Journal of Applied Ecology 2004
41, 344–354

Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya

CHARUDUTT MISHRA*†, SIPKE E. VAN WIEREN*, PIETER KETNER*, IGNAS M. A. HEITKÖNIG* and HERBERT H. T. PRINS*

**Tropical Nature Conservation and Vertebrate Ecology Group, Department of Environmental Sciences, Wageningen University, 69 Bornsesteeg, 6708 PD Wageningen, the Netherlands; and †International Snow Leopard Trust (India Program), Nature Conservation Foundation, 3076/5, IV Cross Gokulam Park, Mysore 570002, India*

Summary

1. The issue of competition between livestock and wild herbivores has remained contentious. We studied the diets and population structures of the mountain ungulate bharal *Pseudois nayaur* and seven species of livestock to evaluate whether or not they compete for forage. The study was conducted in the high altitude Spiti Valley, Indian Trans-Himalaya.

2. We compared resource (forage) availability and bharal population structures between rangelands differing in livestock density. Forage availability was estimated by clipping the standing graminoid biomass in sample plots. Livestock and bharal population structures were quantified through annual censuses. Seasonal diets of livestock were studied by direct observations, while those of bharal were quantified through feeding signs on vegetation.

3. We found that livestock grazing causes a significant reduction in the standing crop of forage. Graminoid availability per unit livestock biomass was three times greater in a moderately grazed rangeland compared with an intensively grazed one.

4. There was considerable diet overlap among the herbivore species. In summer, bharal, yak *Bos grunniens*, horse *Equus caballus*, cow *Bos indicus*, and *dzomo* (yak–cow hybrids) fed predominantly on graminoids, while donkey *E. asinus*, sheep *Ovis aries*, and goat *Capra hircus*, consumed both graminoids and herbs. The summer diet of bharal was a subset of the diets of three livestock species. In winter, depleted graminoid availability caused bharal, yak and horse to consume relatively more herbs, while the remaining livestock species fed predominantly on graminoids. Diet overlap was less in winter but, in both seasons, all important forage species in the bharal diet were consumed in substantial amounts by one or more species of livestock.

5. Comparison of the population structures of bharal between two rangelands differing in livestock density by *c*. 30% yielded evidence of resource competition. In the intensively grazed rangeland, bharal density was 63% lower, and bharal population showed poorer performance (lower young : adult female ratios).

6. *Synthesis and applications*. High diet overlap between livestock and bharal, together with density-dependent forage limitation, results in resource competition and a decline in bharal density. Under the present conditions of high livestock density and supplemental feeding, restricting livestock numbers and creating livestock-free areas are necessary measures for conserving Trans-Himalayan wild herbivores. Mediating competitive effects on bharal through supplemental feeding is not a feasible option.

Key-words: blue sheep, diet, grazing, rangeland, resource, ungulate, wildlife

Journal of Animal Ecology (2004) **73**, 344–354

Correspondence: Charudutt Mishra, Nature Conservation Foundation, 3076/5, IV Cross Gokulam Park, Mysore 570002, India (fax +91 8212513822; e-mail charu@ncf-india.org)

Introduction

Livestock grazing impacts on native wildlife are an important conservation concern globally (Prins 1992; Fleischner 1994; Noss 1994; Voeten 1999). This is especially true in India, which supports the world's largest livestock population (520 million; FAO 2002) that is still increasing (6% increase between 1984 and 1994; WRI 1996). Wildlife reserves cover less than 5% of India's area, and even these are not free from human and livestock impacts. More than 3 million people are estimated to live inside wildlife reserves in India, with livestock grazing being among the most widespread forms of land use (an estimated three-fourths of Indian wildlife reserves support livestock populations; Kothari *et al*. 1989). There have been few attempts to evaluate livestock grazing impacts on native wildlife. Consequently, the debate on what kind of impacts local human resource use has on native wildlife remains ill-informed. The debate on whether local human use of wildlife reserves should be modified, curtailed or encouraged continues to be fuelled by activism rather than by ecology (Mishra & Rawat 1998).

The arid Trans-Himalayan region is spread over 2·6 million km^2, covering the Tibetan plateau and the Tibetan marginal mountains in the rain shadow of the Greater Himalayan range. Most of the region has a pastoral history dating back several millennia (Handa 1994; Schaller 1998). The region also supports a unique wildlife assemblage, including a diverse and endemic large wild herbivore assemblage. This includes globally threatened species such as the wild yak *Bos grunniens* Linnaeus, chiru *Panthalops hodgsoni* Abel and Tibetan gazelle *Procapra picticaudata* Hodgson. Little is known about the diets of either livestock or wild herbivores (but see Harris & Miller 1995). Thus, our understanding of the impacts of livestock on wild herbivores is very limited and, consequently, so is our ability to manage effectively Trans-Himalayan wildlife.

Spiti Valley in the Indian Trans-Himalaya spans an area of 12 000 km^2 and has a pastoral history of more than 3 millennia (Handa 1994). Earlier studies have reported that more than four-fifths of the rangelands in Spiti Valley are currently overstocked, i.e. grazed at such high livestock density that livestock production becomes compromised (Mishra, Prins & Van Wieren 2001). Adult female livestock in these overstocked rangelands show a much lower performance than those grazing in rangelands at lower stocking density, presumably due to density-dependent reduction in resource availability (Mishra 2001; Mishra, Prins & Van Wieren 2001). Livestock populations are maintained beyond points of natural resource limitation through supplemental feeding (Mishra 2001). The impact of this high density of livestock on Trans-Himalayan wild herbivores is unknown. In a theoretical analysis, we deduced that up to four species of wild herbivores might have been driven to extinction in Spiti over the last 3 millennia due to competitive exclusion by livestock (Mishra *et al*. 2002). The impact that livestock has on the remaining wild large herbivores remains unexplored.

