diversity at a local scale (alpha diversity) is determined by the movement of individuals amongst populations (Ricklefs & Schluter, 1993). It is, however, to be noted that metapopulation dynamics are not addressed explicitly in this thesis, and this information here serves as mere information about processes underlying herbivore species-richness patterns. Although it is very important, especially in the context of the large herbivore assemblage in the Trans-Himalaya, and I come back to the subject in the synthesis section.

Macroecological theory and herbivore diversity

Although MacArthur's model and metapopulation based models are useful in explaining species richness patterns at local and regional scales, it does not account for large-scale determinants such as evolutionary history and broad scale biogeography, which are also important in understanding species richness patterns, especially at continental scales (Ricklefs, 2004). Species undergo adaptive radiations by evolving phenotypes that are successful in a novel environment (Ropiquet & Hassanin, 2005), which ultimately lead to speciation. When a species fails to evolve in response to the changing environment, it goes extinct, thereby paving way for another species.

Therefore, apart from ecological factors, historical factors are also important in explaining species distribution at macroecological scales (Ricklefs & Schluter, 1993). For instance, the continental scale biogeographic patterns on the planet are the result of plate tectonics, consequent orogenesis, glaciations and climatic oscillations. The influence of these on large scale biogeography can be studied by examining the faunal relationship between different continents using fossil records (Briggs, 2003). The other factors that are important in explaining continental scale biogeography are dispersal, vicariance, extinction and evolution (Ricklefs & Schluter, 1993).

Despite its importance in understanding the diversity pattern early in the history of ecology, the field of biogeography has been relegated being labeled as a descriptive science. Part of the reason that this field remained less developed is because ecologists took a reductionist approach looking at community patterns and processes at a local scale (Brown, 1985). But with ecologists taking a more macroecological and holistic approach, this important field of biology is being integrated into the mainstream ecology (Brown & Lomolino, 1998).

Herbivore diversity in Ladakh

The Trans-Himalaya encompassing the Tibetan plateau and its marginal mountains (*c.* 2.5 million km²) represents a vast and unique grazing ecosystem in the world as it has a fascinating assemblage of wild herbivores. Small sections of this huge plateau extend into the Indian Territory at several locations in the north and north-eastern parts of the country, and are collectively called the Indian Trans-Himalaya, of which almost 70% is represented by the Ladakh region of the north Indian state of Jammu and Kashmir. Ladakh is located at the intersection of two biogeographic realms *viz.*, Palearctic and Oriental, and contains elements from these realms. But most of the herbivores are Palearctic, a trend also observed in the regions' birds (Namgail & Yom-Tov, 2009). It even harbours species such as cape hare *Lepus capensis* from the Ethiopian realm. Ladakh also represents a biome transition between the vast plains of the Tibetan Plateau and the rugged mountains of Hindukush-Karakoram ranges (Fig. 3), and thus harbours a relatively diverse assemblage of mammalian herbivores with biogeographic affinities to these biomes (Fig. 4). The regional herbivore species-pool comprises twenty mammalian herbivores representing 6 families and 11 genera (Fox et al., 1991; Pfister, 2004).

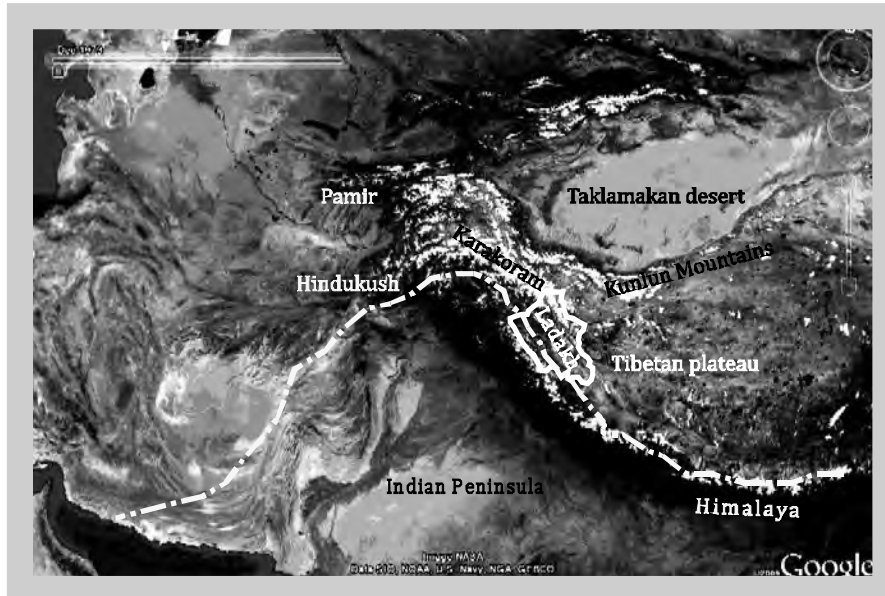


Fig. 3. Location of Ladakh with regard to major mountain ranges in south and central Asia (source Google Earth). The dotted line marks the approximate boundary between the Palearctic and the Oriental Biogeographic realms.

The large herbivores of Ladakh (>2 kg) include eight wild ungulates, *viz.*, Tibetan gazelle *Procapra picticaudata*, Tibetan antelope *Pantholops bodgsoni*, Blue sheep *Pseudois nayaur*, Ladakh urial *Ovis vignei vignei*, Asiatic ibex *Capra ibex siberica*, Tibetan argali *Ovis ammon bodgsoni*, Kiang *Equus kiang* and wild yak *Bos mutus* (Namgail, 2009; see Fig. 4), two marmot species: Himalayan marmot *Marmota bobak*, and the long-tailed marmot *M. caudata* and two hare species: Tibetan woolly hare *Lepus oiostolus* and cape hare. Some of the herbivores like Ladakh urial and Tibetan gazelle are confined to small geographical areas, while others like blue sheep are more widely distributed. Apart from these large herbivores, there are several small mammalian herbivores such as pikas *Ochotona* spp. and

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voles *Alticola* spp. (Pfister, 2004; Bagchi et al., 2006), about which very little is known. The large herbivores have fragmented distributions, and many are endemic and rare with global conservation importance (Namgail, 2009). The mechanistic understanding of the species-richness patterns of these herbivores is therefore important from both academic and applied conservation viewpoints.

Due to the fragmented nature of the species' distributions, and their differential responses to the environmental factors (Mallon, 1983; Namgail et al., 2004), there is a spatial variation in large herbivore species-richness across Ladakh with some parts harbouring higher number of species compared to other areas. Even at smaller spatial scales, some valleys support more and others less species. For instance, the Rumchung valley in the Hemis High Altitude National Park supports three Caprinae species, while the Puyul valley in the proposed Gya-Miru Wildlife Sanctuary has only two species (see Chapter 5). Thus, it is apparent that local assemblages represent small incomplete subsets of the regional species pool.

I investigated this spatial pattern, searching for plausible causes responsible for this pattern. Such a study is crucial for a mechanistic understanding of herbivore diversity pattern of Ladakh as well as other Trans-Himalayan rangelands. The object of this thesis is thus twofold: 1) Understanding the distributional patterns of herbivore species-richness pattern, 2) Exploring plausible causes operating at local as well as regional scale that influence such spatial pattern of herbivore species-richness. Hitherto, most of the studies on large herbivores have been carried out in single assemblages, and the mechanisms that operate at regional scale (macroecological scales) have not been addressed adequately. Since the factors that affect species distribution at different spatial scales are important in conserving biodiversity in the long-run, it is crucial to examine them in detail.

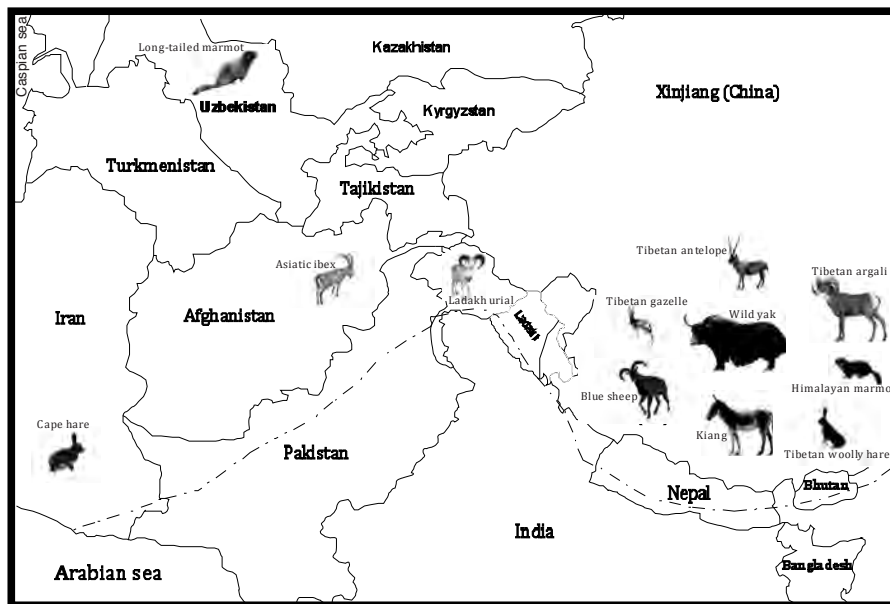


Fig. 4. Study area and species positioned according to their biogeographic affinities (note the conspicuous absence of Oriental species; the cape hare in the bottom left corner of the map is from the Ethiopian Biogeographical realm, which is not shown on the map). The broken line marks the approximate boundary between the Palearctic and the Oriental Biogeographical zones.

The study area and species

Ladakh (32° to 36° N and 75° to 80° E) is the largest province of the northern Indian state of Jammu and Kashmir, and encompasses $\approx 80,000 \text{ km}^2$ (Fig. 5). It is bounded by Karakoram range in the north and the Great Himalaya in the south, and is bounded by the Tibetan plateau in the east and the Hindukush Mountains on the west (see Fig. 3). The greatest extent of the region is northwest to southeast covering $\approx 350 \text{ km}$. It is one of the remotest regions in India, and one of the highest inhabited regions in the world. It has the lowest human population density ($<3 \text{ persons/km}^2$) in India. The inhabitants are mostly nomadic pastoralists in the east, and agro-pastoralists in the west, although this trend is changing (Namgail et al., 2007a). The inhabitants in the east and central parts of Ladakh are predominantly Buddhists with cultural affinities with Tibet, while those in the west are mainly Shia Muslims.

Ladakh is located at the junction of two biogeographic realms: Palaearctic and Oriental and has elements from these biogeographic zones. But most of the mammalian herbivores in the region are Palaearctic in origin with very few smaller herbivores such as the Royle's pika *Ochotona roylei* from the Oriental. There is also one Ethiopian species: cape hare as mentioned earlier. Such a trend was also observed in the region's avifauna (Namgail & Yom-Tov, 2009). On a smaller scale, it is also located at the junction of two biomes: Tibetan plateau and the Hindukush-Karakoram Mountains (including the Ladakh and Zangskar ranges) as alluded to earlier, and thus harbours species that have the core of their ranges in these biomes. The relatively high species richness of large herbivores in the region could perhaps be related to this juxtaposition of biomes.

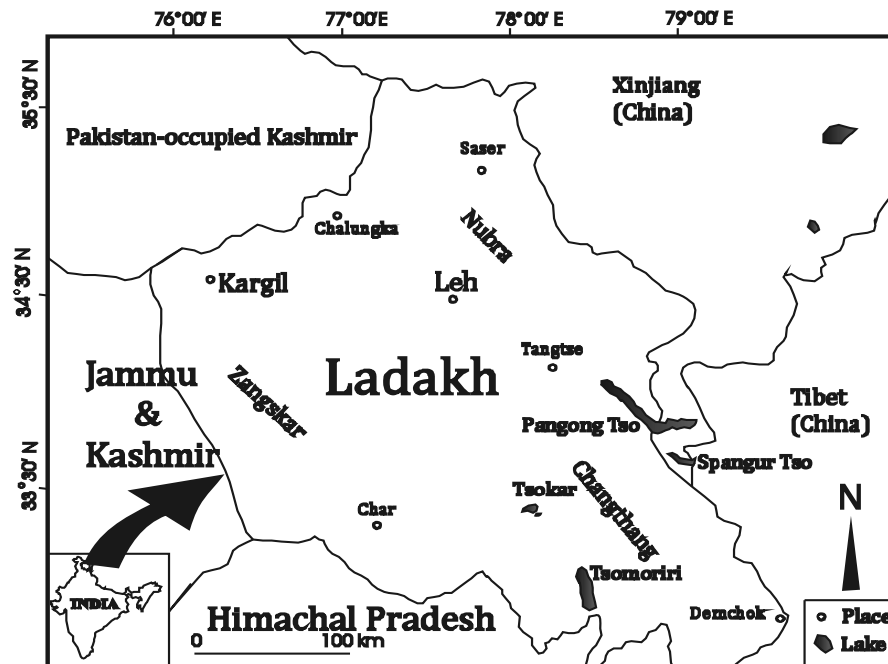


Fig. 5. Ladakh region in the state of Jammu and Kashmir, Indian Trans-Himalaya.

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Climate

The climate is characterised by extreme aridity with an average annual precipitation of *c.* 500 mm, and the region has been classified as a cold desert. Being located in the rain-shadow of the Great Himalaya, it receives only few monsoon clouds. Therefore the precipitation is minimal, mostly in the form of snow in winter, which is associated with the extra-tropical disturbances of mid-latitudes known as “Western Disturbances” (Dhar & Mulye, 1987). The southwestern part of the region, however, gets slightly more precipitation compared to the east and the northeast, and thus is greener (Hartmann, 1983). This discrepancy is indicated by high snowfall on Zuzhi ‘La’ (La means pass in Ladakhi), and less on Chang La and Khardung La, which remain open to traffic during winter except during exceptionally heavy snowfall. The climate is characterised by great extremes of cold (upto -35°C during winter) and heat (upto +35°C during summer), and there is a great diurnal difference in temperature with cool nights and hot days. The humidity fluctuates between 50 and 60% from May to October at various places (Murti, 2001). High-velocity winds blow all through the year, and absence of high humidity helps to keep the atmosphere clear.

Vegetation

Champion and Seth (1968) classified Ladakh as a dry alpine scrub that completely lacks forest cover, except relict populations of juniper *Juniperus* spp. stands in some parts such as Zangskar and Sham. Some other common trees are willows *Salix* spp. and poplars *Populus* spp. that are restricted to areas along rivers and streams. There are also some shrubs such as *Hippophae rhamnoides* and *Myricaria germanica* that grow along streams. Although the vegetation of Ladakh is sparse compared to the vegetation of similar altitudes in the Himalayan range, it is of immense significance as it represents elements from several phytogeographic realms such as the Palaearctic and Oriental. Various botanists have described the vegetation of Ladakh as dry bushes, alpine steppe, dry alpine scrub and alpine stony deserts (Rawat & Adhikari, 2002). Nevertheless, there is a great plant diversity and more than 600 vascular plants have been reported from the region (Kachroo et al., 1977).

Soil

The soils of Ladakh are sandy or sandy-loam, and are generally characterized as poor in organic matter and nitrogen content (Murti, 2001). The pH ranges between 7 and 11 (Bhat, 1965). In the absence of any substantial leaching of minerals from the soil, bases are continuously being added to the soil complex, which result in high pH value; this together with the absence of organic matter turn the soil toward alkalinity (Rawat & Adhikari, 2002). Calcium content is relatively high, but the soil is poor in magnesium. There are, however, adequate plant nutrients in the soil due largely to low precipitation and hence less weathering of rocks. Within Ladakh there are variations in soil composition. For instance, the Nubra and Dras valleys are morainic, and the soils in the Suru valley in Kargil are black due to grey shale; the Puga valley in eastern Ladakh has sulphur and borax deposits.

Geomorphology

One of the unique features of the geology of Ladakh is the presence of a huge plutonic mass, the Ladakh Batholith, which is characterised by a long (*c.* 350 km) ridge with peaks up to 6200 m asl. The northern slope of this batholith is exposed in the Nubra valley, and is in juxtaposition with the Khardung and Shayok volcanics (Bhutani et al., 2009). The southern side of the Indus Valley comprises a series of interfluve ridges of the Indus Molasse that are deeply incised by its tributaries, the largest of which is the Zangskar

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river. The present day Himalaya was once occupied by the Tethys sea, which separated India from Eurasia (Terra & Hutchinson, 1934). In the mid-Eocene, the Indian plate collided against the Asian plate, and the latter buckled under the former and uplifted the Tethys seabed, forming the mighty Tibetan Plateau between Asia and the Indian sub-continent, a process which still continues.

Ladakh displays a geomorphology that is heavily influenced by reworking of frost shattered rock and Quaternary glacial deposits through snowmelt, glacial runoff and mass movement processes. Major damming of rivers has been identified as having had a large influence on the geomorphology that is currently visible in the region. Particularly notable are the lake sediments, such as those found at Lamayuru and Leh, dated to around 35–40 ka BP, where lacustrine deposits are preserved at the distal ends of alluvial fans that discharge into the Indus Valley.

Palaeoenvironment

Ladakh was glaciated during much of the Quaternary period, which is demonstrated by the presence of wide, U-shaped glaciated valleys and extensively glaciogenic sediments along the upper course of major rivers (Pant et al., 2005). Well-developed lateral moraines preserved at many places (e.g., Baralacha La and Shayok and Nubra valleys) clearly indicate that this region experienced at least two glacial advances during the Quaternary period. The Last Glacial Maximum in the Himalaya as well as in western Tibet, however, was less extensive due to weak monsoon.

With the retreat of major valley glaciers, lacustrine and fluvial environments dominated the region. The lacustrine environment was restricted and prevailed in areas where the terminal moraines or landslide debris could block the rivers and create lakes. The terminal phase of lacustrine successions in the region was dominated by varve and rhythmite sedimentation. Similarly, the transformation from meandering to braid-meandering rivers suggests dwindling in hydrological regime. The snowline also retreated leading to the development of hanging glaciers.

Prominent study species

Amongst the eight wild ungulates in Ladakh, four belong to the sub-family Caprinae. These are the Tibetan argali, Ladakh urial, Asiatic ibex and blue sheep. The Tibetan argali is the largest wild sheep in the world, standing 3.5 to 4 feet at the shoulder with the horn measuring 90-100 cm. The animal is light-brown with its rump, throat, chest and belly white. The Ladakh urial is a small wild sheep of about 80 cm high at the shoulder. The coat-color of the upper parts of the body is rufous-grey, while the underparts and legs are whitish. The Asiatic ibex is a majestic wild goat of 80-100 cm high at shoulder. The adult males have long pointed beards and scimitar-shaped horns with prominent ridges on the frontal surface. The blue sheep is a unique mountain ungulate that is placed between sheep and goat as it displays sheep as well as goat-like characteristics. For example, it has a flat tail with bare central surface, lacks facial glands, and during combats the rams rear up and clash their horns like goats, while they lack a beard and rub their faces to the rump of their rivals, which are characteristic features of sheep.

Apart from these there are two antelopes: Tibetan gazelle and Tibetan antelope. The Tibetan gazelle is a small antelope weighing about 15 kg. It has a greyish-brown body and short, black-tipped tail in the center of a heart-shaped white rump-patch. The Tibetan antelope is a graceful animal adapted to the highlands of Tibet. The animal is confined to Aksai Chin and the Chhang Chhenmo areas of northeastern Ladakh. Apart from these there is a bovid: Wild yak, and an equid: Tibetan wild ass, as mentioned earlier. Yak is a sturdy and bulky ungulate with high lung capacity and thick coat, which are adaptations to the high altitude environment of Ladakh and Tibet. Wild yaks are

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mostly black with greyish muzzle, but some are aberrantly brown. The Tibetan wild ass or *Kiang* is the largest wild ass in the world with some stallions standing 1.4 m tall and weighing upto 400 kg. The colour is auburn with white belly, chest and legs, and the sexes are alike.

The thesis

Mammalian herbivores are highly mobile, especially in patchy environments where they need to move constantly to acquire their preferred plant species and other resources, although less than the mammalian carnivores. Therefore, species assembly patterns in mammalian herbivores need to be looked at multiple spatial scales, because factors that operate at different spatial scales may interact. Keeping this in view, this study was carried out at different spatial scales. Chapter 2 presents the results of a biogeographic analysis of the vascular plants of Ladakh in relation to altitude. This chapter also sheds light on the distribution pattern of aboveground biomass in relation to altitude, which has not been assessed before, neither in the Trans-Himalaya nor, to my knowledge, elsewhere.

Chapter 3 deals with the geographical communities of the mammalian herbivores of Ladakh in a spatially explicit way. It explores whether the mammalian herbivore species in the Ladakh Trans-Himalaya form chorotypes or groups sharing distributions, and if so, what explains the congruence in their distributions. It highlights the fact that mammalian herbivore distribution at a regional scale is determined largely by niche conservatism. The chapter further shows that rivers are not effective geographical barriers and thus do not influence the zoogeography of Ladakh.

I then moved on to assemblage level mechanisms to see how they can explain the herbivore species-richness pattern in Ladakh. Since the Trans-Himalayan rangelands are less productive with very low graminoid biomass compared to other natural grazing ecosystems in the world (Mishra, 2001), I expected competition to be an important factor that influences the herbivore assembly structure and in turn the species-richness pattern. Further, since blue sheep is the most abundant wild ungulate in Ladakh, and thus probably the dominant species, I investigated the niche relationship between this species and other sympatric species with similar body size to assess the role of competition in range dynamics of large herbivores. Chapter 4 presents the results of an investigation of the nature of interaction between the Asiatic ibex and blue sheep in winter, which is the pinch period, when herbivore species are more likely to compete.

Chapter 5 assessed the niche dynamics of blue sheep, again at a regional scale. This chapter emphasises the influence of the number of sympatric species on the niche utilization of species. It demonstrates that the habitat-niche width of a species declines in response to the number of sympatric species, whereas the diet-niche width has a hump-shaped relationship with sympatric species richness.

Chapter 6 examines if the blue sheep constrains the range expansion of the Ladakh urial, which is confined to narrow tracts along two river valleys. I studied the co-occurrence pattern of the two species at geographical, landscape and habitat levels. The results indicate that there is a high potential for competition between these two species, especially during winter when the blue sheep descends to avoid snow cover at higher altitudes. The chapter underscores the fact that species co-occur at large spatial scales but segregate at small spatial scales.

Finally, in Chapter 7, I discuss the results of this research in light of the current discourse on herbivore species-richness patterns and the underlying mechanisms. I synthesise by drawing on various chapters of this thesis as well as from my pre-PhD research on the large herbivores of Ladakh. I also underline the implications of the results for mammalian herbivore conservation in Ladakh and other dry alpine

ecosystems. I highlight further gaps in information and research prospects that will foster mechanistic understanding of large herbivore assembly rules in the Trans-Himalaya and other mountainous regions of the world.

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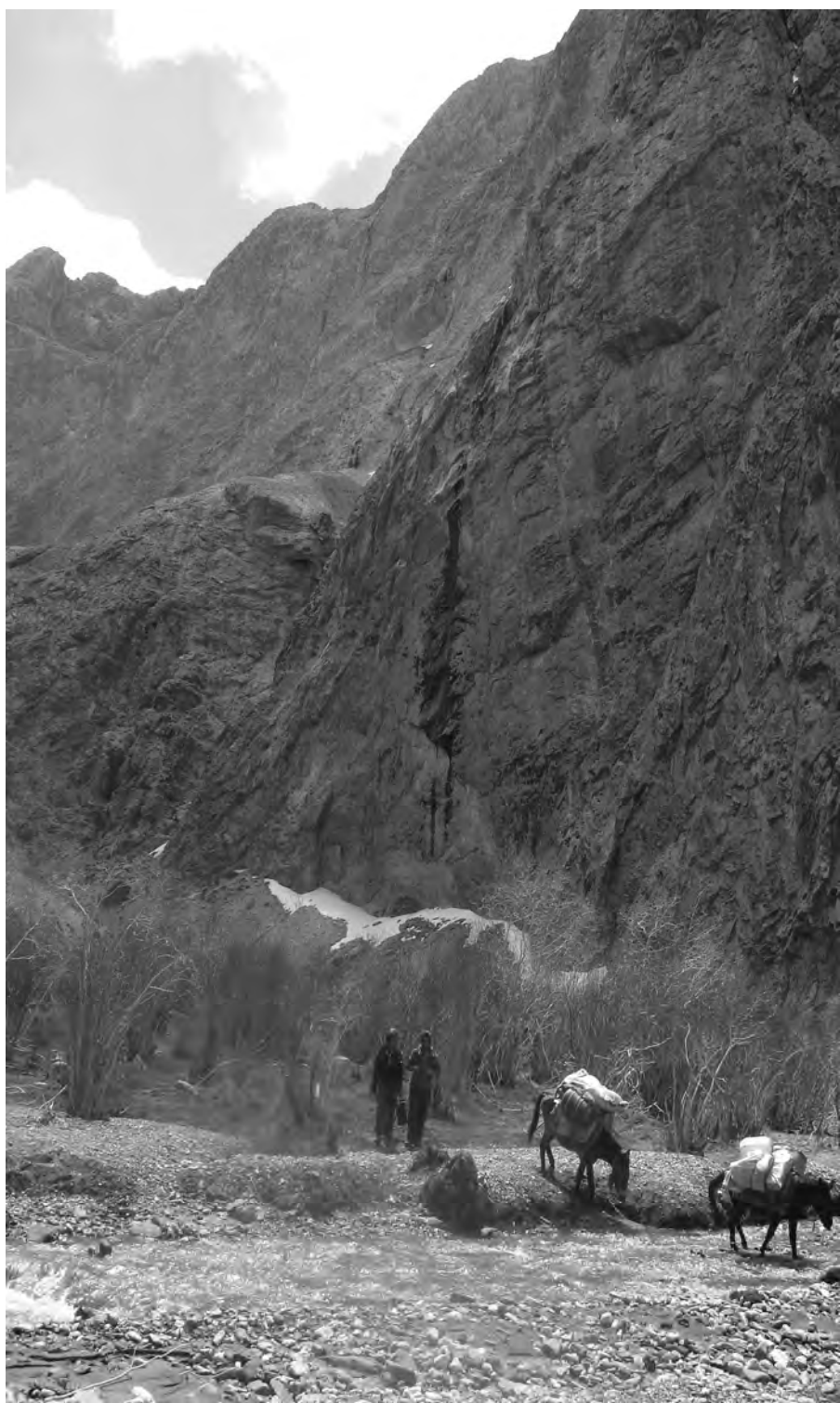
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CHAPTER 2

Aboveground biomass and phytodiversity along altitudinal gradients at different spatial scales in the Ladakh Trans-Himalaya

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'Turning to the east, we are facing a new world of extreme difference: it is the Thibetian naked wastes, deserts of black, wind-worn rocks, wide plains of fine, yellow sand bordered by snow-covered alps. In this chaos of stone there is no connected vegetation: one will seldom find a tree that has not been planted by man. The amount of rainfall is very small. Summer and winter the same blazing sun, seldom veiled by clouds'

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Abstract

The Ladakh region of the Indian Trans-Himalaya harbours more than 600 vascular plants, representing 190 genera and 51 families, but their distributional patterns (both horizontal and vertical) remain little explored. We studied the spatial pattern of vascular plant species-richness in relation to altitude at a geographical as well as a local scale in the region. We used Generalized Linear and Generalized Additive Models to assess the relationships. The relationship between aboveground biomass and altitude was also assessed in four protected areas. We found a hump-shaped relationship between vascular plant species-richness and altitude at both local and geographical scales. The species richness at the local scale in eastern Ladakh (average altitude = 4900 m) peaked between 5000 m and 5200 m above sea level. The cubic smooth spline indicated that the plant species richness at the geographical scale peaked around 4000 m asl. Vegetation cover at this scale peaked at an altitude of about 4300 m. Contrary to our expectation, we found a unimodal relationship between aboveground biomass and altitude. We suggest that such a trend is engendered by excessive grazing by domestic livestock and less precipitation in valley bottoms due to rainshadow effects and high evaporative losses because of high temperature.

Keywords: Vascular plants, species richness, aboveground biomass, altitude, Rapoport's rule, mid-altitude effect, macroecology

Introduction

The spatial variation of biodiversity on earth is an interesting natural phenomenon. The declining species diversity from the tropics to the temperate regions (Rapoport's Latitudinal Rule) is one of the most prominent pattern, which has widely been studied (Pianka, 1966; Ricklefs & Schluter, 1993). Earlier, plant species were thought to be more diverse at lower sites and decline in diversity with altitude. Thus, the altitudinal gradient in species richness in mountainous regions was thought to be analogous to the Rapoport's Latitudinal Rule (Stevens, 1992), but more recent studies have contested this view, and have shown that biodiversity in the mountainous regions does not peak at lower altitudes but somewhere in the middle of the gradient (Rahbek, 1995; Rahbek, 1997), although some did observe a negative linear relationship (Odland & Birks, 1999). The discrepancy was largely attributed to biases engendered by differences in sampling area and effort (Rahbek, 1995).

