

# COEXISTENCE OF WILD AND DOMESTIC UNGULATES IN THE NEPALESE TRANS-HIMALAYA: RESOURCE COMPETITION OR HABITAT PARTITIONING?

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**Coexistence of wild and domestic ungulates in the Nepalese Trans-Himalaya:  
Resource competition or habitat partitioning?**

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## SUMMARY

This thesis deals with the controversial issue of resource partitioning and competition between wild and domestic ungulates in the Trans-Himalayan rangelands. Resource partitioning, or the differential use of resources such as food, space and time is a mechanism by which coexistence among organisms becomes possible despite similar ecological needs.

For centuries, the raising of domestic stock has made it possible for humans to inhabit the Trans-Himalayan rangelands. However, as introduced species, the livestock has the potential to displace wild ungulates. Multi-species rangeland management has therefore become a major conservation concern in the Trans-Himalayan region.

I studied the extent of resource partitioning and competition between naur (blue sheep/bharal, *Pseudois nayaur*), Tibetan argali (*Ovis ammon hodgsoni*), free-ranging domestic yak (*Bos grunniens*) and smallstock (domestic goat *Capra hircus* and sheep *Ovis aries*) in semi-arid, high altitude rangelands, in Nepal. Because clear insights on food habits is required to address the issue of interspecific interactions, I evaluated the suitability of the three most popular field methods used for determining the composition of herbivore diets. The results indicated that feeding site examination and bite-counts were unsuitable methods because of the difficulty in collecting samples that are representative of the entire grazing period and the problem of recording feeding signs correctly. Microhistological analysis of feces appeared to be the most appropriate method, but correction factors are needed to adjust for differential digestion.

A study of seasonal habitat utilization (elevation, vegetation type and slope) showed that naur was more strongly associated with free-ranging yak than with smallstock. The former pair used

similar habitats during most of the year. Naur and smallstock did not form temporal (within season) associations, mainly because smallstock consistently used lower elevations than naur. Alpine meadow was the most important habitat component, as all ungulates preferentially used this vegetation type in most seasons.

Food habits were studied in Damodar Kunda in Mustang District during summer, and a year-long study was undertaken in Phu Valley in Manang District. In both study sites, the results showed that all ungulates fed opportunistically but with different foraging styles: yaks showed a clear grazer trend, goats a browser trend, while naur and domestic sheep were more intermediate feeders. A few species of forbs/legumes were particularly selected, such as *Saussurea graminifolia* and *Sedum* sp. by argali during summer, and *Oxytropis* spp. by most ungulates in spring, summer and autumn. A leguminous low shrub *Chesneya nubigena* was selectively eaten by naur and free-ranging yaks during winter.

Taking an account of habitat and diets together, resource-use overlaps were generally higher between naur and yak than between naur and smallstock in most seasons. This, together with relatively low reproductive success among naur and high total ungulate stocking density, suggested that competitive relationships existed between naur and domestic stock in the study area. Winter, being a period of resource scarcity, was probably the most critical season for naur and yak because they overlapped substantially both in habitat and diet during that period. If stocking densities should increase, the spring and autumn seasons may also become crucial for naur because of more cross-seasonal overlaps in resource-use with domestic goats and sheep.

However, owing to non-equilibrium dynamics of the range ecosystem, the extent of competition was difficult to ascertain. Also, the spatio-temporal heterogeneity in the composition and phenology of forage plants across the gradient of altitude coupled with the rotational grazing system appeared to indirectly facilitate coexistence through partitioning of habitat, especially between naur and smallstock. Thus the traditional grazing system probably buffered against competitive interactions between the wild and domestic species.



## LIST OF PAPERS

This Doctor Scientiarum thesis consists of a synopsis and the following four papers:

I. Summer diets of wild and domestic ungulates in Nepal Himalaya.

(Shrestha, R., P. Wegge, and R. A. Koirala. 2005. *Journal of Zoology* 266:111-119)

II. Determining the composition of herbivore diets in the Trans-Himalayan rangelands: A comparison of field methods.

(Shrestha, R., and P. Wegge. 2006. *Journal of Rangeland Ecology and Management* 59:512-518)

III. Habitat relationships between wild and domestic herbivores in Nepalese Trans-Himalaya.

(Shrestha, R., and P. Wegge. Submitted to *Journal of Arid Environments*)

IV. Wild and domestic ungulates in Nepal Trans-Himalaya: resource partitioning or competition?

(Shrestha, R. and Wegge, P. Manuscript)

## **PART ONE: SYNOPSIS**

### **Background**

Pastoralism is one of the most productive land uses in the semi-arid rangelands of the Trans-Himalaya where cultivated agriculture is of low productive potential (Miller 1997b). Herders here often maintain high stock numbers not only to fulfill their wide range of subsistence needs such as meat, milk, draught power, fuel and farm manure but also as an insurance against losses due to predation and unfavorable climatic conditions (e.g. excessive snowfall). Consequently, the rangelands tend to be overstocked (Mishra et al. 2001). As the high stocking rate is expected to impose resource limitations (Hobbs et al. 1996, Prins 2000), it raises a potential for grazing competition between domestic and sympatric wild herbivores, especially because the two groups are phylogenetically close (similar resource requirements) and also have a recent history of co-occurrence (less resource partitioning).

Furthermore, owing to the maintenance of domestic stock at artificially higher densities by supplemental feeding, shelter and medical attention, they are at a competitive advantage over their wild relatives and may therefore out-compete the latter. Also, the physical disturbance by herders may interfere with natural interaction patterns (Harris and Loggers 2004), thereby displacing wild ungulates to sub-optimal habitats (Namgail et al. 2007). This in turn, is expected to escalate the effect of 'resource competition'.

Understanding the issue of interspecific competition is essential in order to explore the possibility of maintaining domestic stock in an area without detriment to either habitat or wild animals. However, the occurrence and effect of competition is still poorly understood (Arsenault and Owen-Smith 2002), mainly because of the difficulty in demonstrating that resources are

limiting (Schoener 1983). In general, deterioration in range productivity, as indicated by the prevalence of unpalatable “increaser species” (Holzner and Kriechbaum 2000, but see Evju et al. 2006), low biomass of the preferred forage, reduced body growth rates of animals and adverse effects on life –history traits such as fecundity, sexual maturation and survivorship (Fretwell 1972, Saether 1985, Skogland 1986, Reimers et al. 2005), can be used to infer resource limitation under density-dependent dynamics.

Recent studies, however, indicate that semi-arid range ecosystem, including the Trans-Himalaya (Miller 1997a), functions as non-equilibrium systems, where rangeland productivity is governed more by climate than by animal stocking densities (Ellis et al. 1991, Begzsuren et al. 2004). Here, the traditional pastoral systems are considered ‘opportunistic management systems’, characterized by high mobility and herd diversification according to local physiognomic conditions (Coughenour 1991), and they have been acknowledged as an efficient exploitation strategy (Bedunah and Harris 2002). Therefore, in the Trans-Himalaya, it is important to evaluate interspecific herbivore interactions in this perspective besides merely focusing on conventional density-dependent processes.

Information on the impact of livestock grazing on native wildlife in the Trans-Himalaya is generally lacking. Except for a few recent studies in northern India (Bagchi et al. 2004, Mishra et al. 2004, Namgail et al. 2007), knowledge about interspecific relationships between wild and domestic ungulates is limited to comparison of general patterns of habitat use and food habits (Schaller and Gu 1994, Harris and Miller 1995, Fox 1996, Bhatnagar et al. 2000, Shrestha et al. 2005). Results from these studies are inconsistent and authors disagree over the process and the outcome of interspecific interactions. This probably exemplifies the extensive spatial variation

over their large geographical range (Davies et al. 2005, Wang et al. 2006), which has brought about local adaptations across the landscape (Putman 1996). Thus, site-specific studies (Smith et al. 1978), are expected to provide more meaningful results for effective rangeland management.

As a part of the original centre of Caprinae radiation, the Trans-Himalayan region is inhabited by a wide array of endemic caprid taxa ranging from primitive to advanced forms (Schaller 1977, Fox 1997). One such species is naur (blue sheep/bharal *Pseudois nayaur*), which is widely and sympatrically distributed with domestic stock throughout the region (Schaller 1977). As a principal prey of the globally endangered snow leopard (*Uncia uncia*) (Oli et al. 1993), its relationship with livestock (Oli et al. 1994), and its importance as a trophy animal for local revenue generation (Wegge 1976; 1997), the study on this species carries special merits.

### **Aim and outline of the thesis**

This study examines the extent of resource partitioning and competition between wild and domestic ungulates in Nepalese Trans-Himalaya. Achieving this goal requires clear insights into the interspecific food and habitat relationships among the animal species. Hence, first I asked how similar are the different ungulates in their food habits. The summer diets of Tibetan argali (*Ovis ammon hodgsoni*), naur and domestic goats (*Capra hircus*) were studied (Paper I). From that study, I realized the need for assessing methods commonly used to study ungulate diets, as the consistency among methods are known to vary depending on foraging styles (Ortega et al. 1995) and temporal (Mohammad et al. 1996) and spatial (Smith and Shandruk 1979) variation in forage species. Before embarking on a more detailed study of food habits, I therefore compared the 3 most popular field methods, viz. feeding site examination (Pechanec and Pickford 1937), bite-counts (Hubbard 1952) and microhistological analysis of feces (hereafter fecal analysis)

(Baumgartner and Martin 1939) to evaluate their suitability for determining the diets of Trans-Himalayan ungulates (Paper II). Subsequently, I resumed my focus on interspecific interactions and studied the seasonal patterns of habitat utilization, especially focusing on the use of vegetation types, elevation and slope (Paper III). This gave me an idea about when and where the most intense overlap between naur and domestic species was likely to occur, as well as the important habitat components governing their distribution. This was followed by a detailed study of seasonal diets based on fecal analysis (Paper IV), as this technique, when adjusted for differential digestion, appeared to be the most suitable method for comparative studies (Paper II). By combining information on habitat utilization (Paper III) and diet, I then calculated resource-use overlap indices to identify the most similar ungulate pairs as well as the critical periods of the year (Paper IV). In general, studies of potential competition focus on temporal (within season) habitat and diet overlaps. However, successive (cross-seasonal) use of the same habitat and food plants by different herbivores is also important when analyzing competitive relationship. I therefore investigated the cross-seasonal patterns of overlaps as well. Because competition takes place only when shared and essential resources become limited, I tried to detect resource limitation by comparing ungulate biomass density and the population performance of naur with other studies in Nepal and India with differing grazing intensity and range productivity (Paper IV). Finally, I discuss the potential for coexistence of wild and domestic ungulates in Nepal Trans-Himalaya in the context of the existing systems of rotational grazing management and non-equilibrium dynamics in the study area (Paper IV).

## **Study area**

I began my fieldwork in Damodar Kunda in Mustang District ( $29^{\circ} 0' \text{N}$ ,  $84^{\circ} 10' \text{E}$ ) to assess the summer diets of Tibetan argali, naur and domestic goats. Later, a more detailed study on

seasonal habitat utilization and food habits of domestic goats, sheep (*Ovis aries*), yak (*Bos grunniens*), and naur, including population performance of the latter, were undertaken in a 125 km<sup>2</sup> study area in Phu valley of Manang District (28°46'N, 84°17'E). Both Damodar Kunda and Phu study areas lie within the Annapurna Conservation Area and stretch out alongside the southwestern boundary of Tibetan Autonomous Region (TAR) of China (Fig 1). However, Phu is located more towards the south and closer to the Himalaya mountains, and topography here is somewhat more rugged than in Damodar Kunda. Phu (approx 3700 to 7000m asl) is situated in a lower and wider altitudinal range than Damodar Kunda (approx. 4500 to 6500m asl). Both study sites can be described as semi-arid cold deserts with annual precipitation less than 400 mm, half of which occurring in the form of snow during winter. The snow and frozen ground start to thaw in late March/early April. Xerophytic vegetation predominates in both study sites, with the Phu study area more sparsely vegetated compared to Damodar Kunda. Also, the faunal diversity is relatively low in Phu, with naur as the only wild ungulate and mammalian carnivores restricted to snow leopard (*Uncia uncia*) and red fox (*Vulpes vulpes*). In Damodar Kunda, in addition to these, Tibetan argali (*Ovis ammon hodgsoni*), marmot (*Marmotta himalayana*), grey wolf (*Canis lupus*), brown bear (*Ursus arctos*) and Tibetan lynx (*Felis lynx isobellina*) are also found. Pastoral activities also differ between the two study sites. Phu has a permanent settlement, and herders rotate the domestic stock in different seasonal pastures year round. Damodar Kunda is grazed only during summer, but they also practice a rotational grazing system. The stocking densities of domestic stock in Phu and in Damodar Kunda is nearly double that of naur.

## **Methodology**

### **Food habits studies**

Food habit studies were conducted by applying fecal analysis, adjusted for inherent biases by comparing it with bite-counts data obtained in smallstock. In the Damodar Kunda study area, 5 composite samples of argali and 4 composite samples of each of naur and goats were prepared by following the procedure originally developed by Baumgartner and Martin (1939), and later modified by Sparks and Malechek (1968) and Jnawali (1995) (Paper I). Eighteen plant species, which seemed to be eaten by the ungulates from feeding site examinations, were collected for the preparation of reference slides. The first 10 non-overlapping fragments intercepted by the ocular scale line were identified using a compound microscope at 200× magnification. A total of 300 fragments of argali and 240 fragments of each of naur and goat were recorded.

Later in Phu in summer, feeding site examinations, bite-counts and fecal analysis were compared by collecting data from the same animals belonging to one herd of domestic yak (*Bos grunniens*) and two herds of mixed smallstock, consisting of domestic goats (*Capra hircus*) and sheep (*Ovis aries*) (Paper II). Here, I sampled a total of 67 one-m<sup>2</sup> quadrats for feeding site examination, 2 373 bites for bite-counts, and 600 fragments in the fecal analysis. In order to enhance the accuracy and speed of the fecal analysis, a reference slide library consisting of 2 831 high-definition photomicrographs from 63 food plant species was made along with the dichotomous identification keys (Gaylard and Kerley 1995, Carriere 2002). A detailed study on seasonal diets of naur, free-ranging yaks, goats and sheep were conducted (Paper IV) by preparing one composite sample per ungulate per season from a total collection of 397/190/163/153 pellet groups/dung piles of naur, domestic goats, sheep, and yak, respectively, over the four seasons.

The reference slide library prepared earlier (Paper II) was used to identify the fragments of plant species in the fecal samples from Phu.

### **Study on habitat use**

I recorded the seasonal locations of a total 766 groups of naur, 392 herds of yak and, 257 groups of smallstock on a 1:10 000 Topographic Map (Paper III) by systematically searching opposite slopes from fixed vantage points, using 8 × 40 binoculars and a 15 – 60 × variable spotting scope during day-light hours (0600 to 1800 hrs). To control for disturbance by herders, all observations of naur were undertaken in the parts of the range where domestic stock was not attended by herders at the time of observation. The availability and use of elevation, slope and vegetation types were quantified by using the Spatial Analyst extension of Arc View GIS (Environmental Systems Research Institute 1999; 2005). I applied correspondence analysis, an exploratory multi-dimensional graphical technique, to look for seasonal and cross-seasonal associations of animal groups and habitat categories (Beardall et al. 1984, Greenacre 1984). Within each association, interspecific habitat overlaps were quantified by calculating proportional similarity indices (Schoener's Index; Schoener 1968), and subsequently tested for statistical significance by comparing them with null models (Gotelli and Graves 1996). Seasonal preferences for habitat categories by each animal group were assessed following Neu et al. (1974).

### **Resource-use overlaps and naur population data**

The resource-use overlap indices were calculated as the geometric means of the three overlap indices (Case 1983) i.e. plant species in diet (Paper IV), utilization of elevations and of vegetation types (Paper III) and subsequently ordered into three different classes: High ( $\geq 0.70$ ), Moderate (0.51 – 0.69), and Low ( $\leq 0.50$ ).



Demographic data on livestock were obtained through a total count (smallstock and cows) as well as interviews with herders (free-ranging yaks and horses). Naur population size was estimated by total counts through systematically scanning from vantage points (Wegge 1979). The population productivity of naur (number of young/100 adult females) was estimated on the basis of total classified counts made in autumn in Phu (N = 20 groups). Biomass densities of naur and domestic stock were calculated using average adult body mass of each species as reported by Mishra et al. (2002).

## **Major findings and discussion**

### **Methods used to study the botanical composition of herbivore diets**

To address the controversial issue of interspecific competition, reliable information on food habits is needed. Hence, I evaluated the suitability of fecal analysis, bite-counts and feeding site examination – three methods commonly used to study herbivore diets (Paper II). The methods gave different estimates of forage categories (graminoids, forbs and, shrubs) and plant species in both yak and smallstock. Because yaks grazed in other vegetation communities when not observed for bite-counts and feeding signs, the results from the latter methods could not be compared directly with that from fecal analysis. In smallstock, feeding site examination gave higher estimates of graminoids and lower estimates of shrubs than the other two methods, probably because all feeding signs on shrubs were not detected. Feeding signs are known to get readily obscured in plants which are susceptible to disarticulation (Smith 1968, Smith and Shandruk 1979), and shrubs are more likely to be disarticulated because of the prevalence of nodes. Bite-counts and fecal analysis gave comparable results, except that forbs were underestimated by fecal analysis, thereby closely agreeing with our earlier findings (Paper I).

This discrepancy is most likely due to the more complete digestion of forbs (Holechek et al. 1982) as their epidermal tissue is less cutinized compared to many perennials and graminoids (Storr 1961). The fecal analysis consistently identified the highest number of plant species. The wide grazing period represented by the fecal samples together with the extensive coverage of reference plant material and the use of photographic technique might have enhanced the efficiency of the fecal analysis.

Owing to the difficulty of collecting samples that are representative of the entire grazing period and the problem of recording feeding signs correctly, both feeding site examination and bite-counts are unsuitable methods for studying the food habits of free-ranging domestic and wild herbivores. Microhistological analysis of feces appears to be the most appropriate method, but correction factors are needed to adjust for differential digestion.

### **Interspecific habitat relationships**

I examined the seasonal and cross-seasonal habitat relationships between naur and smallstock and naur and domestic yak on the basis of their use of vegetation type, elevation and slope (Paper III). The findings revealed that 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. The summer pastures of naur appeared to receive heavy grazing pressure as yak successively used them not only in summer but also during spring.

The seasonal movement of smallstock across the altitudinal gradient appeared to govern the habitat relationship with naur. The two animal groups rarely formed temporal associations as the smallstock consistently used lower elevations. Naur appeared to avoid grazing areas in the

vicinity of the holding pens of smallstock probably because of lack of good quality forage, as also noted by Zhao et al. (2007). Cross-seasonally, however, in autumn and spring, naur spatially overlapped extensively with the summer range of smallstock, and both preferred the alpine meadow habitat during these periods. Middle elevations and alpine meadows appeared to be the critical habitat components, as alpine meadow was the least abundant vegetation type but consistently and preferentially used by all animal groups across seasons. Earlier studies in an area adjacent to ours (Oli 1996), and elsewhere (Cincotta et al. 1991, Harris and Miller 1995, Schaller 1998), have also reported this vegetation type to be an important habitat component for high altitude ungulates.

### **Interspecific food relationships**

The diet selection by animals can be viewed as an ecosystem process with important implications governing interspecific interactions (Ellis et al. 1976). I examined the diets of wild and domestic ungulates in the two study sites to assess forage selection and extent of food overlap between them. The results indicated that all ungulates were feeding opportunistically but with different foraging styles: goats ate mostly browse (Paper I and IV), yak mostly graminoids (Paper IV), argali mostly forbs in summer (Paper I), while the diet of naur and sheep were more mixed across the seasons (Paper IV). However, the diets of all ungulates were sufficiently mixed to be classified as intermediate feeders according to Hofmann (1989).

Although the diet overlap at the level of plant species between naur and goats was lower in Damodar Kunda compared to Phu, the relative proportions of forage categories in the summer diets of naur and domestic goats were strikingly similar in the two study areas (Paper I and IV). The seasonal variations in the proportions of forage categories (Paper IV) confirmed that the food habits to a large extent are determined by the use habitats (Perez-Barberia et al. 2001) and

hence available vegetation (Gordon and Illius 1989). Therefore the lack of any consistent pattern among previous studies may be explained by the spatio-temporal heterogeneity in the phenology and composition of plant species over the large geographical range of these ungulates (Paper I).

As for important food plants, the results showed that forbs/legumes were strongly selected by all ungulates in both study areas during most part of the year. This is consistent with the report that forbs constitute a major source of nutritious forage in the Tibetan plateau (Long et al. 1999). A few species of forbs were preferentially used, such as *Saussurea graminifolia* and *Sedum* sp. by argali during summer (Paper I), *Oxytropis* sp. by all species throughout the year, except in winter (Paper IV). A leguminous low shrub *Chesneya nubigena* was selectively eaten by naur and free-ranging yaks during winter.

