Journal of Arid Environments 74 (2010) 1162–1169

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Multi-spatial co-distribution of the endangered Ladakh urial and blue sheep in the arid Trans-Himalayan mountains

T. Namgail [a,b,*], S.E. van Wieren [b], C. Mishra [a], H.H.T. Prins [b]

[a] Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore 570002, Karnataka, India
[b] Resource Ecology Group, Department of Environmental Sciences, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands

A R T I C L E I N F O

Article history:
Received 1 October 2009
Received in revised form
8 April 2010
Accepted 23 April 2010
Available online 21 May 2010

Keywords:
Coexistence
Habitat selection
Ladakh
Ovis vignei
Pseudois nayaur
Resource partitioning

A B S T R A C T

Large wild herbivores are important ecologically and economically, and maintaining their populations is a crucial management concern. The Ladakh urial *Ovis vignei vignei* is an endemic and endangered wild sheep inhabiting the arid Trans-Himalayan region of Ladakh, where its population is restricted to narrow tracts along two river valleys. The causes of this restricted distribution of the species are not understood. We asked if competitive exclusion by the more abundant wild ungulate, the blue sheep *Pseudois nayaur*, could explain the limited range of Ladakh urial. To explore this possibility we studied the occurrence patterns of these two species at multi-spatial scales (regional, landscape and habitat). We found that they occurred independently at the regional scale, but co-occurred at the landscape scale, facilitated by divergence in seasonal resource use at the habitat scale. Although the two species segregated along both habitat and diet axes during summer at the habitat scale, there is a high potential for competition during winter, the 'pinch' period, when they overlap in their habitat use due to altitudinal migration. Therefore, the presence of blue sheep seems to limit the population growth and range expansion of the Ladakh urial.

1. Introduction

Almost one in four mammal species in the world is threatened with extinction, and the population of one in two is declining (Schipper et al., 2008). The land mammals of Asia are particularly at great risk. Given this it is crucial to understand the distribution, abundance and diversity patterns of mammals, especially large herbivores, which are important to humans both economically and aesthetically (Gordon et al., 2004). Mechanistic understanding of the distribution and co-occurrence patterns of large herbivores, however, need a multi-spatial scale approach, because species associations change across scales due to factors operating at different spatial scales (Hui, 2009). For instance, factors like biogeographic affinities and dispersal capabilities play roles in species distributions at a regional scale (Ricklefs and Schluter, 1993), whereas species distributions at smaller scales are governed by the availability of essential resources for their growth, reproduction and survival (Begon et al., 1996; MacArthur, 1972).

Large herbivores may not occupy all the available habitats due to presence of potentially competing sympatric species (Namgail et al., 2009). Competitive interactions often set an upper limit on the local diversity of herbivores (Prins and Olff, 1998), and species that coexist in an area do so by diverging in their resource use (Voeten and Prins, 1999), in response to selection pressures generated largely by competition (Mishra et al., 2002). Facilitation is also thought to be an important process determining herbivore species richness in grazing ecosystems (Arsenault and Owen-Smith, 2002; Prins and Olff, 1998), but is perhaps less important in structuring herbivore assemblages in less productive ecosystems where competition tends to be the dominant form of interaction (Mishra et al., 2002, 2004; Namgail et al., 2007).

The Ladakh region (32° to 36° N and 75° to 80° E) of the Indian Trans-Himalaya is a high altitude cold desert, but supports a relatively rich assemblage of eight wild ungulates, perhaps due to its location at the junction of two biomes: the Tibetan plateau and the Hindukush-Karakoram 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 small and patchy distributions (Chundawat and Qureshi, 1999; Fox et al., 1991). Previous studies have documented the importance of livestock grazing as a factor restricting wild ungulate populations in

* Corresponding author. Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore 570002, Karnataka, India. Tel.: +91 821 2515601; fax: +91 821 2513822.
E-mail address: namgail@ncf-india.org (T. Namgail).

0140-1963/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2010.04.013

the region (Bagchi et al., 2004; Mishra et al., 2004; Namgail et al., 2007, 2008). However, the issue of wild ungulates affecting each others ranges has been explored less (but see Namgail, 2006), which could be important, especially in the western part of Ladakh, where the livestock population is declining due to the growth of service sectors such as tourism.

The Ladakh urial *Ovis vignei vignei*, a wild sheep, has only a small population of about 2000 individuals confined to narrow tracts along the banks of the Indus and Shayok Rivers, while the blue sheep *Pseudois nayaur* is the most abundant (approximately 11,000) and widely distributed wild ungulate in Ladakh (Fox et al., 1991). Although the blue sheep's ecology is relatively well known in the region (Namgail, 2006; Namgail et al., 2004), only one study has been carried out on the ecology of Ladakh urial in one area (Raghavan, 2003). These studies have shown that both species prefer areas close to cliffs <250 m. An ecomorphological study also revealed that these two species have appendicular structures adapted to rugged terrain (Van den Tempel and De Vrij, 2006). 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), which implies similar ecological requirements (Prins and Olff, 1998). Therefore, it is likely that they compete for common resources and the presence of the more abundant blue sheep negatively influences Ladakh urial's distribution.