Spiti Valley supports three species of wild medium- to large-sized herbivores: hare *Lepus oiostolus* Hodgson, bharal or blue sheep *Pseudois nayaur* Hodgson and ibex *Capra ibex* Linnaeus (Mishra *et al*. 2002). All available rangelands are grazed by livestock and, consequently, at the rangeland level, there is complete spatial overlap in areas used by livestock and wild herbivores. For instance, all our sightings of bharal in the 31-km^2 intensive study area have been in areas where we have also recorded livestock grazing. Given complete spatial overlap and a high stocking density, we sought to determine whether the extant wild herbivores and livestock compete for food. In this study, we first compared the above-ground graminoid biomass between two adjacent rangelands differing in livestock biomass density, to evaluate if variation in livestock density is associated with variation in resource availability. We then described the diet composition of seven species of livestock and the bharal, which is the most abundant large wild herbivore in the area. We analysed the extent of resource (diet) overlap amongst these various species.

Most studies of large herbivore assemblages have been criticized for falling short of actually demonstrating resource competition, and have been observed to 'merely describe patterns of resource use and partitioning among sympatric species' (Putman 1996; Prins 2000). After evaluating diet overlap, we moved a step further and asked if this overlap actually translates to competition for food between wild herbivores and livestock. Density-dependent decline in forage availability is known to affect reproductive performance in ungulates (Clutton-Brock, Guinness & Albon 1982). Forage availability influences the body condition of females and consequently their fecundity (Clutton-Brock, Guinness & Albon 1982; Skogland 1983; Leader-Williams 1988). Further, there is evidence for density-dependent mortality in neonates and calves (Sæther 1997; Clutton-Brock, Guinness & Albon 1982). We analysed the population structure of bharal in two rangelands differing in livestock stocking density in order to test whether or not they compete for food. We tested two simple predictions. If and when bharal and livestock compete for resources: (i) the density of bharal will decrease with increasing livestock density, and (ii) bharal population performance (young : adult female ratios) will decrease with increasing livestock density.

Materials and methods

Study site

The 186 000 km^2 of the Indian Trans-Himalaya includes parts of both the Tibetan plateau and the Tibetan marginal mountains, immediately north of the Greater Himalayan range. The Spiti region (33°35′–33°0′ N, 77°37′–78°35′ E) in the catchment of the River Spiti is a part of the Trans-Himalayan Lahaul and Spiti district of the Himachal Pradesh state. It is flanked by Greater Himalaya in the south, Ladakh in the north, and Tibet in the east. Agropastoral communities have inhabited the region for more than 2–3 millennia. Parts of Spiti are visited in summer by transhumant pastoralists from Ladakh for barter trade and from the Greater Himalaya for grazing. The livestock assemblage in Spiti includes yak, cattle, cattle–yak hybrids (males and females called *dzo* and *dzomo*, respectively; of the two, our intensive study site only had *dzomo*), horse, donkey, sheep and goat. Livestock grazing occurs in the pastures during most of the year except in the extreme winter. The livestock diet is supplemented by stall feeding in winter. Large carnivores include snow leopard *Uncia uncia*, wolf *Canis lupus* and red fox *Vulpes vulpes* (Mishra 2001). Agricultural and rangeland primary production is limited to the short growing season between May and September. Lying in the rain shadow of the main Himalayan range, the region is cold and arid, with most of the precipitation in the form of snow. The tree layer is absent in these steppe rangelands. The shrub layer is formed by *Caragana* sp. and, to a lesser extent, by *Rosa*, *Potentilla* and *Lonicera* spp. (Mishra 2001). Botanical nomenclature in this paper follows Aswal & Mehrotra (1994). Plant cover is sparse, and the vegetation rarely exceeds a height of 1 m. Several species of herbs and graminoids such as *Stipa*, *Festuca* and *Carex* grow interspersed with the shrubs, rarely exceeding 25–50 cm in height.

DATA COLLECTION

Forage availability

We compared graminoid biomass between two adjacent rangelands differing in livestock biomass density (Table 1). Three years of monitoring (1998–2000) had established that between these two rangelands, livestock in the moderately grazed area showed a much better performance compared with those in the intensively grazed area (Mishra, Prins & Van Wieren 2001). Here, we asked if the variation in livestock density in these rangelands translates into a difference in forage availability.

We clipped above-ground graminoid biomass from 123 plots covering a total of 1434 m^2 spread across the vegetation types in the intensively and moderately grazed rangelands. The plot sizes ranged from 0·0625 to 25 m^2 depending upon the heterogeneity of vegetation and abundance of graminoids. In each dominant vegetation type, plots were distributed randomly (for details on vegetation types see Mishra 2001). In the case of tussock grasses (*Festuca* sp.), we derived a relationship between grass cover and standing biomass (mean biomass ± SD for 100% cover = 2772 ± 1731 kg ha^{-1}). Point intercept transects (50–250 points) were distributed across the vegetation to estimate tussock grass cover, and the derived relationship was used to calculate mean grass biomass. All clippings were done in July–August (2000), the months when vegetation is at its maximum standing biomass. With the aid of a Leica Vector rangefinder (Leica Geosystems, USA), we estimated the total area covered by each of the vegetation types, and thereby estimated the availability of graminoids in the moderately and intensively grazed rangelands. The details of vegetation composition and biomass can be found in Mishra (2001). Here, we restricted our focus to providing an estimate of the graminoid biomass available to livestock in the moderately and intensively grazed rangelands.

Diet

The diet of livestock was recorded through direct observation. Livestock herds were followed to the pastures, and an animal of a given species was selected at random from the herd. This animal was followed continuously while feeding for 15 min, and every 10 seconds the plant species being fed upon was recorded. After the 15-min sample, of approximately 90 bites, we chose another animal of a different species and repeated the procedure. Observations were spread across summer and winter, and across pastures. For bharal, direct observations were not possible as the animals did not allow close approach. We searched for bharal herds and, after locating them, waited until the herd had fed and gradually moved away. We then visited the feeding area and, from feeding signs, recorded which species were fed upon heavily (forming more than 10% plant cover, with most individuals having been fed upon) and

Table 1. Characteristics of rangelands with varying livestock density in Spiti, Indian Trans-Himalaya. On the left are two adjacent rangelands the graminoid biomasses of which were compared. We had earlier established that livestock in the intensively grazed rangeland showed reduced performance compared with the moderately grazed one (Mishra, Prins & Van Wieren 2001). On the right are two distant rangelands the bharal populations of which were compared

	Graminoid biomass		Bharal	
Treatment	Moderately grazed	Intensively grazed	Moderately grazed	Intensively grazed
Altitudinal range (m)	4300–4600	4200–4600	3600–4300	4200–4900
Distance between compared rangelands	Adjoining		40 km	
Area of rangelands (km^2)	5	15	14*	31
Biomass of livestock (kg) (1998 census)	6637 (herded livestock)	38510 (herded livestock)	33432	95851
Biomass density of livestock (kg km^{-2})	1327	2567	2157	3091

*Area available to both bharal and livestock. The latter had another 1·5 km^2 available for grazing that was inaccessible to bharal.

which ones were fed upon moderately (either plants that formed less than 10% cover with feeding signs, or those that were abundant but only a few plants had signs of feeding). These were given scores of 2 and 1, respectively.