### **Resource relationships between naur and domestic ungulates - Potential for resource partitioning and competition**

The resource-use overlap indices were generally higher between naur and yak than between naur and smallstock in most seasons. A closer look indicated that naur overlapped with yak more in elevation and less in plant species while the opposite was true in the case of smallstock (Paper IV). Despite some altitudinal separation, in spring all animal groups preferentially used alpine meadows (Paper III) and fed preferentially on forbs (Paper IV). In summer, naur and free-ranging yaks overlapped extensively as both randomly or preferentially used higher elevation grasslands and alpine meadows, and preferentially fed on graminoids. As summer food plays an important role for winter survival and population performance of ungulates in seasonal environments (Saether et al. 1996), the extensive habitat overlap between yak and naur during this period has the potential to bring about resource competition. Resource-use by naur in autumn, cross-seasonally overlapped with spring and summer of smallstock and the two animals

groups preferentially used middle elevation and alpine meadows during these periods. In winter, as the herders moved smallstock down to winter pastures, they were altitudinally separated from naur. However, substantial overlap occurred between naur and free-ranging yaks during winter as they used similar elevation and both consumed a high proportion of browse.

As competition takes place only when shared and essential resources are in short supply, not only the extent of overlap in resource-use but also animal numbers needs to be considered. In the Damodar Kunda area, competition appeared to be minimal during summer because of little interspecific overlap in diet as well as a low total ungulate biomass compared to other ranges (Paper I). However, this was probably not the case in Phu (Paper IV), because here both total ungulate biomass density (3028 kg/km<sup>2</sup>) and the rather low recruitment of naur (56 young/100 adult females in autumn) compared closely with presumably overgrazed rangeland in the Indian Trans-Himalaya (Mishra et al. 2004). Thus, assuming similar range productivity as that of Mishra et. al. (2004)'s study area in Ladakh, it appears that Phu valley was overstocked and that a competitive relationship existed between naur and domestic stock.

Another factor affecting competitive relationships among domestic and wild ungulates is the interference by herders (Harris and Loggers 2004), as their presence has been shown to displace wild sheep to suboptimal habitats (Namgail et al. 2007). The observed lower density of naur in the intensively grazed area in Ladakh (2.6 animal/ km<sup>2</sup>) compared to ours (9.4 animal/ km<sup>2</sup>) might also be due to a difference in the level of human disturbance between these studies, as Mishra et al. (2004), unlike us, made population counts in a relatively small area (31 km<sup>2</sup>) which was also actively used by herders.

Moreover, recent studies indicate that climate may be more important than density-dependent processes in determining the range productivity in non-equilibrium systems (Ellis et al. 1991, Begzsuren et al. 2004) such as the semi-arid Trans-Himalayan rangelands (Miller 1997a). Hence, the nature of interspecific interactions should be analyzed from this perspective as well. Also, spatial heterogeneity in the composition and phenology of plant species (Cromsigt and Olf 2006) across the gradient of altitude and the existing rotational system of ‘opportunistic grazing management’ appear to be indirectly facilitating the coexistence of naur and domestic stock (Miller 1997a, Bedunah and Harris 2002). This is particularly true in the case of interactions involving naur and smallstock because these two groups of animals share similar foraging regimes owing to their similar mouth morphology, diets and body weights (Schaller and Gu 1994, Shrestha et al. 2005) and behavior (Schaller 1977).

Free-ranging yaks overlapped extensively with naur both temporally and cross-seasonally for the most part of the year. Large grazing animals like yak are expected to facilitate the smaller ones by promoting the growth of high quality forage (Bell 1971, Olf and Ritchie 1998, but see also Woolnough and du Toit 2001). However, this may not be true in less productive environments such as the Trans-Himalaya (Mishra 2001), because here competition rather than facilitation is more likely to take place (Van de Koppel and Prins 1998, Bakker et al. 2006). Owing to their opportunistic foraging styles and quite similar mixed diets, naur is therefore expected to compete more with yak, and our results indicated that the winter season – a period of food scarcity – is particularly crucial in this regard.

### **Perspectives for future studies**

In this study, I identified the critical habitat components, and seasons, which govern the competitive relationships between wild and domestic ungulates. Also, I inferred that the existing

system of rotational grazing may help to buffer resource competition, especially between naur and smallstock.

However, some important questions have to be addressed to obtain further insights into the nature of interspecific interactions. In the non-equilibrium dynamic system of the Trans-Himalaya, the effects of stochastic climatic fluctuations on rangeland productivity and animal population dynamics need to be explored. This can be accomplished by long-term monitoring of population performance of wild animals and their forage plants over a range of climatic conditions and stocking densities (Coughenour et al. 1990, Fernandez-Gimenez and Allen-Diaz 1999, Begzsuren et al. 2004).

As the majority plant species have certain ability to tolerate and/or resist grazing (Myserud 2006) particularly in alpine environments (Austrheim and Eriksson 2001), this will definitely affect the extent of food limitation under different grazing pressures. Evaluation of traits such as plant species' ability to compensate for loss of plant tissue and the herbivore defense mechanisms of major food species such as *Carex* spp., *Kobresia* spp., *Stipa* spp., *Oxytropis* spp., *Chesneya nubigena*, *Saussurea graminifolia*, *Lonicera* spp., *Potentilla fruticosa* will provide much needed information to predict the outcome of interspecific interactions.

Among wild ungulates, low recruitment may be caused by selective predation on newborns and thus not necessarily reflect poor range quality. Thus, further studies are needed to untangle the relative importance of predation and habitat quality on population productivity.

Disturbance by humans may displace wild sheep to sub-optimal habitats (Harris and Bedunah 2001, Harris and Loggers 2004, Namgail et al. 2007). Therefore, I collected data on habitat utilization by naur in the parts of the range where domestic stock was not attended by herders in order to avoid the confounding effect of human presence. Further studies of behaviour and habitat utilization by naur in the presence of herders are needed to evaluate the effect of human disturbance on the natural interaction pattern between naur and domestic species.



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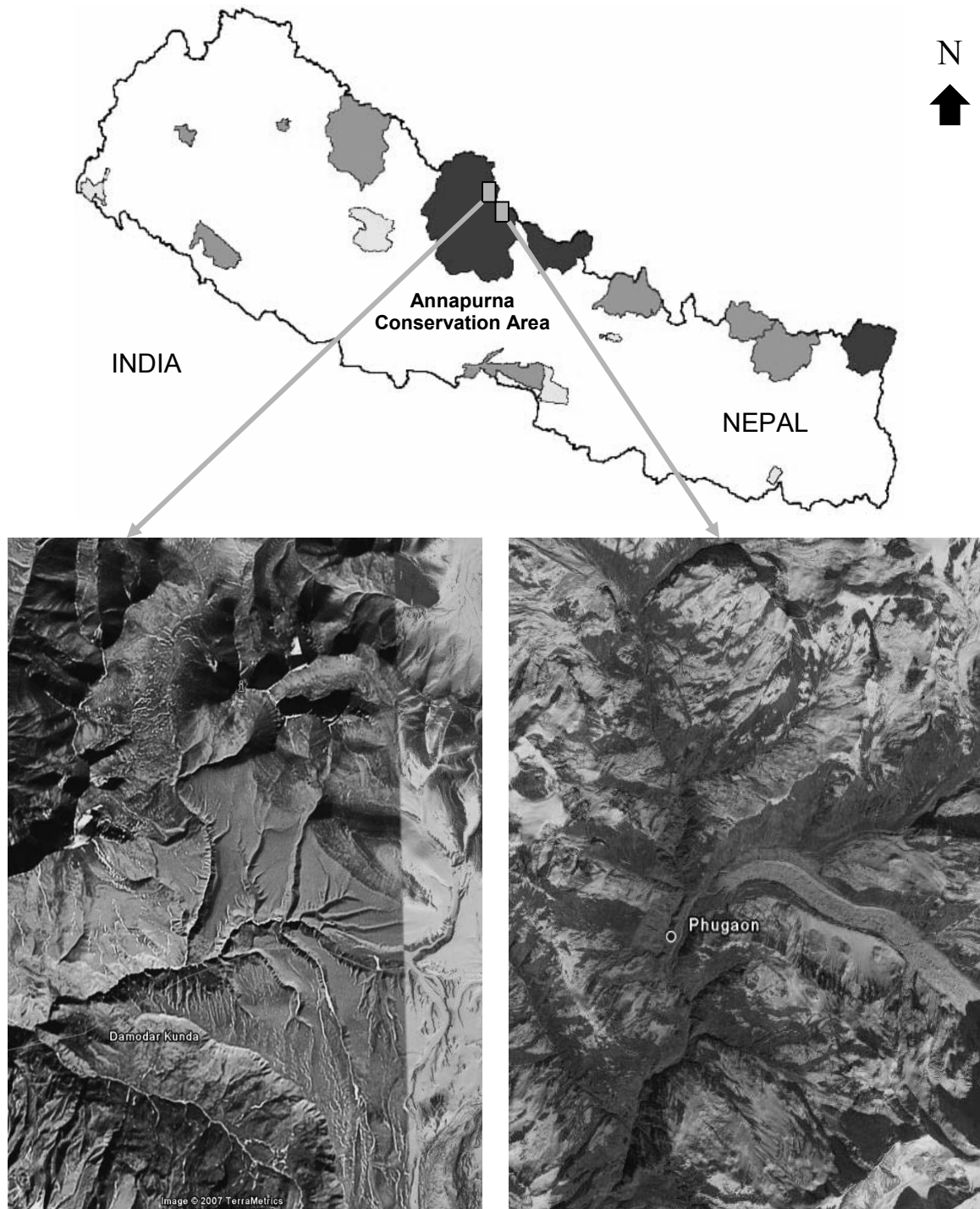


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**Figure 1.** Damodar Kunda study area (left) in Mustang and Phu Study area in Manang (right) within the Annapurna Conservation Area, Nepal (Source: Google 2005).

**PART TWO: COMPILATION OF PAPERS (I-IV)**

# Paper I





# Summer diets of wild and domestic ungulates in Nepal Himalaya

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## Abstract

The selection of summer forage by three sympatric ungulates in the Damodar Kunda region of upper Mustang in north Nepal was studied to assess the extent of food overlap between them. To compare their diets, a micro-histological technique of faecal analysis was used, adjusted for inherent biases by comparing it with bite-count data obtained in domestic goats. Tibetan argali *Ovis ammon hodgsoni*, naur (blue sheep or bharal) *Pseudois nayaur* and domestic goat *Capra hircus* consumed mostly forbs, graminoids and browse, respectively. The proportions of food items in their diets were significantly different both at the plant species ( $P < 0.02$ ) and at the forage category level ( $P < 0.001$ ). Except for sharing three common plants (*Agrostis* sp., *Stipa* sp. and *Potentilla fruticosa*), dietary overlap at the species level was quite low. At the forage category level, naur and domestic goat overlapped more than the other ungulate pairs. Although all three species were opportunistic, mixed feeders, argali was a more selective forb specialist grazer than the other two ungulates. Owing to some spatial separation and little dietary overlap, interspecific competition for summer forage was low. If animal densities increase, however, goats are expected to compete more with naur than with argali because of their more similar diets. Owing to differences in forage selection by argali and naur throughout their large geographical ranges, reflecting adaptations to local ecological conditions, inferences regarding forage competition between domestic livestock and these two wild caprins need to be made from local, site-specific studies, rather than from general diet comparisons.

**Key words:** argali, *Ovis ammon hodgsoni*, blue sheep, *Pseudois nayaur*, *Capra hircus*, diet, faecal analysis, mountain ungulates

## INTRODUCTION

Tibetan argali *Ovis ammon hodgsoni* (hereafter referred to as argali), naur (or blue sheep/bharal) *Pseudois nayaur* (hereafter referred to as naur) and domestic goat *Capra hircus* (hereafter referred to as goat) inhabit the Damodar Kunda rangelands of Mustang district in the trans-Himalayan region of Nepal. Wild and domestic ruminants that forage in the same general habitat may compete for food. Thus, knowledge of feeding ecology is one major pre-requisite for addressing the issue of livestock–wildlife conflicts and for assessing the possibility of multi-species rangeland management (Bagchi, Mishra & Bhatnagar, 2004).

In Nepal, no study has compared the diets of wild and domestic ungulates of the mountain rangelands. Reports

from different localities on the Tibetan Plateau in China (Cincotta *et al.*, 1991; Schaller & Gu, 1994; Harris & Miller, 1995; Miller & Schaller, 1998) have indicated that argali and naur are mixed feeders, but feeding mainly on graminoids, and that the goats are ‘the black sheep’ among livestock by consuming almost everything edible (Schaller, 1977). Many authors (Dzieciolowski *et al.*, 1980; Fox, Nurbu & Chundawat, 1991; Fox & Johnsingh, 1997) speculated that habitat fragmentation and subsequent competition with domestic stock have contributed to a decline in argali populations worldwide, but they did not provide information on food habits. Only a recent study in the Indian trans-Himalaya by Mishra, van Wieren, Ketner *et al.* (2004) has looked specifically at the question of food competition between livestock and naur. Based on feeding site examinations of naur and direct observations of foraging livestock, they concluded that domestic goats and naur have quite similar food habits, which therefore give rise to competition between them. Another study, which addressed the potential competition

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between sympatric Himalayan ibex *Capra sibirica* and domestic smallstock, concluded that competition between these ungulates was minimal because the ibex used different parts of the habitat than the domestic stock (Bhatnagar, 1997). Similarly, a comparative study of argali and naur by Namgail, Fox & Bhatnagar (2004) in Ladakh (India) found that these two species were also spatially segregated due to habitat, and hence did not compete much for forage.

On a more theoretical basis, Mishra, van Wieren, Heitkonig *et al.* (2002) speculated that long-term overgrazing by domestic stock could have excluded large-sized native herbivore species from many trans-Himalayan rangelands, and, based on animal productivity, Mishra, Prins & Van Wieren (2001) provided evidence that overstocking by domestic livestock may be widespread.

The objective of the present study was to compare the summer diets of argali, naur and domestic goat to assess the extent of forage competition between them. In Nepal, argali is a rare species, so far confirmed to exist only in the Damodar Kunda study area. For management it is, therefore, important to know if this species competes for forage with the much larger numbers of naur and domestic goats. Our data were collected during summer, when the nutritional quality of ungulate forage is highest and competition for resources presumably lower than at other times of the year. Nevertheless, as well documented by studies of northern ungulates in similarly seasonal environments in Scandinavia (Reimers, Klein & Sorumgard, 1983), forage quality of summer ranges has pronounced effects on animal physiology and therefore on population performance (Sæther, 1997).

## STUDY AREA

The c. 120 km<sup>2</sup> Damodar Kunda study area (29°0'N, 84°10'E) in Mustang District borders the Tibetan Autonomous Region (TAR) of China. Within an altitudinal range of 4700–5900 m it is contiguous with the Tibetan plateau. This is an open, gently undulating terrain with interspersed round-topped hills, small lakes and gullies, showing the 'sheep ground' features as described by Clark (1964). The lower, south-western zone is more deeply dissected by the headwaters of the Kali Gandaki River, namely Namta and Tehchang rivers and their tributaries, exposing steep slopes, massive cliffs intermingled with grasslands, meadows and scree, thus resembling 'goat ground' (Clark, 1964).

Climate is controlled by the rain shadow effect created by the Himalayas. The general physiognomy can be described as a high elevation cold desert, similar to that of the Tibetan Plateau (Miller, 1994). Total annual precipitation is < 200 mm, with more than half of this occurring as snow during winter. The minimum temperature remains sub-zero from early October to mid April. Snow and frozen land start to thaw at the beginning of April.

Vegetation in general represents high-altitude grasslands, which is Tibetan in character (Stainton, 1972).

Five distinct plant communities (dry grassland, Ionicera community, wet meadow, dry meadow and desert steppe) have been identified (Koirala, Shrestha & Wegge, 2000). For Nepal, Damodar Kunda is an important area in terms of faunal diversity. The mammalian carnivores grey wolf *Canis lupus*, snow leopard *Uncia uncia* and brown bear *Ursus arctos* have been reported (BCDP, 1994), and Tibetan lynx *Felis lynx isobellina* and red fox *Vulpes vulpes* are also suspected to exist there. Naur and argali are the only wild ungulates, with the former outnumbering argali by a factor of > 10 (pers. obs.) and occupying somewhat more rugged terrain than argali. Other mammalian herbivores are marmot *Marmota himalayana*, pika *Ochotona roylei* and woolly hare *Lepus oiostolus*.

Pastoralists have been using the region for grazing domestic stock for a long time. In late June, c. 500–800 livestock, mainly domestic goats, are taken up from the lowland villages and are herded throughout the study area from temporary camps until early September (Koirala & Shrestha, 1997).

## METHODS

Following a reconnaissance survey, the distribution pattern of the 3 ungulate species was identified from direct observations, presence of pellets and tracks, and interviews with local herders. All 3 species had overlapping ranges. Their core areas, however, were clearly separated and differed in vegetative composition. Hence, to detect and compare patterns of food plant selection both within and between species, the study area was subjectively delineated into 3 habitat zones: argali, naur and goat zones. All 3 ungulates occupied these zones, but their relative abundances varied. Detailed habitat and floral characteristics of these 3 zones are described by Koirala *et al.* (2000).

### Microhistological analysis of faeces (faecal analysis)

Initially, an attempt was made to determine food plant selection by examining the sites where animals had foraged. This method was rejected, however, because it was difficult to determine the feeding signs correctly, especially on graminoids; therefore faecal analysis was used instead. Examining faecal samples by a microhistological technique (Baumgartner & Martin, 1939; Sparks & Malechek, 1968) is the most commonly used method for determining the botanical composition of range herbivore diets (Holechek, Vavra & Pieper, 1982; Alipayo *et al.*, 1992). Differential digestibility among plants (Stewart, 1970; Slater & Jones, 1971; Vavra & Holechek, 1980), however, may produce biased estimates (Sanders, Dahl & Scott, 1980; Holechek *et al.*, 1982). To adjust for this, the diet in domestic goats based on microhistological analysis of faeces was compared with the diet derived from direct feeding observations, i.e. the so-called 'bite count' method (Free, Sims & Hansen, 1971;

**Table 1.** Calculation of conversion factors (CFs) based on comparison of forage categories between bite-counts and faecal analysis in domestic goat *Capra hircus*

Forage category	Faecal RIV (%)	Recomputed faecal RIV (%)	Bite counts (%)	Conversion factor <sup>a</sup>	Adjusted RIV <sup>a</sup> (%)
Graminoids	20.0	23.2	28.0	1.208	28.0
Forbs	1.3	1.5	8.0	5.311	8.0
Browse	65.0	75.3	64.0	0.850	64.0
Total	86.3	100.0	100.0		100.0
Unknown	13.7				
Total	100.0				

<sup>a</sup> The conversion factors and adjusted relative importance values (RIVs) were computed as follows:

$$CF_i = \frac{1}{100} \left( \frac{bi \sum_i^n fi}{fi} \right)$$

and, adjusted RIV<sub>*i*</sub> = recomputed faecal RIV<sub>*i*</sub> \* CF<sub>*i*</sub>, where, CF<sub>*i*</sub> = Conversion factor for forage category *i*, *bi* = proportion of forage category *i* in the diet of the ungulate as obtained by bite counts, *fi* = proportion of forage category *i* in the diet of the ungulate as obtained by faecal analysis, *n* = total number of forage categories.

Sanders *et al.*, 1980; Mofareh, Beck & Schneberger, 1997).

During late July and early August 1996, fresh pellets from a total of 42 and 34 pellet groups belonging to 5 and 4 different herds of argali and naur, respectively, were collected and air-dried. Ten randomly selected pellets from each pellet group collected from 1 herd were mixed to form a single composite sample for the herd (Harris & Miller, 1995). Thus, 5 composite samples of argali and 4 composite samples of naur were prepared. Four samples were collected from 4 individual goats comprising both young and adults while feeding on the free range.

The samples were broken into small pieces by hand and ground to pass through a 1-mm screen fitted to an electric mill. The ground material was sieved through Endecotts sieves of 595 and 210 µm mesh size to remove coarse unidentifiable material and dust. Three slides from each faecal sample were prepared following the method used by Sparks & Malechek (1968) and Anthony & Smith (1974), as modified by Vavra & Holechek (1980) and Jnawali (1995).

Eighteen plant species, which seemed to be eaten by the ungulates from the feeding site examinations, were collected for the preparation of reference slides. Individual species were classified into 3 forage categories: graminoids (plants of the grass and sedge families), forbs (broad leaved herbaceous plants) and browse (all woody plants).

Before reading slides from the faecal samples, the reference slides were studied thoroughly as recommended by Holechek & Gross (1982). The first 10 non-overlapping fragments intercepted by the ocular scale line were identified using a compound microscope at 200× magnification. Fragments which could not be classified to species or genera, but to category, were grouped into 'unidentified graminoids', 'unidentified forbs', and 'unidentified browse'. A fourth category 'unknown' included the rest of the fragments that were completely unidentifiable even

to forage category. About 18% of the fragments fell into this group, the rest were identified at least to category level. A total of 300 fragments of argali and 240 of each of naur and goat were recorded. Each sample consisted of 3 slides, and recordings were based on 20 counts per slide.

### Bite count

Before counting bites, we walked with the herd of goats for 3 days to familiarize ourselves with the animals and the available forage. This in turn enabled us to walk very close to the animals, as well as to recognize the forage plants being eaten. A bite was defined as each individual bite taken from the given plant species by the goat. A sample animal was selected randomly from free-ranging animals (not grazing while selected) and observed at close range of 1–2 m for 10 successive bites as soon as it began foraging. Then another animal was selected for the same procedure. Bites were recorded over a 2-week period, and observations for each day were restricted to a single herd as it moved through different vegetation communities. A Dictaphone was used to record 5310 bites. To match the faecal material with the bite counts, fresh pellets from the same group of goats were collected the next morning, i.e. c. 14–22 h after they had been observed in the field.