Information from general surveys suggests that although Ladakh urial's distribution advanced into some of the tributary valleys of the Indus and Shayok, it has not progressed beyond about 15 km from the valley-mouths (Chundawat and Qureshi, 1999; Mallon, 1983). This leads to the obvious question of what hinders its range expansion. Interspecific competition is a possible factor, whereby the more abundant but similar species: the blue sheep competitively excludes the Ladakh urial and prevents its range expansion. Therefore, we investigated whether the limited distribution of Ladakh urial can be explained by possible competition with the blue sheep.

Theory suggests that species that share ecological features may compete and coexist either by geographical partitioning or by resource partitioning along one or more resource axes (Chase and Leibold, 2003; Schoener, 1974). Thus, we hypothesised that blue sheep and Ladakh urial co-occur at larger geographical scales, but diverge in their resource use at the local habitat level.

2. Materials and methods

2.1. Study area

The Ladakh Region (80,000 km^2) is a high altitude cold desert in the northern Indian state of Jammu and Kashmir (Fig. 1). Within this area, Ladakh urial occupies about 3000 km^2 (Chundawat and Qureshi, 1999), while the blue sheep populates about 20,000 km^2. Elevation in Ladakh ranges from 2800 m to 7000 m above sea level. 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 (Namgail, 2009). 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 small groves along glacier-fed streams and rivers (Joshi et al., 2006).

The local habitat scale study was carried out in the Puyul valley (33°43′N, 77°47′E), of the proposed Gya-Miru Wildlife Sanctuary. This valley encompasses about 100 km^2 and is located at about 15 km from the Indus River at Upshi. The valley marks the boundary of Ladakh 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. The altitudinal range of urial was 3700–4500 m during summer and 3840–4400 m during winter, while that of blue

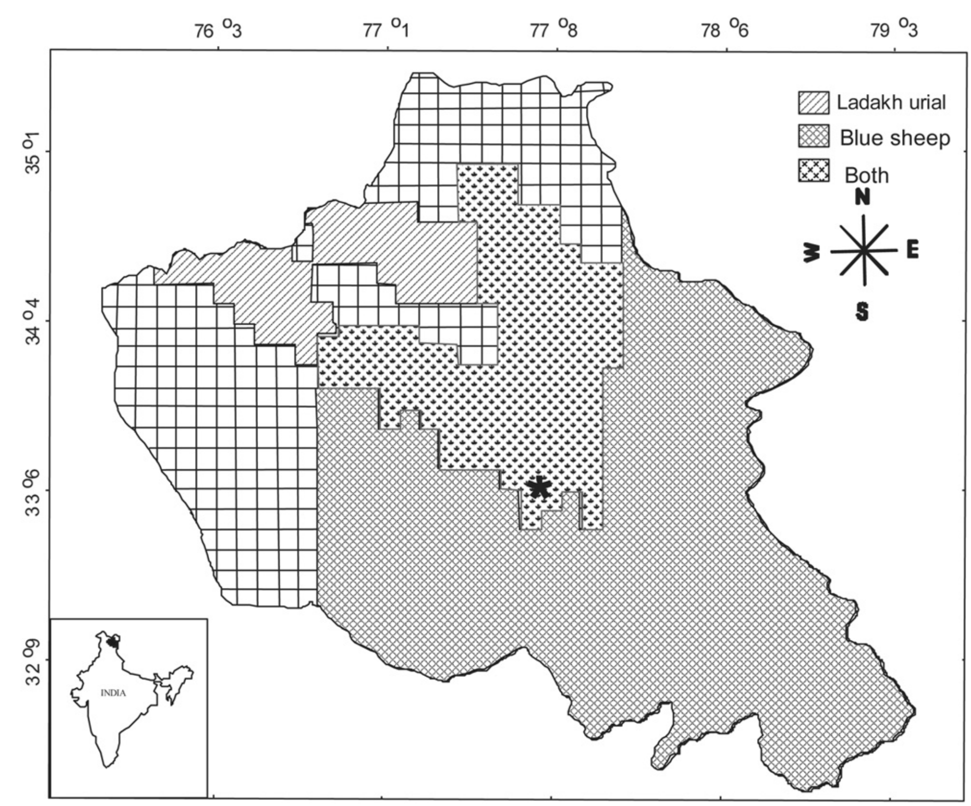

Fig. 1. Ladakh region with the approximate distributional range of Ladakh urial and blue sheep. The location of Puyul, the habitat level study site, is indicated by an asterisk.

sheep was 3850–5400 m during summer and 3160–5040 m during winter. Temperature ranges from −30 °C in winter (Nov.–Mar.) to +35 °C in summer (June–Sept.), and vegetation is characterised by dry alpine steppe (Rawat and Adhikari, 2005).

