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Habitat relationships between wild and domestic ungulates in Nepalese trans-Himalaya

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Abstract

In the semi-arid ecosystems of Asia, where pastoralism is a main subsistence occupation, grazing competition from domestic stock is believed to displace the wild ungulates. We studied the habitat relationships among sympatric naur and domestic yak and smallstock in Phu valley in upper Manang district, Nepal, on the basis of their distribution on vegetation types, elevation and slope. To control for the disturbance effect by humans, we collected the data on naur from those ranges where domestic stock were not being attended by herders. We applied correspondence analysis to explore habitat associations among animal groups ($n = 1415$) within and across-seasons. Within each association, interspecific habitat overlaps and species habitat preferences were calculated. Naur was strongly associated with free-ranging yak as they used similar altitudinal ranges in all seasons, except in spring. Their distributions on vegetation types and slopes were also quite similar, except for a stronger preference for alpine meadows by naur during summer and winter. Naur and smallstock did not form temporal associations as the latter consistently used lower elevations. In autumn and spring, however, naur spatially overlapped with the summer range of smallstock, and both preferred the alpine meadow habitat during these periods. Alpine meadow was the least abundant vegetation type but was consistently and preferentially used by all animal groups across seasons. At high stocking densities, all three animals groups are therefore likely to compete for this vegetation type. The role of spatio-temporal heterogeneity for interpreting the interspecific relationships among ungulates in the semi-arid rangelands of the trans-Himalaya is discussed.

Keywords: Blue sheep; Competition; Habitat partitioning; Naur; Pastoralism; *Pseudois nayaur*

1. Introduction

The trans-Himalayan rangelands have been used by domestic stock along with wild herbivores for centuries (Schaller, 1998). In recent years, there has been a growing concern about conflicts between wildlife conservation and pastoralism in this region (Bagchi et al., 2004; Bhatnagar et al., 2006). This has become even more significant in the Nepalese trans-Himalaya as here pastoralism represents a main subsistence strategy (Oli et al., 1994). One of the fundamental issues underlying this conflict has been the presumed competition for

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resources between wild and domestic animals (Mishra et al., 2004). Knowledge about habitat relationships among sympatric herbivores is a prerequisite for examining resource partitioning and competition (Putman, 1996).

Naur (blue sheep/bharal, *Pseudois nayaur*) is widespread and locally abundant throughout the Himalayas (Schaller, 1977). The domestic stock, on the other hand, was introduced in the region and thus did not co-evolve with naur. Consequently, niche overlap between them is expected. Furthermore, owing to the tendency of herders to maintain their stock at artificially higher densities by supplemental feeding, shelter and medical attention, domestic stock are at a competitive advantage over their wild relatives and may therefore out-compete the latter.

A few studies have attempted to quantify the niche relationships among trans-Himalayan ungulates. However, the authors seem to disagree over the process and the outcome of such interactions. For instance, in a study on livestock and ibex (*Capra sibirica*), Bhatnagar et al. (2000) found that these two groups of animals were spatially separated in summer and along various habitat axes during spring and autumn when they overlapped spatially. From the Tibetan plateau, Schaller and Gu (1994) reported that the summer range use of smallstock and naur overlapped, whereas in Nepal, Shrestha et al. (2005) found them to be spatially separated. Similarly, both Mishra et al. (2004) and Shrestha et al. (2005) concluded that the diet of naur overlapped closely with that of smallstock, but Harris and Miller (1995) found that they differed.

Presence of herders may obscure natural interaction patterns. Recently, Namgail et al. (2006) showed a shift in habitat use and foraging behavior by Tibetan argali (*Ovis ammon hodgsoni*) following the appearance of domestic stock with herders in a pasture in Ladakh, India, thereby implying interference competition between them. Consistent with this, Bagchi et al. (2004) and Harris and Loggers (2004) suggested that the interference by herders should also be considered in addition to exploitative competition when interpreting interactions between wild and domestic herbivores in the trans-Himalaya.