Population structure

We selected two rangelands differing in livestock biomass density and compared their bharal population structures (Table 1). We ensured that these rangelands were neither too close (to ensure the distinct identities of the bharal populations) nor too far (to control for habitat differences). We determined the populations (structure) of all species of livestock and bharal (as defined in Table 2) grazing within these rangelands. This was done through field surveys for bharal, and a livestock census of all families grazing their livestock in these rangelands. Field surveys for bharal were conducted during periods of congregation, at the beginning of winter (November–December 1998) and the end of winter (April–May 2000). Bharal were located from horseback, on foot or from an all-terrain vehicle. They were then approached within 100 m on foot, counted and classified. All snow-free slopes were searched. Care was taken to avoid repeated counts of the same individuals.

In our comparisons of bharal populations as well as those of above-ground graminoid biomass, we designated the rangeland with lower livestock density as 'moderately grazed' and the rangeland with higher livestock density as 'intensively grazed'. We would like to note that this was done for simplicity, the classification being only relative (within the pair of rangelands being compared) and not absolute.

DATA ANALYSES

The mean graminoid biomass and asymmetric 95% confidence intervals were calculated through Monte Carlo simulations (500 permutations using random draws from the observed distribution with replacement; Krebs 1989). The number of plant species eaten per sample by different herbivores and across seasons was compared using ANOVA with unequal replication, and Tukey's honest significant difference tests were employed for within-season *post-hoc* comparisons of the number of species eaten (Zar 1984). The representative seasonal diet for each herbivore was obtained by averaging across replicate samples, i.e. first the proportion that each plant species contributed in each sample was calculated, and then these proportions were averaged across all the samples for a given herbivore in a given season. For bharal we calculated the average diet in two ways. We first ignored the scores assigned to each plant species and used presence/absence (if a species was eaten, it was recorded as 1 irrespective of how intensively it was fed upon) data for plant species across samples for a given season to calculate their contribution to the diet. We then repeated the exercise with the species scores (frequently eaten species being considered twice as important as moderately eaten ones). The average diet obtained from both methods was highly correlated (Pearson's $R = 0{\cdot}97$ in summer and 0·99 in winter; Zar 1984), and we have presented the latter in this paper. Individual species' niche breadth was assessed using Levins' measure, $B = 1/\Sigma p_i^2$ where p_i is the proportion of diet contributed by plant species i (Levins 1968). This was standardized to a scale of 0–1 following Hurlbert (1978), $B_s = (B - 1)/(n - 1)$ where n is the total number of plant species. The total number of species eaten at least once by at least one herbivore in a given season was used to calculate the index.

Overlap in diet of different pairs of species was assessed using the MacArthur & Levins' (1967) index, $O_{jk} = \Sigma p_{ij}p_{ik}/\Sigma p_{ij}^2$, where O_{jk} is the niche overlap of species k on species j, and p_{ij} and p_{ik} represent the proportions that a plant species i contributes to the diets of herbivores j and k. This is an asymmetrical index that, for any given pair of species, separately estimates the extent to which the diet of the first overlaps on the second and the second on the first. In fact, the widely used Pianka's (1973) index is a geometric mean of the two values of MacArthur and Levins' index that characterize any given pair (Krebs 1989). For our purpose, we found the MacArthur & Levins' index (MacArthur & Levins 1967) to be superior because it takes into account the fact that if the diet of the first species of a pair of herbivores is a subset of the diet of the second then, from the point of view of the former, overlap is total, but only partial from that of the second. The Pianka's index (Pianka 1973), on the other hand, gives a single value of overlap for any pair. For each species, Wilcoxon's signed ranks tests were used to test for significant differences in the distribution

Table 2. Summary of age–sex classes (in months) of herbivores as defined in this study

Species	Young	Sub-adult	Adult female	Adult male			
Goat	≤ 6	6–18	> 18	> 18			
Sheep	≤ 6	6–18	> 18	> 18			
Donkey	≤ 12	12–36	> 36	> 36			
Cow	≤ 12	12–36	> 36	> 36			
Dzomo	≤ 12	12–36	> 36	> 36			
Horse	≤ 12	12–36	> 36	> 36			
Yak	≤ 12	12–36	> 36	> 36			
		Yearling		Class I	Class II	Class III	Class IV
Bharal *Pseudois nayaur*	≤ 6	6–18	> 18	18–48	48–72	72–96	> 96

of values of its diet overlap on other species, and of each of the others on the species itself (Zar 1984).

Results

FORAGE AVAILABILITY

The estimated graminoid availability for livestock in the moderately grazed rangeland was 535 kg ha^{-1} (95% confidence limits 434–632 kg ha^{-1}), and 134 kg ha^{-1} (97–194 kg ha^{-1}) in the intensively grazed one (Fig. 1). The overall availability of graminoids was 20·0 kg (13·8–26·8 kg) kg^{-1} of herded livestock in the moderately grazed rangeland, compared with 7·6 kg (6·0–11·8 kg) kg^{-1} of livestock in the intensively grazed rangeland (Fig. 1).

DIETARY PROFILE

Yak

Yaks were recorded feeding on 19 species in summer and 13 species in winter. More than 90% of their diet comprised graminoids in summer (10% herbs), with several graminoid species contributing to the diet (Table 3). In winter, they increased their consumption of herbs (58% graminoids, 36% herbs and 6% shrubs; sample sizes in parentheses in Table 3), although graminoids *Carex melanantha* and *Elymus longe-aristatus* still formed the bulk of the diet.