There are no other wild ungulates in Puyul except the study species, and a small population of domestic sheep and goats (about 700) that grazes the lower areas (3600–4200 m). 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* (Namgail, 2004).

2.2. Field methods

To determine the co-occurrence of blue sheep and Ladakh urial at a regional scale, a grid (20 × 20 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 (10 × 10 km) on a map of Ladakh urial's potential range derived from Chundawat and Qureshi (1999), and then determining the presence–absence of blue sheep and urial in 22 randomly located grid-cells. 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 (Van den Tempel and De Vrij, 2006). Surveys to determine the presence–absence of Ladakh urial and blue sheep in the grid-cells were carried out between June 2006 and August 2008. 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 Ladakh urial were observed from trails along valley bottoms and ridgelines. Scan sampling was the primary method for animal observations, which were aided by 8 × 40 binoculars and a 15–45 X 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 were identified as the most important ones in determining habitat use and partitioning by large herbivores in the Trans-Himalaya (Chundawat and 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°) on an area more than 20 m diameter with vertical drops of more than 5 m. Slope aspect was determined by using a compass. Available habitat variables were sampled from 72 random locations in a similar way as described for habitat use.

Fresh faecal pellets were collected during summer to generate diet profiles of the two 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 about 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 and10 samples for Ladakh urial, which were air-dried and stored in paper bags.

2.3. 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, 10 random grab samples of the residue were then taken, and each droplet was put on a glass slide, spread out evenly and covered with a 2.4 cm cover slip.

We prepared separate reference slides for 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-times 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 (Alipayo et al., 1992).

2.4. Data analysis

Since the species associations depend on the spatial scale of analysis (Hui, 2009), we analysed the data in a hierarchical fashion by first looking at the occurrence patterns at a regional scale (entire Ladakh), landscape level (in and around urial's range) and then at the local habitat level. The co-distribution at the larger spatial scales was determined by a grid-based analysis, and our null model assumed that blue sheep and urial are randomly associated in Ladakh. The presence–absence data were organised into a matrix, where the row represents a species and the column a grid-cell. The species' co-occurrence was quantified using the *C*-score index (Stone and 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 and 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 at the local scale, we first identified the most important variables in habitat choice of each species at a local scale. For this we used the Generalized Linear Model (GLM) by taking used (both species) 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 (Burnham and Anderson, 1998).

Subsequently, we performed Discriminant Function Analysis (DFA) 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 Ladakh 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. All the analyses were carried out in Statistica 7, unless mentioned otherwise.

The niche (both habitat and diet) overlap between the species was determined, using Pianka's Index (Pianka, 1973).

$$O_{jk} = \frac{\sum P_{ij} \cdot P_{ik}}{\sqrt{\sum P_{ij}^2 \cdot \sum P_{ik}^2}}$$

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 $O_{jk} = 0$.

3. Results

3.1. Large scale distributions

At the regional scale, blue sheep occurred in 62 of the 132 grid-cells surveyed, while Ladakh urial occurred in only 10 grid-cells (Fig. 2). 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 (Fig. 3). The co-occurrence analyses showed that blue sheep and urial are distributed independently at the regional 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; $P < 0.05$).

3.2. Habitat scale

A total of 46 observations were made on blue sheep during summer, and 38 observations were made on Ladakh urial during this season. The mean group size of urial during summer was 5 (range = 1–14), while that of blue sheep was 14 (range = 1–53). During winter we made 84 observations on blue sheep, and 20 on Ladakh urial. The mean group size of urial during winter was 10 (range = 6–11), while that of blue sheep was 17 (range = 1–48) during this season.

Akaike Information Criterion for small sample size (AIC_c) indicated that although all physical variables except slope aspect contributed in explaining the variability in the habitat use data of Ladakh urial, altitude is the most important variable during summer as well as winter, as indicated by the inclusion of this variable in the first three consecutive models selected (singly in the best model; Table 1), while blue sheep habitat use is best modelled by using altitude, distance to cliff and slope angle as predictors during summer, and altitude and distance to cliff during winter (Table 2). Aspect was not important in the habitat choice of either species, and hence was dropped from further analyses (DFA) on differences in habitat use by the two species. 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 Ladakh 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.

