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Why should a grazer browse? Livestock impact on winter resource use by bharal *Pseudois nayaur*

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Abstract Many mammalian herbivores show a temporal diet variation between graminoid-dominated and browse-dominated diets. We determined the causes of such a diet shift and its implications for conservation of a medium-sized ungulate—the bharal *Pseudois nayaur*. Past studies show that the bharal diet is dominated by graminoids (>80%) during summer, but the contribution of graminoids declines to about 50% in winter. We tested the predictions generated by two alternative hypotheses explaining the decline: low graminoid availability during winter causes bharal to include browse in their diet; bharal include browse, with relatively higher nutritional quality, in their diet to compensate for the poor quality of graminoids during winter. We measured winter graminoid availability in areas with no livestock grazing, areas with relatively moderate livestock grazing, and those with intense livestock grazing pressures. The chemical composition of plants contributing to the bharal diet was analysed. The bharal diet was quantified through signs of feeding on vegetation at feeding locations. Population structures of bharal populations were recorded using a total count method. Graminoid availability was highest in areas without livestock grazing, followed by areas with moderate and intense livestock grazing. The bharal diet was dominated by graminoids (73%) in areas with highest graminoid availability. Graminoid contribution to the bharal diet declined monotonically (50, 36%) with a decline in graminoid availability. Bharal young to female ratio was 3 times higher in areas with high graminoid availability than areas with low graminoid availability. The composition of the bharal winter diet was governed predominantly by the availability of graminoids in the rangelands. Our results suggest that bharal include more browse in their diet during winter due to competition from livestock for graminoids. Since livestock grazing reduces graminoid availability, creation of livestock-free areas is necessary for the conservation of grazing species such as the bharal and its predators including the endangered snow leopard in the Trans-Himalaya.

Keywords Forage · Diet · Ungulate · Competition · Trans-Himalaya

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Introduction

Early research on understanding large ungulate abundance mainly focused on top-down control of ungulate populations by their predators (Hairston et al. 1960). This body of work ignored the generally low suitability of plant matter as food for ungulates (Murdoch 1966). Plant material available for herbivores, apart from often being of poor quality, is also very diverse, both in its morphological and chemical structure (Short 1971; Robbins et al. 1987). Plant material generally consumed by large herbivores is mainly composed of soluble cell contents and the cell wall (Van Soest

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1982). Nutrients available to a herbivore from a particular plant are determined by the ability of the herbivore to break down its chemical structure into digestible products. In terms of forage types for ungulates, plants may be broadly categorized as graminoids (monocots belonging to families Poaceae, Cyperaceae and Juncaceae) and non-graminoids (the other monocots and all dicots; we henceforth refer to these as "browse"; there are no non-graminoid monocots in our study system). Due to the many inherent differences in the chemical structure of these two plant types, we expect herbivore species to be specialised in digesting graminoids or browse (Hofmann 1989). Hofmann (1989) classified herbivores into grazers, browsers and intermediate feeders based on the adaptations required for specialised feeding on graminoids or browse. Van Wieren (1996) subsequently demonstrated the robustness of this classification by examining the graminoid content in the diet of 45 ruminant species. Intermediate feeders are expected to have adapted to a diet with specific proportions of graminoids and browse because of the broad differences in grass and browse (Christianson and Creel 2009). Yet, despite the specialization, many herbivores show considerable temporal variation in the contribution of graminoids and browse to their diets (Bodmer 1990; Brown and Doucet 1991). Temporal variation in diet often implies that herbivores shift their diet along the grazer browser continuum in response to certain environmental factors. Such diet shifts can either be in response to seasonal changes in forage quality (e.g. *Lepus timidus* L.; Iason and Van Wieren 1999; Hulbert et al. 2001) or due competition from another sympatric herbivore (Hulbert and Andersen 2001) or due to increased predation risk (Morgantini and Hudson 1985). Plants in seasonal environments have a high degree of temporal variation in their chemical composition. Plant nutrient contents are highest during the early growing season and drop to their annual minimum during the lean season (Mattson 1980; Wallace et al. 1995). The availability of forage plants for herbivores also tends to reduce to its lowest during the non-productive season.

Diet shift due to competition with other sympatric species is seen in the roe deer *Capreolus capreolus* in response to competition from mountain hares *Lepus timidus* Linnaeus. Hulbert and Andersen (2001) have shown that during winter roe deer shift from a browse-dominated diet (95% browse 5% graminoids) to a graminoid-dominated diet (40% browse 60% graminoid) in areas where they are sympatric with the mountain hare which mainly browses during this season. A sudden increase in predation pressure can also cause similar diet shifts in ungulates as seen in the wapiti *Cervus elaphus* during the hunting season (Morgantini and Hudson 1985).

While the physiology and anatomy of a herbivore determines the balance of graminoids and browse in its diet, deviation from this balance is expected to have nutritional costs. Deviation from the optimum balance of a graminoid-browse composition in the diet is known to be negatively related to maintenance of body mass during winter in American elk *Cervus elaphus* (Christianson and Creel 2009). Thus, it is evident that such an enforced diet shift can affect important life history parameters such as the body mass of adult female which correlates with vital rates like birth mass, sex ratio, growth rates and survival of young. In this study we examine the cause of such a diet shift in the bharal *Pseudois nayaur* Hodgson, a predominantly grazing mountain ungulate of Central Asia, its potential consequences on population performance, and its conservation-management implications.