Horse

Horses were recorded feeding on 29 species in summer and 14 species in winter. They predominantly fed on graminoids in summer (81% graminoids, 17% herbs and 2% shrubs), with several graminoid species contributing to the diet. In winter, like yaks, horses consumed relatively more herbs (54% graminoids, 35% herbs and 11% shrubs). While *E. longe-aristatus* was an important component of the diet in both seasons, the contribution of *Stipa orientalis* increased substantially in winter.

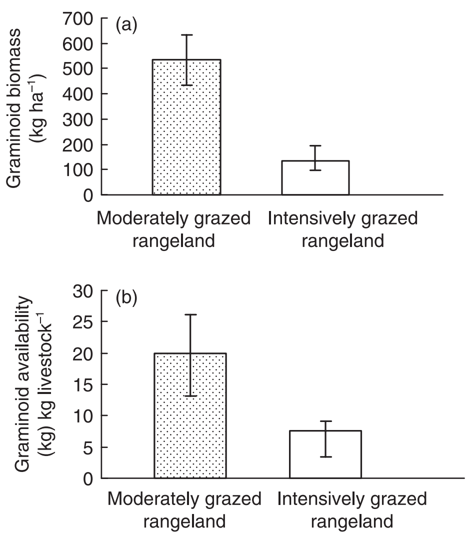

Fig. 1. Mean graminoid biomass in moderately and intensively grazed rangelands in Spiti, Indian Trans-Himalaya. Error bars represent asymmetric 95% confidence limits, based on clipped plots as sampling units. (a) Graminoid biomass in kg ha^{-1}. (b) Graminoid biomass (in kg) per unit livestock biomass (kg).

Dzomo

Dzomo fed on 23 species in summer and seven in winter. They predominantly fed on graminoids in both summer (80% graminoids, 18% herbs and 2% shrubs) and winter (84% graminoids, 13% herbs and 3% shrubs). *Leymus secalinus* and *E. longe-aristatus* together contributed substantially to *dzomo* diet in summer, while in winter *E. longe-aristatus* alone formed the bulk of the diet (Table 3). The importance of *C. melanantha* in the diet increased in winter.

Cow

Cows were recorded feeding on 26 species in summer and seven species in winter. Among these, *E. longe-aristatus* contributed highly to the diet in both summer and winter. The contribution of *Stipa orientalis* and *Carex* spp. in the diet increased markedly in winter. Graminoids contributed 75% of the diet in summer and 80% in winter (herbs and shrubs, respectively, contributed 21% and 3% in summer, and 15% and 5% in winter).

Donkey

Donkeys fed on 31 species in summer and eight species in winter. They fed on both graminoids and herbs in summer (61% graminoids, 30% herbs and 9% shrubs), with several species contributing to the diet. In winter, however, donkeys fed mostly on graminoids (86% graminoids, 14% herbs and no shrubs), with *E. longe-aristatus* alone contributing more than 40% to the diet.

Sheep

Sheep were recorded feeding on 32 species in summer and 12 species in winter. They had a mixed diet in summer (51% graminoids, 48% herbs and 1% shrubs). Several species contributed to the summer diet, but none of them formed the bulk of the diet. In winter, however, sheep largely fed on graminoids, with *E. longe-aristatus* forming the bulk of the diet (82% graminoids, 18% herbs). Sheep, together with goats, had the widest diet breadth in summer (Fig. 2).

Goat

Goats were recorded feeding on 26 species in summer and 14 species in winter. Their diet was similar to sheep in that they fed on both graminoids and herbs in summer (55% graminoids, 42% herbs and 3% shrubs), with no single species forming the bulk of the diet (Table 3).

Table 3. Diet profiles of herbivores in Spiti, Indian Trans-Himalaya. The figures indicate percentage contribution of each plant species to the average diet of each herbivore (sample sizes used to derive the average diet in parentheses, each sample equals approximately 90 bites). The table is simplified in that only species contributing more than 3% to the diet of any herbivore are mentioned. Those contributing less are combined into the others category (last row). Therefore, blank spaces imply either 0% or up to 3% contribution. In the first column the capital letters following species names denote G, graminoid; H, herb; S, shrub

	Yak	Horse	*Dzomo*	Cow	Donkey	Sheep	Goat	Bharal
Summer	(24)	(23)	(12)	(13)	(25)	(13)	(14)	(48)
Elymus longe-aristatus G	16·3	17·9	21·3	23	13·8	11·9	8·6	20·7
Carex melanantha G	10	12·6	13·9	18·2	6·3	9·6	5·3	
Stipa orientalis G	5·6	5·8		8·8	8	6	7·5	24·1
Hieracleum thomsonii H			6·5	4·5		4·8		
C. infuscata G	6·6	15·3	3·4	3·5	13·2	7·7	7·6	5·2
Eurotia ceratoides H				3·3	7·2			3·4
Unidentified forb				3·2				
Nepeta discolor H				3·1				
Carex sp. G	9·6	5·2			7·6	5·3	5·1	6
Festuca olgae G	16·9		8				3	17·2
Lindelophia anchusoides H						5·7	10·2	
Carex sp. G	7·6	4·9			5·7			
Alium H					7·8			
Leymus secalinus G	13·5	13·9	25·6	9·5		9·7	15·7	5·2
Kobresia royaleana G	5·1	3·5						
Astragalus grahamiana S						7·1	8·2	
Potentilla spp. H						3·9	6·6	
Unidentified herb A						5·3	3·7	
Unidentified herb B						3·7		
Cousinia thomsonii H					7			
Others	8·9	20·9	21·4	22·9	23·4	19·4	18·3	19·1
Total	100	100	100	100	100	100	100	100
Winter	(15)	(15)	(6)	(4)	(7)	(32)	(29)	(24)
C. melanantha G	24·5	9·8	24·6	4·4	9·6	11·7	10·6	
E. longe-aristatus G	19·8	17·5	39·1	26·1	40·3	35·2	29·2	19·8
C. thomsonii H	13	14·4			13·8	7·9	5·3	3·7
L. anchusoides H	7·6	3·7	4·4	3·3				
Carex spp. G	7					12·5	17·3	
H. thomsonii H	6·1		8·4	10·7	3·3			16
Eurotia H	5·5	11·1		4·4				
Cicer H	5·4							
L. secalinus G	4·2	4·3				11·4	11·4	9·9
S. orientalis G		20	7·7	27·6	12·4	6·1	3·8	18·5
A. grahamiana S		8·5						
Alium H		3				6·9	10·2	
C. infuscate G			13·3	23·5	15·9			
Caragana S							4·2	
Festuca olgae G								6·2
Scorzonera H								4·9
Polygonum aviculare H								4·9
Arnebia euchroma H								3·7
Rosa webbiana S								3·7
Others	6·9	8·1	2·3	0	4·9	8·4	8	8·7
Total	100	100	100	100	100	100	100	100

They fed mostly on graminoids in winter (75% graminoids, 20% herbs and 5% shrubs), with *E. longe-aristatus* forming the bulk of the diet.

