

Interspecific and seasonal dietary differences of Himalayan thar, chamois and brushtail possums in the central Southern Alps, New Zealand

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Abstract: Himalayan thar or tahr (*Hemitragus jemlahicus*), Alpine chamois (*Rupicapra rupicapra*) and brushtail possums (*Trichosurus vulpecula*) are native to the Himalaya, Europe and Australia, respectively, but are now sympatric in parts of the central Southern Alps, New Zealand. All three species are managed as pests by the Department of Conservation. We analysed the diets of 246 thar, 78 chamois and 113 possums collected in the central Southern Alps during 1988–1996. The diets of thar and chamois strongly overlapped, but thar ate more grasses and less herbs and woody plants than chamois. The diet of possums differed from the diets of thar and chamois, containing a different suite of herbs and almost no grasses. The diets of thar, chamois and possums varied seasonally. Contrary to expectation, the diets of adult male and female thar were similar during the period when they are spatially segregated (October–May). Chamois sampled outside the thar range ate more species than those sampled inside the thar range, suggesting the presence of thar modifies the diet of chamois. If managers wish to protect the dominant *Chionochloa* snow tussocks then thar should be controlled; chamois should be controlled to protect herbs such as *Ranunculus* spp.; and possums should be controlled if *Podocarpus nivalis* or *Muehlenbeckia axillaris* need to be protected. However, managers need to be aware of the potential for chamois to increase in abundance, at least in some sites, if thar are controlled to low abundance, and that this could lead to different impacts on plant populations.

Keywords: competition; *Hemitragus jemlahicus*; Himalayan tahr; Horn's Index; niche overlap; *Rupicapra rupicapra*; *Trichosurus vulpecula*; ungulates

Introduction

The Himalayan thar or tahr (*Hemitragus jemlahicus*) was introduced to the Southern Alps in 1904 (Donne 1924) and now occupies a range of c. 4200 km² (Forsyth & Tustin 2005). Current densities of thar are <1 km⁻² in national parks where they are controlled by the Department of Conservation (DOC) but up to c. 10 km⁻² in areas with no official control (Parkes et al. 2004, unpubl. report LC0304/077). The Alpine chamois (*Rupicapra rupicapra*) was introduced to the Southern Alps in 1907 (Donne 1924). The range of chamois includes all of the thar range but extends north and south (and to lower altitudes), covering nearly 50 000 km² (Forsyth 2005). Densities of chamois seldom exceed 5 km⁻² but are usually c. 1 km⁻² because of commercial helicopter-based hunting and/or avoidance of thar (Forsyth & Hickling 1998; Parkes et al. 2004 unpubl.). The Australian brushtail possum (*Trichosurus vulpecula*) has colonised the Southern Alps from many introduction sites and its geographic range now overlaps that of thar

and chamois (Cowan 2005). Possums are seldom hunted or controlled in the alpine areas of New Zealand because they reach lower densities than in lower-altitude habitats (Hickling & Forsyth 2000; Forsyth & Parkes 2005). Where these species are sympatric there is uncertainty about which species are impacting different plant populations (Forsyth et al. 2000). Therefore, although they are managed as pests by DOC (Parkes & Murphy 2003), identifying the appropriate herbivore to control in order to protect conservation resources can be difficult.

Since thar, chamois and possums evolved on different continents (Asia, Europe and Australia, respectively), competition between these three species in the Southern Alps of New Zealand might be stronger than in co-evolved communities (Connell 1980; Forsyth & Hickling 1998). In particular, competition is expected to be more intense among species of similar size and morphology that share the same resources (Duncan & Forsyth 2006). Because humans are the only predator of thar and chamois in New Zealand, food is assumed to be an important factor

regulating the abundance of these species (review in Forsyth 2006). Hence, competition for food is a potential mechanism for the observed disappearance of chamois from sites that they previously occupied as densities of thar increased in the central Southern Alps (Forsyth & Hickling 1998).

We quantified the diets of thar, chamois and brushtail possums in the central Southern Alps of New Zealand. We use those data to test five ecological predictions (see below) about the diets of thar, chamois and possums. Finally, we highlight how our results inform the management of these herbivores as pests in the central Southern Alps.

1. Diets of thar and chamois should reflect known differences in habitat use

Forsyth (2000) described differences in seasonal habitat selection between chamois and thar in Carneys Creek (eastern Southern Alps) in 1993–1996, with chamois found more often in shrubland than thar, and thar occupying rock and grass bluffs. There was no difference in the species' selection of grassland. The only study of possums in the central Southern Alps suggested this species is most abundant in and around shrubland (Hickling & Forsyth 2000). We therefore predicted that chamois and possums should have more woody species in their diet than thar, but that grasses should be eaten in equal amounts by thar and chamois.

2. Diets of thar, chamois and possums should change seasonally

The central Southern Alps is characterised by large seasonal changes in the availability of plants to thar, chamois and possums. Snow reduces the availability of vegetated habitats in winter (Forsyth 2000). The availability of flowers and fruit is strongly seasonal for most alpine species (Mark & Adams 1995); some (such as *Aciphylla* spp. and *Chionochoa* spp.) produce seeds only periodically (e.g. Schaubert et al. 2002), and a few (such as *Ranunculus* spp.) die back in winter. Both chamois and thar exhibit seasonal changes in habitat selection (Clarke 1986; Tustin & Parkes 1988; Forsyth 2000). Possums in New Zealand forests show strong seasonal changes in diet, particularly with respect to flowers and fruit (Nugent et al. 2000). We therefore predicted that all three species would exhibit seasonal variations in diet.

