



**M. Phil. Thesis in Biology**

**HABITAT SELECTION AND ECOLOGICAL SEPARATION BETWEEN  
SYMPATRIC TIBETAN ARGALI AND BLUE SHEEP  
IN NORTHERN INDIA**

**Tsewang Namgail**

December, 2001



**DEPARTMENT OF BIOLOGY**  
Faculty of Science, University of Tromsø, Norway

## **ABSTRACT**

Summer habitat utilisation and ecological separation between the sympatric mountain ungulates Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudois nayaur* in Hemis High Altitude National Park, Ladakh, India were studied to determine how the two species coexist. I investigated the hypothesis that ecological separation between the blue sheep and Tibetan argali occurs on the basis of physical habitat selection. Such separation was tested for on the basis of expected difference between the species, as related to proximity to cliffs associated with the species-specific anti-predator behaviour. Tibetan argali selected habitats away from cliffs while blue sheep selected habitats close to cliffs. Blue sheep also selected steep slopes whereas argali selected gentle slopes. Slope angle was found to be more important than distance to cliff in shaping the niche relationship. The two species did not differ in their use of habitats in terms of elevation and vegetation cover. They however differed in their use of plant communities; blue sheep selected sub-shrub and grass communities whilst argali selected forb communities. The two species are ecologically separated on the basis of physical habitat (and perhaps food), and presumably do not compete for common resources.

**Key words:** argali, blue sheep, habitat selection, resource partitioning.

## **INTRODUCTION**

Sympatric species with similar niches may compete for common resources and coexist either by geographical partitioning or resource partitioning (Lack, 1971; Schoener, 1974 & 1986; Schaller, 1977). Based on niche theory and its relation to habitat selection (Hutchinson, 1957; Orians & Wittenberger, 1991), similar species with expected similar niches should be allopatric or should show behavioural characteristics that separate them spatially or temporally within the same range. The “Competitive Exclusion Principle” advocates that competing species coexist in a stable environment as a result of resource partitioning; if there is no such partitioning, then one competing species will eliminate or exclude the other (Gause, 1934 & 1935; Hardin, 1960). Competition is considered to be a major selective force causing differential use of resources by coexisting species (MacArthur, 1972; Cody, 1975; Pianka, 1976; Roughgarden, 1983), although processes like predation or different responses of species to environmental gradients may also lead to resource partitioning (Connell, 1975; Wiens, 1977; Strong, 1984; Brown, 1987; Schoener,

1974 & 1986; Putman, 1996). For example, sympatric species that are similar in body size also compete with each other to avoid predators, an interaction known as ‘apparent competition’ (Holt, 1977 & 1984) or competition for ‘enemy-free space’ (Jeffries & Lawton, 1984), and consequently may adopt different escape tactics, often leading to habitat partitioning. Even in food limited conditions competition may be prevented by predation, which keeps the population of the competitors below the level at which food resources become limiting (Hairston, *et al.*, 1960; Putman, 1996). Sometimes, predation and competition together can affect prey communities in a multitude of ways that often interact (Utida, 1953; Connell, 1975; Schoener, 1986; Warner *et al.*, 1983; Holt, 1989).

The pattern of resource partitioning in ungulate communities is widely studied (Jarman, 1971; Jarman & Sinclair, 1979; Hanley & Hanley, 1982; Gordon & Illius, 1989; Fritz *et al.*, 1996; Voeten & Prins, 1999; Forsyth, 2000), but the mechanisms which produce such partitioning remain elusive. The observed pattern of resource partitioning or niche differentiation in ungulate communities could be attributed to both ecological forces (current competition and/or predation) and evolutionary history (ghost of competition past) (see Connell, 1980). In co-evolved communities, the extant species may have competed in the past and evolved different morphological and/or behavioural characteristics, through evolutionary time, thus accomplishing resource partitioning. But this cannot be proved, as we cannot go back in time to check whether the species ever competed or there were some incidences of elimination of other species which competed (Andrewartha & Birch, 1954; Begon *et al.*, 1996). Alternatively, during the course of evolution, they may have responded independently though differently to various selective forces. But again, we cannot in retrospect determine the past processes and check whether they responded independently and differently to selective forces. Therefore, the observed pattern of resource partitioning in ungulate communities can only be tested and interpreted in terms of current ecological forces. It is, however, not easy to disentangle various ecological processes and mechanisms shaping such communities. To ascertain the effect of any dynamic, the natural system must be disturbed away from equilibrium by either adding or removing individuals, but such experimental studies are difficult, if not impossible, in ungulate communities due to management considerations and time constraints (e.g., their long life-span). In any case, competitive structuring implies that inter-specific competition is or has been an important force in determining which species are present in a community as well as their relative abundance and

resource use patterns (Hutchinson, 1959; Sinclair, 1985). If such communities exist it seems reasonable that there should be a limit to the similarity of coexisting species (Hutchinson, 1959).

The Tibetan argali *Ovis ammon hodgsoni* (hereafter termed "argali") and the blue sheep *Pseudois nayaur* are two wild sheep and sheep-like\* species, respectively, of the Bovidae, subfamily Caprinae, and have almost completely overlapping distributions (see Shackleton, 1997) that encompass ca. 2500,000 km<sup>2</sup> over the high Himalaya and the entire Tibetan Plateau. Such a sympatric distribution of related species with similar ecological requirements implies that they do not compete, and there is some degree of resource partitioning. This may be accomplished on the basis of habitat and/or diet separation. Initial food habit studies of argali and blue sheep on the Tibetan plateau (Harris and Miller 1995; Miller and Schaller, 1998; Schaller, 1998) have shown a considerable overlap in diet, suggesting that they accomplish the resource partitioning primarily by habitat separation. Therefore, keeping in view the niche complementarity i.e., species that occupy similar position along one dimension (e.g., food) tend to differ along another dimension (e.g., cover) (Brown, 1975; Schoener, 1986; Pianka, 1994; Begon *et al.*, 1996), I studied the anti-predator habitat selection of the two species to see how such selection contributes to their coexistence. Various anecdotal reports on argali and blue sheep habitat utilisation suggest that although both species are denizens of mountainous areas, blue sheep prefer steep terrain near cliffs whereas argali prefer open and rolling terrain away from cliffs (Clark, 1964; Fox, *et al.*, 1991a; Schaller, 1977 & 1998). The biological basis for this difference in habitat use is explained in terms of contrasting predator avoidance strategies associated with morphological differences between the two species (Geist, 1971 & 1987b; Schaller, 1998). Thus, the long slender legs of argali enhance its cursorial strategy of out-running predators on the open and rolling terrain of its preferred habitat. In contrast, the relatively short and muscular legs of the blue sheep support its agility in steep and rugged terrain (i.e., cliffs) where it retreats to avoid predators which are generally less agile in such habitat. Thus, based on this difference, the blue sheep and argali are expected to show some differences in their use of habitat related to predator avoidance.

---

\* In structure and habits, *Pseudois* is intermediate to *Capra* and *Ovis* but is apparently more closely related to *Capra*. Schaller (1977) described blue sheep as "aberrant goats with sheep-like affinities." He noted that *Pseudois* resembles *Capra* in having a broad, flat tail with a bare central surface, large dewclaws, no inguinal glands, no preorbital glands, and usually no pedal glands.

Various studies (Cerri and Fraser, 1983; Holmes, 1984; Belovsky, 1978; Sih, 1980; Festa-Bianchet, 1988; Boyer *et al.*, 1998) with their implications to “optimal foraging theory” suggest that an animal should forage in areas where its intake rate is highest and predation risk lowest. Thus, the blue sheep and argali are expected to use habitats with high forage availability and low predation risk. In the study area, because food resources are generally more abundant outside of cliffs (escape terrain), blue sheep tend to move outside of such escape terrain for feeding. Wegge (1979) in a study on blue sheep in Nepal, reported it feeding in open habitats, and bedding in more rugged terrain. Blue sheep while in open habitats, however, needs to strike a balance between food acquisition and predator avoidance. Thus, although blue sheep and argali may use the same type of open mountainous terrain for foraging, there should be a distinct difference between the two species in terms of their proximity to cliffs related to the respective anti-predator strategies. This expected difference provides the basis for the present study, especially so because no studies have hitherto actually measured argali habitat use in relation to physical habitat. In fact, there is little documentation of the resource partitioning in ungulates on the basis of habitat separation associated with predator avoidance (Sinclair, 1985). Although more extensive study of argali distribution and habitat selection are planned within the scope of a co-operative research in the Indian Trans-Himalaya (Fox, pers. comm.), the present study provides an initial look at argali and blue sheep relationships in a unique site of argali occurrence in the Indian Trans-Himalaya.

The Tibetan argali is the only subspecies of *Ovis ammon* that is listed as endangered on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and is so listed by the U.S. Fish and Wildlife Service. It is also listed as a threatened species by the Government of India and is a fully protected (schedule 1) species under Jammu & Kashmir Wildlife Protection Act of 1978. The most recent estimate suggests that there are not more than 7,000 Tibetan argali throughout its range (Schaller, 1998). Within India there are only approximately 200 argali remaining, mostly in Ladakh and a few in Sikkim (Fox and Johnsingh, 1997). The blue sheep, in contrast, is the most common mountain ungulate on the Tibetan plateau and its peripheral areas, but since it constitutes a major prey of the endangered snow leopard *Uncia uncia* (Oli *et al.*, 1993; Jackson, 1996), its conservation is important where snow leopards are being protected.

The small population (approx. 20 individuals) of argali within the Hemis National Park in Ladakh, India presents an interesting case where a small group recently established itself in a new

area, and currently presents a focus for conservation of this endangered animal in India. The fact that these argali have not greatly increased in number since the arrival of 3 individuals in 1978 (Fox et al., 1991a and unpubl. data) begs the question as to why. Thus, relying on theoretically based expectations regarding niche (in this case habitat) separation, I have initiated an investigation of habitat use differences between this argali population and the blue sheep that share its range. Because an understanding of this resource separation could have important implications for conservation efforts related to this and other argali populations, I also address these issues.

Based on local knowledge and past studies (e.g., Fox *et al.*, 1991b), I delineated the known range of the small argali population in Hemis NP, and used this as the study area. Within this area I conducted observations on both species to determine if there was indeed the type of physical habitat separation expected on the basis of their predator avoidance strategies. Thus, distance to cliffs was measured, along with other physical variables such as slope angle and elevation that may affect such separation. Although difference in diet was not addressed in this summer season study, easily obtainable data on the related factors of plant community type and vegetation cover were also gathered to assess the differences in vegetation use that could be related to the aforementioned habitat differentiation.

In summary, if predation was important in shaping their niche relationship, I expected blue sheep to use steep habitats near the cliffs and argali to use moderate slopes away from cliffs. Thus, I hypothesised that ecological separation between argali and blue sheep exists on the basis of physical habitat (escape terrain). Such separation was tested for on the basis of expected difference in distance to cliff, with possible additional influences by slope angle and/or elevation.