Bharal

Bharal were recorded feeding on 22 species in summer and 16 species in winter. They fed predominantly on graminoids in summer (80% graminoids, 16% herbs and 4% shrubs). The bulk of the summer diet comprised *S. orientalis*, *E. longe-aristatus* and *Festuca olgae* (Table 3). Bharal had a mixed diet in winter (56% graminoids, 38% herbs and 6% shrubs), although *S. orientalis* and *E. longe-aristatus* retained their importance in the diet. Bharal increased their consumption of *Hieracleum thomsonii* substantially in winter. Of all the species of herbivores, they had the narrowest diet breadth in summer, although in winter their diet breadth was substantially wider (Fig. 2).

COMPARISON OF DIETS

ANOVA (with unequal n), with number of plant species eaten per sample as the dependent variable, and animal

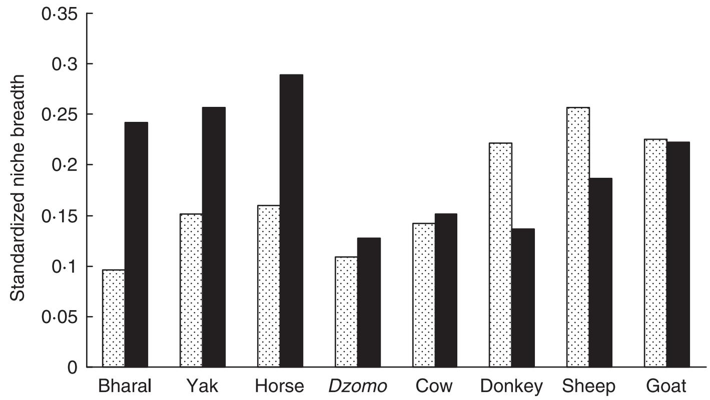

Fig. 2. Seasonal diet spectrum of herbivores in Spiti, Indian Trans-Himalaya, represented by Levins' (1968) niche breadth index, standardized to a scale of 0–1 following Hurlbert (1978). Shaded and black columns represent summer and winter, respectively.

Table 4. Diet overlap in the herbivore assemblage in Spiti, Indian Trans-Himalaya (MacArthur & Levins 1967). In these asymmetrical matrices, the rows represent overlap indices of the diet of a given species (corresponding to the first column) on every other species of herbivore (corresponding to the first row)

	Yak	Horse	*Dzomo*	Cow	Donkey	Sheep	Goat	Bharal
Summer								
Yak		0·85	0·72	0·76	0·81	0·93	0·84	0·61
Horse	0·81		0·7	0·82	0·98	1	0·9	0·48
Dzomo	0·95	0·98		0·95	0·76	1	1	0·49
Cow	0·8	0·91	0·75		0·9	1	0·85	0·56
Donkey	0·57	0·73	0·4	0·6		0·8	0·66	0·43
Sheep	0·57	0·83	0·52	0·65	0·7		0·84	0·4
Goat	0·58	0·66	0·54	0·56	0·65	0·96		0·38
Bharal	0·91	0·74	0·55	0·79	0·9	0·96	0·8	
Winter								
Yak		0·76	0·61	0·39	0·56	0·7	0·72	0·52
Horse	0·69		0·47	0·53	0·55	0·59	0·58	0·69
Dzomo	1	0·91		0·82	0·92	0·96	0·93	0·88
Cow	0·61	0·92	0·72		0·79	0·66	0·61	0·93
Donkey	0·93	1	0·87	0·85		0·97	0·92	0·96
Sheep	0·91	0·86	0·71	0·56	0·76		1	0·83
Goat	0·81	0·72	0·59	0·44	0·62	0·9		0·7
Bharal	0·55	0·81	0·52	0·63	0·61	0·68	0·65	

species and seasons as fixed factors, revealed few differences between animal species (d.f. = 7, $F = 3{\cdot}6$, $P < 0{\cdot}01$) as well as season (d.f. = 1, $F = 36{\cdot}5$, $P < 0{\cdot}01$). Bharal fed on significantly fewer species than cow, goat and sheep in summer, while there was no clear difference in winter. The only other significant difference was between sheep and cow in summer, with the former consuming more species.

Levins' (1968) standardized niche breadth showed a strong negative correlation with proportional graminoid contribution in the diet, i.e. species that fed predominantly on graminoids in a given season had a narrower niche breadth than those feeding on graminoids and herbs (Pearson's $R = -0{\cdot}85$, d.f. = 15, $P = 0{\cdot}001$; Fig. 2). Donkey, goat and sheep showed a decline in diet breadth from summer to winter (they had a mixed diet in summer but largely fed on graminoids in winter), while bharal, yak and horse showed an increase in diet breadth from summer to winter. There was only a marginal increase in diet breadth of cow and *dzomo* from summer to winter: they fed predominantly on graminoids in both seasons.

The values of MacArthur & Levins' (1967) diet overlap index are presented in Table 4, and can range from 0 (no overlap) to 1 (or marginally higher than 1; complete overlap). The diet overlap between members of this herbivore assemblage was high (median = 0·775). In summer, the overlap of diets of *dzomo* and bharal with other species was significantly higher than overlap of others with them (Wilcoxon's signed ranks tests, $z = -2{\cdot}197$, $P = 0{\cdot}028$ for *dzomo* and $z = -0{\cdot}237$, $P = 0{\cdot}018$ for bharal), i.e. their diets tended to be subsets of the diet of other herbivores but not vice versa. This was also reflected in the fact that these species had amongst the narrowest diet breadth in summer (Fig. 2). On the other hand, the diets of sheep and goat showed significantly lower overlap with others compared with overlap of others with them ($z = 2{\cdot}028$, $P = 0{\cdot}043$ for goat and $z = 2{\cdot}366$, $P = 0{\cdot}018$ for sheep). Sheep and goat had amongst the widest diet breadth in summer (Fig. 2). In addition to *dzomo*, the diets of yak, horse and donkey also became subsets of the diets of other species in winter. Overlap of their diets with other species became significantly higher than that of other species with them ($z = -2{\cdot}366$, $P = 0{\cdot}018$ for *dzomo*, $z = -2{\cdot}208$, $P = 0{\cdot}043$ for yak, $z = -2{\cdot}366$, $P = 0{\cdot}018$ for horse and $z = -2{\cdot}197$, $P = 0{\cdot}028$ for donkey).

