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 km² 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, lonicera 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 royeli* 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 analyis)

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[a]	Adjusted RIV[a] (%)
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				

[a] The conversion factors and adjusted relative importance values (RIVs) were computed as follows:

$$\mathrm{CF}i = \frac{1}{100}\left(\frac{bi\sum_{i}^{n} fi}{fi}\right)$$

and, adjusted $\mathrm{RIV}i$ = recomputed faecal $\mathrm{RIV}i * \mathrm{CF}i$, where, $\mathrm{CF}i$ = 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-over-lapping fragments intercepted by the ocular scale line were identified using a compound microscope at $200\times$ 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):

$$\text{DSV}_x = \frac{\text{RIV}_x}{\text{PV}_x}$$

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_λ varies from 0.0 for completely distinct pairs (no food species/forage categories in common) to 1.0 for complete overlap:

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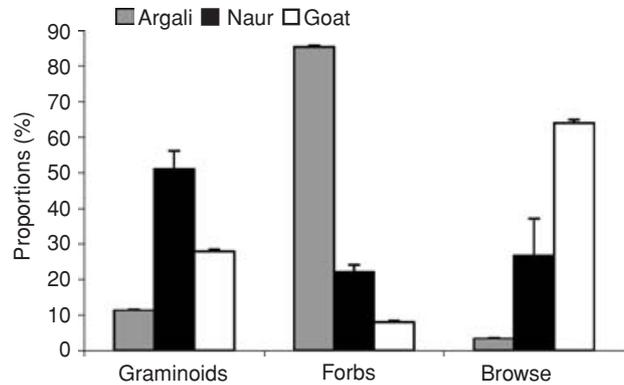

Fig. 1. Relative composition of forage categories (± 1 SD) in the summer diets of argali *Ovis ammon hodgsoni*, naur *Pseudois nayaur*, and domestic goat *Capra hircus* based on faecal analysis. Proportions are adjusted on the basis of bite counts in domestic goats (see text).

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 pygmea* 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 gramonoids 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[a,b]	SD	RIV[a,b]	SD	RIV[a,b]	SD
Graminoids						
Agrostis sp.	0.3	0.1	8.1	3.6	3.5	0.5
Carex sp.	0.0	–	5.0	7.3	0.0	–
Elymus nutans	0.0	–	3.5	2.8	5.3	0.6
Kobresia pygmea	2.9	0.5	–	–	–	–
Stipa 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
Forbs						
Chesneya sp.	–	–	2.1	0.8	0.0	–
Corydalis govaniana	0.0	–	0.0	–	4.9	0.3
Oxytropis sp.	0.0	–	4.2	1.0	0.0	–
Saussurea graminifolia	65.4	0.4	–	–	–	–
Sedum sp.	1.3	0.1	–	–	–	–
Unidentified forbs	18.7	0.8	15.8	4.2	3.1	0.7
Browse						
Lonicera rupicola	–	–	0.0	–	50.9	1.4
Potentilla fruticosa	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

[a] 0, Species present in the habitat but not detected in analysis.
[b] –, 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[a]	48	40	12	44	22	34	39	12	49
Proportion in diet (RIV)									
Adjusted[b]	11	85	3	51	22	27	28	8	64
Non-adjusted[c]	32	55	13	54	6	40	23	2	75
Selection[d]									
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

[a] Prominence values (PV) within the main habitat of each species (%).
[b] Proportions in faecal analysis, adjusted on basis of bite counts (see text).
[c] Proportions in faecal analysis, not adjusted from bite counts.
[d] 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 *Chesnya* sp. (DSV = 7.0). The browse *P. fruticosa* was moderately selected (DSV = 1.3), only exceeded by *Chesnya* 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_λ (Horn 1966) between the summer diets of argali *Ovis ammon hodgsoni*, naur *Pseudois nayaur* and domestic goat *Capra hircus* in Damodar Kunda, Mustang. C_λ: from 0.0 for completely dissimilar diets to 1.0 for complete overlap

Ungulate	Species level[a]	Forage categories[b]
Argali and naur	0.027	0.455
Argali and goat	0.004	0.196
Naur and goat	0.077	0.758

[a] Mostly the genus level.
[b] 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 govaniana* (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. govaniana* 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 *Chesnya* 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. govaniana*.

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 *et al.* (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[a]	Mustang, Nepal	Late summer (faecal)	32	55	13	54	6	40	23	2	75
Adjusted[b]		Late summer	11	85	3	51	22	27	28	8	64

[a] From unadjusted faecal analysis.
[b] 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 (monocotelydons) 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 micronutrients 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^2, with < 0.5 argali/km^2. In the core area of the domestic goats, their density was > 10 animals/km^2, decreasing to an average of < 5/km^2 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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