In the rangelands of Nepalese trans-Himalaya, no study has yet investigated the interactions between wild and domestic herbivores in the use of habitats during all seasons of the year. Nor has any study been undertaken elsewhere, which compares habitat relationships across seasons. In general, studies of potential competition focus on temporal habitat and diet overlaps. However, successive use of the same habitat by different herbivores is also important when analyzing competitive relationships. The objectives of our study were, therefore, as follows: (1) Describe the pattern of associations between naur, domestic sheep (*Ovis aries*) and goats (*Capra hircus*, hereafter collectively termed 'smallstock'), and domestic yak (*Bos grunniens*, hereafter termed 'yak') on the basis of their use of vegetation type, elevation and slope within and between seasons. (2) Within each seasonal or cross-seasonal association of naur and domestic stock, quantify the extent of interspecific habitat overlap and species preferences for vegetation type, elevation and slope.

2. Materials and methods

2.1. Study area

The 125 km^2 study area in Phu valley (28°46′N, 84°17′E) of Manang District in north-central Nepal is located in the rain-shadow of the Annapurna Himalaya. This semi-arid region receives annually less than 400 mm of precipitation (ICIMOD, 1996) and mostly in the form of snow during winter. The mean maximum and minimum temperatures recorded during fieldwork were 5.8 and −7.3 °C in January and 18 and 9.5 °C in July. The snow and frozen ground start to thaw in late March.

Topography is dominated by very rugged terrain. The northern higher part (>4500 m a.s.l.) is less rugged than in the south and has greater affinities with that of the Tibetan plateau. The gradient of altitude and slope governs the composition and distribution vegetation (Kala and Mathur, 2002). Three broad vegetation types were identified on the basis of dominant plant species (Table 1): (1) Alpine meadows are distributed in flat pockets and basins. (2) Scrublands are widespread on rugged and dry, southerly slopes. (3) Alpine grasslands are located at higher elevations, mainly in northern, mesic sites. Faunal diversity is relatively low. Among mammalian carnivores, snow leopard (*Uncia uncia*) is common (Conradi, 2006). Red fox (*Vulpes vulpes*) is also known to exist in the area, whereas wolf (*Canis lupus*) and brown bear (*Ursus arctos*) are absent. Naur is

Table 1
Characteristics of vegetation types in the study area in Phu valley, Nepal

	Alpine meadow	Grassland	Scrubland
Relative Area[a] (%)	13	31	56
Bare ground (%)	29	38	42
Elevation (m)	3800–4900	4200–5200	3640–4700
Slope (deg)	<15	<45	All
Important plant species	*Stellera chasmaejanae*	*Festuca* sp.	*Lonicera spinosa*
	Artemisia spp.	*Carex* spp.	*Astragulus* spp.
	Chesneya nubigena	*Stipa* spp.	*Spiraea* sp.
	Hippophae tibetana		*Cotoneaster* spp.
	Kobresia pygmea		*Caragana jubata*
	Carex spp.		*Rhododendron anthropogon*
			Bistorta sp.

[a]Excluding non-vegetated areas.

abundant and the only large wild ungulate, distributed in a density of approximately 10 animals/km^2 (R. Shrestha, pers. obs.).

The only settlement in the valley, Phu village, is located ca. 7 km from the Tibetan border and consists of 33 households. People follow Tibetan Buddhism, and the abbot of Phu Monastery has placed a ban on hunting, which appears to be strictly followed by the residents. Although some farming takes place, animal husbandry is the main traditional subsistence occupation. The herders own multiple species of domestic stock, yak ($n = 802$), goats ($n = 718$), sheep ($n = 406$), cow ($n = 96$) and horse ($n = 71$). Altogether the total stocking density of domestic animals is nearly double that of naur. As in other parts of Tibetan rangelands, domestic stock is seasonally moved to different pastures. During winter, villagers vacate Phu village and move to lower elevation in the southern part of the study area along with all their stock animals. In spring, the pastures in and around Phu village are used for grazing. In summer and autumn, animals are taken to higher elevations and then herded from both temporary encampments and permanent stone-walled quarters built for seasonal use. For a short period in early autumn, however, they bring their livestock back to Phu village to let them graze in the harvested fields and a nearby pasture. The small stock are usually herded, and periodically moved among different pastures whereas yaks move freely.