The high altitude regions of the Indian Trans-Himalaya are mainly dry alpine steppes that support an assemblage of over 12 species of large wild herbivores (>2 kg) and seven species of domestic ungulates. This region is highly seasonal with a short productive season (May–September) and severe winter (November–March). Bharal, a medium-sized ungulate (mean adult body mass ca. 55 kg) of the sub-family Caprinae, is one of the mountain ungulates found in the high-altitude Trans-Himalayan region (3,000–6,000 m a.s.l.). Five of the six previous studies on bharal have shown that graminoids dominate the diet of bharal during summer (see Shrestha et al. 2005). Craniodental morphology of the bharal also suggests that the species is mainly adapted for a graminoid-dominated diet (Tempel and Vriji 2008) but, studies also report considerable variation, with the graminoid contribution to the bharal diet falling to 50% during winter (Mishra et al. 2004). Thus, we are faced with two questions: why do bharal, seemingly adapted to a graminoid diet, consume large amounts of browse during winter, and what are the potential consequences of this shift in diet for bharal population performance?

In this paper we explore the causes of the decline in graminoids and increase in browse in the bharal diet during winter. We examine two alternate hypotheses to explain the decline of graminoids in the bharal diet: low graminoid availability in winter causes the bharal to include browse in their diet (hypothesis 1; H1); bharal include browse, with relatively higher nutritional quality, to compensate for the poor quality of graminoids during winter (hypothesis 2; H2). H1 predicts that in areas where graminoid availability is relatively high in winter, bharal will continue to be grazers. On the other hand, H2 predicts that the bharal diet will have a high proportion of browse even in areas with high graminoid availability to compensate for the poor graminoid quality. H1 also predicts that bharal populations in areas with high graminoid availability will perform better. In contrast, H2 predicts that bharal populations will perform better in areas where bharal can optimise diet quality. In this paper, we test these predictions by comparing the bharal diet across a gradient of graminoid availability. The chemical composition of all plant species contributing to the bharal diet during winter was also analysed to determine the nutrient content of available forage species. Our objectives were to understand the causes and potential consequences of browse consumption by a graze-adapted species, and to understand the conservation implications of such a diet shift.

Materials and methods

Study area

The study was carried out in the Kibber Wildlife Sanctuary (32°15′–32°22′N, 78°02′–78°13′E), Spiti District, Himachal Pradesh, India. The sanctuary is located along a plateau on the northern banks of the Spiti River. The intense-grazing study area has an altitudinal range of 3,800–5,000 m. The terrain is mainly rolling hills broken occasionally by rocky cliffs and outcrops. During winters the temperature drops to −35°C. The mean maximum temperature in summer is around 25°C. Precipitation is mainly in the form of winter snow, which starts to melt around late March.

The vegetation is dry alpine steppe. Very few shrubs exceed a height of 1 m. The vegetation is mainly dominated by shrubs like *Caragana brevifolia* and *Lonicera spinosa*. Graminoids are represented by species of *Stipa*, *Carex*, *Kobresia*, *Elymus*, and *Festuca* etc. Botanical nomenclature in this paper follows Aswal and Mehrotra (1994).

The indigenous people of the region are mainly agro-pastoralists. Green peas *Pisum sativum*, black peas (a local variety of peas) and barley *Hordeum vulgare* form the main agricultural crops. Domestic livestock includes goat *Capra hircus*, sheep *Ovis aries*, horses *Equus caballus*, donkeys *E. asinus*, cows *Bos indicus*, and yak *Bos grunniens* and dzomo (cow-yak hybrid). Recent research has shown that bharal may face reduced forage availability in winter due to competition with livestock (Mishra et al. 2004). Other sympatric wild herbivores of the region include ibex *Capra sibirica* Linnaeus and hare *Lepus oiostolus* Hodgson. Predators of bharal include large carnivores like snow leopard *Uncia uncia* Schreber, Tibetan wolf *Canis lupus chanco* Gray and golden eagle *Aquila chrysaetos* Linnaeus.

In the study area, we selected sites with three levels of livestock grazing intensity; an ungrazed, a moderately grazed and a heavily grazed site. The ungrazed area consisted of a relatively large village reserve (20 km^2) established as part of a conservation program (led by the Snow Leopard Trust and Nature Conservation Foundation) and protected from livestock grazing since 2005 (two-thirds of the reserve area) and 1999 (one-third of the reserve area), with bharal being the only wild ungulate therein. Among the livestock grazed areas we identified two similar adjoining pastures with summer livestock grazing intensities of 1,326 and 2,163 kg km^{-2} and winter livestock grazing intensities of 337 and 721 kg km^{-2}, respectively. The less grazed of the two areas was used as moderately livestock-grazed treatment (34 km^2) while the other was an intensely livestock-grazed treatment (16 km^2). The altitudes of the three treatments, ungrazed (3,800–5,000 m), moderately livestock grazed (3,900–4,700 m) and intensely livestock grazed (3,800–4,700 m), were comparable.

Estimating forage availability

We estimated forage availability using the biomass of grass and herbs and ground cover, during early winter between 5 and 30 December. Aboveground graminoid and herb biomass was clipped from 87 randomly laid plots, each 3 × 3 m ($n = 40$ in the ungrazed, $n = 30$ in the moderately grazed and $n = 17$ in the intensely grazed treatment). Graminoids and herbs were separated, weighed fresh and oven dried. Shrubs were not clipped.

