



# Behavioural exclusion of chamois by thar in the Southern Alps

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Prepared for: Science and Research Division, Department of Conservation



**Lincoln University  
Wildlife Management Report**

**No.13**

**Lincoln University Wildlife Management Report 13**

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BY THAR IN THE SOUTHERN ALPS**

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Investigation Number: 1894

Key Output: 4.21

**Prepared for:**  
Science and Research Division  
Department of Conservation

April 1997

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## **Behavioural exclusion of chamois by thar in the Southern Alps**

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### **ABSTRACT**

The hypothesis that increasing densities of Himalayan thar (*Hemitragus jemlahicus*) are associated with decreasing densities of chamois (*Rupicapra rupicapra*) in the central Southern Alps was investigated. During 1991-1996 16 sites that contained both thar and chamois during 1978-1979 were resurveyed. There was a six-fold increase in mean thar density between the two counts, whereas chamois density declined significantly. This is evidence that increasing densities of thar *do* exclude chamois from alpine habitats. Observation of 24 interspecific interactions in Carneys Creek showed that chamois moved away from thar significantly more than *vice versa*. We propose that as thar populations grow, increasing numbers of thar select habitats favoured by chamois; the resulting increase in the frequency of interspecific behavioural interactions is the proximate cause of chamois abandoning their home ranges. Behavioural avoidance of thar is an instantaneous, density-dependent mechanism that best explains the recent decline of chamois in the eastern Southern Alps. Control of thar to densities  $<3$  thar/km<sup>2</sup> is likely therefore to result in increased use of some sites by chamois. The conservation significance of such an increase will depend upon the vulnerability of conservation resources to chamois.

### **1. BACKGROUND**

The Department of Conservation has a statutory requirement to manage Himalayan thar (*Hemitragus jemlahicus*) and chamois (*Rupicapra rupicapra*) to protect conservation resources in the Southern Alps. The Himalayan Thar Control Plan (Department of Conservation 1993) defines maximum allowable densities of thar that vary according to land tenure and vegetation. However, since thar are sympatric with chamois throughout their range and there is considerable anecdotal evidence that increasing densities of thar are associated with declining densities of thar, control of thar to low densities ( $\leq 2.5$  thar/km<sup>2</sup>), as required by the Control Plan, may allow chamois populations to increase. The impact of such an increase on conservation resources is unknown but potentially important.

This study aimed to (i) determine whether increasing densities of thar are associated with declining densities of chamois, (ii) test possible mechanisms for any such exclusion of chamois by thar, and (iii) outline the management implications of these results. The study, which began in 1993 and finished in 1997, was conducted under contract to the Department of Conservation.

## 2. INTRODUCTION

Himalayan thar were liberated near Mount Cook, New Zealand (Fig. 1) in 1904 and 1909 to establish a hunting resource. Chamois were released at the same site in 1907 and 1914, also to establish a hunting resource. Both species flourished (Donne 1924). Thar underwent an irruptive oscillation (Caughley 1970a), increasing to peak densities of  $>30$  thar/km<sup>2</sup> (Tustin and Challies 1978). The postulated decline to relatively stable post-peak densities at equilibrium with the food supply has been confounded by commercial hunting since 1971 (Parkes *et al.* 1996). Chamois are inferred to have undergone similar demographic changes (Caughley 1970b; Clarke 1990) but their irruption probably peaked at densities considerably lower than thar (see Clarke and Frampton 1991).

Female thar are gregarious and sedentary on rock bluffs throughout the year (Tustin and Parkes 1988) and at peak density female-juvenile groups  $>30$  were common (Caughley 1967; Tustin and Challies 1978). Chamois in the South Island presently occupy a wide variety of habitats, ranging from low-altitude rainforest in the western Southern Alps (Pekelharing and Reynolds 1983; Yockney 1997) to the high-altitude basins of the central Southern Alps (this study). Chamois are less gregarious than thar, with groups containing more than four adults uncommon even in un hunted populations (Clarke and Frampton 1991). In both species the sexes segregate outside the April-July rut (Shank 1985; Clarke 1986; Forsyth 1997). Thorough accounts of the ecology of thar and chamois in New Zealand are given by Tustin (1990) and Clarke (1990) respectively.

The rapid dispersal of chamois relative to thar (Caughley 1963; Parkes and Clarke 1993; Fig. 2) created an initial wave of chamois colonisation north and south from Mount Cook along the central Southern Alps and lateral ranges (Clarke 1990). Thar represented a subsequent colonising wave, described in detail by Caughley (1970c) and Parkes and Tustin (1985).