2.2. Data collection

Data on habitat use were collected by systematically searching opposite slopes from fixed vantage points using 8×40 binoculars and a 15–60 $\times$ variable spotting scope. Because smallstock were herded from low-elevation to higher pastures and then back again in the evening, we purposely spread our observation throughout the day (600–1800 h). All observations of naur were undertaken in the parts of the range where domestic stock were not attended by herders so as to control for the effect of human interference. A total of 766 groups of naur, 392 herds of yak and, 257 herds of smallstock were observed in winter (4 January–30 March), spring (1 April–15 June), summer (16 June–15 September) and autumn (16 September–3 January). The definition of seasons followed the calendar of local livestock movements. Animal locations were plotted on a 1:10,000 Topographic Map and later transferred to Arc View 3.1 (Environmental Systems Research Institute, Redlands, CA) using software 'World File Generator'. Global positioning system (GPS) readings of animal locations were also taken as and when possible in order to cross-validate the points marked on the topographic map. The use of different habitat categories was obtained using the Geo Processing facility in Arc View 3.1. These were later verified with field records for accuracy.

Habitat availability was assumed to be constant for naur throughout the year. Given the seasonal restrictions imposed on the movement of domestic stock, available habitat was adjusted accordingly for them. Habitat categories such as elevation and slope were mapped by converting the vector contour map (HMG/N, 2001) of the study area into a grid map of 50 m 50 m pixels with the help of Spatial Analyst of the Arc GIS 9 (Environmental Systems Research Institute, Redlands, CA). The accuracy was verified using GPS positions recorded at several reference points in the field. The three vegetation types, which could readily be identified from a distance on the basis of physiognomy and dominant life form (Table 1), were mapped in the field on a 1:10,000 Topographic map. These were later scanned and transferred to a digital map using World File Generator in Arc View 3.1.

2.3. Data analysis

First, we compared altitudinal distributions of animal groups within and across seasons by calculating 99% confidence intervals around their mean altitudinal positions. Differences between naur and domestic stock were tested using Kruskal–Wallis test. Because of unequal sample sizes, Dunn's test was selected for subsequent multiple comparisons (Zar, 1996).

Because correspondence analysis (CA), an exploratory multi-dimensional graphical technique (Greenacre, 1984) has become a popular method for analyzing animal–habitat relationships (Beardall et al., 1984; Dekker et al., 1996; Mwangi and Western, 1998), we then applied this method to look for seasonal and cross-seasonal patterns of association between animal groups and habitat categories. CA was followed by calculating habitat overlap indices and species–habitat preferences for all habitat categories within each association of animal groups as revealed by the CA. A brief description of the procedures is outlined below.

CA was applied by constructing a contingency table of the frequency distributions of naur, smallstock and yak in the following habitat variables: (1) vegetation types; alpine meadow, scrubland and grassland, (2) elevation zones; low (3640–4320 m), middle (4320–4640 m), high (4640–4920 m) and very high (4920–5240 m), and (3) slope categories; flat (0–10^{o}), moderate (11–30^{o}), steep (31–50^{o}), and very steep (51–90^{o}). The initial analysis identified the 'low elevation zone' as an outlier, probably because domestic stock is brought down to low elevation in winter. It was therefore treated as a supplementary variable in the further analysis. The analyses resulted in two principal axes explaining nearly 65% of the total variation. Consequently, a scatter plot was prepared, showing the associations of animal groups on the basis of their seasonal habitat use patterns. We used MINITAB for Windows version 14 to run the analysis.

Habitat overlaps were quantified by calculating proportional similarity indices (Schoener's Index; Schoener, 1968) for the most closely associated animal groups as identified by the CA. It is a symmetric index of niche overlap and approaches 0 for species that share no resources and approaches 1.0 for species pairs that completely overlap in resource use:

$$O_{12}=O_{21}=1.0-0.5\sum|P_{i1}-P_{i2}|,$$

where O_{12} is the overlap of species 1 on species 2, and P_{i1} and P_{i2} are the proportions of habitat i used by species 1 and species 2, respectively.

The statistical significance of the habitat overlaps was determined by comparing them with null models (Gotelli and Graves, 1996), which were obtained by randomizing a matrix comprising data on elevation, slope and vegetation type. We used Winemiller and Pianka's (1990) randomization algorithm 3 (RA 3) to generate 1000 null models. This procedure retains the observed niche breadth of the species, but allows utilization of any of the possible habitat categories. As the habitat categories were not equally distributed in the study area, we weighted the habitat use by their corresponding availability (Gotelli and Graves, 1996; Lawlor, 1980). Thus, the observed overlap was compared with the distribution of simulated mean overlaps and two-tailed probability values were calculated. We used EcoSim software to run the null model analysis (Gotelli and Entsminger, 2004).