Focusing specifically on bharal, it was evident that the bharal diet spectrum in summer was narrow and tended to overlap almost completely with the diet of sheep, yak and donkey (Table 4). In winter, however, bharal had a wider diet breadth and the extent of its diet overlap with other species was reduced. Of the three most important forage species for bharal in summer, *E. longe-aristatus* was consumed substantially by almost all species of livestock, *F. olgae* was consumed substantially by yak, while *S. orientalis* was consumed by all other species in moderate amounts (Table 3). In winter, many livestock species consumed *S. orientalis*, which remained important bharal forage, in substantial amounts. *Hieracleum thomsonii*, which became important in bharal diet in winter, was consumed by at least three other species in moderate amounts.

POPULATION STRUCTURE

The rangelands of which bharal populations were compared varied by 30% in livestock biomass density (Table 1). There was a threefold difference in the average (± SD) density of bharal between the moderately grazed rangeland ($7{\cdot}1 \pm 0{\cdot}2$ km^{-2}) and the intensively grazed one ($2{\cdot}6 \pm 0{\cdot}46$ km^{-2}) (Fig. 3). In terms of performance, again, bharal fitted the predicted pattern; 55 (± 7·1) kids 100 females^{-1} in the heavily grazed rangeland compared with 82·5 (± 16·3) kids 100 females^{-1} in the moderately grazed rangeland (Table 5).

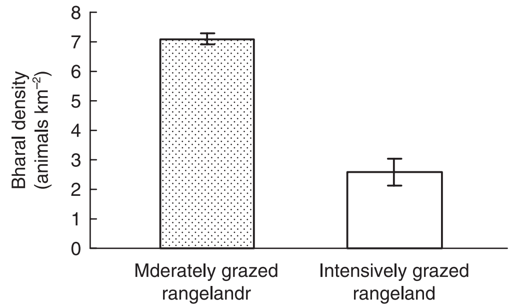

Fig. 3. Mean (± SD as error bars) bharal density in the two censuses (1998 and 2000) in moderately and intensively grazed rangelands in Spiti, Indian Trans-Himalaya.

Discussion

COMPETITION

Competition between species populations has generally been difficult to measure, and the development of theory has long surpassed empiricism (Roughgarden 1979; Goldberg & Barton 1992). Measuring competition among large herbivores has been especially difficult, in part because of the logistic difficulty in conducting experiments or manipulating populations, and in part because research (in temperate ecosystems) has traditionally focused on the role of predation in limiting large herbivore populations, pushing interspecific resource limitation and competition into the background (Kie *et al*. 1991; Sæther 1997; Forsyth 2000). Although competition between livestock and wild herbivores has long been acknowledged to be an important (although contentious) issue, recent reviews indicate a remarkable world-wide scarcity of studies addressing the issue (Putman 1996; Prins 2000). Our study is a contribution in this direction. It establishes that (i) there is high overlap in diets of bharal and Trans-Himalayan livestock; (ii) livestock at high density causes a decline in forage availability for bharal; and (iii) together this results in competition with bharal.

A high degree of resource overlap, by itself, could either imply that consumer species compete with each other (if the resource is limiting) or, alternately, it may indicate an absence of competition and sharing of resources that are abundant (Gordon & Illius 1989; Putman 1996; Mysterud 2000). However, in seasonal environments, when herbivore species do compete for resources, the extent of resource overlap can be expected to decline in

Table 5. Population structure of bharal *Pseudois nayaur* in moderately and intensively grazed rangelands in Spiti, Indian Trans-Himalaya. See Table 2 for description of age–sex classes

	1998		2000	
	Moderately grazed	Intensively grazed	Moderately grazed	Intensively grazed
Total	98	71	102	91
Male class IV	3	4	1	6
Male class III	11	6	4	6
Male class II	5	8	3	14
Male class I	6	5	3	2
Adult female	31	24	16	35
Yearlings	20	12	10	7
Young	22	12	15	21
Unclassified	0	0	50	0
Kids 100 females^{-1}	71	50	94	60

the 'unfavourable season' (lean resource availability). This is because the intensity of resource competition is greater during periods of lean resource availability and, as a species gets outcompeted from preferred resources, it is likely to increase its consumption of less suitable forage (Gordon & Illius 1989; Mysterud 2000). In the Trans-Himalaya, the growing season for vegetation is restricted to the few summer months. In winter, the leaves die off and, in our study area, an estimated 90% of the rangelands become inaccessible for herbivores due to snow cover. Therefore, compared with summer diet where herbivores probably exercise some choice in what they eat, winter diets are expected to be largely constrained by what is available. The relative decline in diet overlap between bharal and livestock in winter in our study therefore points towards resource competition.

Several lines of evidence established competition between bharal and livestock; the overall high diet overlap, the relative decline in diet overlap during the lean season, and the significant density-dependent decline in forage availability caused by livestock. Furthermore, bharal density was 63% lower in the intensively grazed rangeland, a pattern that was in line with our prediction that if bharal and livestock do compete, bharal density would decline as livestock density increases. From the data on bharal population structure, it was also apparent that competition for forage with livestock manifests in reduced reproductive performance (and density) of bharal (Fig. 3 and Table 5). As predicted, bharal showed lowered performance in the intensively grazed rangeland, although the magnitude of difference was much smaller than has been found previously for goat and sheep (Mishra, Prins & Van Wieren 2001). This may be explained by the fact that the maximum offspring produced annually per female in bharal is only one (Schaller 1998) compared with two in goat and sheep. There is some evidence in the literature that, in large herbivores, population performance (fecundity and neonate mortality) is more sensitive to density-dependence compared with adult survival, which appears to be buffered against density-dependent effects (Gaillard, Festa-Bianchet & Yoccoz 1998). Our limited observations on adult bharal mortality in rangelands with varying livestock density show no indication of density-dependence (Mishra 2001).