Early guides and hunters in the Mount Cook region noted that chamois and thar seldom formed mixed groups, despite living in similar habitats when apart (see, for example, McIlbraith 1929). Government hunters, employed to cull thar and chamois from 1937, recorded similar observations. Davison (1946) observed that "where thar are in numbers... there are few chamois. This is most noticeable in the Hooker (Valley) where in 1935 the chamois were numerous and only a few thar... now thar are numerous on both sides and few chamois are seen." More recent workers (e.g., K. Tustin in Schaller 1977) have reported similar observations.

Government-funded ground-based hunting of thar continued until the early 1980s. The advent of helicopter-based hunting for the control of thar in 1967, and the establishment of an overseas market for carcasses in 1970, dramatically reduced the density and distribution of thar in the Southern Alps (Tustin 1980; Parkes and Tustin 1985). Annual commercial harvests of thar peaked at *ca.* 10 000 in 1974 but had fallen to  $<300$  by 1983 (Parkes *et al.* 1996). Chamois harvests followed a similar pattern (Parkes and Clarke 1993). Concern by recreational hunters about the low densities of thar during the early 1980s led to a moratorium prohibiting all commercial and most government hunting in 1983 (Hughey and Parkes 1995). Thus, since 1983 recreational hunting has been the principal form of thar control, and densities of thar have steadily increased in regularly monitored catchments (Department of Conservation 1993).