We followed Neu et al. (1974) and McClean et al. (1998) to assess seasonal preferences for habitat categories by each animal group. G-tests were employed to determine if an animal group used the habitat categories as per availability across seasons (Manly et al., 2002). To determine if a particular habitat category was preferred or avoided, a 95% confidence interval was created for each category by applying Bonferroni corrections to the Z-statistic (Byers et al., 1984; Neu et al., 1974).

3. Results

3.1. Altitudinal distribution

Altitudinal segregation between smallstock and the other two ungulates was apparent throughout the year as the former significantly and consistently used lower altitudes than free-ranging yak and naur in every season ($H = 240$, $k = 11$, $P < 0.01$, Fig. 1). Free-ranging yak and naur, on the other hand, used similar altitudinal range in all seasons (Dunn's test, all $Q < 1.181$, $P > 0.5$, $k = 11$), except in spring ($Q = 3.830$, $P < 0.01$, $k = 11$). Although altitudinally segregated within season (example in spring, Fig. 2a), the summer altitudinal range of

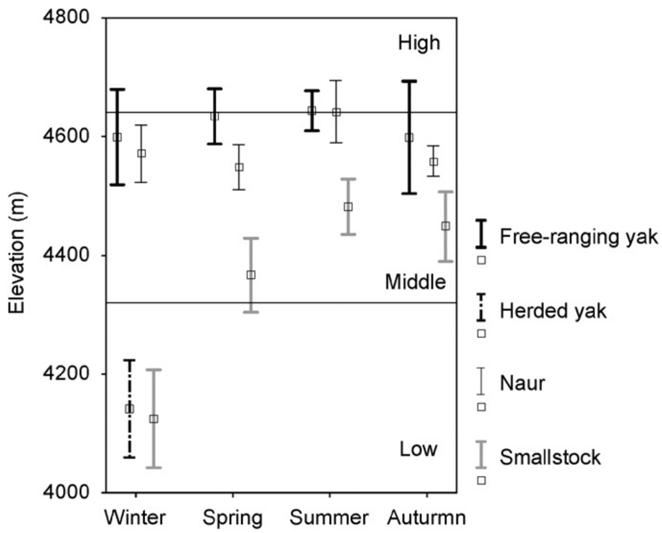

Fig. 1. Altitudinal distribution of animal groups in different seasons. The error bars denote 99% confidence intervals of the means. Three elevation zones (high, middle and low) are also shown in the figure.

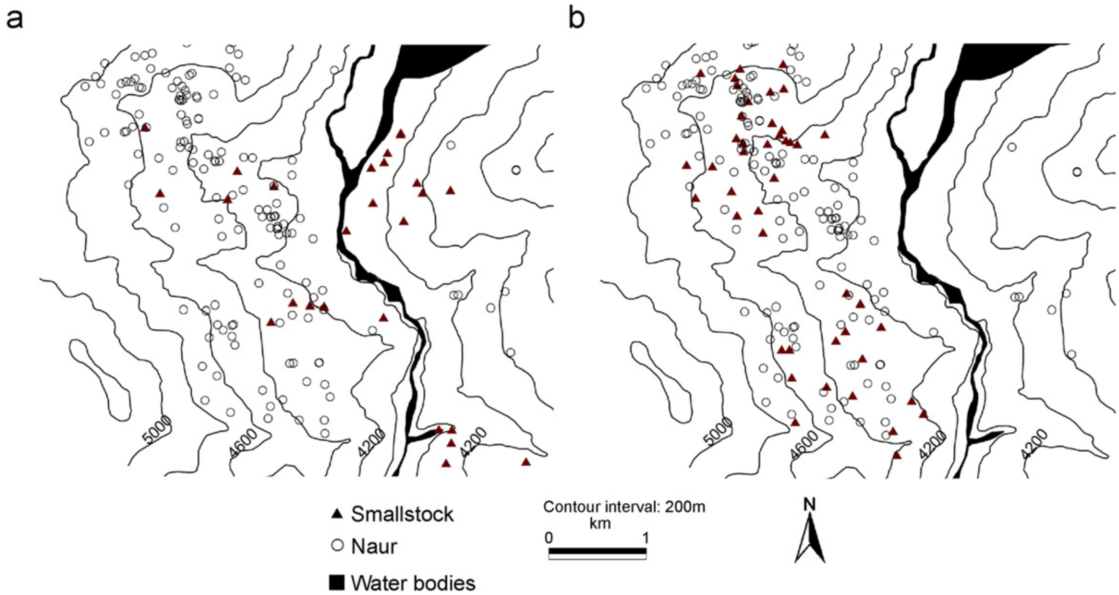

Fig. 2. Spatial distribution of naur and smallstock in the Ramlea basin of the study area: (a) naur and smallstock in spring and (b) naur in spring and smallstock in summer.

