Overwintering strategies and demographic response of bharal (*Pseudois nayaur*) to livestock grazing and removal, in Kibber Wildlife Sanctuary

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By
Kulbhushansingh R. Suryawanshi

Post-Graduate Program in Wildlife Biology & Conservation
Centre for Wildlife Studies
and
National Centre for Biological Sciences
UAS-GKVK Campus
Bangalore – 500 065

Post-Graduate Program in Wildlife Biology and Conservation
National Centre For Biological Sciences, Post Box 6501, GKVK Campus, Hebbal, Bangalore 560 065. India
Tel: 91-80-2363 6421 - 31, Fax: 91-80-2363 6662
Email: msc@wcsindia.org Website: www.wcsindia.org

Declaration

I declare that the thesis entitled "Overwintering strategies and demographic response of bharal (*Pseudois nayaur*) to livestock grazing and removal, in Kibber Wildlife Sanctuary" comprises research work done by me under the guidance of Dr. Charudutt Mishra, and co-guidance of Dr. Yash Veer Bhatnagar. The work is original and has not been done earlier by anyone else. Part of this work, which is related to or similar to work done by other researchers, has been cited in this thesis at appropriate places. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

Charudutt Mishra

Signature of the guide
(Dr. Charudutt Mishra)

Signature of the candidate
(Suryawanshi Kulbhushansingh Ramesh)

Post-Graduate Program in Wildlife Biology and Conservation
National Centre For Biological Sciences, Post Box 6501, GKVK Campus, Hebbal, Bangalore 560 065. India
Tel: 91-80-2363 6421 - 31, Fax: 91-80-2363 6662
Email: msc@wcsindia.org Website: www.wcsindia.org

Certificate

I declare that the thesis entitled "Overwintering strategies and demographic response of bharal (*Pseudois nayaur*) to livestock grazing and removal, in Kibber Wildlife Sanctuary" comprises research work carried out by Suryawanshi Kulbhushansingh Ramesh at the Centre for Wildlife Studies under my guidance, and the co-guidance of Dr. Yash Veer Bhatnagar, during the period 2007-2008, for the Degree of Master of Science in Wildlife Biology & Conservation of the Manipal University. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

Charudutt Mishra

Dr. Charudutt Mishra
Nature Conservation Foundation,
3076/5, IV Cross, Gokulam Park,
Mysore 570 00

Executive Summary

Craniodental morphology of bharal *Pseudois nayaur* indicates that the species is adapted for predominantly feeding on graminoids. Previous studies show that bharal diet is dominated by graminoids (>80%) during summer, but the contribution of graminoids declines to about 50% in winter. I explore the causes of this decline and its implications for bharal conservation.

I test the predictions generated by two alternative hypotheses, (H1) low graminoid availability during winter causes bharal to include browse in their diet, and, (H2) bharal include browse, with relatively higher nutrition, to compensate for the poor quality of graminoids during winter. This field study in the Indian Trans-Himalaya examined bharal diet composition and population structure across a gradient of graminoid availability and livestock grazing during the lean season.

I measured winter graminoid availability in artificially created livestock-free areas, areas with relatively moderate livestock grazing, and those with intense livestock grazing pressures. Chemical composition of plants contributing to bharal diet was analysed. I then compared bharal winter diet composition and population structure across these three treatments. Bharal diet was quantified through feeding signs on vegetation at feeding locations. I also documented the population structures of bharal in the three treatments.

Graminoid availability for bharal was highest in areas with no livestock grazing, followed by areas with moderate and intense livestock grazing. Graminoid quality was relatively lower than browse, but the difference was not statistically significant. Bharal diet was dominated (73%) by graminoids in areas with highest graminoid availability. Graminoid contribution to bharal diet declined monotonically (50%, 36%) with a decline in graminoid availability. Bharal population performance (yearling to female ratio) was three times higher in areas with high graminoid availability than areas with moderate and low graminoid availability. No starvation related adult mortalities were observed in any of the areas.

Composition of bharal winter diet was governed predominantly by the availability of graminoids in the rangelands. The results suggest that the ability to include browse in the diet presumably moderates bharal adult mortality, but this plasticity has a cost in terms of reduced population recruitment. Since livestock grazing reduces graminoid availability, creation of livestock-free areas is necessary for conservation of grazing species such as the bharal and its predators including the endangered snow leopard in the Trans-Himalaya.

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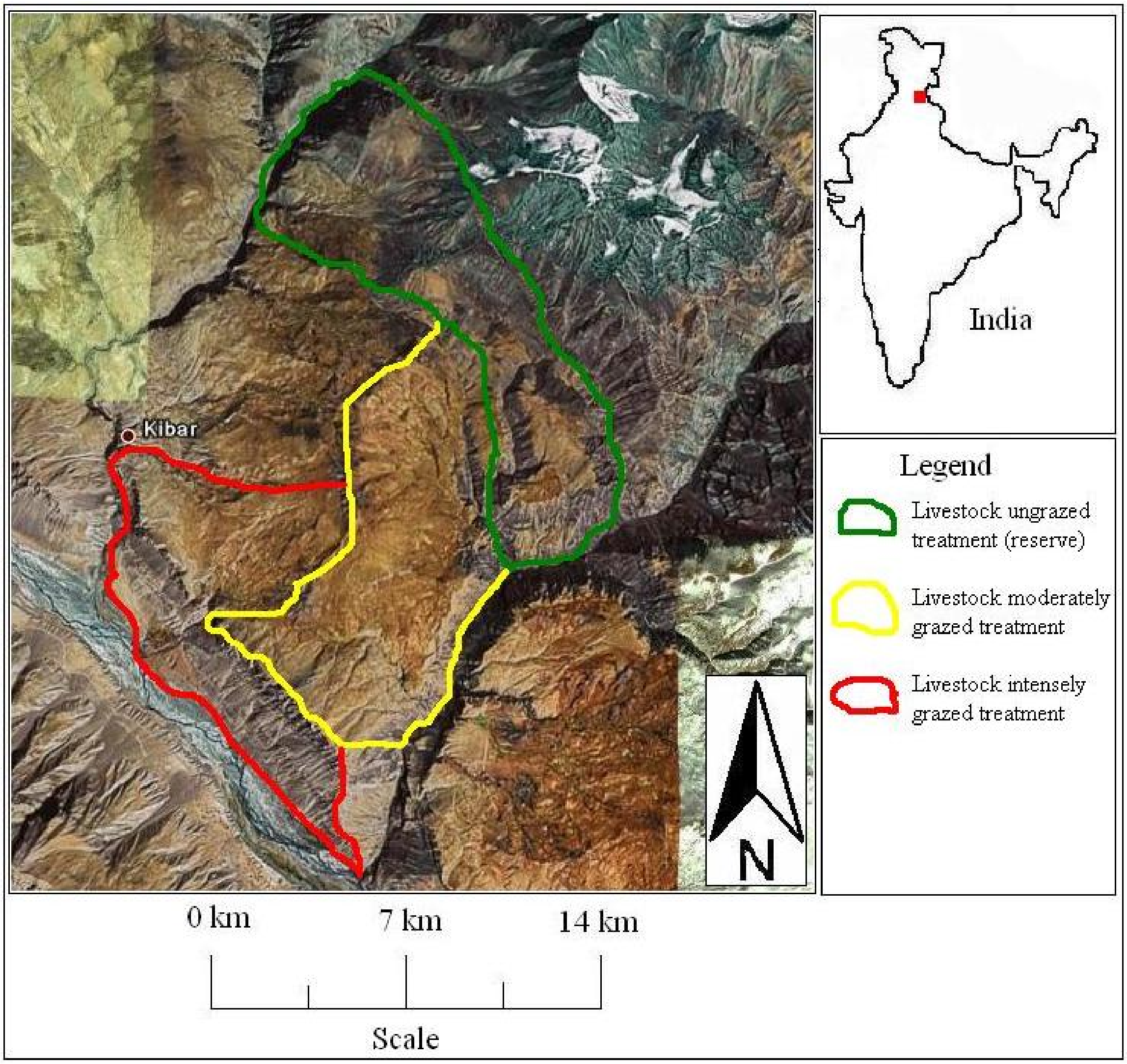