## **STUDY AREA**

This study was carried out in the known argali range in the north-western part of Hemis National Park (34°N, 77°E) in the Ladakh province of Jammu & Kashmir state, India (Fig. 1). The argali range was delineated based on the knowledge of local people and previous observations by others (Fox et al., 1991b; Fox, unpubl. data). The entire argali range currently used encompasses ca. 10 km<sup>2</sup> in the headwaters of the Shingo and Rumbak streams, and is situated in the Zanskar range near the confluence of the Indus and Zanskar rivers. It lies at a distance of ca. 25 km southwest of Leh, the main city of Ladakh. There is a pass, Ganda La (4900 m), in the centre of the study area,

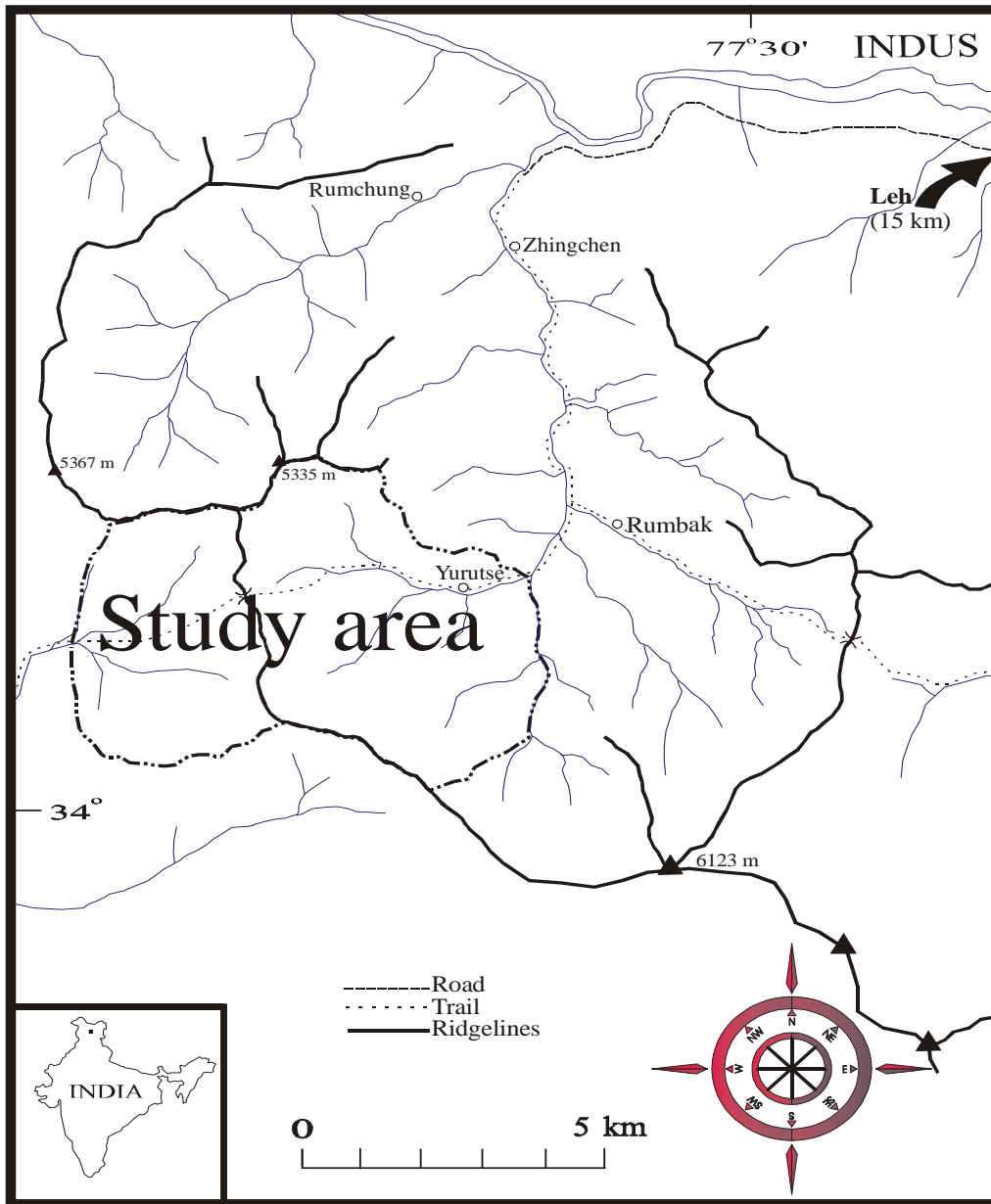
which is used by locals throughout the year and by tourists in the summer. Within the small argali area, topography varies from steep, rocky slopes at higher elevations to gently rolling hills at lower elevations. Elevation within the area used by argali ranges from 4000-5500 m. Hemis National Park is situated in the rain shadow of the great Himalaya, hence the climate is characterised by cold and arid, with low plant productivity that is largely confined to the short growth season in summer. Temperatures in summer (June-Aug.) range from 15-35°C (Chundawat, 1992). Annual precipitation in the Indus valley at Leh is about 100 mm, increasing somewhat south-westward and altitudinally to 500-1,000 mm in valleys at the northern base of the Himalaya (Hartmann, 1983), and is probably about 500 mm in the study area.

## **Flora**

Vegetation is characterised by dry alpine steppe with small shrub (mainly *Caragana* spp., *Artemisia* spp. and *Lonicera* sp.), sub-shrub (mainly *Aconogonum* sp. and *Stachys* sp.), grass (mainly *Poa* spp., *Elymus* spp. and *Festuca* sp.), sedge (*Carex* spp. and *Kobresia* spp.) and forb (mainly *Potentilla* spp., *Oxytropis* spp., *Astragalus* spp., *Thermopsis* sp. *Delphinium* sp., *Dracocephalum* sp. and *Saussurea* spp.) communities present.

## **Fauna**

Besides the blue sheep and argali, there are myriad small mammals including Himalayan marmot *Marmota bobak*, Tibetan woolly hare *Lepus oiostolus*, mouse hare *Ochotona* spp., stone marten *Martes foina*, Himalayan weasel *Mustela sibirica* and red fox *Vulpes vulpes montana*. The major avian species are snowcock *Tetraogallus tibetanus*, chukar *Alectoris chukar*, chough *Pyrrhocorax graculus* and golden eagle *Aquila charysetos*. The large mammalian predators include snow leopard *Uncia uncia*, wolf *Canis lupus chanko*, and wild dog *Cuon alpinus*. These last three prey on blue sheep and argali, while red fox is a threat only to their young lambs. All the above species, except wild dog, were observed in the area during the study period.



**Fig. 1.** Study area in the Rumbak and Shingo catchments of Hemis National Park, Ladakh, India.



## **METHODS**

### *Data collection on habitat use*

The study was conducted during the months of July and August, 2000. Data were collected from selected trails and along ridges, all with good vantage points. Observations were conducted using 8x40 binoculars and a 15-45X spotting scope. Records were made of species type, group size, sex, age, date and time. Individuals were considered to be solitary or belong to different groups when they stood 50 m away from another group. The locations of the blue sheep and argali were plotted on 1:50,000 topographic sheets. Elevation, distance to cliff, slope angle, vegetation type (plant community), and plant cover at the animal locations were recorded. Elevation and slope angle were determined from the topo-map's contour lines, and calculated from the measured distance between the nearest contour lines, respectively. Distance to cliff was determined by measuring the distance between the animal location and the nearest cliff. The vegetation was first classified into five communities based on the physiognomy and dominant species, and mapped on the topo-sheet (Fig. 7). Subsequently, the blue sheep and argali locations were classified as to different vegetation communities. Vegetation cover was estimated in the field, with percentage cover at the animal locations recorded.

Observations were taken between 0600 and 2000 hrs, but most of the observations were obtained from 0600 to 1200 hrs. Since there were only 20 argalis present in the area, pseudoreplication was inevitable. However, dependency was minimised by making only one observation on a group per day. Due to the high fluidity of group membership and movements in and out of the study area, it is difficult to demonstrate that the same groups of blue sheep shared the argali range throughout the summer. In any case, on average ca. 50 blue sheep were daily observed in the study area. This population is a part of the larger population in the whole of Rumbak catchment, thus its habitat selection should not be viewed as absolute, but relative within the argali range.

### **Available habitat**

Availability of a habitat is the quantity of that habitat accessible to the population of animals during the study period (Manly *et al.*, 1993). The animals were assumed to have equal access to

all the available habitats as they could move across the study area within a day. For availability of habitat, a systematic sample of habitat characteristics was obtained from a 1:50,000 topo-map of the study area. For this purpose, a point grid was overlaid on the topo-map and the habitat variables at the location of each point were recorded. Habitat characters (distance to cliff, slope angle and elevation) at 366 points were sampled. Elevation was determined from the contour lines and slope angle was calculated from the measured distance between the nearest contour lines. The distance to cliff was determined by measuring the distance between the respective point and the edge of the nearest cliff. The cliffs, very steep slopes ( $>45^\circ$ ) on an area more than 20 m diameter with vertical drops of more than 3 meters, were identified and mapped in the field.

To assess the vegetation availability, a reconnaissance survey of vegetation was conducted within the study area during the months of July and August, 2000. The plant identification was carried out in the field using “Flowers of the Himalaya” (Polunin and Stainton, 1985) as a reference, and by Dr. Henry Noltie from the Royal Botanic Garden, UK. For the availability of vegetation, a systematic sample of vegetation communities at 366 points was taken, as described earlier.

## **Data analysis**

### **Habitat utilization**

Habitat use was characterised by resource selection functions (RSFs) that are proportional to the probability of a resource being used by an animal. Since individual animals were not identified and were assumed to be randomly sampled, and available population proportion of habitat characteristics was assumed to be known, the habitat selection data conformed to Design 1 with sampling protocol A, according to Manly *et al.* (1993) (see Appendix I). Although availability was sampled, since it was a systematic and intensive sampling with a point grid overlaid on the small study area, I assume that the sample available proportion represents the population proportion.

Measuring habitat preference has often been studied by relating use of a habitat to its availability (Neu *et al.*, 1974; Alldredge and Ratti, 1986 & 1992; Thomas and Taylor 1990; Manly *et al.*, 1993). When resources are used disproportionately to their availability, use is said to be selective (Manly *et al.*, 1993). Resource selection occurs in a hierarchical fashion from the

geographic range of a species, to individual home range within a geographic range, to use of general features (habitats) within the home range, to selection of particular elements (food items) within the general features (or feeding site) (Manly *et al.*, 1993). In this study, habitat selection of blue sheep and argali within the assumed argali home range was investigated.