### Adjustment of the faecal analysis data

As expected, the faecal analysis and the bite counts in goats gave different proportions of browse, forbs and graminoids ( $W = -66$ ,  $P < 0.001$ , Wilcoxon). Because bite counts provide a more accurate picture of the composition of the ingested forage (Sanders *et al.*, 1980), the proportions of forage categories in the faecal analyses were adjusted as follows (Table 1):

(1) The totally unidentified proportions in the faecal analyses (argali 17.3%, naur 21.7% and goat 13.8%)

were removed and the remaining forage proportions recomputed to the summation of 100%.

- (2) In domestic goats, the proportions in the bite counts were divided by the recomputed faecal proportions to yield conversion factors (CFs) for each forage category.
- (3) The recomputed forage proportions in the faecal analyses were then multiplied by their respective conversion factors to give adjusted estimates of the composition of forage categories in the diets.

Assuming that the proportion of individual food plants were biased by the same factors as the category to which they belonged, their proportions were also adjusted by the same factors. Because adjusting the proportions on the basis of bite counts produced quite different results, and because other diet studies on these ungulates have reported non-adjusted values, both estimates are provided for ease of comparison.

### Diet composition

The relative frequency of a plant species in the faeces was calculated and expressed as the relative importance value (RIV), which is the total number of fragments identified for a given food species or forage category divided by the total number of all counts made in the sample, multiplied by 100 (Jnawali, 1995).

### Diet selection

Diet selection value (DSV) was calculated using the following equation, reflecting the consumption (RIV) in relation to the availability (PV) of food plants (Jnawali, 1995):

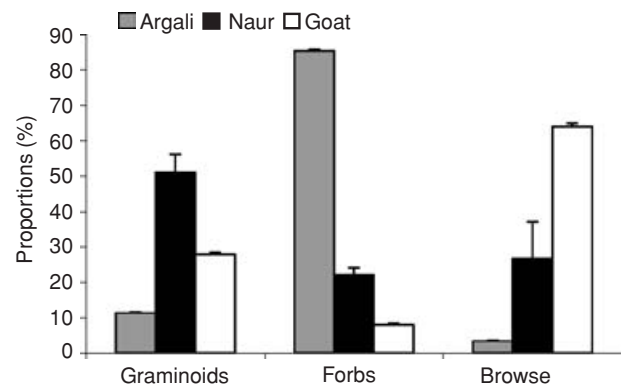
$$DSV_x = \frac{RIV_x}{PV_x}$$

where  $PV_x$  is the prominence value (PV) for species  $x$ . Prominence value reflects the relative availability of plant species in the habitats and is defined as the mean per cent cover of a species multiplied by the square root of the frequency of occurrence of that species in the vegetation sample quadrats (Dinerstein, 1979). The PVs were derived from a vegetation study by Koirala *et al.* (2000).

### Diet overlap and diet comparison

The modified Morisita index of overlap (Horn, 1966) was calculated to estimate the diet overlap between the ungulates and thus to measure their overall diet similarity. The index  $C_\lambda$  varies from 0.0 for completely distinct pairs (no food species/forage categories in common) to 1.0 for complete overlap:

$$C_\lambda = \frac{2 \sum_{i=1}^s x_i y_i}{\sum_{i=1}^s x_i^2 + \sum_{i=1}^s y_i^2}$$



**Fig. 1.** Relative composition of forage categories ( $\pm 1$  SD) in the summer diets of argali *Ovis ammon hodgsoni*, naur *Pseudois nayaur*, and domestic goat *Capra hircus* based on faecal analysis. Proportions are adjusted on the basis of bite counts in domestic goats (see text).

where  $s$  is the total number of food species or taxon/forage categories in the diets, and  $x_i$  and  $y_i$  are the proportion of plant group  $i$  in the total diets of ungulate species  $X$  and  $Y$ , respectively.

Chi-square tests, using adjusted slide counts, were performed to test the following null hypotheses:

- (1) The proportions of forage categories (i.e. graminoids/forbs/browse) are the same for all 3 ungulates.
- (2) The proportions of individual plant species are the same for all 3 ungulates.
- (3) The relative proportions of each forage category (graminoids/forbs/browse) are the same between pairs of ungulates.

## RESULTS

### Diet composition and selection

#### Argali

The Argali diet was strongly dominated by forbs (85.4%) (Fig. 1), among which *Saussurea graminifolia* alone accounted for 65.4% (Table 2). Among the graminoids (11.3%), *Kobresia pygmaea* was the most prevalent species followed by *Stipa* sp. The low proportion of browse (3.3%) was dominated by *Potentilla fruticosa* (2.8%).

Argali strongly selected forbs (DSV = 2.1), followed by quite low and equal selection for graminoids (DSV = 0.2) and browse (DSV = 0.3) (Table 3). The high selection for forbs was mainly the result of very selective foraging on *S. graminifolia* (DSV = 4.2) and *Sedum* sp. (DSV = 3.3).

#### Naur

The diet of naur was dominated by graminoids (51.1%), with forbs and browse making up about equal proportions (Fig. 1). As much as one-fifth of the diet consisted of the browse species *P. fruticosa*. Other important species were four graminoids and the leguminous forb *Oxytropis* sp. (RIV = 3.0–8.1, Table 2).

**Table 2.** Relative importance values (RIVs) of food plants as shown by their adjusted relative frequencies in the composite faecal samples of argali *Ovis ammon hodgsoni*, naur *Pseudois nayaur* and domestic goat *Capra hircus*

Plants	Argali		Naur		Goat	
	RIV <sup>a,b</sup>	SD	RIV <sup>a,b</sup>	SD	RIV <sup>a,b</sup>	SD
<b>Graminoids</b>						
<i>Agrostis</i> sp.	0.3	0.1	8.1	3.6	3.5	0.5
<i>Carex</i> sp.	0.0	–	5.0	7.3	0.0	–
<i>Elymus nutans</i>	0.0	–	3.5	2.8	5.3	0.6
<i>Kobresia pygmaea</i>	2.9	0.5	–	–	–	–
<i>Stipa</i> sp.	1.8	0.3	3.0	2.2	0.6	0.2
Unidentified graminoids	6.3	0.3	31.5	9.3	18.6	0.9
<b>Forbs</b>						
<i>Chesneya</i> sp.	–	–	2.1	0.8	0.0	–
<i>Corydalis govaniiana</i>	0.0	–	0.0	–	4.9	0.3
<i>Oxytropis</i> sp.	0.0	–	4.2	1.0	0.0	–
<i>Saussurea graminifolia</i>	65.4	0.4	–	–	–	–
<i>Sedum</i> sp.	1.3	0.1	–	–	–	–
Unidentified forbs	18.7	0.8	15.8	4.2	3.1	0.7
<b>Browse</b>						
<i>Lonicera rupicola</i>	–	–	0.0	–	50.9	1.4
<i>Potentilla fruticosa</i>	2.8	0.4	20.5	14.7	3.7	0.6
Unidentified browse	0.5	0.2	6.3	6.2	9.4	0.7

<sup>a</sup> 0, Species present in the habitat but not detected in analysis.

<sup>b</sup> –, Species absent in the habitat.

**Table 3.** Relative availability of graminoids (G), forbs (F) and browse (B) in the habitat zones of argali *Ovis ammon hodgsoni*, naur *Pseudois nayaur* and domestic goat *Capra hircus*, their relative proportions in the diets, and their selection as food items

	Argali			Naur			Domestic goat		
	G	F	B	G	F	B	G	F	B
Availability <sup>a</sup>	48	40	12	44	22	34	39	12	49
Proportion in diet (RIV)									
Adjusted <sup>b</sup>	11	85	3	51	22	27	28	8	64
Non-adjusted <sup>c</sup>	32	55	13	54	6	40	23	2	75
Selection <sup>d</sup>									
Adjusted	0.2	2.1	0.3	1.2	1.0	0.8	0.7	0.7	1.3
Non-adjusted	0.7	1.4	1.1	1.2	0.3	1.2	0.8	0.2	1.5

<sup>a</sup> Prominence values (PV) within the main habitat of each species (%).

<sup>b</sup> Proportions in faecal analysis, adjusted on basis of bite counts (see text).

<sup>c</sup> Proportions in faecal analysis, not adjusted from bite counts.

<sup>d</sup> RIV (adjusted and non-adjusted) divided by availability.

In contrast to argali, naur did not display strong selection for any forage category or individual species, except for the forb *Chesneya* sp. (DSV = 7.0). The browse *P. fruticosa* was moderately selected (DSV = 1.3), only exceeded by *Chesneya* sp.

### Goat

The diet of goat was strongly dominated by browse plants (64%), mainly dominated by *Lonicera rupicola* (RIV = 50.9). Graminoids made up 28% and forbs only

**Table 4.** Modified Morisita indices of diet overlap  $C_\lambda$  (Horn 1966) between the summer diets of argali *Ovis ammon hodgsoni*, naur *Pseudois nayaur* and domestic goat *Capra hircus* in Damodar Kunda, Mustang.  $C_\lambda$ : from 0.0 for completely dissimilar diets to 1.0 for complete overlap

Ungulate	Species level <sup>a</sup>	Forage categories <sup>b</sup>
Argali and naur	0.027	0.455
Argali and goat	0.004	0.196
Naur and goat	0.077	0.758

<sup>a</sup> Mostly the genus level.

<sup>b</sup> Includes the categories graminoids, forbs and shrubs.

8% of the diet (Fig. 1). *Elymus nutans* was the most common graminoid followed by *Agrostis* sp. The only identified forb was *Corydalis govaniiana* (RIV = 4.9) (Table 2).

Like naur, goats did not show much selection for any forage category or food plant. The only exception was *C. govaniiana* with a DSV of 5.4. In spite of its importance in the diet, the shrub *L. rupicola* was not a strongly selected species (DSV = 1.5), mainly because it was rather abundant (PV = 32.9%) in the foraging zone of the goats.

Summing up, argali consumed mostly forbs, some graminoids, and hardly any browse, and was very selective on two forb species. Naur ate mostly grasses and about 50:50 forbs and browse, and was not very selective among forage categories or individual plants, except on the forb *Chesneya* sp. Domestic goats ate mainly browse, some graminoids and hardly any forbs, and was not very selective among forage categories or individual plants, except on the forb *C. govaniiana*.

### Diet overlap and diet comparison

The very low overlap ( $C_\lambda < 0.1$ ) at the species level between all the ungulate pairs indicated that their diets were quite different (Table 4). Also, the proportions of forage categories ( $\chi^2 = 464.1$ ,  $P < 0.001$ , d.f. = 4) and the three important and shared food plants, i.e. *Agrostis* sp., *Stipa* sp. and *P. fruticosa* ( $\chi^2 = 12.9$ ,  $P < 0.02$ , d.f. = 4) were significantly different among the three ungulates.

*Argali* and *naur* consumed significantly different proportions of graminoids ( $\chi^2 = 103.0$ ), forbs ( $\chi^2 = 217.7$ ) and browse ( $\chi^2 = 61.8$ , all  $P < 0.001$ , d.f. = 1). Among *argali* and *goat*, overlap both at the forage and at the species level was lowest among all pairs compared. Their relative proportions of graminoids ( $\chi^2 = 24.3$ ), forbs ( $\chi^2 = 319.1$ ) and browse ( $\chi^2 = 232.4$ , all  $P < 0.001$ , d.f. = 1) were also different. *Naur* and *goat* had the most similar diet composition, both in terms of forage categories and plant species (Table 4). Nevertheless, they also differed in the proportions of graminoids ( $\chi^2 = 26.8$ ), forbs ( $\chi^2 = 18.8$ ) and browse ( $\chi^2 = 67.1$ , all  $P < 0.001$ , d.f. = 1).

Only four of the 18 identified species were eaten by all three ungulates, and these food plants did not contribute > 10% to the diets of any of them. The only exception was *P. fruticosa*, which made up c. 20% of the diet of naur.

**Table 5.** Composition of graminoids (G), forbs (F) and browse (B) in the diet of argali *Ovis ammon hodgsoni*, naur *Pseudois nayaur* and domestic goat *Capra hircus* from other studies compared with the results of our study in upper Mustang, Nepal

Author	Location	Season (method)	Argali			Naur			Goat		
			G%	F%	S%	G%	F%	S%	G%	F%	S%
Schaller (1998)	Chang Tang, China	Summer (faecal)	88	9	3	19	81	0	57	31	12
						10	86	4	46	49	5
Harris & Miller (1995)	Qinghai, China	Summer (faecal)	72	27	0	92	8	0	–	–	–
Miller & Schaller (1998)	Chang Tang, China	Autumn (faecal)	24	76	0	62	38	0	–	–	–
Garcia-Gonzalez & Cuartas (1989)	Cazorla mountains, Spain	Autumn (faecal)	–	–	–	–	–	–	3	7	90
Cincotta <i>et al.</i> (1991)	Chang Tang, China	Summer (bite-counts)	–	–	–	–	–	–	46	22	32
Mishra (2001)	Spiti valley, India	Summer (feeding signs)	–	–	–	80	16	4	55	42	3
This Study Unadjusted <sup>a</sup>	Mustang, Nepal	Late summer (faecal)	32	55	13	54	6	40	23	2	75
Adjusted <sup>b</sup>		Late summer	11	85	3	51	22	27	28	8	64

<sup>a</sup> From unadjusted faecal analysis.

<sup>b</sup> From adjusted faecal analysis (see text).

## DISCUSSION

### Correcting faecal analysis from bite counts

The proportion of forbs increased dramatically, and graminoids to a lesser extent, when the faecal proportions were converted from bite counts. This may be owing to several factors. First, the sizes of bites of forbs may have been smaller than the bite sizes of other plants. This is unlikely, as rather the opposite would be expected based on our observations during fieldwork. Second, the identification of forbs by microhistological analysis may be more difficult than identifying other plants. That could be the case, as identification of graminoids (monocotyledons) is quite easy compared to browse and forbs. If so, then a relatively larger fraction of the totally unknown proportion may have consisted of forbs. The conversion method assumed that the three forage categories were distributed in the same proportions in the unknown fraction as in the identified part of the faecal sample. Hence, a bias to overestimate the proportion of forbs may have occurred. As graminoids were even more underrepresented than forbs in the raw faecal analysis, however, this category may then also have been overestimated by the conversion method, if identification of plant categories is a main biasing factor.

Third, more rapid and complete digestion of forbs may have led to a lower proportion of forbs in the faecal analysis than observed during bite counts. This is the general assumption and reason for using bite counts to correct the faecal composition. But if differential digestion leads to a larger proportion of forbs also in the totally unknown fraction, then this alone will bias the converted estimates in favour of forbs. We do not know if this was the case in our samples. However, because the forbs that were

eaten seemed to be more succulent than other ingesta, it is thought that the underlying assumption of differential digestion correctly explains the different results obtained by bite counts and faecal analysis, and therefore that converting the results from the faecal analyses more accurately describes the diets. The conversion assumed that the three ungulate species digest their food categories in a similar way, i.e. their differential digestion of forage categories is the same. We do not know of any study on wild caprins that confirms or contradicts this assumption. If there are differences between species, they are probably not substantial and therefore not expected to alter the general results in this study.

### Diet composition and selection

The diets of the three ungulates were clearly different; goats ate mostly browse, argali mostly forbs and naur mostly graminoids. Their diets were, however, sufficiently mixed across forage categories to be classified as intermediate feeders according to Hofmann (1989).

Previous studies have reported large local differences in the relative composition of forage categories among these species during summer (Table 5). Our results add to this lack of pattern; for instance naur consumed far more browse than reported elsewhere. The lack of any consistent pattern when comparing different studies may be explained partly by the large geographical distributions of argali and naur, with associated local ecological adaptations, and partly by the timing of the different studies. In alpine environments, plant phenology, and hence food quality, changes rapidly; high-quality, sprouting graminoids generally lose their nutritional quality quickly during summer, whereas forbs usually retain their high quality

longer into the autumn. Schaller's (1998) observations at the study site in Changtang (China), that local argalis shifted their diet from 78% grasses in September to 75% forbs in the course of just 1 month later, agree with this.

Schaller & Gu (1994) remarked that ungulates would be opportunistic feeders in simple environments with a short growing season lasting for only 3 months. Our results support this, as the physiognomy of our study area seems to be very similar to theirs in Tibet, with a similarly short growing season. The forb-dominated and selective diet of argali in the presence of more abundant graminoids, however, does not agree with this general prediction. The unexpected result for argali may be explained by the qualities of high-elevation forage plants and their distribution in our study area. Long *et al.* (1999) found forbs to be of better quality (higher metabolizable energy and nitrogen) than shrubs and grasses on the Tibetan plateau during summer. The strong selection of forbs by argali, however, was mainly owing to two species, *Saussurea graminifolia* and *Sedum* sp., and these were only found in the argali habitat. It is therefore suspected that these two plants may contain certain essential micro-nutrients not readily available in other plants, and/or that their proportions of inhibitory compounds are rather low and within the limit that argali is adapted to digest.

Body mass is hypothesized to be the most important trait in explaining differences between feeding styles among ungulates sharing common ancestors (Perez-Barberia & Gordon, 2001). Browsers and selective feeders are expected to be significantly smaller than grazers and mixed feeders. The observed differences in food habits between the goat (average adult male body weight 35 kg; Mishra, van Wieren, Heitkong *et al.*, 2002), and naur (average adult male body weight 57 kg; Wegge, 1979) are to some extent concurrent with this hypothesis. The heaviest argali (average adult male body weight 105 kg; Schaller, 1977), however, was the most selective forager, which contradicts the general theory of an inverse relationship between body size and selective foraging, the so-called Jarman–Bell principle (Jarman, 1974; Demment & van Soest, 1985; Bell, 1986). Again, local adaptations within their wide geographical ranges and pronounced changes in the phenology, and hence quality, of forage plants probably preclude detecting any general evolutionary pattern based on a comparison of late summer diets in a small area like ours.

### Potential for food competition

Because argali, naur and domestic goat are all intermediate feeders with associated opportunistic feeding behaviour, diet overlap seems to be inevitable (Schaller, 1977). Hence, they are expected to compete for the same forage when feeding on the same range. Mishra, van Wieren, Ketner *et al.* (2004) provide empirical data in support of this for naur and livestock.

The results of the present study showed that this is not necessarily true, at least on summer range. Food competition seemed to be low because the relative proportions of

individual food plants and forage categories in their diets were different, and animal densities were not excessive (below). Furthermore, the three plant species shared by the three ungulates, *Agrostis* sp., *Potentilla fruticosa* and *Stipa* sp., were all abundant in all three zones of the study area.

Competition implies that shared and essential resources are in short supply relative to needs. Thus, not only the extent of the same needs but also animal numbers become important. Our results indicate that the extent of the same needs for summer food was rather low, thus competition is not likely to occur unless the density of one or more species increases to a much higher level. A rough estimate of the abundance of naur during fieldwork was between 3 and 6 animals/km<sup>2</sup>, with < 0.5 argali/km<sup>2</sup>. In the core area of the domestic goats, their density was > 10 animals/km<sup>2</sup>, decreasing to an average of < 5/km<sup>2</sup> for the whole study area. If pastoral use should increase, naur, rather than argali, will be affected by forage competition from more smallstock because of their more similar diets. However, in Damodar Kunda such competition is not likely to occur unless numbers of small domestic stock increase to two- or three-fold of the present level. From trans-Himalayan rangelands in India, Mishra, van Wieren, Ketner *et al.* (2004) reported food competition between livestock and naur at lower densities than ours. Their inference, however, was based on observations of the feeding signs of naur; a method that we found to be unsuitable for quantifying the diet composition of this species in our study.

In accordance with Namgail *et al.* (2004), the skewed ratio of naur and argali in our study area can largely be explained by habitat segregation between the two species; naur occupied more rugged terrain than argali. Thus, not only dissimilar diets but also spatial separation will minimize scramble competition between these two species, even if their densities should increase.

The perceived, and to some extent documented, resource competition between domestic livestock and native wild ungulates in the mountain rangelands of Asia (Schaller, 1977, 1998; Shackleton 1997) has recently received more attention by researchers (Harris & Bedunah, 2001; Mishra, 2001; Bagchi *et al.*, 2004). While native species have evolved various ecological characteristics that facilitate coexistence (Schaller, 1998; Namgail *et al.*, 2004), the phylogenetically closely related livestock species are expected to compete with them. Yet, few studies have shown that competition for forage per se by domestic stock is the main driving force behind local declines or the low abundance of wild species. Neither do our results point in that direction. Human disturbance caused by the physical presence of the herding pastoralists themselves (Harris & Bedunah, 2001), often in combination with subsistence 'poaching', may be equally important factors in the presumed conflict between wild and domestic ungulates in the Himalayan rangelands.