Our study focused on and established the importance of 'scramble' competition between livestock and bharal (Begon, Harper & Townsend 1996). However, there are other mechanisms that could potentially result in competition, such as behavioural intolerance of bharal to large livestock herds accompanied by people, causing 'interference' competition (Begon, Harper & Townsend 1996; Forsyth & Hickling 1998). Similarly, susceptibility of bharal to disease or parasites shared with livestock could potentially result in reduced fitness (Forsyth & Hickling 1998). The importance of these mechanisms needs to be investigated in future research.

Facilitation is another form of interaction between herbivores; a large herbivore may 'facilitate' another smaller species by feeding on grass and thereby improving its quality (McNaughton 1979; Prins & Olff 1998). This raises the question of whether bharal could potentially benefit from livestock grazing. Facilitation is an important interaction amongst herbivores under conditions of high graminoid biomass, while competition becomes more important at low biomass (Van de Koppel & Prins 1998). A global comparison has revealed that the Trans-Himalaya fall at the low end of the range in terms of above-ground graminoid biomass (Mishra 2001), and we therefore do not expect facilitation to be an important interaction between livestock and bharal even at low livestock density.

DIET OF LARGE HERBIVORES

The seasonal switch in the extent of graminoid and browse consumption of herbivores in our study appears to be a result of local herding practices and seasonal differences in forage availability. The grazing practice in the study area is such that yak and horse largely range free in distant pastures for most of the year, except during extreme winter when they are herded back and stall-fed (Mishra, Van Wieren & Prins 2003). The pastures that yak and horse use in winter have been used right through summer. As a result, as winter approaches, the plant biomass, especially graminoid biomass, in these pastures becomes depleted, and yak and horse are forced to include more herbs and some shrubs in their diet. In fact, such high consumption of non-graminoid species by horses has perhaps not been reported earlier (Negi *et al.* 1993). Bharal too are apparently forced to include non-graminoids in their diet in winter, because they largely graze in the few snow-free pastures that had been used by livestock throughout the summer. We studied bharal diet only in a rangeland intensively grazed by livestock. We expect that in areas of lower livestock density and consequently higher graminoid biomass, bharal continue to feed predominantly on graminoids in winter.

In contrast, cow and *dzomo* continue to feed on graminoids in winter, as (together with other herded livestock, donkey, sheep and goat) they graze in pastures that are not used in summer but exclusively kept for winter grazing (Mishra, Van Wieren & Prins 2003). These pastures have greater graminoid availability compared with those used by yak and horse. Why the summer mixed feeders, donkey, sheep and goat, which use the same winter pastures as cow and *dzomo*, should also feed predominantly on graminoids in winter is not very clear. It is probably related to greater graminoid biomass availability in those pastures compared with herbaceous biomass during winter, although we do not have data to establish this.

MANAGEMENT RECOMMENDATIONS

Rangelands might be overstocked in most areas with agropastoral land use in the Trans-Himalaya;

supplemental feeding from forage produced in crop fields allows livestock populations to be maintained beyond points of natural resource limitation (Mishra 2001; Mishra, Prins & Van Wieren 2001). Even in areas that traditionally had purely pastoral land use, there is increasing government and international aid to provide supplemental feed for livestock (Mishra 2000; Yash Veer Bhatnagar, personal communication). Our study strongly suggests that this high density of supplementary-fed livestock may cause competition with wild herbivores. One option for conservation management is to mediate competitive effects on bharal through supplemental feeding. As bharal populations appear to be resource limited, we predict that supplemental feeding would increase bharal density. However, our study suggests that although the significance of forage availability in winter (the lean season) cannot be discounted, the condition of summer pastures is an important determinant of bharal density (Mautz 1978). This resource limitation in summer rangelands is presumably the main cause of reduced bharal performance. Therefore, for supplemental-feeding to be an effective conservation management option, bharal populations would need to be supplemented not just during the 'unfavourable season' but also during the summer 'productivity pulse' (Keddy 1989) because there is forage competition even during summer.

Centuries of intensive livestock grazing and water harvest for agriculture have caused the degradation of rangeland vegetation and a significant reduction in graminoid biomass in Spiti Valley (Mishra 2001). The expected numerical response of bharal to supplemental feeding would escalate the grazing pressure and would cause further vegetation degradation. Together with the need for year-round investment, this means that supplemental feeding of bharal to enhance their population has limited feasibility or long-term merit.

Our results suggest that a reduction in livestock density should elicit a numerical response from bharal. Conservation management therefore must initiate a reduction in livestock density in areas identified for wildlife conservation. Additionally, conservation managers need to address the fact that presently, in the Indian Trans-Himalaya, there is a complete absence of conservation areas that are free from livestock grazing (Mishra 2001). The only exception known to us is a small (500-ha) rangeland near our intensive study site that we have maintained free of livestock grazing at an experimental scale: the bharal density here has increased significantly following 4 years of protection from livestock grazing (Mishra *et al*. 2003). Creating livestock-free areas and monitoring the responses of wild herbivore populations within them must become the top priority for conservation management in the Trans-Himalaya.

Acknowledgements

This research was made possible by a grant from Netherlands Foundation for the Advancement of Tropical Research (WOTRO), a body residing under the Netherlands Organization for Scientific Research (NWO). Pieter Ketner was also supported by the NWO. We thank M. D. Madhusudan and Rohan Arthur for valuable suggestions, and Tandup Dorje and Lobsang Gialson for invaluable help. We are grateful to Dr G. S. Rawat for help with plant identification. We also thank the Department of Forest Farming and Conservation, Himachal Pradesh, for permission to conduct the fieldwork.

References

Aswal, B.S. & Mehrotra, B.-N. (1994) *Flora of Lahaul-Spiti*. Bishen Singh Mahendra Pal Singh Publishers, Dehradun, India.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: Individuals, Populations and Communities*, 3rd edn. Blackwell Science, Oxford, UK.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer: Behaviour and Ecology of Two Sexes*. Wildlife Behaviour and Ecology Series. The University of Chicago Press, Chicago, IL.