3. Diets of adult male and female thar should differ when segregated

Male and female thar aggregate on steep, snow-free bluffs during the rut and winter (c. June–September) but otherwise are segregated. Female–kid groups are sedentary on rock and grass bluffs throughout the year (Tustin & Parkes 1988). In contrast, male thar (≥ 2 years old) leave the female-based groups in spring and use tall grassland and some shrubland habitats at lower altitudes (Tustin &

Parkes 1988; Forsyth & Tustin 2005). In Carneys Creek, habitat selection by the two sexes differed significantly in spring and summer, marginally in autumn but not in winter (Forsyth 2000). We predicted that adult male and female thar would have more similar diets when aggregated compared with when segregated.

4. Diets of thar and chamois should be more similar to each other than to possums'

Thar and chamois (Order: Artiodactyla) are more closely related to each other than to possums (Order: Diprotodontia) (Bininda-Emonds et al. 2007), and this is reflected in features such as body size, oral and dental morphology, and digestive anatomy that are considered to be important predictors of diet (e.g. Hofmann 1989; Hume 1999). Hence, we predicted that the diets of thar and chamois should be more similar to each other than to that of possums.

5. Diet of chamois should be broader outside the thar range

Because data show that (1) chamois are excluded from previously occupied sites by high densities of thar (Forsyth & Hickling 1998) and (2) chamois move away from thar far more frequently than vice versa (Forsyth & Clarke 2001), we believe chamois modify their habitat selection in the presence of thar (but not vice versa). We therefore predicted that chamois living outside the breeding range of thar would have a broader diet than chamois living inside the breeding range of thar: this prediction assumes that plant communities are similar inside and outside the thar breeding range.

Methods

Thar and chamois diets

During 1988–1995, recreational and commercial hunters supplied us with samples of the rumen contents of thar and chamois they had shot. All animals were taken from the eastern side of the Main Divide (Fig. 1). Thar were taken over their whole range in this eastern zone and chamois from both this area and the eastern Southern Alps south to the Shotover River and north to the southern catchments of the Waimakariri River (Fig. 1).

Hunters were asked to take c. 500 ml of rumen contents, mix these with 40 ml of 10% formalin, and then freeze the samples as soon as possible. For each sample, hunters provided the following information: species, sex, age (kid, juvenile or adult), elevation (m), date, and location (catchment) killed.

In the laboratory each of the defrosted rumen samples was thoroughly mixed, and a subsample of at least 100–200 ml was washed over a 4-mm sieve and sorted under a binocular microscope. (Method follows C Thomson, JP

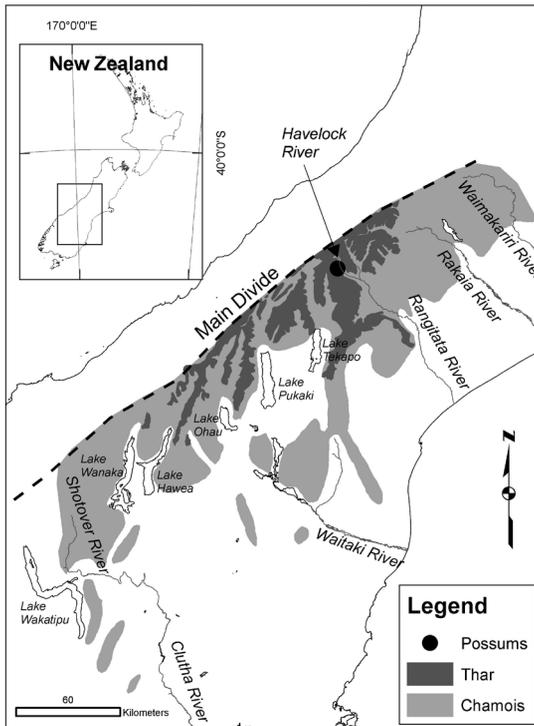


Figure 1. Map of the central Southern Alps, New Zealand, showing the approximate boundaries of the areas in which our samples of thar, chamois and possums were obtained.

Parkes, MC Coleman (1994) unpubl. report LC9394/096.) The sorted material, including the unidentified component, was then oven-dried (60°C for 72 h) and weighed. The percentage of each plant species in the diet of an animal was thus estimated using the dry weight (DW). We could not distinguish between two genera of grasses, *Poa* and *Rytidosperma*; we therefore present pooled data for the two genera.

Possum diets

During 1993–1996, we collected stomachs from possums killed in each season in the Havelock catchment of the Rangitata River (primarily from Camp Stream, Carneys Creek and the Forbes River) (Fig. 1): most possums were poisoned with cyanide paste (Trappers Cyanide Co., Styx Mill Road, Christchurch, NZ) but also some were shot with the aid of a spotlight. We took the possums from shrubland, grassland and bluff habitats likely to be used by thar and chamois in this area, as defined by Forsyth (2000). All of the stomach contents of each possum were placed into a plastic bag, mixed with 10% formalin, and then frozen as soon as possible.

