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Habitat segregation between sympatric Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudois nayaur* in the Indian Trans-Himalaya

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Abstract

Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudois nayaur* have almost completely overlapping distributions encompassing most of the Tibetan plateau and its margins. Such a sympatric distribution of related species with similar ecological requirements implies that there is some degree of resource partitioning. This may be accomplished on the basis of habitat and/or diet separation. This study evaluated such ecological separation on the basis of physical habitat partitioning by these two sympatric ungulates in Hemis High Altitude National Park, Ladakh, India, in an area where the argali established a small new population in 1978. Such separation was tested for on the basis of expected difference between the species in their proximity to cliffs, associated with 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. The two species did not differ in their use of habitats in terms of elevation. They did, however, differ in their use of plant communities; blue sheep selected sub-shrub and grass-dominated communities whilst argali selected forb-dominated communities. We suggest that the two species coexist in this site as a result of the differential use of habitat associated with their species-specific anti-predator strategies.

Key words: argali, *Ovis ammon hodgsoni*, blue sheep, *Pseudois nayaur*, habitat selection, resource partitioning, niche relationship

INTRODUCTION

The pattern of resource partitioning in ungulate communities is widely studied (Jarman, 1974; Jarman & Sinclair, 1979; Gordon & Illius, 1989; 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 (i.e. current competition and/or predation) and evolutionary history (i.e. ghost of competition past) (Connell, 1980). In coevolved communities, the extant species may have competed in the past and developed different morphological and/or behavioural characteristics through evolutionary time, thus accomplishing resource partitioning. There is however an inherent problem in invoking the so-called ‘ghost of competition past’, as we cannot in retrospect determine the past processes and check whether they competed in the past or not (Begon, Harper & Townsend, 1996). Therefore, the pattern of resource partitioning in ungulate communities can only be tested and interpreted in terms of current ecological forces.

Resource partitioning studies have addressed mountain ungulate–livestock interaction for the Asiatic ibex *Capra ibex sibrica* (Bhatnagar *et al*., 2000) and blue sheep *Pseudois nayaur* (Mishra, 2001) in the relatively dry areas of the Indian Himalayan region, but other than theoretically (Mishra *et al*., 2002) niche separation among wild species has not been addressed in this area. Study of ecological separation among musk deer *Moschus chrysogaster*, goral *Nemorhaedus goral*, serow *Capricornis sumatraensis* and sambar *Cervus unicolor* has indicated that, in the moist and productive areas of the Greater Himalaya, these dissimilar sympatric species apparently partition the abundant resources (Green, 1987). Ungulates in the drier Trans-Himalayan region, however, live in a relatively impoverished environment (Mishra, 2001), where they are expected to compete for common resources, and coexist either by geographical or resource partitioning (Schaller, 1977). In recent years, there has been a great controversy on the relative importance of competition and predation in structuring ecological communities (see reviews by Sih *et al*., 1985; Gurevitch,

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Morrison & Hedges, 2000). Much of the literature has focused on competition as a plausible factor influencing differential use of resources by coexisting species (MacArthur, 1972; Pianka, 1976; Fritz, de Garine-Wichatitsky & Letessier, 1996), while importance of predation in resource partitioning is little understood. Predation may lead to resource partitioning provided the species are safest from predators in different habitats (Sih *et al*., 1985; Repasky, 1996).

The Tibetan argali *Ovis ammon hodgsoni*, henceforth 'argali', and the blue sheep *P. nayaur* are two wild ungulates of the Bovidae subfamily Caprinae, with almost completely overlapping distributions (see Shackleton, 1997) that encompass the Tibetan plateau and its peripheral areas. Although other subspecies of *O. ammon* occur in areas without blue sheep, where overlap occurs as with *O. a. hodgsoni* such sympatric distribution of related species with similar ecological requirements implies that they avoid any high degree of competition, and that 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 & Miller, 1995; Miller & Schaller, 1998) have shown a considerable overlap in diet, suggesting that they accomplish the resource partitioning primarily by habitat separation.