For the determination of resource selection, the variables were classified into distinct categories containing at least five observations each, with few exceptions. The distance to cliff was categorised into "very close to cliff" (<50 m), "close to cliff" (51-250 m), "away from cliff" (251-450 m) and "farther away" (>450 m). Slope angle was categorised into "flat" (<10°), "moderate" (11-30°), "steep" (31-50°) and "very steep" (>50°). Elevation was categorised into "low" (<4300 m), "middle" (4301-4600 m), "high" (4601-4900 m) and "very high" (>4900 m). Likewise, vegetation was categorised into the following communities: Shrub, Sub-shrub, Grass, Sedge and Forb. The selection ratio for each category was calculated as

$$\hat{w}_i = o_i / \pi_i \quad (\text{eqn 1})$$

where  $\hat{w}_i$  is the selection ratio,  $o_i$  is the proportion of used units in category  $i$ , and  $\pi_i$  is the proportion of available resource units in category  $i$ . The standardised selection ratio  $B_i$  was also calculated for each category to check for relative preference between categories. To statistically test significant departures of use from availability, the modified  $X^2$ : log-likelihood chi-square test ( $X_L^2$ ) was calculated as

$$X_L^2 = 2 \sum_{i=1}^I u_i \log_e \{u_i / u_+ \pi_i\} \quad (\text{eqn 2})$$

where  $u_i$  is the number of used resource units in category  $i$ ,  $u_+$  is the total number of used resource units sampled and  $\pi_i$  is the proportion of available resource units in category  $i$ . If the  $X_L^2$  was significant, the null hypothesis: all habitats are used in proportion to their availability (no selection) was rejected. Subsequently, for each habitat category, the Bonferroni-adjusted 100 (1- $\alpha$ ) % confidence intervals were constructed as

$$o_i \pm Z_{\alpha/2I} \sqrt{\{o_i (1-o_i) / u_+\}} \quad (\text{eqn 3})$$

where  $o_i$  is the proportion of used units in category  $i$ ,  $u_+$  is the total number of used resource units sampled and  $I$  is the number of habitat categories. A habitat category was selected if the lower confidence interval for that category was greater than the corresponding population proportion. Similarly, a habitat category was avoided when the upper confidence interval for that category excluded the corresponding population proportion.

### Ecological separation

Although the chi-square analyses and the subsequent Bonferroni-adjusted confidence intervals shed light on the resource partitioning, a multivariate approach was used mainly to determine the most crucial variable that separated the two species. For this purpose, continuous variables were used, and data were screened to check for the assumptions of normality and homogeneity of variance. All but blue sheep's distance to cliff and argali's elevation were close to normal. The blue sheep's distance to cliff was log-transformed to better approximate normality; however, transformation of argali's elevation did not improve the normality as the variable had a bimodal distribution.

To check for differences in means of variables, namely slope angle, distance to cliff, elevation and vegetation cover for blue sheep and argali, the t-test for independent samples was used—as this is less sensitive to the assumption of normality, especially when the sample size is large (Manly, 1994). The multivariate Hotelling's  $T^2$  test was used to check the differences in means taking all the variables together, thus taking proper account of the correlation between variables (Manly, 1994).

Those variables with significant mean differences were selected for further analysis of resource partitioning. Independent Linear Discriminant Analysis was used to determine whether animal locations could be discriminated on the basis of their environmental characteristics. Discriminant analysis is a multivariate statistical technique useful for investigating within and between group variability, testing differences in the composition of groups and identifying variables most useful in determining the most likely group membership of individual cases. In this study all locations of blue sheep comprised one group and all locations of argali the other.

## RESULTS

A total of 82 groups of blue sheep and 105 groups of argali were observed (Fig. 2) during the two month study period. The argali population was composed of three adult males, eleven adult females, one yearling and five lambs. Most of the blue sheep observed consisted of all-male groups.

### Habitat utilization

In all the tables below, the available sample proportion represents the available population proportion of the study area (see methods).

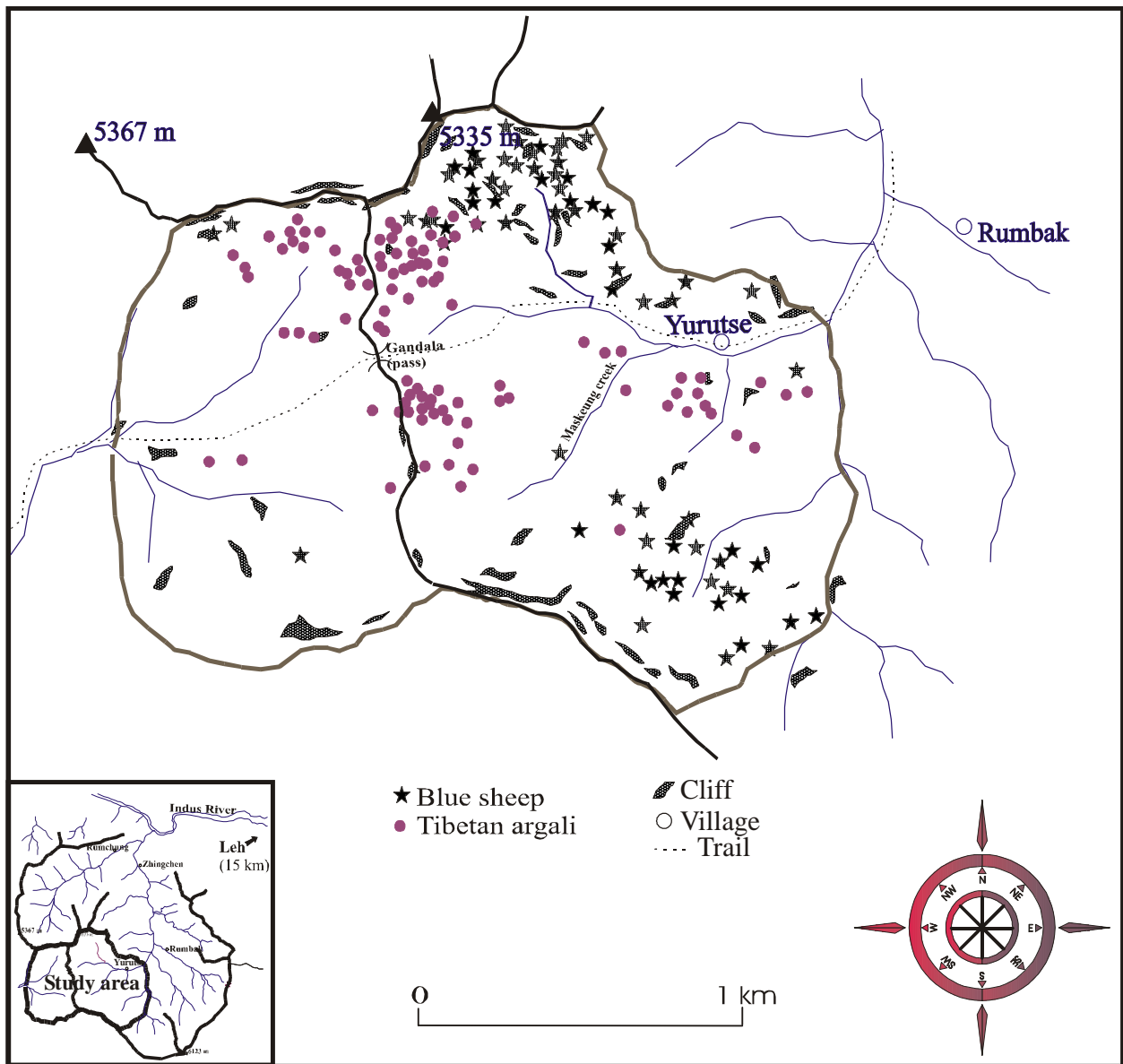
#### Distance to cliff

For argali, the calculated chi-square test ( $X_L^2 = 19.53$ ,  $p < 0.01$ ) was highly significant, thus rejecting the null hypothesis of no selection. The lower limit of the habitat category “away from cliff” was greater than the population proportion, indicating its selection (Table 1, Fig. 3). Likewise the upper limit of the category “very close to cliff” excluded the population proportion, indicating its avoidance. Argali tended to avoid habitat “farther away” from cliff, while it tended to select habitat “close to cliff” (Table 1). The argali’s probability of using habitat “away from cliff” ( $B_3 = 0.390$ ) was 3 times greater than the probability of using habitat “farther away” ( $B_4 = 0.179$ ).

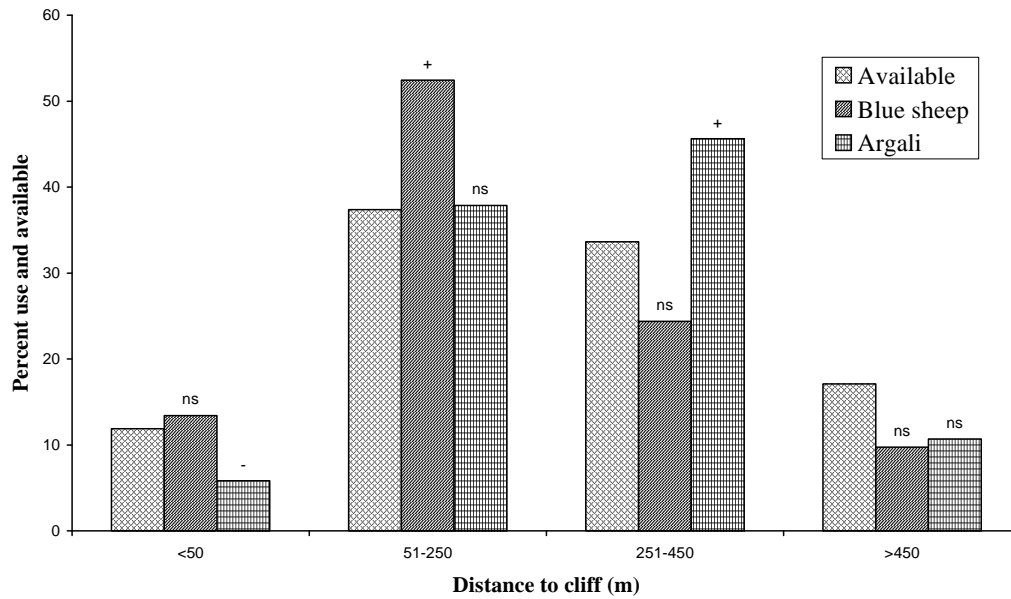
**Table 1.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals for distance to cliff use by argali.

Distance to cliff (meters)	Available sample		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Very close to cliff (<50m)	41	0.119	6	0.058	0.490 <sup>-</sup>	0.141	0.002	0.114
Close to cliff (51-250m)	129	0.374	39	0.379	1.013 <sup>ns</sup>	0.291	0.264	0.494
Away from cliff (251-450m)	116	0.336	47	0.456	1.357 <sup>+</sup>	0.390	0.339	0.573
Farther away (>450m)	59	0.171	11	0.107	0.624 <sup>ns</sup>	0.179	0.034	0.180
Total	345	1.000	103	1.000	3.484	1.000		

Selection (+), avoidance (-) and non significant trends (ns)



**Fig. 2.** Observations of the Tibetan argali and blue sheep along with locations of cliffs in the argali range in the Shingo and Rumbak catchments.



**Fig. 3.** Percent use and availability of distance to cliff for argali and blue sheep, indicating selection (+), avoidance (-) and non-significance (ns) based on Bonferroni-adjusted 95% confidence intervals.

For blue sheep, the calculated  $X_L^2$  statistic ( $X_L^2 = 9.7$ ,  $p < 0.05$ ) was significant, indicating that at least one habitat category was selected. The habitat category “close to cliff” was apparently selected significantly more often than is expected from the population proportion of this category (e.g.,  $\pi_2 = 0.374$  is below the lower limit of the confidence interval 0.392-0.656) (Table 2, Fig. 3). In fact, the probability of habitat “close to cliff” being selected by blue sheep was three times greater than that of the habitat “away from cliff” ( $B_2 = 0.366$ ,  $B_3 = 0.190$ ). Blue sheep tended to select habitats very close to cliff, while it avoided areas “away” and “farther away” from cliff, though not significantly (Table 2, Fig. 3).