Because possums chew their food more finely than ruminants, we washed their stomach contents over a 2-mm sieve. We then randomly selected, using the point subsampling method outlined by Sweetapple and Nugent (1998), and identified 100 of the remaining plant fragments. Although the sieving method (Thomson et al. 1994 unpubl.) has subsequently been shown to produce some bias, particularly for herbs and fruits (Sweetapple & Nugent 1998), we are confident the method is adequate for meeting the objectives of this study. However, our method may have overestimated the amount of fruit in the diet of possums (Sweetapple & Nugent 1998).

Statistical analyses

We summarised the diet of the three herbivores by listing those identifiable plant species that constituted $\geq 5\%$ by DW of the diet of one of the animals. Otherwise, food items were pooled by genera.

We tested seasonal differences in the amount of principal food items ($\geq 5\%$ DW) in the diet of each of the three herbivores using the Kruskal–Wallis one-way classifications by ranks approximation of chi-square (Siegel & Castellan 1988). We set the level of significance for all statistical tests at $\alpha = 0.05$.

To test whether the sexual segregation of thar outside the rut affected the diet of adult male thar, we assumed adult male (>2 yr) and all female thar were aggregated between June and September and were segregated between October and May (Forsyth & Tustin 2005). We pooled diet data into three major categories of plants (grasses, herbs and woody shrubs) and used Horn's Index (H ; Horn 1966) of niche overlap to estimate dietary overlap between adult male and all female thar in each of the two periods:

$$H = \frac{\sum (p_{ij} + p_{ik}) \log(p_{ij} + p_{ik}) - \sum p_{ij} \log p_{ij} - \sum p_{ik} \log p_{ik}}{2 \log 2}$$

where p_{ij} is the proportion of food item i in the diet of sex j and p_{ik} is the proportion of food item i in the diet of sex k . Horn's Index varies from 0 (the diets are completely different) to 1 (the diets are identical). We calculated 95% confidence intervals for H using 10 000 bootstrap samples (Manly 1997).

We used Horn's Index to test whether the diets of thar and chamois were more similar to each other than to possums' diet, with j and k representing species rather than sex in each of the pairwise comparisons.

To test whether the diet of chamois was broader outside the thar range, we used Horn's Index to compare the diets of chamois shot inside and outside the thar breeding range (as defined in Fig. 1). We also compared the numbers of species recorded in the diets and used Wilcoxon two-sample tests to compare the ranking of common ($\geq 3\%$ by DW) genera.

We used Horn's Index to estimate dietary overlap because simulation studies have shown it to have less bias

than other indices (Krebs 1999). Bias in Horn's Index can be minimised in two main ways (Krebs 1999). First, bias may be reduced by having equal sample sizes. However, because chamois were far less abundant than thar within the thar breeding range during our study (Forsyth & Hickling 1998), our sample size for chamois in this area was substantially smaller than for thar (see below). Second, bias is reduced by minimising the number of resource categories. We thus used only three resource categories (grasses, herbs and woody plants) for tests of predictions about dietary overlap.

Results

Scope of data

We analysed diet samples from 246 thar, 78 chamois (27 sampled within the thar breeding range) and 113 possums. Seasonal sample sizes were most similar for male thar and least balanced for chamois (Table 1). All species recorded in the rumens of the thar and chamois are listed in Forsyth et al. (2002), and plant species recorded in the stomachs of possums are listed in Appendix 1.

Diets of thar, chamois and possums

Grass was far more common in the diet of thar than for both chamois and possums (Table 2). Hence, our prediction that grasses should be eaten in equal amounts by thar and chamois was not supported by the data. Whereas *Chionochloa* and *Poa* spp. dominated the diet of thar, these genera were eaten far less by chamois and hardly at all by possums. Chamois and possums ate similar amounts of herbs, more so than thar. However, different species dominated the herb components of the diets. Whereas *Celmisia* and *Aciphylla* were the dominant herbs eaten by thar, they were much less abundant in chamois and were hardly recorded in possums. *Ranunculus* spp. (mainly *R. lyallii*) dominated the herb component of chamois diet, but were much less common in the diet of thar, and not recorded in the stomachs of possums. Rather, possums ate more *Hieracium* spp. and *Trifolium* spp., the latter not being recorded in the rumens of either thar or chamois.

Our prediction that chamois and possums would have more woody plants in their diet than thar was supported by our data. However, woody plants were also important for thar. The genera *Gaultheria*, *Carmichaelia*, *Hebe*, and *Dracophyllum* were the most important woody plants for both chamois and thar, but were very small constituents of the diet of possums. Instead, possums ate the leaves of *Podocarpus nivalis*, *Muehlenbeckia* spp. and *Aristotelia serrata*.

Fruit was a major component (21%) of the diet of possums, but not for thar or chamois (c. 0.2%). The key fruits eaten by possums, in descending order of importance, were: *Coprosma* spp., *Coriaria* spp., *Muehlenbeckia axillaris*, *Podocarpus nivalis*, *Pseudopanax* spp., *Aristotelia fruticosa*, *Exocarpus bidwillii*, and *Gaultheria depressa*. Ferns and fungi were small components of the diets of possums, but were rare or absent in thar and chamois (Table 2).

Do the diets of thar, chamois and possums change seasonally?