Various anecdotal reports on argali and blue sheep habitat utilization 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 (Fox, Nurbu & Chundawat, 1991; 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; Main, Weckerly & Bleich, 1996). 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 (Bleich, 1999; Geist, 1999). Thus, based on this difference, the blue sheep and argali are expected to show some differences in their use of habitat 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 escape terrain.

Although the species argali is widely distributed in mountainous regions of central Asia, the Tibetan argali is one of the two subspecies of *Ovis ammon* that are listed as endangered on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The most recent estimates suggest that, although other subspecies are much more numerous, there are < 7000 Tibetan argali left in the wild (Shackleton, 1997; Schaller, 1998). Within India there are only *c*. 200 argali remaining, mostly in Ladakh and a few in Sikkim (Fox & Johnsingh, 1997). The small population (*c*. 20 individuals) of argali within the Hemis High Altitude National Park in Ladakh presents an interesting case where three individuals established a new population in 1978 (Fox *et al*., 1991). The fact that these argali have not greatly increased in number since their arrival concerns the park managers.

Relying on theoretically-based expectations regarding niche (in this case habitat) separation, we have initiated an investigation of habitat use differences between this argali population and the blue sheep that share its range. This has clear implications for conservation efforts in the Hemis population, and perhaps with other argali populations. If predation was important in shaping their niche relationship, we expected blue sheep to use steep habitats near the cliffs and argali to use moderate slopes away from cliffs. Current predation does appear to be an important ecological factor in the study area, as several large predators are known to prey on these wild ungulates (Chundawat, 1992; Fox & Chundawat, 1995). Thus, we hypothesized that ecological separation between argali and blue sheep exists on the basis of physical habitat (escape terrain), and tested for this on the basis of expected difference in distance to cliff, with possible additional influences related to slope angle and/or elevation.

The study was carried out in summer (July–August) as the blue sheep, mostly males, migrate to higher elevations, where the argali occur, during this season (Chundawat, 1992). Although difference in the diet was not addressed in this summer season study, easily obtainable data on plant community type were also gathered to assess the differences in vegetation use that could be related to the aforementioned habitat differentiation.

METHODS

Study area

Our study was carried out in the north-western part of Hemis High Altitude National Park (34°N, 77°E) in the Ladakh Province of Jammu & Kashmir State, India (Fig. 1). The known range of the small argali population in the Park was delineated from local knowledge and past studies (e.g. Fox *et al.*, 1991). The entire argali range currently used encompasses *c*. 10 km^2 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 about 20 km from Leh, the principal town of Ladakh.

Elevation within the area used by argali ranges from 4000 to 5500 m. The argali range is relatively higher than the overall blue sheep range in the whole of the Rumbak catchment (Chundawat, 1992). Within the small area of argali use, topography varies from steep, rocky slopes along the highest ridgelines to gently rolling in the mid-elevation zone and steeper again at the lowest sites. Hemis National Park is situated in the rain shadow of the Great