Map showing boundaries of the three grazing treatments. Inset shows the location of the Kibber Wildlife Sanctuary in India (top right).
Google Earth URL: http://earth.google.com/intl/en/GooleEarth4.3. 2008. GeoEye TerraMetrics (image taken on 7th January 2007) (Accessed on 30th June 2008)

Overwintering strategies and demographic response of bharal (*Pseudois nayaur*) to livestock grazing and removal

Introduction

Importance of wild ungulates

Large bodied ungulates are important drivers of energy flow and nutrient recycling in grazing ecosystems (McNaughton 1976, Frank et al. 1998). They also have strong direct and indirect feedbacks on plant community structure, composition and productivity of grasslands (McNaughton 1976, Milchunas & Laurenroth 1993, Frank et al. 1998, Koppel & Prins 1998, Frank et al. 2002, Augustine & McNaughton 2006). Wild ungulates are the primary prey of most large carnivores across the world, and their density is an important determinant of carnivore density (Karanth et al. 2004). Large ungulates also contribute to the local economies of many regions. Areas supporting large ungulates benefit through enterprises such as tourism and sport hunting (over 10.3 million people hunted in the United States spending US $ 5.1 billion in a single hunting season in 1991; Conover 1997). Wildlife tourism generates around US $ 400 million per annum in Kenya, it also opens opportunities for employment for local and regional communities (Barnes et al. 1999, Ogutu 2002). While the ecological importance and economic potential of wild ungulates is being explored further (Gordon et al. 2004), human activities like hunting, land conversions for agriculture and pastoralism pose threats to ungulate diversity across the world. Fifteen percent of the world land area is currently under agriculture and another 25% is under managed grazing; over 90% of natural grasslands of the world have been converted for agriculture during the past 150 years (Prins 2000, Prins & Gordon 2008).

Challenges faced by foraging ungulates

What determines the abundance of ungulates?, while being an important conservation question, also poses a fundamental question in ecology, *viz.* what determines distribution and abundance of organisms? (Andrewartha & Birch 1972). Early research on large ungulate abundance mainly focused on top-down control of ungulate populations by their predators (Hairston et al. 1960). This body of work did not recognise the generally low suitability of plant matter as food for ungulate (Murdoch 1966). Mammals require high amount of metabolisable nitrogen (N) for synthesis of proteins which form the structural building blocks of mammal tissue. Plant tissue is mainly composed of carbohydrates and very low amounts of protein (Mattson 1980). Thus, ungulates need to invest a large amount of energy and time harvesting enough forage to sequester the necessary amount of N from plants (Mattson 1980, Iason & Van Wieren 1999). Additionally, mammalian herbivores are relatively poor at utilising available N as their excretion contains substantial amount of N compounds (Mattson 1980). Plants also have lignin and secondary compounds that reduce digestibility (Robbins et al. 1987a, b, Cordon 2007). Since ungulates are limited by the amount of forage they can consume due to limited gut capacity, there is a minimum level of N that is required in any potential forage species for an ungulate to be able to utilise it (Mattson 1980, Iason & Van Wieren 1999). Thus the quantity and suitability of available forage have subsequently been recognised as important factors limiting ungulate populations (Iason & Van Wieren 1999). The debate on bottom-up versus top-down control of herbivore populations continues.

Plant material available for herbivores, apart from often being of poor quality, is also very diverse, both in its morphological and chemical structure (Short et al. 1974, Robbins et al. 1987a). Plants can be broadly classified as graminoids (monocotyledonous) and non-graminoids (dicotyledonous) (Short 1971). The differences between these two groups from a foraging herbivore's viewpoint are summarised in Table 1. Different ungulate taxa have adapted to feeding on these different forage groups (Janis 2008).

Table 1. Differences between graminoid (monocotyledonous) and non-graminoid (dicotyledonous) plant structures as forage for ungulates

	Graminoids	Non-gaminoids	***Reference***
Chemical properties			
Protein content	Generally less crude protein (less nitrogen)	Higher crude protein, but some of it bound to secondary compounds and thus un-available for herbivores	(Dougall et al. 1964, Codron et al. 2007)
Fibre content	High proportion of cell wall, major portion of which is cellulose (cellulose can be digested by gut micro-flora fermentation)	Relatively lesser proportion of cell wall and much of it is lignified (lignin is non-digestible)	(Short 1971)
Secondary compounds	Low secondary compounds	High secondary compounds, which, apart from being poisonous, also affect digestibility negatively	(Freeland & Janzen 1974, Iason & Van Wieren 1999)
Physical properties			
Abrasive silica	Presence of abrasive silica that wears down tooth enamel	Negligible silica	(Dougall et al. 1964, McNaughton et al. 1985)
Resistance to chewing (Hypothesised)	Higher masticatory force required for comminuting	Lesser mastiacatory force required	(Solounias & Dawson-Saunders 1988, Mendoza et al. 2002)
Homogeneity in nutrient distribution	Relatively homogeneous distribution of nutrient across plant parts	Relatively heterogeneous distribution of nutrients across plant parts	(Iason & Van Wieren 1999)
Digestibility			
Overall digestibility	Yield more energy per unit forage fermented	Less energy per unit forage fermented	(Codron et al. 2007)
Speed of digestion	Rate of fermentation is slower throughout	Rate of fermentation is faster in the initial stages of fermentation	(Short 1971)

With the emergence of graminoids around 25 million years ago, forest dwelling browsing ungulates diversified to exploit the new niche opened in the form of grasslands (Janis 2008). Availability of grass and browse led to diversification of ungulates that were adapted in their craniodental and digestive morphology and physiology to the different forage types (Janis 2008). The differences in the tissue lignification and secondary chemical compounds led to the requirement of special adaptations in the physiology of ungulates exploiting specific forage types (graminoids and browse) (Janis 2008). Thus grazers and browsers evolved to deal with their forage in different and specialised ways.

Although a certain degree of plasticity exists, the ability of ungulates to utilise these different types of forage, appears to be limited due to specialisation. Based on these adaptations, Hoffman (1989) divided ungulates into three groups, namely, grazers, browsers and intermediate feeders (Table 2).

Table 2. Feeding adaptations of grazers and browsers

	Grazers	Browsers	***Reference***
Digestion	Ready fibre (NDF) digestion	Low fibre (NDF) digestion	(Perez-Barberia et al. 2004; Van Wieren 1996)
Anatomy	Adaptation to tooth abrasion due to silica, broader muzzle width, larger omasum	No adaptation to abrasion, narrower muzzle for selective feeding, larger salivary gland	(Janis 1990; Cordon et al. 2007)
Daily food intake	Higher daily forage intake	Lower daily intake	(Clemens & Maloiy 1983)
Digestion kinetics	High forage retention time	Low retention time	(Hummel et al. 2006)
Tannin binding salivary protein	Absent	Present	(Austin et al. 1989
Secondary metabolite tolerance	Low (expected)	High (expected)	Weak support (Brooker et al. 1994)

Ungulates in seasonal environments

Plants as forage matter for ungulates in seasonal environments also have a high degree of temporal variation in their chemical composition. The N content of plant tissue is highest during the growing season and drops lowest during the lean season (Mattson 1980). Fibre content of plants is also highest during the lean season (Wallace et al. 1995). As a result, in seasonal environments the nutritional quality of most perennial plants drops during the lean season. The digestibility of plant tissue also shows a negative relationship with age of the plant (Mattson 1980; Wallace et al. 1995). This drop is mainly due to increasing fibre content in their tissue as plants approach senescence (Mattson 1980; Wallace et al. 1995). As annuals from seasonal environments die off during the lean season the forage quality is at an annual minimum during the lean season. Thus various strategies have evolved in ungulate species to fulfil their energy requirements during the lean season (Iason & Van Wieren 1999).