The diets of thar, chamois and possums changed greatly with season (Table 3). Although grasses were similarly important to thar in all four seasons (50–57%), *Chionochloa* spp. were eaten most in autumn, winter and spring, and *Poa/Rytidosperma* spp. were most important in spring, summer and autumn. Possums ate more grass in spring than in other seasons, and chamois ate more grass in summer than in other seasons. Both thar and chamois ate most *Celmisia* in winter. *Gaultheria* was eaten in similar amounts in all seasons by thar and chamois. Thar ate most *Carmichaelia* in autumn and spring, but there was no evidence of a seasonal pattern in chamois. *Ranunculus* was important for chamois in all seasons but winter (when above-ground biomass dies), but was important for thar only in summer. *Coprosma* was only important ($\geq 5\%$) to chamois, and only in winter and spring. *Hieracium* was eaten more by possums in spring and summer than in autumn and winter. Fruits were very important to possums in autumn and winter (c. 40%), important in summer, but were not eaten at all in spring.

Table 1. Number of thar, chamois and possums sampled by season and age–sex class.

Species	Season				Total
	Spring	Summer	Autumn	Winter	
Adult male thar (>2 yr)	24	22	24	22	92
Female thar	33	20	10	40	103
Juvenile/kid thar	27	11	6	7	51
All thar	84	53	40	69	246
Chamois	11	25	21	21	78
Possums	36	25	17	35	113

Table 2. Comparison of the overall diets of 246 thar, 78 chamois and 113 possums by percentage of total dried weight (\pm 95% CL). Note that columns do not sum to 100.0 because of rounding error.

Dietary item	Thar	Chamois	Possums
Grasses			
<i>Chionochloa</i> spp.	29.8 \pm 3.6	2.3 \pm 2.2	0.0
<i>Poa/Rytidosperma</i>	13.9 \pm 1.9	5.1 \pm 1.6	0.2 \pm 0.1
Other grasses	12.1 \pm 1.9	14.4 \pm 2.5	0.9 \pm 0.4
Total grasses	55.8 \pm 2.9	21.9 \pm 4.5	1.1 \pm 0.4
Other monocots	2.7 \pm 0.7	1.3 \pm 1.0	0.0
Herbs			
<i>Celmisia</i> spp.	6.7 \pm 1.4	3.8 \pm 1.8	0.4 \pm 0.5
<i>Aciphylla</i> spp.	4.3 \pm 0.9	0.2 \pm 0.1	0.0
Other herbs	3.4 \pm 0.6	8.0 \pm 0.5	15.5 \pm 3.2
<i>Ranunculus</i> spp.	1.5 \pm 0.9	11.3 \pm 4.7	0.0
<i>Anisotome</i> spp.	1.1 \pm 0.3	3.2 \pm 1.5	0.9 \pm 0.8
<i>Hieracium</i> spp.	0.4 \pm 0.2	1.1 \pm 1.0	9.1 \pm 2.8
<i>Epilobium</i> spp.	0.4 \pm 0.3	3.2 \pm 1.6	1.2 \pm 0.8
<i>Trifolium</i> spp.	0.0	0.0	4.1 \pm 1.9
Total herbs	17.9 \pm 2.0	30.8 \pm 5.3	31.2 \pm 4.9
Woody plants			
<i>Gaultheria</i> spp.	6.4 \pm 1.0	16.7 \pm 2.9	0.5 \pm 0.4
<i>Carmichaelia</i> spp.	6.2 \pm 1.7	12.6 \pm 4.8	0.0
<i>Hebe</i> spp.	3.7 \pm 0.9	3.9 \pm 1.3	0.0
Other woody plants	2.9 \pm 0.4	5.6 \pm 1.6	13.8 \pm 2.0
<i>Dracophyllum</i> spp.	1.5 \pm 0.4	1.5 \pm 0.8	0.0
<i>Coprosma</i> spp.	0.9 \pm 0.4	3.3 \pm 1.9	0.3 \pm 0.2
<i>Podocarpus nivalis</i>	0.9 \pm 0.5	0.0	10.6 \pm 3.0
<i>Coriaria</i> spp.	0.6 \pm 0.4	1.0 \pm 0.8	0.6 \pm 0.3
<i>Muehlenbeckia</i> spp.	0.2 \pm 0.4	0.6 \pm 0.4	5.0 \pm 2.1
<i>Aristotelia serrata</i>	0.0	0.0	6.6 \pm 2.0
Total woody plants	23.2 \pm 2.4	45.2 \pm 6.3	37.2 \pm 4.8
Fruit	0.2 \pm 0.1	0.3 \pm 0.1	21.2 \pm 5.4
Ferns	0.1 \pm 0.1	0.1 \pm 0.0	4.4 \pm 2.0
Fungi	0.0	0.0	3.1 \pm 2.2
Lichens	0.0	0.3 \pm 0.2	0.0
Animal matter	0.0	0.0	1.3 \pm 1.1
Total	99.9	99.8	99.7

Table 3. Seasonal differences in the use of principal foods of thar, chamois and possums. Mean dried weight \pm 95% CL. T = thar, C = chamois, P = possums.