smallstock were similar to the spring (Fig. 2b) and autumn ranges of naur ($Q = 2.63$ and 2.76, respectively, $k = 11$, $P > 0.05$, both, Fig. 1).

3.2. Animal–habitat associations within and across seasons

Component 1 of the CA (elevation and vegetation type) explained about 42% and component 2 (steepness) about another 22% of the variation (Fig. 3a). The scatter plot using these two components revealed four associations between naur and domestic stock within and across seasons (Fig. 3b). Significant habitat overlap indices (O) between animal groups within each of these associations ($O > 0.86$, $P < 0.01$) supported the results obtained in the CA. However, further analyses of species habitat preferences within associations showed similarities and differences among them on a finer scale.

3.2.1. Association I: Naur and free-ranging yak in winter

Within this association, naur significantly preferred alpine meadows, avoided grassland and used scrublands randomly, while yak used all three vegetation types randomly (Table 2). Conversely, the latter were more selective on elevation, as they significantly preferred both middle and high elevation and avoided low and very high elevation, while naur preferred only the middle elevation zone (Table 3). As for slope, both used all the slope categories randomly except for very steep slope, which was significantly avoided by free-ranging yaks (Table 4).

3.2.2. Association II: Naur in spring and free-ranging yak in autumn

Naur in spring preferentially used alpine meadows (Table 2), and avoided very high elevation (Table 3) and steeper slopes (Table 4), like free-ranging yak did in autumn. However, naur avoided the scrubland and grassland vegetation types while yak used these in proportion to availability (Table 2).

3.2.3. Association III: Naur in summer and free-ranging yak in summer and spring

The habitat use of naur during summer was closely associated with that of yak in spring and summer. Both species similarly either preferred or randomly used alpine meadows and grasslands (Table 2), middle and high elevation zones (Table 3) and flat and moderate slopes (Table 4). They avoided scrublands, low and very high elevation zones, and steeper areas (all $P < 0.05$).

3.2.4. Association IV: Naur in autumn and smallstock in summer

In contrast to the close seasonal associations between naur and yak, the former interacted with smallstock only spatially, but not temporally. In autumn, naur used the summer habitats of smallstock (Fig. 3b), and then both preferentially used alpine meadow (Table 2) and middle elevation zone (Table 3) and avoided scrublands as well as very high elevation and very steep areas (Table 4). However, grasslands were randomly used by smallstock whereas naur avoided them (Table 2).

In addition, the spring habitat use by naur was also closely related with that of smallstock in summer (Tables 2–4). The CA did not reveal a spatial association between them probably because smallstock were more randomly distributed on slope categories than naur (Table 4).

4. Discussion

4.1. Habitat overlap

Owing to altitudinal segregation, naur and smallstock did not overlap temporally. Previous studies have suggested (Bagchi et al., 2004; Harris and Loggers, 2004; Oli, 1996; Shrestha et al., 2005) as well as documented (Namgail et al., 2006), that the disturbance by humans causes displacement of wild herbivores from their range. To control for this factor, we collected our habitat data on naur from those ranges where domestic stock were not being herded. Under such conditions, greater habitat overlap between the two animal groups was expected if interference by humans is a major displacement factor. Instead of human disturbance, a possible reason for the observed temporal habitat separation might have been poor quality of the pastures