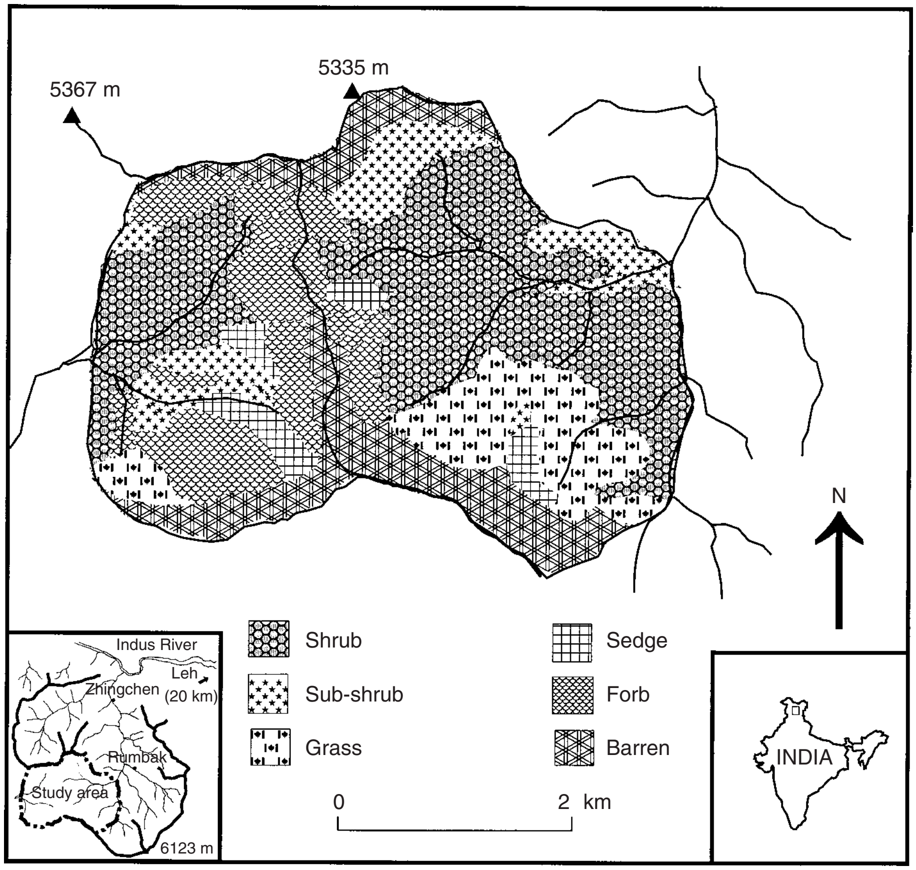

Fig. 1. Distribution of vegetation communities in the study area, north-western Hemis National Park, Ladakh, India.

Himalaya; hence the climate is characterized by cold and arid conditions, with low plant productivity confined to the 3-month growing season in summer (June–August). Diurnal temperatures in the Park in summer range from 15 °C to 35 °C (Chundawat, 1992). Annual precipitation in the Indus Valley at Leh is *c.* 100 mm, increasing somewhat south-westward and altitudinally to 500–1000 mm in valleys at the northern base of the Himalaya (Hartmann, 1983), and is probably *c.* 500 mm in the study area.

Vegetation of Hemis National Park is characterized by dry alpine steppe. Within the study area there are no trees, and vegetation consists of small shrubs, sub-shrubs, grasses, sedges and forbs (Fig. 1; see Namgail (2001) for a complete description of the vegetation). Predators of the argali and blue sheep include snow leopard *Uncia uncia*, wolf *Canis lupus chanko*, and wild dog *Cuon alpinus*, with red fox *Vulpes vulpes montana* and golden eagle *Aquila chrysaetos* a threat only to the young lambs.

Habitat use

Data were collected by searching for argali and blue sheep from selected trails and ridges, all with good vantage points. Observations were conducted using 8 × 40 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. Observations on argali and blue sheep were taken between 06:00 and 20:00, but most of the observations were obtained from 06:00 to 12:00, when animals were active, and effects of human-related disturbance minimal. Although not distributed evenly throughout the day, these observations can reasonably be considered a representative sample for anti-predator related habitat use. All observations were made by 1 person, thus there was no inter-observer bias.

The locations of the blue sheep and argali groups were plotted on 1:50 000 topographic sheets with elevation contour intervals of 40 m. Elevation, distance to cliff, slope angle and vegetation type (plant community) at the animal locations were recorded. Elevation was determined from the topographic sheet, and slope angle calculated from the measured distance between the nearest contour lines. Distance to cliff was determined by measuring the distance between the animal location and the nearest cliff on the map. Cliffs, very steep slopes (> 45°) on an area of >30 m diameter with vertical drops of >3 m, were identified and mapped in the field. The vegetation was classified into 5 communities, based on physiognomy and dominant species, and mapped on the topographic sheet (Fig. 1). Subsequently, the mapped blue sheep and argali locations were classified as to different vegetation communities.