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# Paper II



# Determining the Composition of Herbivore Diets in the Trans-Himalayan Rangelands: A Comparison of Field Methods

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## Abstract

In late summer, in a semi-arid mountain range in Nepal, we compared 3 field methods for determining the botanical composition of herbivore diets. Data were collected from the same animals belonging to 1 herd of domestic yak (*Bos grunniens*) and 2 herds of mixed smallstock, consisting of domestic goats (*Capra hircus*) and sheep (*Ovis aries*). Bite count, feeding site examination, and microhistological analysis of feces gave different estimates of forage categories and plant species in both animal groups. Because yaks grazed in other vegetation communities when not observed for bite-counts and feeding signs, the results from the latter methods could not be compared directly with that from fecal analysis. In smallstock, feeding site examination gave higher estimates of graminoids and lower estimates of shrubs than the other 2 methods, probably because all feeding signs on shrubs were not detected. Bite-counts and fecal analysis gave comparable results, except that forbs were underestimated by fecal analysis, presumably due to their more complete digestion. Owing to the difficulty in collecting samples that are representative of the entire grazing period and the problem of recording feeding signs correctly, both feeding site examination and bite-counts are unsuitable methods for studying the food habits of free ranging domestic and wild herbivores. Microhistological analysis of feces appears to be the most appropriate method, but correction factors are needed to adjust for differential digestion. The systematic use of photomicrographs improves the speed and accuracy of the fecal analysis.

## Resumen

A fines del verano, en un pastizal semiárido montañoso de Nepal, comparamos 3 métodos de campo para determinar la composición botánica de la dieta de herbívoros. Los datos fueron colectados de los mismos animales pertenecientes a un hato de yaks (*Bos grunniens*) domésticos y dos hatos de rumiantes menores combinados de cabras domésticas (*Capra hircus*) y ovinos (*Ovis aries*). El conteo de bocados, la examinación del sitio de alimentación y el análisis microhistológico de heces dieron diferentes estimaciones de las categorías de forraje y especies de plantas en ambos grupos de animales. Debido a que los yaks apacentaron otras comunidades vegetales, cuando no se observaron para el conteo de bocados y signos de alimentación, los resultados de este método no pudieron ser comparados directamente con los del análisis fecal. El examen del sitio de alimentación de los ruminantes menores produjo estimaciones más altas de las graminoides y más bajas de los arbustos que los otros dos métodos, probablemente porque todos los signos de alimentación en los arbustos no fueron detectados. El conteo de bocados y el análisis fecal produjeron resultados comparables, excepto para las hierbas que fueron subestimadas por el análisis fecal, presumiblemente debido a su más completa digestión. Debido a la dificultad en colectar las muestra que son representativas del periodo completo de apacentamiento y el problema de registrar correctamente los signos de alimentación, tanto el examen del sitio de alimentación como el conteo de bocados son métodos inadecuados para estudiar los hábitos alimenticios de los animales domésticos en libre pastoreo y la fauna silvestre. El análisis microhistológico de las heces parece ser el método más apropiado, pero se necesitan factores de corrección para ajustar el diferencial de digestión. El uso sistemático de fotomicrográficas mejora la velocidad y certeza del análisis fecal.

**Key Words:** bite-count, *Bos grunniens*, *Capra hircus*, fecal analysis, feeding site examination, food habits, *Ovis aries*

## INTRODUCTION

Knowledge of the food habits of wild and domestic herbivores is a basic requirement for the management of rangeland resources. During the past 60 years, several techniques have been developed to study herbivore food habits (Holechek et al. 1982; Alipayo et al. 1992). Yet, one of the crucial problems

confronting range scientists is to select the most practical and reliable method (Barker 1986). The 3 most popular field methods are feeding site examination (Pechanec and Pickford 1937), bite-counts (Hubbard 1952) and microhistological analysis of feces (hereafter fecal analysis) (Baumgartner and Martin 1939). Feeding site examination involves enumeration of feeding signs in sample quadrats where animals have been feeding. The bite-count method is undertaken by observing an animal at close range and recording the number of bites on different plant species. Fecal analysis requires the identification of plant fragments in fecal sample material on the basis of the histological characteristics of specific plants or plant parts.

Although many studies have compared these methods, none have included them in one study. The comparative studies

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carried out so far reveal that the consistency among methods is affected primarily by the feeding behavior of the ungulates (Ortega et al. 1995) and the temporal (McInnis et al. 1983; Mohammad et al. 1995) and spatial (Smith and Shandruk 1979; Mofareh et al. 1997) variation in the composition of the available forage species (Free et al. 1971; Bartolome et al. 1995). Therefore, any method that is judged to be appropriate for a given ungulate species in a given habitat may not be suitable for a different species in a different habitat.

Except for the study by Shrestha et al. (2005), to the best of our knowledge no studies have yet been undertaken in the Trans-Himalayan rangelands to evaluate the bite-count technique, the feeding site examination and fecal analysis as methods to estimate the botanical composition of herbivore diets. In order to compare the diets of domestic and wild species, Shrestha et al. (2005) adjusted the results obtained from fecal analysis by comparing them with bite-counts data obtained in domestic goat (*Capra hircus*). However, as their study was not specifically designed to compare the methods, it was difficult to draw any conclusion about their accuracy.

The objective of the present study was to evaluate the suitability of the aforementioned 3 methods for determining the diets of domestic goats and sheep (*Ovis aries*) (henceforth referred to as "smallstock") and domestic yaks (*Bos grunniens*) (henceforth referred to as "yak").

Such an assessment of methods is needed for field studies addressing the controversial issue of competition among wild and domestic ungulates in these marginal lands (Harris and Miller 1995; Miller and Schaller 1996; Mishra et al. 2004; Shrestha et al. 2005).

## METHODS

### Study Area

The study was conducted in the Phu valley (lat 84°15' to 84°20'E and, long 28°43' to 28°50'N) of Manang District of north-central Nepal. It lies in the rain shadow of Annapurna range and shares its northern border with the Tibetan plateau. The area receives annually less than 400 mm of precipitation (ICIMOD 1996) and most of it occurs in the form of snow during winter. The mean maximum and minimum temperatures recorded during this study were 5.8°C and -7.3°C in January and 18°C and 9.5°C in July. The snow and frozen ground start to thaw in March.

Animal husbandry is an age-old strategy of subsistence livelihood in this region (Miller 1987). It is practiced by employing the indigenous grazing management system of rotating livestock herds across different seasonal pastures. The smallstock are usually herded while grazing in the open pastures, and then corralled when they return in the evening. Except for milking yaks and juveniles, other yaks are free-ranging throughout the year.

Three adjacent summer pastures, viz. Tshea, Dhungparpa and Napu, were selected for this study. Data on smallstock were collected from Tshea and Dhungparpa pastures, both of which were located in north-eastern aspects in an altitudinal range of 4 000–4 800 m. Data on yak were collected in the Napu pasture, at 4 400–5 000 m on south-easterly slopes.

Vegetation composition is dominated by bunchgrasses and low, densely matted shrubs, which are typical of the semi-arid Tibetan Plateau (Miller 1987). Altitude and aspect appear to govern the distribution of vegetation communities. *Lonicera* spp. L. vegetation community spreads over most of the lower and middle slopes on southern and eastern aspects. Pockets of *Caragana jubata* (Pall.) Poir. are distributed on the northern aspects and the *Artemisia* spp. L.–*Stellera chamaejasme* L. meadow vegetation type is prevalent in the basins. Alpine grasslands dominated by *Carex* spp. L., *Kobresia* spp. Willd. and *Festuca* spp. L. are widespread in the higher slopes.

Fieldwork was conducted during late August and early September. At the onset of data collection, grazing herds of yaks and smallstock were followed for 4 days to familiarize us with the animals and the available vegetation composition and also to identify practical problems associated with the methodology. The feeding site examinations could not be conducted separately for goats and sheep because they were herded together in mixed flocks. We therefore merged our goats and sheep data in the bite-count as well as in the fecal analyses to facilitate comparisons with the feeding site examinations. This was done by weighing the frequencies by the proportion of goats (67%) and sheep (33%) in the smallstock herds. We followed Polunin and Stainton (1987), and Stainton (1988) to identify the forbs and shrubs in field.

### Bite-counts

Following Sanders et al. (1980), the bite-count data were spread over 3 periods of the day, viz. morning (06:00–10:00 hours), afternoon (10:00–14:00 hours) and evening (14:00–18:00 hours). A bite was defined as an individual bite taken from a given plant species (Mofareh et al. 1997; Henley et al. 2001). The plant species being eaten every 10<sup>th</sup> second by a randomly selected feeding individual was recorded on a dictaphone during 15-minute observation periods (Mishra et al. 2004), thereby yielding a maximum of 90 bites per observation period. The animals were observed from a distance of ca. 2 m and a total of 935 and 723 bites were recorded for goats and sheep, respectively, from 2 sites over successive 2 days in Tshea and Dhungparpa pastures. Yaks were observed 1 day in Napu pasture which yielded 715 bites. The locations of the sites were recorded by Global Positioning System (GPS) readings and also marked by using physical features such as boulder outcrops, gullies, scree, etc. as reference points for later feeding site examinations.

### Feeding Site Examination

Within hours after completing the bite-count, the feeding site examinations were carried out by a second observer in exactly the same locations where the bite-counts had been recorded. One-m<sup>2</sup> quadrats were placed at 10 m intervals along the feeding routes. Signs, such as exudation of sap, crushed tissue and fresh clippings were used to judge if a plant species had been eaten. A method similar to the Ocular-Estimate-by-Plot method as described by Pechanec and Pickford (1937) and adopted by Laycock et al. (1972) was used in quantifying the consumption. Thirty-eight quadrats from 2 different sites were sampled for smallstock, and 29 quadrats from 1 site were sampled for yaks.

## Fecal Analysis

Fecal samples were collected next morning from the same livestock herds, which had been subjected to bite-counts and feeding site examinations the day before. Pellets from 7 and 9 different goats and 7 and 8 different sheep were collected from the 2 different pastures shortly after defecation by observing the animals in their holding pens. Yaks were free-ranging and not corralled at night. Hence, fresh yak dung ( $N = 12$ ) were collected on the pasture. The samples were air dried and stored in paper bags in the field. The reference slides were prepared from 63 plant species that included most of the species judged to be eaten based on field observations and interview of herders.

**Preparation of Slides.** Two composite samples were prepared for the smallstock and 1 composite sample was prepared for yak. Sample preparation began by randomly selecting 10 pellets and ca. 5 g of dung from each individual smallstock and yak sample, respectively. Five slides from each composite fecal sample were prepared following the method developed by Sparks and Malechek (1968) and later modified by Vavra and Holechek (1980); Jnawali (1995); Shrestha et al. (2005); and Wegge et al. (2006). Also, separate slides for the plant parts such as leaf, stem, flower, seed, and root were prepared.

**Preparation of Photomicrographs.** The diagnostic features of the plant epidermis such as cells, fibres, trichomes, pores, stomata, vessels, intercellular structures, etc., from each reference slide were photographed using a Leica DFC camera fitted to an optical microscope at 100 $\times$  and 400 $\times$  magnification. In order to ensure wide representation, successive photographs were taken until the same type of tissue was encountered repeatedly along a transect. Thus, a reference slide library was made of 2 831 images. These photomicrographs were given specific file names with dichotomous identification keys, describing the general orientation and color, shape, size and type of epidermal tissues (e.g., with cells—cork cells, sponge cells, silica cells, guard cells, etc.), and general texture (density) of each diagnostic feature. This was done in order to facilitate the screening of photomicrographs for the identification of fecal fragments during later analysis. All photomicrographs were organised using Picasa 2 software (Google 2005). Considering the massive number of photomicrographs from the plant reference slides, this method appeared to be efficient and practical both in terms of speed and accuracy.

**Slide Reading.** The images of fecal fragments were compared with the plant reference photomicrographs at the similar level of magnification (100 $\times$  and 400 $\times$ ), exposure, brightness, and colour conditions. The first 20 nonoverlapping fragments intercepted by a randomly selected transect line were counted. A total of 5 slides and 2 transects per slide yielded 200 counts per composite sample. Out of the 2 composite samples of smallstock and 1 composite sample of yaks, a total of 400 and 200 fragments were examined, respectively.

Fragments that could not be identified to species or genera, but to forage category were grouped into 'unidentified graminoids', 'unidentified forbs', and 'unidentified shrubs'. A few fragments in smallstock (ca. 5%) and in yak (ca. 2%) were classified as 'unidentified dicots', as they could not be distin-

guished into shrub or forb categories. The completely unknown fragments, which accounted to ca. 7% in smallstock and ca. 4% in yak, were included in the 'unknown' category.

## Data Analysis

Relative frequencies were calculated for each forage category and plant species in bite-count, fecal analysis, and feeding site examination. In feeding site examination, the relative frequencies were calculated by weighting the consumption by production in each quadrat (Smith 1968), as follows:

$$f_i = u_i \times p_i / \sum_{i=1}^n (u_n \times p_n) \quad [1]$$

where,

$f_i$  = relative frequency of plant species  $i$  consumed by an ungulate in the quadrat.

$u_i$  = proportion of total horizontal cover of the plant species  $i$  consumed by an ungulate in the quadrat,

$p_i$  = proportion of the plant species  $i$  relative to the total vegetative cover in the quadrat.

$n$  = total number of species in the quadrat.

As the unknown dicots and completely unknown proportions made up negligible amounts in the fecal analysis, they were adjusted by distributing them proportionately to the shrubs and forbs, and to all 3 categories, respectively. This was done by assuming that the ratio of identifiable and unidentifiable fragments was proportional to each other for each plant species in the microscopic analysis (Free et al. 1971).

Differences between estimated proportions of forage categories by fecal analysis, bite-count and feeding site examination of smallstock and yak were assessed by Chi-square tests (Alipayo et al. 1992). In doing so, the following null hypotheses were tested:

1. Within each group of herbivores, the estimated proportions of forage categories are the same by *all 3 methods*,
2. Within each group of herbivores, the estimated proportions of *all 3 forage categories* are the same by any given *pair of methods*,
3. Within each group of herbivores, the estimated proportion of *each forage category* is the same by any given *pair of methods*.

The relationships between pair of methods in estimating forage categories were assessed by the Pearson's product moment correlation coefficient ( $r$ ). The similarity between a pair of methods (Chapuis et al. 2001) was assessed by Schoener's Index (Schoener 1968), which is identical to the percent similarity index as introduced by Renkonen (1938):

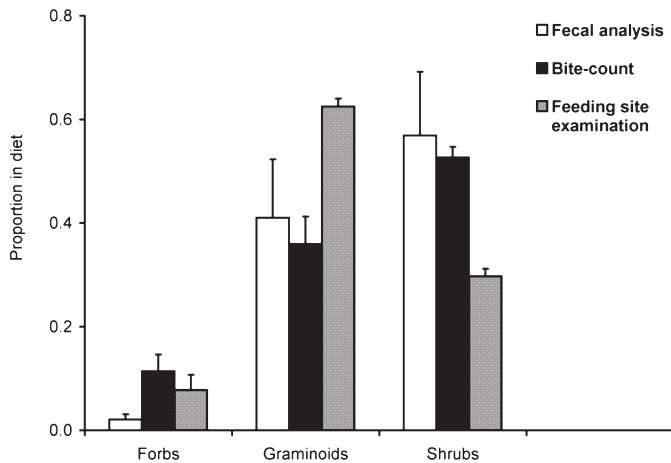
$$\text{Schoener's Index} = 1 - 0.5 \sum |p_{xi} - p_{yi}| \quad [2]$$

where,

$p_{xi}$ : proportion of food item  $i$  detected by method  $x$

$p_{yi}$ : proportion of food item  $i$  detected by method  $y$ .

The index varies from 0.0 for completely dissimilar to 1.0 for completely similar diet compositions as detected by methods.



**Figure 1.** Comparisons between fecal analysis, bite-count, and feeding site examination in estimating the botanical composition of diets of smallstock in the Phu Valley of upper Manang, Nepal. Error bars denote the standard deviation.

The 3 plant species contributing the highest proportion to the diet by each method were analysed by Chi-square tests to test for differences between pair of methods and between all the 3 methods combined. Pearson correlation coefficient ( $r$ ) and Schoener's Index were used to determine the relationship and the similarity between the methods in estimating proportions of different plant species.

## RESULTS

### Comparison at the Level of Forage Categories

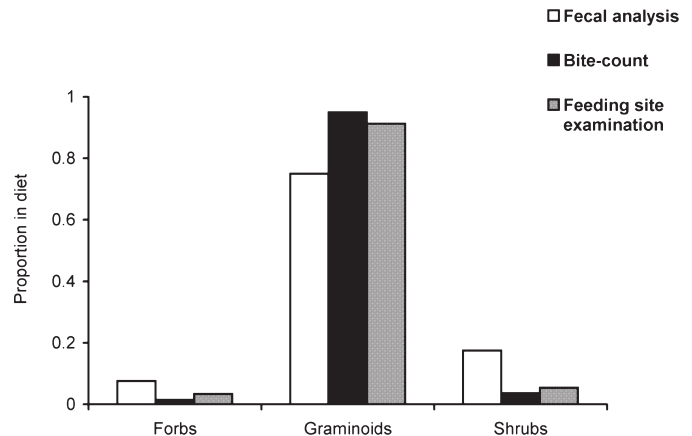
The 3 methods differed in estimating forage categories in the diets of both smallstock ( $\chi^2 = 23.83$ ,  $P < 0.01$ ,  $df = 4$ ; Fig. 1) and yak ( $\chi^2 = 21.09$ ,  $P < 0.01$ ,  $df = 4$ ; Fig. 2).

**Fecal Analysis vs. Bite-count.** Fecal analysis and bite-counts differed significantly both in smallstock and in yak (Table 1). In the former, this was mainly due to a lower estimate of forbs by the fecal analysis ( $\chi^2 = 6.66$ ,  $P = 0.01$ ,  $df = 1$ ; Fig. 1) as there were no significant difference in shrubs ( $\chi^2 = 0.32$ ,  $P < 0.57$ ,  $df = 1$ ) or in graminoids ( $\chi^2 = 0.53$ ,  $P < 0.48$ ,  $df = 1$ ).

**Fecal Analysis vs. Feeding Site Examination.** For both animal groups, fecal analysis also differed from feeding site examination (Table 1) because it gave higher estimates of shrubs and lower estimates of graminoids (Figs. 1 and 2). However, the lower estimate of forbs by fecal analysis was significant only in the smallstock ( $\chi^2 = 3.726$ ,  $P = 0.05$ ,  $df = 1$ ).

**Bite-count vs. Feeding Sites.** Bite-counts and feeding site examination differed only in smallstock (Table 1); the feeding site examination gave lower estimates of shrubs ( $\chi^2 = 11.25$ ,  $P < 0.01$ ,  $df = 1$ ) and higher estimates of graminoids ( $\chi^2 = 13.986$ ,  $P < 0.01$ ,  $df = 1$ ). In yak, no differences were detected in any of the forage categories by the two methods.

**Similarities and Relationships.** In smallstock, the bite-count was most similar (Table 2) and closely related (Table 3) to the fecal analysis. In yak, the bite-count was more similar to the



**Figure 2.** Comparisons between fecal analysis, bite-count, and feeding sites examination in estimating diets of yak in Phu valley of upper Manang, Nepal.

feeding site examination than to the fecal analysis (Table 2). As the data were collected for only one day from a single site, we were unable to use correlation test on data in yaks.

### Comparison at the Level of Plant Species

Fecal analysis consistently identified the highest number of plant species both in smallstock and yak (Table 4). In smallstock, feeding site examination detected the least number of plant species, but the 3 methods varied less in total number identified relative to yak. In yak, bite-count and feeding site examination detected only one-fourth, and one-half of the species, respectively, than that identified by fecal analysis.

As with the forage categories, the 3 methods differed in estimating the proportions of the 3 most important food species in both smallstock ( $\chi^2 = 25.44$ ,  $P < 0.01$ ,  $df = 6$ ) and yaks ( $\chi^2 = 89.29$ ,  $P < 0.01$ ,  $df = 10$ ). Pair-wise comparisons revealed that feeding site examination differed from bite-count and fecal analysis in both animal groups, but the difference between the latter 2 methods was not significant in the smallstock (Table 1). The ranking of the important food species in smallstock further attests to this, as the bite-count and fecal analysis gave consistently higher ranks to the 2 important food species *Poa pagophila* (Bor.) Kew Bull. and *C. jubata* than that by the feeding site examination (Table 5). In the case of yak, no methods were in agreement in estimating the 3 most important plant species (Table 1).

Further analysis based on Schoener's Index and Pearson's product moment correlation coefficient showed a pattern consistent with the previous results on forage categories. They showed that in smallstock, fecal analysis was most similar (Table 2) and more closely related (Table 3) to bite-count than to feeding site examination.

## DISCUSSION

The 3 methods differed in estimating the diets of smallstock and yak both at the forage category and at the plant species level. In smallstock, feeding site examination gave higher estimates of graminoids and lower estimates of forbs and shrubs than the



**Table 1.** Pair-wise comparisons of methods in estimating the proportions of forage categories and the 3 most important plant species in smallstock and yak.

	Forage category						Plant species <sup>1</sup>					
	Smallstock			Yak			Smallstock			Yak		
	$\chi^2$	<i>P</i>	df	$\chi^2$	<i>P</i>	df	$\chi^2$	<i>P</i>	df	$\chi^2$	<i>P</i>	df
Fecal analysis vs. bite-count	6.7	0.03	2	15.85	< 0.01	2	2.08	0.56	3	56.37	< 0.01	5
Fecal analysis vs. feeding site examination	16.63	< 0.01	2	10.36	0.01	2	10.32	< 0.02	3	38.29	< 0.01	5
Feeding site examination vs. bite-count	14.21	< 0.01	2	1.19	0.55	2	23.63	< 0.01	3	31.31	< 0.01	4

<sup>1</sup>Average proportions of the 3 plant species with the highest contribution in each sample collection.

other two methods. Furthermore, fecal analysis underestimated the proportion forbs compared with bite-count. In yak, bite-count and feeding site examination gave similar results, with consistently higher estimates of graminoids and lower estimates of forbs and shrubs than fecal analysis.