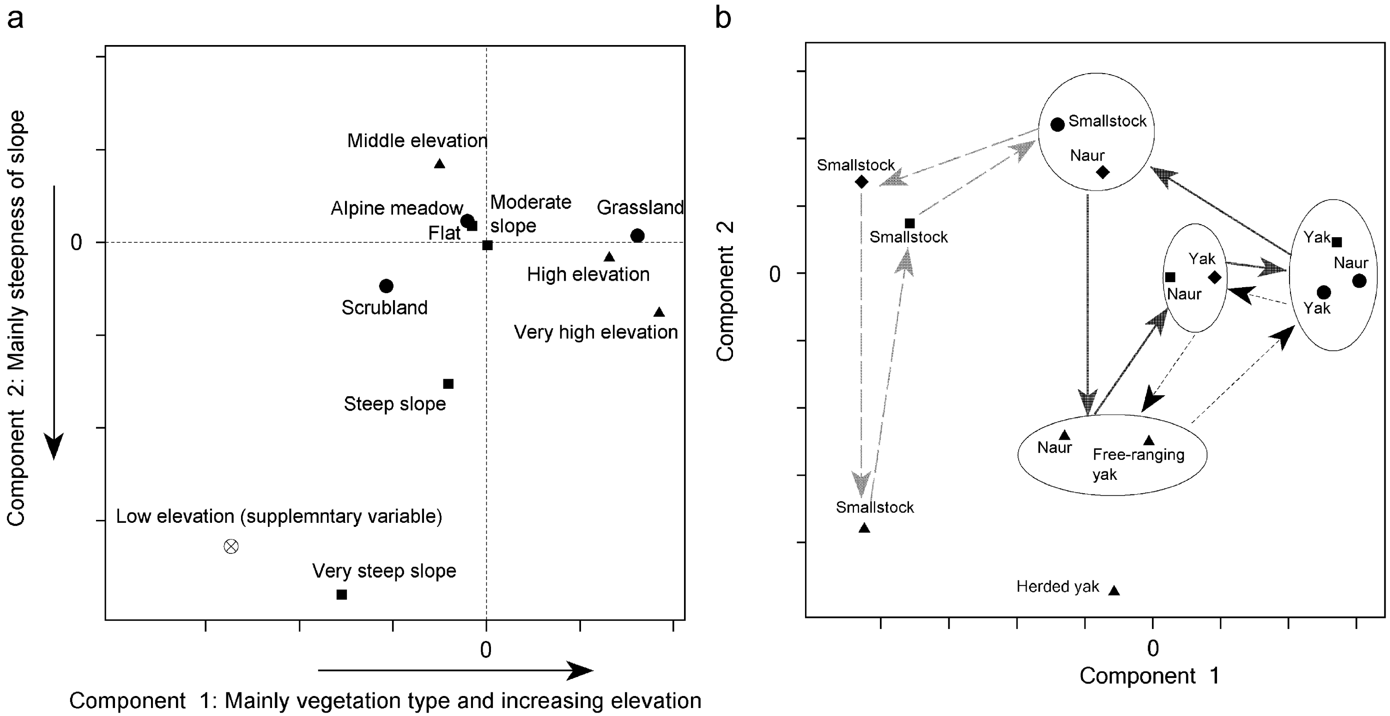

Fig. 3. Animal–habitat associations within and across seasons as revealed by the correspondence analysis: (a) habitats, (b) animal groups, where seasonal locations were indicated by symbols: squares (spring), circles (summer), diamonds (autumn), and triangles (winter) and movements by arrows: long-dashed gray (smallstock), straight black (naur) and short-dashed black (free-ranging yaks).

Table 2
Seasonal use of vegetation types by domestic stock and naur in Phu valley, Nepal

Seasons	Vegetation type	Availability[a] (%)		Utilization (%)				Selection[b]			
		All	Domestic stock	Smallstock	Naur	Free-ranging yak	Herded yak	Smallstock	Naur	Free-ranging yak	Herded yak
Spring	Alpine meadow	13.3	13.3	28.6	45.8	30.2		+	+	+	
	Grassland	31.2	31.2	8.8	18.9	44.8		–	–	+	
	Scrubland	55.5	55.5	62.6	35.2	25.0		0	–	–	
Summer	Alpine meadow	13.3	13.8	44.1	32.7	22.7		+	+	0	
	Grassland	31.2	30.4	25.4	39.6	38.7		0	0	0	
	Scrubland	55.5	55.8	30.5	27.7	38.7		–	–	–	
Autumn	Alpine meadow	13.3	13.8	37.2	35.7	35.4		+	+	+	
	Grassland	31.2	30.4	0.0	22.7	22.9		–	–	0	
	Scrubland	55.5	55.8	62.8	41.6	41.7		0	–	0	
Winter	Alpine meadow	13.3	12.1	22.9	28.9	24.4	37.0	0	+	0	+
	Grassland	31.2	33.2	11.4	13.3	20.0	33.3	–	–	0	0
	Scrubland	55.5	54.7	65.7	57.8	55.6	29.6	0	0	0	–