Factors such as plant height and vegetation cover were expected to affect the availability of graminoids for bharal after snow fall. Bharal do not dig in the snow (personal observation) and feed largely on the exposed vegetation, above the snow. The availability of a plant depended on: (1) the height of the plant, and (2) the abundance of the plant, so we measured the tallest height of each plant species in the ungrazed and the moderately grazed treatments. However, due to heavy snow fall, plant height could not be recorded correctly in the intensely grazed treatment. The height of the tallest plant of each species was measured within 79 ($n = 19$ in ungrazed, $n = 59$ in moderately grazed) randomly laid plots. Ground cover was recorded from 30 to 50 points at 50-cm intervals along 210 transect lines. Plant species, bare ground or rock touching each point along the transect line was recorded. The lines were systematically placed with a random start.

Estimating the bharal diet

Bharal were located and observed from a distance of about 50 m with a pair of 8 × 32 (Olympus) binoculars and a 20–60 × 60 spotting scope (KONUSPOT 60s). After the bharal had moved away, the feeding site was examined for fresh feeding signs. A 3 × 3-m plot was laid at the intense-grazing site. Any species covering >10% of ground with >50% being fed on was given a score of 2; species covering <10% of the feeding area with most individuals being fed on or species with abundant cover but with only a few individuals being fed on were scored as 1; species that were not fed on were scored 0, following Mishra et al. (2004)

($n = 81$ in ungrazed, $n = 122$ in moderately grazed and $n = 170$ in intensely grazed plots). Data on the winter diet of livestock in the same region are available from Mishra et al. (2004).

Sampling for chemical composition of plant species

Samples of each species that was fed on by bharal were clipped from four randomly selected locations every month from each of the three treatments. These samples were oven dried, homogenised and analysed for: (1) total ash, (2) crude fat, (3) crude protein (Kjeldahl nitrogen × 6.25), (4) crude fibre, (5) acid detergent fibre (ADF), (6) acid detergent lignin (ADL); following AOAC (1990). Neutral detergent fibre (NDF) was calculated following Van Soest et al. (1991).

Population estimation

We did a total count to assess bharal population structures in two of the three treatments. The bharal population structure of the moderately grazed treatment was ignored as this treatment was continuous with the ungrazed treatment north of it and the intensely grazed treatment south of it. The ungrazed and intensely grazed treatments were at least 6 km apart at the closest point. Although we doubt the distinct identities of the bharal population in these two treatments, based on our field observations, we assumed that the main herds were restricted to the respective treatments. The census was conducted on 2 April 2008, a period when the populations are congregated in the few snow-free sites, where reliable counts are possible (Mishra et al. 2004). Each treatment was thoroughly searched by two teams of two persons independently. The census was conducted from horseback, on foot and from all terrain vehicles. After encountering a group, their location and population structure were recorded. Bharal were classified as per Mishra et al. (2004).

Data analysis

Each clipped plot was used as a sampling unit to calculate mean above-ground forage biomass across treatments. We used each feeding site of bharal as a sampling unit to assess the bharal diet. Scores for each plant species were added and divided by the sum of all the scores across all species which yielded the proportionate contribution of each plant species to the bharal diet following Mishra et al. (2004). The 95% confidence limits for mean above-ground biomass and the composition of the bharal diet were calculated through Monte-Carlo simulations. We carried out 1,000 permutations with repeated draws from the observations with replacement (Krebs 1989) to calculate the parameter of interest. The percent nutrient content of the bharal diet was assessed as a product of the composition of the bharal diet and nutrient content of each plant species in the bharal diet. Ninety-five percent confidence limits were calculated by assessing the nutrient content of 1,000 permutations obtained from repeated draws of bharal-diet composition with replacement from the observations.

ANOVA was used to assess the difference in the number of plant species in the diet among various treatments and to assess the differences in plant heights across moderately grazed and ungrazed treatments. We grouped food species into graminoids (*Stipa orientalis*, *Elymus longe-aristatus*, *Carex* sp. and *Leymus secalinus*), herbs (*Astragalus grahamiana*, *Cousinia thomsonii*, *Lindelophia anchusoides*, *Bupleurum candollei*, *Ephedra gerardiana*, *Hieracleum thomsonii*, *Saussurea jacea*, *Crepis flexuosa* and *Scrophularia koelzii*) dwarf shrubs (shrubs < 50 in height; *Caragana brevifolia*, *Eurotia ceratoides*) and shrubs (*Ribes orientale*, *Rosa webbiana*).

We assessed the suitability of plant species for bharal by examining their foraging preferences following Vanderploeg and Scavia (1979). The electivity index (E^*) was calculated as: $E_i^* = [W_i - (1/n)]/[W_i + (1/n)]$, where n is the number of plant species $W_i = (r_i/p_i)/\sum(r_i/p_i)$, the proportion of the ith plant species in the diet is denoted by r_i and the proportion available is denoted by p_i.