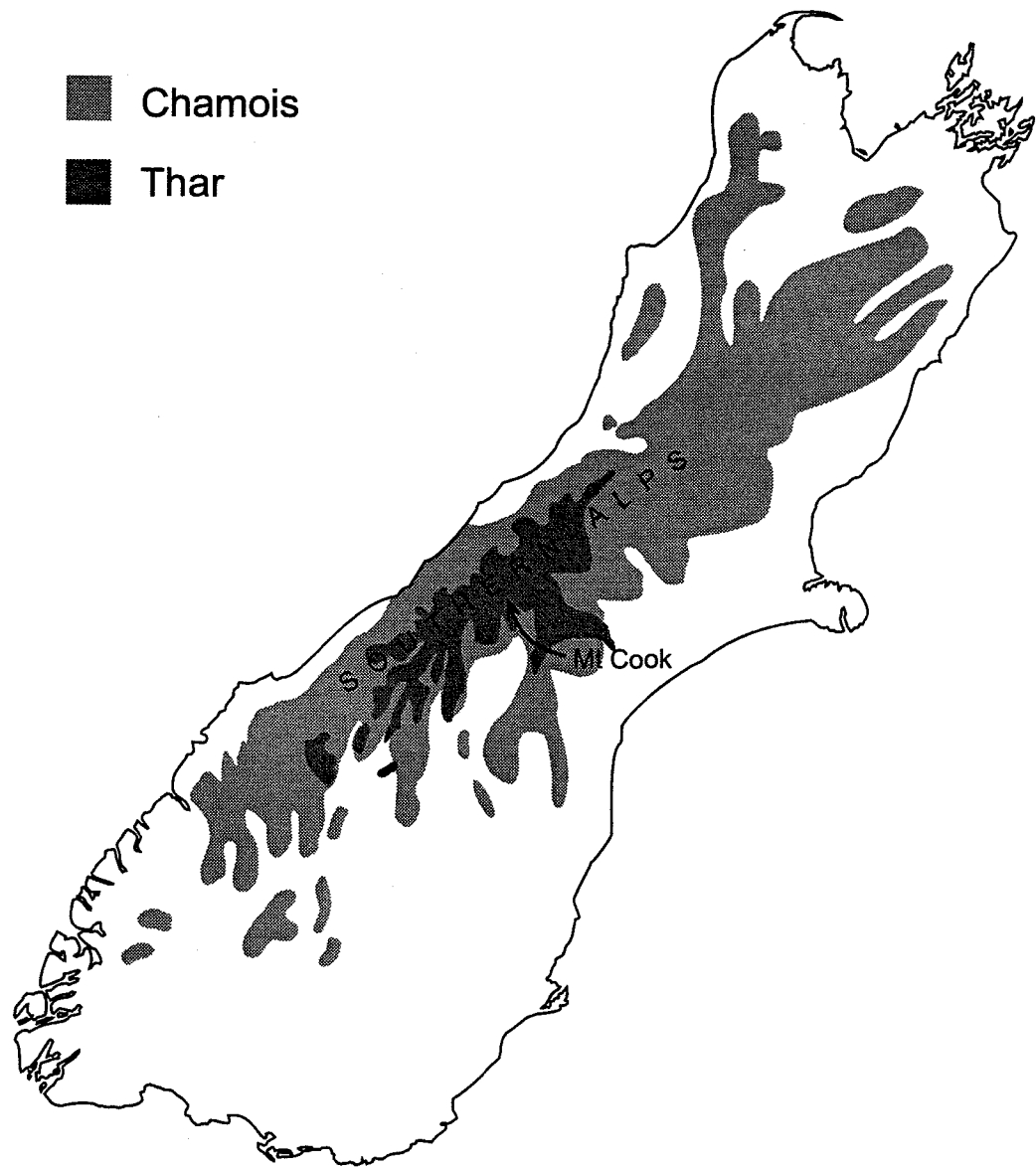


Figure 1. Liberation site (Mt. Cook) and 1996 distributions of Himalayan thar and chamois in the South Island of New Zealand (updated from Department of Conservation 1993 and Parkes and Clarke 1993).

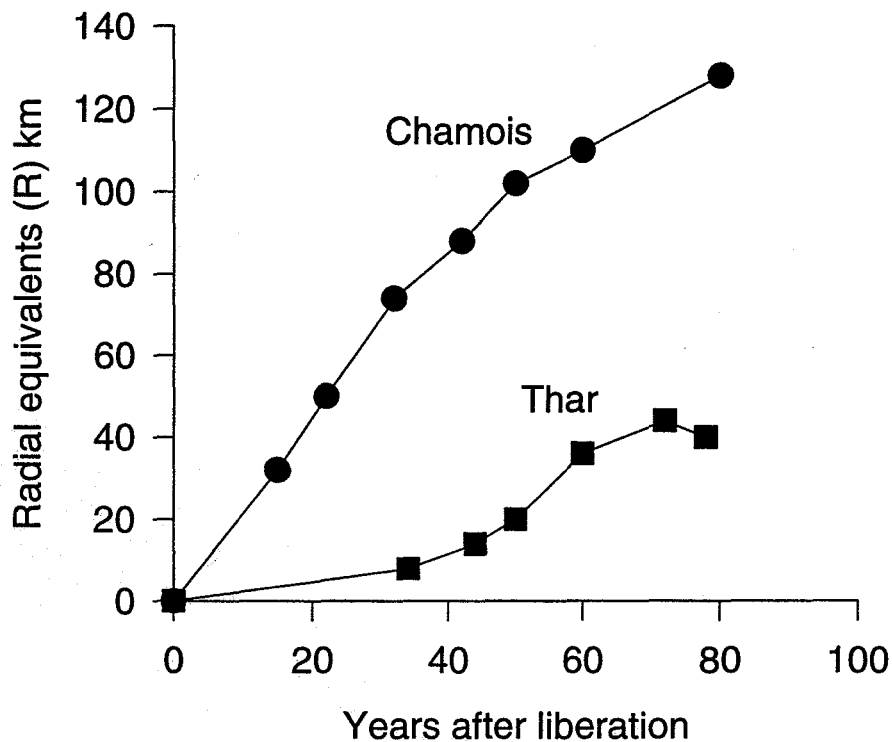


Figure 2. Dispersal of Himalayan thar and chamois liberated at Mt. Cook, New Zealand (after Parkes and Clarke 1993). The size of the breeding range is expressed as the radius of a circle of equivalent area to the observed range. Parkes and Clarke (1993) suggested that a linear model ( $y=12.76 + 1.51x$ ) provided the best fit to chamois dispersal ( $R^2=0.96$ ), and an exponential model ( $y=0.6 e^{0.07x}$ ) the best fit to thar dispersal ( $R^2=0.99$ ).

Although reliable evidence (*sensu* Romesburg 1981) for interspecific competition is best provided by removal experiments (e.g., Redfield *et al.* 1977), such experiments have not been performed with ungulates for practical reasons (Caughley and Sinclair 1994). For example, chamois in Europe have apparently been displaced by re-introductions of ibex (*Capra ibex*) (Schröder and Kofler 1984, 1985) and moufflon (*Ovis musimon*) (Gonzalez 1985), and by domestic sheep (*Ovis aries*) (Rebollo *et al.* 1993), but these studies were descriptive and provided no statistical evidence of a decline in chamois numbers related to the presence of the other ungulate. Although such data are difficult to collect, they are nevertheless required to prove competitive exclusion of one species by another (Schoener 1983; Hastings 1987). Recent events have presented a unique opportunity to test hypotheses about the numerical response of chamois to increasing densities of thar.