The daytime sampling period in yak for both bite-count and feeding site examination probably explains the observed discrepancy between fecal analysis and these 2 methods. Although not studied systematically, we observed that yaks shifted to lower slopes during nighttime. The vegetation in these low-lying areas was dominated by dicots with higher species richness than the upper alpine grasslands. Hence, it is likely that yaks consumed more dicots when we did not collect data on bite-count and feeding site examination.

Unlike yak, the smallstock were kept in an enclosure when they returned from the pasture. Also they were confined to the same pasture for more than 5 days during the data collection period, and the vegetation community was relatively homogeneous where the smallstock foraged. Hence under these conditions, the asynchronous sampling period between fecal analysis and the other two methods can not account for the observed discrepancy in smallstock (Smith and Shandruk 1979). In the following section, we discuss the possible biasing factors in each studied method.

### Feeding Site Examination

Feeding signs are known to get readily obscured in plants which are susceptible to disarticulation (Smith 1968; Smith and Shandruk 1979). Shrubs are more likely to be disarticulated because of the prevalence of nodes. For this reason, feeding site examination probably overlooked some of the feeding signs on shrubs. In addition, the method employed in quantifying the consumption of forage species might also have contributed to underestimation of shrubs in the feeding site examination. Owing to the difficulty in estimating consumption on the basis

**Table 2.** Similarity (Schoener's Index) between pairs of methods in estimating the proportions of forage categories and the 3 most important plant species in smallstock and yak.

Method pairs	Smallstock		Yak	
	Forage category	Plant species	Forage category	Plant species
Bite-count vs. fecal analysis	0.89	0.83	0.80	0.53
Bite-count vs. feeding site examination	0.73	0.65	0.96	0.74
Fecal analysis vs. feeding site examination	0.72	0.69	0.84	0.62

of counting all feeding signs on individual plants, we estimated utilization by cover values, similar to the Ocular-Estimate-by-Plot method (Pechanec and Pickford 1937; Laycock et al. 1972). This method restricted our observation mainly to the horizontal part of the shrub canopy.

### Bite-count Technique

Inaccurate identification of plants and differential bite size are the major factors affecting the accuracy of the bite-count data. Identification of plants is influenced by the forage category (Henley et al. 2001), terrain conditions (Sanders et al. 1980), and the training of the observer (Free et al. 1971). The bias due to these factors per se was minimized in the present study because the bites were recorded by approaching the domestic animals within a distance as close as 2 m by an observer, who had nearly 1 year of experience with the local flora.

The bite size is reported to vary according to season (Free et al. 1971), size of the leaves (Mofareh et al. 1997; Henley et al. 2001), and mouth morphology of the ungulate (Ortega et al. 1995; Mofareh et al. 1997). Free et al. (1971) showed that bite weight was roughly constant in spring and summer, but variable during autumn when the forage began to mature and leaves began to dry and curl. If this is the case, our bite-count data were less biased due to variation in bite size because they were collected in summer. Henley et al. (2001) concluded that bite-counts tend to underestimate the dietary contribution of large-leaved plants (e.g., forbs). However, in the dry trans-Himalayan rangelands, leaves of forbs and shrubs are small and rather similar in size. Lastly, Mofareh et al.'s (1997) conclusion of more uniform bite sizes in narrow-muzzled ungulates such as deer and small bovids compared to cattle seems to correctly explain our results of similar proportion of shrubs and graminoids by bite-counts and fecal analysis.

Therefore, our bite-count data in smallstock probably gave rather accurate results. It is likely that the reason for the discrepancy between this method and fecal analysis in estimating forbs has more to do with the fecal analysis method than with the bite-count method.

### Fecal Analysis

The fecal analysis consistently gave lower proportions of forbs than bite-count also when tested separately for goats ( $\chi^2 = 11.33$ ,  $P < 0.01$ ,  $df = 1$ ) and sheep ( $\chi^2 = 18.54$ ,  $P < 0.01$ ,  $df = 1$ ). These findings closely agree with the study undertaken in summer in domestic goats in an area adjacent to the present study area (Shrestha et al. 2005) and elsewhere (Smith and Shandruk 1979; McInnis et al. 1983; Alipayo et al. 1992;

**Table 3.** Relationships (Pearson's product moment correlation coefficient,  $r$ ) between pairs of method in estimating the proportions of forage categories and the 3 most important plant species in smallstock and yak.

	Forage category			Plant species <sup>1</sup>					
	Smallstock			Smallstock			Yak		
	$r$	$P$	$n$	$r$	$P$	$n$	$r$	$P$	$n$
Fecal analysis vs. bite-count	0.97	< 0.01	6	0.84	< 0.02	7	0.78	0.07	6
Fecal analysis vs. feeding site examination	0.57	0.23	6	0.80	0.03	7	0.65	0.17	6
Feeding site examination vs. bite-count	0.48	0.33	6	0.45	0.31	7	0.95	< 0.01	4

<sup>1</sup>Average proportion of plant species with the highest contribution in each sample collection.

Bartolome et al. 1995). Considering the authors' previous experience with the fecal analysis method and knowledge of the local flora, the bias was not due to incorrect identification of plant species, which is often the case with untrained observers (Free et al. 1971; Holechek and Gross 1982; Alipayo et al. 1992). Besides, detailed collection of reference specimens comprising plant tissues from flower, seed, stem, leaf, and root, and the use of photomicrographs improved the accuracy, as evidenced by the low proportions of completely unknown fragments in the present study.

Instead, the bias most likely was due to differential digestion of ingested plant material. Persistence of plant material after passage through the gut varies according to the digestibility of the plant species (Pulliam 1978). Digestibility depends to a large extent on the lignification of epidermal tissue. Many perennial species (e.g., shrubs) have highly lignified epidermal tissue, and proportionally more of such plants will therefore "survive" digestion compared with annuals, including forbs (Storr 1961). Moreover, the epidermal tissue in xeric shrubs is known to be more cutinized than forbs, thereby further reducing the extent of their digestion. For these reasons, forbs are more susceptible to digestion (Vavra et al. 1978; Bartolome et al. 1995) relative to shrubs (Holechek and Gross 1982), and this is especially true in semi-arid environments like ours (Long et al. 1999). This appears to be the most obvious reason why fecal analysis gave lower estimates of forbs compared to bite-count in our study.

Precision is expected to increase during winter (Vavra et al. 1978; Chapuis et al. 2001) when digestibility (Long et al. 1999) and/or abundance of forbs are low. Fecal analysis is also found to be more precise in grazers like sheep and cattle (Vavra et al. 1978; Alipayo et al. 1992; Bartolome et al. 1995; Mohammad et al. 1995; Mofareh et al. 1997) than in browsers such as deer (Holisova et al. 1986; Lewis 1994). This supports the report that fecal analysis is less accurate when the diet consists more of shrubs and forbs than of monocots (Slater and Jones 1971). Our results suggest that it is not the amount of shrubs but probably the amount of forbs, which give rise to a bias in the fecal analysis.

**Table 4.** Total number of plant species identified by fecal analysis, bite-count and feeding site examination in smallstock and yak.

	Smallstock	Yak
Ungulates		
Fecal analysis	26	29
Bite counts	22	8
Feeding site examination	18	13

## CONCLUSION AND MANAGEMENT IMPLICATIONS

Both the feeding site examination and the bite-count method gave biased estimates of the diet of the free-ranging yaks because the data from these methods did not cover the late evening and night feeding bouts. Apart from this, the former method did not detect all the feeding signs in shrubs and is also unsuitable when more than one herbivore uses the range. Although rather precise, the bite-count method can only be used for tame animals, which are not free-ranging. Considering this, the fecal analysis appears to be the most appropriate method for comparing food habits of wild and domestic ungulates in the Trans-Himalayan rangelands. However, this method is quite time-consuming and demands a great deal of skill in identifying the plant species in the fecal samples. Using high definition photomicrographs together with the development of dichotomous identification keys of reference plant species and their parts can mitigate these problems. Also, the problem of differential digestion in the fecal analysis can be addressed by developing appropriate correction factors (Brand 1978; Barker 1986). In doing so, the phenological stage of the plants and type of ungulate should be taken into consideration.

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**Table 5.** Ranking of the 3 most important food species<sup>1</sup> by 3 different methods in smallstock. The ranking is based on the average of 2 composite fecal samples and 2 days of observations of bite-counts and feeding site examinations.

Plant species	Fecal analysis		Bite-count		Feeding site examination	
	Percent of diet	Rank	Percent of diet	Rank	Percent of diet	Rank
<i>Carex</i> sp.	11.46	1	16.23	2	47.15	1
<i>Lonicera spinosa</i>	8.11	2	19.34	1	14.12	2
<i>Poa pagophila</i>	4.58	4	14.16	3	1.52	11
<i>Caragana jubata</i>	4.17	6	9.11	4	1.08	12
<i>Spiraea</i> sp.	5.65	3	6.79	5	8.51	3
<i>Agrostis</i> sp.	1.49	11	0.15	18	4.70	5
<i>Danthonia jacquemontii</i>	0.67	15	1.68	11	8.25	4

<sup>1</sup>Species with the highest contribution in each sample collection.

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# Paper III



# **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 was not being herded. 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 non-equilibrium systems such as 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 (Mishra and Rawat, 1998). 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 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 of livestock and ibex (*Capra sibirica*), Bhatnagar et al. (2000) found these two species to be spatially separated. 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<sup>2</sup> 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 °C and -7.3 °C in January and 18 °C 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. 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. 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 abundant and the only large wild ungulate, distributed in a density of approximately 10 animals/km<sup>2</sup> (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 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. While in pastures, the smallstock are usually herded, whereas yaks move freely.

## *2.2. Data collection*

Data on habitat use were collected by systematically searching opposite slopes from fixed vantage points using  $8 \times 40$  binoculars and a 15 - 60X variable spotting scope during daylight hours (0600 to 1800 hrs). All observations of naur were undertaken in the parts of the range where domestic stock were not attended by herders. A total of 766 groups of naur, 392 herds of yak and, 257 herds of smallstock were observed in winter (4 January to 30 March), spring (1 April to 15 June), summer (16 June to 15 September) and autumn (16 September to 3 January). The definition of seasons followed the calendar of local livestock movements. Animal locations

were plotted on a 1:10000 Topographic Map and later transferred to Arc View 3.1 (Environmental Systems Research Institute, Redlands, CA). using software 'World File Generator'. 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 50m by 50m 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 1:10000 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 percent confidence intervals around their mean altitudinal positions. Differences between naur and domestic 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; Scogings et al., 1990), 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 correspondence analysis. A brief description of the procedures is outlined below.

Correspondence analysis 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 – 4319 m), middle (4320 – 4639 m), high (4640 – 4919 m) and very high (4920 – 5239 m), and 3) slope categories; flat (0 - 10 degrees), moderate (11 - 30 degrees), steep (31 - 50 degrees), and very steep (51 - 90 degrees). 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 2 principal axes explaining nearly 65 percent 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 correspondence analysis. 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 1 000 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, 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 spatially segregated within season, the summer altitudinal range of smallstock was similar to the spring 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*

The first two components of correspondence analysis explained about 65% of variation. The scatter plot using these two components revealed three distinct habitat complexes (Fig. 2a). The upper left quadrant of the plot represents the steeper and highly rugged, low elevation zones, consisting mostly of scrublands. Lower left and more towards the middle portion, near the origin of the plot, refers to middle elevation zones with flat to moderate slopes. The third habitat complex comprised mainly the high elevation alpine grasslands and is located in the middle and right hand side of the scatter plot.



Four associations between naur and domestic stock within and across seasons emerged in the scatter plot (Fig. 2b). 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 correspondence analysis. 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 appeared to be more selective on vegetation types than free-ranging yak as they significantly preferred alpine meadows, avoided grassland and used scrublands randomly, while the latter used all three vegetation types randomly (Table 2). On the other hand, free-ranging yaks were more selective on elevation than naur, as they significantly preferred middle and high elevation and avoided low and very high elevation, while naur showed a significant preference only for 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 (Bonferroni, all  $P < 0.05$ ) 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. 2b), 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 correspondence analysis did not reveal a spatial association between them probably because smallstock was more randomly distributed on slope categories than naur (Table 4).

## 4. Discussion

### 4.1. Habitat overlap

Due 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 (Bagchi 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 was 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 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 (Zhao et al., 2007). A high proportion of increaser species such as *Stellera chamaejasme*, *Oxytropis tatarica* and *Artemisia* spp etc. (Holzner and Kriechbaum, 2000), as was also noted by Sherpa and Oli (1988) in a previous survey, 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 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, the three herbivores may coexist through food resource partitioning because of differences in body size (adult male body weights: smallstock 35 kg (Wilson, 1997), naur 57 kg (Wegge, 1979), and yak 300 kg (Wilson, 1997)). Food quality and quantity are the two main niche axes which ungulates partition on the basis of body weights (Jarman, 1974; Voeten and

Prins, 1999). The smaller species, with their higher per mass metabolic rate, are expected to be selective browsers, whereas the larger species, with their lower per mass metabolic rate, are expected to be generalist grazers (Belovsky, 1997; Olf et al., 2002). Further information on the food habits of the three animal groups is therefore needed to understand the nature of their interactions.

Moreover, density-dependent effects of competition should be cautiously interpreted (Saether et al., 1996; Wang et al., 2006). Arid and semi-arid rangelands like the trans-Himalaya are known to be non-equilibrium grazing systems, controlled more by abiotic than by biotic factors (Ellis and Swift, 1988; Vetter, 2005). Also, 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 probably facilitates the coexistence of potentially competing herbivores (Alhamad, 2006), as has been shown by theoretical analysis (Ritchie and Olf, 1999), experimental (Cromsigt and Olf, 2006), and observational studies in other natural environments (Metzger et al., 2005; Voeten, 1999).

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

	Alpine Meadow	Grassland	Scrubland
Relative Area <sup>a</sup>	13%	31%	56%
Bare ground	29%	38%	42%
Elevation (in meters)	3800-4900	4200-5200	3640- 4700
Slope (in degree)	< 15 degree	< 45 degree	All
Important plant species	<i>Stellera chasmaejanae</i> , <i>Artemesia</i> spp., <i>Chesneya nubigena</i> , <i>Hippophae tibetana</i> , <i>Kobresia pygmea</i> , <i>Carex</i> spp.	<i>Festuca</i> sp., <i>Carex</i> spp., <i>Stipa</i> spp.	<i>Lonicera spinosa</i> , <i>Astragalus</i> spp., <i>Spiraea</i> sp., <i>Cotoneaster</i> spp., <i>Caragana jubata</i> , <i>Rhododendron anthropogon</i> , <i>Bistorta</i> sp.

<sup>a</sup>Excluding non-vegetated areas

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

Seasons	Vegetation type	Availability <sup>a</sup> (%)		Utilization (%)				Selection <sup>b</sup>			
		All	Domestic stock	Small-stock	Naur	Free ranging yak	Herded yak	Small-stock	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	-

<sup>a</sup>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.

<sup>b</sup>Symbols (+, 0, -) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).

**Table 3.** Seasonal use of elevation zones by domestic stock and naur in Phu valley, Nepal. Low, middle, high and very high elevation zones refers to (3640 - 4319m), (4320 - 4639m), (4640 - 4919m), and (4920-5239m), respectively.

Seasons	Elevation zones	Availability <sup>a</sup> (%)		Utilization (%)				Selection <sup>b</sup>			
		All	Domestic stock	Small-stock	Naur	Free ranging yak	Herded yak	Small-stock	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	-	-	-	-

<sup>a</sup>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.

<sup>b</sup>Symbols (+, 0, -) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).

**Table 4.** Seasonal use of slope categories by domestic stock and naur in Phu valley, Nepal. Flat, moderate, steep and very steep categories refers to (0 - 10), (11 - 30), (31 - 50), and (51-90) degrees of slope, respectively.

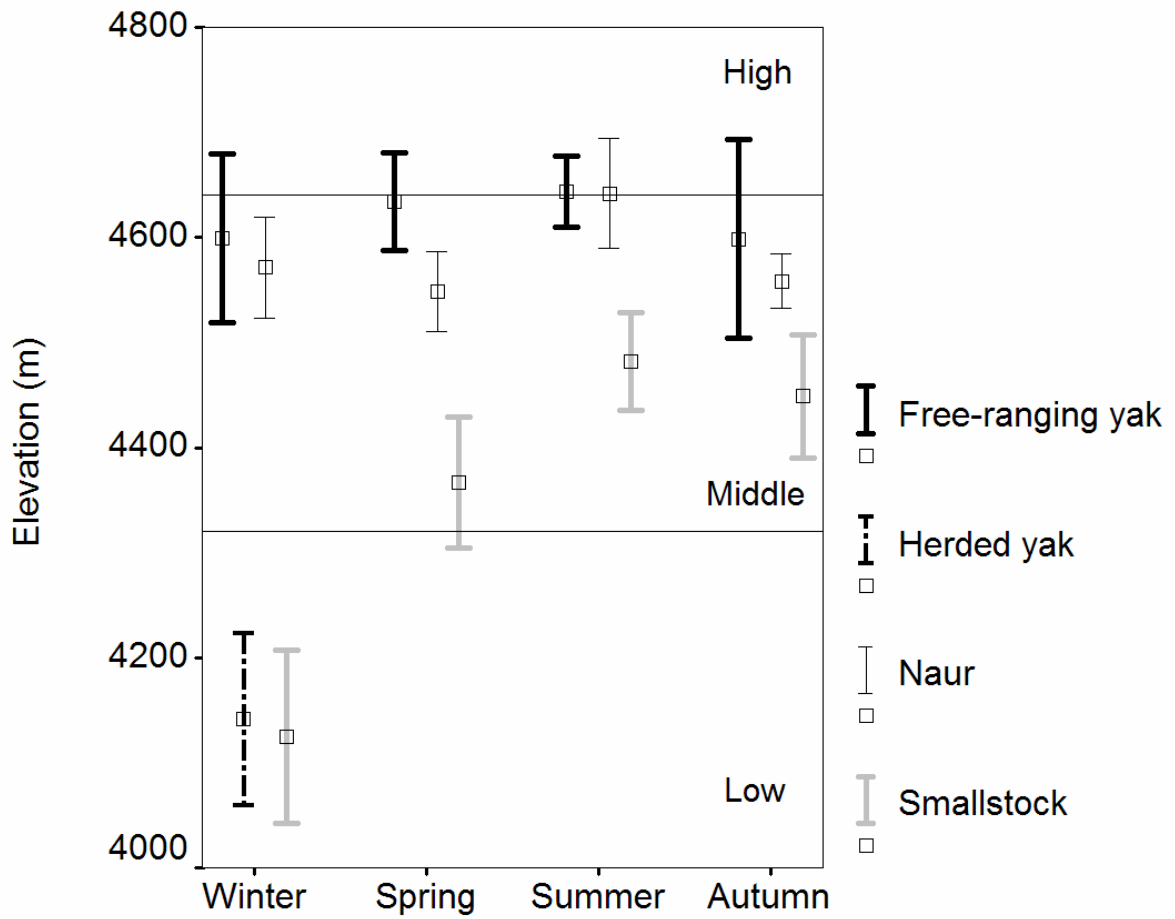
Seasons	Slope categories	Availability <sup>a</sup> (%)		Utilization (%)				Selection <sup>b</sup>			
		Domestic		Free		Free		Free		Herded	
		All	stock	Small-stock	Naur	ranging yak	Herded yak	Small-stock	Naur	ranging yak	Herded yak
Spring	Flat	34.4	34.4	51.0	42.7	59.0		+	+	+	
	Moderate	30.5	30.5	37.3	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

<sup>a</sup>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.

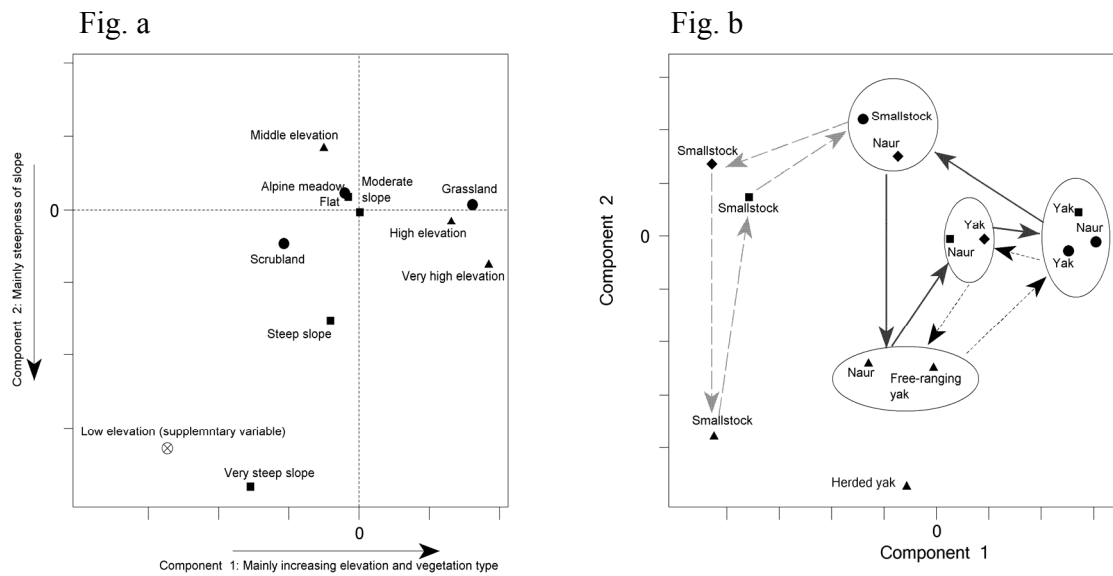
<sup>b</sup>Symbols (+, 0, -) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).