The E^* value for any forage species close to zero indicated that bharal fed on the species in proportion to its availability, while negative values indicated avoidance and positive values indicated preference for the species. For the electivity analysis, we converted the data into a presence/absence and fed/not fed format. If a particular plant species was present at a feeding site it was scored 1 for presence in the sample. If a species was present and had been fed on by bharal then it was scored 1. The p_i of a particular species i was calculated as: $p_i = x_i/y$, where x_i is the number of sites where ith plant species was present and y is the sum of x for all i. The proportion of the species i in the diet (r_i) was calculated as: $r_i = v_i/w$, where v_i is the number of sites where the ith plant species was foraged upon by bharal and w is the sum of v for all i. The data were pooled within plant types to calculate the E^* for each plant type.

The difference across treatments in the ratio of young (6–18 months old; youngest age group of the population during the census) to adult females (an indirect measure of population performance or fecundity) was tested through repeated sampling. We bootstrapped the census data with each herd as a sampling unit. One hundred thousand permutations of sample sizes equal to those observed in the field were drawn with replacement from the pool of all the bharal herds encountered in the census across all the three treatments. The number of times the young to female ratio from these randomly drawn samples showed a difference as large as the one observed in the field was recorded. These were the chance events, and their proportion in the 100,000 permutations was the probability of observing the difference due to random chance alone.

We did not use any other measure like density of bharal to compare across treatments because the actual areas available to bharal in each of the treatments were the wind swept patches that were free of snow. The number and size of such patches varied across the study duration.

Results

Forage availability and vegetation structure

The mean above-ground dry graminoid biomass was 15.6 kg ha^{-1} (95% confidence interval 10.6–22.3 kg ha^{-1}), 18.4 kg ha^{-1} (14.8–22.7 kg ha^{-1}) and 7.1 kg ha^{-1} (5.6–9.1 kg ha^{-1}) in the ungrazed, moderately grazed and intensely grazed treatments, respectively (Fig. 1a). The mean above-ground dry herb biomass was 26.4 kg ha^{-1} (19.6–33.7 kg ha^{-1}), 36.1 kg ha^{-1} (23.7–51.9 kg ha^{-1}) and 22.1 kg ha^{-1} (17.7–26.7 kg ha^{-1}) in the ungrazed, moderately grazed and intensely grazed treatments, respectively. The ground cover was dominated by bare soil and rock in all the three treatments. Vegetation cover was highest in the ungrazed (31.2%) followed by moderately grazed (28.37%) and intensely grazed (11.09%) treatments. Dwarf shrubs dominated vegetation cover with over 90% of the vegetation represented in the ungrazed, 76% in the moderately grazed and only 26% in the intensely grazed site (Fig. 1b).

We tested for differences in plant height between the ungrazed and the moderately grazed treatments for the four most common species (one graminoid, one herb and two dwarf shrubs) for which enough data were available. The mean height of *S. orientalis* (graminoid) was significantly greater ($F = 7.95$, $P = 0.06$) in the ungrazed treatment (10.8 cm) compared to the moderately grazed treatment (5.0 cm), suggesting greater graminoid availability in the ungrazed treatment (Fig. 2). The differences were not significant for any other plant species: *C. brevifolia* ($F = 1.33$, $P = 0.25$), *E. ceratoides* ($F = 2.15$, $P = 0.15$), *B. candollei* ($F = 0.41$, $P = 0.53$).

Winter diet of bharal

During the study, 34 plant species were recorded from bharal feeding sites. Twenty-seven of these had been fed upon by bharal at least once. Only 16 plant species contributed more than 1% each to the winter diet, which consisted of 46.2% graminoids, 17.8% dwarf shrubs, 32.3% herbs and 4.4% shrubs. The contribution of graminoids to the bharal diet was highest (74.3%) in the ungrazed treatment, 49.7% in the moderately grazed treatment and 36.6% in the intensely grazed treatment (Fig. 3). The proportion of herbs was similar in the ungrazed and in the moderately grazed treatments at 10%, but was over 50% in the intensely grazed treatment. Dwarf shrubs contributed the most to the diet in the moderately grazed treatment (40%). In the ungrazed treatment a single species of grass, *S. orientalis*, comprised 56% of the diet (Table 1).