A mechanistic understanding of the altitudinal gradient in species richness is crucial for the management of natural resources largely in the light of the current climatic changes. The altitudinal gradient in plant diversity has been the centre of attention of plant ecologists in the last couple of decades, and studies were carried out in all the mountainous regions of the world, including the Himalayas (Bhattarai & Vetaas, 2003; Oommen & Shanker, 2005). Altitudinal gradient is one of the most decisive factors for spatial pattern of phytodiversity, because it presents changes in availability of abiotic factors such as heat, moisture and nutrients, which determine the growth of plants. Nevertheless, there are alternative hypotheses that account for this pattern, including area (Rosenzweig, 1995), hard boundaries (Colwell & Hurtt, 1994) and climate (Currie & Paquin, 1987). But hitherto almost all the studies on the subject were carried out in the tropics and temperate regions, and information remains rudimentary from the alpine systems, which in fact are ideal for studying biodiversity patterns along altitudinal gradients as the environment in these systems can change within short distances.

Aboveground plant biomass is an important component of grazing ecosystems and determines the stocking density of herbivores. It is therefore crucial to understand the spatial pattern of aboveground biomass for effective and sustainable management of rangelands for wild as well as domestic herbivores. Nevertheless, although the spatial pattern of net primary productivity and its relation with climatic factors was studied in Trans-Himalayan mountains (Yang et al., 2009) and other natural grassland ecosystems (Sala et al., 1988; Epstein et al., 1997; Jobbagy et al., 2002), the pattern of aboveground biomass along an altitudinal gradient has not been explored in a spatially explicit way, neither in the Trans-Himalaya nor, to our knowledge, elsewhere. Altitude, as alluded to earlier, is an important gradient along which aboveground biomass is expected to decline due to declining temperature and nutrients, which get washed down (Rastetter et al., 2004). But there has been no apparent effort to document this with empirical evidence, and it is less clear if such a trend can be expected in drier environments of deserts with little complexity in vegetation structure.

The Ladakh region (32° to 36° N and 75° to 80° E) of the Indian Trans-Himalaya is a high altitude cold desert and supports a unique assemblage of flora adapted to extreme environmental conditions (Rawat & Adhikari, 2005a). The region has unrivaled geographical and topographic features, and an altitudinal range from 2800 to 7,670 m above sea level, which provides an array of habitats for alpine plants. Ladakh is located at the intersection of two major biogeographical zones: Palearctic and Oriental, and hence has elements from these realms. Kachroo *et al.* (1977) reported 611 vascular plants from the region, representing 190 genera and 51 families. The spatial pattern of plant distribution and plant community structure in this area is however poorly known, and

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some information on these aspects have started to come in only recently (see Kala & Mathur, 2002; Rawat & Adhikari, 2002; Klimes, 2003).

The main objective of this study was to understand the vascular plant distribution and abundance along an altitudinal gradient at different spatial scales in Ladakh. We were interested to know whether these parameters are monotonically or unimodally related to altitude. Based on information from literature, we predicted 1) a hump-shaped relationship between vascular plant species-richness and altitude, 2) a negative relationship between aboveground biomass and altitude.

Materials and methods

Study area

Ladakh is situated in the Indian Trans-Himalaya, covering an area of $\approx 80,000 \text{ km}^2$. It is unique in terms of geography, geology and edaphic features (Kachroo et al., 1977). The vegetation community is diverse due to these and the great altitudinal range mentioned earlier. Ladakh is characterized by high, steep and rugged mountains separated by deep valleys into which the Indus and Zangskar rivers and their tributaries flow. The climate is characterized by long, cold periods without favourable conditions for growth in winter and short growth seasons in summers, and there is a marked diurnal variation in temperature. The soil is nutrient-poor, consisting of sandy clay and at places coarse gravel or murram, and become more alkaline in some parts. The region supports very sparse vegetation cover consisting of low shrubs, stunted grasses and herbs (Chaurasia & Singh, 1997; Rawat & Adhikari, 2005b) largely due to the short growing season, harsh climatic conditions and poor soil.

Ladakh is bounded by the Great Himalayan range on the south and the Karakoram range on the north. The former range blocks most of the monsoon bearing clouds, making the region arid. Winter precipitation is mostly in the form of snow, which is associated with the extra-tropical disturbances of mid-latitudes known as “Western Disturbances” (Dhar & Mulye, 1987). The south-western part of the region, however, gets slightly more precipitation compared to the east and the north-east, and thus is greener (Hartmann, 1983). The vegetation of eastern Ladakh is largely dominated by Hemicryptophytes, followed by Therophytes and Chamaephytes (Klimes, 2003). Champion and Seth (1968) described the vegetation of Ladakh as ‘dry alpine scrub’ that is characterised by complete absence of forest cover, except relict patches of juniper *Juniperus polycarpus* stands in some parts of Zangskar and Sham. Other prominent trees are willow *Salix* spp. and poplar *Populus* spp. that are restricted mainly to cultivated areas along rivers. There are also other shrubs such as seabuckthorn *Hippophae rhamnoides turkestanica* and *Myricaria elegans* that grow along stream and river banks.

Ladakh harbours a relatively rich assemblage of wild mammals such as Tibetan gazelle *Procapra picticaudata*, Tibetan antelope *Pantholops hodgsoni*, Blue sheep *Pseudois nayaur*, Ladakh urial *Ovis vignei vignei*, Asiatic ibex *Capra ibex siberica*, Tibetan argali *Ovis ammon hodgsoni*, Tibetan wild ass or Kiang *Equus kiang* and wild yak *Bos mutus*. The prominent predators include the endangered snow leopard *Uncia uncia* and Tibetan wolf *Canis lupus chanco*. The mountain slopes (or the rangelands) are used by the local communities for grazing a variety of domestic livestock including yak, sheep, goat, horse, donkey, cow and dzo (hybrid between yak and cow). *Pashmina* or cashmere wool, obtained from a local breed of goat called *Changra*, is the most valuable product from these rangelands. The local people in the western part are agropastoralists with major emphasis on agriculture, while those in the east are mainly nomadic pastoralists (Namgail et al., 2007). Ladakh has the lowest human population density in India with less than 3 persons/km².

Sampling methods

Plant species diversity

Sampling for the local scale investigation was carried out in July 2004 (during peak standing biomass) in the Hanle Valley of eastern Ladakh. Two transects (each covering 1000 vertical meters between 4500 and 5500 m asl with no variation in aspect) were walked on a hillside, and plant species richness was sampled using a line-intercept method (Muller-Dumbois & Ellenberg, 1974). We placed 20 m line intercepts at intervals of 50 vertical meters, and recorded plant species (or any other substrate such as soil or rock) at every 0.5 m interval along the line intercept. The species richness of graminoids and non-graminoids along each transect were recorded separately. The highest altitude sampled was the top of the hill.

Data for assessing the species richness at a regional scale were collected between July and September 2007. We drove from Rangdum in the west to Hanle in the east (approx. 600 km; altitudinal range, 2800 to 6000 m asl), and Turtuk in the north to Sarchhu in the south (approx. 300 km; altitudinal range, 2860 to 4900 m asl), at an average speed of 50 km/hour, stopping every one hour and laying 20 m transects (similar to the local scale method) on randomly selected adjacent slopes. When the road was rough, which slowed us down, we increased the time interval between samplings to avoid spatial autocorrelation. We also avoided sampling on human-modified landscape. Plants were identified in the field using field guides (e.g., Kachroo et al., 1977; Polunin & Stainton, 1990; Aswal & Mehrotra, 1994). Those species that could not be identified in the field were brought to the Herbarium at the Wildlife Institute of India for identification.

To assess the relationship between species richness pattern and climate at the regional scale, we obtained climatic variables: precipitation in the wettest quarter of the year (abbreviated in the figures as PreWetQ), mean annual precipitation (AnnPrec), precipitation in the driest quarter (PreDriQ), annual mean temperature (AnMeTe), mean temperature of the coldest quarter (MTeCoQ), mean temperature of the warmest quarter (MTeWaQ) at 1 km² resolution from the WorldClim database (Hijmans et al., 2005). These variables were extracted from all the transect locations in a GIS environment (ArcView, 9; ESRI, 1996).

Plant biomass

Data for assessing the relationship between aboveground biomass and altitude were collected between July and September 2007. Sampling was done in four established and proposed protected areas: the proposed Ridzong Wildlife Sanctuary (34°20' N, 77°04' E), Hemis National Park (34°06' N, 77°23' E), the proposed Gya-Miru Wildlife Sanctuary (33°40' N, 77°47' E) and the Changthang Wildlife Sanctuary (33°19' N, 78°29' E). A transect was laid on an altitudinal gradient at every 200 m, alternately on either side of a valley, starting at the valley-mouth. Each transect was then divided into 50 m vertical segments, and a 2 x 2 m plot was sampled at every 50 m intercept. Vegetation was clipped to the ground level in these quadrats and stored in paper bags. They were then sun-dried and weighed to the nearest 0.1 g to estimate aboveground biomass. We avoided sampling in human-modified landscape and along river and stream banks, which generally support high biomass of woody species due to high moisture from them.

Vegetation cover

We estimated vegetation cover (in cover classes of ten percent) in association with altitude and slope. Data for this were collected in August 2006. We explored the area between Lamayuru and Sarchhu in the Zangskar mountains. First we walked along the upper reaches of the Zangskar River, over the Sisir-la Pass (4700 m) and Singge-la Pass

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(4825 m), and then along the Tsarap, Lingti and Kargyak rivers at about 4200 to 4800 m, over the Shingo-la Pass (5050 m), and finally along the Sangpo and Jankar rivers at about 4500 to 3700 m. Locations and altitudes were determined through a global positioning system (Garmin GPS 12) and an altimeter (Origo Accusense Multi-sensor). In total we walked about 250 km at an average altitude of 4800 m asl.

Statistical analysis

First we analysed the data using Generalized Linear Models, but when we assessed the difference between a logarithmic link and an identity link function (assuming normal distributions of error) by drawing diagnostic Q-Q plots (Q stands for quantile) of the residual variation, the Poisson Model had a slightly better fit, perhaps due to fewer counts. Therefore, we used Generalized Additive Models (GAM) assuming a Poisson distribution. Within the GAM framework, we used a cubic smooth spline so that any abrupt change in vegetation distribution could be captured (Hastie & Tibshirani, 1990). This is especially appropriate because Ladakh represents two biogeographic provinces: Tibetan plateau in the east and the Hindukush-Karakoram mountains (including Ladakh and Zangskar ranges) in the west, and there might be abrupt changes in flora. Graminoids and non-graminoids were analysed separately at the local scale. We regressed species richness against the climatic variables to evaluate the influence of climate on species richness. All these tests were carried out in Statistica 7.

We used Canonical Correspondence Analysis (CCA) to explore the relationship between plant species distribution and environmental variables, putting all species in a continuous environmental perspective. This method is useful in measuring the amount of variation in the species distribution data that can be explained by different explanatory variables. The statistical significance of this relationship was assessed using a permutation test, which has an added advantage of the ability to check which variables contribute most to the relationship. The analysis was carried out using the CANOCO software version 4.5 (Ter Braak, 1986).

Results

A total of 91 plant species were recorded during the investigation at the regional scale, while only 28 species were recorded during sampling at the local scale in Hanle. Plant species richness varied along the altitudinal gradient at both geographical and local scales. Species richness had a hump-shaped relationship with altitude, peaking at mid-altitude at both spatial scales (Figs. 1 and 2).

Species richness

Local scale

Plant species in 74 transects were recorded to assess the relationship between species richness and altitude at the local scale. Both graminoids and non-graminoids had hump-shaped relationships with altitude (Fig. 1). The smooth spline with four degrees of freedom for these functional groups indicated a sharp hump between 5000 and 5200 m. It also indicates a steep decline in species richness above 5200 for both functional groups. For the graminoids there was also a sharp increase in species richness before it slumps, while for non-graminoids the increase and decrease were more gradual (Fig. 1).

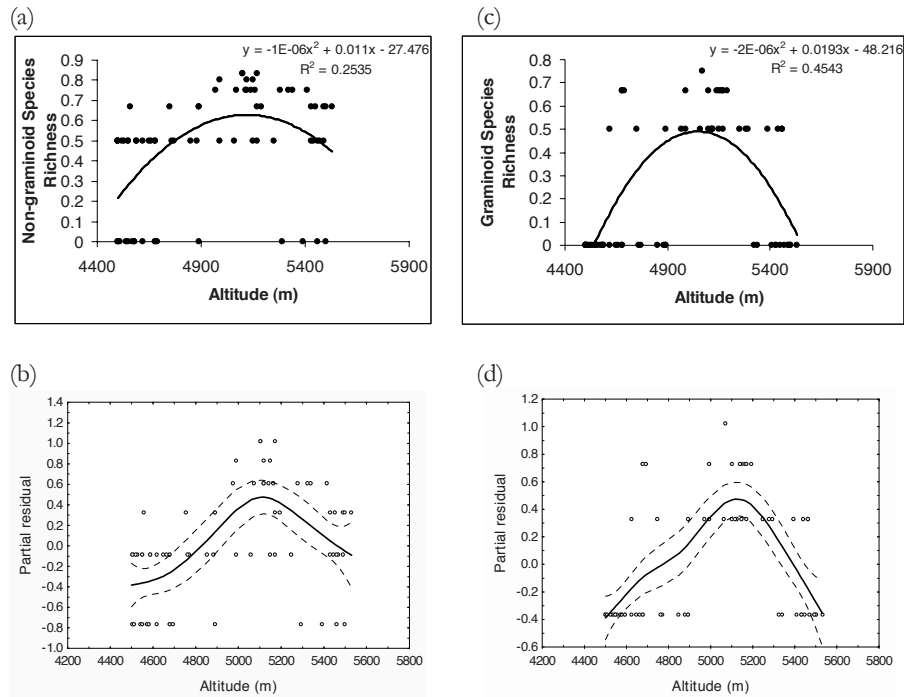


Fig. 1. Unimodal relationship between non-graminoid (a, b) and graminoid (c, d) species richness (Simpson's index) and altitude at a local scale. In figure b and d, the solid lines are the cubic smooth splines and the dashed lines are 95% confidence limits.

Geographical scale

We sampled plants from 55 transects spanning entire Ladakh. Twenty-nine plant species were encountered most frequently during the sampling at this scale (Table 1). The plant species richness had a hump-shaped relationship with altitude (Fig. 2a), and peaked at 4000 m asl (Fig. 2b), and dominance was lowest around this altitude (Fig. 3).

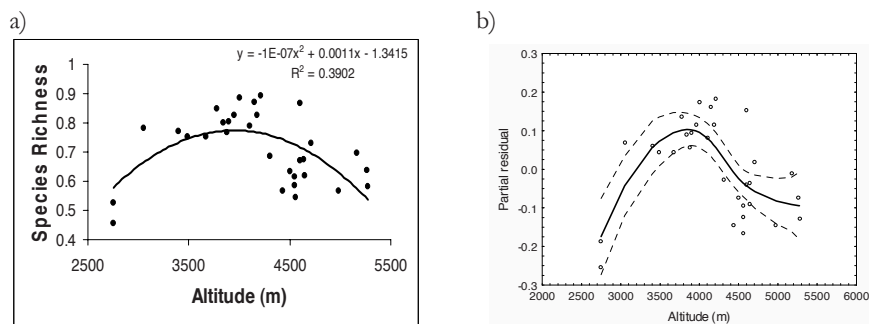


Fig. 2. Scatterplot of relationship between plant species richness (Simpson's index) and altitude at a regional scale. In figure b the solid line is the cubic smooth spline and the dashed lines are the 95% confidence limits.

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On average, Caprifoliaceae and Crassulaceae had higher altitudinal range, while Iridaceae had the lowest altitudinal range (Fig. 4). *Cargana versicolor*, *Krascheninnikovia ceratoides* and *Tanacetum tibeticum* are some of the most common species that occurred at high altitude drier areas, while *Artemisia maritima*, *Ephedra gerardiana* and *Echinops cornigerus* occurred at lower regions of Ladakh (Fig. 5).

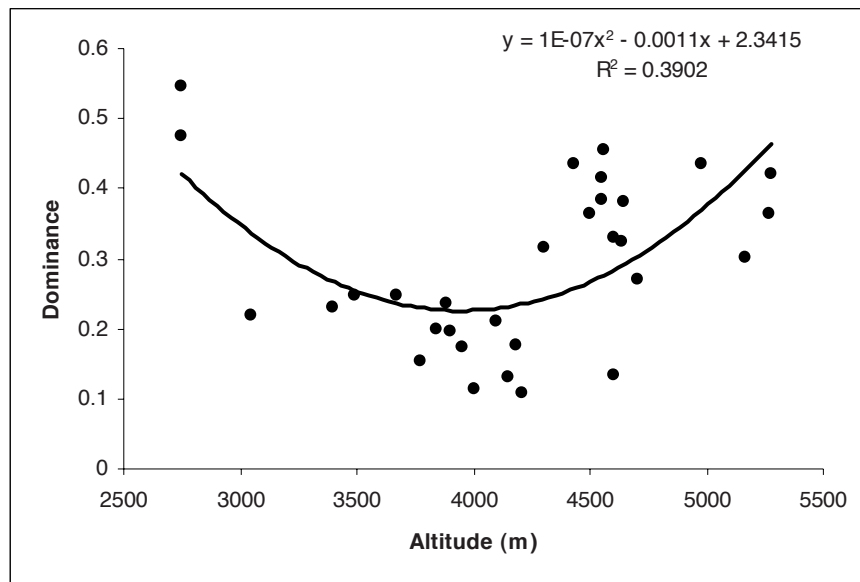


Fig. 3. Dominance pattern of plant species along an altitudinal gradient at a geographical scale in Ladakh

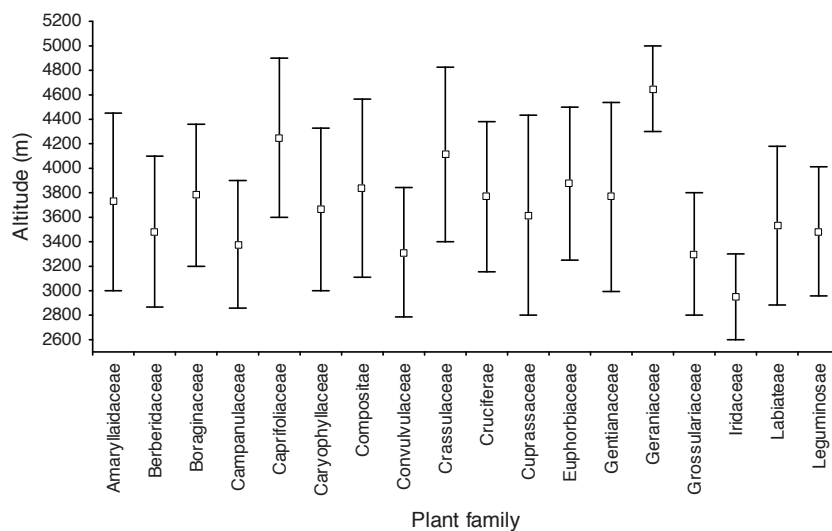


Fig. 4. Altitudinal range of some common families of plants in the Ladakh Trans-Himalaya.

Phytogeography of Ladakh

Table 1. Plant species that were encountered in more than 50% of the transects at the regional scale.

Species	Family	Abbr. in CCA
<i>Aconogonum tortuosum</i>	Polygonaceae	Aco-tor
<i>Rosa webbiana</i>	Rosaceae	Ros-web
<i>Potentilla fruticosa</i>	Rosaceae	Pot-fru
<i>Saussurea taraxacifolia</i>	Compositae	Sau-bra
<i>Saussurea bracteata</i>	Compositae	Sas-tar
<i>Echinops cornigerus</i>	Compositae	Ech-cor
<i>Artemisia brevifolia</i>	Compositae	Art-bre
<i>Artemisia maritima</i>	Compositae	Art-mar
<i>Waldheimia stoliczkaei</i>	Compositae	Wal-sto
<i>Tanacetum tibeticum</i>	Compositae	Tan-tib
<i>Cicer microphyllum</i>	Papilionoideae	Cic-mic
<i>Caragana versicolor</i>	Papilionoideae	Car-ver
<i>Acantholimon lycopodiodes</i>	Phimbaginaceae	Aca-lyc
<i>Androsace mucronifolia</i>	Primulaceae	And-muc
<i>Ephedra gerardiana</i>	Ephedraceae	Eph-ger
<i>Lindelia longiflora</i>	Boraginaceae	Lin-lon
<i>Rheum webbiana</i>	Polygonaceae	Rhe-web
<i>Dracocephalum heterophyllum</i>	Labiatae	Dra-het
<i>Heracleum pinnatum</i>	Umbelliferae	Her-pin
<i>Geranium sibiricum</i>	Gentianaceae	Ger-sib
<i>Krascheninnikovia ceratoides</i>	Chenopodiaceae	Kra-cer
<i>Arenaria bryophylla</i>	Caryophyllaceae	Are-bry
<i>Oxytropis microphylla</i>	Leguminosae	Oxy-mic
<i>Astragalus rhizanthus</i>	Papilionoideae	Ast-rhi
<i>Pedicularis cheilanthifolia</i>	Scrophulariaceae	Ped-che
<i>Carex melanantha</i>	Gramineae	Car-utr
<i>Stipa orientalis</i>	Gramineae	Sti-ori
<i>Elymus nutans</i>	Gramineae	Ely-nut

Table 2. The regression of climatic variables and plant species richness. PreWetQ = Precipitation in the Wettest Quarter of the year, AnnPrec = Mean Annual Precipitation, MTeCoQ = Mean Temperature of the Coldest Quarter, AnMeTe = Annual Mean Temperature)

Variable	Beta	Standard error beta	B	Standard error B	t(24)	P-level
PreWetQ	-2.317	0.419	-0.010	0.002	-5.520	<0.001
AnnPre	2.278	0.390	0.004	0.000	5.839	<0.001
MTeWaQ	0.791	0.750	0.003	0.002	1.054	0.302
AnMeTe	-0.892	0.709	-0.003	0.002	-1.258	0.220

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Aboveground biomass

We estimated aboveground biomass from 65 randomly selected quadrats in the four protected areas that spanned a range of climatic and geographical regimes. The relationship between aboveground biomass and altitude was also hump-shaped ($F = 9.803$, $P = 0.003$; Fig. 6).

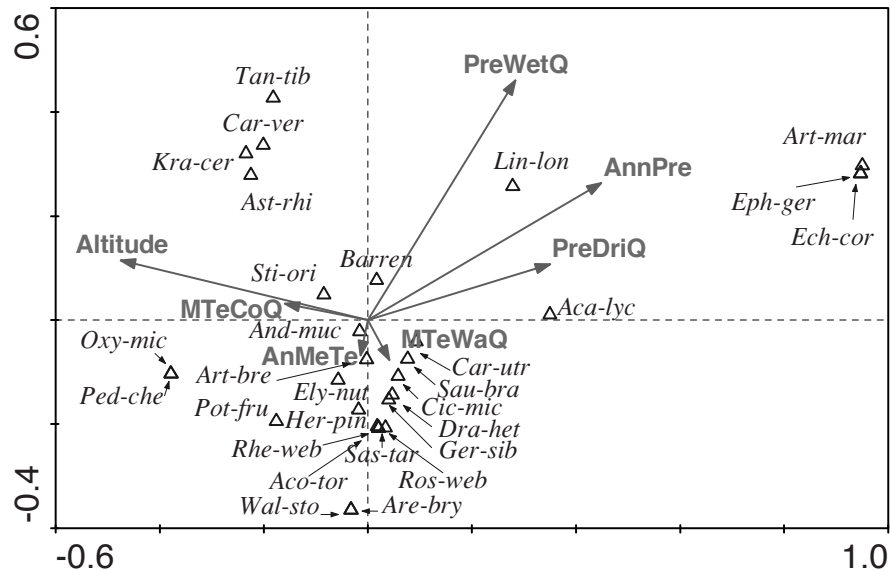


Fig. 5. CCA ordination of some common plant species in Ladakh and the environmental variables. See Table 1 for species identity. (PreWetQ = Precipitation in the Wettest Quarter of the year, AnnPrec = Mean Annual Precipitation, PreDriQ = Precipitation in the Driest Quarter, AnMeTe= Annual Mean Temperature, MTeCoQ = Mean Temperature of the Coldest Quarter, MTeWaQ = Mean Temperature of the Warmest Quarter).

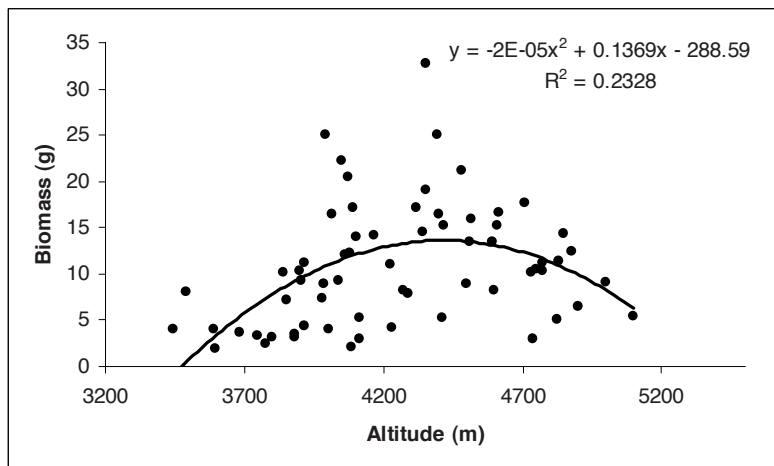


Fig. 6. Non-linear relationship between aboveground plant biomass (dry weight) and altitude in Ladakh.

The mean aboveground biomass (dry weight) for the entire region was 5.4 g m^{-2} (range 1 to $16.4 \text{ g dry weight}$). The mean aboveground biomass in the proposed Ridzong Wildlife Sanctuary was 3.9 g m^{-2} , Hemis National Park was 4.3 g m^{-2} , Gya-Miru Wildlife Sanctuary was 6.4 g m^{-2} , and that in Changthang Wildlife Sanctuary was 5.6 g m^{-2} .

Vegetation cover

Vegetation cover varied as a function of altitude and slope angle. It peaked in areas at an altitude of 4200 m and zero to 10 degree sloped angle (Fig. 7). Low altitudes ($<3600 \text{ m}$) and very high areas ($>5000 \text{ m}$) had very little vegetation cover ($<10\%$). Similarly, very steep areas ($>45^\circ$) had little vegetation cover, which is in line with our biomass data.

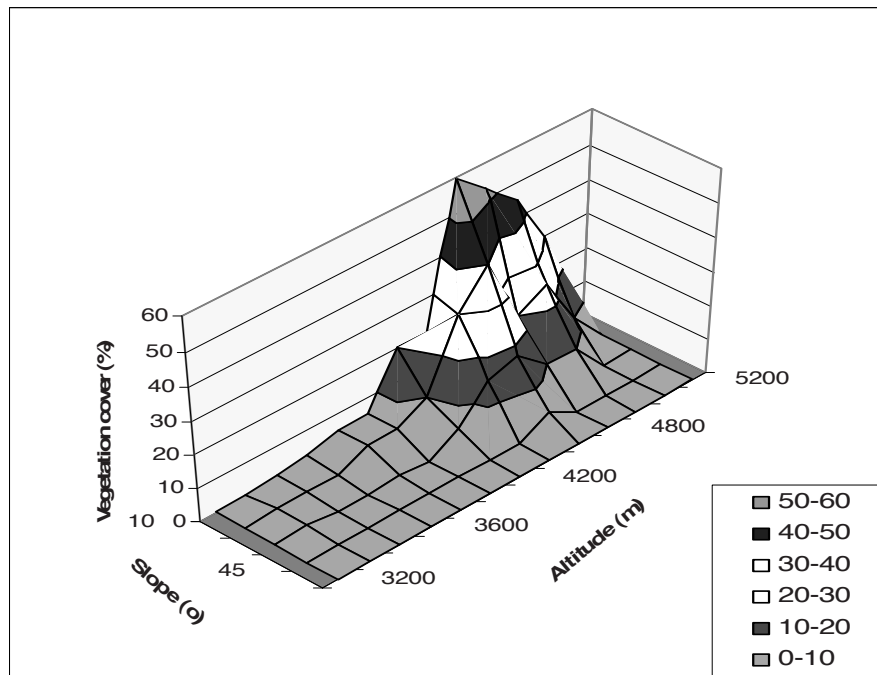


Fig. 7. Vegetation cover (%) as a function of slope angle and altitude during peak of vegetation growth in the mountainous region of Ladakh, India.

The CCA showed that amongst the most commonly encountered species, the distribution of *Artemisia maritima*, *Ephedra gerardiana*, *Echinops cornigerus* and *Lindlofia longiflora* occur in areas with high precipitation (Fig. 5). *Krascheninnikovia ceratoides*, *Tanacetum tibeticum*, *Caragana versicolor* and *Astragalus rhizanthus* occur in drier, high altitude habitats. Temperature is not a good determinant of plant species distributions (Table 2; Fig 5).