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



**Fig. 2.** 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 grey (smallstock), straight black (naur) and short-dashed black (free-ranging domestic yaks).



# Paper IV



# **Wild and domestic ungulates in Nepal Trans-Himalaya: resource partitioning or competition?**

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## Abstract

We examined the extent of resource partitioning and competition between naur (blue sheep/bharal, *Pseudois nayaur*) and domestic goat (*Capra hircus*), sheep (*Ovis aries*) and free-ranging yak (*Bos grunniens*) in a semi-arid, high altitude rangeland in Phu valley in Nepal by combining information on habitat utilization and diet. Seasonal diets were studied using micro-histological analysis of feces after adjusting for differential digestion. Information on seasonal habitat-use (elevation and broad vegetation types) was derived from another study in the area. We determined resource-use overlaps by calculating the geometric means of the 3 overlap indices, viz. elevation, vegetation types and food plant species. Besides merely comparing within-season or temporal resource-uses, we also investigated the cross-seasonal patterns of overlap as the successive use of the same resources by different herbivores provides additional insights into competitive relationships, particularly in seasonal environments. In order to detect resource limitation, we compared ungulate biomass density and the population performance of naur, as expressed by the ratio of young to adult females, with other areas in Nepal and India with differing grazing intensity and range productivity. All four ungulates had mixed diets and foraged opportunistically. Few plants, which were also the most abundant in the study area, made up the bulk of the diet of all animal groups. However, their foraging styles differed as yaks showed a clear grazer trend, goats a browser trend, while naur and sheep were more intermediate feeders. Alpine meadow was an important habitat component, and legumes *Oxytropis* spp. and *Chesneya nubigena* appeared to be critical food resources; the former was preferentially eaten by all ungulates in spring, summer and autumn and the latter by naur and free-ranging yaks during winter. Relatively high total ungulate biomass density (3028 kg/km<sup>2</sup>) and low recruitment (56 young per 100 adult females in autumn) of naur compared to other studies provided some evidence of resource limitation and interspecific competition. However, owing to the non-

equilibrium dynamics of the range ecosystem of the Trans-Himalaya, the extent of competition was difficult to ascertain. The spatio-temporal heterogeneity in the composition and phenology of forage plants across the steep gradient of altitude together with rotational grazing management appeared to indirectly facilitate co-existence through spatial partitioning of naur and smallstock. However, disturbance from herder attendance and/or higher stocking densities are likely to impose competition between these two groups due to high cross-seasonal overlaps in elevation, vegetation types and diet. Temporally, naur overlapped more with free-ranging yak than with smallstock. Similar habitat use and diets in winter suggests that competition between these two species is most likely to take place during this season.

Key words: bharal, blue sheep, diet, grazing, habitat, livestock, naur, overlap, *Pseudois nayaur*, yak

## **Introduction**

The controversy surrounding the issue of interspecific competition has been a major bottleneck for effective multi-species range management in Trans-Himalaya and elsewhere. Information on when (temporally) and where (spatially) related ungulates interact with respect to their use of resources is required in order to understand the processes of resource partitioning and competition (de Boer and Prins 1990). The extent of overlap in habitat and food tells us the degree to which coexisting species have similar resource requirements (Putman 1996). Competition takes place only when shared resources become limited (de Boer and Prins 1990). However, owing to the difficulty of demonstrating resource limitation (Schoener 1983), the occurrence and effects of competition are poorly understood (Arsenault and Owen-Smith 2002). An indirect approach for detecting competition is observation of negative effects on populations or individuals resulting from overlapping use of resources (Putman 1996), as overstocking is known to reduce animal body growth and adversely affect life-history traits such as fecundity, sexual maturation and survivorship (Fretwell 1972, Saether 1985, Skogland 1986, Reimers et al. 2005). However, these approaches work in systems where the environmental conditions are relatively constant one year to another (Ellis and Swift 1988), allowing herbivore populations to increase until they are stabilized by density-dependent limitations.

Recent studies indicate that many semi-arid rangeland ecosystems (Ellis et al. 1991, Fernandez-Gimenez and Allen-Diaz 1999), including the Trans-Himalaya (Miller 1997) function as a non-equilibrium system, where rangeland productivity is governed mainly by the fluctuations in the climatic factors and thus it would be difficult to ascertain the extent of competition merely on the basis of conventional density-dependent models in these regions.



Naur (blue sheep/bharal, *Pseudois nayaur*) and domestic stock are widely and sympatrically distributed throughout the Trans-Himalaya (Schaller 1998). While the former is an important prey species of the globally endangered snow leopard (*Uncia uncia*) (Oli et al. 1993), the latter constitutes an integral part of local subsistence livelihoods (Lensch 1995). Owing to close phylogenetic relationship and the recent history of co-occurrence, naur and domestic stock are expected to show limited resource partitioning. Also, because of the tendency of herders to maintain domestic stock at artificially higher densities by supplemental feeding, shelter and medical attention, domestic stock is at a competitive advantage over their wild relatives and may therefore out-compete the latter.

Information on the impact of livestock grazing on native wildlife in the Trans-Himalaya is generally lacking. Except for a few recent studies in northern India (Bagchi et al. 2004, Mishra et al. 2004, Namgail et al. 2007), knowledge about interspecific relationships between wild and domestic ungulates is limited to comparison of patterns of habitat use and food habits (Schaller and Gu 1994, Harris and Miller 1995, Fox 1996, Bhatnagar et al. 2000, Shrestha et al. 2005).

Naur are mixed feeders (Shrestha et al. 2005) and are commonly found in proximity to rugged mountain slopes (Wegge 1979, Oli 1996, Namgail et al. 2004). In the Indian Trans-Himalaya, Mishra et al. (2004) reported substantial diet overlap with livestock and concluded that this adversely affected the naur population. Spatial overlap was also reported by Schaller and Gu (1994) between naur and domestic stock during summer in Tibet. On the other hand, Harris and Miller (1995) reported both diet and habitat separation between the two animal groups during summer, also in Tibet. In Nepal, while they overlapped in their summer diet, spatial separation was noticed among them (Shrestha et al. 2005).

These discrepancies might be due to the extensive spatial variation (Davies et al. 2005, Wang et al. 2006) over their large geographical range, which has brought about local adaptations across the landscape (Putman 1996). Also, the presence of herders may alter the natural interaction patterns (Namgail et al. 2007); thus the effect of herders has to be taken into account when studying interactions among wild and domestic ungulates (Harris and Loggers 2004, Mishra et al. 2004).

In mountainous regions, altitude plays a crucial role in determining abundance and distribution of ungulates across the landscape (Green 1987, Mysterud et al. 2001). Yet, this important component of the habitat has seldom been adequately accounted for by other studies in the Trans-Himalaya (but see Bhatnagar et al. 2000). Furthermore, studies undertaken so far have focussed only on the overlaps in habitat and diet within the same season (Bagchi et al. 2004, Mishra et al. 2004), although the successive use of the same habitat or food plants by different herbivores is also important (Bell 1971, Jarman and Sinclair 1979). Cross-seasonal overlap can be facilitating for another herbivore, if feeding by one species increases the access to and/or quality of forage for the other (McNaughton 1976, Arsenault and Owen-Smith 2002), as well as competing, if such utilization brings about resource limitation to the other species (Illius and Gordon 1987).

In our study area, previous work has shown that the alpine meadow vegetation type is a critical resource, as both naur and domestic stock used this vegetation type preferentially throughout the year (Shrestha and Wegge unpubl. data). In this follow-up paper, we describe the botanical composition of seasonal diets of the interacting ungulates (naur and domestic yak *Bos grunniens*,

goats *Capra hircus* and sheep *Ovis aries*). By combining information on habitat utilization and diet, we identify the most closely related species pairs (both within and between seasons) as well as the critical periods of the year. Finally we discuss our results with regards to resource competition and partitioning in light of the current stocking densities of the range and the reproductive performance of naur.

## **Methods**

### ***Study area***

We conducted the fieldwork within a 125 km<sup>2</sup> study area in the Phu valley (28°46' N, 84°17' E) of Manang District in Nepal (Figure 1). The study area adjoins the Tibetan plateau to the north and spreads across an altitudinal range of approx. 3700 to 7000m. The topography is dominated by steep slopes, massive cliffs and glacier fields. The local climate is influenced by the rain shadow effect of the Annapurna Himalaya. Total precipitation is less than 400 mm annually (ICIMOD 1996) and occurs mostly in the form of snow during winter. The mean maximum and minimum temperatures recorded during fieldwork were 5.8 °C and -7.3 °C in January and 18 °C and 9.5 °C in July. The snow and frozen ground start to thaw in late March. The area is sparsely vegetated by xerophytic plants, characterized by aromatic, dwarf, cushionoid, and hairy species. In general, altitude and slope govern the distribution of vegetation types. Three broad vegetation types were identified based on dominant life forms: 1) alpine meadows, distributed in pockets of relatively flat areas; 2) alpine grasslands, located at higher elevations in mesic sites; and 3) scrublands, widespread on dry rugged slopes. Among these types, alpine meadow is the least abundant and is mainly distributed in middle elevations (Figure 1; Table 1). Faunal diversity is generally low; naur is the only large wild ungulate and snow leopard (*Uncia uncia*) is common, whereas wolf (*Canis lupus*) and brown bear (*Ursus arctos*) are absent.

Phu village, sparsely populated by 33 households, is the only permanent settlement in the study area. People here follow Tibetan Buddhism, and the local abbot has imposed total ban on hunting, which is strictly followed by the villagers. The main subsistence occupation is animal husbandry, followed by agriculture. The herders own multiple species of domestic stock, yak (38%), goats (34%), sheep (19%), cow (5%) and horse (3%). Altogether the total stocking density of domestic animals is nearly double that of naur. Herders move their stock to different seasonal pastures throughout the year. While in the pastures, yaks are generally free-ranging and the sheep, goats and cows are herded. During winter, except for free-ranging horses and non-lactating yaks, the domestic stock is supplementally stall-fed.

### ***Data collection***

#### **Food habits**

We applied microhistological analysis of feces to study the food habits (Sparks and Malechek 1968, Shrestha et al. 2005) and used correction factors to adjust for differential digestion of forage categories (Shrestha and Wegge 2006).

Each season, fresh fecal samples of free-ranging yaks and naur were collected from different parts of the study area. To detect seasonal changes in diet, we collected the samples from more or less the same sites across seasons by consistently following the same trails throughout the year. A total of 397 pellet groups of naur and 153 dung piles of yak were sampled over the four seasons (winter: 1 January to 30 March, spring: 1 April to 15 June, summer: 16 June to 15 September, and autumn: 16 September to 31 December). The definition of seasons followed the calendar of local livestock movements. Fresh pellets of 190 goats and 163 sheep were collected

in their holding pens over the year. The samples were stored in paper bags and air-dried in the field.

As composite fecal samples yield similar results as that of the means from individual samples (Jenks et al. 1989), they were composited to speed up the laboratory work (Harris and Miller 1995). One composite sample per season per ungulate was prepared by randomly selecting 5 pellets and ca. 5 g of dung from each individual naur, goats and sheep and yak sample, respectively. Five slides from each composite fecal sample were prepared following the procedure detailed in Shrestha and Wegge (2006). Moreover, we used a plant reference slide library consisting of 2 831 photomicrographs of 63 different plant species in our study area that had been prepared by Shrestha and Wegge (2006) to identify the plant fragments in the feces. While doing so, the fecal images were maintained at similar level of magnification (100x and 400x), brightness, and colour conditions as that of the reference photomicrographs. The first 20 non-overlapping fragments intercepted by a randomly selected transect line were counted. A total of 5 slides and 2 transects per slide yielded 200 counts per composite sample. Thus, a total of 800 fragments were counted for each ungulate in four seasons.

Fragments, which could not be identified to species or genera but to forage category were grouped into ‘unidentified graminoids’, ‘unidentified forbs’, ‘unidentified browse’, and ‘unidentified dicots’. The completely unknown fragments were included in the ‘unknown’ category.

### **Habitat Use**

Vegetation type and elevation were the most influential variables in explaining the distribution of ungulates in our study area. We therefore used the data on utilization of vegetation types and elevation from our earlier habitat study (Appendix I and II) (Shrestha and Wegge unpubl. data). To exclude the confounding effect of human presence, the habitat data on naur were collected from those parts of the rangeland where domestic stock were not attended by herders at the time of observation.

### **Forage availability**

We conducted a vegetation survey in summer to estimate the abundance of forage plants. A total of 639 quadrats (each 1-m<sup>2</sup>), were randomly laid in the 3 vegetation types (N; alpine meadow = 237, grassland = 133, and scrubland = 274). The percentage cover of individual species in each quadrat was estimated visually following the procedure described by Smartt et al. (1976). In addition, we recorded the GPS position, altitude, aspect, slope and percentage of bare ground to assess general habitat characteristics. We followed Pohle (1990), Polunin and Stainton (1987) and Stainton (1988) to identify the plant specimens during the fieldwork. Moreover, a herbarium of all the plant species encountered in the field was prepared and the unidentified specimens (mostly graminoids) were later identified with the help of experts.

### **Stocking densities and naur reproductive success**

Numbers of domestic species were obtained through a total count (smallstock and cows) as well as interviews with herders (free-ranging yaks and horses). To estimate the naur population size, we did total counts in autumn (October – December) by systematically scanning from vantage points (Wegge 1979). The number of young (< 1 year) and adult females (> 2 years) in each

group were recorded. The population productivity of naur was analyzed using only those observations where we could classify all the members of a group (N = 20 groups). Biomass densities of naur and domestic stock were calculated using average adult body mass of each species as reported by Mishra et al. (2002).

### ***Data Analysis***

#### **Diet composition**

First, we adjusted the data on diet composition by applying conversion factors (forbs  $\times$  3.85, graminoids  $\times$  0.90, browse  $\times$  0.89; Appendix III), which were derived from a comparative study of methods in the same study area (Shrestha and Wegge 2006). Because yaks grazed in other vegetation communities when not observed for bite-counts, the data were not comparable with the fecal analysis and as such we could not develop a separate conversion factor for yaks. Thus we used the average of the conversion factors for goat and sheep assuming that the degree of bias due to differential digestion is the same for all four ungulates. Because cattle, goats and sheep are known to digest forage in a similar manner (Huntington and Givens 1997), we expect this assumption to be realistic. Besides adjusting the forage categories, the proportions of individual food plants were also adjusted by using the same factors as the category to which they belonged (Shrestha et al. 2005). We did not apply conversion factors for our winter data because bias due to differential digestibility is considered to be minimal during that period (Chapuis et al. 2001). We then calculated the relative frequencies for each forage category and plant species by dividing the total number of fragments identified for a given category (forage category or plant species) by the total number of all counts made in the sample, multiplied by 100.

We applied G-tests (Log likelihood Chi-square tests) in two and three dimensional contingency tables to test for significant differences of the proportions of forage categories, plant species over the year (Zar 1996). Equal sample sizes allowed us to use one-tailed tests by dividing the resultant  $P$  by 2 in order to ascertain the directional change between pairs (Zar 1996). Statistical tests were carried out using Microsoft Excel add-in Pop Tools (Hood 2005) and the Sigma Stat (SPSSInc 2003).

### **Diet selection**

To estimate the relative abundance of food within the study area, we computed the relative frequencies of the mean cover values of each plant species and forage category for each vegetation type. Because the spatial overlap between the four ungulates occurred mostly in the altitudinal range of 4200 – 4700 m in all seasons, except for domestic goats and sheep during winter (Shrestha and Wegge unpubl. data), we weighted the available forage on the basis of proportionate area occupied by each vegetation type within this altitudinal range. In winter, when the domestic goats and sheep were confined to the altitudinal range of 3700 – 4200 m, the available forage was weighted accordingly.

We then examined if an ungulate used the forage categories and plant species according to availability in each season by applying G-tests (Manly et al. 2002). To determine if a particular forage category or plant species was preferred or avoided, 95 % confidence intervals were created by applying Bonferroni corrections to the Z-statistic (Neu et al. 1974, McClean et al. 1998). Because availability data were recorded in summer they were somewhat overestimated for the winter and spring seasons. Hence, any preferential usage in these periods was conservative.



### **Diet and habitat overlap**

The seasonal (hereafter termed temporal) and cross-seasonal overlaps in diet (plant species) and habitat (elevation and vegetation types) between naur and domestic stock were calculated using proportional overlap indices (Schoener's Index; Schoener 1968):

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

where,  $O_{12}$  is the overlap of species 1 on species 2, and  $P_{i1}$  and  $P_{i2}$  are the proportions of resource (vegetation types, elevation and food plant species)  $i$  used by species 1 and species 2, respectively.

This index has been shown to be relatively robust against differential availability of resources as well as the number of resource categories considered for the analysis (Hanski 1978). The index approaches 0 for species that share no resources and approaches 1.0 for species pairs that completely overlap in resource use.

### **Resource-use overlap**

Following Case (1983), we computed the geometric mean of the three overlap indices; viz. 1) plant species in diet, 2) elevation, and 3) vegetation type, in order to obtain the combined measure of resource-use overlap between naur and domestic stock:

$$O_{\text{resource-use}} = \sqrt[3]{O_{\text{vegetation type}} \times O_{\text{elevation}} \times O_{\text{plant species}}}$$

where,  $O_{\text{resource-use}}$ ; resource-use overlap,  $O_{\text{vegetation type}}$ ; overlap in the vegetation types,  $O_{\text{elevation}}$ ; overlap in the elevation,  $O_{\text{plant species}}$ ; the overlap in the food plant species.

We used this measure because the distribution of elevation, vegetation type and diet can neither be completely independent (whereby overlaps along each niche dimension are multiplied) nor be totally dependent (whereby the arithmetic mean is taken) of each other (May 1975, Hanski 1978). The resource-use overlap indices thus obtained were ordered into three different classes: High ( $\geq 0.70$ ), Moderate (0.51 – 0.69), and Low ( $\leq 0.50$ ). Although these overlap indices did not provide statistical inferences about ecological relationships between species, they provide a relative measure of ecological similarity among them (Krebs 1999).

## Results

### *General diet composition*

The proportions of forage categories ( $\chi^2 = 411.4$ ,  $df = 30$ ,  $P < 0.01$ ) and plant species ( $\chi^2 = 1760.0$ ,  $df = 540$ ,  $P < 0.01$ ) differed between the four ungulates during the year. Goats consumed mostly browse, graminoids dominated the yak diet for most part of the year, while the diets of naur and sheep were more mixed across the seasons (Fig. 2). Only few plant species, such as forbs *Oxytropis* spp. (mean 6.3%), sedges *Carex* spp. (mean 10.2 %) and the shrub *Lonicera spinosa* (mean 7.5%) made up the bulk of the diets throughout the year (Table 2).

### **Naur**

Forbs dominated the diet at the start of growing season in spring. Its proportion decreased in the successive seasons as browse steadily increased during autumn and winter, while in summer the 3 forage categories did not differ significantly (Fig. 2a;  $\chi^2 = 13.5$ ,  $df = 2$ ,  $P = 0.28$ ). *Carex* spp. was the most common food species throughout the year, while the shrub *Chesneya nubigena* dominated in the winter browse diet comprising over 13 %, followed closely by *L. spinosa* and

*Artemisia* spp. (Table 2). Among forbs, *Oxytropis* spp. contributed the highest amount in all seasons, except in summer.

### **Domestic goat**

The proportion of browse increased gradually in the diet as the season advanced from spring to winter (Fig. 2b). Compared with naur, goats ate significantly more shrubs in spring and in summer (both;  $\chi^2 > 9.8$ ,  $df = 1$ ,  $P < 0.01$ ) and less graminoids in summer and in autumn (both;  $\chi^2 > 7.4$ ,  $df = 1$ ,  $P < 0.01$ ). Among browse, *L. spinosa* and *Astragalus* sp. were the most common species (Table 2). In spring and autumn, the proportions of forbs were significantly higher than that of graminoids (both;  $\chi^2 > 5.29$ ,  $df = 1$ ,  $P < 0.02$ ), while the opposite was true in winter ( $\chi^2 = 22.41$ ,  $df = 1$ ,  $P < 0.01$ ). In summer, goats ate about equal proportion of forbs and graminoids ( $\chi^2 = 0.11$ ,  $df = 1$ ,  $P = 0.75$ ). *Carex* spp. dominated among the graminoid component for most part of the year, and *Oxytropis* spp. made up the bulk of the forb diet (Table 2).

### **Domestic sheep**

Unlike goats, sheep did not show any consistent pattern in the consumption of forage categories (Fig. 2c). Their diet closely resembled that of naur in spring and in autumn (both;  $\chi^2 < 0.12$ ,  $df = 2$ ,  $P > 0.12$ ), while in summer and in winter sheep ate significantly more graminoids than naur (both;  $\chi^2 > 7.0$ ,  $df = 1$ ,  $P < 0.01$ ). During summer, *Carex* spp. were the most common graminoids followed by *Poa* sp. (Table 2). The former also dominated the spring diet, together with the two shrubs *Astragalus* sp. and *L. spinosa*. In autumn *L. spinosa* was most abundant, whereas the grass *Pennisetum flaccidum* dominated in winter. Among forbs, *Oxytropis* spp. dominated the diet for the most part of the year, closely followed by *Saussurea fastuosa*, *Iris* spp. and *Tanacetum nubigenum*.