3.3. Habitat use and partitioning

3.3.1. Summer

Discriminant Analysis showed that altitude had the highest loading on root or function 1 in the habitat use during summer (Table 3), indicating that it was one of the most important factor in discriminating the locations used by the Ladakh urial from those used by blue sheep and unused but available locations. Fig. 4 suggests that blue sheep during summer used higher areas which were more available, whereas Ladakh urial occurred in the lower areas. These

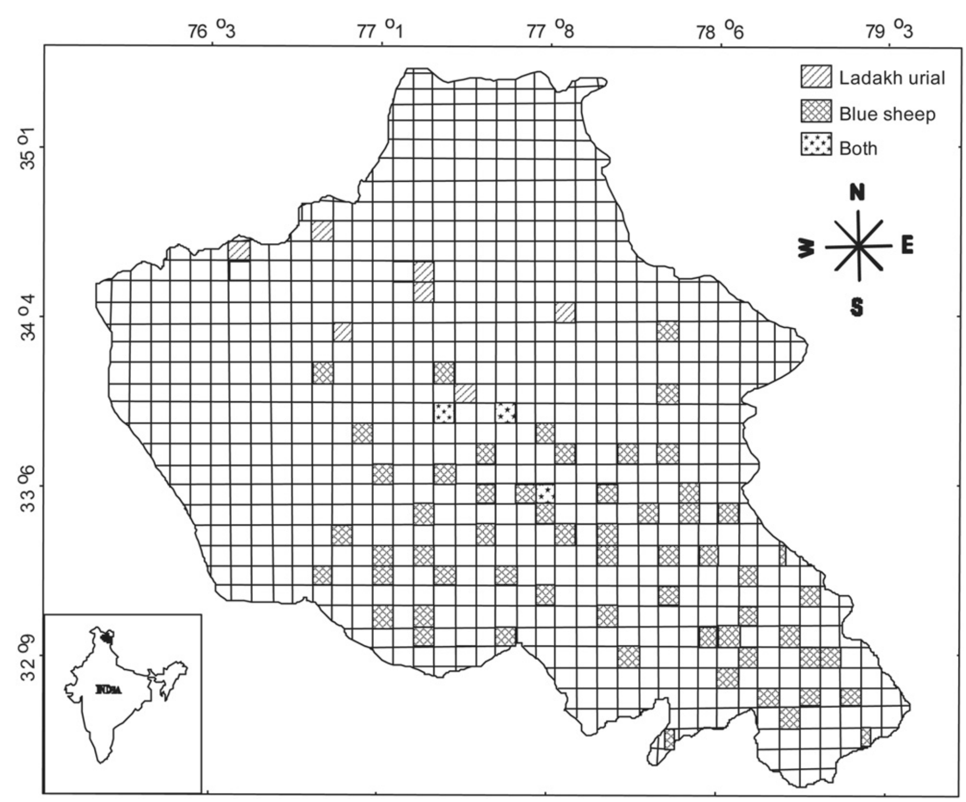

Fig. 2. Gridded map of Ladakh showing the random grid-cells (20 × 20 km) sampled that harboured Ladakh urial and blue sheep.