As there were only 20 argali present in the area (Namgail, 2001), pseudo-replication was inevitable

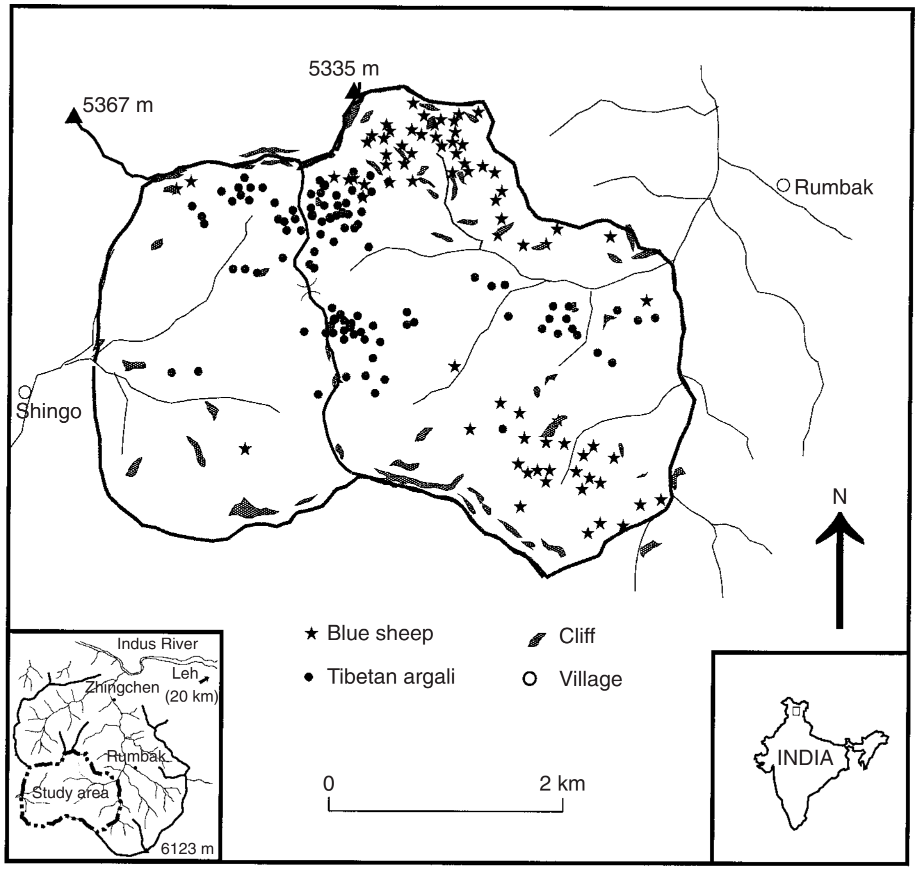

Fig. 2. Locations of Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudois nayaur* and cliffs in the upper Rumbak and Shingo catchments of Hemis National Park, Ladakh, India.

(Machlis, Dodd & Fentress, 1985), although frequent regrouping lessened the dependency. Owing to the high fluidity of group membership for blue sheep, and movements in and out of the study area (Namgail, 2001), it is difficult to demonstrate that the same groups shared the argali range throughout the study period. Nevertheless, a group of *c.* 27 males was frequently observed in the area through the entire study period. Blue sheep nursery groups used lower and more rugged areas in the vicinity of the study area, where they may be more secure from predators, similar to that observed for bighorn sheep *Ovis canadensis* (Bleich, Bowyer & Wehausen, 1997).

Available habitat

Availability of a habitat is the quantity of that habitat accessible to the population of animals during the study period (Manly, McDonald & Thomas, 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, and sometimes did. For availability of habitat, a systematic sample of habitat characteristics was obtained from a 1:50 000 topographic sheet of the study area. For this purpose, a point grid was overlaid on the topographic sheet 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. These variables were determined in the same way as described for the animal habitat use.

To assess the vegetation availability, a reconnaissance survey of vegetation was conducted in the area during the study period. The plant identification was carried out in the field, using Polunin & Stainton (1985) as a reference. Once the 5 plant communities were mapped on the topographic sheet (Fig. 1), a systematic sample at the same 366 points was taken to determine their availability.

Data analysis

Habitat preference was determined by relating use of a habitat to its availability. When resources are used disproportionately to their availability, use is said to be selective (Manly *et al*., 1993). 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). Although availability was sampled, since it was a systematic and intensive sampling with a point grid overlaid on the small study area, we assume that the sample available proportion represents the population proportion.