Food class/item	Species	Mean % dried weight				χ^2	P
		Summer	Autumn	Winter	Spring		
<i>Chionochloa</i>	T	13.7 \pm 4.6	30.5 \pm 8.4	42.0 \pm 7.2	29.6 \pm 6.3	32.1	<0.0001
	C	0.1 \pm 0.1	4.1 \pm 5.3	4.0 \pm 5.9	0.8 \pm 1.5	5.1	0.16
	P	0	0	0	0		
<i>Poa / Rytidosperma</i>	T	18.0 \pm 4.2	13.6 \pm 4.8	8.0 \pm 2.9	16.3 \pm 3.4	27.9	<0.0001
	C	8.0 \pm 4.1	4.2 \pm 2.1	3.2 \pm 1.8	4.3 \pm 3.7	5.2	0.16
	P	0	0	0.1 \pm 0.2	0.5 \pm 0.3		
<i>Ranunculus</i>	T	5.9 \pm 3.7	0.3 \pm 0.2	0	0.7 \pm 0.8	39.0	<0.0001
	C	13.0 \pm 9.2	18.9 \pm 9.6	1.1 \pm 1.9	12.3 \pm 16.2	16.4	0.0009
	P	0	0	0	0		
<i>Aciphylla</i>	T	4.0 \pm 1.9	6.3 \pm 3.2	3.3 \pm 1.4	4.3 \pm 1.6	7.7	0.05
	C	0.1 \pm 0.1	0.3 \pm 0.2	0.1 \pm 0.1	0.5 \pm 0.7	3.6	0.31
	P	0	0	0	0		
<i>Celmisia</i>	T	5.7 \pm 2.6	2.6 \pm 1.3	12.2 \pm 3.9	4.7 \pm 1.7	16.5	0.0009
	C	1.5 \pm 1.5	4.2 \pm 2.6	6.8 \pm 5.7	2.7 \pm 3.5	9.4	0.02
	P	0	2.1 \pm 3.3	0	0.2 \pm 0.4		

<i>Hieracium</i>	T	1.3 ± 1.0	0.1 ± 0.1	0	0.2 ± 0.2	27.4	<0.0001
	C	1.5 ± 2.1	0.2 ± 0.5	0	3.5 ± 5.0	9.1	0.03
	P	10.1 ± 3.6	1.5 ± 1.9	4.5 ± 2.5	16.5 ± 7.5	15.6	0.001
<i>Trifolium</i>	T	0	0	0	0		
	C	0.1 ± 0.1	0	0	0		
	P	5.7 ± 2.9	2.7 ± 4.8	0	7.6 ± 5.4	30.1	<0.0001
<i>Gaultheria</i>	T	6.1 ± 2.4	4.8 ± 1.7	6.5 ± 2.2	7.1 ± 1.5	6.2	0.10
	C	17.5 ± 6.0	13.2 ± 6.4	19.1 ± 6.4	16.6 ± 6.4	3.1	0.38
	P	0	0.1 ± 0.1	0.7 ± 1.0	0.9 ± 0.7	8.6	0.04
<i>Carmichaelia</i>	T	4.8 ± 2.6	10.9 ± 5.6	3.2 ± 2.2	7.3 ± 3.3	16.7	0.0008
	C	5.2 ± 5.2	12.7 ± 9.7	20.0 ± 11.9	15.0 ± 9.8	3.7	0.30
	P	0	0	0	0		
<i>Hebe</i>	T	4.1 ± 2.4	2.4 ± 1.2	3.7 ± 2.1	4.0 ± 1.1	9.1	0.03
	C	3.0 ± 1.9	3.8 ± 2.7	4.4 ± 2.1	5.2 ± 5.3	1.7	0.65
	P	0	0	0	0		
<i>Podocarpus nivalis</i>	T	0	1.6 ± 2.0	2.0 ± 1.1	0.1 ± 0.1	29.8	<0.0001
	C	0.1 ± 0.2	0	0	0		
	P	9.4 ± 5.9	11.5 ± 9.4	8.3 ± 4.8	13.2 ± 5.7	0.6	0.9
<i>Coprosma</i>	T	0.1 ± 0.1	1.2 ± 1.3	1.0 ± 0.7	1.1 ± 0.7	11.2	0.01
	C	0.1 ± 0.1	1.2 ± 1.1	8.6 ± 5.6	4.6 ± 5.8	17.4	0.0006
	P	0.1 ± 0.2	0	0.5 ± 0.3	0.4 ± 0.5	13.7	0.003
<i>Muehlenbeckia</i>	T	0.1 ± 0.1	0.1 ± 0.1	0	0.6 ± 1.1	9.1	0.02
	C	1.1 ± 0.9	1.0 ± 0.8	0	0	17.0	0.0007
	P	13.8 ± 7.6	2.0 ± 1.1	3.6 ± 2.7	1.7 ± 1.2	12.8	0.005
<i>Aristotelia serrata</i>	T	0	0	0	0		
	C	0	0	0	0		
	P	9.2 ± 4.7	3.4 ± 3.5	5.2 ± 2.9	7.7 ± 4.4	5.2	0.15
All grass	T	50.2 ± 5.5	54.3 ± 7.5	59.1 ± 5.8	57.2 ± 4.7	5.3	0.15
	C	31.8 ± 8.0	19.2 ± 6.7	14.9 ± 8.9	18.1 ± 12.9	12.0	0.007
	P	0.3 ± 0.2	0.4 ± 0.5	0.7 ± 0.5	2.2 ± 1.0	11.9	0.008
All herbs	T	26.0 ± 5.1	14.7 ± 3.5	18.9 ± 4.2	13.5 ± 2.6	18.9	0.0003
	C	29.7 ± 9.7	42.3 ± 9.1	21.5 ± 8.3	28.9 ± 16.3	9.6	0.02
	P	36.2 ± 9.2	19.1 ± 9.9	17.1 ± 6.9	47.3 ± 8.9	31.1	<0.0001
All shrubs	T	19.1 ± 4.4	25.6 ± 6.0	20.3 ± 4.1	25.6 ± 4.4	7.0	0.07
	C	36.0 ± 9.5	35.5 ± 11.8	60.3 ± 12.5	51.2 ± 15.6	10.9	0.01
	P	33.1 ± 9.5	23.2 ± 10.6	26.1 ± 8.7	34.5 ± 7.6	5.4	0.14
All trees	T	0	2.1 ± 3.0	0	0.6 ± 0.6	5.9	0.12
	C	0.2 ± 0.3	1.8 ± 3.5	0.5 ± 0.9	0	0.8	0.9
	P	4.5 ± 3.2	16.3 ± 10.4	4.7 ± 3.6	7.7 ± 4.3	2.2	0.5
All ferns	T	0.3 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0	23.8	<0.0001
	C	0	0.2 ± 0.2	0	0	5.9	0.11
	P	13.7 ± 7.1	0.4 ± 0.8	0.1 ± 0.1	4.0 ± 2.7	41.3	<0.0001
All fruits	T	0.7 ± 0.4	0.4 ± 0.3	0	0.1 ± 0.1		
	C	0.6 ± 0.3	0.2 ± 0.3	0	0		
	P	11.7 ± 6.2	39.7 ± 16.1	40.8 ± 10.5	0	62.0	<0.0001