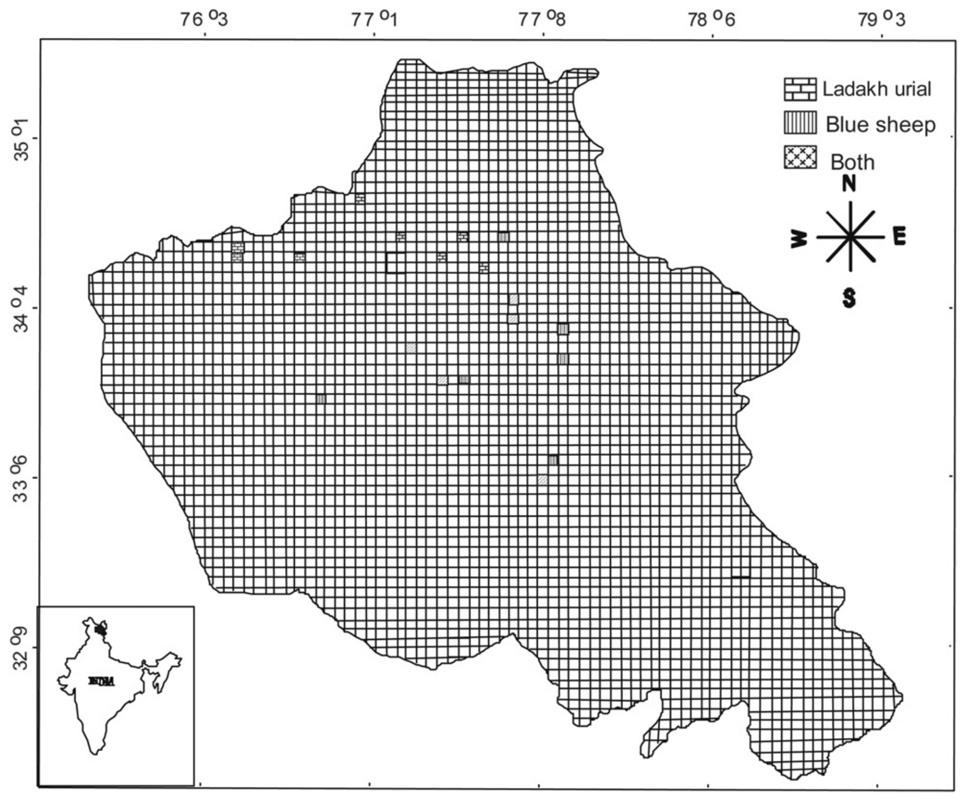

Fig. 3. Gridded map of Ladakh showing random grid-cells (10 × 10 km) sampled that harboured the Ladakh urial and blue sheep.

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, $P < 0.001$).

Comparison of the habitat use of blue sheep and Ladakh urial with a paired t-test also showed a similar trend ($t = 7.92$, $P = 0.0001$; Table 4), which was further suggested 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 ($F_{3,\ 80} = 23.028$, $P < 0.001$).

3.3.2. *Winter*

Altitude and slope angle had the highest loadings on root or 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. 5 suggests that during winter 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 this season ($t = 0.452$, $P = 0.652$), as also indicated by the greater habitat overlap along this axis ($O_{jk} = 0.885$). They differed only marginally in the use of distance to cliff ($t = 1.931$, $P = 0.056$; $O_{jk} = 0.890$).

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, which are useful in explaining the variability in the data (Burnham and Anderson, 1998).

Number	Model	k	Summer		Winter	
			AIC$_c$	Δ	AIC$_c$	Δ
1	Altitude	2	65.304	**0.000**	56.068	**0.000**
2	Distance + Altitude	3	65.712	**0.408**	57.925	**1.857**
3	Distance + Slope + Altitude	4	67.021	**1.716**	59.925	3.857
4	Slope + Altitude	3	67.061	**1.756**	58.068	2.000
5	Altitude + Aspect	3	74.516	9.212	59.222	3.154
6	Distance + Altitude + Aspect	4	74.744	9.440	60.687	4.618
7	Distance + Slope + Altitude + Aspect	5	75.485	10.180	62.598	6.530
8	Slope + Altitude + Aspect	4	75.714	10.410	61.181	5.113
9	Slope	2	142.519	77.215	100.244	44.175
10	Distance + Slope	3	144.464	79.160	90.354	34.286
11	Distance	2	145.092	79.788	88.459	32.391
12	Slope + Aspect	3	149.561	84.257	86.684	30.616
13	Aspect	2	150.699	85.395	84.970	28.901
14	Distance + Slope + Aspect	4	151.519	86.214	71.671	15.602
15	Distance + Aspect	3	152.087	86.783	69.686	13.618

Distance = Distance to cliff (m), Slope = Slope angle (deg) and Altitude (m).

Table 2
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 blue sheep in Gya-Miru, Ladakh. The figures in bold are AIC differences (Δ) of less than two, which are useful in explaining the variability in the data (Burnham and Anderson, 1998).

Number	Model	*k*	Summer		Winter	
			AICc	Δ	AICc	Δ
1	Distance + Slope + Altitude	4	130.221	**0.000**	118.185	**1.959**
2	Distance + Slope + Altitude + Aspect	5	132.665	2.444	122.124	5.898
3	Distance + Slope + Aspect	4	134.115	3.894	143.847	27.621
4	Slope + Altitude	3	134.393	4.172	139.250	23.024
5	Distance + Slope	3	134.484	4.264	157.540	41.314
6	Slope + Altitude + Aspect	4	136.348	6.128	143.041	26.815
7	Distance + Altitude	3	138.922	8.701	116.226	**0.000**
8	Slope + Aspect	3	139.422	9.201	192.231	76.005
9	Slope	3	140.542	10.321	210.221	93.995
10	Distance + Altitude + Aspect	4	143.466	13.246	120.157	3.931
11	Distance	2	144.273	14.052	155.568	39.342
12	Distance + Aspect	3	146.017	15.796	141.954	25.728
13	Altitude	2	150.085	19.865	137.927	21.701
14	Altitude + Aspect	3	153.067	22.846	141.749	25.523
15	Aspect	2	159.237	29.017	198.546	82.320

Distance = Distance to cliff (m), Slope = Slope angle (deg) and Altitude (m).