What "successful" ungulates do: The bharal

Amongst mammals the strategies to deal with the lean season include reduced metabolism, hibernation, behavioural adaptations such as heat preserving body posture and migration (Albon & Langvatn 1992), increased consumption rates, prolonged feeding and digestion time, specialised alimentary canal and digestive systems that depend on symbiotic microbes (Gross et al. 1985, Bozinovic 1995, Hammond & Wunder 1995, Derting & Noakes 1995). Temperate and alpine ungulates mainly depend upon fat reserves built during the season of resource abundance to survive the lean season (Young 1976; Loison et al. 1999; Mautz 1978; Souve 2005). Shift in habitat use within the same landscape (Wallace et al. 1995; Luccarini et al. 2006) or a seasonal shift in diet to obtain better quality forage are also successful lean season strategies, while there are limitations to the shift (Mattson 1980). These limitations are mainly due to low or negative digestibility of available N of the new forage type, which can lead to increased weight loss during this season (Iason & Van Wieren 1999).

The high altitude regions of the Indian Trans-Himalaya are mainly dry alpine steppe regions that support an assemblage of over ten species of large wild herbivores (>2 kg), namely, Himalayan woolly hare (*Lepus oiostolus*), Cape hare (*Lepus capensis*), Himalayan Marmot (*Marmota himalayana*), long-tailed marmot (*Marmota caudata*), Tibetan antelope (*Panthalops hodgsoni*), Tibetan gazelle (*Procapra picticaudata*), bharal/blue sheep (*Pseudois nayaur*), Himalayan ibex (*Capra sibirica*), kiang (*Equus kiang*), Ladakh urial (*Ovis vignei*), Tibetan argali (*Ovis ammon*) and wild yak (*Bos grunniens*) and a further seven species of domestic ungulates, namely goat, sheep, donkey, cattle, horse, cattle yak hybrid and domestic yak. This region is amongst some of the least productive grass-dominated systems of the world (Mishra et al. 2001). There is empirical information showing forage limitation for wild ungulates due to competition from livestock in the region (Mishra et al. 2004). Recent research from the Himachal Pradesh Trans-Himalaya established the decline of wild mountain ungulate species such as the bharal and ibex due to forage competition with livestock (e.g. Mishra et al. 2004, Bagchi et al. 2004). There is theoretical evidence showing local extinction of four species of wild ungulates due to competitive exclusion from livestock from the same region (Mishra et al. 2002).

Bharal, a medium sized ungulate (*mean adult body mass* 55 kg) of the sub-family Caprinae, is one of the most widespread and abundant large herbivore in the Trans-Himalaya and the Tibetan plateau (Miller & Schaller 1996; Johnsingh et al. 2006). Bharal craniodental morphology suggests that the species is mainly adapted for a graminoid-dominated diet

(Tempel & Vriji 2008). Five of the six previous studies on bharal have shown that graminoids form the dominant forage type in bharal diet (see Shrestha et al. 2005). While all these studies suggest that bharal are adapted for a graminoid diet type, studies also reported that the graminoid contribution to bharal diet drops to 50% during winter (Mishra et al. 2004). Thus, we are faced with two questions (I) why do bharal, seemingly adapted to graminoid diet, include large amount of browse in their winter diet?, and, (II) what are the consequences of this shift in diet for bharal population dynamics?

Why do they do it?

In this thesis I explore the causes of decline in graminoids in the bharal diet during winter. I examine two alternate hypotheses to explain the decline of graminoids in bharal diet H1: Low graminoid availability in winter causes the bharal to include browse in their diet. H2: Bharal include browse, with relatively higher nutrition, to compensate for the poor quality of graminoids during winter. 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 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 its diet quality.

The draft manuscript titled "Why do grazers browse: livestock impact on winter resource use of bharal *Pseudois nayaur*" is prepared for submission to the *Journal of Applied Ecology.*

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Why do grazers browse: livestock impact on winter resource use of bharal *Pseudois nayaur*

Kulbhushansingh R. Suryawanshi[1, 2]

[1] Post-graduate Program in Wildlife Biology and Conservation, National Centre for Biological Sciences, Bangalore, India

[2] Wildlife Conservation Society—India Program, Centre for Wildlife Studies, Bangalore, India

Corresponding author: Kulbhushansingh R. Suryawanshi
269, 5th Main,
Canara bank layout,
Kodigehalli,
Bangalore 560097
India

Email: Kulbhushansinghs@gmail.com

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Summary

1. Craniodental morphology of bharal *Pseudois nayaur* indicates that the species is adapted for predominantly feeding on graminoids. Previous studies show that bharal diet is dominated by graminoids (>80%) during summer, but the contribution of graminoids declines to about 50% in winter. I explore the causes of this decline and its implications for bharal conservation.

2. I test the predictions generated by two alternative hypotheses, (H1) low graminoid availability during winter causes bharal to include browse in their diet, and, (H2) bharal include browse, with relatively higher nutrition, to compensate for the poor quality of graminoids during winter. This field study in the Indian Trans-Himalaya examined bharal diet composition and population structure across a gradient of graminoid availability and livestock grazing during the lean season.

3. I measured winter graminoid availability in artificially created livestock-free areas, areas with relatively moderate livestock grazing, and those with intense livestock grazing pressures. Chemical composition of plants contributing to bharal diet was analysed. I then compared bharal winter diet composition and population structure across these three treatments. Bharal diet was quantified through feeding sign on vegetation at feeding locations. I also documented the population structures of bharal in the three treatments.

4. Graminoid availability for bharal was highest in areas with no livestock grazing, followed by areas with moderate and intense livestock grazing. Graminoid quality was relatively lower than browse, but the difference was not statistically significant. Bharal diet was dominated by graminoids (73%) in areas with highest graminoid availability. Graminoid contribution to bharal diet declined monotonically (50%, 36%) with a decline in graminoid availability. Bharal population performance (yearling to female ratio) was three times higher in areas with high graminoid availability than areas with moderate and low graminoid availability. No starvation-related adult mortalities were observed in any of the areas.

5. *Synthesis and application*: Composition of bharal winter diet was governed predominantly by the availability of graminoids in the rangelands. My results suggest that the ability to include browse in the diet presumably moderates bharal adult mortality, but this plasticity has a cost in terms of reduced population recruitment. Since livestock grazing reduces graminoid availability, creation of livestock free areas is necessary for conservation of grazing species such as the bharal and its predators including the endangered snow leopard in the Trans-Himalaya.

1. Introduction

What determines the abundance of ungulates?, while being an important conservation question, also poses a fundamental question in ecology, *viz*. what determines the distribution and abundance of organisms? (Andrewartha & Birch 1972). Early research on large ungulate abundance mainly focused on top-down control of ungulate populations by their predators (Hairston, Smith & Slobodkin 1960). This body of work did not recognise 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). Plants can be broadly classified as graminoids (monocotyledonous) and non-graminoids (dicotyledonous) (Short 1971). Plant material consumed by herbivores is mainly composed of soluble cell contents and the cell wall (Van Soest 1982). Nutrients available to herbivore from a particular plant are determined by the ability of the herbivore to break down its chemical structure into digestible products. Due to the many inherent differences in the chemical structure of graminoids and browse, 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 Weiren (1996) has demonstrated the robustness of this classification by examining the graminoid content in the diet of 45 ungulates species. While the classification explains the graminoid content in ungulate diet, it fails to explain the seasonal variability in diet.