## **Domestic yak**

Contrary to the other ungulates, yak consumed mostly graminoids throughout the year (Fig. 2d,  $\chi^2 = 86.5$ ,  $df = 6$ ,  $P < 0.01$ ), and the proportions of forage categories differed from naur in every season (four seasons;  $\chi^2 > 23.5$ ,  $df = 2$ ,  $P < 0.01$ ). They fed more on shrubs than forbs in spring and winter compared to the other seasons (spring only;  $\chi^2 = 56.01$ ,  $df = 1$ ,  $P < 0.01$ ). *Carex* spp., closely followed by *Stipa* sp., dominated the graminoids component for the most part of the year (Table 2). *Chesneya nubigena* and *L. spinosa* were the two most important shrubs; together they accounted for 1/3 of the total shrub intake both in winter and spring. Among forbs, *Oxytropis* spp. dominated in all seasons.

## ***Resource-use overlap***

### **General pattern**

Among the 3 resource categories, highest overlap occurred in vegetation types between all ungulates, while lowest overlap occurred in elevation between naur and smallstock, and in food plant species between naur and yak (Fig. 3). The resource-use overlap indices were generally higher between naur and yak than between naur and smallstock for most part of the year (Fig. 3). The pattern of overlap between naur and goats and naur and sheep was similar; greatest temporal overlap occurred during spring and summer while the lowest was in winter. Such seasonal pattern was not apparent between naur and yak.

In general, temporal and cross-seasonal overlaps occurred at similar frequencies between naur and domestic species, with a tendency of more overlap between naur and yak (Table 3). As high

overlap in resource use signifies greater potential for interspecific competition, we subsequently describe our results focusing on those pairs with high overlap indices ( $\geq 0.70$ ):

### **Spring resource-use by naur**

In spring, the temporal and cross-seasonal resource-use overlap indices were high between naur and all three species of domestic stock (Fig. 3a). High temporal overlap with smallstock occurred in spring as all strongly preferred alpine meadows (Appendix I, Shrestha and Wegge unpubl. data) and forbs (Table 4). Out of the 3 preferred species of forbs by naur, *Oxytropis* sp. was preferentially eaten by sheep while *Potentilla multifida* was avoided and *Corydalis govaniiana* was randomly eaten (Table 4). Goats consumed these 3 species randomly.

Also later in summer, domestic goats overlapped extensively with naur resource-use in spring (Fig. 3a), mainly due to strong overlap in vegetation types and moderate overlap both in plant species and elevation. Cross-seasonally, both ungulates preferred alpine meadows and avoided scrublands (Appendix I). They then fed preferentially on *Oxytropis* spp. (Table 4). Two other preferred spring forbs of naur, *C. govaniiana* and *P. multifida*, were significantly avoided by goats in summer.

High resource-use overlap between naur and yak occurred temporally in spring, and cross-seasonally in autumn (Fig. 3a). During these seasons, both preferentially used alpine meadows (Appendix I) and then they ate forbs and graminoids preferentially or randomly, while shrubs were avoided. Again, both preferred *Oxytropis* spp. (Table 4).

### **Summer resource-use by naur**

The overlap with domestic stock was generally low in summer compared with other seasons, as high overlap occurred only between naur and yak (Fig. 3b). The high temporal overlap between yak and naur occurred as both randomly or preferentially used middle and high elevation, alpine meadows and grasslands (Appendix I and II). Graminoids were then significantly preferred by both ungulates (Table 4).

The resource-use by yak earlier in spring also overlapped extensively with that of naur in summer (Fig. 3b). This was mainly because their consistent preference for middle elevation and alpine meadows during these periods (Appendix I and II). As for the diet, both preferentially fed on graminoids (Table 4). However, the two plants preferred by yak in spring, (*Oxytropis* spp. and *Carex* spp.), were only randomly eaten by naur in summer.

### **Autumn resource-use by naur**

The resource-use overlap pattern in autumn was quite similar to that in spring (Fig. 3c). Smallstock preferentially used alpine meadows in spring and summer like naur did in autumn (Appendix I). However, except for selective feeding on *Oxytropis* spp. during these seasons, their diet selection did not match, possibly because more random consumption of forage categories and plant species by naur in autumn (Table 4).

Naur in autumn also overlapped markedly with yak in spring (Fig. 3c), as both preferentially used the alpine meadows and avoided the scrublands (Appendix I and II). Both yak and naur significantly preferred *Oxytropis* sp. during these seasons (Table 4).

### **Winter resource-use by naur**

In winter, high temporal overlap occurred only with free-ranging yak (Fig. 3d), because other domestic stock was kept at lower elevations. Both naur and yak used middle and high elevations and alpine meadows and scrublands (Appendix I and II). Both fed randomly or preferentially on graminoids and browse and avoided forbs (Table 4). Out of two preferred shrubs by naur, *Chesneya nubigena* was significantly preferred also by yak.

Naur in winter overlapped with all three domestic species in spring (Fig. 3d). Then all three preferentially used middle elevation and alpine meadows like naur did in winter (Appendix I and II). However, naur avoided the grasslands in winter, while yak in spring preferred them. Likewise, shrubs were preferentially eaten by naur in winter but avoided by yak and sheep in spring (Table 4). The two most preferred shrubs (*C. nubigena* and *Artemisia* spp.) by naur in winter were eaten randomly by all domestic species in spring.

### ***Stocking densities and naur reproductive success***

Our study area was being grazed by a total of 802 yaks, 718 goats, 406 sheep, 96 cows and 71 horses totalling a density of 16.7 animals/km<sup>2</sup> or biomass of 2509 kg /km<sup>2</sup>. This, together with a density of naur at 9.4 animals/km<sup>2</sup> (519 kg/km<sup>2</sup>), yielded a total ungulate biomass density of 3028 kg/km<sup>2</sup>. The autumn counts of naur yielded 56 young per 100 adult females in a total classified count of 213 individuals belonging to 20 herds. Both total ungulate biomass density and ratio of young to adult females compared closely with Mishra et al. (2004)'s intensively grazed rangeland in Ladakh, India. Recruitment rate was lower than that reported from Mishra et al. (2004)'s moderately grazed rangeland and other ranges elsewhere in Nepal (Schaller 1977,

Wegge 1979, Wegge and Oli 1988, Oli and Rogers 1996), but higher than that reported by Schaller (1977) from presumably highly overgrazed rangelands in Shey, Nepal (Table 5).

## **Discussion**

### ***Diet composition***

In all seasons, the four ungulates had mixed diets with varying proportions of forage categories and plant species. However, judging by dominant forage categories on an annual basis, yaks showed a clear grazer trend, goats a browser trend, while naur and sheep were more intermediate feeders.

The seasonal variations in the proportions of forage categories confirmed that the food habits to a large extent are determined by the use of habitats (Perez-Barberia et al. 2001) and hence available vegetation (Gordon and Illius 1989). At the start of the growing season, all preferentially used alpine meadows (Shrestha and Wegge unpubl. data). Here, the forbs, which are highly nutritious in spring (Larter and Nagy 2001), were most abundant. All ungulates, except yak, consumed greater amounts of forbs in this period compared to other seasons. Yaks preferentially used grasslands in spring, and hence graminoids then comprised the bulk of their spring diet. In summer, all ungulates increased their consumption of graminoids. Graminoids are reported to contain highest concentration of nutrients during summer and then lose nutrients more rapidly compared to forbs and shrubs (Long et al. 1999). In autumn through winter, the proportion of shrubs increased in the diets of all ungulates, except domestic sheep. Shrubs are known to be very important food for yak on the Tibetan plateau, especially during autumn and winter, as the level of secondary compounds decreases during these periods (YanJun et al. 2002), and shrubs therefore serve as an alternative source of protein (Shikui et al. 2002). As the goats



and sheep were shifted to lower pasture during winter, they fed more on graminoids. In summer and autumn, the winter pastures are protected from grazing by domestic stock, hence graminoids were more abundant in the vicinity of the winter settlement.

Only few species made up the bulk of the diet of all four ungulates for most part of the year. Again, these plants were among the most abundant forage species in the study area. The high consumption of the grass *Pennisetum flaccidum* and the shrub *Clematis* sp. by goats and sheep during winter can also be explained by their availability; the former was the most abundant graminoid in the winter pasture, while the latter was given as supplementary feed during this period. Therefore, consistent with previous studies (Schaller and Gu 1994, Mishra et al. 2004, Shrestha et al. 2005), all ungulates in our study were feeding opportunistically, and this trait was particularly evident in naur and domestic sheep.

The two legumes *Oxytropis* spp. and *Chesneya nubigena* appeared to be crucial food plants as they were selected by most ungulates in the same season as well as in successive seasons. The shrub *Chesneya* was used only during winter by naur and yak when they did not feed on *Oxytropis*. This switch probably occurred because of difficult access (snow) and depleted availability (continuously fed on by most of the ungulates in other seasons) of *Oxytropis* during winter, rather than a change in nutritive quality. Generally, legumes are reported to be at their peak digestibility in spring, and they are also known to retain higher amount of protein in summer through winter compared to graminoids (Long et al. 1999, Larter and Nagy 2001). The strong selection for *Oxytropis* spp. by all ungulates deserves a special note because plants belonging to the genera *Oxytropis* are known to be toxic. The ungulates in our study area might have become 'habituated' to consuming *Oxytropis* (Molyneux and Ralphs 1992) possibly due to

adaptation of rumen microbes to secondary compounds (Menke et al. 1992), as this plant represents a significant food resource that enable ungulates to survive on rangeland with a prolonged dormant period when more preferred defenceless species are absent (Papachristou et al. 2005).

### ***Resource-relationships between naur and domestic ungulates***

Naur overlapped with yak more in elevation and less in plant species while the opposite was true in the case of smallstock. The seasonal and cross-seasonal overlaps among naur and smallstock appeared to be governed mainly by seasonal movement across the gradient of altitude.

In spring, as the herders brought the domestic stock back up from winter pastures, high overlap (both seasonal and cross-seasonal) took place between them and naur. In seasonal environments, spring is a crucial period for ungulates because of the need for replenishing depleted fat reserves and producing offspring. Most parturition (especially naur and yak) takes place during this season, and good quality forage is essential for lactating females. Alpine meadows are known to be a principal source of good quality forage in the Trans - Himalaya (Long et al. 1999). Hence, all ungulates concentrated in the alpine meadows during spring. Despite some separation in elevation between naur and smallstock in spring (Shrestha and Wegge unpubl. data), it is highly likely that they would compete for food, particularly for *Oxytropis* sp. if stocking densities increase.

In summer, goats and sheep were taken to higher elevation pastures and then they greatly overlapped with the habitat that naur had used in spring. Naur had then moved to higher elevation, and as they then consumed more graminoids, they overlapped more extensively with

yak. Excessive grazing by yak both in spring and summer might limit the availability of graminoids for naur during summer and hence lead to interspecific competition. For temperate ungulates, summer nutrition is known to be important for winter survival and population performance (Reimers et al. 2005).

The resource-use pattern by naur in autumn resembled the spring and summer use by domestic goats and yak in spring. Since middle elevation and alpine meadows were heavily used by all ungulates during these periods, this habitat complex appeared to be a critical resource during these periods.

During winter, goats and sheep were shifted to low-lying winter pastures, thus separating them from naur altitudinally, and thereby minimizing potential for competition. However, in winter naur overlapped extensively with the free-ranging yaks as they used similar elevation and both consumed high proportions of browse.

### ***Potential for competition and partitioning of resources***

Acknowledging density-dependent effects on population performance (Skogland 1986), and assuming similar range productivity as that of Mishra et al. (2004)'s study area in Ladakh, India, it appears that our study area was overstocked. The observed low ratio of young to adult females in autumn, which was similar to Mishra et al. (2004)'s intensively grazed study area, suggests a competitive relationship between naur and domestic stock in the study area.

In general, high niche overlap among different species translates into competition only when shared resources become limited (de Boer and Prins 1990, Putman 1996). Another factor

affecting competitive relationships among domestic and wild ungulates is the interference by herders (Harris and Loggers 2004), and their presence has been shown to displace wild sheep to suboptimal habitats (Namgail et al. 2007). The lower density of naur observed in the intensively grazed area in Ladakh (2.6 animal/ km<sup>2</sup>) compared to ours (9.4 animal/ km<sup>2</sup>) might also be due to a difference in the level of human disturbance between these studies, as Mishra et al. (2004), unlike us, made population counts in a relatively small area (31 km<sup>2</sup>) which was also actively used by herders.

Predicting competition on the basis of conventional density-dependent models alone is difficult in non-equilibrium systems (Fernandez-Gimenez and Allen-Diaz 1999) such as the Trans-Himalaya (Miller 1997), where the rangeland productivity is believed to be controlled more by the climatic variations rather than stocking density (Ellis et al. 1991). Also, the spatio-temporal heterogeneity in the composition and phenology of plant species across the gradients of altitude might mitigate the effects of interspecific competition through partitioning of resources (Cromsigt and Olff 2006). The existing system of seasonally rotating the domestic stock in different key pastures based on local climatic patterns is a human-adapted strategy to optimize the use of limited food resources for domestic stock production (Miller 1997, Bedunah and Harris 2002). Coincidentally, such a system probably also facilitates coexistence with naur through partitioning of resources. This may especially be true in the case of goats, as their foraging regime closely resembles naur owing to similar mouth morphology, diets and body weights (Schaller and Gu 1994, Shrestha et al. 2005) and behaviour (Schaller 1977).

On the other hand, both temporal and cross-seasonal resource-use overlaps were consistently high for the most part of the year between naur and free-ranging yaks. Large grazing animals are

expected to facilitate the smaller ones by promoting the growth of high quality forage (Bell 1971, Olff and Ritchie 1998, but see also Woolnough and du Toit 2001). However, this may not be true in less productive environments such as the Trans-Himalaya (Mishra 2001), because here competition rather than facilitation is more likely to take place (Van de Koppel and Prins 1998, Bakker et al. 2006). Owing to their opportunistic foraging styles and quite similar mixed diets, naur is therefore expected to compete more with yak, and our results indicated that the winter season – a period of food scarcity – is particularly crucial in this regard. Also, if livestock densities should increase, the spring and autumn seasons may become crucial for naur because of more cross-seasonal overlaps with smallstock. Because we collected the habitat data on naur from those parts of the rangeland where domestic stock were not attended by herders, human disturbance from the normal practice of herding may accentuate the effect of resource competition.

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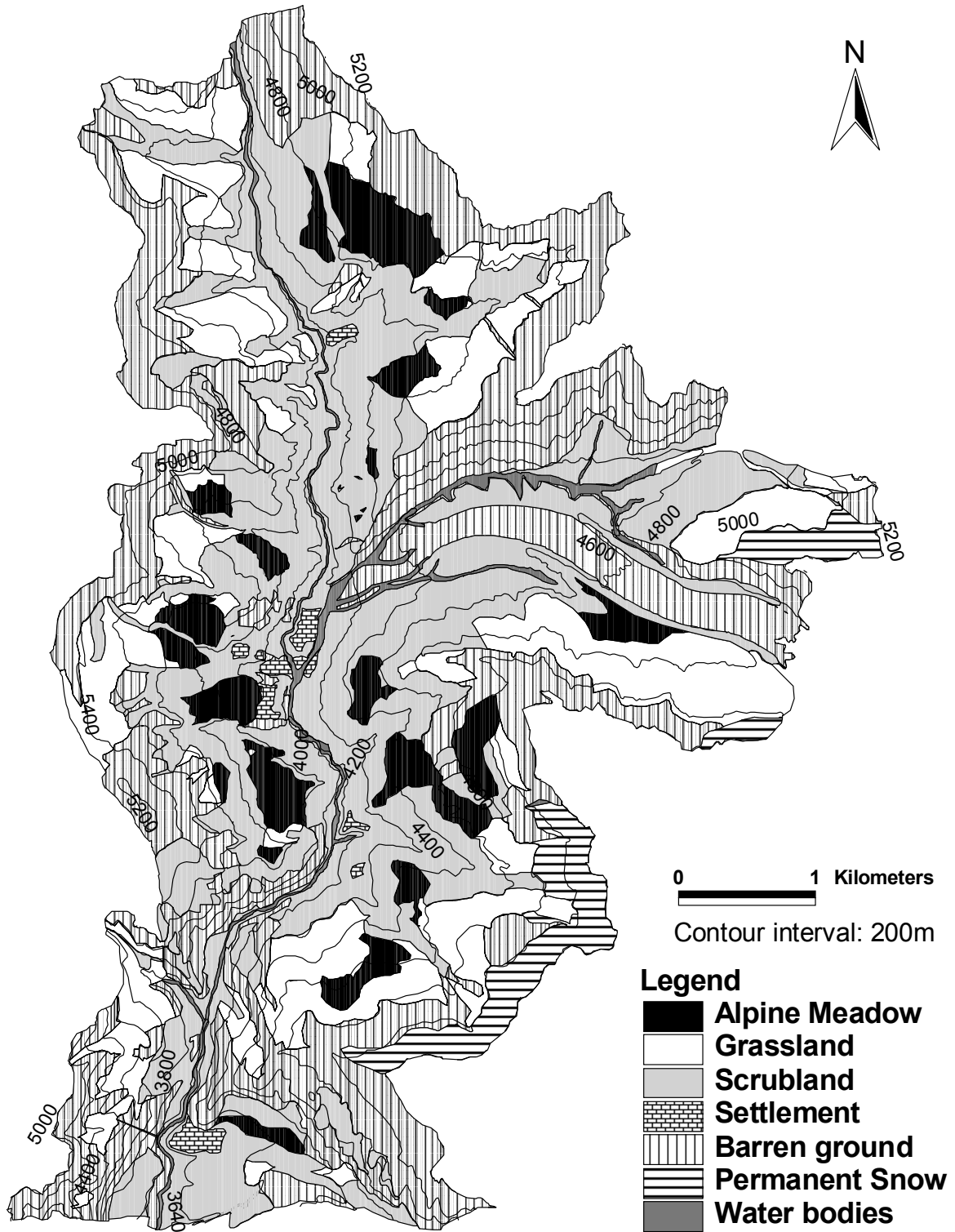
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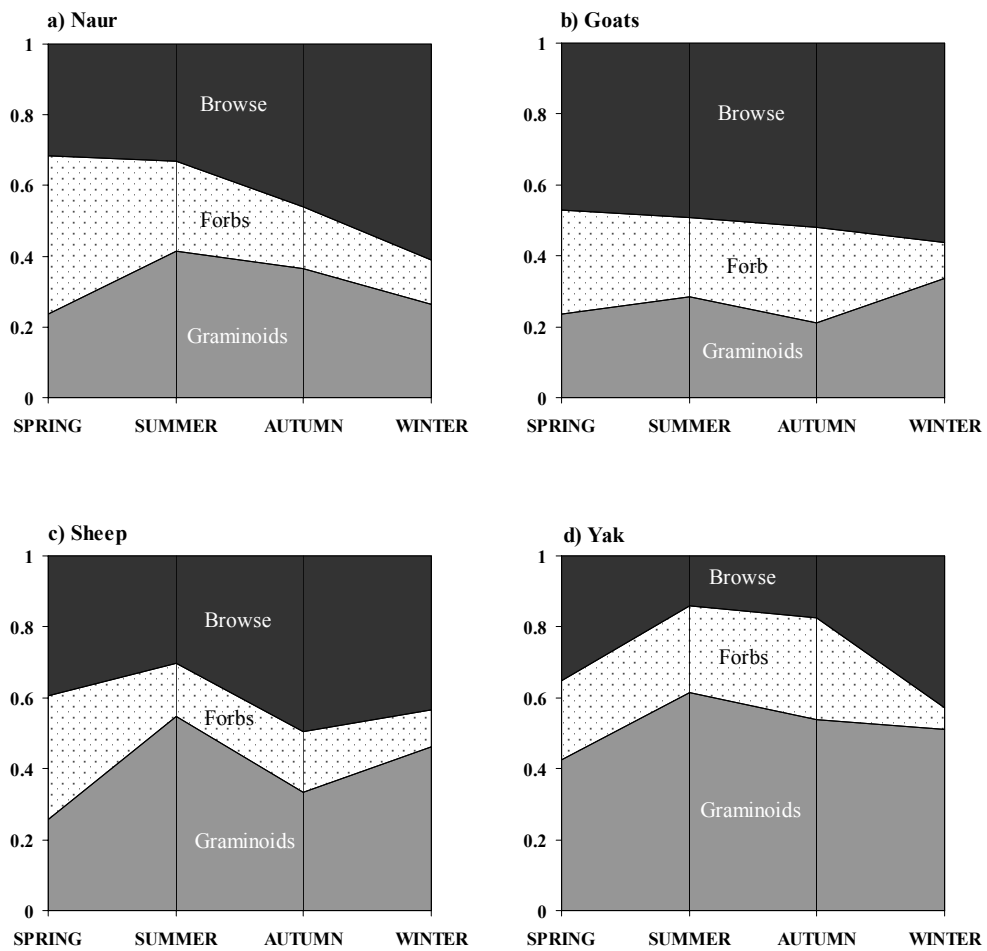
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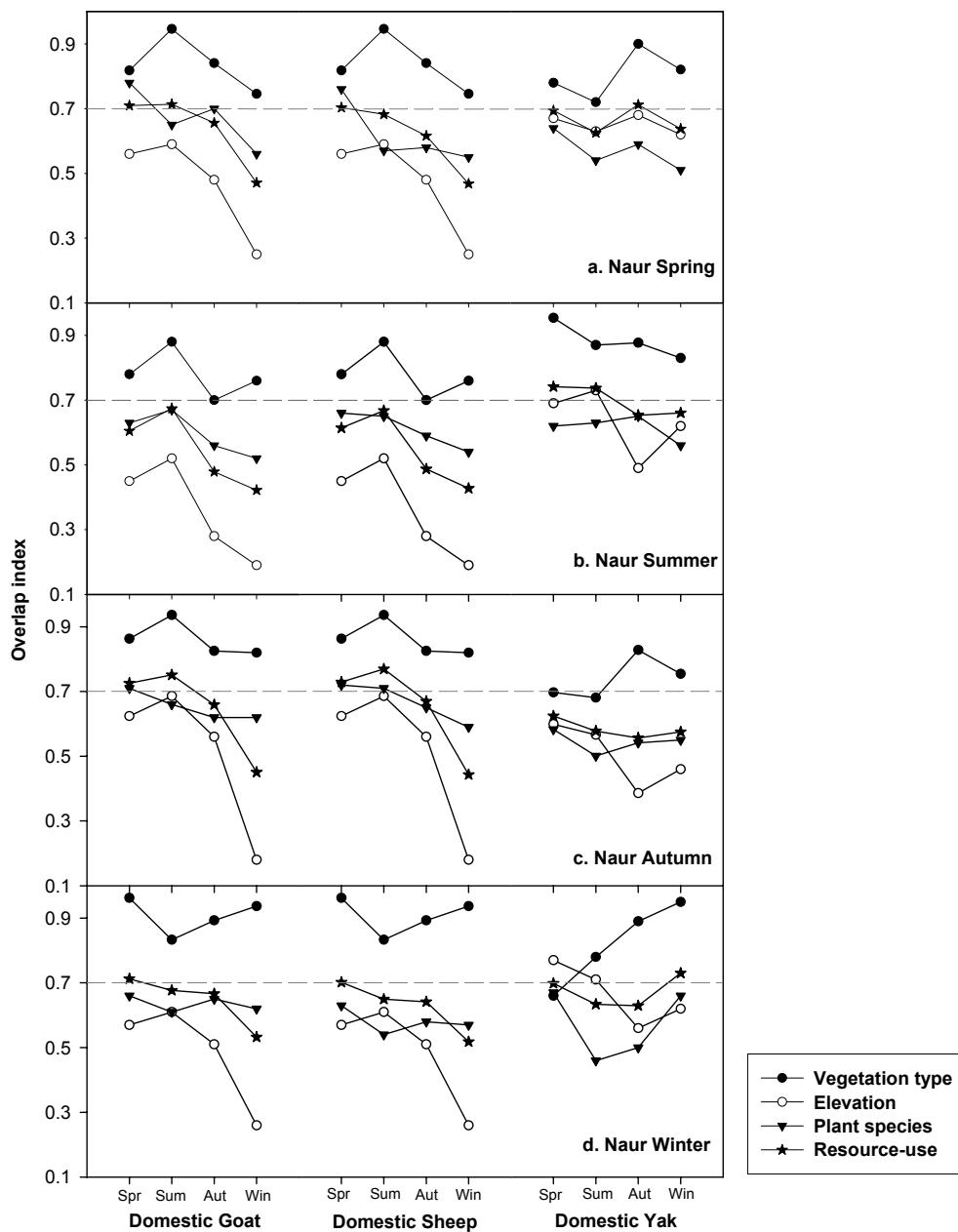
**Figure 1.** Map of study area showing vegetation types and other habitat features in Phu valley in Manang, Nepal.