3.4. Diet profile and overlap

Diets of blue sheep and urial were dominated by non-graminoids (Table 5), but 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 ($O_{jk} = 0.293$).

4. Discussion

Ladakh urial and blue sheep are distributed independently at the regional scale, which 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). Although there was no association between the two species at the regional scale, they did co-occur in and around the urial's range at a smaller scale, namely at that of the landscape level. Thus, our hypothesis that they co-occur at large spatial scales (regional and landscape) was only partially supported. It is however to be noted that the regional analysis was carried out merely to decipher the spatial scale at which their co-occurrence becomes apparent. When their distribution interface was analyzed more closely at the habitat level, they were observed to diverge largely along an altitudinal gradient, which is in line with our hypothesis. 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 (cf. Zeng et al., 2010). Thus, urial might be at a disadvantage during this season, given that blue sheep has higher population density in Ladakh (Fox et al., 1991), perhaps due to its versatility in resource use (Namgail et al., 2009). At any rate, 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 (Albon and Langvatn, 1992; Liu et al., 2002; Zeng et al., 2010). This is tenable because large herbivores do take advantage of

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)	0.053335	0.621171	−0.575613	−0.448963
Slope angle (deg)	0.093429	−0.637678	−0.093372	0.785858
Altitude (m)	−0.993386	−0.153163	−0.747958	0.573143

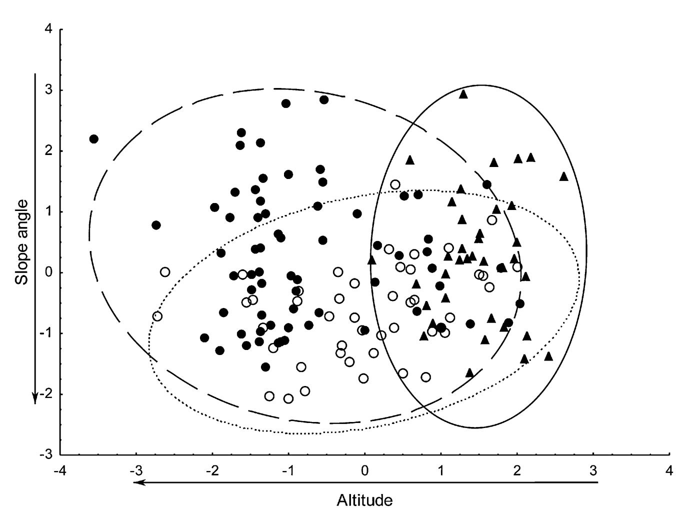

Fig. 4. Output of linear discriminant function Analysis to examine whether the areas used by Ladakh urial (triangle), blue sheep (open circle) and those available (filled circle) during summer could be discriminated on the basis of habitat features in the areas.

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

Variable	Blue sheep				Ladakh urial				Available ($n=72$)	
	Summer ($n=46$)		Winter ($n=84$)		Summer ($n=38$)		Winter ($n=20$)			
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Distance	114	109	60	65	209	156	99	128	238	184
Slope	34	7	31	10	30	9	27	13	27	8
Altitude	4530	341	4160	465	4051	164	4113	170	4762	351

Distance = Distance to cliff (m), Slope = Slope angle (deg) and Altitude (m).

Table 5
Proportions 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		
Calamagrostis sp.	1.6	12.0
Dactylis sp.	2.3	0.0
Elymus sp.	2.3	1.1
Festuca ovina sp.	4.9	9.5
Stipa 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		
Aconogonum sp.	0.7	0.0
Allium sp.	0.5	0.0
Arenaria/Cerastium sp.	17.6	0.0
Artemisia sp.	5.8	4.3
Biebersteinia sp.	0.5	0.0
Iris sp.	0.7	0.0
Lavandula sp.	1.2	0.9
Lonicera sp.	1.2	0.0
Malva sp.	0.2	0.0
Nepeta sp.	0.7	0.0
Oxytropis sp.	0.9	0.0
Polygonum sp.	2.8	0.0
Thermopsis sp.	20.0	0.0
Caragana sp.	3.2	21.2
Ephedra 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		
Artemisia flower heads	0.0	4.7
Asteraceae stems/flower head	1.4	2.9
Rumex flower and stem	3.9	11.7
Urtica flower	0.0	0.4
Veronica 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

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; Zeng et al., 2010). The higher reaches are also cooler and free from insects, which are known to harass wild ungulates (Hagemoen and Reimers, 2002).

Although both species included a higher proportion of non-graminoids in their diets during summer, they fed on different plant species within this functional group. Thus, the two species diverged in their dietary preferences during summer, perhaps as a consequence of the differential habitat use and differential availability of forage plants along an altitudinal gradient (Namgail, unpubl. data). Ladakh urial incorporated a relatively higher proportion of generative parts such as flowers, fruits and seeds of non-graminoids in its diet, perhaps as a strategy to reduce competition with blue sheep.