Discussion

The hump-shaped relationship between vascular plant species-richness and altitude observed in Ladakh conforms to the general trend observed in studies on this subject (Rahbek, 1995). Such a pattern could be related to several environmental and biological factors that vary along an altitudinal gradient. For example, the lower number of plant species at lower altitude could be related to the competitive exclusion of some species by other plant species with higher adaptation and tolerance towards heat, moisture and high

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soil nutrients, while the less species richness at higher altitudes may be related to the instability of substrates on the steep slopes in higher areas as well as to lower temperature (Klimes, 2003). It is, however, to be noted that since altitude represents a combination of several climatic variables closely correlated with numerous other environmental properties, it is difficult to single out important factors individually. Local topography, soil conditions and snow deposition pattern that vary along an altitudinal gradient can influence plant species diversity along such gradients (Chapin & Korner, 1995; Rawat & Adhikari, 2005b).

Temperature is known to decrease monotonically with altitude with a lapse rate of 0.6 °C per 100 m, while precipitation has a more erratic pattern. Given these, and assuming that they have positive effects on species richness, one could expect a monotonic inverse relationship between vascular plant species-richness and altitude. But we found a hump-shaped relationship, suggesting that climatic factors have less influence on the relationship, and local microtopography and soil conditions are more important as reported by Rawat and Adhikari (2005b) in Tsokar Basin, Ladakh. Nevertheless, precipitation seems to have an effect at the regional scale as regression analysis showed a strong relationship between precipitation and species richness at this scale, but temperature did not affect the relationship, as also indicated by less contribution of this variable in the CCA of species distribution. Very high moisture levels also lead to dominance by few moisture-loving plants, which exclude other plants (Olff et al., 2002), thereby negatively affecting the plant species richness. This was indicated by the negative relationship between plant species richness and precipitation during the wettest quarter of the year in Ladakh.

Although the climatic factors might determine the relationship between altitude and plant species richness at the regional scale, biotic factors might become more important in determining the relationship at a local scale. For instance, biological factors such as competing species might competitively exclude plant species, with less tolerance towards high temperature and nutrient levels, from the lower slopes. Alternatively, since the species richness peaked at the mid-altitudes and then declines precipitously as the mountain-top is approached, it could also be related to hard boundaries: mountain tops and valley bottoms (see Colwell & Hurtt, 1994).

The unimodal relationship between plant biomass and altitude is contrary to our expectation. Generally, one would predict a higher plant biomass at lower altitudes as the plant cover is higher at the base of a mountain due to greater availability of moisture and nutrients (Rastetter et al., 2004), but we found less plant biomass at lower altitudes, which is intriguing. One possibility is that plants at low altitudes could be sparse and stunted due to trampling and feeding by the domestic livestock. It is also to be noted that because of the high temperature, the limited moisture in the air fail to precipitate at lower altitudes, which makes these areas dry and perhaps less vegetated. Moreover, the high mountains cause a rainshadow in the deeper valleys.

Pastoralists also collect species like *Caragana* sp. from the lower slopes for fuelwood, which leads to soil erosion (Rawat & Adhikari, 2005b) and perhaps to lower plant diversity. These leguminous plants are known to influence fertility as its root-nodules have nitrogen-fixing bacteria. Further they help retaining moisture in the soil. Therefore, extraction of this plant might have led to the impoverishment of flora at lower slopes. Anthropogenic pressures such as excessive livestock grazing and collateral activities are known to influence the phytogeography in the alpine grazing ecosystems. A discussion on this issue has been started in the Himalayan region (Saberwal, 1996; Mishra & Rawat, 1998), and the potential role of livestock grazing in creating spatial pattern of plant distribution and abundance need to be studied in detail, because the livestock population on the rangelands of Ladakh is increasing apace (Namgail et al., 2007).

Vegetation cover peaked at around 4300 m. Such a trend could be related to the high moisture content at higher altitudes due to low temperature and thus high precipitation, as alluded to earlier. Rawat and Adhikari (2005b) reported an increase in plant cover with altitude until the nival zone, and related the trend to a high precipitation and thus high soil moisture content.

The main conclusions of the study are as follows: plant species richness peaked at mid-altitude at both local and geographical scales. At the local scale the graminoids had a narrower peak than the non-graminoids. Precipitation affected the relationship between altitude and species richness at the geographical scale, but temperature did not influence the relationship. Contrary to the general belief, the plant biomass also had a hump-shaped relationship with altitude. Perhaps, excessive grazing by livestock at the lower altitudes, low precipitation at low altitudes might have caused such a spatial pattern, either singly or in tandem. To our knowledge, this is the first study on the relationship between aboveground biomass and altitude, and has both theoretical and conservation implications. Furthermore, this is the first study of this kind in Ladakh at multiple spatial scales, and thus establishes a basis for further experimental work and mechanistic understanding of plant distributional patterns in the region.

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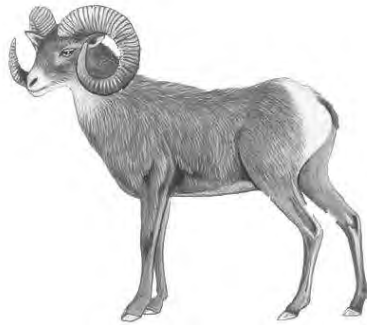
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CHAPTER 3

Biogeography of mammalian herbivores in Ladakh: distribution in relation to environmental and geographical barriers

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'To understand the biota of a region one must determine the distributions of its organisms beyond that region as well as the distributions of their closest relatives'

Alfred Russel Wallace

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Abstract

The Trans-Himalayan region of Ladakh harbours 20 species of mammalian wild herbivores representing 6 families and 11 genera. We studied their distributional patterns and asked if they form chorotypes or groups of species with similar distributions. We sampled presence-absence of 20 mammalian herbivores from 39 quadrats or operative geographical units (OGU; 20 x 20 km). A probabilistic similarity technique was used to look for herbivore species with distributions more similar than expected at random. Baroni-Urbani & Buser's similarity index was applied to the presence-absence data of herbivores in the OGUs, and the Unweighted Pair-Group Method using Arithmetic Average (UPGMA) was used to classify the species according to their distributions. Statistical significances of the groups obtained were assessed by G-test of independence. We used the Canonical Correspondence Analysis (CCA) to explore the relationship between environmental variables and the chorotypes. We obtained six chorotypes including two large ones, of which one was composed of nine species, and occurred in the open high plains of eastern Ladakh. The other comprised six species and occurred in the rugged mountains of north and south-western Ladakh. Seventy six percent of the variation in species distribution was explained by environmental variables. Some of the environmental variables were spatially structured, and a partial constrained ordination showed that eight percent of the variability in species distribution is explained by non-spatial environmental variation, 55% by spatially structured environmental variation and 13% by pure spatial variation. The remaining 24% of the variation was unexplained by the variables used, suggesting the importance of rivers, high mountains and other historical factors as geographical barriers hindering animal movements.

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

Introduction

The distributional patterns of species and the underlying processes are important aspects of biogeography (Myers & Giller, 1995). Species either occur alone, responding differently to environmental gradients or they share ranges. In the latter case, specific groups can be classified into biogeographical units corresponding to environmental (Gómez-González *et al.*, 2004) as well as historical factors (Myers & Giller, 1995). Studies on congruence or shared geographical ranges have been carried out extensively in several taxa (Marquez *et al.*, 1997; Gómez-González *et al.*, 2004; Oertli *et al.*, 2005), but is poorly understood in mammalian herbivores, especially large herbivores such as ungulates. Given that large herbivores occupy almost 50% of the earth's surface, and many of them have historically been useful to humans, more so since the dawn of civilisation (Diamond, 1997), there is an urgent need to understand their biogeography.

Analytical biogeography, applying hypothetico-deductive approach, is an objective way of studying distributional patterns of animals (Myers & Giller, 1995). The distributional associations of species, termed 'Chorotype' (Baroni-Urbani *et al.*, 1978), have often been studied by probabilistic approaches using similarity indices (Real & Vargas, 1996; Armenteras *et al.*, 2003), which are deemed crucial for understanding the distribution of animal assemblages at large geographical scales. Cross-taxon analysis of congruence or shared distributions of species is also helpful in evaluating the suitability of some taxa or guilds as surrogate for others while prioritizing conservation areas with limited time and budget (Williams & Gaston, 1994; Balmford & Long, 1995; Warman *et al.*, 2004). This is especially relevant in gathering information on biodiversity in mountainous regions where species inventorying is constrained by terrain ruggedness and inaccessibility.

The mountainous region of Ladakh in northern India supports a relatively diverse assemblage of 20 mammalian herbivorous species representing 6 families and 11 genera (Fox *et al.*, 1991a; Pfister, 2004). Most of these are Palearctic, a trend also observed in the region's birds (Namgail & Yom-Tov, 2009). Perhaps because the tropical lowland organisms do not overcome high mountain passes of the Trans-Himalaya (see Janzen, 1967). In any case, the mammalian herbivore assemblage includes twelve wild ungulates including endangered species like the Tibetan antelope *Pantholops hodgsoni* and Ladakh urial *Ovis vignei vignei*, and also several rodents and lagomorphs (Pfister, 2004).

Although some studies were carried out to understand the status and distribution of wild ungulates in Ladakh (Fox *et al.*, 1991a; Mallon, 1991; Chundawat & Qureshi, 1999; Bhatnagar & Wangchuk, 2001), information on their precise distributional ranges are lacking. On the basis of limited ecological information, the distributions of these ungulates were mapped through habitat suitability modeling (Chundawat & Qureshi, 1999), which still need to be ground-truthed across entire Ladakh. The distribution and diversity patterns of smaller herbivores such as rodents and lagomorphs, however, remain unknown except for some prominent places in the protected areas. Furthermore, even in the case of ungulates, apart from few studies on autecology and coexistence of species pairs, hitherto no apparent effort has been made to understand the assembly patterns at a multispecies level. Such information are, however, crucial for a comprehensive understanding of the Zoogeography of Ladakh.

Macro-level distributional patterns of species and the underlying mechanisms were often investigated in distinct ecosystems and communities (Holland *et al.*, 1991; Risser, 1995), but remain obscured for transition areas where one biome meets another. Transition areas, known as ecotones, are thought to be richer in biodiversity as they are more diverse in habitats, thereby supporting a greater number of species. Ecotones are thus thought to be dynamic biodiversity-hotspots where novel and unique evolutionary forms are generated (Kark & van Rensburg, 2006).

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Ladakh (32° to 36° N and 75° to 80° E) is located at the junction of two biomes: the Tibetan plateau in the east and Hindukush-Karakoram mountains (including Ladakh and Zangskar ranges) in the west. The former is characterised by vast open plains interspersed with rocky outcrops, while the latter is characterised by rugged and broken terrain. Thus, Ladakh's mammalian herbivores are perhaps adapted to two types of terrain features from these biomes (Mallon, 1991; Pfister, 2004). However, apart from anecdotally, it is not known as to whether the species belonging to the two biomes form either distinct geographical groups corresponding to their evolutionary histories or individual species from different biomes respond independently to environmental gradients. Although some studies have been carried out on local scales, as mentioned earlier, assessing the coexistence of species pairs (Namgail et al., 2004; Namgail, 2006b), there has been no large scale study encompassing multi-species at larger spatial scales. Therefore, the present study investigated the association/dissociation of mammalian herbivores with different biogeographic affinities at the entire Ladakh level. Recognising the apparent lack of knowledge on smaller herbivores in Ladakh, we also gathered information on their distributions and included them in the analysis.

As far as the ecology of the wild ungulates are concerned, only a few studies have been carried out (Namgail et al., 2004; Bhatnagar et al., 2006b; Namgail, 2006b) in Ladakh, as alluded to earlier, although information is also available from studies on some species like the blue sheep *Pseudois nayaur* and Asiatic ibex *Capra ibex* from the neighbouring Spiti valley, which addressed the interaction between these and the domestic livestock (Johnsingh et al., 1999; Bagchi et al., 2004; Mishra et al., 2004). Anecdotal information and limited studies on single or species-pairs addressing habitat use have suggested that the large herbivore species in the region partition space on the basis of altitude, slope angle and distance to cliff (Mallon, 1991; Fox et al., 1992; Chundawat & Qureshi, 1999; Namgail et al., 2004; Namgail, 2006b). Chundawat and Qureshi (1999) identified these variables as the most important factors determining the distribution of wild ungulates in Ladakh. There is not much information on the habitat use of wild yak *Bos mutus*, Tibetan antelope and the Tibetan gazelle *Procapra peticandata* in Ladakh, but studies from the Tibetan plateau showed that these animals partition resources along an altitudinal gradient (Harris & Miller, 1995).

The scanty dietary information on these ungulates suggest that amongst the four Caprinae species, Tibetan argali *Ovis ammon hodgsoni* and blue sheep include a higher proportion of graminoids such as *Carex* spp. and *Stipa* spp. in their diets, while the Ladakh urial and Asiatic ibex incorporate a higher proportion of non-graminoids in their diet (Johnsingh et al., 1999; Mishra et al., 2004; also see Van den Tempel & De Vrij, 2006). The Tibetan gazelle and Tibetan antelope are known to feed mainly on non-graminoids such as forbs except the male Tibetan antelope during summer (Harris & Miller, 1995). The Tibetan wild ass and the wild yak are known to feed predominantly on graminoids such as *Stipa*, *Carex* and *Kobresia* (Harris & Miller, 1995; Schaller, 1998). Nonetheless, the information on habitat and diet of the smaller herbivores remain elusive, as alluded to earlier, although they are urgently needed, as many of these smaller herbivores face persecution by humans due to a preconception that they degrade pastures (Bagchi et al., 2006).

So what does all these niche utilisation patterns of large herbivores and the landscape configuration in Ladakh tell us about their distribution in the region? Can the distribution of landscape features explain the distributional patterns of these large herbivores on the basis of their niche preferences? Do species from different biomes respond differently to the environmental conditions in Ladakh or they adapt to novel conditions, thereby converging in their resource use pattern irrespective of their evolutionary histories? If so, then do they share distributions? Can we also say something

about the distribution and diversity patterns of the smaller herbivores on the basis of the distribution of the larger ones (>2 kg) like the ungulates. These were some the questions that stimulated us to start this investigation. These are interesting research questions that need to be answered in order to understand the overall herbivore assembly pattern in a transition area like Ladakh.

Given the paramount importance of topographical features in the distribution of these herbivores (Chundawat & Qureshi, 1999; Namgail et al., 2004), we largely focused on the role of physical factors in understanding the congruence, or lack thereof, in distribution of herbivores from the two biomes. Although vegetation is more important than climatic ones in determining the distribution of herbivores, especially at smaller spatial scales, we did not use vegetation as an explanatory factor in this study because there is no reliable vegetation map for the region. The vegetation distribution in Ladakh is very sparse, and there are no trees except along some river banks (Kachroo et al., 1977; Rawat & Adhikari, 2005b). This and the barren nature of the landscape make it difficult to get remotely sensed data on vegetation. We, however, investigated the influence of climatic factors such as temperature and precipitation, as proxy factors, that can explain the large herbivore distributions.

Thus, given the fact that there is a topographical gradient, and species from different biogeographic zones might respond differently to such gradients leading to association of some species, while dissociation of others as observed between species pairs, we hypothesised that mammalian herbivores of Ladakh form geographical groups on the basis of their biogeographic affinities, and physical and climatic variables like altitude and slope angle determine such grouping patterns. We explore the importance of major rivers in determining geographical distribution of mammalian herbivores in Ladakh, and also discuss the possible role of mountain ranges in their distributions.

Study area

Ladakh is the biggest province, encompassing an area of $\approx 80,000 \text{ km}^2$, in the north-Indian state of Jammu and Kashmir. The region has some of the highest mountain ranges in the world, and the largest stretch of glaciers beyond the polar region (Namgail, 2003). Altitude in the region ranges from 3000 to 7600 m, providing a variety of habitats for mammalian herbivores. Trans-Himalaya, of which Ladakh is a part, came into being as a result of the collision between the Indian and Eurasian plates ≈ 35 million years ago (Dewey et al., 1988). The subsequent buckling of the Indian plate under the Eurasian one uplifted the Himalaya and the Tibetan plateau, leaving its legacy on the present distribution of flora and fauna. The tectonic movement and orogenic processes influenced the climate of the Trans-Himalaya making it progressively drier (Ramstein et al., 1997), and a predominantly endemic assemblage of herbivores developed in the region (Schaller, 1998). Following the initial rise of the Himalaya, several species especially of the family Bovidae underwent adaptive radiations by evolving ecological and phenotypic diversities, occupying the newly created mountainous niches (Ropiquet & Hassanin, 2005).

Ladakh has three mountain ranges: Zangskar, Ladakh and Karakoram that run almost parallel to one another and a network of rivers and 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 & Adhikari, 2005a). Some trees like poplar *Populus* spp. and willow *Salix* spp. grow along river-valleys. The rangelands of the region are also characterised by low graminoid biomass (Mishra, 2001). Ladakh is a very remote region in India, and remains cut-off from the rest of the country for almost seven months of the year due to heavy snow on the high passes. Due to the inhospitable

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environment and low productivity, the human population is low with a density of less than three persons/km², which is the lowest for India.

Data collection

We collected presence-absence data of mammalian herbivores from 39 quadrats or operative geographical units (OGUs) of 20 x 20 km². This quadrat-size was chosen to strike a balance between covering a maximum geographical area and capturing the essence of possible influence of environmental factors on the shared distributions amongst species. Although, we surveyed 95 quadrats, the remaining 56 were not analysed as we could not survey them thoroughly for smaller mammals, and there was little information in the literature. It was especially difficult to establish the absence of small herbivores such as pikas *Ochotona* spp. and voles *Alticola* spp., which are less visible compared to the larger ones: ungulates. The 39 quadrats used, however, spanned entire Ladakh and thus had a representative sample from each landscape unit: rugged terrain and open plain.

Although we opportunistically accumulated information on species presence-absence in the 39 quadrats over a period of seven years beginning in early 2000, proper surveys in the OGUs were carried out between May 2006 and June 2008. Animals were located from trails and vantage points. Apart from direct observations, presence of body parts such as horns of ungulates was recorded as presence of a species (de Vrij & van den Tempel, 2006). The occurrence of fossorial herbivores such as marmots and pikas were determined also by locating burrows followed by intensive search to establish their presence. Information on herbivore occurrence in the quadrats was gathered also by interviewing wildlife officials and researchers working in different areas. We triangulated such information by carrying out a questionnaire survey through post, whereby people from villages in or nearby a quadrat filled out a form on presence-absence of animals and sent it back to us. Apart from these, we also used data from published sources (e.g., Fox et al., 1991a; Mallon, 1991; Pfister, 2004). Such multiple sources of data ensured a thorough sampling from each quadrat.

To look at the relationship between environmental variables (physical and climatic) and chorotypes, we recorded mean altitude ($n = 50$) and slope angle ($n = 50$; an index of terrain ruggedness) from each quadrat. To detect geographical trends in the distributions of chorotypes, we also took into consideration the geographical longitude and latitude of the quadrats. The climatic variables (mean annual temperature and mean annual precipitation) at 1 km² resolution were obtained from the WorldClim database (Hijmans et al., 2005). We obtained these variables in a GIS (Geographic Information System; ArcView, New York, USA) environment (ESRI, 1996).

There are two major rivers: Indus and Zangskar that could influence the zoogeography of Ladakh. The former runs from east to west dividing Ladakh into two almost equal halves, while the Zangskar runs from south to north, dividing Ladakh in western and eastern parts, before it drains into Indus. Therefore, we also assessed their importance as geographical barriers. For this, we recorded the number of species that occur on one side of the river but not on the other, and evaluated whether these rivers restrict the range of mammalian herbivores in Ladakh.

Statistical Analysis

Chorotypes

To classify species according to their distributions, we used the similarity index of Baroni-Urbani & Duser (1976) to each pair of species a and b as

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

where A is the number of quadrats where only species a is present, B is where only species b is present, C is where both are present, and D is the number of quadrats from which both are absent.

A dendrogram of the biogeographical relationship between species was obtained by applying the Unweighted Pair-Group Method using Arithmetic Average (UPGMA) to the matrix of values of Baroni-Urbani & Buser's similarity index. This procedure is an agglomerative one that produces the lowest distortion in relation to the original distances between samples (Sneath & Sokal, 1973). The statistical significance of each similarity value was evaluated using the statistical table in Baroni-Urbani & Duser (1976). In this way a matrix of significant similarities was generated by substituting the similarity values with a '+', '-', or '0' sign when the similarities were, respectively, higher, lower or similar than would be expected at random. We then converted the similarity matrix of species \times locations to a secondary matrix of similarity coefficients.

We used G-tests to statistically test the significance of each group in the dendrogram (McCoy et al., 1986). This method distinguished species that occur together more frequently than expected at random from those that are artifacts of the cluster analysis. The null hypothesis was that no geographical groups or chorotypes are formed by the Trans-Himalayan mammalian herbivores. For each comparison, we took a sub-matrix, (corresponding to a sub-group in the dendrogram) of significant similarities, which we divided into three zones: A and B corresponding to each group compared, and zone AxB corresponding to the intersection of both groups.

We considered species to form chorotypes or show similarity in distribution when significantly similar species (+) tended to be located in zones A and B, but not in A \times B. If, on the other hand, the significantly less similar species (-) occurred in zone A \times B, but not in A or B, we considered the two groups of species to be strongly segregated. The parameters DW (A \times A) and DW (B \times B) measure the internal homogeneity of each group, whereas DS measures strong segregation between groups. A group of species was considered to be a weakly segregated chorotype when DW>0 and GW was statistically significant, and a strongly segregated one when DS>0 and GS was statistically significant. This procedure determines whether the clusters identified have any biogeographical meaning, or are the artifacts of the analysis having to form clusters.

Ordination method

The geographical communities or chorotypes could be influenced by ecological as well as historical factors. We used the Canonical Correspondence Analysis (CCA) to explore the relationship between the identified chorotypes and the environmental variables, putting all species in a continuous environmental perspective. This method is useful in measuring the amount of variation in the species distribution data that can be explained by different explanatory variables. The statistical significance of this relationship was assessed using a permutation test, which has an added advantage of the ability to check which variables contribute most to the relationship. The analysis was carried out using the CANOCO software (Ter Braak, 1986).

Since environmental variables could be spatially structured, and confound the results, we performed the so-called partial constrained ordinations suggested by (Borcard et al., 1992), and controlled for a second set of variables by using them as covariates. Therefore, we carried out four types of CCA: (1) between species and environmental variables, (2) between species and environmental variables with spatial variables (latitude

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and longitude) as covariates, (3) between species and spatial variables and (4) between species and spatial variables with environmental variables as covariates.

Results

We sampled 20 mammalian herbivores from the 39 OGUs. These comprised eight ungulates, seven lagomorphs and five rodents (Table 1). Fifty percent of the species ($n = 20$) were present in more than 10 OGUs. Blue sheep was the most common mammalian herbivore occurring in more than 25 OGUs, followed by the Asiatic ibex *Capra ibex siberica* and long-tailed marmot *Marmota caudata* (Fig. 1). The similarity between species distributions are shown by the dendrogram created through UPGMA (Fig. 2). The matrix of significant similarity between species distributions are presented in Table 2. The significant segregations of species based on their distributions are presented in Table 3.

Chorotypes

A total of six chorotypes were identified (Fig. 2). Chorotype I was composed of only one species: Tibetan antelope *Pantholops hodgsoni*, which had significantly different distribution from all other herbivores. Chorotype II was strongly segregated from all others, and comprised six species: long-tailed marmot (abbreviated as Lo'T Mar), Asiatic ibex (Asi Ibx), Large-eared pika (LaE Pik) *Ochotona macrotis*, Nubra pika (Nub Pik) *Ochotona nubrica*, Cape hare (Cap Har) *Lepus capensis* and Ladakh urial (Lad Uri; Fig. 2; Table 3). Chorotype III again comprised one species: wild yak (Wil Yak) with a distribution unique to itself. Chorotype IV was formed by the Royle's pika (Roy Pik) *Ochotona roylei* and Royle's mountain vole (RoM Vol) *Alticola roylei*, while Chorotype V comprised one species: Tibetan gazelle (Tib Gaz) *Procapra picticaudata*, although it was weakly segregated from others.

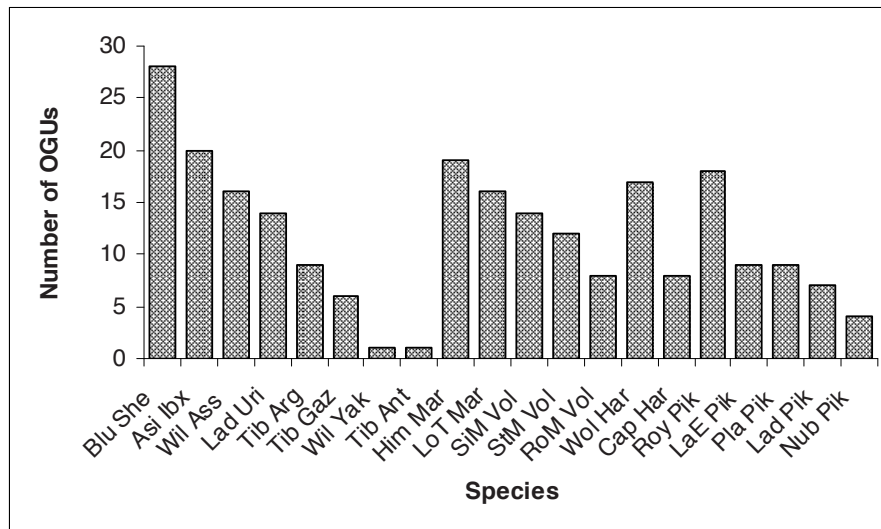


Fig. 1. Number of operative geographical units (OGUs) occupied by mammalian herbivores in the Ladakh Trans-Himalaya. See Table 1 for species identity.

Zoogeography of Ladakh

Chorotype VI was the largest of all with nine species that included Silvery mountain vole (SiM Vol) *Alticola argentatus*, Tibetan woolly hare (Wol Har) *Lepus oiostolus*, Himalayan marmot (Him Mar) *Marmota bobak*, Tibetan wild ass (Wil Ass) *Equus kiang*, Ladakh pika (Lad Pik) *Ochotona ladacensis*, Plateau pika (Pla Pik) *Ochotona curzoniae*, Stoliczka's mountain vole (StM Vol) *Alticola stoliczkanus*, Tibetan argali (Tib Arg) *Ovis ammon hodgsoni* and blue sheep (Blu She; Fig. 2).

Table 1. Mammalian herbivores in the Ladakh Trans-Himalaya and their abbreviation used in the study.

Order/Family	Scientific name	Common name	Abbr.
Artiodactyla			
Bovidae	<i>Capra ibex siberica</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

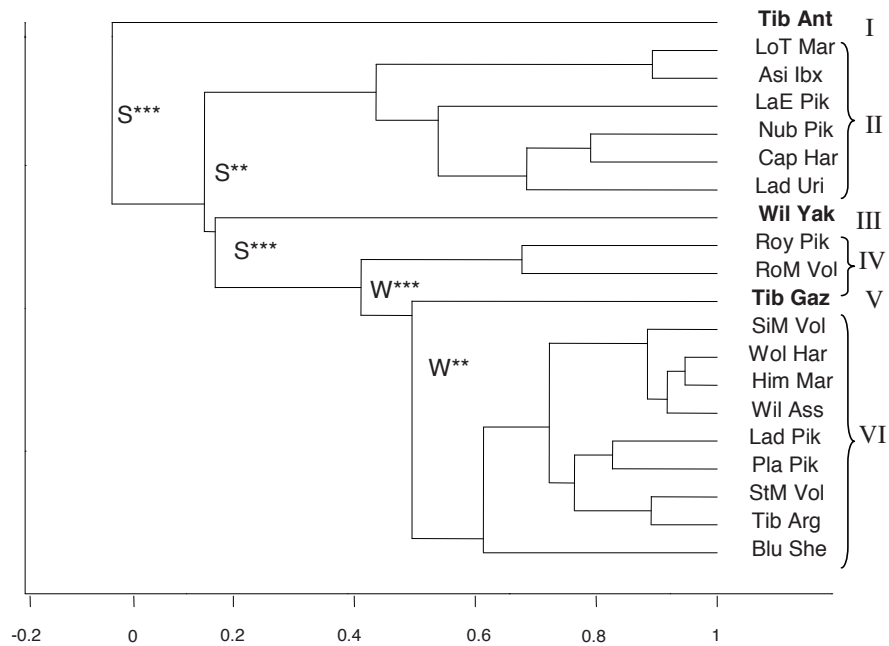


Fig. 2. Classification dendrogram of the distribution of mammalian herbivores in Ladakh. Species in bold represent chorotypes of single species and roman numerals indicate chorotype number; see Table 1 for species identity. S is strong and W is weak segregation amongst species distributions. ** $P < 0.01$; *** $P < 0.005$.