Plants in seasonal environments have a high degree of temporal variation in their chemical composition. Plant nutrient contents are highest during the 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. In seasonal environments some herbivores show a shift towards intermediate foraging during the lean season (*Lepus timidus* Linnaeus; Iason & Van Wieren 1999; *Pseudois nayaur* Hodgson, Mishra *et al.* 2004). In this study I examine the cause of such a dietary shift in a grazing mountain ungulate, and its effects on the population dynamics.

The high altitude regions of the Indian Trans-Himalaya are mainly dry alpine steppe regions 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 *Pseudois nayaur* Hodgson, a medium sized (*ca.*55 kg) ungulate of the sub-family Caprinae, is one of the mountain ungulates found in the high altitude Trans-Himalayan region (3000m to 6000m ASL). Bharal is the primary prey species of the snow leopard in its distributional range (Oli 1994; Bagchi & Mishra 2006). Bharal craniodental morphology suggests that the species is mainly adapted for a graminoid-dominated diet (Tempel & Vriji 2008). Five of the six previous studies on bharal have shown that graminoids form the dominant forage type in bharal diet in summer (see Shrestha, Wegge & Koirala 2005). While all these studies suggest that bharal are adapted for a graminoid diet type, studies also reported that the graminoid contribution to bharal diet drops to 50% during winter (Mishra *et al.* 2004). Thus, we are faced with two questions (I) why do bharal, seemingly adapted to graminoid diet include large amount of browse in their winter diet?, and, (II) what are the consequences of this shift in diet for bharal population dynamics?

In this paper I explore the causes of the decline in graminoids and increase of browse in the bharal diet during winter. I examine two alternate hypotheses to explain the decline of graminoids in bharal diet H1: Low graminoid availability in winter causes the bharal to include browse in their diet. H2: Bharal include browse, with relatively higher nutrition, to compensate for the poor quality of graminoids during winter. 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 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 the latter predicts that bharal populations will perform better in areas where bharal can optimise it diet quality.

I tested these predictions by comparing bharal diet composition in areas with varying graminoid availability in a semi-experimental framework. Chemical composition of all plant species contributing to bharal diet during winter was also analysed to determine nutrient content of available forage species.

2. Methods and study area

2.1. 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 the plateau on the northern banks of the Spiti River. The intensive study area had an altitudinal range from 3800 m to 5000 m. The terrain was mainly rolling hills broken occasionally by rocky cliffs and outcrops. During winters the temperature drops up to -35° C. Summer has mean maximum temperatures around 25° C. Precipitation is mainly in form of winter snow. The winter snow starts to melt around late March.

The vegetation is 'dry alpine steppe'. Very few shrubs exceed a height of one meter. 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 & Mehrotra (1994).

People of the region are mainly agro-pastoralists. Green peas, black peas (local variety of peas) and barley form the main agricultural crops. Domestic livestock include goats, sheep, horses, donkeys, cows, and yak and cow-yak hybrid. 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.

The study area consisted of three levels of livestock grazing intensity; ungrazed (reserve), a moderately grazed and heavily grazed. The ungrazed area consisted of a relatively large village reserve (15-20 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 village reserve area) and 1999 (one third of the reserve area), with bharal being the only wild ungulate therein. Among the livestock grazed areas I identified two similar adjoining pastures that differed by at least 50 % in their livestock density (Table 1). The less grazed of the two areas was used as moderately livestock grazed treatment while the other was intensely livestock grazed treatment. The treatments were adjoining each other. Because of the large size of the treatments I expect the bharal populations to have distinct identities across the treatments.

Table 1. Stocking densities of livestock in three grazing treatments in the study area

Livestock grazing pressure	Altitude (m)	Livestock grazing pressure kg km $^{-2}$		***Total area (km^2)***
		Summer	Winter	
None	3800-5000	Nil	Nil	20
Moderate	3900-4900	1326	337	34
Intense	3800-4700	2163	721	16

2.2. Methods:

2.2.1. Estimating forage availability: I estimated forage availability using biomass of grass and herbs and ground cover, during early winter between 5 and 30 December. Above ground graminoid and herb biomass was clipped from 87 randomly laid plots, each of 3 m x 3m (n=40 in un-grazed, n=30 in moderately grazed and n=17 in intensely grazed treatment). Graminoids and herbs were separated, weighed fresh and oven dried. Shrubs were not clipped. Plant height was expected to affect forage availability after events of snowfall, so I measured the tallest height of all plant species in reserve and moderately grazed treatments. A similar system of systematic plots with a random start was followed. The height of the tallest plant of each species within the plot was measured.

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.

2.2.2. Estimating diet of bharal: 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 intensive feeding site. Any species covering >10% of ground and with >50% feeding was given a score of 2, and species covering <10% of the feeding area with most individuals been fed on or species with abundant cover but with only few individuals been fed on were scored as 1, species that were not fed on were scored 0, following Mishra *et al*. (2004). (n=81 in reserve, n=122 in moderately grazed and n=170 in intensely grazed)

2.2.3. 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, Robertson & Lewis (1991).

2.2.4. Population estimation: I did a total count to assess bharal population structures across the three treatments. The census was conducted on 2nd April 2008. 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 structure was recorded. Bharal were classified as per Mishra *et al.* (2004).

2.3. Data Analysis: Each clipped plot was used as a sampling unit to calculate mean above ground forage biomass across treatments. I used each feeding site of bharal as a sampling unit to assess bharal diet. Scores for each plant species were added and divided by the sum of all the scores across all species which gave me the proportionate contribution of each plant species to bharal diet following Mishra *et al*. (2004). The 95% confidence limits for mean above ground biomass and bharal diet composition were calculated through Monte-carlo simulations. I carried out 1000 permutations with repeated draws from the observations with replacement (Krebs 1989) to calculate the parameter of interest. The percent nutrient content of bharal diet was assessed as a product of bharal diet composition and nutrient content of each plant species in bharal diet. The 95% confidence limits were calculated by assessing the nutrient content of the 1000 permutations obtained from repeated draws of bharal diet composition with replacement from the observations.

Analysis of variance (ANOVA) was used to asses the difference in the number of plant species in the diet among various treatments. Welch two sample t-test was used to asses the differences in plant heights across moderately grazed and reserve treatments.

I grouped food species into graminoids, herbs, sub-shrubs (shrubs < 50 in height) and shrubs. The groups comprised of the following species:

Graminoids: *Stipa orientalis, Elymus longe-aristatus, Carex sp.* and *Leymus secalinus*.

Herbs: *Astragalus grahamiana*, unidentified herb A (unid A), *Cousinia thomsonii, Lindelophia anchusoides*, unidentified herb B (unid B), *Bupleurum candollei*, *Ephedra gerardiana*, unidentified herb C (unid C) and *Hieracleum thomsonii.*

Shrubs: *Ribes orientale*, *Rosa webbiana*.

Sub-shrubs: *Caragana brevifolia, Eurotia ceratoides*.

I 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 i^{th} plant species in the diet is denoted by r_i and the proportion available is denoted by p_i.

Electivity index 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, I 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 one for presence in the sample. If a species was present and had been fed on by bharal then it was scored one for feeding in the sample. The proportional availability (p_i) of a particular species i was calculated as:

$p_i = x_i / y$

Where x_i is the number of sites where i^{th} 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 i^{th} plant species was foraged upon by bharal and y is the sum of v for all i

The data were pooled within plant types to calculate the electivity index for each plant type.

The difference across treatments in the ratio of yearlings to adult females (an indirect measure of population performance or fecundity) was tested through repeated sampling. I bootstrapped the census data with each herd as a sampling unit. 1,00,000 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 yearling 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 1,00,000 permutations was the probability of observing the difference due to random chance alone.