Therefore, although the Ladakh urial may co-exist with blue sheep in some valleys as a result of the summer resource partitioning, competition with the latter during winter might be hindering its population growth, and thus range expansion. Even during summer, urial may be competitively excluded from the more favourable higher areas, which have high abundance of nutritious plants and are insect-free, as discussed earlier. But these need to be explored further. At any rate, blue sheep seems to have a competitive edge over the Ladakh urial, perhaps due to its flexibilty in habitat use and high density.

It is, however, to be noted that, compared to other Caprinae species, Ladakh urial was hunted more in the past for trophy and meat (Mallon, 1983), as it occurs along the Leh-Srinagar highway (the capitals of Ladakh and Kashmir, respectively), and probably its population was affected by livestock grazing (Raghavan, 2003). Yet, since the conservation laws are enforced more strictly in the recent years (Jigmet Takpa, pers. comm.), and the livestock population in the potential urial habitat is declining (T. Namgail, unpubl. data), currently these are less likely to constrain Ladakh urial's distribution.

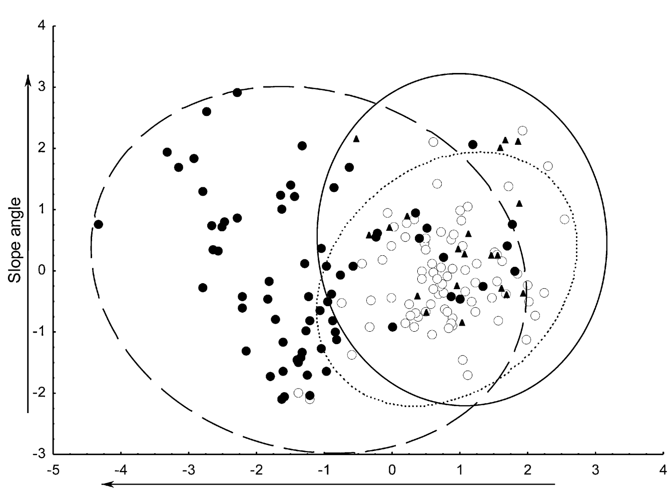

Fig. 5. Output of linear discriminant function analysis to examine whether the areas used by Ladakh urial (triangle), blue sheep (open circle) and those available (filled circle) during winter could be discriminated on the basis of habitat features in the areas.

5. Conclusions

Blue sheep and Ladakh urial occurred independently at the regional 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 they 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.

Acknowledgements

The study was financed by the Wildlife Conservation Society, Rufford Foundation and Wageningen University. We thank Christine de Jong for guidance in laboratory and Yash Veer Bhatnagar for support. We thank the officials of the Jammu and Kashmir Wildlife Protection Department for granting research permission, and Karma Sonam, Mipham, Gyalson and Namgyal for assistance.

References

Albon, S.D., Langvatn, R., 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65, 502–513.

Alipayo, D., Valdez, R., Holecheck, J.L., Cardenas, M., 1992. Evaluation of microhistological analysis for determining ruminant diet botanical composition. Journal of Range Management 45, 148–152.

Arsenault, R., Owen-Smith, N., 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos 97, 313–318.

Bagchi, S., Mishra, C., Bhatnagar, Y.V., 2004. Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the Trans-Himalayan mountains. Animal Conservation 7, 121–128.

Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology: Individuals, Populations and Communities. Blackwell Scientific Publications, Oxford.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: a Practical Information Theoretic Approach. Springer, Berlin.

Chase, J.M., Leibold, M.A., 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, Chicago, USA.

Chundawat R.S., Qureshi Q., 1999. Planning Wildlife Conservation in Leh and Kargil Districts of Ladakh, Jammu & Kashmir. Unpublished Report Submitted to the Wildlife Institute of India, Dehradun, India.

de Jong, C.B., van Wieren, S.E., Gill, R.M.A., Munro, R., 2004. Relationship between diet and liver carcinomas in roe deer in Kielder Forest and Galloway Forest. Veterinary Record 155, 197–200.

Diamond, J.M., 1975. Assembly of species communities. In: Cody, M.L., Diamond, J. M. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Massachusetts, USA.

Festa-Bianchet, M., 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75, 580–586.

Fox, J.L., Nurbu, C., Chundawat, R.S., 1991. The mountain ungulates of Ladakh, India. Biological Conservation 58, 167–190.

Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41, 1021–1031.

Gotelli, N.J., Entsminger, G.L., 2001. EcoSim: Null Models Software for Ecology. Version 7.72. Acquired Intelligence Incorporation and Kesey-Bear. http://www.uvm.edu/~biology/Faculty/Gotelli/Gotelli.html.