Ordination of species

Environmental variables influenced the distribution of the chorotypes as their relationship established by CCA was statistically significant (F-ratio = 4.57; $p = 0.002$). They explained 63% of the variation in geographical distributions of species. The first axis ordered mammalian herbivores along a gradient of decreasing altitude and increasing slope angle, while the second axis ordered species along a gradient of decreasing precipitation and increasing temperature. This ordering indicated that Asiatic ibex, long-tailed marmot, Ladakh urial, Nubra pika and cape hare occur in steeper areas at lower altitude with high temperature (Fig. 3). Large-eared pika and Royle's mountain vole occur in areas with high precipitation, while Tibetan argali, Tibetan wild ass, Himalayan marmot, Tibetan woolly hare, Stoliczka's mountain vole and silvery mountain vole occur in flatter and drier areas at high altitude with less temperature (Fig. 3). Precipitation and altitude contribute little along the two ordination axes (Fig. 4), suggesting that these variables are spatially structured. In figure 4, species are arranged by increasing altitude and decreasing slope angle along axis one, while they are ordered along a gradient of decreasing temperature and precipitation on the second axis.

Some of the species are related differently to environmental variables after removing the effect of spatial structure. For example, in the first analysis without the spatial variable as covariate (Fig. 3), blue sheep was grouped with Tibetan argali, Tibetan woolly hare and Himalayan marmot, but it is associated more closely with Ladakh urial and cape hare after the spatial structure was eliminated (Fig. 4).

Zoogeography of Ladakh

Table 2. Matrix of significant similarities between the distributions of mammalian herbivores in Ladakh. See table 1 for species identity. + similarities more than expected, - similarities less than expected and ° as expected at random.

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																		+	+

Table 3. Significant segregation of species distributions as indicated by the forks of the dendrogram obtained by UPGMA. DW ($A \times A$) and DW ($B \times B$) indicate internal homogeneity, while GW and (DS) GS indicate weak and strong segregations, respectively (see McCoy *et al.*, 1986 for a detailed methodology).

Groups obtained by UPGMA			Aggregation			Segregation		
<i>Group A</i>	<i>Group B</i>	<i>Similarity Coeff.</i>	DW ($A \times A$)	DW ($B \times B$)	Weak GW	P	Strong DS	GS P
Wol Har-Him Mar	Wil Ass	0.917	0.00	0.00	1.05	NS	-0.71	0.00 NS
SiM Vol	Wol Har-Wil Ass	0.885	-0.71	0.00	1.59	NS	-0.71	0.00 NS
Lad Pik-Pla Pik	StM Vole-Tib Arg	0.764	0.00	0.00	2.09	NS	-0.71	0.00 NS
SiM Vol-Wil Ass	Lad Pik-Tib Arg	0.723	0.00	0.00	6.05	NS	-0.71	0.00 NS
Nub Pik-Cap Har	Lad Uri	0.685	0.00	-0.71	1.05	NS	-0.71	0.00 NS
SiM Vol-Tib Arg	Blu She	0.614	0.00	-0.71	1.76	NS	-0.71	0.00 NS
LaE Pik	Nub Pik-Lad Uri	0.539	-0.71	0.00	1.59	NS	-0.71	0.00 NS
Tib Gaz	StM Vole-Blu She	0.495	-0.63	0.08	19.54	***	-0.52	0.00 NS
LoT Mar-Asi Ibx	LaE Pik-Lad Uri	0.436	0.31	0.31	1.24	NS	-0.07	0.00 NS
Roy Pik-RoM Vol	Tib Gaz-Blu She	0.412	0.18	0.15	23.41	***	-0.37	2.64 NS
Wil Yak	Roy Pik-Blu She	0.170	-0.07	0.52	3.50	NS	0.47	15.19 ***
LoT Mar-Lad Uri	Wil Yak-Blu She	0.152	0.27	0.30	17.32	NS	0.11	27.12 **
Tib Ant	LoT Mar-Blu She	0.000	0.00	0.03	0.00	NS	0.30	56.86 ***

** $p < 0.05$; *** $p < 0.005$; NS: Non-significant

Table 4. Results of the CCAs performed excluding the effects of different set of variables.

Explanatory variables	Covariables	% explained	P
Environmental	None	63	<0.01
Environmental	Spatial	8	<0.01
Spatial	None	78	<0.01
Spatial	Environmental	13	<0.01

A CCA between species and spatial variables accounted for 78% of the variation in the species distribution data (Table 4). From Fig. 5, three prominent groups can be distinguished: (1) Large-eared pika, Nubra pika, Ladakh urial and cape hare occur in northern part of Ladakh, (2) Asiatic ibex, long-tailed marmot, Royle's pika and Royle's mountain vole are distributed in the southwestern part of Ladakh, while (3) Tibetan gazelle, Ladakh pika, plateau pika, Tibetan argali, Tibetan wooly hare, Stoliczka's mountain vole, silvery mountain vole, Himalayan marmot and Tibetan wild ass occur in the eastern part of Ladakh. Blue sheep has a broad distribution with no apparent geographical trend as indicated by its position near the intersection of the two axes.

When environmental variables were used in the CCA as covariates, spatial variables accounted for 13% of the variation in species distribution data (Table 4; Fig 6). Species ordered along the two axes leads to almost the same groups as in Fig. 5, suggesting that species distribution is not completely explained by spatial variation in environmental data. The percentage of total variation in the species distribution accounted for by each component of the partial constrained ordination was as follows: eight percent by non-spatial environmental variation, 55% by spatially structured environmental variation and 13% by pure spatial variation. The remaining 24% of the variation was unexplained by these variables.

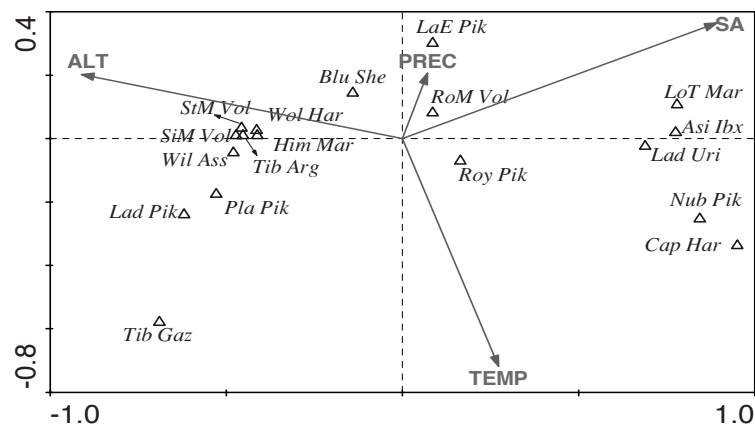


Fig. 3. First two axes of CCA ordination of the species and environmental variables (with no covariables). See Table 1 for species identity. (SA = Slope angle, Alt = Altitude, PREC = Precipitation, TEMP = Temperature).

Chapter 3

Rivers as geographical barriers

Two species of lagomorphs: cape hare and Nubra pika, which constitute 29% of this taxon ($n = 7$) found in Ladakh, occurred only in quadrats north of the Indus River, while all other mammalian herbivores occurred on both sides of the river. Similarly, five ungulates (62% of the taxon found in Ladakh, $n = 8$), two rodents (40%, $n = 5$) and four lagomorphs (71%, $n = 7$) occurred only in quadrats east of the Zangskar River, while all others occurred on both sides of the river.

Discussion

The biogeographical characteristics of Ladakh Trans-Himalaya is unique with an interesting assemblage of mammalian herbivores adapted to diverse habitats. The present study has shown that the mammalian herbivores in the region form groups based on their biogeographic affinities, which was hitherto presumed but not tested. The Trans-Himalaya is thought to be the cradle of Caprinae evolution (Schaller, 1977), and Ladakh Trans-Himalaya is one of the few areas in central Asia that harbour the highest number of species belonging to this taxon. Thus, Ladakh is an important biogeographic unit from both ecological and evolutionary perspectives. Although biogeographical analysis of mammals have been carried out elsewhere (Badgley & Fox, 2000; H. 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 the distribution of wild ungulates in the Trans-Himalaya and other alpine rangeland areas.

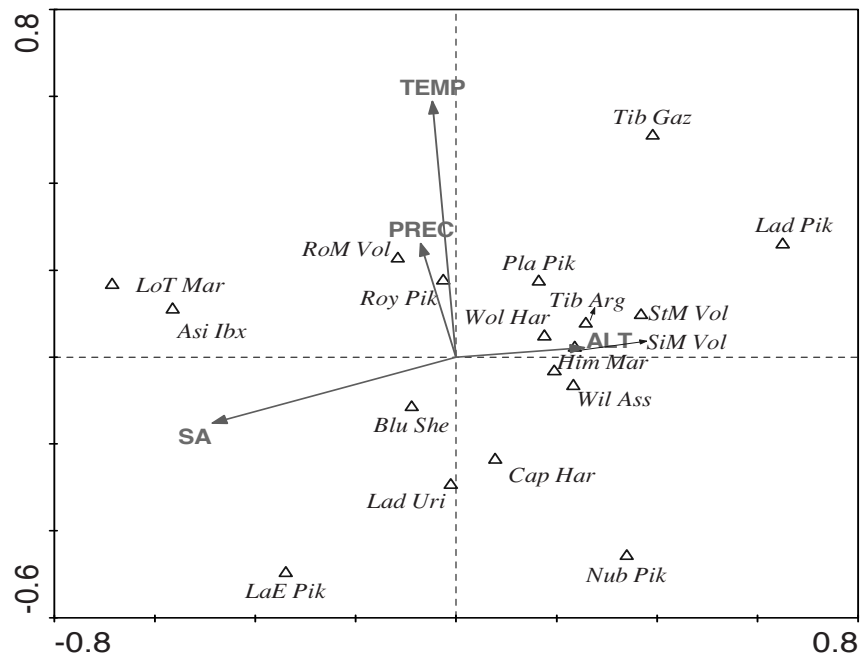


Fig. 4. First two axes of CCA ordination of the species and environmental variables (explanatory) with spatial variables (covariates). See Table 1 for species identity. The abbreviations of environmental variables are same as in Fig. 1.

It seems that there are two main biogeographic units of mammalian herbivores in the region, as indicated by the strong segregation between chorotype II comprising six species and all the other species, nine of which belong to chorotype VI. Chorotype II belongs to the north and south-western rugged parts of Ladakh, while species in other chorotypes correspond to the eastern plain of Changthang. These conform to the anecdotal information on their distributional patterns in Ladakh (Fox et al., 1991a; Mallon, 1991). The environmental variables that best characterise Chorotype II are rugged terrain with steep slopes, typical of north and south-western part of Ladakh. In chorotype II, Asiatic ibex and long-tailed marmot are more similar in their distributions than the rest of the members. When looked at their global distributions, both seem to have relatively wide and overlapping distributions in central Asia, with the ibex having somewhat wider distribution. The areas in Ladakh with the core of their ranges are characterised by rugged, relatively lower and thus higher temperature. Ibex distribution in central Asia seems to be determined largely by topography, as it is known to use steep cliffs as escape terrain (Fox et al., 1992; Namgail, 2006b), but the role of terrain ruggedness in the habitat selection of long-tailed marmot is not known. There could be another factor that is causing the convergence of their distribution, which can only be known by studying their habitat utilization patterns in detail.

There are three chorotypes each with a single species, which have very restricted distributions unique to themselves. These are the Tibetan gazelle, Tibetan antelope and wild yak. Both wild yak and Tibetan gazelle faced precipitous decline in their populations in Ladakh during the last century; excessive hunting and livestock grazing have been listed as the most important causes of these declines (Bhatnagar et al., 2006a; Namgail et al., 2007; Namgail et al., 2008). The Tibetan antelope, on the other hand, did not have a wide distribution in Ladakh in the past too. The animal is known for its long latitudinal migration, and perhaps it does not have a bigger population in Ladakh because there is not enough open areas in a north-south orientation in this region, as it is bounded by the Karakoram range on the north and the Great Himalayan range on the south.

Chorotype IV is formed by the Royle's pika and Royle's mountain vole. There is no information on the ecology of these species in Ladakh, except anecdotal information about their distribution in few areas (Pfister, 2004). Their global distribution is, however, restricted to the Himalayan region (Smith & Boyer, 2008), where their distributions span an altitudinal range between 2500 and 4300 m asl. Further, mountain vole is endemic to India and is the only small mammalian herbivore of Ladakh that is listed as 'Near Threatened' on the IUCN red list of threatened animals, as all others are listed as 'Least Concern' (IUCN, 2008). Anecdotal information suggests that both Royle's pika and vole occur in rocky habitats in Ladakh (Pfister, 2004) at lower altitudes with slightly higher precipitation (pers. obs.), perhaps due to the spatial structuring in environmental variables (see discussion below). The role of temperature and precipitation in their distributions is also indicated by the CCA results.

All other species are clubbed into chorotype VI, in which some species are more similar in distribution than others, although not significantly. All the species in this chorotype have the core of their ranges on the Tibetan plateau except for three species: silvery mountain vole, Himalayan marmot and Ladakh pika, which are distributed mainly in the marginal mountains of the plateau (Molur, 2008; Molur & Shreshtha, 2008; Smith & Johnston, 2008). Within this chorotype, woolly hare and Himalayan marmot are more similar to each other than they are to others. Globally both species have similar distributions along an altitudinal gradient (Molur & Shreshtha, 2008), thus altitude might be a factor that is leading to the congruence in their distributions in Ladakh, which needs to be explored. Further, within this chorotype, blue sheep stands apart from others, indicating that although it shares habitat features with other members of the chorotype,

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its distribution is idiosyncratic in some ways. This could be related to its ubiquity, as it is the most abundant and widely distributed wild ungulate in Ladakh as indicated by the CCA analysis (see also Fox et al., 1991a; Namgail, 2006b).

The congruence pattern of mammalian herbivore distribution in Ladakh indicates that their distributions are influenced by both current ecological and historical factors, as the environmental factors did not explain all the the geographical groups obtained in the cluster analysis. A substantial variation in the species distributional data was also explained by the spatial variables, suggesting that some environmental variables have a spatial structure and consequently their effect is confounded by the geography. The results of the partially constrained ordinations suggest that altitude and precipitation have a latitudinal and/or longitudinal component. When the topographical and climatic maps of Ladakh are examined closely, it is apparent that south-western part of Ladakh receives more precipitation (Hartmann, 1983), and the eastern part is higher than the rest.

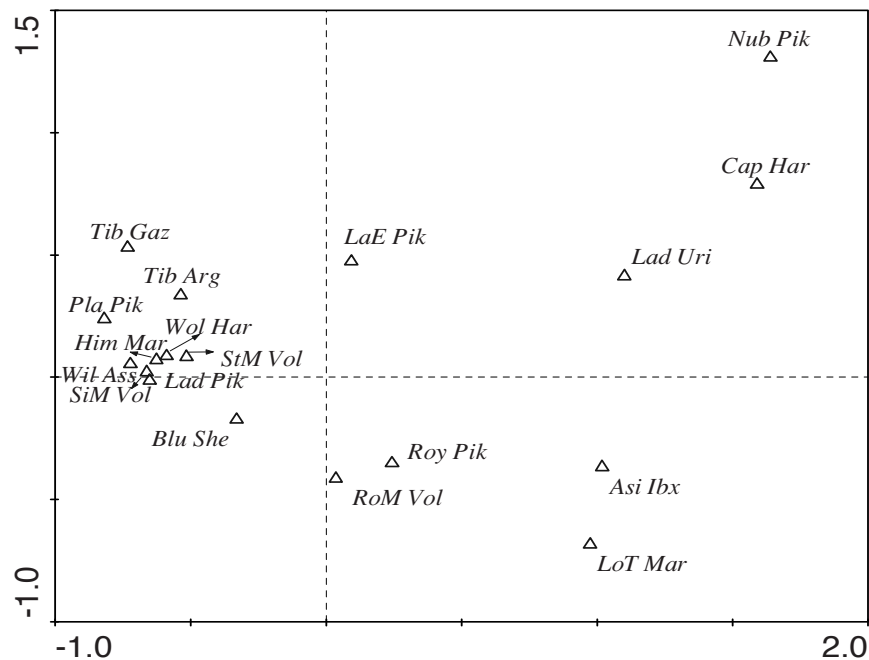


Fig. 5. First two axes of CCA ordination of the species and spatial variables. See Table 1 for species identity.

The 24% of the variation in species distribution that remained unexplained suggests that there are factors that influence their distributions but were not included in this analysis, as alluded to earlier. Such factors could be both current ecological and historical factors. The most plausible such factors are vegetation, humans and their endeavours, rivers and high mountains as geographical barriers. One of the major caveats of this study is the lack of information on the vegetation, but this would not have influenced the overall conclusion of the study for a couple of reasons: 1) physical habitats explained most of the variation on distributional pattern of herbivores, especially the larger ones, 2) the climatic variables used in the study would have accounted for the variation in the

vegetation distribution to some extent, as they influence the vegetation growth and regeneration (Chapter 2).

There are more mammalian herbivores in the eastern than in the western part of Ladakh (Pfister, 2004), as also shown by the cluster and CCA analysis. One wonders why there is a discrepancy in species richness across the landscape. One of the main factors accounting for this could be the topographical features, as indicated by the CCA. Because the eastern part is flatter and open that might facilitate free movement of animals, while the western part is more rugged with myriad glaciers that may restrict animal movement. But there is no denial that anthropogenic pressures might also have played a role, as different species might respond differently to gradients created by humans. The largest chorotype occurred in the eastern part of Ladakh, which is the centre of *Pashmina* or cashmere wool production in India. The people in this part of Ladakh are predominantly nomadic pastoralists and rear a variety of livestock including yak, horse, sheep and goat. Could it be that there are more species of wild herbivores here than in the western part because these livestock act as a buffer for the wild herbivores against predators, implying that the predators in the west, with declining livestock population (Raghavan, 2003), have a more controlling effect on wildlife populations. The level of hunting by humans has been reported to be higher in the western part (Namgail, 2006a), which might exacerbate the aforementioned negative influence of predators. Further discussion on this topic is beyond the scope of this paper, but such issues need to be addressed to have a comprehensive understanding of the species richness pattern of mammalian herbivores in Ladakh.

The role of rivers and high mountains in the herbivore species richness pattern in Ladakh has never been assessed. Given that 24% of the variability in the distributional patterns of mammalian herbivores remain unexplained it is possible that the present assemblage of large herbivores in Ladakh are shaped by these geographical features. Some species like the cape hare and Nubra pika occurred only in quadrats north of the Indus river, which indicate that this river could be restricting their southward expansion. Further, most of the species that have the core of their ranges on the Tibetan plateau occurred only on the eastern side of the Zangskar river, suggesting that it might be a more important determinant of Ladakh's zoogeography. The river's influence on animal distributions might, however, be confounded by the terrain configuration (animals not being able to adapt to rugged terrain), as there is an interface between western rugged terrain and eastern plains that runs almost parallel to the river, although located approx. 30 km east of the river.

Therefore, we looked for species that occur in the area between the river and the terrain interface to disentangle their effects, and found one ungulate: Tibetan argali and three lagomorphs in this area, suggesting that Zangskar might constrain the distributional ranges of these species, but not that of the others, which might be constrained by the topography. Yet, literature suggests that Tibetan argali is also adapted to open areas (Namgail *et al.*, 2004), and there is only one small population of this species within 10 km from the river that colonised the area in 1978 (Fox *et al.*, 1991b). Thus, the rivers do not seem to influence the distribution of large herbivores in Ladakh, perhaps because animals cross the rivers during winter when they freeze, although they might restrict the ranges of some of the less mobile species such as smaller herbivores.

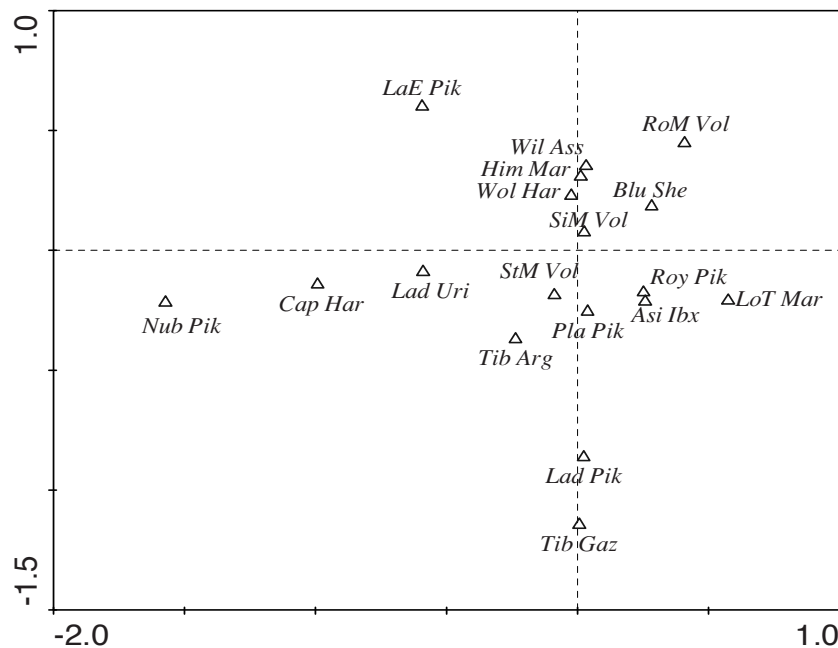


Fig. 6. First two axes of CCA ordination of the species and spatial variables (explanatory) and environmental variables (covariates). See Table 1 for species identity.

The unexplained variation in the species distribution, therefore, could largely be accounted for by historical factors associated perhaps with orogenesis. The rise of the Himalaya as a result of the collision of the Indian and Eurasian plates led to the formation of formidable mountains in the region, which might have acted as barriers, confining species with similar modes of dispersal to similar areas. The Himalaya is still geologically active, and the mountains are rising rapidly due to block faulting (Valdiya, 1991). Thus, the geographical grouping of mammalian herbivores in Ladakh could, to some extent, be attributed to the high and formidable mountains that restrict their movements. This perhaps is vouched by the fact that the open plains of eastern Ladakh, where animals can move freely, is more diverse in mammalian herbivores compared with the rugged areas of the western part.

Furthermore, the role of high and formidable mountains in herbivore distributions is perhaps also indicated by the absence of large herbivores in Ladakh from the Oriental region, because the Himalayan range hindered their northward expansion (see Chapter 7). Similarly, there are less species from west Asia, and more from the Tibetan plateau in Ladakh's regional herbivore species-pool, which is perhaps due to the geographical barrier comprising a jumble of mountains to the west of Ladakh, that represent the end of several mountain ranges such as the Kunlun Shan, Tian Shan and the Himalaya. Although these are just a few facts to support the plausible role of high mountain ranges influencing Ladakh's zoogeography, a thorough discussion on the issue is beyond the scope of this paper. The results of this study merely serve as baseline information for further studies that will enhance our understanding of biogeography, phylogeny and evolution of mountain ungulates.

Conservation implications

The populations of many mammalian herbivores in Ladakh are declining precipitously (Bhatnagar et al., 2006a; Namgail et al., 2009). Amongst the eight wild ungulates, two are listed as 'Endangered', two as 'Vulnerable' and one as 'Near Threatened' on the IUCN red-list of threatened animals (IUCN, 2008). The status of less prominent taxa like lagomorphs and rodents remains little known, although some species are known to be persecuted by humans as pest control measures (Bagchi et al., 2006). This calls for enhanced research, monitoring and conservation programs. Nevertheless, the harsh environment and the difficult terrain make it difficult to develop such programs. Thus, there is an urgent need for innovative ways to study and conserve this unique but threatened group of animals. Our study has shown that there is cross-taxon congruence in the distribution of the mammalian herbivores of Ladakh. Under such a scenario, larger and easily located taxa like ungulates can be used as surrogates for other less prominent taxa such as pikas and voles while planning conservation strategies and prioritising areas for conservation of these high-altitude animals.

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CHAPTER 4

Winter habitat partitioning between Asiatic ibex and blue sheep in Ladakh, northern India

Tsewang Namgail

‘.....parts of the Himalaya remain virtually unknown, zoogeographically speaking. The precise limits of species have seldom been defined, and the fascinating ecological problems raised when two related species occupy the same range have been largely ignored’

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Abstract

Asiatic ibex *Capra ibex siberica* and blue sheep *Pseudois nayaur* are the most abundant wild ungulates in the Ladakh Region of the Indian Trans-Himalaya. Both species use rugged terrain to escape predation, and the competitive exclusion principle suggests that the distribution of one species may be affected by the presence of the other. I evaluated habitat use by these mountain ungulates in the Shun Gorge, at the eastern boundary of ibex distribution in the Zangskar Mountains, Ladakh, India. I hypothesised that due to their high affinity toward cliffs as a predator escape strategy, ibex and blue sheep overlap in their habitat use, especially in winter when they are likely to be confined by snow cover. Resource selection indices and chi-square statistics revealed that both ibex and blue sheep prefer habitat close (1-50 m) to cliffs. The two species were also similar in their use of habitat in terms of slope angle, except that ibex avoided gentle slopes ($<15^{\circ}$) and blue sheep avoided very steep slopes ($>45^{\circ}$). Both used habitats in terms of elevation and snow cover non-selectively except that blue sheep avoided very low areas (<4000 m), and ibex avoided snow-free areas. I suggest that there is high potential for competition between the two species, and the presence of one species may negatively influence the distributional pattern of the other.

Key words: Asiatic ibex, *Capra ibex*, blue sheep, *Pseudois nayaur*, resource selection, habitat partitioning, Zangskar, Ladakh, Trans-Himalaya

Introduction

Large herbivores with similar ecological requirements are expected to partition resources to coexist, especially in areas where the resources are in short supply (Wiens, 1977; De Boer & Prins, 1990). Understanding the mechanism of such resource partitioning is a central issue in community ecology (Ricklefs, 1990). Resource partitioning is accomplished through evolutionary divergence of resource use by co-occurring species (Walter, 1991), apparently in response to competition. Nevertheless, some ecologists argue against the importance of competition in the differential use of resources by sympatric species, and contend that predation may also lead to niche differentiation (Hairston et al., 1960; Holt, 1977; Repasky, 1996), as predatory risk provides an axis along which habitat partitioning can occur (Holt, 1989). Nevertheless, in areas where competition does structure communities, species should segregate along at least one resource dimension in the Hutchinsonian niche hypervolume (Schoener, 1974).

As per the competitive exclusion principle, when two species co-occur in an area and depend on the same limited resources, the dominant species competitively exclude the subordinate one, as exemplified by Gause's experimental work (Gause, 1934). Therefore, the range of a species can be reduced by the presence of other species with similar ecological requirements (Connell, 1961). Studies on resource partitioning by ecologically similar wild ungulates were carried out extensively in North America and Africa (Lamprey, 1963; Jarman & Sinclair, 1979; Hanley & Hanley, 1982; Jenkins & Wright, 1988; Voeten & Prins, 1999), but there is little information on the niche separation amongst wild ungulates of the Trans-Himalayan ecosystem of south Asia. Wildlife managers in this mountainous region, therefore, rely on information generated from studies in the tropical and sub-tropical regions, which may not necessarily be applicable to this dry alpine ecosystem with a unique assemblage of large herbivores.

In this study, I looked at the differential habitat use by two mountain ungulates: Asiatic ibex *Capra ibex siberica* (hereafter ibex) and blue sheep *Pseudois nayaur* in the Zangskar Mountains of Ladakh, India. These are the most abundant wild ungulates in the region with blue sheep's population (\approx 11,000 individuals) reaching almost double the number of ibex (Fox et al., 1991). Blue sheep also has a wider distribution in the region, mostly in the eastern part and ibex has a relatively narrower distribution in the western part (Fox et al., 1991). Fox et al. (1992), however, reported a relatively higher abundance of ibex in central Ladakh (despite its dryness and low vegetation), which they attributed to the lack of snowpack that might had encouraged ibex populations to overwinter in the region. The two species constitute the most important prey species of the highly endangered snow leopard *Uncia uncia* (Mallon, 1991; Oli et al., 1993).

Ibex and blue sheep have similar anti-predator habitat requirements, as both use rugged terrain to escape predation (Bhatnagar, 1997; Namgail et al., 2004). Preliminary observations on the habitat use by these species also revealed that they are similar in the use of habitat variables such as altitude, slope angle, rock type etc. (Mallon, 1991). Therefore, it is possible that they compete for some resources, and the presence of one species could negatively affect the other species. There is anecdotal information on their distributions that support such contentions, e.g., across large mountainous tracts of northwestern Tibetan Plateau, the distributions of these species demarcate often abruptly, thereby suggesting competitive exclusion of one species by the other (Schaller, 1998).

Blue sheep may use large boulders and scree of slate talus as escape terrain in parts of the Tibetan Plateau with low availability of cliffs (Harris & Miller, 1995). Furthermore, in other areas where the two species co-occur, blue sheep are reported to explore the open slopes near cliffs more often than ibex (Wegge, 1989; pers. obs.). The former is therefore more flexible in its habitat use, and may have a competitive advantage

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over ibex. The Shun Gorge marks the eastern boundary of ibex distribution in the Zangskar Mountains of the Indian Trans-Himalaya (Namgail, 2004), while along the Himalayan Range to the south its eastern limit terminates abruptly at the Sutlej Defile (Fox et al., 1992). Based on the competitive exclusion principle, one can therefore speculate that competition with blue sheep may limit its eastward distribution. A study was thus carried out in the Shun Gorge to assess the degree of overlap and possible competition between these ecologically similar species. Based on their similar anti-predator habitat requirements, I predicted a high overlap between the two species in the use of habitat, especially in winter when snow cover is likely to restrict them to limited grazing grounds.