FAO (2002) *FAO Statistical Databases*. http://apps.fao.org; accessed November 2003. Food and Agricultural Organization of the United Nations, Rome, Italy.

Fleischner, T.L. (1994) Ecological costs of livestock grazing in western North America. *Conservation Biology*, **8**, 629–644.

Forsyth, D.M. (2000) Habitat selection and coexistence of the Alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) in the eastern Southern Alps, New Zealand. *Journal of Zoology (London)*, **252**, 215–225.

Forsyth, D.M. & Hickling, G.J. (1998) Increasing Himalayan tahr and decreasing chamois densities in the eastern Southern Alps, New Zealand: evidence for interspecific competition. *Oecologia*, **113**, 337–382.

Gaillard, J., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.

Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist*, **139**, 771–801.

Gordon, I.J. & Illius, A.W. (1989) Resource partitioning by ungulates on the Isle of Rhum. *Oecologia*, **79**, 383–389.

Handa, O.C. (1994) *Tabo Monastery and Buddhism in the Trans-Himalaya: Thousand Years of Existence of the Tabo Chos-Khor*. Indus Publishing Co, New Delhi, India.

Harris, R.B. & Miller, D.J. (1995) Overlap in summer habitats and diets of Tibetan plateau ungulates. *Mammalia*, **59**, 197–212.

Hurlbert, S.H. (1978) The measurement of niche overlap and some relatives. *Ecology*, **59**, 67–77.

Keddy, P.A. (1989) *Competition*. Population and Community Biology Series. Chapman & Hall, London, UK.

Kie, J.G., Evans, C.J., Loft, E.R. & Menke, J.W. (1991) Foraging behaviour by mule deer: the influence of cattle grazing. *Journal of Wildlife Management*, **55**, 665–674.

Kothari, A., Pande, P., Singh, S. & Variava, D. (1989) *Management of National Parks and Wildlife Sanctuaries in India: A Status Report*. Indian Institute of Public Administration, New Delhi, India.

Krebs, C.J. (1989) *Ecological Methodology*. Harper & Row Publishers, New York, NY.

Leader-Williams, N. (1988) *Reindeer in South Georgia: The Ecology of an Introduced Population*. Cambridge University Press, Cambridge, UK.

Levins, R. (1968) *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, NJ.

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, **101**, 377–385.

McNaughton, S.J. (1979) Grazing as an optimisation process: grass–ungulate relationships in the Serengeti. *American Naturalist*, **113**, 691–703.

Mautz, W.W. (1978) Sledding on a bushy hillside: the fat cycle in deer. *Wildlife Society Bulletin*, **6**, 88–90.

Mishra, C. (2000) Socioeconomic transition and wildlife conservation in the Indian Trans-Himalaya. *Journal of the Bombay Natural History Society*, **97**, 35–32.

Mishra, C. (2001) *High altitude survival: conflicts between pastoralism and wildlife in the Trans-Himalaya*. PhD Thesis. Wageningen University, Wageningen, the Netherlands.

Mishra, C. & Rawat, G.S. (1998) Livestock grazing and biodiversity conservation: comments on Saberwal. *Conservation Biology*, **12**, 712–714.

Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A. & Prins, H.H.T. (2003) The role of incentive programs in conserving the snow leopard *Uncia uncia*. *Conservation Biology*, **17**, 1512–1520.

Mishra, C., Prins, H.H.T. & Van Wieren, S.E. (2001) Overstocking in the Trans-Himalayan rangelands of India. *Environmental Conservation*, **28**, 279–283.

Mishra, C., Van Wieren, S.E., Heitkönig, I.M.A. & Prins, H.H.T. (2002) A theoretical analysis of competitive exclusion in a Trans-Himalayan large herbivore assemblage. *Animal Conservation*, **5**, 251–258.

Mishra, C., Van Wieren, S.E. & Prins, H.H.T. (2003) Diversity, risk mediation, and change in a Trans-Himalayan agropastoral system. *Human Ecology*, **31**, 595–609.

Mysterud, A. (2000) Diet overlap among ruminants in Fennoscandia. *Oecologia*, **124**, 130–137.

Negi, G.C.S., Rikhari, H.C., Ram, J. & Singh, S.P. (1993) Foraging niche characteristics of horses, sheep and goats in an alpine meadow in the Indian Central Himalaya. *Journal of Applied Ecology*, **30**, 383–394.

Noss, R.F. (1994) Cows and conservation biology. *Conservation Biology*, **8**, 613–616.

Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, **4**, 53–74.

Prins, H.H.T. (1992) The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation*, **19**, 117–123.

Prins, H.H.T. (2000) Competition between wildlife and livestock in Africa. *Wildlife Conservation by Sustainable Use* (eds H.H.T. Prins, J.G. Grootenhuis & T.T. Dolan), pp. 51–80. Kluwer Academic Publishers, Boston, MA.

Prins, H.H.T. & Olff, H. (1998) Species-richness of African grazer assemblages: towards a functional explanation. *Dynamics of Tropical Communities* (eds D. M. Newbery, H. H. T. Prins & N. D. Brown), pp. 449–490. The British Ecological Society, London, UK.

Putman, R.J. (1996) *Competition and Resource Partitioning in Temperate Ungulate Assemblies*. Chapman & Hall, London, UK.

Roughgarden, J. (1979) *Theory of Population Genetics and Evolution Ecology: An Introduction*. Macmillan, New York, NY.

Sæther, B.-E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology and Evolution*, **12**, 143–149.

Schaller, G.B. (1998) *Wildlife of the Tibetan Steppe*. The University of Chicago Press, Chicago, IL.

Skogland, T. (1983) The effects of density dependent resource limitation on size of wild reindeer. *Oecologia (Berlin)*, **60**, 156–168.

Van de Koppel, J. & Prins, H.H.T. (1998) The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *Journal of Tropical Ecology*, **14**, 565–576.

Voeten, M.M. (1999) Living with wildlife: coexistence of wildlife and livestock in an East African savanna system. PhD Thesis. Wageningen University, Wageningen, the Netherlands.

WRI (1996) *World Resources Report 1996*. World Resources Institute, Washington, DC.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall, Englewood Cliffs, NJ.

Received 29 December 2002; final copy received 15 November 2003