Table 1. Estimated habitat use for Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudois nayaur* in Hemis National Park, India. π_i, proportion of available resource units in category i; u_i, number of used resource units in category i; o_i, proportion of used units in category i and s_i, selection of habitat category i

		Tibetan argali			Blue sheep		
Variable	π_i	u_i	o_i	s_i	u_i	o_i	s_i
Distance to cliff (m)							
Very close to cliff (< 50)	0.119	6	0.058	–	11	0.134	0
Close to cliff (51–250)	0.374	39	0.379	0	43	0.524	+
Away from cliff (251–450)	0.336	47	0.456	+	20	0.244	0
Farther away (> 450)	0.171	11	0.107	0	8	0.098	0
Total	1.000	103	1.000		82	1.000	
Slope angle (degrees)							
Flat (< 10)	0.014	1	0.010	0	0	0.000	–
Moderate (11–30)	0.437	64	0.610	+	22	0.268	–
Steep (31–50)	0.522	40	0.381	0	57	0.695	+
Very steep (> 50)	0.027	0	0.000	–	3	0.037	0
Total	1.000	105	1.000		82	1.000	
Elevation (m)							
Low (< 4300)	0.075	4	0.038	0	2	0.024	–
Middle (4301–4600)	0.242	15	0.143	–	6	0.073	–
High (4601–4900)	0.372	31	0.295	0	33	0.402	0
Very high (> 4900)	0.311	55	0.524	+	41	0.500	+
Total	1.000	105	1.000		82	1.000	
Vegetation type							
Shrub	0.383	27	0.257	–	18	0.220	–
Sub-shrub	0.186	19	0.181	0	35	0.427	+
Grass	0.077	1	0.010	–	17	0.207	+
Sedge	0.038	0	0.000	–	4	0.049	0
Forb	0.071	57	0.543	+	1	0.012	–
Barren	0.246	1	0.010	–	7	0.085	–
Total	1.000	105	1.00		82	1.000	

+, Selection; −, avoidance; 0, use: in proportion to availability based on Bonferroni-adjusted 95% confidence intervals for habitat use.

For the determination of habitat selection, the variables were classified into distinct categories. To statistically test significant departures of use from availability, the modified χ^2: log-likelihood chi-square test (χ^2_L) was calculated (see Manly *et al*., 1993). If the χ^2_L 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 for habitat use were constructed. 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.

RESULTS

A total of 82 observations on blue sheep and 105 observations on argali was recorded during the 2-month study period (Fig. 2). The argali population was composed of three adult males, 11 adult females, one yearling and five lambs (Namgail, 2001). Eighty five percent of blue sheep observations were of all-male groups, with 6% mixed groups, and 9% nursery groups.

Argali selected the habitat category ‘away from cliff’, and avoided the category ‘very close to cliff’ ($\chi^2_L = 19.53$, $P < 0.01$). Blue sheep in contrast selected the category ‘close to cliff’ ($\chi^2_L = 9.7$, $P < 0.05$), and its use of other categories were in proportion to the respective availabilities (Table 1). Argali also selected ‘moderate’ slopes, and avoided ‘very steep’ slopes ($\chi^2_L = 9.26$, $P < 0.05$). Blue sheep use of ‘steep’ slopes was significantly higher than expected, and they avoided ‘moderate’ slopes ($\chi^2_L = 29.80$, $P < 0.01$).

Argali used the ‘very high’ elevation category more than expected from its availability, and avoided the middle elevation habitats ($\chi^2_L = 21.56$, $P < 0.01$), while it used the other two categories as expected (Table 1). Blue sheep also exhibited a similar pattern of habitat use ($\chi^2_L = 29.80$, $P < 0.01$). Regarding vegetation, argali selected forb communities (dominated by *Potentilla* spp., *Oxytropis* spp., *Astragalus* spp., *Thermopsis* sp., *Delphinium* sp., *Dracocephalum* sp. and *Saussurea* spp.), and avoided shrub (mainly *Caragana* spp. and *Artemisia* spp.), grass (mainly *Festuca* sp., *Poa* spp. and *Elymus* spp.), and sedge (*Carex* spp. and *Kobresia* spp.) ($\chi^2_L = 189$, $P < 0.0001$) (Table 1). Blue sheep, however, avoided forb communities, and selected sub-shrub (dominated by *Aconogonum* sp. and *Stachys* sp.) and grass communities ($\chi^2_L = 55.0$, $P < 0.001$).