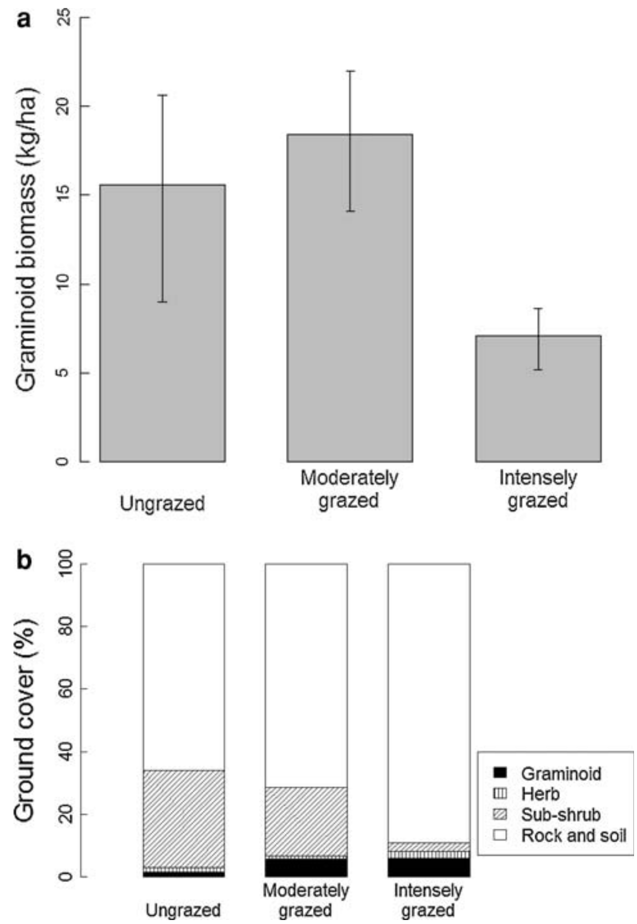

Fig. 1 **a** Mean winter graminoid biomass, and **b** percent ground cover in treatments not grazed, moderately grazed and intensely grazed by livestock during winter in Sipti, Himachal Pradesh, India. **a** *Error bars* represent asymmetric 95% confidence limits, based on clipped plots as sampling units

ANOVA (unequal *n*) for number of species available per feeding site as dependant variable and grazing treatments as fixed factors showed significant differences ($df = 2$, $F = 5.21$, $P = 0.005$). Plant species available per feeding site was highest in the intensely grazed treatment followed by the moderately grazed treatment and ungrazed treatment. A similar analysis for the number of species in the bharal diet per sample also differed significantly ($df = 2$, $F = 22.23$, $P < 0.0001$). Bharal fed on a greater number of species in the intensely grazed treatment than in the moderately grazed and ungrazed treatments.

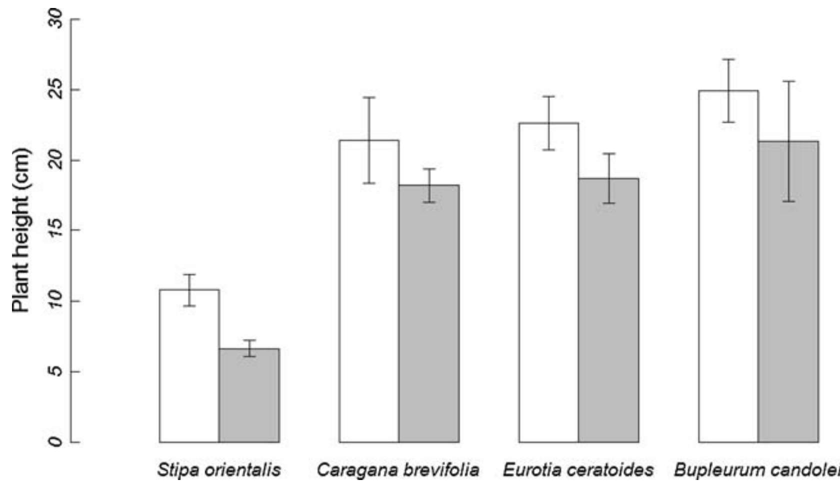

Fig. 2 Mean plant height in treatments not grazed (*white bars*) and moderately grazed (*shaded bars*) by livestock. *Error bars* represent ±1 SE. Plant height was not measured in the intensely grazed treatment due to logistic constraints

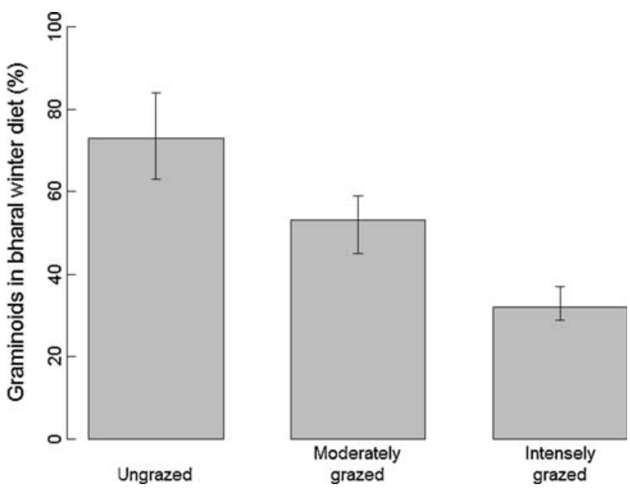

Fig. 3 Graminoid contribution to the bharal winter diet in the treatments not grazed, moderately grazed and intensely grazed by livestock in Spiti. *Error bars* indicate 95% confidence limits, based on each feeding site as a sampling unit

The E^* calculated following Vanderploeg and Scavia (1979) was positive for all the four species of graminoids and four species of herbs, namely *S. koelzii*, *H. thomsonii*, *L. anchusoides* and *E. gerardiana*, indicating selective preference for these species. All other herbs, shrubs and dwarf shrubs had negative values, and thus were eaten less in proportion to their availability. *E. ceratoides*, one of the dwarf shrubs, had an index very close to zero ($E^* = -0.03$), indicating feeding in proportion to availability of the species (Fig. 4).

Among plant types, the E^* was positive only for graminoids (0.28), while it was negative for shrubs (−0.30) and dwarf shrubs (−0.27), and close to zero for herbs ($E^* = -0.003$). E^*s for herbs, dwarf shrubs and shrubs in the presence of graminoids at the feeding site were 0, −0.31 and −0.27, respectively which increased to 0.04, −0.14 and 0.05, respectively in the absence of graminoids. The change in the E^* for dwarf shrub from −0.27 to 0.05 indicates that dwarf shrubs were the most preferred plant types for bharal in the absence of graminoids. The E^* for graminoids remained constant in the presence and absence of herbs, dwarf shrubs and shrubs from the feeding site. This result indicated that presence/absence of graminoids affected bharal foraging decisions disproportionately compared to the presence/absence of other plant types.