[a]Availability was assumed to be constant for naur in all seasons, but it was adjusted for domestic stock according to the seasonal restrictions imposed on certain pastures by herders.
[b]Symbols (+, 0, –) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).

used by smallstock. As the smallstock are usually herded in the vicinity of their overnight holding pens, their foraging areas receive a heavy grazing pressure as was also observed by Zhao et al. (2007) in the Tien Shan mountains. A high proportion of increaser species such as *Stellera chamaejasme*, *Oxytropis tatarica* and *Artemisia* spp. etc. as was also noted by Sherpa and Oli (1988) in a previous survey in Phu, supports this.

As smallstock were shifted to higher altitudes during summer, we found them to use the spring and autumn elevations of naur. The effect of summer grazing by smallstock appeared to be particularly important as both preferentially used alpine meadow in these periods. Nevertheless, the quality and quantity of autumn forage are probably not reduced as a consequence of summer use by smallstock. Tibetan plateau domestic ungulates are considered not to be limited by forage quantity in autumn (Long et al., 1999). Also, forbs, which are most abundant in alpine meadows, are expected to retain good quality well into autumn relative to graminoids (Long et al., 1999). This might also explain why naur is attracted to alpine meadows in autumn.

Unlike the weak temporal association with smallstock, naur appeared to be more closely related with yak as both consistently used similar elevations for most part of the year. Earlier studies have also reported a closer association between free-ranging yaks and naur (Harris and Miller, 1995) and ibex (Bagchi et al., 2004) than with smallstock in the use of habitats.

The summer pasture of naur appeared to receive heavy grazing pressure as yak used it not only in summer but also during spring. Generally, ecologists consider food not to be a limiting factor during summer because of the abundant plant growth. However, reports from temperate environments in Europe (Saether et al., 1996) and North America (Bowyer, 1991) show that summer food plays a significant role for ungulate winter survival and for population performance. Likewise, on the Tibetan Plateau, nutritional quality of forage during summer is suggested to be a mediator of livestock survival during the remainder of the year (Cincotta et al., 1991).

Spatial overlap also occurred as yak descended from high elevation zones in autumn and subsequently used naur spring range. As already pointed out, naur spring pasture was also used by smallstock in summer. The successive use of the same habitat complex by all three animal groups across different seasons raises an

Table 3
Seasonal use of elevation zones by domestic stock and naur in Phu valley, Nepal

Seasons	Elevation zones	Availability[a] (%)		Utilization (%)				Selection[b]			
		All	Domestic stock	Smallstock	Naur	Free-ranging yak	Herded yak	Smallstock	Naur	Free-ranging yak	Herded yak
Spring	Low	17.8	17.8	34.3	18.3	5.2		+	0	–	
	Middle	23.2	23.2	52.9	41.9	38.1		+	+	+	
	High	32.0	32.0	12.7	31.5	47.0		–	0	+	
	Very high	26.9	26.9	0.0	8.3	9.7		–	–	–	
Summer	Low	17.8	9.6	11.7	5.2	2.4		0	–	–	
	Middle	23.2	24.7	73.3	39.7	39.0		+	+	+	
	High	32.0	36.1	15.0	40.5	54.5		–	0	+	
	Very high	26.9	29.7	0.0	14.7	4.1		–	–	–	
Autumn	Low	17.8	9.6	15.7	4.9	11.5		0	–	0	
	Middle	23.2	24.7	70.6	64.0	40.4		+	+	0	
	High	32.0	36.1	13.7	28.1	32.7		–	0	0	
	Very high	26.9	29.7	0.0	3.0	15.4		–	–	–	
Winter	Low	17.8	35.5	86.4	14.8	10.2	88.2	+	0	–	+
	Middle	23.2	20.1	11.4	45.1	40.8	5.9	0	+	+	–
	High	32.0	23.3	2.3	33.1	42.9	5.9	–	0	+	–
	Very high	26.9	21.1	0.0	7.0	6.1	0.0	–	–	–	–