Methods

Study area

The Shun Gorge (33°N, 77°E) is located in the Zangskar Range, Ladakh, India, and encompasses c. 70 sq. km. As other parts of Zangskar, it remains cut off from the rest of Ladakh in winter (Nov.-Apr.), when the only motorable road from Kargil is blocked by heavy snow. Thus during winter, it can only be accessed through a trek of c. 15 days over the frozen Zangskar, Lungnak and Tsarab rivers. Topographically, the area is characterised by rugged terrain, with low river bluffs along the Tsarab River. Elevation ranges from 3500-5000 m. Precipitation is mostly in the form of snow during winter (Nov.-Feb.), and during the study period, I recorded about a meter of snow on the upper slopes.

No ungulates are found in the area except the study species and domestic yak, horse, sheep and goats. The sheep and goats were herded on the river bluffs near the villages, and were sometimes taken to the side-valleys, depending on the depth of snow. The yaks and horses ventured out far away from the villages but not far enough to disturb the ibex and blue sheep, which generally occurred on higher reaches. There are two villages viz., Yarshun (7 households) and Marshun (3 households) in the study area, with a total human population of c. 50 people.

Both wild and domestic ungulates are preyed on by the snow leopard, wolf *Canis lupus chanco*, and to a less extent by lynx *Lynx l. isabellina*. Avian predators like the golden eagle *Aquila chrysaetos* sometimes prey on the lambs of both domestic and wild ungulates. See Namgail (2004) for more information on wildlife and natural history of Zangskar.

Field methods

The study was conducted between 12 Jan. –20 Feb. 2002. The length of the study period was constrained by the remoteness and inaccessibility of the study area. During the study, I walked on the frozen Tsarab River, looking for ibex and blue sheep. Two permanent trails: one upstream (c. 5 km) and one downstream (c. 3 km) from Marshun Village were established on and along the river. Each trail was walked at least 15 times during the study period. The observations were aided by 8x40 binoculars and a 15-45X spotting scope.

Whenever a group of animals was encountered, I recorded the time, date, species and habitat characteristics such as distance to cliff, slope angle, elevation and snow cover. All these habitat variables were visually estimated except elevation, which was determined from a 1: 250, 000 topographic map, and the accuracy was often checked by using a Global Positioning System (GPS). For estimating the proportions of available habitat, 149 random points were plotted on a 1: 250,000 topographic map of the area (Marcum & Loftsgaarden, 1980), which were then located on the ground and the habitat characteristics at these sites were sampled in the same way as described for habitat use.

Analytical methods

The selection of habitat by ibex and blue sheep were determined by estimating selection ratios (ratio of the proportion of habitat use and available) for different habitat units. The value of the selection ratio of a habitat unit is proportional to the probability of that unit being utilized by the study animals (Manly et al., 1993). Due to the small size of the study populations, I needed to include re-sighted groups in the analysis, but the long observation interval (one observation on a group/day) should minimise the autocorrelation. Since the available habitat was estimated, and individual animals were not identified, the data conformed to the design I format (Thomas & Taylor, 1990) with sampling protocol A (Manly et al., 1993). For statistical analyses, the habitat variables were classified into distinct categories, and the selection ratio (\hat{w}_i) for each category was calculated as

$$\hat{w}_i = o_i / \pi_i \quad \text{Eqn. 1}$$

where o_i is the proportion of used units in category i , and π_i is the proportion of available resource units in category i . Subsequently, the standard error of a selection ratio was calculated as

$$se(\hat{w}_i) = \hat{w}_i \sqrt{\{1/u_i - 1/u_+ + 1/m_i - 1/m_+\}} \quad \text{Eqn. 2}$$

where u_i is the used resource units in category i , u_+ is the total number of used units sampled, m_i is available resource units in category i and m_+ is the total available units in category i .

To statistically test for habitat selection, i.e., whether sample proportion of used resource units were significantly different from the sample proportion of available units, the modified χ^2 : log-likelihood Chi-square statistic (χ^2_L) for each habitat variable was calculated as

$$\chi^2_L = 2 \sum \{u_i \log \{u_i/E(u_i)\} + m_i \log \{m_i/E(m_i)\}\} \quad \text{Eqn. 3}$$

where $E(u_i)$ is the expected value of u_i , and $E(m_i)$ is the expected value of m_i . If the χ^2_L was significant for a habitat variable (i.e., habitat selection), simultaneous Bonferroni-adjusted 95% confidence intervals were calculated for each category of that variable (to check which categories are creating the significance) as

$$\hat{w}_i \pm Z_{\alpha/(2I)} se(\hat{w}_i) \quad \text{Eqn. 4}$$

where I is the number of habitat categories and $se(\hat{w}_i)$ is the standard error of selection ratio. A habitat was used selectively, if the confidence limit for that habitat excluded 1. If selected, a habitat was preferred if the interval was > 1 , and avoided if < 1 (Manly et al., 1993).

Univariate t-tests were used to statistically test for significant differences in the use of habitat in terms of distance to cliff, slope angle, elevation and snow cover by ibex and blue sheep. The slope angle and elevation were normally distributed, and distance to cliff and snow cover were log and arcsine transformed, respectively, to fulfill the assumption of normality. Overlap in habitat use by ibex and blue sheep was calculated using Pianka's index (Pianka, 1973).

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$$O_{jk} = \frac{\sum P_{ij}.P_{ik}}{\sqrt{\sum P_{ij}^2 \cdot \sum P_{ik}^2}} \quad \text{Eqn. 5}$$

where O_{jk} is the measure of overlap between species j and k , and P_{ij} and P_{ik} are the proportions of time spent by species j and k respectively on resources i - n . Overlap is complete when $O_{jk} = 1$ and absent when $O_{jk} = 0$.

Results

Forty-six observations on ibex and 70 on blue sheep were made during the study period. During surveys in the study area, I counted a maximum of 35 ibex and 67 blue sheep. Assuming that I counted all the animals in the c. 70-km²-gorge, the above figures translate to an ibex density of 0.5/km² and a blue sheep density of 0.96/km². Habitat selection pattern by the two species is given in Table 1, while Table 2 presents the means (\pm SE) of the habitat variables used by the two species and their overlap.

Habitat use and overlap

Ibex preferred habitats close to cliffs (1-50 m; $\chi^2_L = 8.92$, $p < 0.05$), and their use of other distance categories were in proportion to their respective availabilities (Table 1). Blue sheep showed a similar pattern of habitat use, but used cliffs (0 m) significantly less than in proportion to their availability ($\chi^2_L = 14.2$, $p < 0.05$). Ibex also avoided gentle slopes ($<15^\circ$; $\chi^2_L = 8.59$, $p < 0.05$), while blue sheep avoided very steep slopes ($>45^\circ$; $\chi^2_L = 8.80$, $p < 0.05$), but both species used other slope categories similarly and non-selectively (Table 1).

Table 1. Estimated habitat selection indices for Asiatic ibex and blue sheep in Zangskar, Ladakh, India. \hat{w}_i estimated habitat selection ratio; $se(\hat{w}_i)$ standard error of selection ratio; $\hat{w}_i(l)$ and $\hat{w}_i(u)$ 95% lower and upper confidence limits, respectively.

Variable	\hat{w}_i	Asiatic ibex			\hat{w}_i	Blue sheep		
		$se(\hat{w}_i)$	$\hat{w}_i(l)$	$\hat{w}_i(u)$		$se(\hat{w}_i)$	$\hat{w}_i(l)$	$\hat{w}_i(u)$
Distance to cliff (m)								
0	0.560 ⁰	0.198	0.116	1.004	0.322 ⁻	0.125	0.042	0.602
1-50	1.709 ⁺	0.293	1.053	2.365	1.626 ⁺	0.263	1.037	2.215
51-100	0.560 ⁰	0.262	0.000 [†]	1.147	1.030 ⁰	0.322	0.309	1.751
>100	0.689 ⁰	0.375	0.000 [†]	1.529	0.792 ⁰	0.351	0.006	1.578
Slope angle (deg.)								
<15	0.395 ⁻	0.237	0.000 [†]	0.926	0.952 ⁰	0.338	0.195	1.709
16-30	0.945 ⁰	0.197	0.504	1.386	1.341 ⁰	0.202	0.889	1.793
31-45	1.809 ⁰	0.423	0.861	2.757	0.905 ⁰	0.251	0.343	1.467
>45	0.448 ⁰	0.272	0.000 [†]	1.057	0.196 ⁻	0.145	0.000 [†]	0.521
Elevation (m)								
<4000	0.704 ⁰	0.209	0.236	1.172	0.294 ⁻	0.113	0.041	0.547
4001-4150	1.313 ⁰	0.326	0.583	2.043	1.776 ⁰	0.351	0.990	2.562
4151-4300	1.976 ⁰	0.606	0.619	3.333	2.077 ⁰	0.575	0.789	3.365
>4300	0.560 ⁰	0.347	0.000 [†]	1.337	0.490 ⁰	0.273	0.000 [†]	1.102
Snow cover (%)								
0	0.395 ⁻	0.160	0.037	0.753	0.909 ⁰	0.209	0.441	1.377
1-25	2.239 ⁰	1.047	0.000 [†]	4.584	0.736 ⁰	0.436	0.000 [†]	1.713
26-75	1.990 ⁰	0.586	0.677	3.303	1.553 ⁰	0.451	0.543	2.563
>75	0.833 ⁰	0.194	0.398	1.268	0.890 ⁰	0.173	0.502	1.278

⁺ (preference); ⁻ (avoidance); ⁰ (use in proportion to availability); [†] inferences are less reliable due to very few observations ($n_i < 5$).

Interaction between ibex and blue sheep

Both species used elevation non-selectively, except that blue sheep avoided habitats at very low elevation (<4000 m; $\chi^2_L = 23.49$, $p < 0.05$; Table 1). They also used areas with varying snow cover non-selectively except that ibex avoided snow-free areas ($\chi^2_L = 12.21$, $p < 0.05$). The t-test statistics also revealed a high similarity in habitat use, differing significantly only in the use of slope angle ($t = 2.589$, $p < 0.01$; Table 2), which was further confirmed by the relatively less overlap ($O_{jk} = 0.88$) between the two species in the use of this variable (Table 2).

Table 2. Mean (\pm SE) of habitat use and overlap (O_{jk}) between ibex and blue sheep in Zangskar, Ladakh, India.

Habitat variable	<i>Blue sheep</i>	<i>Asiatic ibex</i>	t-value	p	O_{jk}
Distance to cliff (m)	42 \pm 4.905	36 \pm 5.871	0.247	0.810	0.92
Slope angle (degrees)	27 \pm 1.122	32 \pm 1.634	2.589	0.010*	0.88
Elevation (m)	4143 \pm 13.211	4092 \pm 32.576	1.751	0.082	0.95
Snow cover (%)	52.143 \pm 4.873	53 \pm 5.496	1.902	0.060	0.98

* Statistically significant

Discussion

My results showed that ibex and blue sheep overlap in their habitat use. Nevertheless, mechanisms other than snow cover restricting the two species to limited grazing grounds are responsible for such high overlap, because the two species did not prefer the snow-free areas as expected under this assumption. During the study period, the two species were seen feeding in close proximity (<20 m) on three occasions. Such sociality is a common feature of the ungulate communities of eastern Africa, and has been viewed as a response to high predation pressure (Sinclair, 1985). The high overlap between ibex and blue sheep in their habitat use could be related to their occurrence in close proximity for mutual protection against predator.

The high overlap in habitat use by these species in the Zangskar Mountains may also imply: (a) that resources are abundant and they can coexist without strong competition (b) that they differ in the use of their diet (c) that not enough time has elapsed for evolutionary divergence of resource use. The first explanation is untenable, since the Trans-Himalayan Mountains support very low plant biomass (Chundawat & Rawat, 1994; Mishra, 2001). The second explanation is likely to account for the high overlap in habitat use, as diet separation allows the co-occurrence of species in the same habitat (Schoener, 1974; Pianka, 1994). The dietary use and overlap between them need to be investigated to shed light on this aspect. The third explanation is also defensible, as the resource partitioning between co-occurring species is an evolutionary process (Walter, 1991).

The high preference for habitat close to cliff (1-50 m) by both species is consistent with the results obtained in other studies on these wild ungulates (Wilson, 1989; Bhatnagar, 1997; Longva, 1998; Namgail et al., 2004). Such preferences reflect the importance of cliffs as escape terrain, and perhaps a high predation pressure in the area, as indicated by a relatively high abundance of snow leopard signs such as scrapes, spray marks and droppings (Namgail, Unpubl. data). The high affinity of these ungulates toward cliffs may also make them relatively less vulnerable to disturbance associated with livestock grazing, as such terrain types are used less frequently by livestock herders (pers.

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obs.). The relatively higher number of these species in Ladakh (Fox et al., 1991) could be due to a low level of competition with domestic livestock, which has the capability of out-competing ibex and blue sheep as shown by theoretical (Mishra et al., 2002) as well as empirical studies (Bagchi et al., 2004; Mishra et al., 2004).

The overlap in habitat use by ibex and blue sheep suggests a high potential for competition between them, as habitat overlap can lead to exploitation as well as interference competition (Begon et al., 1996). But comparative data from both sympatric and allopatric populations, encompassing all seasons need to be collected to demonstrate competition. However, given the relatively higher density of blue sheep in the Shun Gorge, it is possible that this species negatively influences the population and distribution of ibex in the Zangskar Mountains and other areas where they come together.

Conclusion

There was substantial overlap in habitat use by ibex and blue sheep, which is in contrast to the prediction of competition theory. Such high overlap in habitat use by the two species in a region with inherently low plant productivity, especially in the resource-limited winter months, suggests a high potential for competition. A thorough understanding of resource selection of both sympatric and allopatric populations of ibex and blue sheep is desirable to demonstrate competition.

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CHAPTER 5

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

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"...spying a small herd feeding on a hillside, I marked out an area with my glasses and visited a spot. After much search I found a few blades of grass and an alpine plant or two. Measuring a space of 100 yards by 10, I systematically collected every scrap of vegetation, and in the end had secured seventeen withered blades of coarse grass and seven small alpine plants, in fact, less than one would feed a guinea-pig on, and yet these herds of sheep and asses graze contentedly and with success on those barren hillsides. Their means of subsistence is still a puzzle to me"

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Abstract

The distributions of the Trans-Himalayan large herbivores are fragmented, engendering a spatial heterogeneity in their species-richness. We capitalised on this natural-experiment situation to understand the niche dynamics of herbivores in relation to the number of sympatric species. 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 almost similar environmental features but varying wild ungulate species richness, and studied the species' diet and habitat utilization in them. Habitat variables were observed in the field and microhistological faecal analysis was carried out to determine the habitat and diet width of the animal in the three areas with different ungulate species richness. The habitat- and diet-niche widths were determined using the Shannon's H' Index. The results showed that habitat width of blue sheep has 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 greater number of sympatric species, and the widest diet spectrum in areas with moderate species richness. We suspect that the narrow diet width in allopatry is out of choice, while it is out of necessity in areas with greater number of sympatric species due to resource partitioning. We suggest that interactions with sympatric species lead to niche adjustment of mountain ungulates, and underscore the importance of including biotic interactions in species distribution models, which have often been neglected.

Keywords: Ladakh, niche width, *Pseudois nayaur*, species diversity, Trans-Himalaya

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 either as a result of 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 goes extinct from a community, niche space (habitat supplying resources for a species' survival) is expected to become vacant that can either be 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. 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 selecting 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 due to resource constraint brought 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, though 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

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sympatric species richness. For this, we studied its habitat and diet in areas where it occurs allopatrically and contrasted it 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 to 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 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 (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' to 34°40'N and 75 °40' to 79 °30'E) is classified as a cold desert. The moisture-laden monsoon clouds hardly reach this region due to 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 (Dec-Jan) to +35°C in summer (June-Aug). 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 were as follows: a) 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, b) Puyul valley (33°43'N, 77°47'E) of the proposed Gya-Miru Wildlife Sanctuary (hereafter Gya-Miru) and c) Rumchung valley (34°08'N, 77°24'E) of the Hemis National Park (hereafter Hemis) are administratively 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; 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 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 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. It, however, exhibits an altitudinal migration by coming down to lower elevations during winter, when upper reaches get covered with heavy snow (Namgail, 2006b). The animal has been reported to feed largely on graminoids such as *Carex/Kobresia* and *Stipa* during summer (Harris & Miller, 1995; Mishra et al., 2004). It 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 Aug. 2007. Blue sheep herds were located from trails and vantage points (Namgail et al., 2004). We searched the mountain slopes with 8x40 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 like slope aspect and slope position, only the aforementioned variables were used to estimate the habitat-niche width of the animal; a model selection procedure (Akaike Information Criterion) identified these as the most important variables in blue sheep habitat use (Namgail, 2006a). An altitudinal gradient provides different habitats for plants, and thus the vegetation diversity and abundance vary along such a gradient in Ladakh (Chapter 2), whereas distance to cliff provides a gradient in vegetation biomass (more vegetation away from cliffs) and predation risk for blue sheep 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 and Miller (1995) on blue sheep's microhistological faecal analysis-based diet in Yenniugou 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 the diet information from the two studies are comparable. Initially, we also did direct observations on feeding animals, but given the workload in the field: estimating habitat use, availability and plant sampling during two seasons in all the different study sites, we found it less practical in this large scale study. Thus, one of us handled the laboratory work, while another estimated habitat use and collected faecal pellets. 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 9 from Hemis.

These samples were air-dried and stored in paper bags before boiling in water for about 1 h and soaking overnight. They were then crushed in the laboratory, and the inner tissue was separated from the epidermis and cuticle by mixing a 5 g sub-sample with water for 1 minute in a Waring blender, and was strained over a plankton sieve following 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, ten 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

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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 mm²) 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 taken from Mishra (2001), while 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 x 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 x 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 were determined using the Shannon-Wiener Index (Magurran, 1988). This index varies from 0 for minimum resource items to about 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, while 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 to 5300 m), slope angle (5 degrees; 0 to 65 degrees) and distance to cliff (50 m; 0 to 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 with a special t-test with the Shannon-

Wiener indices as $t = \frac{H_1' - H_2'}{[\text{var}(H_1') + \text{var}(H_2')]^{1/2}}$, 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. In order 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, while that during winter was 15 (Table 1). In Gya-Miru, 46 observations were made during summer and 86 were made during winter. A total of 74 observations during summer and 28 during winter were made in Hemis. Median group size between seasons

Species richness and niche dynamics

(winter = 15, summer = 14) or between areas were not significantly different, and the average group size of blue sheep was thus 13.7.

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

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).

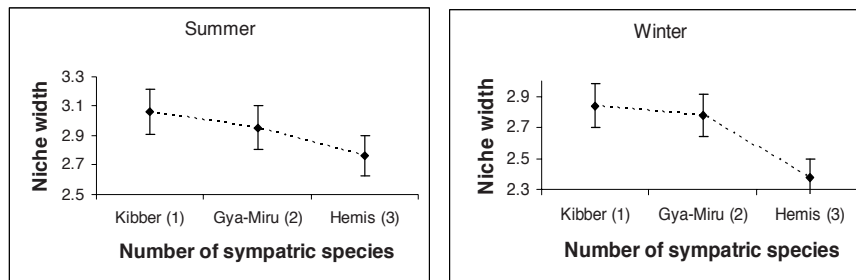


Fig. 1. The relationship between blue sheep's habitat-niche width (Shannon-Wiener indices with 95% confidence intervals) and the number of sympatric species (in parentheses) in the Indian Trans-Himalaya.

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

Area pair	Summer		Winter	
	t-value	P	t-value	P
Kibber and Gya-Miru	1.546	0.123	1.077	0.282
Kibber and Hemis	3.660	<0.001	2.495	0.013
Gya-Miru and Hemis	1.621	0.106	3.664	<0.001

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

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($F = 23.26$, $p < 0.001$; 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 m and 46 m, respectively (Table 4). The species also differed in terms of 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 3 & 4).

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	df	P
Distance to cliff (m)	Species	20.01	2	<0.001
	Season	23.26	1	<0.001
	Species x Season	1.75	2	0.174
	Available	0.02	1	0.885
Slope angle (deg)	Species	8.47	2	<0.001
	Season	0.38	1	0.539
	Species x Season	4.56	2	0.011
	Available	2.17	1	0.141
Elevation (m)	Species	36.15	2	<0.001
	Season	18.55	1	<0.001
	Species x Season	6.33	2	<0.001
	Available	3.93	1	0.048

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, while 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).

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, and the widest in Gya-Miru ($H' = 2.81$) with one sympatric species, and again narrower ($H' = 2.36$) in Hemis with two sympatric species.

Species richness and niche dynamics

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

Variable*	Kibber			Gya-Miru			Hemis		
	<i>Avail.</i>	<i>Summer</i>	<i>Winter</i>	<i>Avail.</i>	<i>Summer</i>	<i>Winter</i>	<i>Avail.</i>	<i>Summer</i>	<i>Winter</i>
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
Alt	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 = Distance to cliff (m), Slope = Slope angle (deg.) and Alt = Altitude (m); Avail. = Available

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 Yenuigou with six sympatric species, which was significantly different from blue sheep's diet width in Gya-Miru ($t = 5.245$, $p < 0.001$) and Hemis ($t = 4.499$, $p < 0.001$; Table 5).

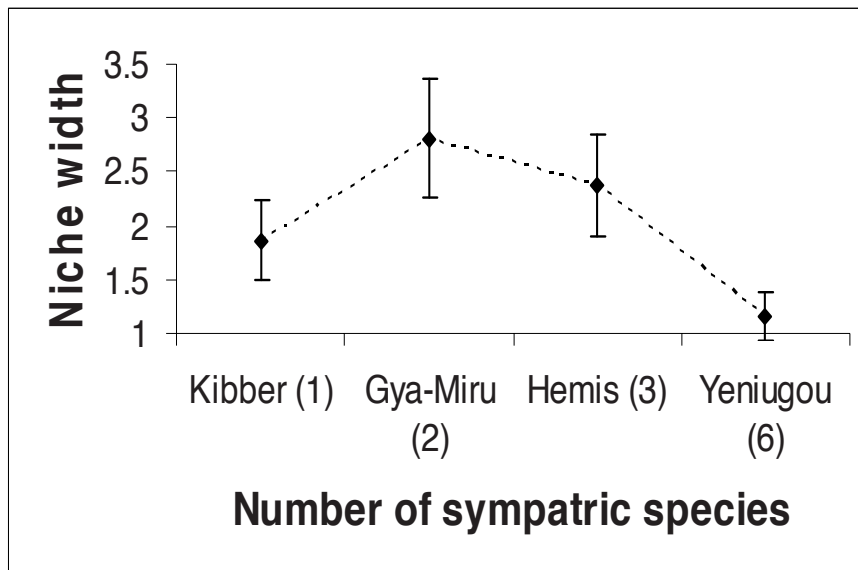


Fig. 2. Relationship between blue sheep's diet-niche width (Shannon-Wiener indices with 95% confidence intervals) and the number of sympatric species (in parentheses) in the Trans-Himalaya (data source for Yenuigou: Harris and Miller, 1995).

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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
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

Plant availability

There were 21 plant species in Gya-Miru, 17 in Hemis, 16 in Kibber, 20 in Yeniugou that are known to be important constituent of the diet of mountain ungulates in the Trans-Himalaya. *Carex*, *Kobresia*, *Stipa*, *Festuca*, *Astragalus*, *Oxytropis*, *Leymus*, *Potentilla*, *Nepeta* and *Artemisia* were some of the most abundant genera in the four 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 $6.31 (\pm 3.7) \text{ g/m}^2$, while that in Hemis was $4.15 (\pm 2.67) \text{ g/m}^2$, 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 in any of our study sites. This pattern is in contradiction 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 due to 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 other hand, 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 niche of herbivores in terms of habitat and diet have 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 localised distribution in moist areas such as stream-banks with higher vegetation cover (Alfred et al., 2006), 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, for the field work in more areas in this observational study would have ensued more environmental (natural as well as man-made) heterogeneity amongst the study sites, thereby confounding the effect of sympatric species richness on blue sheep's niche width. We however 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 change the competitive balance of the co-occurring species. Furthermore, the plant species richness was comparable in the three study areas. 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). Blue sheep's wide distribution thus may be the result of its dietary and habitat flexibility, suggesting that compared to other Caprinae species, it may face fewer constraints to recolonise 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 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 because animals cannot occupy all the suitable habitats due to 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 reexamined especially in low productive environments like the Trans-Himalaya, where availability of resources is minimal due to low plant diversity and biomass, which further declines in winter due to senescence and snow cover. From a conservation point of view, it is obvious that given the tendency of the wild ungulates to shift their niche 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 due to the relationship between mechanisms underlying local and regional species richness (Ricklefs & Schluter, 1993).

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CHAPTER 6

Coexistence of Ladakh urial and blue sheep at multi-spatial scales in the Trans-Himalayan mountains

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Competition for resources would be inevitable and coexistence impossible without a geographic partitioning of ranges. Sympatric survival is not possible in a simple habitat for caprids of a similar size'

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Abstract

Large wild herbivores are important ecologically and economically, and maintaining their populations is an important management priority. However, herbivores might not be able to occupy all suitable habitats due to the presence of other potentially competing wild or domestic species. The Ladakh urial *Ovis vignei vignei* is an endemic and endangered wild sheep inhabiting the mountainous region of Ladakh, northern India, where its population is restricted to narrow tracts along two river-valleys. The causes of this restricted distribution of the species are not understood. Excessive grazing by domestic livestock in this landscape is considered as an important factor influencing wild herbivore populations, but whether a wild ungulate can influence another wild ungulates' range is less known. We asked if competitive exclusion by the more abundant wild ungulate, the blue sheep *Pseudois nayaur*, could explain the singular distributional pattern of Ladakh urial. To explore this possibility, we studied the occurrence patterns of these two species at multiple scales (geographical, landscape and habitat). We found that they occurred independently at the geographical scale, but co-occurred at the landscape scale, facilitated by divergence in seasonal resource use observed at the habitat scale. Although the two species segregated along diet as well as habitat dimensions in summer, enabling their coexistence at the landscape level, there remained a high potential for competition during winter when they overlapped in their habitat use. We conclude that while human and livestock impacts may currently affect its distribution, the presence of blue sheep appears to be an important historical factor limiting the population growth and range expansion of the Ladakh urial.

Keywords: *Ovis vignei*, *Pseudois nayaur*, niche relationship, habitat selection, resource partitioning, Trans-Himalaya.

Introduction

Understanding spatial distributions of animals and the underlying mechanisms have both theoretical and practical value (Andrewartha & Birch, 1954). Mechanistic understanding of the geographical distribution of a species needs a multi-scale approach. Factors like immigration and emigration play important roles in species distributions at a regional scale (Ricklefs & Schluter, 1993), whereas species distributions at smaller scales are governed by the availability of crucial resources for their growth, reproduction and survival (MacArthur, 1972; Begon et al., 1996). Nevertheless, species often cannot locally occupy all the available habitats as other biological factors prevent them from using their full potential range. For instance, utilization of all potential areas may be impeded by interactions with other ecologically similar species (Hutchinson, 1959).

It is well established that energetic constraints set a limit to the number of species that an area can support (MacArthur, 1972; Olff & Ritchie, 1998). Competitive interactions may set an upper limit on local diversity, and the role of competition in structuring ecological communities has become a central issue in community ecology (Diamond, 1975; Connor & Simberloff, 1979). Species that coexist in an area do so by diverging in their resource use over an evolutionary period, largely in response to selection pressures generated by competition. Such adaptive divergence in resource use by co-occurring species is called resource partitioning (Schoener, 1974; Walter, 1991), and has been documented in several taxa (Toft, 1985 in reptiles and amphibians; Albrecht & Gotelli, 2001 in birds; Namgail et al., 2004 in mammals). Facilitation is also thought to be an important process determining herbivore species richness in grazing ecosystems (Arsenault & Owen-Smith, 2002). Although it may enhance species richness in communities in high productive areas in the Tropical systems (Huisman & Olff, 1998), it is less important in structuring herbivore assemblages in less productive ecosystems where competition tends to be the dominant form of interaction (Mishra et al., 2002; Mishra et al., 2004; Namgail et al., 2007).