**Figure 2.** Proportions of forage categories in the diets of a) naur, b) domestic goat, c) domestic sheep, and d) free-ranging domestic yaks in spring, summer, autumn and winter in Phu valley in Manang, Nepal.



**Figure 3.** Seasonal and cross-seasonal overlaps in vegetation types, elevation, food plant species shown by proportional overlap indices (Schoener's Index) between naur and 3 species of domestic stock. Resource-use overlap refers to the combined overlap in vegetation types, elevation and the plant species. Dashed horizontal lines that cross the y-axis at 0.7 denote high resource-use overlap (see text).





**Table 1.** Percent distribution of habitat types in different elevation zones in Phu valley in Manang, Nepal.

Habitat types	Elevation categories			Total
	3680 - 4200m	4201 - 4700m	4701 - 5200m	
Alpine Meadow	2.0	11.0	6.7	6.6
Grassland	5.1	15.8	25.4	15.4
Scrubland	60.6	51.1	10.1	40.6
Others <sup>a</sup>	32.3	22.1	57.8	37.4
Total	100.0	100.0	100.0	100.0

<sup>a</sup> Includes settlement, barren land, permanent snow and water bodies.

**Table 2:** Estimated proportions (%) of available forage categories and plant species in two altitudinal ranges of the study area and their percent consumption by naur and domestic goats, sheep and yak in spring, summer, autumn and winter in Phu valley of Manang, Nepal. The bold letters denote significant preferences (based on 95% Bonferroni confidence intervals) by ungulates within the altitudinal range of 4200– 4700m in all seasons, except by smallstock during winter; they then used an altitudinal range of 3700 – 4200m and their preferences are shown accordingly in the table.

Plant species	Availability <sup>a</sup>																	
	(cover %) in																	
	altitudinal range (4201- 4700m)			Spring			Summer			Autumn			Winter					
	Goat	Sheep	Naur	Yak	Goat	Sheep	Naur	Yak	Goat	Sheep	Naur	Yak	Goat	Sheep	Naur	Yak		
<b>Graminoids</b>	30.5	24.5	23.6	25.7	23.7	<b>42.5</b>	28.3	<b>54.9</b>	<b>41.5</b>	<b>61.5</b>	21.2	33.3	36.5	<b>53.8</b>	<b>33.5</b>	<b>46.1</b>	26.4	<b>51.1</b>
<i>Carex</i> spp.	6.5	4.6	9.5	8.8	9.7	<b>15.3</b>	12.4	<b>15.6</b>	8.9	<b>16.6</b>	5.3	7.4	9.6	8.6	5.9	6.3	11.0	12.2
<i>Stipa</i> spp.	5.5	5.2	1.7	7.3	1.8	4.4	0.9	5.2	3.8	8.5	0.4	1.4	2.7	11.1	1.6	5.8	4.4	11.7
<i>Poa</i> sp.	3.0	4.0	2.1	2.3	1.4	1.5	5.6	<b>10.4</b>	5.9	3.0	1.3	3.7	2.7	1.2	0.5	6.3	0.5	0.5
<i>Danthonia jacquemontii</i>	2.8	1.8	3.7	0.8	1.8	1.1	1.3	4.3	0.8	3.4	3.5	0.0	3.6	6.6	1.1	3.1	1.1	8.0
<i>Festuca</i> sp.	2.8	1.2	0.8	1.5	0.7	2.2	0.4	2.8	8.0	4.7	0.9	1.4	3.6	5.7	1.1	0.0	0.0	3.7
<i>Pennisetum flaccidum</i>	1.9	0.7	0.4	0.8	1.4	0.2	0.0	0.0	1.3	0.0	0.0	0.9	1.4	0.8	<b>11.9</b>	<b>11.5</b>	0.5	1.6
<i>Elymus nutans</i>	1.7	1.5	0.8	0.8	1.1	1.1	0.9	0.9	0.4	3.8	0.9	1.8	0.9	2.1	1.6	2.6	2.2	2.1
<i>Kobresia</i> spp.	1.6	0.7	0.4	0.8	0.7	4.9	1.3	0.0	0.8	3.8	0.9	1.4	2.3	2.9	0.5	1.6	0.5	1.6
<i>Agrostis</i> sp.	0.7	0.7	1.7	0.0	1.4	0.0	2.6	3.3	0.4	1.3	1.3	0.5	0.5	0.0	0.5	1.0	0.5	0.0
Other graminoids <sup>b</sup>	3.9	4.2	2.5	2.7	3.6	<b>11.7</b>	3.0	<b>12.3</b>	<b>11.0</b>	<b>16.6</b>	6.6	<b>14.8</b>	9.1	<b>14.8</b>	8.6	7.9	5.5	9.6
<b>Forbs</b>	19.6	17.7	<b>29.4</b>	<b>35.0</b>	<b>44.6</b>	22.3	22.5	14.8	25.3	24.3	26.7	17.0	17.5	<b>29.0</b>	10.3	10.6	12.7	6.0
<i>Oxytropis</i> spp.	1.9	1.9	5.5	<b>10.1</b>	<b>10.5</b>	<b>7.6</b>	<b>7.5</b>	<b>9.9</b>	3.9	6.1	6.2	2.4	<b>10.9</b>	<b>10.3</b>	1.7	1.7	3.6	2.4
<i>Tanacetum nubigenum</i>	1.6	1.6	1.8	0.0	1.7	0.0	3.8	2.5	5.9	2.0	2.1	0.0	0.0	4.1	0.0	0.0	1.2	0.0
<i>Saussurea fastuosa</i>	0.3	0.3	<b>5.5</b>	3.4	3.5	0.0	0.0	0.0	0.0	0.0	2.1	0.0	2.2	2.1	3.4	2.8	0.6	1.2
<i>Iris</i> spp.	1.8	1.8	0.0	3.4	1.7	0.0	1.9	0.0	2.0	0.0	2.1	2.4	0.0	0.0	2.9	2.8	1.2	1.8
<i>Potentilla multifida</i>	1.1	1.0	5.5	0.0	<b>7.0</b>	2.2	0.0	0.0	0.0	2.0	2.1	0.0	0.0	0.0	0.0	0.0	0.6	0.0
<i>Taraxacum officinale</i>	1.9	1.3	1.8	1.7	0.0	3.3	1.9	0.0	2.0	0.0	0.0	2.4	0.0	2.1	0.0	0.0	1.2	0.0

Plant species	Proportion in diet (%)																
	Availability <sup>a</sup> (cover %) in						Season										
	altitudinal range (4201- 4700m)		Spring		Summer		Autumn		Winter								
<i>Corydalis gowaniana</i>	0.3	0.1	1.8	1.7	5.2	3.3	0.0	0.0	0.0	0.0	2.1	0.0	0.6	1.8	0.0		
<i>Leontopodium</i> sp.	1.4	1.1	0.0	0.0	1.7	0.0	1.9	0.0	3.9	4.1	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Cremanthodium</i> spp.	0.8	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	1.1	0.6	0.0	0.0	
<i>A. rupicola</i>	0.1	0.0	1.8	1.7	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	
Other forbs <sup>b</sup>	8.3	8.1	5.5	13.2	11.4	6.0	5.6	2.5	7.7	8.1	12.3	9.7	2.2	1.1	1.7	2.4	0.6
<b>Browse</b>	49.9	57.8	47.0	39.3	31.7	35.2	49.2	30.3	33.2	14.1	52.0	49.7	46.1	56.2	43.4	61.0	42.9
<i>Lonicera spinosa</i>	13.7	17.3	9.8	6.6	6.9	7.8	7.4	5.2	3.6	4.2	11.5	11.3	7.6	10.9	7.2	8.4	9.7
<i>Spiraea</i> sp.	13.4	16.2	4.3	4.3	2.8	3.3	6.5	6.3	4.5	1.9	6.2	6.8	4.6	3.4	3.9	5.4	2.4
<i>Chesneya nubigena</i>	2.2	2.1	6.0	5.4	4.1	7.1	3.0	3.4	5.5	3.3	5.3	3.4	7.1	6.9	3.3	13.3	10.3
<i>Astragalus</i> sp.	4.4	5.1	7.7	7.4	4.5	1.0	10.4	4.6	6.8	0.5	2.9	7.9	9.1	4.6	1.7	6.0	2.4
<i>Clematis</i> sp.	0.1	0.0	3.8	2.7	3.3	1.5	2.2	1.1	2.3	0.5	8.6	7.3	3.5	9.2	7.8	2.4	0.6
<i>Artemisia</i> spp.	2.2	2.7	1.7	0.8	0.8	1.5	0.4	0.0	0.5	1.4	4.8	2.8	1.5	2.3	1.7	8.4	1.2
<i>Potentilla fruticosa</i>	2.7	2.2	1.7	1.2	1.2	1.3	1.3	2.3	2.7	0.9	1.9	4.0	1.5	2.3	2.2	0.0	4.2
<i>Caragana jubata</i>	1.1	0.9	1.7	3.1	0.4	0.8	7.4	3.4	1.8	0.0	0.0	1.1	2.5	1.1	0.0	0.0	0.0
<i>Ephedra Gerardiana</i>	1.4	1.1	1.3	1.6	0.8	1.3	1.7	1.1	0.0	0.5	2.4	1.1	3.0	2.3	0.0	4.2	0.0
<i>Hippophae tibetana</i>	1.7	2.0	2.1	0.4	1.6	1.0	0.4	0.0	2.3	0.0	1.0	1.1	0.5	2.9	2.2	1.2	0.6
<i>Berberis</i> spp.	0.7	0.7	0.9	1.2	1.2	1.3	3.0	1.7	0.5	0.9	1.0	0.6	1.5	0.6	2.2	1.2	0.6
<i>Juniperus</i> spp.	2.1	2.7	0.0	1.2	0.0	0.0	1.3	0.0	0.0	0.0	1.0	0.0	0.0	1.7	2.2	1.8	0.0
<i>Ribes orientale</i>	0.4	0.5	1.3	0.8	0.0	0.8	0.0	0.0	0.0	0.0	0.0	1.7	0.5	2.3	1.7	0.6	1.2
<i>Salix</i> sp.	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	1.0	0.6	1.7	0.0	1.8
Other shrubs <sup>b</sup>	3.7	4.1	4.7	2.7	4.1	6.6	3.9	1.1	2.3	0.0	5.7	0.6	2.0	5.2	5.6	7.8	7.9

Note:

a) Weighted on the basis of relative areas of three vegetation types within the specified altitudinal range.

b) Includes unidentified portions and species with a total contribution of less than 5% to the annual diet of all ungulates.

**Table 3.** Proportions of temporal and cross-seasonal high ( $\geq 0.70$ ), moderate (0.50 - 0.69), and low ( $\leq 0.49$ ) resource-use overlaps between naur and 3 species of domestic stock in Phu Valley in Manang, Nepal.

	High overlap		Moderate overlap		Low overlap	
	Temporal	Cross-seasonal	Temporal	Cross-seasonal	Temporal	Cross-seasonal
Naur and Goat	0.3	0.3	0.8	0.3	0.0	0.3
Naur and Sheep	0.3	0.3	0.8	0.4	0.0	0.3
Naur and Yak	0.5	0.3	0.5	0.7	0.0	0.0

**Table 4.** Degree of preference for forage categories and plant species by naur and domestic goats, sheep and yak in spring, summer, autumn and winter seasons. Symbols (+, 0, -) represent plant species or forage categories that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals). Only those plant species which were found to be preferred in at least one diet are shown.

	Spring			Summer			Autumn			Winter			
	Goat	Sheep	Naur	Goat	Sheep	Naur	Goat	Sheep	Naur	Goat	Sheep	Naur	Yak
	ACD	ACD	BCD	AC	C	AB	Yak	Goat	Sheep	Naur	Yak	Yak	Yak
<b>High resource-use overlap (&gt;70%) with naur<sup>a</sup></b>													
<b>Forage categories</b>													
Forbs	+	+	0	0	0	0	0	0	0	0	+	-	-
Graminoids	0	0	+	0	+	+	+	-	0	0	+	+	0
Browse	0	-	-	0	-	-	-	0	0	0	-	-	0
<b>Plant species</b>													
<i>Corydalis govianiana</i>	0	+	0	-	-	-	-	-	-	-	0	0	-
<i>Oxytropis</i> spp.	0	+	+	+	+	0	0	0	0	+	+	0	0
<i>Potentilla multifida</i>	0	-	0	-	-	-	0	0	-	-	-	-	-
<i>Saussurea fastuosa</i>	+	0	-	-	-	-	-	0	-	0	0	0	0
<i>Carex</i> spp.	0	0	+	0	+	0	+	0	0	0	0	0	0
<i>Pennisetum flaccidum</i>	-	0	-	-	-	0	-	-	0	0	0	+	0
<i>Poa</i> spp.	0	0	0	0	+	0	0	0	0	0	0	-	-
Other graminoids	0	0	+	0	+	+	+	0	+	0	+	0	0
<i>Caragana jubata</i>	0	0	0	+	0	0	-	-	0	0	-	-	-
<i>Chesneya</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	+
<i>Clematis</i> sp.	0	0	0	0	0	0	0	+	+	0	0	+	0
<i>Artemisia</i> spp.	0	0	0	-	-	-	0	0	0	0	0	0	+

a) The letters A, B, C and D denote high resource-use overlap (> 70% ; Fig 3) of domestic species with naur in spring, summer, autumn and winter, respectively.

**Table 5.** Comparison of population productivity (number of young per adult female in autumn) between the study area in Phu valley, Nepal and other locations.

Season	young per 100 adult female	N	Location	Source
Autumn	40	1952	Shey, Nepal	Schaller 1977
Autumn	73	435	Khansar, Manang, Nepal	Wegge and Oli 1988
Autumn	70	703	Upper Marsyangdi, Manang, Nepal	Oli and Rogers 1996
Autumn	84	1271	Dhorpatan, Nepal	Wegge 1979 <sup>a</sup>
Autumn	71	98	Ladakh, India	Mishra 2004 <sup>b</sup>
Autumn	50	71	Ladakh, India	Mishra 2004 <sup>c</sup>
Autumn	56	213	This study <sup>d</sup>	

<sup>a</sup> Average figure for the counts made during 1974 -1977

<sup>b</sup> Moderately grazed rangeland - Ungulate biomass density (naur and domestic stock) 2586 kg/km<sup>2</sup>

<sup>c</sup> Intensively grazed rangeland – Ungulate biomass density 3248 kg/km<sup>2</sup>

<sup>d</sup> Ungulate biomass density 3037 kg/km<sup>2</sup>

**Appendix I.** Seasonal use of vegetation types by domestic stock and naur in Phu valley in Nepal.

(Source: Shrestha and Wegge unpubl. data).

Seasons	Vegetation type	Availability <sup>a</sup> (%)		Utilization (%)			Selection <sup>b</sup>		
		All	Domestic stock	Small stock	Naur	Free ranging yak	Small stock	Naur	Free ranging 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	0	+	0
	Grassland	31.2	33.2	11.4	13.3	20.0	-	-	0
	Scrubland	55.5	54.7	65.7	57.8	55.6	0	0	0

<sup>a</sup> Availability was assumed to be constant for naur in all seasons, but was adjusted for domestic stock according to seasonal restrictions imposed on certain pastures by herders.

<sup>b</sup> Symbols (+, 0, -) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).

**Appendix II.** Seasonal use of elevation zones by domestic stock and naur in Phu valley in Nepal. Low, middle, high and very high elevation zones refers to 3640 - 4320m, 4320 - 4640m, 4640 - 4920m, and 4920-5240m, respectively. (Source: Shrestha and Wegge unpubl. data).

Seasons	Elevation zones	Availability <sup>a</sup> (%)		Utilization (%)			Selection <sup>b</sup>		
		All	Domestic stock	Small-stock	Naur	Free ranging yak	Small-stock	Naur	Free ranging 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	+	0	-
	Middle	23.2	20.1	11.4	45.1	40.8	0	+	+
	High	32.0	23.3	2.3	33.1	42.9	-	0	+
	Very high	26.9	21.1	0.0	7.0	6.1	-	-	-

<sup>a</sup> Availability was assumed to be constant for naur in all seasons, but it was adjusted for domestic stock according to seasonal restrictions imposed on certain pastures by herders.

<sup>b</sup> Symbols (+, 0, -) represent vegetation types that are preferred, randomly used, or avoided according to their availability (based on 95% Bonferroni confidence intervals).



**Appendix III.** Conversion factors based on comparison of forage categories in bite-counts and in fecal analysis of domestic goats *Capra hircus* and sheep *Ovis aries*. Two composite samples for each species (Goat 1 and Goat 2; Sheep 1 and Sheep 2) were used in the analysis. Data adapted from Shrestha and Wegge (2006).

Forage category	Fecal proportion <sup>a</sup>						Bite proportions						Conversion factor <sup>b</sup>							
	Goat 1		Goat 2		Sheep 1		Sheep 2		Goat 1		Goat 2		Sheep 1		Sheep 2		Mean	SE		
Forbs	0.03	0.03	0.03	0.03	0.05	0.05	0.05	0.12	0.12	0.17	0.17	0.18	0.18	1.91	3.61	6.43	6.43	3.44	3.85	1.33
Graminoids	0.45	0.26	0.58	0.48	0.34	0.34	0.24	0.24	0.52	0.52	0.49	0.49	0.75	0.93	0.90	0.90	1.02	0.90	0.90	0.08
Browse	0.52	0.71	0.40	0.47	0.61	0.61	0.64	0.64	0.31	0.31	0.33	0.33	1.17	0.91	0.79	0.79	0.71	0.89	0.14	0.14

Note : <sup>a</sup> Recomputed fecal proportions after removing the totally unidentified proportions and unidentified dicots.





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