Nutrient contents of bharal winter diet

The nutrient content of the bharal diet was calculated as the product of the nutrient content of each plant species (Tables 2, 3) and the contribution of the plant species to the bharal diet in each of the three treatments. Nutrient (total ash + crude protein) content of the bharal diet did not show any difference across the treatments (Figs. 5, 6). The percent NDF, ADF, ADL and crude fibre content of the bharal diet did not show any significant differences across treatments either. These results show that the nutrient content available to the bharal across the three treatments was similar.

Population structure

A total of 151 bharal were recorded in the ungrazed and intensely grazed treatment. The young to adult female ratios were 0.9 and 0.28 in the ungrazed and intensely grazed treatments, respectively (Table 4). The difference in the ratio between the ungrazed and intensely grazed treatments was significant ($P < 0.0001$; bootstrap, 100,000 permutations).

Discussion

Hofmann (1989) first classified ungulates based on their morphological and physiological adaptations which he suggested were profitable for feeding on graminoids or browse.

Table 1 The contribution (%) of different plant species which formed 95% of the winter diet of the bharal *Pseudois nayaur* in the treatments not grazed, moderately grazed and intensely grazed by livestock in Spiti, Himachal Pradesh, India

Plant species	Overall winter	ungrazed	Moderately grazed	Intensely grazed
Ribes orientale (S)	0.6	0.0	A	1.8
Astragalus grahamiana (H)	0.7	A	1.8	0.4
Saussurea jacea (H)	0.7	A	A	2.2
Cousinia thomsonii (H)	1.2	A	1.2	2.6
Lindelophia anchusoides (H)	1.4	A	0.6	3.6
Crepis flexuosa (H)	1.6	1.2	0.3	3.5
Bupleurum candollei (H)	2.3	3.8	0.9	2.2
Ephedra gerardiana (H)	2.3	0.6	0.9	5.5
Rosa webbiana (S)	2.4	A	A	7.5
Scrophularia koelzii (H)	3.5	A	A	10.8
Carex sp. (G)	3.6	A	7.4	3.5
Elymus longe-aristatus (G)	5.7	10.2	4.7	2.2
Leymus secalinus (G)	7.4	5.7	6.2	10.4
Caragana brevifolia (DS)	7.8	8.3	15.1	0.2
Hieracleum thomsonii (H)	8.0	1.9	5.0	17.2
Eurotia ceratoides (DS)	10.8	9.0	21.0	2.6
Stipa orientalis (G)	35.1	56.4	28.7	20.3
Others	4.2	2.6	6.2	3.8

G Graminoids, *H* herbs, *S* shrubs, *DS* dwarf shrubs, *A* absent

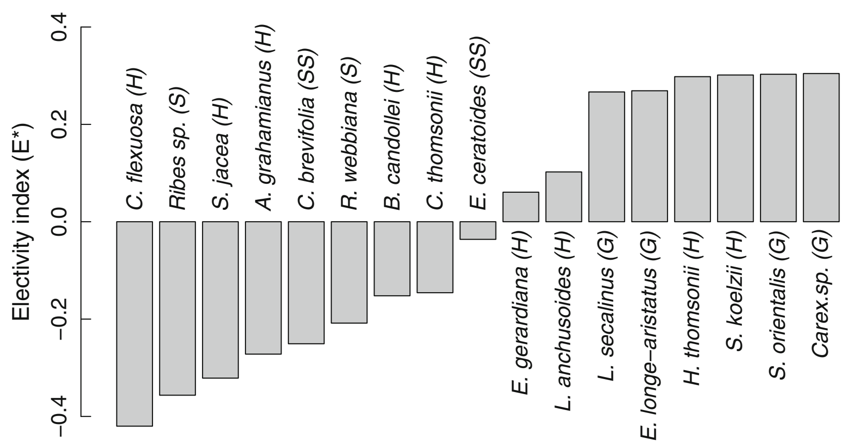

Fig. 4 Electivity indices calculated following Vanderploeg and Scavia (1979) for plant species contributing more than 1% to the bharal diet. *Positive values* indicate preference for a species while *negative values* indicate avoidance. Values closer to zero indicate feeding in proportion to availability. *G* Graminoids, *H* herbs, *S* shrubs, *SS* dwarf shrubs

Table 2 Nutritional parameters of plant types during winter in Spiti

	Total ash	Crude fat	Crude protein	Crude fibre	Neutral detergent fibre (NDF)	Acid detergent fibre (ADF)	Acid detergent lignin (ADL)
Graminoids	5.6 (1.1)	1.6 (0.4)	2.1 (0.2)	34.9 (2.1)	74.3 (1.8)	46.8 (3.4)	17.1 (2.8)
Shrubs	4.7 (0.6)	1.1 (0.03)	2.4 (0.2)	27.7 (1.7)	53.2 (0.4)	43.4 (1.4)	18.9 (2.6)
Dwarf shrubs	4.9 (0.6)	1.6 (0.4)	5.6 (1.4)	32.5 (1.2)	73.4 (5.0)	52.3 (4.0)	17.5 (4.4)
Herbs	8.5 (2.1)	1.4 (0.2)	3.0 (0.5)	31.7 (1.9)	63.7 (4.3)	46.0 (3.5)	16.9 (1.2)