The Ladakh region (32° to 36° N and 75° to 80° E; 80,000 km²) of the Indian Trans-Himalaya is a high altitude cold desert, but supports a rich assemblage of eight wild ungulates, perhaps due to its location at the junction of two biomes: Tibetan plateau and Hindukush-Pamir mountains. Amongst these ungulates, two are listed as 'Endangered', two as 'Near Threatened' and one as 'Vulnerable' on the IUCN red-list of threatened animals (IUCN, 2008). All of them except the blue sheep have relatively patchy distributions, generating a spatial heterogeneity in herbivore diversity (Fox et al., 1991; Chundawat & Qureshi, 1999). Previous studies have documented the importance of livestock grazing as an important factor restricting wild ungulate populations in the region (Bagchi et al., 2004; Mishra et al., 2004; Namgail et al., 2007; Namgail et al., 2008). However, the importance of competition amongst the wild ungulates themselves has not been explored as a potential mechanism for species distributions (but see Namgail, 2006). Unlike in tropical environments, the plants in the Trans-Himalaya are stunted and sparsely distributed, and the simple vegetation structure does not appear to allow niche partitioning amongst large herbivores, as seen in tropical systems (Voeten & Prins, 1999; Cromsigt & Olff, 2006). Therefore, instead of plants, the terrain features are more important in niche separation amongst the herbivores in the region (Namgail et al., 2004; Namgail, 2006).

The Ladakh urial has a small population (*c.* 2,000) in Ladakh, confined to narrow tracts along the banks of the Indus and Shayok rivers, while the blue sheep is the most abundant (*c.* 11,000) and widely distributed wild ungulate (Fox et al., 1991). Amongst all the wild ungulates, the Ladakh urial suffered the most due to anthropogenic pressure associated with modern development as it inhabits the lowest slopes along the Srinagar-Leh highway, the lifeline of Ladakh (Mallon, 1983). The species was persecuted by

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hunters for trophy and meat due to its occurrence along the highway (Mallon, 1983). Apart from these the animal also suffered due to pasture degradation associated with excessive livestock grazing (Chundawat & Qureshi, 1999), and persecution by farmers as it reportedly damage their crops. Nonetheless, although these pressures might have led to decline in its density, the range of the species have historically been restricted (Mallon, 1983). Currently, although urial's distribution has penetrated the tributary valleys of the Indus and Shayok, it has not progressed beyond *c.* 15 km from the valley-mouths (Mallon, 1983). This leads to the obvious question of what restricts the distribution of the species to this narrow belt.

Interspecific competition is a possible factor, whereby more abundant species like the blue sheep competitively exclude the Ladakh urial, or prevent its range expansion. Therefore, we asked if the limited distribution of Ladakh urial can be explained by possible competition with the blue sheep, given that amongst all the wild large herbivores of the region, the body masses of these two species (mean = 52 kg) are most similar (Mishra et al., 2002), and thus they probably have similar ecological requirements. Theory suggests that species that share ecological features may compete and coexist either by geographical partitioning or resource partitioning along one or more resource axes (Schoener, 1974). Thus we hypothesised that blue sheep and Ladakh urial have non-overlapping geographical distributions and/or diverging resource utilization patterns at a local scale. We aimed to understand the nature of interaction (in terms of habitat and diet) between the two species at smaller spatial scales and its implications for their occurrence at larger spatial scales, which will shed light on the possible role of competition with blue sheep in hindering the range expansion of urial. Understanding the factors limiting urial distribution is crucial given that the species is endemic to Ladakh and is listed as an 'Endangered' species on the IUCN red-list of threatened animals (IUCN, 2008).

Materials and Methods

Study area

The Ladakh Region (*c.* 80,000 km²) is a high altitude cold desert in the northern Indian state of Jammu and Kashmir. Within this area, Ladakh urial occupy *c.* 3000 km². Elevation in Ladakh ranges from 2900 m to 7000 m. The region is deprived of the monsoon clouds due to the rain-shadow effect of the Greater Himalaya, and hence has very low primary productivity. The growth season is confined to a short period of 3-4 months during summer. Trees like poplar *Populus* spp. and willow *Salix* spp. are confined to oases along glacier-fed streams and rivers.

The Puyul valley (33°43'N, 77°47'E), the habitat scale study site in the proposed Gya-Miru Wildlife Sanctuary, encompasses *c.* 100 km² and is located at *c.* 15 km from the Indus River at Upshi. The valley marks the boundary of urial distribution along the tributary stream of Gya. Elevation in the area ranges from 3900 to 6500 m asl, and provides diverse habitats ranging from rugged tracts at higher altitudes and relatively open areas in lower areas. Temperature ranges from -30 °C in winter to +30 °C in summer, and vegetation is characterised by dry alpine steppe (Rawat & Adhikari, 2005).

There are no other wild ungulates in the area except the study species, and a small population of domestic sheep and goats (*c.* 700) that grazes the area. There are however several small mammals: Tibetan woolly hare *Lepus oiostolus*, mouse hare *Ochotona* sp. and marmot *Marmota bobak* that share the pastures with the study species. Mammalian predators include the snow leopard *Uncia uncia*, wolf *Canis lupus*, lynx *Lynx l. isabellina* and red fox *Vulpes v. montana*.

Field methods

To determine the co-occurrence of blue sheep and urial at a geographical scale, a grid (20x20 km) was overlaid on a map of Ladakh, and presence-absence of the two species was determined in 136 random grid-cells scattered all over Ladakh. Co-occurrence at the landscape level was assessed by overlaying a grid (10x10 km) on a map of Ladakh urial's potential range, and then determining the presence-absence of blue sheep and urial in 22 randomly located grid-cells. Most of these grid-cells were located on the ground and the presence-absence of the species in them was determined by direct observation of the animals as well as by indirect evidence such as the presence of horns etc. Information on presence-absence of a species was also gleaned from the literature as well as from knowledgeable local people and wildlife officials.

For the determination of habitat use at a local scale, data were collected between June 2006 and March 2007. Herds of blue sheep and urial were observed from trails along valley bottoms and ridgelines. Scan sampling was the primary method for animal observations, which were aided by 8x40 binoculars and a 15-45X spotting scope. Records were made of species type, group size and date.

Habitat variables *viz.*, altitude, distance to cliff, slope angle and aspect at the animal locations were recorded. These variables have been identified as important in determining habitat use and partitioning by large herbivores in the Trans-Himalaya (Chundawat & Qureshi, 1999; Namgail et al., 2004). Altitude was determined from a topographic map, while slope angle and distance to cliff were visually estimated. A cliff was defined as a very steep slope ($>45^\circ$) on an area more than 20 m diameter with vertical drops of more than 5 meters. Slope aspect was determined by using a compass.

Fresh faecal pellets were collected to generate diet profiles of the species and to assess the diet overlap. 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.* 150 pellets was collected from each herd of the animals. Subsequently, five pellets were randomly drawn from each group to form one sample for the respective herd. Thus there were 11 samples for blue sheep and 10 samples for Ladakh urial, which were air-dried and stored in paper bags.

Laboratory methods

The dried faecal samples were boiled in water for about 1 h, soaked overnight, and then crushed. The inner tissue was separated from the epidermis and cuticle by mixing a 5 g subsample with water for 1 min in a Waring blender, and was strained over a plankton sieve following 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, ten 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 the plant parts such as leaf, stem, flower and seeds. For this, small pieces of plant parts were cleaned in household bleach overnight, washed in water, and then fragments of epidermis were 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 (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 (Cid & Brizuela, 1990; Alipayo et al., 1992).

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Data analysis

To assess the co-occurrence at geographical and landscape levels, our null model assumed that blue sheep and urial are randomly associated. The presence-absence data were organised into a matrix following Connor and Simberloff (1979), where the row represents a species and the column a grid-cell. The species' co-occurrence was quantified using the *C*-score index (Stone & Roberts, 1990), calculated as $C_{ij} = (r_i - S)(r_j - S)$, where r_i is the number of grid-cells with species i and r_j the number of grid-cells with species j and S being the number of shared grid-cells. This index quantifies the 'checkerboard units' (*sensu* Diamond, 1975) for the species pair, and the larger the index the less co-occurrence of the species. Significance of the observed *C*-scores was assessed through Monte Carlo simulations (1000 iterations) using the co-occurrence module of Ecosim 7.72 software (Gotelli & Entsminger, 2001). Observed *C*-score is significantly smaller than expected at random, when $P(\text{Observed} > \text{Expected}) < 0.05$.

For assessing the differential habitat use by the two species, we first identified the most important variables in habitat choice of each species at a local scale. For this we used Generalized Linear Model (GLM) by taking used and unused (but available) habitats as a binary response variable and distance to cliff, slope angle, aspect and altitude as predictor variables. Subsequently, we used Akaike's Information Criterion for small samples (AIC_c) and their differences (Δ) to select the most parsimonious model with fewest variables (lower the Δ , more parsimonious the model) that explain most of the variation in the data. All models with AIC_c differences (Δ) of less than two are useful in explaining the variability in the data.

Subsequently we performed Discriminant Analysis to determine whether the areas used by blue sheep, urial and the unused but available ones could be discriminated on the basis of the most crucial variables identified. We tested for significant differences between these areas on the canonical scores of the first two functions or axes with a one-way ANOVA followed by *post hoc* Fisher's LSD test. Significant differences between blue sheep and urial habitat use were also assessed by using t-tests for independent samples. The multivariate Hotelling's T^2 test was used to check for differences taking all the variables together and thus taking into account the relationship between them. The habitat-niche (all four variables) and diet-niche overlap between the species was determined using Pianka's Index (Pianka, 1973).

$$O_{jk} = \frac{\sum P_{ij}.P_{ik}}{\sqrt{\sum P_{ij}^2 \cdot \sum P_{ik}^2}} \quad \text{Eqn. 1}$$

where O_{jk} is the measure of overlap between species j and k , and P_{ij} and P_{ik} are the proportions of taxon i in the diet of species j and k respectively. Overlap is complete when $O_{jk} = 1$ and absent when $O_{jk} = 0$.

Results

Large scale distributions

At the geographical scale (entire Ladakh) blue sheep occurred in 62 of the 132 grid-cells surveyed, while Ladakh urial occurred in only 10 grid-cells. At the landscape scale (in and around urial's range), blue sheep occurred in 11 grid-cells while the Ladakh urial occurred in 13 of the 22 grid-cells surveyed. The co-occurrence analyses showed that blue sheep and urial are distributed independently at the geographical scale (*C*-score = 110; $P = 0.82$), but their co-occurrence was significantly higher than expected by chance at the landscape level (*C*-score = 48; $P < 0.05$).

Co-distribution of urial and blue sheep

Habitat scale

Akaike Information Criterion for small sample size (AIC_c) indicated that altitude is the most important variable determining habitat choice by urial during summer as well as winter (Table 1), while blue sheep habitat use is best modeled by using distance to cliff, slope angle and altitude as predictors during summer, and distance to cliff and altitude during winter (Table 2).

Table 1. Akaike's information criterion scores (AIC_c), their differences (Δ) and number of model parameters (k) for habitat models developed for seasonal habitat use by the Ladakh urial in Gya-Miru, Ladakh. The figures in bold are AIC differences (Δ) of less than two.

No.	Model	K	Summer		Winter	
			AIC _c	Δ	AIC _c	Δ
1	Altitude	2	65.30	0.00	56.07	0.00
2	Distance + Altitude	3	65.71	0.41	57.92	1.86
3	Distance + Slope + Altitude	4	67.02	1.72	59.92	3.86
4	Slope + Altitude	3	67.06	1.76	58.07	2.00
5	Altitude + Aspect	3	74.52	9.21	59.22	3.15
6	Distance + Altitude + Aspect	4	74.74	9.44	60.69	4.62
7	Distance + Slope + Altitude + Aspect	5	75.49	10.18	62.60	6.53
8	Slope + Altitude + Aspect	4	75.71	10.41	61.18	5.11
9	Slope	2	142.52	77.21	100.24	44.17
10	Distance + Slope	3	144.46	79.16	90.35	34.29
11	Distance	2	145.09	79.79	88.46	32.39
12	Slope + Aspect	3	149.56	84.26	86.68	30.62
13	Aspect	2	150.70	85.39	84.97	28.90
14	Distance + Slope + Aspect	4	151.52	86.21	71.67	15.60
15	Distance + Aspect	3	152.09	86.78	69.69	13.62

Aspect was not important in the habitat choice of both species, and hence was dropped from further analysis. Based on the AIC_c differences (Δ), the models in Table 1 are ranked from the best (lowest Δ value) to the worst (highest Δ value) for habitat use by urial during summer, while for winter they are arranged haphazardly for the sake of comparison with the summer data. The habitat models for blue sheep in Table 2 are also arranged in a similar fashion.

Habitat use and partitioning

Summer

Discriminant Analysis showed that altitude had the highest loading on function 1 in the habitat use during summer (Table 3), indicating that it was the most important factor in discriminating the locations used by urial from those used by blue sheep and unused but available locations. Fig. 1 suggests that blue sheep during summer used higher areas which were more available, whereas Ladakh urial occurred in the lower areas. These differences were significant when these areas were contrasted on the basis of the canonical scores of the first two functions or axes with a one-way ANOVA ($F=35.96$, $df = 4$, $P<0.001$).

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Table 2. Akaike's information criterion scores (AICc), their differences (Δ) and number of model parameters (k) for habitat models developed for seasonal habitat use by the blue sheep in Gya-Miru, Ladakh. The figures in bold are AIC differences (Δ) of less than two.

No.	Model	K	Summer		Winter	
			AICc	Δ	AICc	Δ
1	Distance + Slope + Altitude	4	130.22	0.00	118.18	1.96
2	Distance + Slope + Altitude + Aspect	5	132.66	2.44	122.12	5.90
3	Distance + Slope + Aspect	4	134.11	3.89	143.85	27.62
4	Slope + Altitude	3	134.39	4.17	139.25	23.02
5	Distance + Slope	3	134.48	4.26	157.54	41.31
6	Slope + Altitude + Aspect	4	136.35	6.13	143.04	26.81
7	Distance + Altitude	3	138.92	8.70	116.23	0.00
8	Slope + Aspect	3	139.42	9.20	192.23	76.00
9	Slope	3	140.54	10.32	210.22	93.99
10	Distance + Altitude + Aspect	4	143.47	13.25	120.16	3.93
11	Distance	2	144.27	14.05	155.57	39.34
12	Distance + Aspect	3	146.02	15.80	141.95	25.73
13	Altitude	2	150.08	19.86	137.93	21.70
14	Altitude + Aspect	3	153.07	22.85	141.75	25.52
15	Aspect	2	159.24	29.01	198.55	82.32

Comparing the habitat use of blue sheep and urial with a paired t-test also showed a similar trend ($t = 7.92$, $P = 0.0001$; Table 4), which was further strengthened by the little overlap between the two species along an altitudinal gradient ($O_{jk} = 0.222$). Similarly, blue sheep used habitats significantly closer to cliffs (mean = 114 m), while urial selected habitats away from cliffs (mean = 209 m; $t = 3.24$, $P = 0.001$; Table 4). These differences were significant taking all the variables together ($F_{3,80} = 23.028$, $P < 0.001$).

Table 3. Standardized coefficients of discriminant function coefficients of seasonal habitat use by Ladakh urial and blue sheep in Gya-Miru, Ladakh.

Variable	Summer		Winter	
	Root 1	Root 2	Root 1	Root 2
Distance to cliff (m)	0.053	0.621	-0.575	-0.448
Slope angle (deg)	0.093	-0.637	-0.093	0.785
Altitude (m)	-0.993	-0.153	-0.747	0.573

Table 4. Mean (\pm SD) of the habitat features used by the blue sheep, Ladakh urial and those available.

Var.	Blue sheep				Ladakh urial				Available	
	Summer		Winter		Summer		Winter			
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
DTC	114	109.13	60	65.09	209	156.61	99	128.07	238	184.78
SA	34	7.55	31	10.26	30	9.41	27	13.62	27	8.12
Alt	4530	341.15	4160	465.19	4051	164.94	4113	170.73	4762	351.85

DTC = Distance to cliff, SA = Slope angle, Alt = Altitude

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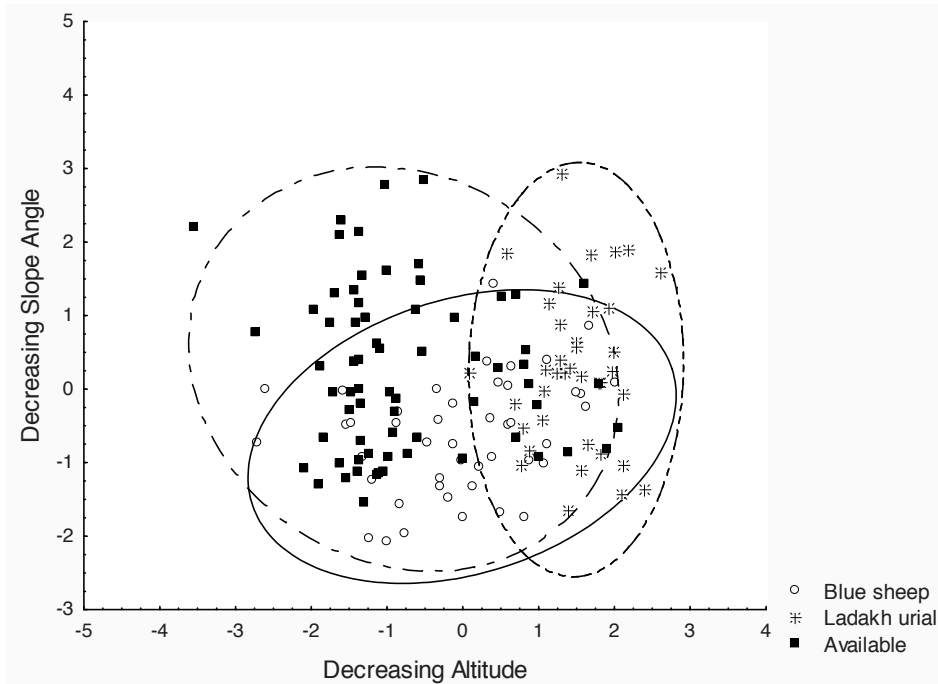


Fig. 1. Output of Linear Discriminant Function Analysis to examine whether the areas used by Ladakh urial, blue sheep and those available during summer could be discriminated on the basis of habitat features in the areas.

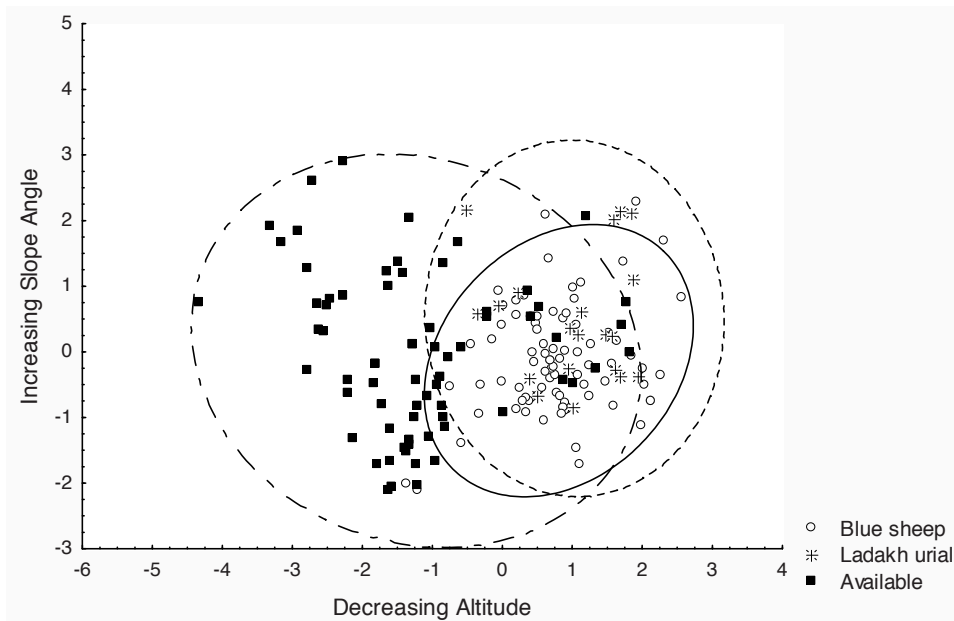


Fig. 2. Output of Linear Discriminant Function Analysis to examine whether the areas used by Ladakh urial, blue sheep and those available during winter could be discriminated on the basis of habitat features in the areas.

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Winter

Altitude and slope angle had highest loadings on function 1 and function 2, respectively, during winter (Table 3), indicating that these variables were important in discriminating between the three locations: blue sheep, urial and available (random). Fig. 2 suggests that both blue sheep and urial used significantly lower areas than those available ($F=32.02$, $df=4$, $P<0.001$). Therefore, they did not differ in habitat use on an altitudinal gradient during winter ($t = 0.452$, $p = 0.652$), as also indicated by the greater habitat overlap along this axis ($O_{jk} = 0.885$). The animals were also similar in the use of slope angle ($t = 1.405$, $p = 0.163$; $O_{jk}=0.965$), although they differed only marginally in the use of distance to cliff ($t = 1.931$, $p = 0.056$; $O_{jk}=0.890$).

Diet profile and overlap

Diets of blue sheep and urial were dominated by non-graminoids (Table 5). Ladakh urial consumed a high proportion of generative parts (flowers, fruits and seeds) of the plants. The diet spectrum of blue sheep encompassed six species of graminoids and 16 species of non-graminoids, while that of urial encompassed 5 species of graminoids and 8 species of non-graminoids. Within non-graminoids, *Thermopsis* sp. (20%) and *Arenaria* sp. (17.6%) were the most dominant species in blue sheep's diet, while *Caragana* sp. (21%) and *Rumex* sp. (11.7%) were the most dominant in urial's diet (Table 5). Although both species consumed a greater proportion of non-graminoids, they fed on different plant species as indicated by the less overlap in diet ($O_{jk} = 0.293$).

Discussion

Blue sheep and urial are distributed independently at the geographical scale, which conforms to the disjoint potential distributions of these species modeled in a GIS environment (Chundawat & Qureshi, 1999). This distributional independence could be related to their differing biogeographical affinities; urial having advanced into Ladakh from the western Hindukush mountains by penetrating the Indus and Shayok valleys (Schaller, 1977), and blue sheep colonizing the region from the eastern Tibetan plateau (Namgail et al., 2004). But when we zoomed in at the landscape level, the two species co-occur, often inhabiting the same catchments. When their distribution interface was analyzed more closely, they were observed to diverge in their resource use at the habitat level. Ladakh urial used lower areas whereas blue sheep occurred in higher reaches during summer. Such habitat partitioning, which is known to prevent both resource and interference competition, might have allowed their co-occurrence at the landscape level.

They however overlapped in habitat use during winter when the blue sheep descended to lower slopes due to snow accumulation in the higher areas. Thus, urial might be at a disadvantage given that blue sheep has a higher density (Fox et al., 1991), perhaps due to their versatility in resource use (Chapter 5 and 7). Thus, since winter is the season with a severe resource crunch in the Trans-Himalaya due to plant senescence and heavy snow cover (Mishra, 2001; Namgail, 2006), there is a high potential for competition between them during this season. At least five groups of urials were observed to leave the study area during this season, perhaps in response to the high density of blue sheep in the lower areas.

The altitudinal separation between the two species during summer could be related to competitive exclusion of urial from the higher areas, which are considered to be more profitable in terms of energy gain as higher habitats have more nutritious plants during this season. This is tenable because large herbivores do take advantage of such altitudinal differences in the availability of energy sources by moving to higher reaches where fresh plants sprout later in the summer (Festa-Bianchet, 1988). The higher reaches

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are also cooler and free from insects, which are known to harass wild ungulates (Hagemoen & Reimers, 2002).

Table 5. Proportion of plant fragments in the diet of Ladakh urial and blue sheep during summer in Gya-Miru, Ladakh.

Plants	Blue sheep	Ladakh urial
Graminoids vegetative		
<i>Calamagrostis</i> sp.	1.6	12.0
<i>Dactylis</i> sp.	2.3	0.0
<i>Elymus</i> sp.	2.3	1.1
<i>Festuca ovina</i> sp.	4.9	9.5
<i>Stipa</i> sp.	2.1	3.1
Unidentified grass	2.3	6.5
Graminoids generative		
Glumes	0.5	1.6
Fruits	0.0	0.9
Non-graminoid vegetative		
<i>Acogonum</i> sp.	0.7	0.0
<i>Allium</i> sp.	0.5	0.0
<i>Arenaria/Cerastium</i> sp.	17.6	0.0
<i>Artemisia</i> sp.	5.8	4.3
<i>Biebersteinia</i> sp.	0.5	0.0
<i>Iris</i> sp.	0.7	0.0
<i>Lavandula</i> sp.	1.2	0.9
<i>Lonicera</i> sp.	1.2	0.0
<i>Malva</i> sp.	0.2	0.0
<i>Nepeta</i> sp.	0.7	0.0
<i>Oxytropis</i> sp.	0.9	0.0
<i>Polygonum</i> sp.	2.8	0.0
<i>Thermopsis</i> sp.	20.0	0.0
<i>Caragana</i> sp.	3.2	21.2
<i>Ephedra</i> sp.	0.0	0.5
Dicot stems	5.3	0.7
Unidentified dicot 1	3.9	2.9
Unidentified dicot 2	1.2	0.0
Non-graminoid generative		
<i>Artemisia</i> flower heads	0.0	4.7
Asteraceae stems/flower head	1.4	2.9
<i>Rumex</i> flower and stem	3.9	11.7
<i>Urtica</i> flower	0.0	0.4
<i>Veronica</i> fruit	0.0	0.4
Unidentified fruit	2.3	3.6
Unidentified flower	0.0	0.5
Seeds	0.9	0.0
corky stem/scale/fruit	1.6	8.4
Others		
Unidentified cuticles	7.4	2.3

Although both animals included a higher proportion of non-graminoids in their diets during summer, they fed on different species within this functional group. Thus, the two species diverged in their dietary preferences during summer, perhaps as a consequence of

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the differential habitat use and differential availability of forage plants on an altitudinal gradient. Ladakh urial incorporated a remarkable proportion of generative parts such as flowers, fruits and seeds of non-graminoids, presumably to avoid competition with blue sheep.

Thus, although the two species might co-occur in some valleys as a result of the summer resource partitioning, competition with blue sheep during winter might be hindering the growth of urial population, thereby making it difficult for the species to expand its range further. It is, however, to be noted that the urial range in Ladakh, being located along two major rivers, are also fertile and is used for cultivation and limited grazing by domestic livestock (Raghavan, 2003). There is also a highway between Leh, the capital city of Ladakh and Srinagar, the capital of Kashmir passing through urial habitat along the Indus valley, which made their habitat more accessible to hunters (Mallon, 1983). Therefore, although anthropogenic pressure might have played a crucial role in decimating its population more recently, urial's range historically might had been constrained by the presence of blue sheep.

Conclusions

Blue sheep and Ladakh urial associated independently at a geographical scale (entire Ladakh), but they co-occurred at the landscape level. An investigation of the resource utilisation pattern by the two species at a smaller (habitat) scale showed that the animals partition resources associated with their habitat segregation along an altitudinal gradient during summer, as the blue sheep occurred at higher areas than urial during this season. Such a separation at the habitat level might have enabled co-occurrence at the landscape level. Nevertheless, the two species overlapped in their habitat use during winter when the blue sheep descended to lower slopes due to high snow cover in the higher reaches, which appeared to displace urials from their preferred sites. Such displacement of urial during winter with a resource crunch suggests a competitive interaction, which might ultimately be constraining the range of Ladakh urial despite the niche separation during summer. Keeping these in view, it is crucial to look for areas with less abundance or absence of common species like blue sheep, if possible, when it comes to prioritising areas for the conservation of endangered Ladakh urial in the Trans-Himalayan mountains.

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CHAPTER 7

Mammalian herbivore species-richness: synthesis

Tsewang Namgail

'There's a mighty big difference between good sound reasons, and reasons that sound good'

Burton Hillis

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Introduction

Despite being one of the oldest patterns observed in the field of ecology, the spatial heterogeneity in species diversity on earth and the processes that generate it have remained unresolved. Ecological literature is replete with accounts of species diversity patterns and processes underlying them, listed in the beginning (Chapter 1), but hitherto there is no consensus on the primary mechanisms. It is stressed in this thesis that the issue is rather complex and its resolution will require a new synthesis drawing upon disciplines like ecology, evolution, biogeography, systematics, phylogeography and paleontology that developed during the last century but drifted apart at the same time. Because the phenomenon of species diversity spans such diverse fields, the comprehensiveness of the research efforts required to tackle the phenomenon must equally be great. This thesis is written in the hope that the contents will generate more light than heat on this general, but important discourse that transcends the field of ecology.

Since the distribution and diversity patterns of mammalian herbivores of the Himalaya and the regions beyond remain poorly understood, I focused on the mammalian herbivore distribution and diversity patterns in the Ladakh region of the Indian Trans-Himalaya, about which very little is known. Ecological information on the processes underlying herbivore assembly patterns in the region have started to come in only recently (Namgail et al., 2004; Namgail, 2006; Namgail et al., 2008). The results of this research project have implications not only for understanding the formation and maintenance of herbivore assemblages in the region but also for developing conservation strategies for the threatened mammalian herbivores.