Hagemoen, R.I.M., Reimers, E., 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology 71, 883–892.

Hui, C., 2009. On the scaling patterns of species spatial distribution and association. Journal of Theoretical Biology 261, 481–487.

IUCN, 2008. 2008 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

Joshi, P.K., Rawat, G.S., Padilya, H., Roy, P.S., 2006. Biodiversity characterization in Nubra Valley, Ladakh with special reference to plant resource conservation and bioprospecting. Biodiversity and Conservation 15, 4253–4270.

Liu, X., Skidmore, A.K., Wang, T., Yong, Y., Prins, H.H.T., 2002. Giant Panda movement patterns in Foping Nature Reserve, China. Journal of Wildlife Management 66, 1179–1188.

MacArthur, R.H., 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row.

Mallon, D., 1983. The status of Ladakh urial *Ovis orientalis vignei* in Ladakh, India. Biological Conservation 27, 373–381.

Mishra, C., 2001. High Altitude Survival: Conflicts Between Pastoralism and Wildlife in the Trans-Himalaya. Ph.D. Thesis. Wageningen University, The Netherlands.

Mishra, C., Van Wieren, S.E., Heitkonig, I.M.A., Prins, H.H.T., 2002. A theoretical analysis of competitive exclusion in a Trans-Himalayan large-herbivore assemblage. Animal Conservation 5, 251–258.

Mishra, C., Van Wieren, S.E., Ketner, P., Heitkonig, I.M.A., Prins, H.H.T., 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. Journal of Applied Ecology 41, 344–354.

Namgail, T., 2004. Eurasian lynx in Ladakh. Cat News 40, 21–22.

Namgail, T., 2006. Winter Habitat Partitioning between Asiatic Ibex and Blue Sheep in Ladakh, Northern India. Journal of Mountain Ecology 8, 7–13.

Namgail, T., Fox, J.L., Bhatnagar, Y.V., 2004. Habitat segregation between sympatric Tibetan argali Ovis ammon hodgsoni and blue sheep *Pseudois nayaur* in the Indian Trans-Himalaya. Journal of Zoology 262, 57–63.

Namgail, T., Fox, J.L., Bhatnagar, Y.V., 2007. Habitat shift and time budget of the Tibetan argali: the influence of livestock grazing. Ecological Research 22, 25–31.

Namgail, T., Bagchi, S., Mishra, C., Bhatnagar, Y.V., 2008. Distributional correlates of the Tibetan gazelle *Procapra picticaudata* in Ladakh, Northern India: towards a recovery programme. Oryx 42, 107–112.

Namgail, T., Mishra, C., de Jong, C.B., van Wieren, S.E., Prins, H.H.T., 2009. Effects of herbivore species richness on the niche dynamics and distribution of blue sheep in the Trans-Himalaya. Diversity and Distributions 15, 940–947.

Pianka, E.R., 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4, 53–74.

Prins, H.H.T., Olff, H., 1998. Species richness of African grazer assemblages: towards a functional explanation. In: Newberry, D.M., Prins, H.H.T., Brown, N.D. (Eds.), Dynamics of Tropical Communities. Blackwell Science., London, UK, pp. 449–490.

Raghavan, B., 2003. Interactions Between Livestock and Ladakh Urial (*Ovis vignei vignei*). M.Sc. Thesis. Saurashtra University, India.

Rawat, G.S., Adhikari, B.S., 2005. Floristics and distribution of plant communities across moisture and topographic gradients in Tso Kar basin, Changthang plateau, eastern Ladakh. Arctic Antarctic and Alpine Research 37, 539–544.

Ricklefs, R.E., Schluter, D. (Eds.), 1993. Species Diversity in Ecological Communities. University of Chicago Press, Chicago, USA.

Schaller, G.B., 1977. Mountain Monarchs: Wild Goat and Sheep of the Himalaya. University of Chicago Press, Chicago, USA.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., et al., 2008. The status of the World's land and marine mammals: diversity, threat, and knowledge. Science 322, 225–230.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27–39.

Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. Oecologia 85, 74–79.

Van den Tempel, C., De Vrij, M., 2006. Cranial and Appendicular Morphologies Functionally Related to Feeding Type and Habitat of Trans-Himalayan Caprinae. M.Sc. Thesis. Wageningen University, The Netherlands.

Voeten, M.J., Prins, H.H.T., 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120, 287–294.

Zeng, Z., Beck, P.S.A., Wang, T., Skidmore, A.K., Song, T., Gong, H., Prins, H.H.T., 2010. Plant phenology and solar radiation drive seasonal movements of Golden takin in the Quinling Mountains, China. Journal of Mammalogy 91, 92–100.