Do the diets of adult male and female thar differ when segregated?

The diets of adult male and all female thar were broadly similar when the two classes were aggregated ($H=0.996$; $0.972-0.999$), and, in contrast to our third prediction, broadly similar when the two classes were segregated ($H=0.999$; $0.988-0.999$) (Table 4). The two classes of thar also ate a similar number of species; 13.9 for adult males and 13.7 for females ($t_{190}=0.38$, $P=0.7$).

Are the diets of thar and chamois more similar to each other than to possums'?

When analysed as three categories (grasses, herbs or woody plants), the diets of thar and chamois strongly overlapped ($H=0.900$; 95% CI, $0.868-0.929$). However, there was much less overlap between the diets of thar and possums ($H=0.573$; $0.542-0.602$) and chamois and possums ($H=0.769$; $0.749-0.788$). Our fourth prediction, that the diets of thar and chamois should be more similar to each other than to that of possums, was supported by the data.

Table 4. Comparison of the diets (mean \pm 95% CL) of adult male and female thar when males are aggregated with (June to September) and segregated from (October to May) females.

Food category	Males with females		Males segregated from females	
	Males	Females	Males	Females
Grasses	62.2 \pm 9.0	58.8 \pm 7.2	53.3 \pm 6.0	54.7 \pm 5.0
Herbs	13.7 \pm 6.0	18.8 \pm 4.8	19.5 \pm 4.4	17.3 \pm 3.6
Shrubs	22.8 \pm 7.3	20.9 \pm 5.2	23.2 \pm 4.9	22.1 \pm 5.2

Table 5. Mean rankings of major food items ($\geq 3\%$ dried weight) in the diets of chamois sampled inside and outside the breeding range of thar.

Food item	Mean rank inside thar range	Mean rank outside thar range	Wilcoxon test (W) statistic and P -value
<i>Celmisia</i> spp.	27.8	45.7	$W = 1003$; $P < 0.001$
<i>Ranunculus</i> spp.	32.4	43.3	$W = 881$; $P = 0.03$
<i>Epilobium</i> spp.	33.1	42.9	$W = 869$; $P = 0.07$
<i>Anisotome</i> spp.	32.9	43.0	$W = 866$; $P = 0.05$
<i>Chionochoa</i> spp.	35.7	41.5	$W = 791$; $P = 0.1$
<i>Poa/Rytidosperma</i>	39.0	39.8	$W = 703$; $P = 0.9$
Other grasses	42.9	37.7	$W = 571$; $P = 0.3$
<i>Coprosma</i> spp.	36.2	41.3	$W = 779$; $P = 0.3$
<i>Hebe</i> spp.	43.9	37.2	$W = 571$; $P = 0.2$
<i>Gaultheria</i> spp.	37.0	40.8	$W = 757$; $P = 0.5$
<i>Carmichaelia</i> spp.	42.9	37.7	$W = 598$; $P = 0.3$

Is the diet of chamois broader outside the thar range?

Horn's Index indicated strong overlap in the percentages of the three food categories eaten by chamois inside and outside the breeding range of thar ($H = 0.983$; 95% CI, 0.949–0.997). However, our prediction that chamois diet would be broader outside the thar range was supported by the data. Chamois sampled outside the thar range ate significantly more plant species (mean = 14.6; 95% CI, 13.4–15.8) than those sampled inside the thar range (mean = 12.0; 10.8–13.2) ($t_{76} = 2.77$, $P = 0.007$). For chamois sampled outside the thar range, *Celmisia*, *Ranunculus*, and perhaps *Epilobium* and *Anisotome* were more important in the diet than for chamois sampled inside the thar range (Table 5).