This section of the thesis takes a synthetic approach, drawing on the results presented in the various chapters as well as on results from my previous investigations on the mammalian herbivores in the highlands of Ladakh. Unlike my previous approaches of focusing on single assemblages, the present investigation strived to understand the mechanisms of mammalian herbivore distribution and species-richness pattern at larger geographical scales. To address various biogeographical issues in the region, I capitalised on both niche theory (MacArthur & Levins, 1967) and macroecological theory (MacArthur & Wilson, 1967; Brown & Maurer, 1987).

Perhaps the best way to start will be with a tribute to the four 19th century scientists: Charles Darwin, Joseph Hooker, Alfred Russel Wallace and Philip Sclater, who revolutionised our understanding of the spatial heterogeneity in biological diversity on the planet. They shared a common interest of understanding the origin, diversification and distribution of the world's biota. Darwin devoted several years of his early career investigating geology and natural history around the world, which later led to formulation of the Theory of Natural Selection. Wallace traveled widely around the world collecting specimens, and proposed a division of the world in six biogeographical realms. Sclater collected information on the distribution of birds, and proposed a division of the world on the basis of avifaunal distribution. Hooker was the first botanist who attempted to understand the plant diversity pattern on earth, and was the first European to collect plants in the Himalayas.

The Himalayan mountains represent a treasure-trove of flora due to the great altitudinal gradient that provides varied habitats to plants. The floral diversity of the Himalayan range is increasingly being studied. One of the issues that are being investigated currently is the plant diversity along altitudinal gradients. But hitherto most of the studies focused on patterns at smaller scales with steep altitudinal gradients, and it is not known as to what pattern emerges, if we investigate this relationship at a regional scale with a gradual altitudinal gradient. This is where Chapter 2 of this thesis contributes, demonstrating that plant diversity has a hump-shaped relationship even at a regional

scale with moderate altitudinal gradient over hundreds of kilometers. Further, although spatial distribution of aboveground plant biomass has been investigated in the Trans-Himalaya as well as other grazing ecosystems, we still need to understand how it varies along an altitudinal gradient. It is generally presumed that it has a negative relationship with altitude, but it might not be the case in mountain desert ecosystems with simple vegetation structure and high topographical heterogeneity. Chapter 2 also addresses this important issue, and shows that aboveground plant biomass in dry alpine areas varies unimodally with altitude, which is in contradiction to the general belief that it declines monotonically with altitude. The chapter discusses this unexpected trend, especially in light of the biome idiosyncrasies and increasing livestock population in Ladakh.

Subsequently, I investigated the herbivore distribution and diversity patterns in Ladakh. Most of the biogeographical studies on herbivores were carried out in single ecosystems or biomes, but the distribution and diversity pattern of herbivores are less known in transition areas between discrete biomes. Recognising the fact that Ladakh is located at the intersection of two biomes, Chapter 3 strives to fill this gap in information. The work presented in the chapter investigated as to how mammalian herbivores with different biogeographic affinities interact, i.e., whether they mingle or form separate groups on the basis of their evolutionary histories. It became apparent that mammalian herbivores in Ladakh form geographical groups, which underscores the fact that it is important to examine the biogeographical backgrounds of species to understand herbivore assembly patterns at local scales, presented in Chapter 4 and 6.

After studying these large scale biogeographic patterns, I shifted my focus on niche-related diversity patterns. Studies addressing herbivore assembly patterns in the past examined the niche relationships only between constituent species in a single assemblage, but it is not known as to how the niche of a species can vary across assemblages with varying number of sympatric species. Chapter 5 strives to understand this issue, and reports the niche dynamics of blue sheep *Pseudois nayaur* in response to herbivore species-richness. This chapter along with Chapter 4 and 6 also underline the importance of interspecific interactions in species distributions. It thus emphasises the need to include interspecific competition in distribution models, which has often been neglected, thereby overestimating species' distributional ranges.

At a local scale, the essence of herbivore species assembly structure is the co-existence of invading herbivores with the native ones. When an invading species is similar to the native herbivores in its ecological requirements, either one native species that is less efficient than the invading species in extracting resources or the invading species will be excluded from the assemblage over a period of time, unless they find a way to partition resources amicably, promoting long-term coexistence. In high altitude environments, interspecific competition might become more intense in winter when the resource level is at its minimal due to plant senescence and snow cover. Thus the presence of one species might constrain the distributional range of another. Empirical support for this is presented in Chapter 4.

Some species are more efficient in utilizing scarce resources and competitively exclude other species. Since the comprehension of negative influence of dominant species on the distribution of subordinate species is crucial for understanding spatial heterogeneity in herbivore species-richness, the issue is further explored in Chapter 6, which addresses the interaction between two similar-sized Caprinae species at different spatial and temporal scales. The study was designed recognising the fact that hitherto most of the studies that investigated species coexistence were carried out at a single spatial scale. This study highlights the fact that species co-existence is contingent upon spatial scale of analysis; they co-occur at larger spatial scales, but segregate at smaller

spatial scales. Furthermore, even at smaller spatial scales, species coexist in some seasons when resources are abundant but not in others when there is resource scarcity.

Geography of species richness

Biogeography has a long history as a branch of science, striving to understand the spatial patterns of biological diversity. Nevertheless, it remained relatively dormant for some time because it was labeled as a descriptive science until Robert H. MacArthur and Edward O. Wilson breathed new life into it with their famous Island Biogeography Theory (MacArthur & Wilson, 1967). Subsequently, some biogeographers also used experimental approaches to address biogeographical issues (Simberloff & Wilson, 1969). In the following decades there was a renaissance of the field due largely to parallel developments in macroecology (Brown, 1985). Currently, biogeography is an emergent and synthetic discipline, relying on ecology, evolutionary biology, population biology, systematics and earth sciences.

The relegation of biogeography in the past was also related to the difficulty associated with testing the effects of historical factors on species distribution and diversity patterns. However, recent development in tools in the field of genetics, paleontology, geology, systematics, spatial ecology (Remote Sensing and GIS) and robust computer softwares have enabled analyses that can account for these factors. It is, however, difficult to do controlled experiments in biogeography because of its manifestation at large spatial and temporal scales. Nonetheless, given the current scenario of climate change that affects systems at large spatial scales, it is crucial to approach systems at macroecological scales (Chapter 2 and 3).

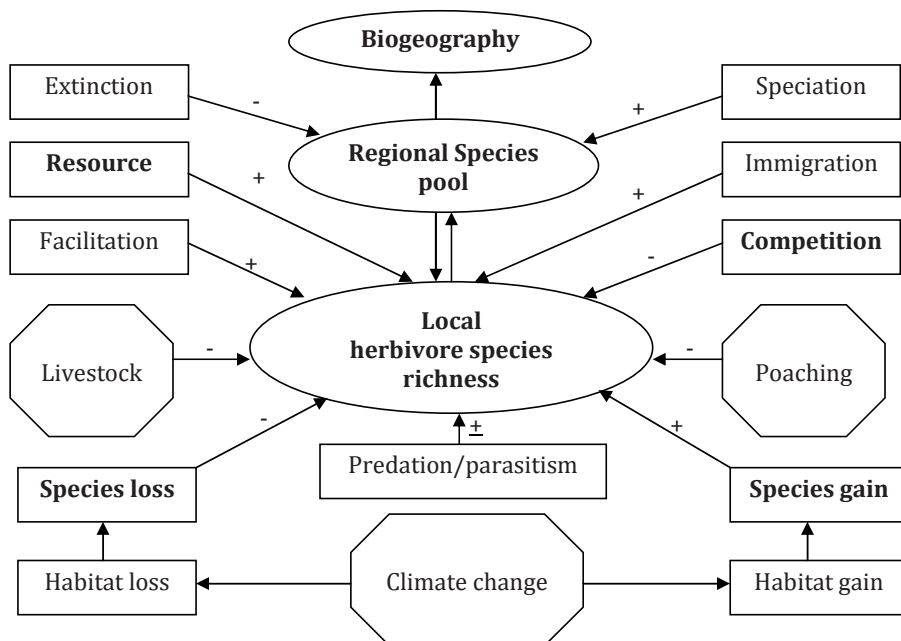


Fig. 1. Schematic representation of herbivore species-richness pattern and the underlying processes in the Indian Trans-Himalaya. The oval-shaped boxes represent patterns, the rectangular boxes are processes (arranged from top-global to bottom-local) and the octagonal boxes are the major plausible causes. The patterns and processes in bold texts are the ones dealt with in this thesis.

Nevertheless, it is important to note that local-scale processes (Chapter 4 and 6) are also important in understanding large-scale distribution and diversity patterns of mammalian herbivores. Fig. 1 provides a schematic representation of how these patterns and processes are interdependent.

In the following sections, I establish the relevance and contribution of the various chapters of this thesis to the literature on herbivore distribution and diversity patterns, especially in alpine environments. First, I discuss the plant diversity pattern along altitudinal gradients at different spatial scales, and then mammalian herbivore distribution and species-richness patterns in the light of their evolutionary history and current ecological factors.

Biogeography of Ladakh

Phytogeography

Understanding distributional patterns of plants at different spatial scales is crucial for understanding the biogeography of herbivores. Earlier, plant diversity was thought to decrease monotonically with altitude (Stevens, 1992), but numerous studies on the subject showed that plant diversity peaks at the mid-altitude instead at lower altitudes. This led to a flurry of research in the mountainous regions all across the planet, and most of the studies showed the same hump-shaped relationship, and any deviation from this has largely been attributed to discrepancies in sample size and efforts. Majority of the studies were also carried out at smaller spatial scales with steep altitudinal gradients. I investigated this relationship both at local and regional scales to see if different patterns emerge. It is to be noted that the altitudinal gradient in the larger scale investigation is very gradual, spanning hundreds of kilometers. The results indicated that plant species-richness peak at mid-altitudes at local as well as at large geographical scales (Chapter 2).

Although, spatial pattern of net primary productivity and its relation with climatic factors was studied in Trans-Himalayan mountains (Yang et al., 2009) and other grassland ecosystems (Sala et al., 1988; Epstein et al., 1997; Jobbagy et al., 2002), the pattern of aboveground biomass along an altitudinal gradient has not been explored before in a spatially explicit way, neither in the Trans-Himalaya nor, to my knowledge, elsewhere. Altitude, as alluded to earlier, is an important gradient along which aboveground biomass is expected to decline due to declining temperature and nutrients, which get washed down (Rastetter et al., 2004). But there has been no apparent effort to document this with empirical evidence, and it is less clear if such a trend can be expected in drier environments of deserts with little complexity in vegetation structure. The present study has shown that aboveground biomass of plants in drier alpine regions varies unimodally with altitude (Chapter 2). When the geography of the species richness of large herbivores in Ladakh was examined, I found more species in central Ladakh, which falls in the middle of the altitudinal gradient used in the study of plant diversity pattern at the regional scale. Thus, it is likely that there is a positive relationship between plant species richness and/or productivity and herbivore species richness. Analysis on this association is underway, which will shed light on the dynamics of phyto- and zoogeography.

Zoogeography: role of ecotone

Ladakh's location at the junction of two biomes makes it an interesting system for studying the distribution and diversity pattern of mammalian herbivores. These two biomes are the vast and open Tibetan plateau in the east, encompassing ≈ 2.5 million km² and the rugged Hindukush-Karakoram mountains (including Ladakh and Zangskar ranges) in the west. These mountains in the latter biome form a jumble of mountains, also encompassing the ends of several other ranges: Kunlun Shan, Pamir, Himalaya and

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Tian Shan. These mountain ranges perhaps played a greater role in shaping the biogeography of central Asia than biogeographers think. Today, many large herbivore species are present on the Mongolian plateau north of the Kunlun Shan but are absent from the Tibetan plateau. Similarly, several species with the cores of their ranges in the Himalaya and the Gangetic plains are absent from the Tibetan plateau (see Fig. 2). Therefore, it seems likely that the Tibetan species developed as a result of vicariance, which needs to be explored. The Kunlun in the north and Himalaya in the south probably isolated the large herbivores of the Tibetan plateau over an evolutionary period. Although the species expanded their ranges westwards, they are perhaps stopped by the aforementioned jumble of mountains. Similarly, there are several large herbivores including Mouflon *Ovis roientalis* that are distributed in the drier environments of the west Asian deserts, but are missing from Ladakh. This could be due to the aforementioned jumble of mountains hampering their eastward progress (see further discussion below).

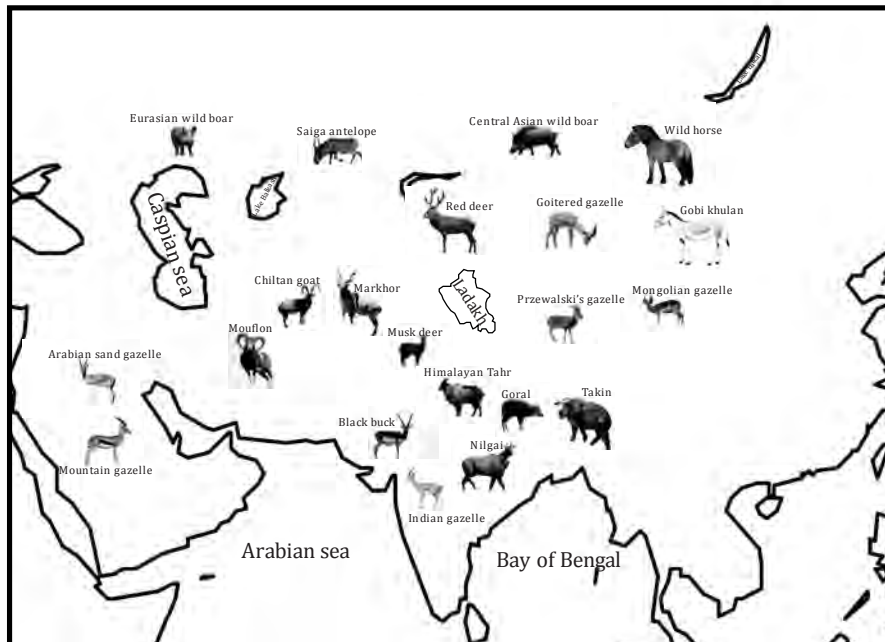


Fig. 2. Some Palaearctic and Oriental large herbivores (positioned in the map in relation to their approx. distributional ranges) that are missing from the herbivore species-pool of Ladakh.

The geographical groupings of mammalian herbivores in Ladakh on the basis of their biogeographic affinities (Chapter 3) are telltale signs of the termination of their range expansions due to high and formidable mountain ranges. Thus, hard boundaries do seem to influence herbivore species distribution and diversity patterns as predicted by Colwell & Lees (2000). The two large groups of herbivores with similar distributions in Ladakh might correspond to the two biomes that meet in Ladakh, as mentioned above, which was presumed earlier, but was never tested. The importance of topographical factors such as slope angle and altitude in explaining the shared distributions of these herbivores further support this speculation. Rivers are also likely to affect large herbivore distributions, but they do not seem to influence their distributions in Ladakh (Chapter 3), perhaps because they freeze during winter allowing the animals to cross over.

Transition zones between biomes, or ecotones, are known to harbour unique and endemic species and alleles, which may support the notion that ecotones serve as centers of speciation (Wiens & Graham, 2005). Evolutionary advanced species occur in transitional ecotones in central Africa (Fjeldså & Rahbek, 1998). Moritz et al. (2000) further proposed that areas such as the central African ecotones hold concentrations of young species and evolutionary novelty, and are important for maintaining the evolutionary processes. The Ladakh urial *Ovis vignei vignei*, which is an endemic and endangered species, is the most advanced wild sheep in the evolutionary history of the genus *Ovis* (Geist, 1987). This evolutionary novelty could be related to Ladakh's location at the interface between two biomes. Currently the species has a narrow distribution only along two major rivers and its range expansion is perhaps hindered by the abundant and similar-sized blue sheep advancing into Ladakh from the Tibetan plateau in the east (Chapter 6). Thus, the Ladakh urial is perhaps trying to find a niche in an assemblage with species co-evolved over a long evolutionary period (see further discussion below).

Because environmental conditions generally closely correspond to a species' ecological requirements at the center of its range (Brown, 1984), the environmental suitability for a species is expected to decline towards the periphery of its range. Most of the mammalian herbivore populations in Ladakh represent species' populations at the edge of their ranges (Namgail, 2009). Therefore, the less population densities of large herbivores in the region (Fox et al., 1991) could be attributed to their locations at the edge of species' ranges. Furthermore, given that the presence-absence of a species in an area essentially reflects the balance between colonization and extinction (Ricklefs, 1987; Huston, 1999), the recolonisation potential of a species is also expected to decline towards the edge of its range (MacArthur, 1972). Thus, the probability of occurrence of a species (i.e., density) at regional scales is expected to decline from the center of its range to the periphery due to a decline in the recolonisation potential. The fragmented populations of mammalian herbivores in Ladakh engendering a spatial heterogeneity in their species-richness could also be due to such edge related effects.

Influence of evolutionary history

There are myriad studies on the role of physical and biological factors in determining herbivore distribution and species richness patterns, but the role of evolution and historical distributions in the formation and maintenance of herbivore assemblages has not been addressed adequately. This is intriguing, given that the taxonomic components of a community organisation can be comprehended only by placing the local community in its historical and biogeographical context (Chapter 3). One cannot understand the geographical variation in species diversity solely by studying dynamical interactions among species within assemblages, as in Chapter 4. Geological, evolutionary and historical factors play important roles in determining niche occupancy, assembly structures and perhaps other attributes of herbivore communities, as alluded to earlier.

The specialization of a species as a result of long-term evolution of its morphology in a particular topographic setup limits its dispersal capability. Recent examination of skeletal morphology of the Caprinae species in Ladakh has revealed that they are different in terms of their appendicular structures associated with adaptations to different topographical features (Van den Tempel & De Vrij, 2006). Thus, distributions of the mammalian herbivores of Ladakh are perhaps determined by niche conservatism, and species ranges are restricted to areas with environmental features to which they are best adapted through long-term evolution. The formation of two large geographical groups of mammalian herbivores in Ladakh (Chapter 3) could be related to this fact.

The small mammalian herbivores such as pikas *Ochotona* spp. and voles *Alticola* spp. in the central Asian rangelands form taxa that remain little-known. It is, however,

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important to know their distributions and diversity pattern, because they enhance plant species richness in the Trans-Himalayan rangelands (Bagchi et al., 2006), and have been identified as indicator species of pasture degradation in the rangelands of central Asia (Holzner & Kriechbaum, 2001). Chapter 3 demonstrates that there is congruence in the distributions of large herbivores and these smaller mammalian herbivores. Despite the caveats mentioned in the Chapter, the biogeographical analysis of these little known taxa in the context of overall herbivore assemblage in Ladakh has important implications for understanding their distribution pattern, which has not been addressed before.

Role of interspecific competition

The role of competition in structuring animal assemblages has been disputed for over three decades. It is, therefore, one of the most contested topics in ecology; controversy raged over its supremacy in structuring ecological communities, and acrimonious discussions ensued amongst ecologists (Diamond, 1975; Connor & Simberloff, 1979; Gotelli & McCabe, 2002). The competition driven 'assembly rules' suggested by Diamond were downplayed by Connor and Simberloff, who suggested using null models to test for non-random co-occurrence of species. Following this debate, myriad studies were carried out to assess the role of competition in structuring species assemblages, but most of them investigated niche dynamics in single assemblages, and it is not known as to how an individual species' niche can vary across assemblages responding to the number of competing species in those assemblages.

Today, there is consensus amongst ecologists that when two species rely on the same resources that are in short supply, the subordinate species usually get competitively excluded (Chapter 4 and 6). A species cannot inhabit all the available habitats, and thus occupies only a subset of the available habitat, often referred to as the 'realized niche' (Hutchinson, 1959). Therefore, assuming that all animals have similar growth rates, dispersal abilities and there are no geographical barriers, the structure of herbivore assemblages is largely determined by species coexistence. However, whether two species co-exist or not also depends on the spatial scale, as species do co-occur at large geographical scales, but often separate along one or more niche axes at the local scale (Chapter 6).

The blue sheep is the most abundant and widespread wild ungulate in Ladakh (Namgail, 2009), perhaps as a result of the flexibility in terms of resource use compared to rare and endangered species (Chapter 6). When the diet width of this species and that of Ladakh urial were studied in two locations with different number of herbivore sympatric species, it had a narrower diet width in the area with high number of species, whereas urial's diet width did not differ between the two areas (see Fig. 3), suggesting that blue sheep is flexible in its resource use. Further, blue sheep specialized by consuming both vegetative and generative parts of plant species in areas with higher number of sympatric species (Fig. 5). Therefore, owing to its versatility in resource utilisation, blue sheep is likely to outcompete other similar-sized species with different evolutionary histories. Therefore, I studied its interaction with other Caprinae species: Asiatic ibex (Chapter 4) and Ladakh urial (Chapter 6) which are similar to blue sheep in their body sizes but have different biogeographic affinities (Chapter 3). Blue sheep has high potential for competition with both these species especially in winter, when the resources are at their minimal levels due to plant senescence and snow cover. The study on blue sheep and Ladakh urial was carried out at multiple spatial scales (Chapter 6), and the role of spatial scale in species co-existence became apparent as the two species associated randomly at the geographical scale but they co-occurred at the landscape level as a result of resource partitioning at the local-level habitat.

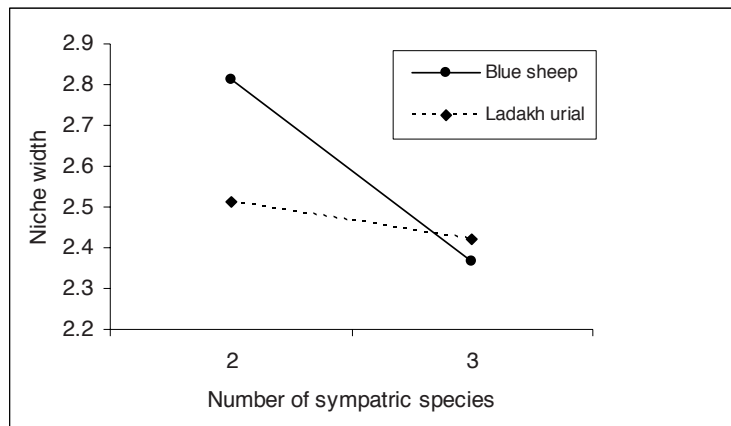


Fig. 3. The diet-niche width of blue sheep and Ladakh urial in relation to the number of sympatric large herbivore species in the Trans-Himalayan mountains (Note the sharp decline in blue sheep's niche width).

Urial has a very limited distribution in Ladakh, and is endemic to the region. It is probably an evolutionary novel species, 'trying' to fit in a large herbivore assemblage that evolved over eons as speculated earlier. I investigated this by studying the species packing in the large herbivore assemblage in Ladakh, including hare and marmots. I related the natural log-transformed body weight with species rank on the basis of weight ratio, first without urial and then with urial in the assemblage. I found a slightly stronger relationship in the imaginary assemblage without urial than that in the assemblage with urial (Fig. 4), suggesting that the species perhaps did not evolve with the rest of the large herbivore species in Ladakh.

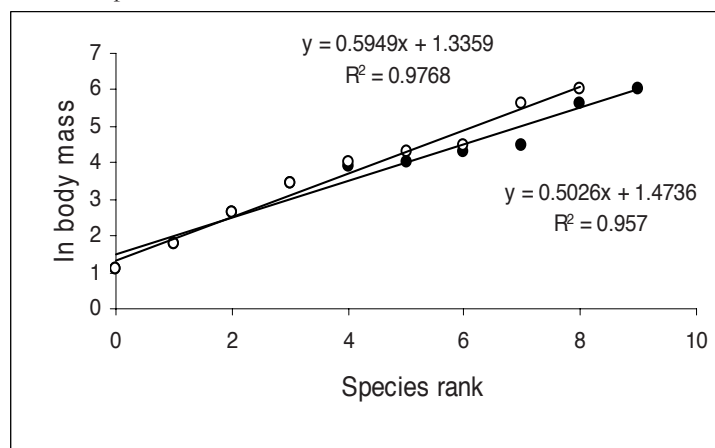


Fig. 4. Relationship between species rank (increasing weight by a constant proportion) and log-transformed body masses of large herbivores in Ladakh. The open circles represent the assemblage without Ladakh urial, and the filled circles represent the assemblage with Ladakh urial.

The potential for competition in the Trans-Himalayan large herbivores is further indicated by the expansion of blue sheep's niche width with decrease and contraction

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with increase in the number of sympatric species in an assemblage (Chapter 5). This relationship, however, differed between the habitat-niche width and diet-niche width. The habitat width declined monotonically with the number of sympatric species, whereas the diet width had a hump-shaped relationship with the number of sympatric species. The former pattern is understandable that as the number of sympatric species increases in an assemblage there would be less habitat-space available for a particular species, but the hump-shaped relationship between diet-niche width and herbivore species richness is intriguing. I suggest that the narrow diet width in allopatry is out of choice as the animal can eat the most nutritious plants available to itself, and the narrow diet width in species-rich areas is out of necessity as it needs to narrow down its diet spectrum, feeding on fewer plant species that are spared by the competitors (see Chapter 5). Thus, the animal seems to specialize on some plant species in species-rich assemblages, perhaps feeding on both vegetative and generative parts such as flowers and seeds (see Fig. 5).

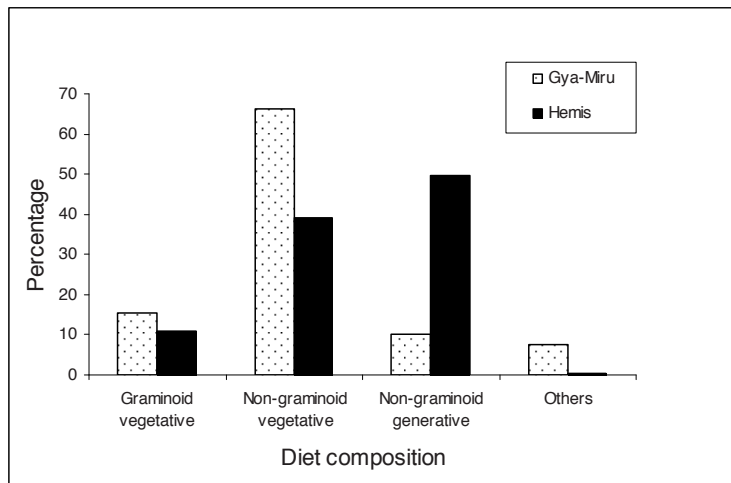


Fig. 5. Diet profile of blue sheep in Gya-Miru with one sympatric species and Hemis with two sympatric species (Note that in Hemis it is consuming a higher proportion of generative parts such as flowers and seeds, perhaps to avoid competition with other species).

Chapters 4, 5 and 6, thus, indicate that competition might play a role in structuring herbivore assemblages at local scales (alpha diversity) in Ladakh. These results also have wider implications for understanding large herbivore assemblages in other alpine ecosystems, and warrants inclusion of interspecific interactions in species distribution models, which until now were constructed largely on the basis of the availability of the physical environment. Consequently, many species distribution models tend to overestimate the range of a species, as the animals actually do not occur in some parts of the predicted range because potentially competing species exclude them from those potential areas. Furthermore, it became apparent that topography is more important in resource partitioning by large herbivores in the high altitude drier environments of Ladakh with less complexity in vegetation structure (Namgail et al., 2004; Chapter 3 to 6). The discourse in Chapter 5 takes us back to the concept of fundamental and realized niches propounded by Evelyn Hutchinson five decades ago (Hutchinson, 1959): species cannot occupy their full potential ranges (fundamental niche) because they are not able to survive in areas with strong competitors, and thus they need to confine themselves to

smaller habitats (realized niche). Most of the species distribution models till now predicted the distribution in terms of fundamental niche, but what is needed is the distribution in terms of the realized niche to delineate more accurate ranges of species.

Although blue sheep might interact negatively with similar-sized species from other biomes (Chapter 4 and 6), it does not compete with similarly-sized species from the same biome, perhaps by virtue of their shared evolutionary history. For instance, a resource partitioning study between the Tibetan argali *Ovis ammon hodgsoni* and blue sheep in the past showed that these species are different in terms of their use of terrain feature with the former using more open areas and the later using rugged terrain (Namgail et al., 2004), which resulted in differential use of plant communities. This is perhaps determined by their skeletal morphology evolved over a long evolutionary period (Van den Tempel & De Vrij, 2006). Thus, the Tibetan argali's range is perhaps constrained due to niche conservatism. However, they might have competed in the past and evolved different morphological features, but this cannot be proven as we cannot in retrospect see if species competed in the past or not.

Did competition shape the regional species pool?

The current regional herbivore species-pool in Ladakh is perhaps a culmination of competition amongst wild herbivores over eons. Otherwise, why are there only 12 large herbivores (> 2 kg) in Ladakh? Given that the region is located at the junction between the Oriental and Palaearctic biogeographic realms, one would expect the region to have at least one large herbivore from the Oriental, but there is none. All are Palaearctic except one: Cape hare from the Ethiopian realm. Further, why not more from the Palaearctic, which has scores of large herbivores in areas with almost similar environmental conditions as those of Ladakh. For instance, the Przewalski's horse *Equus caballus przewalskii* and Mongolian gazelle *Procapra gutturosa* that occur in south-western Mongolia (c. 2000 km from Ladakh) are absent from Ladakh (see Fig. 2). It is possible that the Przewalski's horse was competitively excluded by the almost same-sized kiang *Equus kiang*, and the Mongolian gazelle was outcompeted by the similar-sized Tibetan antelope *Pantholops hodgsoni*.