**Table 2.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals for distance to cliff use by blue sheep.

Distance to cliff (Meters)	Available sample		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Very close to cliff (<50m)	41	0.119	11	0.134	1.129 <sup>ns</sup>	0.295	0.044	0.244
Close to cliff (51-250m)	129	0.374	43	0.524	1.402 <sup>+</sup>	0.366	0.392	0.656
Away from cliff (251-450m)	116	0.336	20	0.244	0.725 <sup>ns</sup>	0.190	0.130	0.358
Farther away (>450m)	59	0.171	8	0.098	0.570 <sup>ns</sup>	0.149	0.020	0.176
Total	345	1.000	82	1.000	3.827	1.000		

Selection (+), avoidance (-) and non significant trends (ns)

### Slope angle

For argali use of slope angle, the null hypothesis that all habitat categories are used in proportion to their availabilities was rejected thereby supporting the hypothesis that at least one habitat category was used disproportionately ( $X_L^2 = 9.26$ ,  $p < 0.05$ ). The population proportion for the “moderate” slope ( $\pi_2 = 0.437$ ) was below the lower limit of the 95% confidence interval (0.496-0.724), which indicates that this category is selected significantly (Table 3, Fig. 4). Argali avoided “very steep” slopes. It also avoided “flat” and “steep” terrain, although not significantly (Table 3, Fig. 4). Nevertheless, the lower confidence limit of the category “flat” is negative, therefore needs to be interpreted with some reservation. Argali’s probability of using moderate slopes ( $B_2 = 0.494$ ) was twice more than that of using steep slopes ( $B_3 = 0.259$ ).

**Table 3.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals for slope angle use by argali.

Slope angle (degrees)	Available sample		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Flat (<10)	5	0.014	1	0.010	0.697 <sup>ns</sup>	0.247	0.000 <sup>†</sup>	0.033
Moderate (11-30)	160	0.437	64	0.610	1.394 <sup>+</sup>	0.494	0.496	0.724
Steep (31-50)	191	0.522	40	0.381	0.730 <sup>ns</sup>	0.259	0.267	0.525
Very steep (>50)	10	0.027	0	0.000	0.000 <sup>-</sup>	0.000	–	–
Total	366	1.000	105	1.000	2.821	1.000		

Selection (+), avoidance (-) and non significant trends (ns)

<sup>†</sup>A negative value for the lower confidence limit for “Flat” was replaced with a 0 value since a proportion can not take a negative value.

The alternative hypothesis of blue sheep selecting at least one slope category was supported ( $X_L^2 = 29.80$ ,  $p < 0.01$ ) significantly. The probability of selecting very steep terrain ( $B_4 = 0.408$ ) was 4 times greater than that of moderate terrain ( $B_2 = 0.187$ ). The Bonferroni-adjusted 95% confidence intervals for the categories, “flat”, “steep” and “moderate” slopes excluded their respective population proportions, which indicate that these habitat types are used non-randomly. The lower confidence limit for the habitat category “steep” slope excluded the available population proportion thus indicating its selection; the upper confidence limits for “flat” and “moderate” terrain were lower than their respective population proportions thereby indicating the



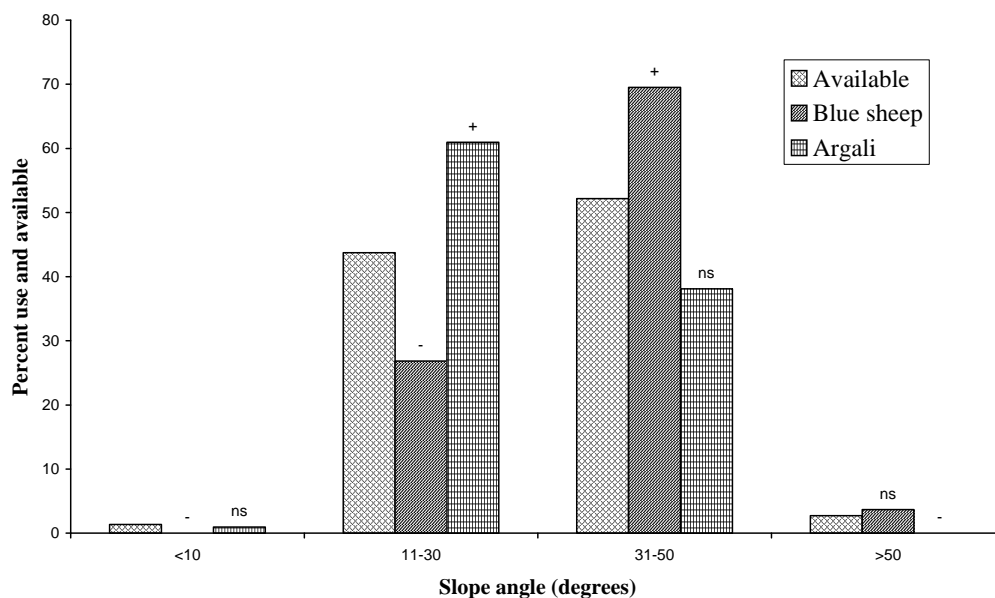
avoidance of these categories (Table 4, Fig. 4). Blue sheep tended to select very steep slopes. This however needs to be interpreted with some reservation due to a negative lower limit.

**Table 4.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals for slope angle use by blue sheep.

Slope angle (degrees)	Available sample		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Flat (<10)	5	0.014	0	0	0.000 <sup>-</sup>	0.000	-	-
Moderate (11-30)	160	0.437	22	0.268	0.614 <sup>-</sup>	0.187	0.151	0.385
Steep (31-50)	191	0.522	57	0.695	1.332 <sup>+</sup>	0.405	0.573	0.817
Very steep (>50)	10	0.027	3	0.037	1.339 <sup>ns</sup>	0.408	0.000 <sup>†</sup>	0.087
Total	366	1.000	82	1.000	3.285	1.000		

Selection (+), avoidance (-) and non significant trends (ns)

<sup>†</sup>A negative value for the lower confidence limit for “very steep” slope was replaced with a 0 value since a proportion can not take a negative value.



**Fig. 4.** Percent use and availability of slope angle for argali and blue sheep, indicating selection (+), avoidance (-) and non-significance (ns) based on Bonferroni-adjusted 95% confidence intervals.

## Elevation

For argali use of elevation, test statistic was highly significant ( $X_L^2 = 21.56$ ,  $p < 0.01$ ), thus supporting the hypothesis that at least one habitat category is used non-randomly. The lower limit for the very high elevation category excluded the population proportion, thus this habitat category was used more than expected (Table 5, Fig. 5). The probability of argali using “very high” elevations ( $B_4 = 0.471$ ) was markedly higher than the probability of using other elevation categories ( $B_1 = 0.142$ ,  $B_2 = 0.165$  and  $B_3 = 0.222$ ). The same relationship holds between the unstandardised ( $\hat{w}_i$ ) values. The upper limit for the middle elevation was lower than the population proportion, thus showing its avoidance. The confidence limit for low elevation is unreliable due to a negative lower limit.

**Table 5.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals for elevation use by argali.

Elevation (meters)	Available sample		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Low (<4300m)	26	0.075	4	0.038	0.508 <sup>ns</sup>	0.142	0.000 <sup>†</sup>	0.083
Middle (4301-4600)	84	0.242	15	0.143	0.590 <sup>-</sup>	0.165	0.061	0.225
High (4601-4900)	129	0.372	31	0.295	0.794 <sup>ns</sup>	0.222	0.188	0.402
Very high (>4900)	108	0.311	55	0.524	1.683 <sup>+</sup>	0.471	0.407	0.641
Total	347	1.000	105	1.000	3.576	1.000		

Selection (+), avoidance (-) and non significant trends (ns)

<sup>†</sup>A negative value for the lower confidence limit for “low” elevation was replaced with a 0 value since a proportion can not take a negative value.

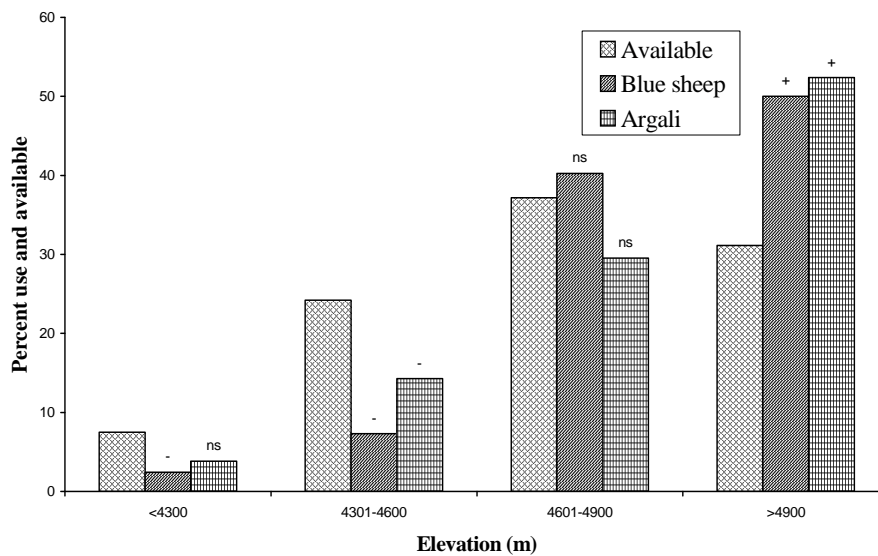
The calculated chi-square ( $X_L^2 = 29.80$ ,  $p < 0.01$ ) for blue sheep use of elevation was highly significant, indicating that proportion use of at least one habitat category was non-random (Table 6, Fig. 5). The standardised selection ratio for the use of “very high” elevation by blue sheep ( $B_4 = 0.484$ ) was greater than the corresponding ratio for “high” elevation ( $B_3 = 0.326$ ), which reveals that the probability of using habitats at “very high” elevation is higher than that of using habitats at “high” elevation. Blue sheep significantly avoided both low and middle elevations, whilst they tended to select high elevations. The lower confidence limit for the “very high” elevation category was greater than the population proportion thus indicating its selection (Table 6).

**Table 6.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals for elevation use by blue sheep.

Elevation (meters)	Available sample		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Low (<4300)	26	0.075	2	0.024	0.326 <sup>-</sup>	0.098	0.000 <sup>†</sup>	0.046
Middle (4301-4600)	84	0.242	6	0.073	0.302 <sup>-</sup>	0.091	0.004	0.142
High (4601-4900)	129	0.372	33	0.402	1.083 <sup>ns</sup>	0.326	0.273	0.531
Very high (>4900)	108	0.311	41	0.500	1.606 <sup>+</sup>	0.484	0.367	0.633
Total	347	1.000	82	1.000	3.317	1.000		

Selection (+), avoidance (-) and non significant trends (ns)

<sup>†</sup>A negative value for the lower confidence limit for “low” elevation was replaced with a 0 value since a proportion can not take a negative value.



**Fig. 5.** Percent use and availability of elevation for argali and blue sheep, indicating selection (+), avoidance (-) and non-significance (ns) based on Bonferroni-adjusted 95% confidence intervals.