Discussion

As predicted, the diets of thar and chamois were more similar than those of thar and possums and chamois and possums. Although Himalayan thar, Alpine chamois and Australian brushtail possums evolved on different continents, thar and chamois are much more closely

related to each other than to possums and are thus more similar in many features that are important predictors of diet. In particular, possums are hind-gut fermenters with a simple stomach but well-developed colon and caecum (Hume 1999) whereas thar and chamois continually mix their foods in their multi-chambered stomachs and through re-mastication (Hofmann 1989). Our results provide support for the generality that morphologically more similar non-indigenous species will compete more than less morphologically similar species (Duncan & Forsyth 2006).

Although thar and chamois ate the same genera/species, the percentages varied greatly. Thar ate more grasses than did chamois, particularly *Chionochoa* and *Poa/Rytidosperma*. Chamois ate more herbs (particularly *Ranunculus* spp.) and more woody plants (especially *Gaultheria* and *Carmichaelia* spp.) than did thar. Possums ate almost no grasses, instead eating herbs (especially *Hieracium* and *Trifolium*), woody plants (*Podocarpus nivalis*, *Muehlenbeckia* spp. and *Aristotelia serrata*) and fruits, none of which were important in the diets of thar or chamois.

Our results broadly match those of a previous study of thar diet. Tustin (1990) reported that *Chionochoa* spp. was the dominant food item in the rums of 72

thar shot in the Macaulay Valley (eastern Southern Alps) in August 1975 (93% by DW), followed by *Podocarpus nivalis* (3.8%) and *Dracophyllum* spp. (1.7%). The only published study of chamois diet was from 40 animals shot during spring and summer in forested habitats in central Westland (Yockney & Hickling 2000). In that study, only five species (all woody plants) averaged >5% by dry weight: *Carmichaelia* spp., *Coprosma* spp., *Weinmannia racemosa*, *Griselinia littoralis*, and *Melicactus ramiflorus*. Clarke (1986) described chamois in the Avoca River region (eastern Southern Alps) feeding mostly on herbaceous species and short sward grasses. In Cupola Basin (northern Southern Alps), chamois were thought to feed mainly on the grasses *Poa colensoi*, *Chionochloa* spp. and *Festuca* spp. and the *Dracophyllum* spp. shrubs (Batcheler & Christie, cited in Gibb & Flux 1973).

Clarke (1990) described chamois as 'essentially grazers', implying they ate mainly grasses. In our study, chamois ate more woody plants than they did either herbs or grasses, and in the forests of central Westland the diet of chamois shot in spring and summer comprised $\leq 8\%$ grasses (Yockney & Hickling 2000). The high percentage of grasses in the faeces of chamois in Cupola Basin (cited in Gibb & Flux 1973) may have been (1) due to differences in food availability, (2) an artefact of herbaceous plants and leaves from woody species being relatively more digestible than grasses, and/or (3) due to high densities of red deer at that time somehow forcing chamois to utilise more grass. Along the grazer–browser continuum defined by Hofmann (1989), we would rank thar as more grazers than chamois.

Seasonality of diets

Our prediction that all three herbivores would exhibit seasonal differences in diet composition was supported by the data. The changes in diet are unsurprising given the strong seasonal changes in the central Southern Alps environment. Seasonal changes in snow cover, solar radiation, and plant quantity and quality generate strong seasonal changes in habitat use and feeding locations for thar (Tustin & Parkes 1988; Forsyth 2000) and chamois (Clarke 1986; Forsyth 2000). As well as snow making many plants 'unavailable' to animals, many alpine plant species undergo seasonal changes likely to modify their attractiveness to herbivores.

Segregation of male and female thar

One hypothesis to explain sexual segregation in ungulates is that males need to maximise their intake of high-quality food before the rut, while females with young need to avoid predation (Bleich et al. 1997). Adult male thar segregate from female groups in spring to utilise different catchments (Forsyth 1999), or at least different parts of catchments. Within Carneys Creek, adult males also preferred grassland and shrubland more than did females

in spring and summer but used habitats similarly during the rut (Forsyth 2000). Thus, we were surprised by the similarity of the diets of adult male and all female thar during October–May.

Competition between chamois and thar

We found evidence that thar influenced the diet of chamois. Relative to chamois shot inside the breeding range of thar, chamois shot outside the breeding range of thar ate both more plant genera/species and higher percentages of *Ranunculus* and *Celmisia*. Diet overlap may be an indicator of potential competition for food between ungulates (Putman 1996). Our data suggest it is possible that sustained high densities of thar could reduce the availability of plant species eaten by chamois, and there is anecdotal evidence to support this. For example, in the 1960s thar greatly reduced the biomass of *Ranunculus* spp., an important food of chamois (Tables 2 and 3), in Mount Cook National Park (Burrows 1974). Modelling based on the Lotka–Volterra competition model and parameterised with the data reported here indicates that thar can drive chamois to local extinction. However, the model showed that chamois may be able to persist when foods of differentially high value for that species relative to thar are present (J. Kean, AgResearch, Lincoln, pers. comm.).