3. Results

3.1. 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 reserve, moderately grazed and intensely grazed treatments respectively (Fig. 1.a). 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 reserve, moderately grazed and intensely grazed treatments respectively (Fig 1.a). The ground cover was dominated by bare soil and rock in all the three treatments. Vegetation cover was highest in the Reserve (31.2%) followed by moderately grazed (28.37%) and intensely grazed (11.09%) treatments. Sub-shrubs dominated vegetation cover with over 90% of vegetation representation in the reserve, 76% in moderately grazed and only 26% in intensely grazed (Fig. 1.b).

Plant height data were collected on the four commonest plant species (one graminoid, one herb and two sub-shrubs) from two treatments (reserve & moderately grazed) that had similar above ground biomass. Height of *S. orientalis* (graminoid) was significantly different between reserve and moderately grazed treatments while there was no difference in the height of sub-shrubs. The mean height of *S. orientalis* (graminoid) was 10.8 and 5.5 cm in reserve and moderately grazed treatments respectively, the differences grass height across the two treatment was statistically significant (t = -3.08, P = 0.009) (Fig. 2). The differences were not significant for any other plant species, *C. brevifolia* (t = -0.94, P = 0.36), *E. ceratoides* (t = -1.49, P = 0.14), *B. candollei* (t = -0.63, P = 0.58). As a result of the taller grass (*S. orientalis*) in reserve treatment I expect the availability of graminoids to be higher in reserve treatment than in moderately grazed treatment and the least in the intensely grazed treatment.

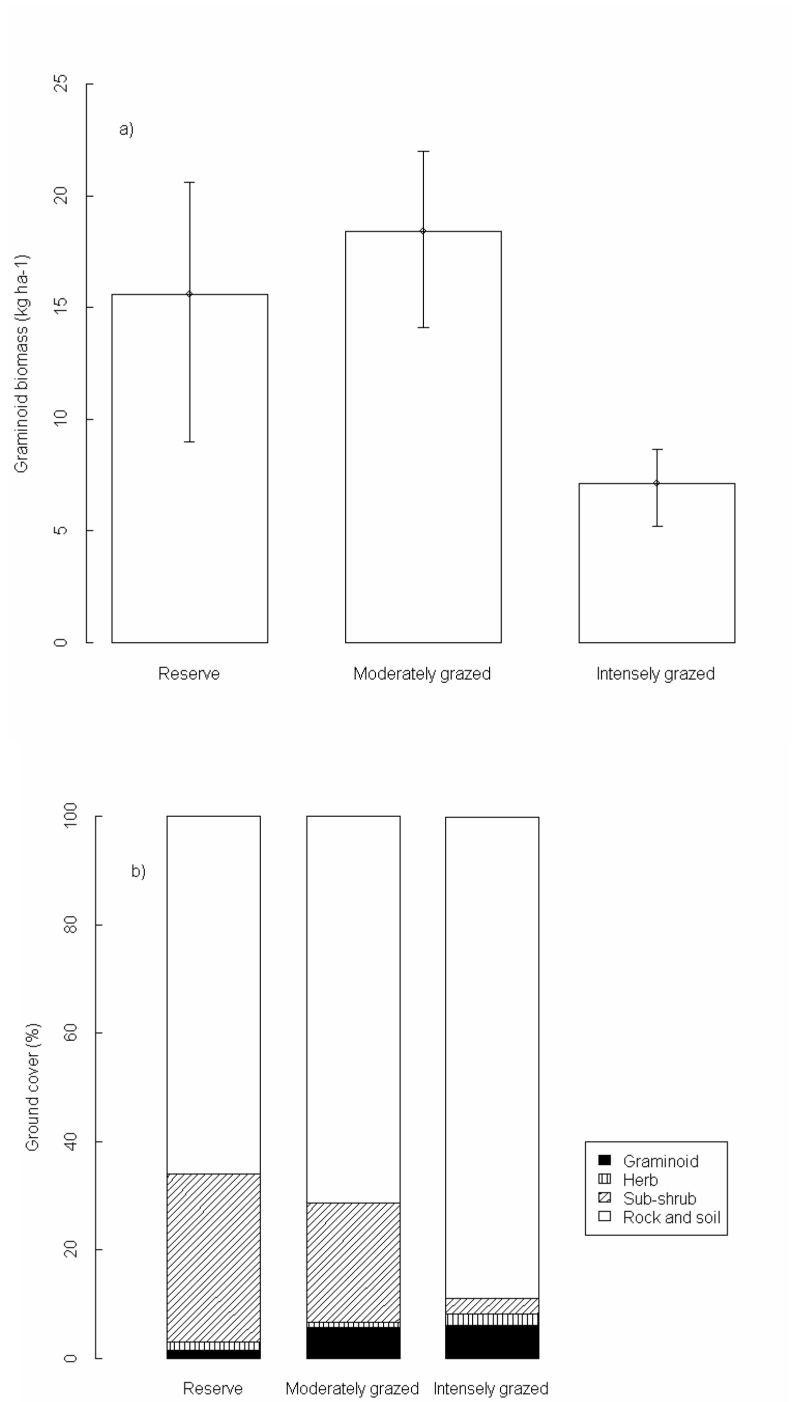

Fig.1. (a) Mean winter graminoid biomass, and (b) Percent ground cover in livestock ungrazed (reserve), moderately grazed and intensely grazed treatments during winter in Sipti, India. Error bars in (a) represent asymmetric 95% confidence limits, based on clipped plots as sampling units.

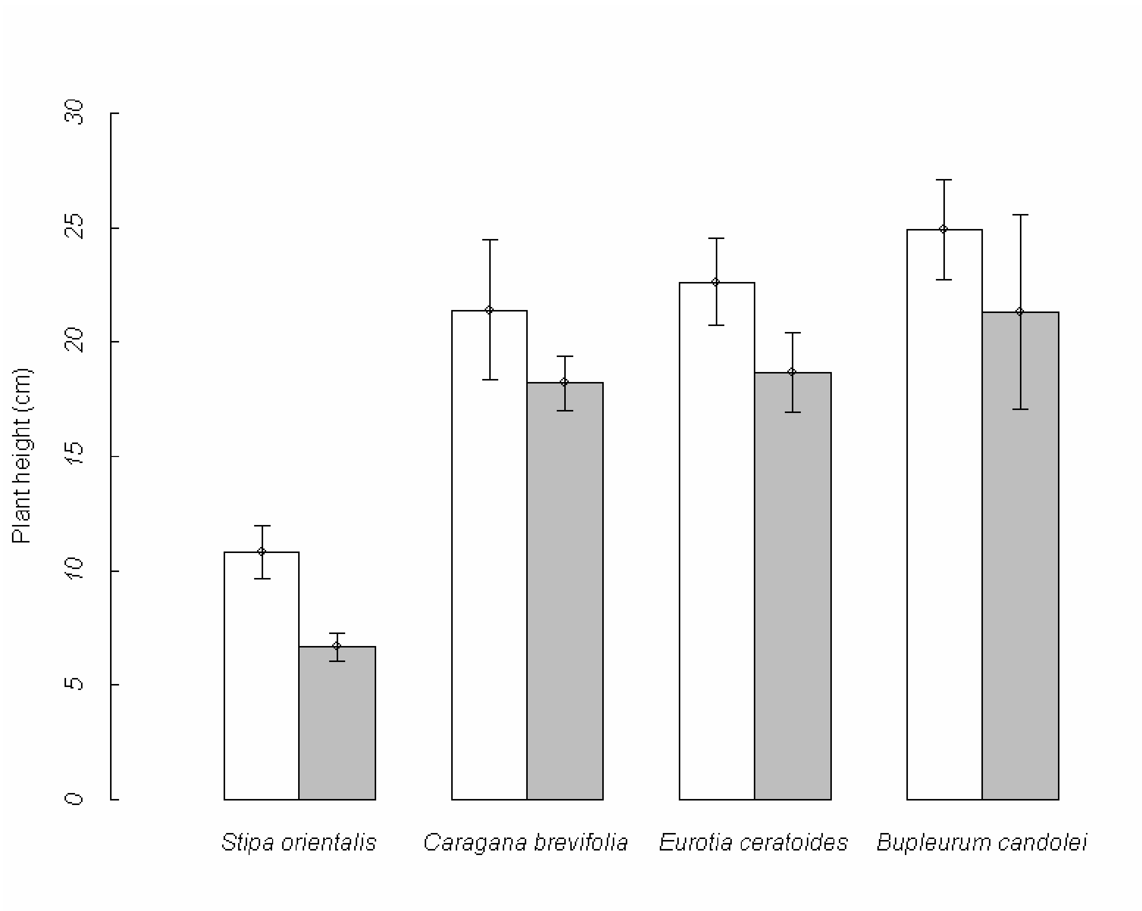

Fig.2. Mean plant height in livestock un-grazed (Reserve) and livestock moderately grazed (Moderate) treatments. White and shaded represent reserve and moderately grazed respectively. Error bars represents ± one standard error.