## Vegetation

The  $X_L^2$  test statistic for argali's selection of vegetation was highly significant ( $X_L^2 = 189$ ,  $p < 0.0001$ ), indicating that the use of at least one vegetation category was non-random. The probability of forb community being used by argali was the highest ( $B_5 = 0.809$ ) followed by the probability of sub-shrub ( $B_2 = 0.103$ ). The lower confidence limit for the community "forb" was greater than the population proportion thus it was used disproportionate to its availability (Table 7, Fig. 6). Argali avoided shrub, grass, sedge and barren, as indicated by the exclusion of the population proportions of these communities by their respective upper confidence intervals. The confidence limits for grass and barren, although statistically significant under present assumptions, are unreliable due to negative lower limits.

**Table 7.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals for vegetation community use by argali.

Vegetation community	Available sample □		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Shrub	140	0.383	27	0.257	0.672 <sup>-</sup>	0.071	0.145	0.370
Sub-shrub	68	0.186	19	0.181	0.974 <sup>ns</sup>	0.103	0.082	0.280
Grass	28	0.077	1	0.010	0.124 <sup>-</sup>	0.013	0.000 <sup>†</sup>	0.035
Sedge	14	0.038	0	0.000	0.000 <sup>-</sup>	0.000	–	–
Forb	26	0.071	57	0.543	7.642 <sup>+</sup>	0.809	0.415	0.671
Barren	90	0.246	1	0.010	0.039 <sup>-</sup>	0.004	0.000 <sup>†</sup>	0.035
Total	366	1.000	105	1.000	9.451	1.000		

Selection (+), avoidance (-) and non significant trends (ns)

<sup>†</sup>Negative values for the lower confidence limits for "Grass" and "Barren" were replaced with 0 values since a proportion can not take a negative value.

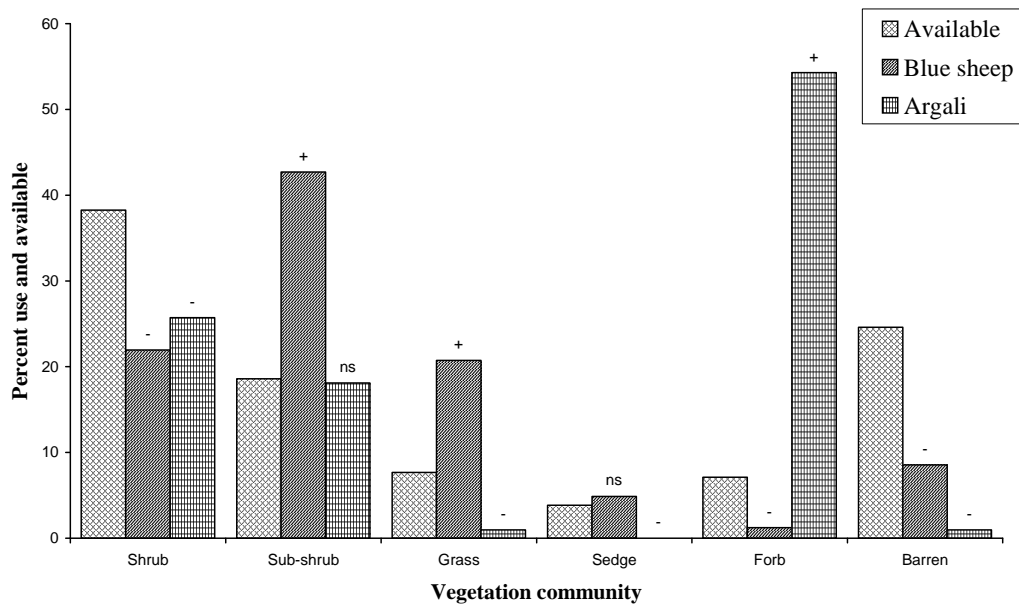
For blue sheep use of vegetation, the standardised ratio for sub-shrub and grass ( $B_2 = 0.312$  and  $B_3 = 0.367$ ) were almost equal, and were considerably higher than the corresponding ratios for all other categories, which reveals that these categories have higher probabilities of being selected. Blue sheep significantly avoided forb, shrub and barren, while it tended to select sedge (Table 8). The test statistic for the detection of selection was highly significant ( $X_L^2 = 55.0$ ,  $p < 0.001$ ). The lower confidence limits for "sub-shrub" and "grass" excluded their respective population proportions thereby indicating their selections (Table 8, Fig. 6).

**Table 8.** Estimated selection indices, relative probabilities and Bonferroni confidence intervals of vegetation communities used by blue sheep.

Vegetation community	Available sample $\square$		Use sample		Selection index ( $\hat{w}_i$ )	Standardised index ( $B_i$ )	Confidence intervals	
	Count ( $m_i$ )	Proportion ( $\pi_i$ )	Count ( $u_i$ )	Proportion ( $o_i$ )			Lower	Upper
Shrub	140	0.383	18	0.220	0.574 <sup>-</sup>	0.078	0.099	0.341
Sub-shrub	68	0.186	35	0.427	2.297 <sup>+</sup>	0.312	0.283	0.571
Grass	28	0.077	17	0.207	2.710 <sup>+</sup>	0.367	0.089	0.325
Sedge	14	0.038	4	0.049	1.275 <sup>ns</sup>	0.173	0.000 <sup>†</sup>	0.112
Forb	26	0.071	1	0.012	0.172 <sup>-</sup>	0.023	0.000 <sup>†</sup>	0.044
Barren	90	0.246	7	0.085	0.347 <sup>-</sup>	0.047	0.004	0.166
Total	366	1.000	82	1.000	7.375	1.000		

Selection (+), avoidance (-) and non significant trends (ns)

<sup>†</sup>Negative values for the lower confidence limits for “Sedge” and “Forb” were replaced with 0 values since a proportion can not take a negative value.



**Fig. 6.** Percent use and availability of vegetation communities for argali and blue sheep, indicating selection (+), avoidance (-) and non-significance (ns) based on Bonferroni-adjusted 95% confidence intervals.

## Ecological separation

The slope angle used by blue sheep and argali differed significantly with regard to their means ( $t = -5.76$ ,  $p < 0.001$ ) (Table 9). Distance to cliff also showed significant difference ( $t = 2.68$ ,  $p < 0.01$ ) (Table 9). There was also evidence of an overall difference between argali and blue sheep, taking all the variables viz., elevation, slope angle, distance to cliff and vegetation cover together (Hotelling's  $T^2 = 37.82$ ,  $F(4, 182) = 9.3006$ ,  $p < 0.001$ ). The means for elevation and vegetation cover did not differ.

**Table 9.** Comparison of mean values for argali and blue sheep with variables taken one at a time.

Variable	Argali		Blue sheep		t (185 d.f.)	p-value
	Mean	S.D.	Mean	S.D.		
Elevation	4837.43	235.58	4866.10	200.02	-0.88	0.379 <sup>ns</sup>
Slope angle	31.00	7.19	36.77	6.25	-5.76	0.000***
Distance to cliff	286.52	154.06	224.15	163.03	2.68	0.008**
Vegetation cover	33.43	17.31	30.10	22.96	1.13	0.259 <sup>ns</sup>

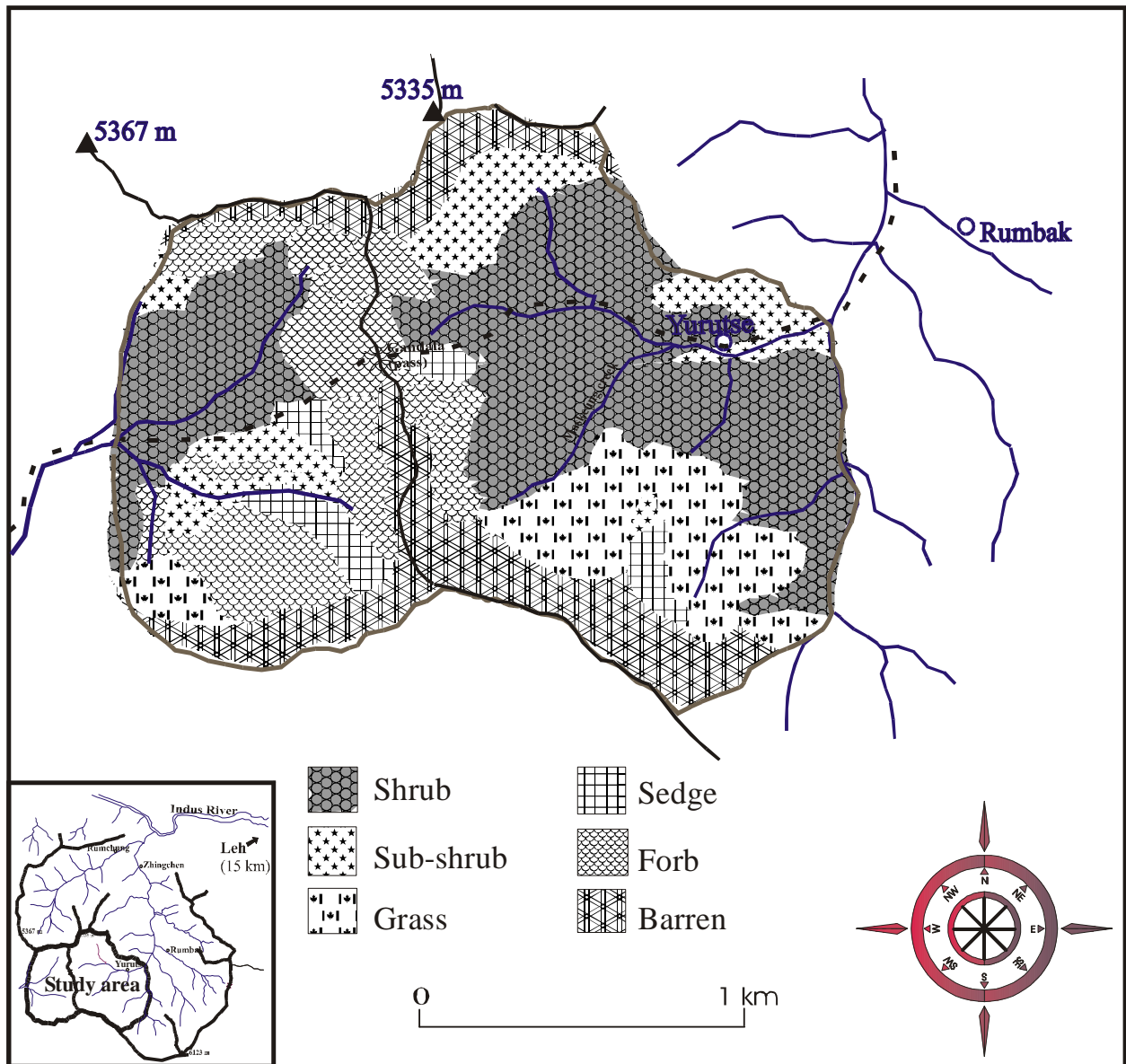
$P < 0.001$ \*\*\*,  $P < 0.01$ \*\* , ns = non significant

Only those variables with significant mean differences were entered in the linear discriminant function analysis. Since only two variables, namely slope angle and distance to cliff differed significantly with regard to their means and thus entered in the model, the locations selected by argali and blue sheep were separated by only one discriminant function (Table 10). Slope angle was the more important variable for discrimination between the animal locations (Wilk's lambda = 0.96,  $p < 0.001$ ). Distance to cliff, however did not add much contribution to the discrimination. Forty percent of the variability was explained by differences between groups ( $\chi^2 = 31.92$ ,  $p < 0.001$ ).