DISCUSSION

Our results support the hypothesis that ecological separation between argali and blue sheep exists on the basis of physical habitat selection. Observations of the two species showed a distinct niche divergence, with argali using relatively open terrain, and blue sheep using more rugged terrain, which conforms to previous anecdotal reports (Fox *et al*., 1991; Schaller, 1977, 1998). Ecologists have long considered that habitat segregation serves to reduce both interference and exploitation competition, and facilitates coexistence of ecologically similar species (Pianka, 1978). Thus the habitat segregation, in terms of proximity to cliff and slope steepness, by blue sheep and argali in Hemis National Park may minimize competition and facilitate their coexistence. Although the species also differed in their association with different vegetation communities, implications regarding diet are speculative.

As there is evidence of substantial predation pressure in the study area (Chundawat, 1992), prey species may actively lower risk of predation by selecting habitat that serves as effective refuge against predators (Houtman & Dill, 1998). During the present investigation, 65% of the sightings of blue sheep were within 250 m from cliffs (escape terrain). Such high affinity by blue sheep toward cliffs, which generally support less vegetation, suggests that forage is not the only constraint in their habitat use. In contrast, 64% of the argali observations were beyond 250 m from cliffs, which illustrates the importance of open terrain in the determination of habitat use by argali. This difference in the use of habitat, in terms of proximity to cliff can be attributed to the species-specific anti-predator behaviour.

Various studies (Belovsky, 1978; Sih, 1980; Festa-Bianchet, 1988; Houtman & Dill, 1998) with their implications to the 'optimal foraging theory' suggest that an animal should forage in areas where its intake rate is highest and predation risk lowest. Although the blue sheep may be safer in the cliffs (escape terrain), there is generally less forage available in them (Namgail, 2001). Therefore, they move out of such escape terrain for feeding (Wegge, 1979). Blue sheep probably need to strike a balance between food acquisition and predator avoidance, while feeding outside the escape terrain. Their high affinity for the neighbourhood of cliffs may thus minimize overlap with argali.

Although diet competition was not addressed in this summer season study, as food is not likely to be limiting during this season (Miller & Schaller, 1998), association with plant communities was assessed. Blue sheep selected grass and sub-shrub communities, which were more abundant in vicinity of the cliffs. Argali, on the other hand, showed higher affinity for forb-dominated communities, which were more abundant in the open areas. Assuming that each species feeds on the dominant plants, such a selection pattern is at least consistent with the results of some diet-based studies (Koirala & Shrestha, 1997; Miller & Schaller, 1998) that record a preponderance of forbs in argali diet, and graminoids in blue sheep diet.

As for the nutritional relationships associated with interspecific differences in body size (Bell, 1971; Gagon & Chew, 2000), one would expect blue sheep (relatively smaller) to show a forb-dominated diet and argali a graminoid-dominated diet. The converse relationship observed in this study could be dictated by the plant community use associated with anti-predator habitat selection. In any case, because forage is not limiting at this time of year, such expectation for diet differences may not be appropriate.

The study has shown that despite the sparse vegetation (Chundawat, 1992), argali and blue sheep coexist in Hemis National Park, apparently by differential anti-predator habitat selection by the two species. The differential use of habitat as well as vegetation communities suggests little overlap on these dimensions, and presumably a reduced possibility of competition between argali and blue sheep. Although the continued presence of argali in the area thus seems possible, the slow growth of this new population may simply be the result of the limited amount of appropriate habitat here for this species. Other factors, such as possible competition with livestock may be important (Namgail, 2001); a threat that should also be assessed soon because of the precarious overall status of argali in India.

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