Data are percent dry weight contents (1 SE)

His argument was based on the physical, structural and chemical differences between graminoids and browse. Since then, the question “are grazers different from browsers?” has been debated (Gordon 2003; Robbins et al. 1995). Hofmann (1989) suggested that herbivores showing adaptation for a specific forage type (graminoids or browse) should prefer to feed on that type. Bharal show a shift from a mainly graminoid-dominated diet in summer to a mixed diet during winter (Mishra et al. 2004). In this study we tested the predictions of two alternative hypotheses to explain the decline of graminoids in the bharal diet during winter. Our results were in agreement with the hypothesis

Table 3 Various nutritional parameters of plants that contributed more than 1% to the bharal winter diet in Spiti

Plant species	Total ash	Crude fat	Crude protein	Crude fibre	NDF	ADF	ADL
Lindelophia anchusoides (H)	23.2	1.38	5.22	18.81	42.9	37.33	17.52
Stipa orientalis (G)	7.18	2.80	2.44	27.66	68.75	36.84	16.03
Caragana brevifolia (SS)	5.93	2.19	7.64	34.25	66.3	46.52	11.20
Elymus longe-aristatus (G)	3.97	0.75	1.62	38.26	78.99	45.59	17.08
Crepis flexuosa (H)	3.97	0.25	0.80	36.79	80.30	63.78	22.82
Eurotia ceratoides (SS)	4.05	1.02	3.65	30.80	80.56	57.99	23.72
Bupleurum candollei (H)	2.52	1.61	4.43	36.60	76.73	57.26	16.90
Astragalus grahamiana (H)	4.31	1.06	2.41	27.13	69.94	52.08	17.62
Cousinia thomsonii (H)	11.77	1.17	4.43	30.91	52.14	40.95	13.94
Leymus secalinus (G)	8.31	0.97	1.62	37.35	75.83	48.63	09.69
Rosa webbiana (S)	3.78	1.07	2.80	30.15	53.73	41.46	22.64
Ribes orientale (S)	5.65	1.17	2.03	25.33	52.59	45.51	15.07
Ephedra gerardiana (H)	6.06	0.35	1.63	31.04	44.04	27.17	23.08
Saussurea jacea (H)	6.58	2.00	4.02	32.49	65.37	41.92	14.22
Hieracleum thomsonii (H)	4.67	2.36	2.81	37.73	70.98	52.78	15.84
Scrophularia koelzii (H)	13.35	2.18	1.62	33.93	70.65	41.01	10.20
Carex sp. (G)	3.03	1.94	2.85	36.45	73.48	56.03	25.59

Data are percent content per unit dry matter. For abbreviations, see Tables 1 and 2

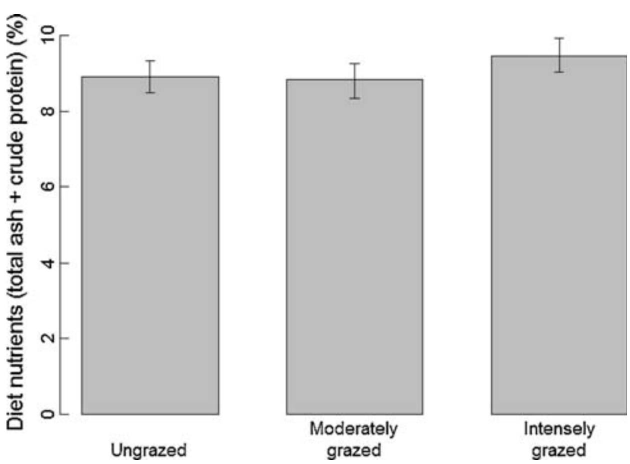

Fig. 5 Percent nutrient (total ash + crude protein) content of the bharal diet during winter across treatments which were ungrazed, moderately grazed and intensely grazed by livestock in Spiti. *Error bars* represent 95% confidence limits calculated based on each feeding site as a sampling unit

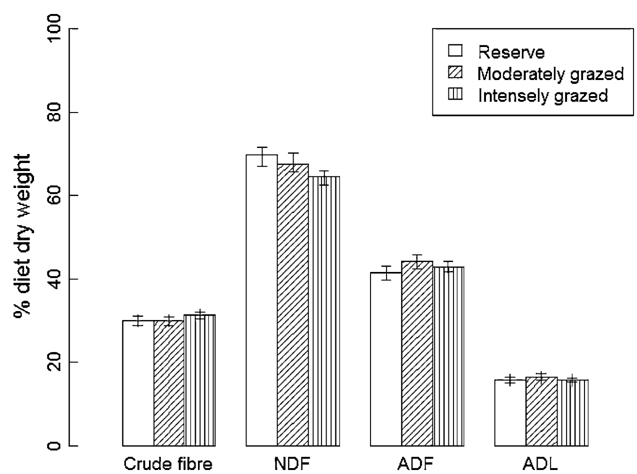

Fig. 6 Crude fibre, neutral detergent fibre (*NDF*), acid detergent fibre (*ADF*) and acid detergent lignin (*ADL*) content in the bharal diet during winter in Spiti. *Error bars* represent ±1 SE