Similarly, species such as the Indian gazelle or Chinkara *Gazella bennettii* that occur in the Gangetic plains south of the Himalaya do not occur in Ladakh (Fig. 2). Many species like the musk deer *Moschus chrysogaster* and Himalayan tahr *Hemitragus jemlahicus* that are distributed in the Himalaya are also missing from the regional species pool of Ladakh (Fig. 2). Probably, the Tibetan gazelle *Procapra picticaudata* and Asiatic ibex *Capra ibex siberica*, respectively, out-competed these species from Ladakh. A small population of musk deer was present in western Ladakh until very recently (Pfister, 2004). It is possible that the 'adventurers' could not establish viable populations due to lack of metapopulation dynamics as movement of the animals were restricted by the high mountain passes. Another possibility is that the animals occurring at lower latitudes and altitudes in the Indian Peninsula are physiologically constrained, as they cannot store fat to survive in the extremely low temperatures of the Trans-Himalaya. One might also ask why megaherbivores like the elephants *Elephas maximus indicus* and rhinoceros *Rhinoceros unicornis* are not present in Ladakh. The apparent answer to that would be inadequate resources for these animals to survive.

Another interesting fact about the regional species pool of Ladakh is that there are two antelopes from the east: Tibetan gazelle and Tibetan antelope, but not a single one from the west. Several antelopes occur in the Arabian Peninsula including the Mountain gazelle *Gazella gazella cora*, Arabian sand gazelle *Gazella subgutturosa marica* and Goitered gazelle *Gazella subgutturosa*, but are missing from the herbivore species pool of Ladakh. This might reflect the possibility that high mountains in Hindukush and Pamir

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ranges hindered their eastward progress, further suggesting the role of high mountains as geographical barriers. These need to be explored to understand the herbivore diversity patterns as well as evolution and dispersal routes of mountain ungulates in central Asia.

This thesis and biogeographic machinery

Harking back to the objects of this research, i.e., understanding (1) species richness pattern, and (2) the plausible causes operating at local and regional scales, I now examine with the help of a conceptual model whether these have been achieved and where do the chapters contribute towards understanding the overall machinery of biogeography (see Fig. 6). Chapter 2 explores the plant species-richness and aboveground biomass pattern at local as well as geographical scale (objects 1 and 2). Chapter 3 contributes towards understanding the herbivore species-richness pattern (object 1). Chapter 4 helps in understanding the cause of species richness at a local scale (object 2). Chapter 5 augments our understanding of the plausible causes of herbivore species-richness at a regional scale (object 2). Chapter 6 explores co-existence of herbivores at both local and regional scales (objects 1 and 2).

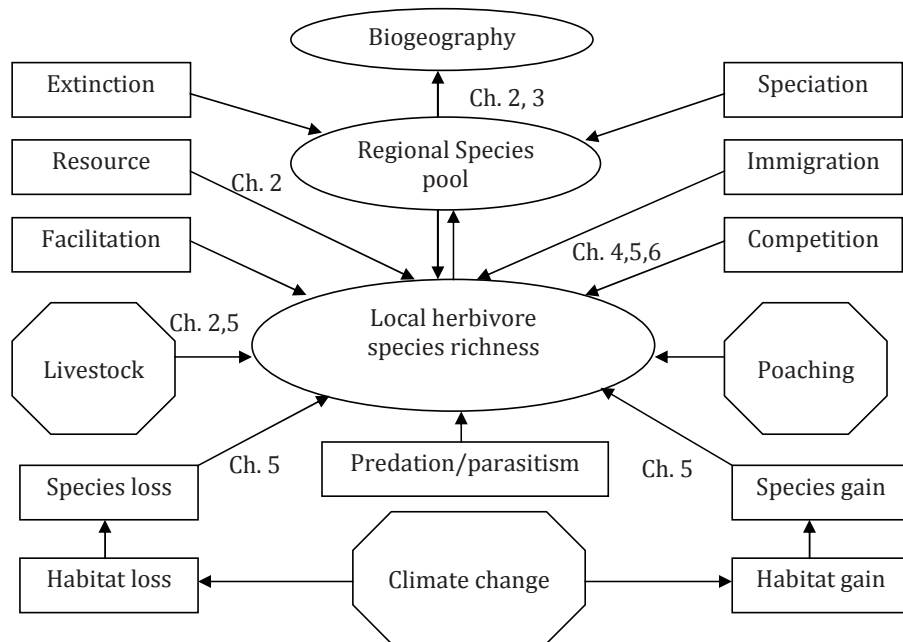


Fig. 6. Map showing the contributions of various chapters to the broad scheme of biogeography (see Fig. 1 for the meaning of the shapes of different compartments).

Management implications

The loss of herbivores from the face of the planet has become a major concern and efforts to stem such loss are stymied by lack of information on proximate and ultimate factors influencing the spatial pattern of herbivore diversity at different spatial and temporal scales. Large herbivores are especially threatened due to a plethora of human endeavours, and given that large herbivores play a unique role in ecosystem functioning, are economically and aesthetically important (Gordon et al., 2004), there is an urgent need to understand the mechanisms governing their species-richness pattern, so that

their loss from grazing ecosystems can be stemmed. This thesis contributes towards developing conservation strategies for the large herbivores in the Trans-Himalayan region of Ladakh, which are highly threatened, and some are on the verge of local extinction (Namgail, 2009).

Amongst the eight wild ungulates of Ladakh, two are listed as 'Endangered', two as 'Near Threatened' and one as 'Vulnerable' on the Red List of Threatened Species by the International Union for Conservation of Nature (IUCN, 2008). Several smaller mammalian herbivores are also threatened due to human endeavours associated with livestock grazing (Bagchi et al., 2006), yet information on their distributions and diversity patterns is very scanty (Chapter 3). The population of several wild ungulates, especially those of the Tibetan gazelle and Tibetan argali declined precipitously in the last century due to habitat degradation associated with livestock grazing and many other natural and manmade factors (Bhatnagar et al., 2006; Namgail et al., 2007b; Namgail et al., 2008). Currently, these and several other species have highly fragmented populations in Ladakh as well as globally (Schaller, 1977; Schaller, 1998; Namgail, 2009). The results of this project contribute towards understanding the distributional pattern and plausible causes of the fragmented nature of their distribution, which will help in prioritising areas for their conservation.

Chapter 2 underscores the importance of mid-altitude areas for the conservation of floral wealth of Ladakh, and perhaps herbivore species. Hence, mid-altitude areas are needed to be considered first while prioritising areas for protection of flora in Ladakh. Chapter 3 emphasises the importance of the topography more than the climatic factors in determining the distribution and diversity patterns of mammalian herbivores in Ladakh. Further, it shows that when research and monitoring are constrained by time and money, the large and prominent herbivores such as ungulates can be used as proxy species to prioritise areas for the conservation of smaller herbivores such as pikas and voles (difficult to locate in the field), because there is a congruence in the distribution of these herbivorous taxa.

Chapters 4 through 6 emphasise the importance of interspecific competition in the present distributional patterns of mammalian herbivores in Ladakh. They showed that abundant and wide-spread species like the blue sheep are flexible in their resource use, and can competitively exclude other species such as the Asiatic ibex and Ladakh urial that are perhaps more specialized in their habitat and diet use. Such competitions are more likely between species that are similar in body-size but are different in their biogeographic affinities. For instance, both blue sheep and Tibetan argali that have the core of their ranges on the Tibetan plateau, suggesting similar evolutionary histories, do not compete, and partition resources on the basis of the physical habitat (Namgail et al., 2004). Thus, above facts need to be considered while developing conservation strategies for endangered species like the Ladakh urial.

The niche shift of wild herbivores (Chapter 5) in response to the number of sympatric species is of concern to wildlife conservationists largely in the light of increasing livestock population in the region (Namgail et al., 2007a). Domestic livestock deplete rangeland resources (Namgail et al., 2008) and competitively exclude wild herbivores from some rangelands (Mishra et al., 2002; Mishra et al., 2004). Livestock grazing also relegates the wild herbivores to sub-optimal habitats, thereby affecting the vital activities important for their growth and reproduction (Namgail et al., 2007b). Almost all the protected areas in the Trans-Himalaya are grazed pervasively by domestic livestock, which thwarts conservation efforts. Given these and the results of chapter 5, livestock grazing should be curtailed or stopped in ecologically sensitive areas with endangered wild species.

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Future Directions

Despite the various caveats, the various chapters in this thesis contribute towards understanding distribution and community dynamics of large herbivores in Ladakh, and more importantly serve as baseline information for further studies on the herbivore assembly rules and biogeography of the Trans-Himalaya and perhaps other alpine regions. The thesis also serves as a precursor to studies exploring the origin of Himalayan ungulates, their evolution and routes of dispersal, which hitherto remain unclear. The Himalayan region is thought to be the cradle of evolution of the sub-family Caprinae (Schaller, 1977). Unfortunately the Caprinae arose and diversified during a turbulent period when climates changed and the earth heaved and folded. Being essentially adapted to hills and cliffs, the distributional patterns of the animals were thus altered, and since bones are seldom preserved in mountains the Caprini have revealed little of their fossil past (Schaller, 1977).

Not much has been done on the geographical distribution of Caprinae and the associated taxa, because of the remoteness and inaccessibility of the mountainous areas where they inhabit. Understanding the geography of the diversity pattern of the Trans-Himalayan mammalian herbivores including the caprids, their evolution and dispersal routes is also constrained by lack of information on their phylogeny. Therefore, this particular field needs to be researched further by taking advantage of the recent developments in the fields of genetics and molecular biology.

To understand the community dynamics of mammalian herbivores, it is crucial to know whether herbivore species richness also affects the secondary productivity, i.e., whether it affects the population dynamics of the constituent species of an assemblage. We know that plant species richness enhances aboveground biomass (Spehn et al., 2000) and consumer species richness (Wright & Samways, 1998), but it is not known if consumer species-richness leads to a greater consumer biomass. There are two possible mechanisms that can lead to this process: (a) higher herbivore species-richness leads to greater efficiency in utilizing the primary productivity, and (b) facilitation of one herbivore species by another or complete exploitation of the primary productivity leads to higher consumer biomass irrespective of the energy transfer efficiency (Prins & Fritz, 2008). The apparent assumption is that all the members of the assemblage are similar in body size.

Although there are several other fields that need attention, it is not possible to list them all here. Therefore, finally, the metapopulation dynamics of large herbivores in the Trans-Himalaya needs to be explored, which remains elusive not only in this assemblage but also in assemblages in other ecosystems (see Elmhagen & Angerbjörn, 2001). This lack of information is largely related to the long generations of large herbivores, and the difficulty associated with dealing with large spatial scales. But with the development of macroecology, landscape genetics and spatial statistics, it is becoming more feasible to study population dynamics of large herbivores at regional and continental scales. Metapopulation studies are especially relevant in the herbivore assemblage of the Trans-Himalaya, where species have highly fragmented distributions. Such studies will help not only in understanding their phylogeny and dispersal routes, but also in establishing protected areas and corridors linking them.

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Summary

The spatial heterogeneity in biological diversity on earth is one of the most fascinating natural phenomena. Deciphering the underlying mechanisms of this phenomenon is a major challenge as it is a complex issue that requires insights from various biological and non-biological fields like geology and geography. One of the most discernible biodiversity patterns is the declining biological diversity as one move from the tropics to the temperate and arctic regions. Even at a continental scale some biogeographic zones are richer in biodiversity than others. Thus the pattern repeats itself at different scales in a hierarchical fashion. Relying on the niche theory as well as on macroecological theory, I investigated the spatial heterogeneity in mammalian herbivore species-richness in a little known herbivore assemblage of the Ladakh Trans-Himalaya. This Trans-Himalayan region in north Indian state of Jammu and Kashmir is located at the junction of two biogeographic realms: Palaearctic and Oriental. At a smaller spatial scale, it forms an ecotone between the Tibetan plateau in the east and the Hindukush-Karakoram mountains (including the Ladakh and Zaskar ranges) in the west.

The study took a multi-scale approach by first understanding the broad phytogeographical and zoogeographical patterns and subsequently studying the mechanisms operating at smaller spatial scales. At the outset, I investigated the diversity and aboveground biomass patterns of vascular plants in relation to altitude. The diversity and biomass were spatially structured at both local and regional scales. At the local scale both graminoid and non-graminoid species-richness had a hump-shaped relationship with altitude. The phytodiversity also varied unimodally along an altitudinal gradient at a regional scale. Further, the aboveground biomass also had a non-linear relationship with altitude, which is contradictory to the popular belief that biomass decreases monotonically with altitude. Since the sampling was done mostly in high pastures with livestock grazing, such a non-linear trend could be related to depletion of plants by livestock at the lower altitudes, which were grazed more intensively. But the pattern could also be related to low precipitation at lower altitudes due to higher temperature.

Secondly, I asked if the mammalian herbivores in Ladakh form chorotypes or groups that share distributions. I found that they formed two large geographical groups that perhaps correspond to the two biomes: Tibetan plateau and Hindukush-Karakoram mountains. One of them occurred in the vast eastern plains of Changthang, while the other occurred in the rugged mountains of north and south-western Ladakh. Such groupings could be related to niche conservatism, as the species in each group had similar biogeographic affinities. Topographical features were more important than the climatic ones in explaining the geographical groupings of mammalian herbivores. Rivers did not influence the geography of herbivore species-richness. I suggest that the relatively high diversity of mammalian herbivores in Ladakh is because of its location at the intersection of two biogeographical realms and two biomes.

Subsequently, I shifted my focus on patterns and processes operating at local scales, which might influence spatial heterogeneity in large herbivore species-richness at meso- and mega scales. More specifically I studied the nature of interaction between large herbivores that have comparable body sizes and perhaps similar ecological requirements. It became apparent that the formation and maintenance of large herbivore assemblages could also be influenced by competitive interaction between species that are similar in body sizes but different biogeographic affinities. For instance, the distribution of the Asiatic ibex *Capra ibex siberica* seemed to be constrained by similarly-sized species like the blue sheep *Pseudois nayaur*. It is suggested that interspecific competition can influence the assembly patterns of mammalian herbivores in the dry alpine grazing ecosystems.

Recognising the fact that studies on niche relationship amongst large herbivores were carried out only in single assemblages, I also examined the niche dynamics of blue

sheep in response to the number of sympatric species in an assemblage. The results showed that a species' habitat-niche width and diet-niche width differ in their relationships with herbivore species-richness, as the former declines monotonically whereas the latter has a hump-shaped relationship with the number of sympatric species in assemblages. The former association is understandable, but it is more difficult to explain the latter. It is suggested that narrow diet width in allopatry is due to a species' feeding on the most nutritious plants available to itself, whereas the narrow diet width in areas with high number of sympatric species is due to a species' specialisation on fewer plant species that are more profitable as the sympatric species do not prefer them.

The influence of interspecific competition on assembly patterns of large herbivores is further indicated by the adverse niche relationship between Ladakh urial *Ovis vignei vignei* and blue sheep. First, the results suggested that the coexistence of the two species depends on the spatial scale of analysis. For instance, their distributions were not related at large geographical scales as they associated randomly, but they co-occurred at the landscape level. When their distributions and interactions were further evaluated at the local habitat level, I found that they separate along an altitudinal gradient. Blue sheep used the higher pastures but it descended to lower slopes during winter when the higher pastures got covered with thick snow, thereby increasing the potential for competition with the Ladakh urial that used the lower slopes. Thus, although they might co-occur at the landscape level as a result of the niche separation during summer, there is a high potential for competition during winter, the pinch period, which perhaps negatively influence the reproductive performance of Ladakh urial, thereby hampering its range expansion.

Samenvatting

De ruimtelijke heterogeniteit van de biologische diversiteit op aarde is een van de meest fascinerende natuurlijke fenomenen. Het ontcijferen van de onderliggende mechanismen van dit fenomeen vormt een grote uitdaging, omdat het een complex onderwerp is wat inzichten vergt van verschillende biologische en niet-biologische disciplines zoals geologie en geografie. Een van de makkelijkst waarneembare patronen is de afname van biologische diversiteit van de tropen naar de gematigde en Arctische zones. Zelfs op een continentale schaal zijn sommige biogeografische zones rijker dan andere. Zo herhaalt het patroon zich op hiërarchische wijze op verschillende schalen. Vanuit de niche theorie en macro-ecologische theorie heb ik de ruimtelijke heterogeniteit van de soortenrijkdom van plantenetende zoogdieren onderzocht in een weinig bekende assemblage van herbivoren in Ladakh Trans-Himalaya. Deze Trans-Himalaya regio in de Noord-Indische staten Jammu en Kashmir bevindt zich op het grensvlak van twee biogeografische rijken: het Palearctische en het Oriëntaalse. Op een kleinere schaal vormt het een ecologische gradiënt tussen de Tibetaanse hoogvlakte in het oosten en het Hindukush-Kardakoram gebergte (inclusief de Ladakh en Zangskar bergketens) in het westen.

Deze studie volgt een benadering op meerdere schaalniveaus door eerst de algemene phytogeografische en zoogeografische patronen te proberen te begrijpen en daarna de mechanismen die op kleinere schaal opereren te bestuderen. In eerste instantie heb ik de patronen in diversiteit en bovengrondse biomassa van vaatplanten onderzocht in relatie tot hoogte. De diversiteit en biomassa waren ruimtelijk gestructureerd op zowel een lokale als een regionale schaal. Lokaal vertoonden zowel de soortenrijkdom van grasachtigen als die van niet-grasachtigen een optimum curve in relatie tot de hoogte. De phytodiversiteit varieerde ook unimodaal langs een hoogtegradiënt op regionale schaal. De bovengrondse biomassa had een niet-lineaire relatie tot hoogte, in tegenstelling tot de algemene aanname dat biomassa evenredig afneemt met hoogte. Omdat de bemonstering voornamelijk plaatsvond op hooggelegen weidegronden die door vee worden begraaasd, kan deze non-lineaire trend gerelateerd zijn aan de uitputting van planten op relatief lage hoogten, waar intensiever begraaasd wordt. Het patroon kan echter ook gerelateerd zijn aan de lagere hoeveelheid neerslag op lage hoogten, vanwege hogere temperaturen.

Daarnaast heb ik de vraag gesteld of de plantenetende zoogdieren van Ladakh chorotypen of groepen vormen die hun verspreidingsgebied delen. Ik heb gevonden dat zij twee grote geografische groepen vormen, die misschien overeenkomen met de twee biomen: de Tibetaanse hoogvlakte en het Hindukush-Kardakoram gebergte. Een van hen bestrijkt de oostelijke steppen van Changthang, terwijl de andere de ruige bergen van noord en zuidwest Ladakh beslaat. Een dergelijke groepering zou gerelateerd kunnen worden aan niche conservatisme, omdat de soorten van beide groepen een soortgelijke biogeografische affiniteit hebben. Topografische eigenschappen hadden een grotere verklarende waarde dan klimatologische eigenschappen voor de geografische groepering van de plantenetende zoogdieren. Rivieren hadden geen invloed op de geografie van de soortenrijkdom van herbivoren. Ik stel voor dat de relatief hoge soortenrijkdom van plantenetende zoogdieren in Ladakh is te danken aan zijn locatie op het grensvlak van twee biogeografische rijken en twee biomen.

Vervolgens heb ik mijn focus verlegd naar patronen en processen op lokale schaal, welke de ruimtelijke heterogeniteit in de soortenrijkdom van grote herbivoren op meso- en megaschaal kan beïnvloeden. Ik heb specifiek de aard van de interactie tussen grote herbivoren met vergelijkbare lichaamsgrootte en mogelijk vergelijkbare ecologische behoeften bestudeerd. Het werd duidelijk dat de vorming en handhaving van soortenassemblages ook beïnvloed kon worden door competitieve interacties tussen soorten met vergelijkbare lichaamsgrootte maar verschillende biogeografische affiniteiten. De verspreiding van de Aziatische Ibex *Capra ibex siberica*, lijkt bijvoorbeeld te worden

beperkt door de even grote Blauwschaap *Pseudois nayaur*. Dit suggereert dat interspecifieke competitie de assemblagepatronen van plantenetende zoogdieren in droge alpine ecosystemen kan beïnvloeden.

Rekening houdend met het feit dat de studies naar niche relaties tussen grote herbivoren slechts in enkele assemblages zijn uitgevoerd, heb ik de nichedynamiek van Bharal onderzocht in relatie tot het aantal sympatrische soorten in een assemblage. De resultaten laten zien dat de habitat-nichebreedte en de dieet-nichebreedte verschillen in hun relatie met de soortenrijkdom van herbivoren, omdat de eerste evenredig afneemt met het aantal sympatrische soorten in een assemblage, terwijl de laatste een unimodale optimumcurve laat zien. De eerste relatie is makkelijk te begrijpen, maar het is moeilijker om de laatste te verklaren. Het suggereert dat een smalle dieet-nichebreedte in allopatrie veroorzaakt wordt doordat een soort zich voedt met de meest voedselrijke plant die beschikbaar is, terwijl een smalle dieet-nichebreedte in gebieden met een groot aantal sympatrische soorten veroorzaakt wordt doordat een soort zich specialiseert in een kleiner aantal plantensoorten die beschikbaar zijn omdat sympatrische soorten ze minder graag eten.

De invloed van interspecifieke competitie op assemblage patronen wordt verder geïllustreerd door de tegenovergestelde niche-verhouding tussen Ladakh Oerial *Ovis vignei vignei*, en de Bharal. Aanvankelijk leken de resultaten af te hangen van de ruimtelijke schaal van de analyse. Hun verspreiding was bijvoorbeeld niet geassocieerd op grote geografische schaal, waar deze een willekeurig patroon lieten zien, maar op landschapsniveau kwamen ze op dezelfde plekken voor. Na verdere evaluatie van hun verspreiding en interactie op lokaal habitatniveau, heb ik gevonden dat zij zich onderscheidden langs een hoogtegradiënt. De Bharal gebruikten de hogere weiden, maar daalde af in de winter naar lagergelegen hellingen wanneer de hoge weiden bedekt zijn met een dikke laag sneeuw, waarbij het potentieel voor competitie met de Ladakh Oerial die met name de lagergelegen hellingen gebruiken, toeneemt. Hieruit volgt dat, hoewel ze samen voorkomen op landschapsniveau als gevolg van niche specialisatie gedurende de zomer, er een groot potentieel is voor competitie gedurende de winter, de kritieke periode, wat mogelijk een negatief effect heeft op de voortplantingsprestaties van de Ladakh Oerial en een beperking is voor de uitbreiding van het areaal van de Ladakh Oerial.

Afterword

The core of this thesis touches upon an old issue in ecology on which controversy raged for a long time, namely whether ecological communities are well-defined functional units of species that are interdependent or are loose assemblages of independent species interacting randomly. This thesis supports the latter school of thought. Species come across novel environmental conditions and either evolve morphologically, physiologically and/or behaviourally, engendering new species over a period of evolutionary time, or go extinct. At a shorter temporal scale, individuals of a species emigrate from one area/population and join new assemblages, and either coexist or compete with the native species and consequently exclude one of the native species or get excluded over a period of time.

Such capabilities of species and the spatial heterogeneity in the environment leave no room for doubt that ecological communities are open and dynamic assemblages. There have also been propositions that communities act like super organisms, evolving as a whole, i.e., consistently maintaining the number of species in a particular functional group (e.g., grazers) across ecosystems, and adding or eliminating species depending on the environmental scenario. Even if such processes occur in nature, it would be difficult to detect in the contemporary world because there is no place left on earth where humans have not meddled with the system. Nevertheless, there would still be remnant processes that would be worth a look.

One of the implicit objects of this research project was to understand why some species have restricted distributions in Ladakh? Although this is a parochial question, it has universal relevance, and applies to the entire planet earth. For instance, why Kangaroos are found only in Australia? Why Lemurs are confined to Madagascar? Why snow leopards roam only in central Asian mountains and not in the European Alps? Why Guanacos did not move out of South America? Why Giraffes are found only in Africa? These questions lie at the heart of biogeography. In a letter to John Dalton Hooker in 1845, Charles Darwin referred to the study of geographic distribution as "...that almost keystone subject of the laws of creation". This opinion implies that these questions stimulated the Theory of Natural Selection.

So what are the plausible answers to these questions? There are more answers than one would think exist, of which few were addressed in this thesis. These include: (1) the areas where a species does not occur were historically unsuitable, but became suitable recently, and species have not colonized them yet, (2) Diffuse competition prevents the species from persisting in the gap areas, (3) The vacant areas are not habitable, only our ignorance makes us think otherwise, (4) These areas had once supported the species, which went extinct locally, (5) The species in the regional pool are poor dispersers, (6) Anthropogenic pressures prevented species from colonizing vacant areas. Even if species did colonize, the 'adventurers' were driven to extinction before they could establish a population, (7) Geographical barriers such as mountains and rivers hindered species movement.

The above answers and numerous others suggest that the issue is complex. This thesis only serves as the first step of a long journey. Although the questions deal with fundamental issues in ecology, they have conservation implications. Thus, it is hoped that the scientific knowledge generated through this research would help not only in understanding the formation and maintenance of herbivore assemblages but also in protecting the large herbivores of Ladakh for posterity.



VITA

Tsewang Namgail was born in Skurbuchan, Ladakh, on the 3rd of May 1974. He completed his secondary school education at Government Hari Singh Higher Secondary School in 1991, and then B.Sc. at Government Gandhi Memorial Science College, Jammu in 1995. Thereafter, he studied Zoology (Honours) at the Panjab University, Chandigarh, and graduated in the year 1998. He worked on insect pests of poplar trees in Chandigarh for his M.Sc. dissertation. He then went to the University of Tromsø, Norway, to pursue an M.Phil. Degree in Wildlife Science. For the dissertation, he worked on the Tibetan argali under the supervision of Dr. Joe Fox. Subsequently he acquired financial support from several national and international organisations to work on coexistence of mountain ungulates, wildlife-livestock interactions, herbivore behaviour, herbivore-plant interactions, human-carnivore conflicts, breeding biology and assembly patterns of birds in Ladakh.

He joined the Ph.D. program at the Resource Ecology Group, Wageningen University, in September 2005. In addition to scientific research, he helps local people in managing natural resources in a sustainable way. He, in collaboration with colleagues, has started various conservation programs in Ladakh. He also had a short stint at the Wildlife Institute of India, continuing the work on Tibetan argali. He was conferred PE & RC Publication Award 2008 for the work on argali. Apart from these, he conducted several surveys in Ladakh to know the status and distribution of mammalian herbivores. He was interviewed on the local radio and television several times, and his work was featured in several Indian newspapers. He is fond of music and plays several instruments including flute and harmonica, and won a bronze medal in a national orchestra competition in New Delhi. Currently he works with the Nature Conservation Foundation, India.

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PROFESSIONAL ACTIVITIES

Referee: Animal Conservation, Oryx, Mammalia, Environmental Management, Journal of Natural History

Member: International Society of Zoological Sciences, International Association for Ecology, World Association of Young Scientists, Snow Leopard Network, Mountain Forum, Indian Crane and Wetland Working Group

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review of Literature (4.2 ECTS)

- Herbivore species diversity at multi-spatial and temporal scales (2005)

Writing of Project Proposal (7 ECTS)

- Herbivore species richness in the Trans-Himalaya: understanding the causes of spatial variation (2006)

Post-Graduate Courses (4.4 ECTS)

- Community ecology; SENSE (2005)
- Advanced statistics; PE&RC (2007)
- Multivariate analysis; PE&RC (2009)

Deficiency, Refresh, Brush-up Courses (1.7 ECTS)

- Basic statistics; PE&RC (2006)
- Use of geo-information and remote sensing; ITC (2007)
-

Competence Strengthening / Skills Courses (4.2 ECTS)

- Information literacy; PE&RC (2006)
- Scientific publishing; SENSE (2007)
- Techniques for writing and presenting a scientific paper; SENSE (2007)
- Project and time management; SENSE (2007)
- Science, media and general public; SENSE (2009)

Discussion Groups / Local Seminars and Other Scientific Meetings (4 ECTS)

- Forest and conservation ecology (2005-2007)
- Spatial methods (2007-2009)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (1.2 ECTS)

- PE&RC Annual meeting: "Truth of Science" (2005)
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International Symposia, Workshops and Conferences (11.5 ECTS)

- 12th Benelux Congress of Zoology; Wageningen, the Netherlands (2005)
- IV World Congress on Mountain Ungulates; Munnar, India (2006)
- 11th Meeting of the Goose Specialist Group; Ladakh, India (2008)
- V World Congress on Mountain Ungulates, Granada, Spain (2009)
- 12th Meeting of the Goose Specialist Group; Sweden (2009)

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