**Table 10.** Result of stepwise linear discriminant function analysis to test whether argali and blue sheep could be separated based on different environmental characteristics.

Function	Eigen value	% of var.	Can. Cor.	$\chi^2$	Standardised coefficients	Can.	Disc.	Func.
1	0.189	100	0.40	31.92 ***	-0.92 (Slope angle)			
					0.24 (Distance to cliff)			

$P < 0.001$ \*\*\*



**Fig. 7.** Distribution of vegetation communities in the study area.

## DISCUSSION

The results of this study support the hypothesis that ecological separation between argali and blue sheep exists on the basis of physical habitat. Observations of the two species showed a distinct niche divergence, with argali using undulating terrain and blue sheep using more rugged terrain, which conforms to anecdotal reports (Fox *et al.*, 1991a; Schaller, 1977 & 1998). This distinct difference in the use of environmental features may be related to the species-specific anti-predator strategies. Although the species also differed in their association with different vegetation communities, it is difficult to conclude that they differ with regard to their diet. Nevertheless, habitat separation has been considered as the most common mode of resource partitioning in animals, followed by food (see Schoener, 1974). Much of the literature has focussed on competition as a plausible factor influencing such separations (Jenkins and Wright, 1988; Murray and Illius, 2000), while importance of predation in resource partitioning, although studied extensively in other taxa (e.g., Mittelbach, 1984; Mercurio *et al.*, 1985), is little understood in ungulate communities. Predation may lead to habitat partitioning, provided the species are safest from predation in different habitats (Repasky, 1996). During the present study, carried out in the summer season when food competition is less likely, the two species partitioned habitat in terms of variables deemed to be important in escaping predators, implying that predator related-mortality may be an important fitness component, placing a premium on predator escape ability. Hence, predation is a conceivable agent of selection responsible for the evolution of habitat partitioning.

As expected, argali selected habitats “away from cliffs” and the blue sheep selected habitats “close to cliffs” (Tables 1 & 2, Fig. 3). The latter is consistent with the result obtained by Chundawat (1992) in the whole of Rumbak catchment. Longva (1998), in a study of blue sheep’s anti-predator habitat utilisation in the area, also found it using habitats significantly closer to cliffs than that available. During the present study, 65% of the sightings of blue sheep were within 250 m from cliffs (escape terrain). Such high affinity of blue sheep toward cliffs, which generally support less vegetation, suggests that forage is not the only constraint in their habitat use. In contrast, over half of the argali’s observations were above 250 m from cliffs, which illustrates the importance of open terrain in the determination of habitat use by argali. Furthermore, blue sheep tended to select the habitat category “very close to cliff”, whilst argali avoided this category (Fig. 3). Such differential habitat use by the two species, as related to



proximity to cliff implies little overlap on this dimension. However, adequate comparative data needs to be collected to determine the degree of overlap and possible competition.

The lack of adequate habitat (mainly for argali) and vegetative diversity & productivity in the area is likely to increase the possibility of an overlap in habitat and/or diet use, and thus competition between the two species. Such competition may however be averted by either spatial or temporal separation at the microhabitat level (Pianka, 1994), as demonstrated in several mammalian sympatric species (e.g., Brown and Lieberman, 1973; M'Closkey and Fieldwick, 1975; Dueser and Shugart 1978). Temporal separation was not addressed in this study, but some spatial separation was apparent in their use of microhabitat (Fig. 2). This segregation could be due to a combination of competition and predation, and consequently to the resource (food, cover etc.) partitioning by the two species. However, if competition was important in shaping the niche relationship, the blue sheep's population should have declined following the argali's arrival in the area. But the former's population has shown a slight increase during the last decade (Fox, unpubl. data). Hence, predation may be the rather more important factor influencing this spatial separation. Predatory risk provides an axis along which microhabitat partitioning can occur based on trade-offs involving predator avoidance and competitive abilities (Holt, 1989). Such separation may also occur as a result of the behavioural avoidance of one species by the other, a pattern seen in other mountain ungulates (e.g., Forsyth, 2000).

Blue sheep's selection of steep slopes, in contrast to argali's selection of gentle slopes, reflects its agility and capability to negotiate steeper slopes. Blue sheep also tended to select "very steep" slopes, whereas argali completely avoided this category (Table 3 & 4), which further strengthens the relationship. This notable difference in the use of slope, especially in such rugged terrain affirms that they are ecologically separated, which may partly be attributed to the morphological differences associated with predator avoidance. This fundamental difference may preclude or minimise any competitive interaction between the two species in this study area as well as other areas where they come together. The tendency of blue sheep to select "very steep" slopes during the present study is comparable to the result obtained by Chundawat (1992), who reported blue sheep using very steep slopes ( $>40^\circ$ ) in proportion to its availability during summer, whilst it avoiding such slopes during all other seasons. Such a selection pattern conforms to the contention that ungulates are more concerned about predators during summer when the food is abundant.

Ecological separation may also be accomplished through altitudinal zonation of species (Green, 1987). During the present investigation, the insignificant difference in means of elevational use by the two species (Table 9), and therefore the considerable overlap in the altitudinal distribution rules out such separation on an altitudinal gradient, thereby increasing the possibility of a competitive interaction. The fine-grained partition of habitat, as discussed earlier, may however reduce any such interaction. The selection of high altitude by both argali and blue sheep (Table 5 & 6) may be attributed to the delayed phenology of plants at higher elevations (Johnston *et al.*, 1968; Hoefs, 1979), and their attempt to take advantage of freshly sprouting forage at such elevations during summer. Both species are reported to use lower elevations in the area during winter (Mallon, 1991; Fox *et al.*, 1991a). Seasonal migration over an altitudinal gradient has been reported in other mountain sheep, such as bighorn *Ovis canadensis* (see Geist, 1971). In the case of blue sheep it might also be a strategy of reducing competition with the lactating females, as most of the observations of blue sheep at high elevations were male groups. To maximise their reproductive fitness, males that have bred females ought to vacate the areas used by these females while they are lactating (Geist and Petocz, 1977). The differential habitat use by sexes as observed in other ungulate species (Festa-Bianchet, 1988; Forsyth, 2000), however could not be analysed in this study due to paucity of data on different sexes. The argali's high altitudinal distribution is also likely to be linked to disturbance by livestock. The female and nursery groups were seen at lower elevations during the morning, and at higher elevations during the day when the herders tended the livestock at lower elevations. Such displacement of argali to higher elevations by livestock has also been observed in the Mongolian Altai (Dzieciolowski *et al.*, 1980). Nonetheless, further investigation needs to be carried out, possibly with an experimental approach, to assess the effect of livestock grazing on the argali's habitat use on an altitudinal gradient, and as a consequence its (argali) interaction with the blue sheep.

There was no difference in the mean vegetation cover of the habitats selected by the two species (Table 9). Given the high affinity of blue sheep towards cliffs as an anti-predator strategy, and the heterogeneous distribution of forage in the area (i.e., more vegetation outside of cliffs, and the presumed positive relationship between distance to cliff and vegetation cover), one would expect lower vegetation cover in habitats selected by the blue sheep than those selected by argali. But no such difference was observed. This may pertain to argali's habitat shift in response to the

growing population of livestock, i.e., argali might have moved towards cliffs to avoid livestock related activities, thereby feeding in habitats similar to those used by blue sheep.

Sympatric ungulates tend to use different vegetation communities (Gordon, 1989). Therefore selection of vegetation communities was studied, but with an objective of understanding the differential habitat use; dietary partitioning is deferred to future studies. However, the vegetation community preferences observed during the present investigation agree to some extent with diet-based results of previous food habit studies on the Tibetan plateau (Schaller and Gu, 1994; Harris and Miller, 1995; Miller and Schaller, 1998), and Nepal Himalaya (Koirala and Shrestha, 1997). In assessing my results, these need to be compared with some reservation because other results are based on diet analysis. Blue sheep in the present study selected sub-shrub and grass communities (Table 8). This could be related to the preponderance of these communities in vicinity of the cliffs. Argali on the other hand predominantly selected forb communities (Table 7), which is consistent with the diet-based results obtained by Koirala & Shrestha (1997) and Miller and Schaller (1998). Both blue sheep and argali avoided shrub communities (dominated by *Caragana* sp. and *Artemisia* spp.).

As per the nutritional relationships associated with interspecific differences in body size (Bell, 1971; McNaughton and Georgiadis, 1986; Illius and Gordon, 1987; Myrnerud, 1998; Gagon and Chew, 2000), one would expect blue sheep (relatively smaller) to show greater affinities for forb communities, and argali to demonstrate greater preference for grass communities. But, as discussed above, a converse relationship was observed during this study. This could be ascribed to the preponderance of forbs in the argali's realised niche determined mainly by livestock grazing in the area. Moreover, although blue sheep were found in the grass-dominated communities, they may selectively feed on more nutritive species within such communities. In any case, the differential vegetation preference in this preliminary study suggests minimal overlap in diet. But diet analysis needs to be carried out to proclaim any dietary separation, and to ascertain the significance of such separation in their coexistence.

Despite the fact that argali use habitat away from cliff and blue sheep use habitat close to cliff, distance to cliff did not play a major role in discriminating between the two species when slope angle was included in the discriminant function analysis (Table 10). It is however to be noted that both species tended to avoid the category "farther away" from cliff, indicating that

they do not differ much in the use of habitat in terms of proximity to cliff, as they do in terms of slope angle. This may well reflect the preponderance of cliffs in the area. In any case, it is obvious that slope angle is an important factor in argali's choice of habitat, and in determining its coexistence with blue sheep. Distance to cliff may also be an important factor, but it seems like that the argali does not have much choice in this particular study area. Nonetheless, as alluded to earlier, the lack of argali's selection of areas far from cliffs may also be attributed to the influence of livestock on the argali's choice of habitat. The daily herding of livestock in the area may displace argali from their preferred sites and push them towards the cliffs, which may in turn increase the overlap in habitat use by the two wild ungulates. On an average, three herds, each comprising of ca. 200 sheep and goats, graze in the area on a daily basis during the short summer (pers. obs.). The argali's preference for open and rolling slopes makes them more vulnerable to livestock associated disturbances, mainly due to the shepherds bias towards herding on more open slopes (Fox *et al.*, 1994; Koirala and Shrestha, 1997; Herders, pers. comm.). The influence of livestock on argali's population dynamics has been envisaged elsewhere (Fedosenko, 1985; Fedosenko *et al.*, 1995).

Blue sheep on the other hand is less likely to be affected by the tended livestock because of their association with the cliffs. Longva (1998) found no considerable effect of livestock herding on blue sheep's habitat use, i.e., blue sheep used the same slopes irrespective of livestock presence. However, the displacement of argali from its preferred habitats, as discussed above, may increase the likelihood of its competition with the blue sheep, thereby affecting the latter's habitat use pattern. Thus the livestock may also affect the blue sheep population indirectly. During the present study, the argali was observed keeping a distance from the sheep and goats, perhaps as a response to the presence of the herder. In contrast, it was observed feeding or resting very close to cattle such as dzos (hybrid of yak and cow), which are free ranging at least for the few summer months. Harris and Miller (1995) also found argali feeding in close proximity to wild yaks, on the Tibetan plateau, without any agonistic behaviour. Thus only the tended livestock, mainly sheep and goats, might displace argali from their preferred habitats, i.e., push argali towards the cliffs where the vegetation may be less and interaction with the blue sheep more. In other words, livestock possess the potential not only to compete for forage with argali, but also to exclude them from the desired sites due to their mere presence or the presence of associated herders and sometimes dogs.