Competition for food is only one of the possible explanations for changes in the abundance of thar and chamois in New Zealand. The introduction of ibex (*Capra ibex*) into parts of the range of Alpine chamois in the European Alps apparently led to the decline of chamois, and it was suggested this was due to high dietary overlap and the ability of ibex to eat poorer-quality food (Schröder & Kofler 1984). However, the behavioural avoidance of thar by chamois may be a more likely mechanism than food competition for the exclusion of chamois from previously used sites by increasing densities of thar (Forsyth & Hickling 1998; Forsyth & Clarke 2001).

Limitations of the study

Our main assumption in comparing diets across the study area was that the availability of major food classes was similar, particularly inside and outside the breeding range of thar. We did not quantify the availability of food resources, but pairing such data with usage data (this study) would allow dietary preferences to be estimated (Manly et al. 2002). However, it would be extremely difficult to estimate the seasonal availability of food resources in the shrubland, grassland, scree and rock-bluff habitats of the central Southern Alps.

Although thar and chamois were collected widely within their sympatric eastern Southern Alps range, possums were collected from a much smaller area (Fig. 1). The diet of possums sampled from the same areas as thar and chamois may have been different from that reported

here. Studies of possum diet elsewhere in the central Southern Alps are needed to determine the generality of our results for this species. We therefore suggest that, until other studies are published, our conclusions about the diets of possums, and hence their similarity with thar and chamois, should be treated with caution.

We had a large sample size for thar but only moderate sample sizes for chamois and possums. These sample sizes became much smaller and unbalanced for the analyses of seasonal variation in diet, the diet of chamois inside and outside the range, and the diets of adult male and all female thar when aggregated and segregated.

Managing thar, chamois and possums as pests

Forsyth et al. (2000) advocated a precautionary approach to the management of thar, chamois, and possums in the central Southern Alps, recommending that the whole suite of exotic herbivores (including red deer *Cervus elaphus* and European hares *Lepus europaeus*) needs to be managed to achieve protection of the native biota. However, the results of this study show that thar, chamois and possums have different diets, indicating that the impacts of these three herbivores will not often be cumulative. The three herbivores seem to exploit plant communities in different ways, and a manager would need to evaluate the effect of a particular herbivore on a particular plant population. However, managers need to be aware of the potential for chamois to increase in abundance, at least in some sites, if thar are controlled to low abundance (Forsyth & Hickling 1998), and that this could lead to different impacts on plant populations. As rules of thumb, if managers are interested in protecting or restoring the dominant *Chionochloa* spp. then they should control thar (see also Parkes et al. 2004 unpubl.); if they are more interested in protecting *Ranunculus* spp., then chamois should be the primary target; possums should be controlled if *Podocarpus nivalis* or *Muehlenbeckia axillaris* need to be protected.

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Appendix 1. Plant species identified in the diet of possums (* includes fruit). Plant names follow the Ngā Tipu o Aotearoa – New Zealand Plants database of the Allan Herbarium (<http://nzflora.landcareresearch.co.nz>).

Trees	Woody plants	Herbs	Ferns
<i>Aristotelia fruticosa</i> *	<i>Coprosma</i> spp.*	<i>Acaena</i> spp.	<i>Asplenium richardii</i>
<i>Griselinia littoralis</i>	<i>Coriaria angustissima</i> *	<i>Anisotome aromatica</i>	<i>Blechnum novae-zelandiae</i>
<i>Hoheria lyallii</i>	<i>Coriaria sarmentosa</i>	<i>Anisotome flexuosa</i>	<i>Blechnum penna-marina</i>
<i>Metrosideros umbellata</i>	<i>Dolichoglottis scorzonerooides</i>	<i>Anisotome haastii</i>	<i>Hymenophyllum</i> spp.
<i>Nothofagus solandri</i>	<i>Dracophyllum uniflorum</i>	<i>Brachyglottis</i> sp.	<i>Polystichum vestitum</i>
<i>Pittosporum tenuifolium</i>	<i>Exocarpos bidwillii</i> *	<i>Celmisia</i> spp.	<i>Pteridium esculentum</i>
<i>Pseudopanax colensoi</i> *	<i>Gaultheria crassa</i>	<i>Crepis capillaris</i>	
<i>Raukaua simplex</i> *	<i>Gaultheria depressa</i> *	<i>Epilobium macropus</i>	
	<i>Melicytus alpinus</i>	<i>Epilobium chlorifolium</i>	
	<i>Muehlenbeckia axillaris</i> *	<i>Gingidia montana</i>	
	<i>Muehlenbeckia complexa</i>	<i>Anaphalioides bellidioides</i>	
	<i>Myrsine divaricata</i>	<i>Hieracium praealtum</i>	
	<i>Myrsine nummularia</i>	<i>Hieracium pilosella</i>	
	<i>Parahebe linifolia</i>	<i>Hypochaeris radicata</i>	
	<i>Parsonsia capsularis</i>	<i>Leucogenes grandiceps</i>	
	<i>Phyllocladus alpinus</i>	<i>Oreomyrrhis colensoi</i>	
	<i>Pimelea</i> sp.	<i>Myosotis</i> sp.	
	<i>Podocarpus hallii</i>	<i>Raoulia tenuicaulis</i>	
	<i>Podocarpus nivalis</i> *	<i>Rumex acetosella</i>	
	<i>Rubus cissoides</i>	<i>Taraxacum officinale</i>	
	<i>Rubus schmidelioides</i>	<i>Trifolium repens</i>	
		<i>Viola cunninghamii</i>	
		<i>Wahlenbergia albomarginata</i>	