3.2. Chemical composition of forage plant species (Nutrients available):

Bharal winter forage plant species were analysed for seven nutritional parameters. Sub-shrubs had highest amount of crude protein but the differences were not significant. Herbs had higher ash content than shrubs and sub-shrubs but only marginally higher than graminoids. The crude fat content of all types of plants was relatively similar. Crude fibre and NDF content of shrubs was lower than other plant types. There were no significant differences among the ADF and ADL content of the four plant types (Table 2 & 3). Welch two sample t-test was used to test for significance of differences. None of the plant types differed significantly in any of the seven parameters. Altogether there was no significant difference in the nutritional quality of any of the four plant types.

Table 2. Various nutritional parameters of plants that contributed more than one percent to bharal winter diet in Spiti, Himachal Pradesh, India. Figures in the table are percent content of the particular parameter (column) per unit dry matter of the species (row). In the first column capital letter(s) following plat species name inside parenthesis denote G, Graminoids; H, Herbs; S, Shrubs; SS, Sub-shrubs.

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

Table. 3. Nutritional parameters of plants types during winter in Spiti, Himachal Pradesh, India. Figures in the table are percent dry weight content (one standard error) of the particular parameter (column) for every plant type (row).

	Total ash	Crude fat	Crude protein	Crude fibre	NDF	ADF	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)
Sub-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)

3.3. Winter diet of bharal: During the study, 34 plant species were recorded from bharal feeding sites. Twenty seven of these had been fed on at least once. Only 16 plant species contributed more than one percent each to the winter diet, which consisted of 46.2% graminoids, 17.8% sub-shrubs, 32.3% herbs and 4.4% shrubs. Graminoid contribution was highest in the reserve (74.3%), 49.7% in the moderately grazed treatment and 36.6% in the intensely grazed treatment (Fig. 3.). The proportion of herbs was equal in the reserve and in the moderately grazed area at 10%, but over 50% in intensely grazed treatment. Sub-shrubs contributed highest to the diet in the moderately grazed treatment; (40%). In the reserve a single species of grass, *S. orientalis* formed 56% of the diet.

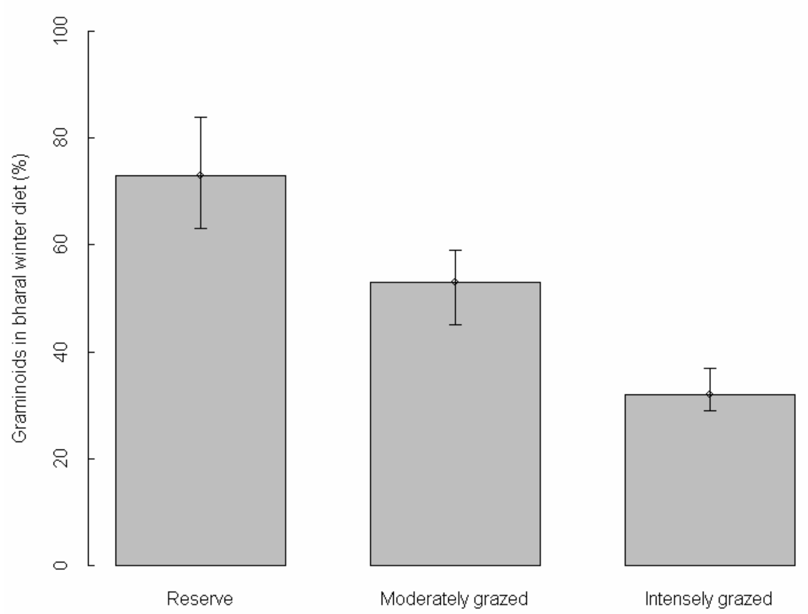

Fig.3. Winter diet composition of bharal in reserve, moderately grazed and intensely grazed treatments in Spiti, India. Error bars indicate 95% confidence limits, based on each feeding site examination as a sampling unit.

Table 4. The contribution (%) of different plant species which formed 95% of the winter diet of bharal in the livestock ungrazed reserve, moderately grazed and intensely grazed treatments in Spiti, India. G, Graminoids; H, Herbs; S, Shrubs; SS, Sub-shrubs. a- absent from the habitat

Plant species	Overall winter	Reserve	Moderately grazed	Intensely grazed
Ribes orientale. (S)	0.6	0.0	A	1.8
Astragalus grahamiana (H)	0.7	A	1.8	0.4
Unidentified herb A (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
Unidentified herb B (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
Unidentified herb C (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 (SS)	7.8	8.3	15.1	0.2
Hieracleum thomsonii (H)	8.0	1.9	5.0	17.2
Eurotia ceratoides (SS)	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

ANOVA (unequal n) for number of species available per feeding site as dependant variable and grazing treatments as fixed factors showed significant differences (d.f. = 2, $F = 5.21$, $p = 0.005$). Plants species available per feeding site were highest in the intensely grazed treatment followed by the moderately grazed treatment and reserve treatment. Similar analysis for number of species in bharal diet per sample also differed significantly (d.f. = 2, F 22.23, $p < 0.0001$). Bharal fed on greater number of species in the intensely grazed treatment than in the moderately grazed and reserve treatments.

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

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

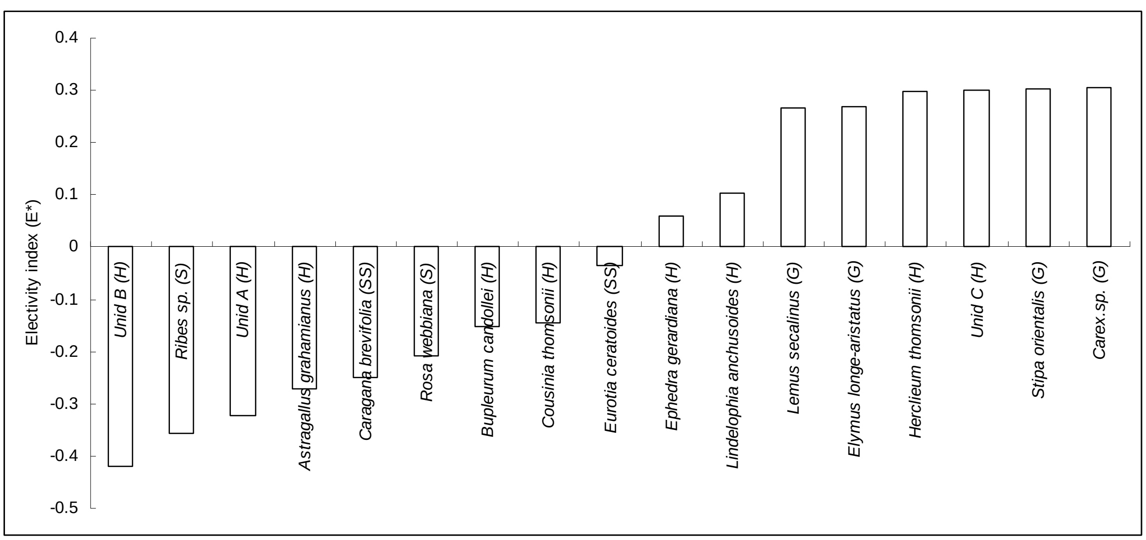

Fig.4. Electivity indices (E*) calculated following Vanderploeg and Scavia (1979) for plant species contributing more than one percent to bharal diet. Positive values indicate preference for a species while negative values indicate avoidance. Values closer to zero indicate feeding in proportion to availability. G, Graminoids; H, Herbs; S, Shrubs; SS, Sub-shrubs.