Because of these circumstances associated with livestock disturbance, the argali may fall prey to both snow leopard (which stalks from the edge of terrain breaks such as cliffs) and wolf (which hunts in the open). The slow growth of the argali population in the area may be a reflection of this situation. Two snow leopards were encountered in the area, and a pack of three wolves was also observed traversing the argali home range frequently during the present study. For blue sheep even the small cliffs may serve as refuge against predators, especially wolf, thus reducing its depredation rate. Harris and Miller (1995) noticed blue sheep using boulder and scree of slate talus in Yeniugou, on the Tibetan plateau where availability of cliffs is low. Thus blue sheep may have a slight edge over argali in escaping predators in this area. Argali in this study area may be both resource and predator limited, and such questions should be addressed in further detail.

Another anthropogenic effect on argali's habitat use is the heavy tourist traffic in this area during the summer months. The argali range lies on the popular Markha trek route. This makes argali prone to tourism related developments. Argali have been seen running uphill when disturbed by the trekkers. This may leave argali with less energy for other vital activities important for its growth, reproduction and survivability. Moreover, the ponies used by the trekking groups for transporting their gear also graze in the area during the night, when the latter camp, which may further increase the grazing pressure.

## **Potential for competition between argali and blue sheep**

The strong affinity of blue sheep toward cliffs is likely to reduce both interference and exploitation competition with argali, and may contribute to their coexistence. However, more extensive studies with sufficient comparative data from all seasons need to be carried out to understand the interaction properly. Although competition aspects on the food dimension was not addressed in this study, argali's selection of forb community, and blue sheep's selection of sub-shrub and grass communities suggest a minimal overlap in diet, and presumably a reduced possibility of competition in the dietary realm. Furthermore, since there is a spatial separation at the microhabitat level, and food is not likely to be limiting during the summer (Schaller and Gu, 1994; Miller and Schaller, 1998), there is little prospect for competition (both exploitation and

interference) between the two species during this season. Their zone of sympatry, and overlap in resource use however are likely to increase, should populations expand or availability of habitat decline, thereby enhancing the potential for both food and habitat competition between them. An increase in blue sheep's population may also increase the possibility of an apparent competition (Holt, 1977) between the two species. Just as consumer species can reciprocally reduce each others abundance via depleting a shared resource, prey species can sometimes indirectly depress each other by increasing the abundance of a shared enemy (Holt, 1977; Holt & Lawton, 1993). Thus, increase in blue sheep's population may elicit a numerical response from the predators in the area, which may in turn decrease the argali's population. This phenomenon and the limiting environment for argali in the area could work in tandem to keep its population low.

## **Management implications**

The resource selection pattern observed during the present study may be useful in predicting foraging areas and habitat distribution of blue sheep and argali. Such pattern may also offer additional insight into their ecology and habitat requirements. The increased preference of moderate slopes by argali suggests that such terrain types must be managed for the long-term persistence of this species. Despite the lack of vegetative diversity and productivity, Hemis National Park provides a mosaic of habitats with unique aggregation of rare and endangered wild animal species. It is certainly one of the prime habitats for blue sheep (Fox and Nurbu, 1990). However, the slow growth of the small argali population raises the question of suitability of this park for argali conservation. The Rumbak catchment of the park where argali is located is rugged and precipitous, and has limited open area preferred by argali. Furthermore, a road to Rumbak village is currently under construction, the completion of which may facilitate a greater influx of tourists to the area thereby posing more threat to the continued survival of the aforementioned population of argali. Thus, Hemis NP may not be the best place for future argali conservation, and attention may better be diverted to other areas such as the proposed Gya-Meeru wildlife sanctuary when it comes to managing and conserving this argali subspecies in India.

The livestock number in Hemis National Park has shown a slight increase during the past decade (Bhatnagar *et al.*, 1999). Therefore, the question of its compatibility with wildlife conservation in the area needs to be addressed. On an average, three herds of domestic sheep and

goats graze daily in the argali range during the short summer (June-August), as discussed earlier. Approximately one third of the population of livestock that graze in the area during this season belong to villages outside the boundary of Hemis NP. Of these, the non-lactating cattle such as dzos are free ranging while the sheep and goats are herded by the park residents on lease, for manure. This may lead to an overstocking, which may expedite the resource depletion and exclusion of the wild ungulates from the area. The excessive grazing by livestock during summer may also limit forage availability during winter for the wild ungulates, especially argali, as it does not have enough suitable habitat to move around. Furthermore, on average five ponies used by trekking groups to transport their gear, graze in this area each day through the short summer. Likewise, grazing by small herbivores such as marmot and Tibetan woolly hare may further increase the grazing pressure. In summary, given the limited habitat, and the present amount of disturbance and grazing pressure in the area, long term persistence of the small population of argali is highly uncertain.

## **ACKNOWLEDGEMENTS**

I wish to express profound gratitude to my supervisor, Dr. Joseph L. Fox for his zealous interest, constructive criticism and expert guidance throughout the study. I am greatly indebted to him for giving me the opportunity to study the animals that lived in the mountains next to my home yet I was oblivious to them. I also express my sincere gratitude to Dr. Yash Veer Bhatnagar, Wildlife Institute of India, for his guidance and constant encouragement both in the field and through the writing process.

I should like to thank Dr. Henry Noltie, Royal Botanic Garden, UK, for his help in the identification of plant specimens. Statistical advice of Dr. Rolf Anker Ims, is thankfully acknowledged. I am also thankful to Mr. Abdul Rauf Zargar, Wildlife Warden, Department of Wildlife Protection, Leh, for granting permission to work in the Hemis National Park. I wish to express my gratitude to Anne Høydal, Administrative Head, and all other staff at the Department of Biology who helped me in one way or the other. My gratitude is also due to all the fellow students at the said Department, especially Kishor, Bård and Rolf for their help and encouragement throughout the study.

Heartfelt thanks go to the Department of Biology, University of Tromsø for financial support and necessary equipment for the fieldwork. The additional financial support for fieldwork from the Center for Environment and Development, University of Tromsø, Statens Lånekasse and Earthwatch Institute, USA are equally acknowledged.

I owe a special thanks to Paul, Rigmor, Odd and Elinor for their kind hospitality, and for providing me a home away from home.

Last but not the least, I am grateful to all the members of my family for their moral support. I am also thankful to the Snow Leopard Trails, and its entire staff for their help, especially Mr. Sonam Morup for his two months company in the field. The fieldwork was spiced up by the sight of two snow leopards, an animal that I always considered as elusive as the Himalayan Yeti and the North American Sasquatch.

## **LITERATURE CITED**

- Allredge, J.R. and J.T. Ratti, 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* **50**, 157-165
- Allredge, J.R. and J.T. Ratti, 1992. Further comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* **56**, 1-9
- Andrewartha, H.G. and L.C. Birch, 1954. *Distribution and Abundance of Animals*. University of Chicago Press, Chicago
- Begon, M., J.L. Harper and C.R. Townsend, 1996. *Ecology: Individuals, Populations and Communities*, pp. 945, Blackwell Scientific Publications, Oxford
- Bell, R.H.V., 1971. A grazing ecosystem in the Serengeti. *Sci. Amer.* **255**, 86-93
- Belovsky, G.E., 1978. Diet optimisation in a generalist herbivore: the moose. *Theor. Popul. Biol.* **14**, 105-134
- Bhatnagar, Y., R. Wangchuk and R. Jackson, 1999. A survey of depredation and related wildlife-human conflicts in Hemis National Park, Ladakh, Jammu & Kashmir, India. International Snow Leopard Trust, Seattle
- Boyer, R.T., G.K. John and V.V. Ballenberghe, 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *J. Mammal.* **79**, 415-425
- Brown, J.H., 1975. Geographical Ecology of Desert Rodents. In: Cody, M.L. and J.M. Diamond (eds) *Ecology and Evolution of Communities*, pp. 315-341, Belknap, Cambridge



- Brown, J.H., 1987. Variation of desert rodent guilds: patterns, processes, and scales. In: Gee J.H.R. and P.S. Giller (eds) *Organisation of Communities: Past and Present*. Blackwell Scientific Publications, Oxford
- Brown, J.H. and G.A. Lieberman, 1973. Resource utilisation and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology*, **54**, 788-797
- Cerri, R.D. and D.F. Fraser, 1983. Predation and risk in foraging minnows: balancing conflicting demands. *Am. Nat.* **121**, 552-561
- Chundawat, R.S., 1992. The ecological studies of snow leopard and its associated prey species in Hemis National Park, Ladakh, India. PhD thesis, University of Rajasthan
- Clark, J.L., 1964. *The great arc of the wild sheep*, pp. 247, University of Oklahoma Press, Norman
- Cody, M.L., 1968. On the methods of resource division in grassland bird communities. *Am. Nat.* **102**, 107-148
- Cody, M.L., 1975. Towards a theory of continental species diversities. In: Cody, M.L. and J.M. Diamond (eds) *Ecology and Evolution of Communities*, pp. 214-257, Belknap, Cambridge
- Connell, J.H., 1975. Some mechanisms producing structure in natural communities. In: Cody, M.L. and J.M. Diamond (eds) *Ecology and Evolution of Communities*, pp. 460-490, Belknap, Cambridge
- Connell, J.H., 1980. Diversity and the co-evolution of competitors, or ghost of competition past. *Oikos*, **35**, 131-138
- Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**, 661-696
- Dueser, R.D. and H.H. Shugart, Jr., 1978. Microhabitats in forest-floor small mammal fauna. *Ecology*, **59**, 89-98
- Dzieciolowski, R., J. Krupka, Bajandelder and R. Dziedzic, 1980. Argali and ibex populations in the Kuhsyrh Reserve in Mongolian Altai. *Acta. Theriol.* **25**, 213-219
- Fedosenko, A.K., 1985. Present status of argali sheep populations in U.S.S.R. In: Hoefs, M. (ed) *Wild sheep: distribution, abundance, management and conservation of the sheep of the world and closely related mountain ungulates*, pp. 200-210, Northern Wild sheep and goat council, Yukon Wildlife Branch, Whitehorse, Canada