Low, middle, high and very high elevation zones refers to (3640–4320 m), (4320–4640 m), (4640–4920 m) and (4920–5240 m), respectively.
[a]Availability was assumed to be constant for naur in all seasons, but it was adjusted for domestic stock according to the seasonal restrictions imposed on certain pastures by herders.
[b]Symbols (+, 0, –) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).

important question as to what attracts them to the naur spring range. As the alpine meadows were consistently preferred by all animal groups, this vegetation type was clearly an essential habitat for all ungulates. Earlier studies undertaken in an area adjacent to ours (Oli, 1996), and elsewhere (Cincotta et al., 1991; Harris and Miller, 1995; Schaller, 1998), have also reported alpine meadow to be an important habitat component. The selection for alpine meadow is not surprising because of its high abundance of sedges and forbs (Koirala et al., 2000). Consumption of nitrogen-rich forages such as sedges and forbs is essential for microbial fermentation and increasing the efficiency of utilization of grasses (Long et al., 1999). This is especially true in the case of free-ranging animals in less productive environments, because here they have to rely heavily upon the efficiency of the microbial activities of the gastro-intestinal tract for extracting the maximum possible nutrients from poor quality feeds (Sahu and Kamra, 2002).

4.2. Potential for competition

Competition is expected among sympatric ungulates when shared resources are in short supply (Pianka, 1978). In our study, all animal groups preferentially used alpine meadows at the same altitudinal range either simultaneously or in different seasons. As alpine meadow was the least abundant vegetation type, exploitative competition is likely to occur. However, in the absence of evidence of resource limitation, we are unable to assess the competitive relationships among them.

Furthermore, in semi-arid and rugged rangelands like the trans-Himalaya, rapid and pronounced changes in the composition and phenology of plant species across gradients of altitude (spatial) and season (temporal) probably promotes the formation of different temporal or spatial ‘patches’ (Putman, 1996) across the landscape (Pickett and Cadenasso, 1995). Such spatio-temporal heterogeneity is expected to facilitate the coexistence of potentially competing herbivores (Alhamad, 2006), as has been shown by theoretical analysis

Table 4
Seasonal use of slope categories by domestic stock and naur in Phu valley, Nepal

Seasons	Slope categories	Availability[a] (%)		Utilization (%)				Selection[b]			
		All	Domestic stock	Smallstock	Naur	Free-ranging yak	Herded yak	Smallstock	Naur	Free-ranging yak	Herded yak
Spring	Flat	34.4	34.4	51.0	42.7	59.0		+	+	+	
	Moderate	30.5	30.5	37.3	39.0	25.4		0	+	0	
	Steep	30.3	30.3	10.8	18.3	14.2		–	–	–	
	Very steep	4.9	4.9	1.0	0.0	1.5		–	–	–	
Summer	Flat	34.4	41.7	51.7	42.2	43.9		0	0	0	
	Moderate	30.5	30.6	30.0	43.1	40.7		0	+	0	
	Steep	30.3	25.9	18.3	14.7	15.4		0	–	–	
	Very steep	4.9	1.7	0.0	0.0	0.0		–	–	–	
Autumn	Flat	34.4	41.7	52.9	49.8	51.9		0	+	0	
	Moderate	30.5	30.6	29.4	38.2	34.6		0	+	0	
	Steep	30.3	25.9	17.6	11.2	13.5		0	–	–	
	Very steep	4.9	1.7	0.0	0.7	0.0		–	–	–	
Winter	Flat	34.4	19.9	50.0	36.6	30.6	35.3	+	0	0	0
	Moderate	30.5	30.0	25.0	29.6	34.7	32.4	0	0	0	0
	Steep	30.3	38.8	22.7	31.7	34.7	26.5	–	0	0	0
	Very steep	4.9	11.4	2.3	2.1	0.0	5.9	–	0	–	0

Flat, moderate, steep and very steep categories refers to (0–10), (11–30), (31–50) and (51–90) degrees of slope, respectively.
[a]Availability was assumed to be constant for naur in all seasons, but it was adjusted for domestic stock according to the seasonal restrictions imposed on certain pastures by herders.
[b]Symbols (+, 0, –) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).

(Wilson and Abrams, 2005), experimentally (Cromsigt and Olff, 2006), and in observational studies in other natural environments (Metzger et al., 2005; Voeten, 1999).

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