3.4. Nutrient contents of bharal winter diet:

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

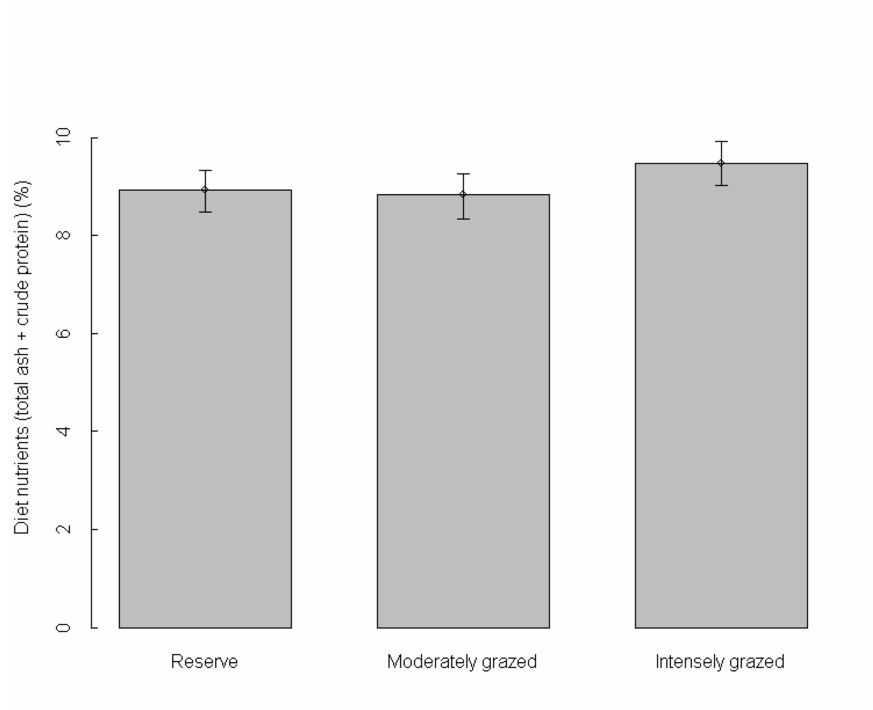

Fig.5. Percent nutrient (total ash + crude protein) content of bharal diet during winter across livestock ungrazed, livestock moderately grazed and livestock intensely grazed treatments in Spiti, Himachal Pradesh. Error bars represent 95% confidence limits calculated based on each feeding site as a sampling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

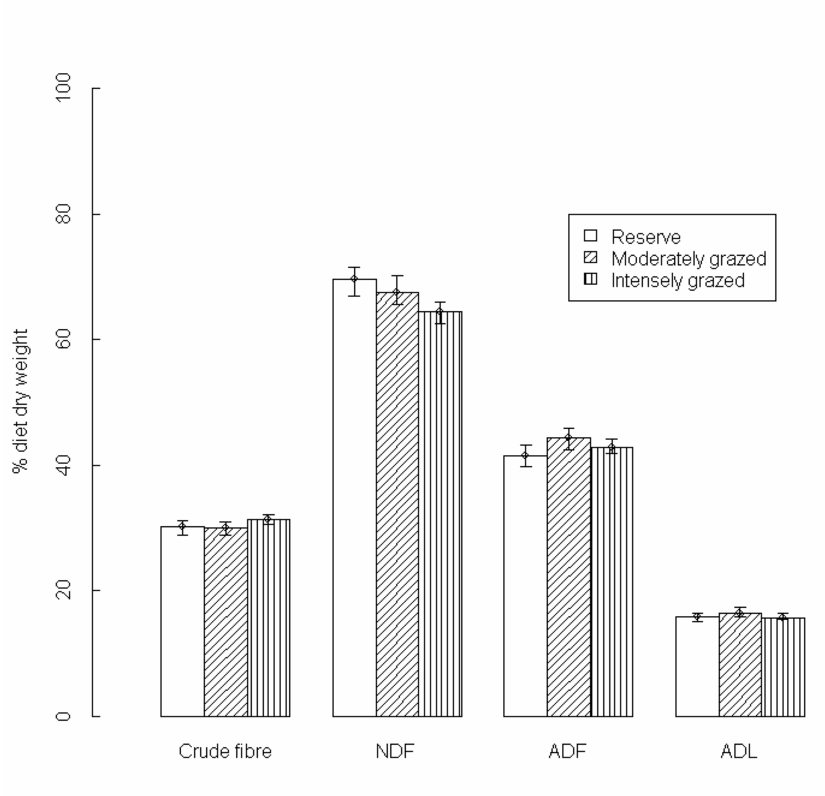

Fig.6. Crude fibre, Neutral detergent fibre (NDF), Acid detergent fibre (ADF) and Acid detergent lignin (ADL) content in bharal diet during winter in Spiti, Himachal Pradesh. Error bars represent ± one standard error.

3.4. Population structure: The yearling to adult female ratio was 0.9, 0.24 and 0.28 in the reserve, moderately grazed and intensely grazed treatments respectively. The difference between the reserve and other two treatments was significant ($p < 0.0001$; bootstrap, 100,000 permutations). The difference between the yearling to female ratio across moderately grazed and intensely grazed treatments was not significant (Table 5).

Table 5. Population structure of bharal *Pseudois nayaur* in livestock ungrazed, moderately grazed and intensely grazed rangeland in Spiti, Indian Trans-Himalaya. Figures in parenthesis in the first row are the number of herds of bharal recorded in the respective treatment.

	Reserve (7)	Moderately grazed (7)	***Intensely grazed (6)***
Adult females	21	21	36
Yearlings	19	5	10
Class I to IV male	17	31	48
Yearling 100 females $^{-1}$	90	24	28
Total	57	57	94

4. Discussion

I tested the predictions of two alternative hypotheses to explain the decline of graminoids in bharal diet during winter. My results were in agreement with the prediction of the hypothesis that low graminoid availability during winter causes bharal to include more browse in their diet during winter. I did not find any support for the hypothesis that bharal include browse, with relatively higher nutrition, to compensate for the poor quality of graminoids during winter.

Forage availability: The graminoid above-ground biomass was similar in the livestock ungrazed reserve and the moderately livestock grazed treatments, and lowest in the intensely grazed treatment. Yet, there were other factors such as plant height and vegetation cover that affected the availability of graminoids for bharal after snow fall. Bharal do not dig craters in the snow (personal observation) and fed largely on the vegetation that was exposed out of the snow. Emergence of a plant from the snow depended on two factors: 1. Height of the plant; 2. Percent vegetation cover of the region. Grass (*S. orientalis*) was double its height in the reserve treatment than in the moderately grazed treatment. No other plant species differed significantly in height across the two treatments. Vegetation cover was also higher in the reserve treatment. Thus I conclude that during winter (after snow fall), when most of the diet sampling was carried out, graminoid availability (especially *S. Orientalis*) was highest in the reserve treatment.