- Fedosenko, A.K., P.I. Weinberg and R. Valdez, 1995. Argali sheep survey in the headwaters of the Korunduk River, Kirghizstan. *Mammalia*, **59**, 452-455
- Festa-Bianchet, M., 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia (Berl.)*, **75**, 580-586
- Forsyth, D.M., 2000. Habitat selection and coexistence of the Alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) in the eastern Southern Alps, New Zealand. *J. Zool., Lond.* **252**, 215-225
- Fox, J.L. and A.J.T. Johnsingh, 1997. Country report for India. In: Shackleton, D.M. (ed) *Wild sheep and goats and their relatives*, pp. 215-231, IUCN, Gland, Switzerland and Cambridge, UK
- Fox, J.L. and C. Nurbu, 1990. Hemis, a national park for snow leopard in India's Trans-Himalaya. *Int. Ped. Book of snow leopards*, **6**, 71-84
- Fox, J.L., C. Nurbu and R.S. Chundawat, 1991a. Tibetan argali (*Ovis ammon hodgsoni*) establish a new population. *Mammalia*, **55**, 448-451
- Fox, J.L., C. Nurbu and R.S. Chundawat, 1991b. Mountain ungulates of Ladakh, India. *Biol. Conserv.* **58**, 167-190
- Fox, J.L., C. Nurbu, S. Bhatt and A. Chandola, 1994. Wildlife conservation and land-use changes in the Trans-Himalayan region of Ladakh, India. *Mount. Res. Devel.* **14**, 39-60
- Fritz, H., M. de Garine-Wichatitsky & G. Letessier, 1996. Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. *J. Appl. Ecol.* **33**, 589-598
- Gagon, M. and A.E. Chew, 2000. Dietary preferences in extant African Bovidae. *J. Mammal.* **81**, 490-511
- Gause, G.F., 1934. *The struggle for existence*. Baltimore:Williams & Wilkins.
- Gause, G.F., 1935. Experimental demonstration of Volterra's periodic oscillation in the numbers of animals. *Journal of Experimental Biology*, **12**, 44-48
- Geist, V., 1971. *Mountain sheep: A study of behaviour and Evolution*, pp. 383, University of Chicago Press, Chicago
- Geist, V., 1987b. On the evolution of the Caprinae. In: Soma, H. (ed) *The biology and management of Capricornis and related mountain antelopes*, pp. 3-40, Croom Helm, London

- Geist, V. and R.G. Petocz, 1977. Bighorn sheep in winter: do rams maximise reproductive fitness by spatial and habitat segregation from ewes? *Can. J. Zool.* **55**, 1802-1810
- Gordon, I.J., 1989. Vegetation community selection by ungulates on the Isle of Rhum. *J. Appl. Ecol.* **26**, 65-79
- Gordon, I.J. and A.W. Illius, 1989. Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* (Berl.), **98**, 167-175
- Green, M.J.B., 1987. Ecological separation in Himalayan ungulates. *J. Zool., Lond.* **1**, 693-719
- Hairston, N.G., F.E. Smith and L.B. Slobodkin, 1960. Community structure, population control and competition. *Am. Nat.* **94**, 421-425
- Hanley, T.A. and K.A. Hanley, 1982. Food resource partitioning by sympatric ungulates on Great Basin rangeland. *Journal of Range Management*, **35**, 152-158
- Hardin, G., 1960. The competitive exclusion principle. *Science*, **131**, 1292-1297
- Harris, R.B. and J.D. Miller, 1995. Overlap in summer habitats and diets of Tibetan Plateau ungulates. *Mammalia*, **59**, 197-212
- Hartmann, H., 1983. Pflanzengesellschaften entlang der Kashmirroute in Ladakh. *Jb. Ver. Schutz der Bergwelt*, 131-37
- Hoefs, M., 1979. Flowering plant phenology at Sheep Mountain, southwest Yukon Territory. *Can. Field. Nat.* **93**, 183-187
- Holmes, W.G., 1984. Predation risk and foraging behaviour of the hoary marmot in Alaska. *Behav. Ecol. Sociobiol.* **15**, 293-301
- Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Pop. Biol.* **12**, 197-229
- Holt, R.D., 1984. Spatial heterogeneity, indirect interactions and the coexistence of prey species. *Am. Nat.* **124**, 377-406
- Holt, R.D., 1989. Predation and competition: the interaction of two types of species interactions. *Oikos*, **54**, 256-263
- Holt, R.D. and J.H. Lawton, 1993. Apparent competition and enemy-free space in insect host-parasitoid communities. *Am. Nat.* **142**, 623-645
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symposia in Quantitative Biology*, **22**, 415-427

- Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145-159
- Illiuss, A.W. and I.J. Gordon, 1987. The allometry of food intake in grazing ruminants. *J. Anim. Ecol.* **64**, 481-492
- Jackson, R.M., 1996. Home range, movements and habitat use of snow leopard (*Uncia uncia*) in Nepal. Ph.D. dissertation, University of London
- Jarman, P.J., 1971. Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia, (Berl.)*, **8**, 157-78
- Jarman, P.J. and A.R.E. Sinclair, 1979. Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair, A.R.E. & M. Norton-Griffiths (eds) *Serengeti, dynamics of an ecosystem*, pp. 130-166, University of Chicago Press, Chicago
- Jeffries, M.J. and J.H. Lawton, 1984. Enemy-free space and the structure of ecological communities. *Biol. J. Linn. Soc.* **23**, 269-286
- Jenkins, K.J. and R.G. Wright, 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. *J. Appl. Ecol.* **25**, 11-24
- Johnston, A., L.M. Bezeau and S. Smoliak (1968). Chemical composition and in vitro digestibility of alpine tundra plants. *J. Wildl. Manage.* **32**, 773-777
- Koirala, R.A. and R. Shrestha, 1997. Floristic composition of summer habitats and dietary relationships between Tibetan argali (*Ovis ammon hodgsoni*), naur (*Pseudois nayaur*) and domestic goat (*Capra hircus*) in the Damodar Kunda region of Upper Mustang in Nepal Himalaya. M.Sc. thesis, Agricultural University of Norway
- Lack, D., 1971. *Ecological Isolation in Birds*, pp. 404, Blackwell Scientific Publications, Oxford
- Longva, K.S., 1998. Flexibility in blue sheep anti-predator habitat selection, as influenced by predator type. M.Sc. thesis, University of Tromsø
- MacArthur, R.H., 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton
- Mallon, D.P., 1991. Status and conservation of Large Mammals in Ladakh. *Biol. Conserv.* **56**, 101-119
- Manly, B.F.J., 1994. *Multivariate Statistical Methods*. Chapman and Hall, London
- Manly, B.F.J., L.L. McDonald, and D.L. Thomas, 1993. *Resource selection by animals*. Chapman and Hall, London

- M'Closkey, R.T. and B. Fieldwick, 1975. Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). *J. Mammal.* **56**, 119-129
- McNaughton, S.J., 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science*, **191**, 92-94
- McNaughton, S.J. and N.J. Georgiadis, 1986. Ecology of African grazing and browsing mammals. *Ann. Rev. Ecol. Syst.* **17**, 39-65
- Mercurio, K.S., 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. *Ecology*, **66**, 1417-1425
- Miller, J.D. and G.B. Schaller, 1998. Rangeland dynamics in the Chang Tang Wildlife Reserve, Tibet. In: Stellrecht, I. (ed) *Karakorum-Hindukush-Himalaya: Dynamics of Change*, pp. 125-147, Rudiger Koppe Verlag, Koln, Germany.
- Mittelbach, G.G., 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology*, **65**, 499-513
- Murray, M.G. and A.W. Illius, 2000. Vegetation modification and resource competition in grazing ungulates. *Oikos*, **89**, 501-508
- Mysterud, A., 1998. The relative role of body size and feeding type on activity time of temperate ruminants. *Oecologia*, **113**, 442-446
- Neu, C.W., C.R. Byers and J.M. Peek, 1974. A technique for analysis of utilisation-availability data. *J. Wildl. Manage.* **38**, 541-545
- Oli, M., I.R. Taylor and M.E. Rogers, 1993. Diet of the snow leopard (*Panthera uncia*) in the Annapurna Conservation Area, Nepal. *J. Zool.* **231**, 365-370
- Orians, G.H. and J.F. Wittenberger, 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* **137**, s29-s49
- Pianka, E.R., 1976. Competition and niche theory. In: May, R.M. (ed) *Theoretical Ecology*. Blackwell Scientific Publications, Oxford
- Pianka, E.R., 1994. *Evolutionary ecology*, pp. 486, HarperCollins College Publications, New York
- Polunin, O. and A. Stainton, 1985. *Flowers of the Himalaya*, pp. 580, Oxford University Press
- Putman, R.J., 1996. *Competition and resource partitioning in temperate ungulate assemblies*. London: Chapman and Hall

- Rachlow, J.L. and R.T. Boyer, 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *J. Zool., Lond.* **254**, 457-465
- Repasky, R.R., 1996. Using vigilance behaviour to test whether predation promotes habitat partitioning. *Ecology*, **77**, 1880-1887
- Roughgarden, J., 1983. Competition and theory in community ecology. *Am. Nat.* **122**, 583-601
- Schaller, G.B., 1977. *Mountain Monarchs, Wild Sheep and Goats of the Himalaya*, pp. 425, University of Chicago Press, Chicago
- Schaller, G.B., 1998. *Wildlife of the Tibetan Steppe*, pp. 373, University of Chicago Press, Chicago
- Schaller, G.B. and B. Gu, 1994. Ungulates in Northwest Tibet. *National Geographic Research & Exploration*. **10**, 266-293
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science*, **185**, 27-39
- Schoener, T.W., 1986. Resource partitioning. In: Kikkawa, J. and D.J. Anderson (eds) *Community Ecology: Pattern and Process*, pp. 91-126, Blackwell Scientific Publications, Oxford
- Shackleton, D.M. (ed), 1997. *Wild sheep and goats and their relatives*. IUCN, Gland, Switzerland and Cambridge, UK
- Sih, A., 1980. Optimal behaviour: can foragers balance two conflicting demands? *Science*, **210**, 1041-1043
- Sinclair, A.R.E., 1985. Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.* **54**, 899-918
- Strong, D.R., 1984. Exorcising the ghost of competition past: phytophagous insects. In: Strong, D.R., D. Simberloff, L.G. Abele and A.B. Thistle (eds) *Ecological Communities: Conceptual Issues and the Evidence*, pp. 390, Princeton University Press, Princeton
- Thomas, D.L. and E.J. Taylor, 1990. Study designs and tests for comparing resource use and availability. *J. Wildl. Manage.* **54**, 322-330
- Utida, S., 1953. Interspecific competition between two species of bean weevils. *Ecology*, **34**, 301-307
- Voeten, M.M. & H.H.T. Prins, 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, **120**, 287-294

Wegge, P., 1979. Aspects of the population ecology of blue sheep in Nepal. *Journal of Asian Ecology*, **1**, 10-20

Werner, E.E., J.F. Gilliam, D.F. Hall and G.G. Mittelbach, 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540-8

Wiens, J.A., 1977. On competition and variable environments. *Am. Sci.* **65**, 590-597

## **APPENDIX I**

Resource selection may be detected and measured by comparing any two of the three possible sets (use, unused, and available) of resource units (Manly *et al.*, 1993).

Three common sampling protocols have been identified based on these three sets:

**SP-A** Available units are either randomly sampled or censused and used resource units are randomly sampled.

**SP-B** Available resource units are either randomly sampled or censused and a random sample of unused resource units is taken.

**SP-C** Unused resource units and used resource units are independently sampled.

Three general study designs for evaluating selection have been identified:

**Design 1-** Measurements of use and availability are made for the collection of all animals in the study area; individual animals are not identified.

**Design 2-** Individual animals are identified and the use of resources is measured for each, but availability is measured at the population level.

**Design 3-** Individuals are identified and availability is measured for each animal.