that low graminoid availability causes bharal to include browse in their diet, as in winter the diet continued to be dominated by graminoids in areas with higher graminoid availability. In rangelands where the graminoid availability was lower, bharal tended to include more browse in their diet. The selection for graminoids by bharal in spite of their relatively lower crude protein, and moderate ash content indicates that nutritional levels of plants had less influence on the bharal winter diet selection compared to the influence of plant type (graminoid or browse). These results suggest that the availability of graminoids determined the bharal diet composition, and the quality of non-graminoids did not have a significant effect on the winter diet of bharal. The high positive E^* for graminoids and the influence of graminoid presence on the E^* for other plant types indicate that bharal preferred graminoids to any other forage type, which is consistent with its summer diet (Mishra et al. 2004; Shrestha et al. 2005) and the craniodental adaptations of the species (Tempel and Vriji 2008) which suggest bharal to be a grazer.

Chemical analyses show that the differences in the nutrient quality across plant types during winter were not significant. The selection of graminoids in such a scenario

Table 4 Population structure of bharal in rangeland ungrazed and intensely grazed by livestock in Spiti

	Ungrazed ($n = 57$)	Intensely grazed (94)
Adult females	21	36
Young	19	10
Class I–IV male	17	48
Young (100 females)$^{-1}$	90	28

Population structure of the moderately grazed treatment was ignored due to its continuity with ungrazed and intensely grazed treatments

Table 5 Percent contribution of graminoids and browse to the winter diet of seven species of livestock in Spiti

	Yak	Horse	Dzomo	Cow	Donkey	Sheep	Goat
Graminoid (%)	55.5	51.6	84.7	81.6	78.2	76.9	72.3
Non-Graminoid (%)	44.5	48.4	15.3	18.4	21.8	23.1	27.7

Data compiled from Mishra et al. (2004)

indicates the importance of adaptation for a particular diet type, in this case, for a grazing diet. Yet, the nutrient quality of all plant species (except *C. brevifolia*, a dwarf shrub, and *L. anchusoides*, a herb) was below maintenance level [<5% crude protein; estimated for *Ovis canadensis* Shaw (Hebert 1976 cited in Goodson et al. 1991)]. Our study thus shows again the role of fat accumulation during summer (productive season) in temperate and alpine species such as the bharal. Our results also show that bharal, while remaining dependent on graminoids, have the plasticity to be able to utilise browse in areas where the preferred forage is unavailable. Such plasticity has been seen in other herbivores like the mountain hare that live in similar seasonal environment and do not hibernate (Iason and Van Wieren 1999). Feeding plasticity could be important for herbivores in areas with unpredictable weather affecting forage availability.

Fat reserves acquired during summer, together with winter diet and nutrition, are presumably the major factors determining the body weight of bharal during winter (the gestation period). Female weight during pregnancy (during winter in the bharal) is known to be an important determinant of the birth weight of the young (born just at the end of winter; late April–early May; Illius and Gordon 1999). As survival of young through the first year is related to their weight at birth (Clutton-Brock et al. 1987; Loison et al. 1999) the winter nutrition of females is expected to be a key factor in determining the first year survival of neonate bharal.

The young to female ratio (population performance) in the treatment ungrazed by livestock was 3 times higher than in the intensely grazed treatments. We recognize that the location of the two treatments, being only 6 km apart, does not preclude exchange of individuals between these two areas, and our results should be treated as preliminary. Nevertheless, they indicate high fecundity and first-year survival for bharal in areas not grazed by livestock. These results, while being consistent with our hypothesis that low graminoid availability causes bharal to include non-graminoids in their diet, are also consistent with previous studies showing suppression of fecundity in areas of high livestock density (Mishra et al. 2001, 2004) and survival of bharal young due to reduced forage availability in areas with high livestock densities (Gaillard et al. 1998). Our result points to the importance of foraging at the equilibrium of graminoids and browse being determined by evolutionary adaptations. Deviations from this equilibrium can impose nutritional penalties resulting in reduced fitness.

The above-ground standing biomass of graminoids in our study area is among the lowest in the world (Mishra 2001). Other studies from similar low productivity systems such as tundra and steppe have shown that their herbivore populations are often resource limited (Aunapuu et al. 2008; Crete and Huot 1993; Turchin and Batzli 2001; Zhong et al. 2008). Our study provides additional evidence that low productivity systems could be limited by forage availability.

There is evidence showing reduced forage availability for bharal in areas with a high livestock grazing pressure (Mishra et al. 2004). Five species of livestock predominantly grazed during winter (graminoids contributing more than 70% to their diet) while two fed intermediately (graminoids contributing 40–60% to their diet; Table 5). The inclusion of higher amounts of browse in the bharal diet in livestock-grazed areas also suggests that bharal shift from a graminoid-based diet in summer to a mixed diet in winter mainly due to a reduced availability of graminoids, resulting from competition from domestic livestock. Thus, livestock, which heavily outnumber wild ungulates in these areas, seem to severely limit the availability of graminoids for wild ungulates. The findings of our study emphasise the need to enhance graminoid availability in key areas for wild grazing ungulates such as the bharal. The creation of livestock-free areas is thus necessary for the conservation of grazing species such as the bharal and its predators, including the endangered snow leopard in the Trans-Himalaya.

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