Forage quality: The results show that the differences in the nutrient quality across plant types during winter were not significant. Selection of graminoids in such a scenario 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*; sub-shrub and *L. anchusoides*; herb) was below maintenance level (<5% crude protein; estimated for *Ovis Canadensis* Shaw (Hebert 1976 in Goodson, Stevens & Bailey 1991), and thus I expect bharal to be losing weight during winter, even in areas that were rich in their preferred forage type, the graminoids.

Bharal diet: My results were in agreement with the hypothesis that low graminoid availability causes bharal to include browse in their diet, as bharal diet in winter 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 the diet. The selection for graminoids by bharal in spite of their relatively lower crude protein, and moderate ash content indicates that nutritional levels of plant types had little influence on bharal winter diet selection. These results suggest that the availability of graminoids determines bharal diet composition, and the quality of non-graminoids does not have a significant effect in determining the winter diet of bharal. The high positive electivity index for graminoids and the influence of graminoid presence on the electivity index for other plant types indicate that bharal preferred graminoids to any other plant type.

My results show that bharal while remaining dependent on graminoids, also have the plasticity to be able to utilise other forage types 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 during winter (Iason & Van Wieren 1999). Feeding plasticity could be important for herbivores in areas with unpredictable weather affecting forage availability. High snowfall even over short durations usually covers up most graminoids, making them inaccessible for bharal. Plasticity to include other plant types in the diet in such condition can thus positively affect survival.

Although my results show that the nutrient quality of bharal diet was uniform across the three treatments, my data do not include digestibility of the plant species. Bharal, being a grazer, is expected to have lower physiological ability to digest or utilise digested non-graminoids due to the presence of secondary chemical compounds in them. Therefore, bharal efficiency at utilising the available nutrients is expected to be lower for a non-graminoid diet. Thus, I expect the amount of nutrients obtained by bharal to be lower in areas with low graminoid availability due to the higher proportion of browse in the diet which could be the possible cause of the lower yearling to female ratio in these areas. There is a possibility that availability of graminoids also affects the intake rate of bharal but I have not examined this in my study.

Population performance: The yearling to female (Y:F) ratio (population performance) in the livestock in the ungrazed reserve treatment was three times higher than in the other two treatments. This indicates high fecundity and first year survival for bharal in this treatment. These results, while being consistent with my hypothesis that low graminoid availability causes bharal to include non-graminoid in their diet, are also consistent with previous studies showing suppression of fecundity (Mishra, Prins & Wieren 2001; Mishra *et al*. 2004) and survival of young of bharal due to reduced forage availability in areas with high livestock densities (Gaillard *et al.* 1998).

Conclusion: Hofmann (1989) first classified ungulates based on their morphological and physiological adaptations which he suggested were profitable for feeding on graminoids and browse. 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, Spalinger & Van Hoven 1995).

Hofmann (1989) suggested that herbivores showing adaptation for a specific forage type (graminoids or browse) should prefer to feed on the same forage type. My study shows that bharal prefer graminoids, which is consistent with the craniodental adaptations of the species (Tempel *and* Vriji 2008) and its summer diet (Mishra *et al*. 2004; Shrestha *et al*. 2005) which suggests bharal to be a grazer.

Since I did not observe any starvation related adult mortality in bharal, which is not reported by other studies either (Mishra *et al.* 2004), I expect feeding plasticity to be important for adult survival in areas with unpredictable weather affecting forage availability. On the other hand, my data show that the change in the diet shown by a grazer such as the bharal (to include more browse) may have its costs in the recruitment of the population. The yearling to female (Y:F) ratio (a measure used to quantify population performance) in the livestock ungrazed (reserve) treatment was three times higher than the other two treatments (moderately & intensely grazed). This result brings to light the potential importance of graminoid availability in influencing fecundity and first year survival of bharal.

The below-maintenance level nutrient quality of forage during winter (lean season) observed in my study also emphasises the role of fat accumulation during summer (productive season) in temperate and alpine species such as the bharal. Fat reserves acquired during summer, together with winter diet and nutrition, are the major factors determining body weight of bharal during winter (the gestation period). Female weight during pregnancy (winter for bharal) is know to be an important determinant of the birth weight of the young (born just at the end of winter; late April- early May) (Illius & Gordon 1999). As survival of young through the first year is related to its weight at birth (Clutton-Brock *et al.*1987; Loison, Langvatn & Solberg 1999) winter nutrition available for females is expected to be a key factor in determining the first year survival neonate bharal. Thus while diet plasticity seems to increase adult bharal survival, inclusion of browse in the diet presumably compromises the fecundity and the first year survival of bharal.

Conservation implications: The Trans-Himalayan and Tibetan grassland system are one of the largest grazing systems of the world (the Tibetan rangeland being over 130 million ha; Miller 2002). This region supports over ten species of wild ungulates and five species of large carnivores (Schaller 1998) making it an extremely important conservation area. This region also has a livestock grazing history of over three millennia (Mishra *et al.* 2003; Miller 2002). Over 39 million people depend on these rangelands on the Tibetan plateau alone (Miller 2002).

Three of the seven species of livestock of the region are predominantly grazers while the rest are predominantly intermediate feeder (at least 50% graminoid in diet) (Mishra *et al.* 2004). At least six of the ten species of wild ungulates also mainly feed on graminoids (Miller & Schaller 1996). Enhancing of graminoid availability in key bharal areas, by removal of livestock grazing pressure is likely to lead to increase in bharal population by influencing its fecundity and recruitment.

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Appendix 1: The relevance of the nutritional parameters estimated for bharal forage species

Nutritional parameter	Represents	Importance for ungulate foraging	Method of estimation
Total Ash	Macro minerals required in relatively large amounts by ungulates. Include calcium (Ca), phosphorus (P), magnesium (Mg), potassium (K), chlorine (Cl), sulphur (S) and sodium (Na). Micro (or Trace) Minerals: Minor minerals required in very small amounts. Includes manganese (Mn), copper (Cu), zinc (Zn), selenium (Se), iron (Fe), cobalt (Co), iodine (I) and fluorine (Fl).	Total ash represents the sum of all the different minerals present in the forage. Herbivores, like all organisms, need a certain amount of these minerals for various metabolic functions.	AOAC (1990)
Crude fat	Measured as ether extract, it represents the total amount of fat in the plant	One of the sources of energy for herbivores.	AOAC (1990)
Crude protein	An estimate of the total protein content of forage; calculated as the product of Total nitrogen (N) and 6.25; Crude protein includes true protein and other nitrogen-containing substances such as ammonia, amino acids, nitrates.	N being the most important component animal tissue forms the most important component of forage. Herbivores are limited by minimum levels of crude protein below which they spend more energy trying to digest the small quantity N and lose weight in the process.	(Kjeldahl nitrogen × 6.25) AOAC (1990)
Crude fibre	Represents the total amount of fibre present in the forage	Fibre content is negatively related to digestibility.	AOAC (1990)
Neutral detergent fibre (NDF)	Complex carbohydrates including cellulose, hemicellulose, lignin and pectin that form the plant cell wall. Non-lignified	Total forage intake is negatively related to NDF. Most ungulates can consume only up to	Van Soest, Robertson & Lewis (1991)

	cellulose can be digested by the gut microbial flora. Hemicellulose is partially digestible. Lignin is completely indigestible.	1.2% NDF of their total body weight.	
Acid detergent fibre (ADF)	Primarily cellulose, lignin and variable amounts of silica	Acid detergent fibre (ADF) is the less digestible fibre portion of the forage. The higher the ADF level, the lower the energy.	AOAC (1990)
Acid detergent lignin (ADL)	Represents the total lignin content of the plant sample. Lignin is a polyphenolic component of cell walls that impart mechanical strength to the plant tissue	Lignin is the prime factor influencing the digestibility of plant cell wall material. Increase in lignin usually causes decrease in digestibility, intake, and animal performance.	AOAC (1990)