Forsyth (1997) described three mechanisms that could account for thar excluding chamois in the eastern Southern Alps. Briefly, the two most likely mechanisms were: (1) Dietary competition. In the absence of hunting thar attain very high densities and typically share their range with other introduced herbivores such as red deer (*Cervus elaphus scoticus*), brown hare (*Lepus europaeus occidentalis*), brushtail possum (*Trichosurus vulpecula*), and chamois. Sustained grazing by these species reduces the distribution and abundance of preferred plant species (see, for example, Caughley 1970a). Modelling has shown competition between food-limited generalist herbivores,



such as thar and chamois, to depend upon the fractions of shared and exclusive resources (Belovsky 1986). Since sympatric thar and chamois in the eastern Southern Alps feed on the same species, albeit in different proportions according to season (Parkes and Thomson 1995), chamois may have been excluded by thar through scramble competition for food.

(2) Behavioural avoidance of thar by chamois. Miller (1967) proposed that intraspecific behaviours could govern interspecific interactions between mammal species; gregarious species would be expected to dominate less gregarious species. Chamois in New Zealand are highly mobile (Clarke 1986) and space themselves by "mutual avoidance" (Clarke 1990; Clarke and Frampton 1991). In contrast, female thar are sedentary and highly social (Caughley 1967; Tustin and Challies 1978; Tustin and Parkes 1988; Tustin 1990). These innate differences in sociality may result in chamois avoiding thar groups.

Both mechanisms require habitat selection by sympatric thar and chamois to overlap, and there is *a priori* reason to believe that this may occur. Observation of chamois in the northern Southern Alps indicated a preference for habitats with "numerous rock outcrops, bluffs and steep slopes" (Christie 1963:112). Transects in the Nina Valley (eastern Southern Alps) showed chamois defecations to be most common in extensive bluff systems, steep broken country and sub-alpine shrubland (Espie 1976). Clarke (1986) observed a preference of chamois in the Birdwood Range (eastern Southern Alps) for steep and broken country. The three cited studies were all outside the breeding range of thar. Female-juvenile groups of thar live on steep, rock bluff habitats (Tustin and Parkes 1988; Tustin 1990). Thus, the potential for thar and chamois to select the same habitat appears high.

Niche theory (Gause 1934; Diamond 1978) states that when two species co-exist (termed sympatric) their habitat selection and diet will not completely overlap. Rosenzweig (1981) proposed that when resources are limiting, competing species should specialize and contract their habitat selection. If one species dominates the other (e.g., through behavioural mechanisms) and is more efficient in all habitats, then the subordinate species will be excluded (Morse 1974; Rosenzweig 1981). We propose that such a process may be responsible for the exclusion of chamois by increasing densities of thar in parts of the eastern Southern Alps, New Zealand.

### **3. OBJECTIVES**

- To test whether increasing densities of thar are associated with declining densities of chamois in the eastern Southern Alps.
- To describe seasonal changes in habitat selection by sympatric thar and chamois in Carneys Creek.
- To test whether chamois behaviourally avoid thar.
- To outline management recommendations based on the results to the preceding objectives.

## 4. METHODS

### 4.1 Do Thar Exclude Chamois?

#### 4.1.1 Densities of Thar and Chamois in 1978

Between November 1978 and April 1979 (hereinafter termed '1978') New Zealand Forest Service hunters visited 53 sites within the then breeding range of thar (Parkes and Tustin 1985) and chamois (Clarke 1990) in the eastern Southern Alps (Fig. 3). The hunters aimed to reduce the densities of thar and chamois within these sites. Sites were of variable area and selected on previous knowledge of high animal densities (i.e., non-randomly). Binoculars (8-10 X) were used to count animals from vantage points in the 4 hour post-dawn and pre-dusk periods when thar and chamois are most active (Christie 1963; Tustin and Parkes 1988; Clarke 1990). Animals were then hunted by pairs of hunters. These counts were assumed to provide an index (Caughley and Sinclair 1994) of abundance.

Figure 3. Location of 53 sites in the eastern Southern Alps, New Zealand, in which Himalayan thar and/or chamois were observed during November 1978-April 1979.

The area searched and the number of thar, chamois and other ungulates seen at each site were recorded on a 1 : 63 360 scale map. Details of the sites are given in Forsyth (1997). For each site the area searched was digitised using ARC/INFO™ (Environmental Systems Research Institute Inc. 1991) and the density of thar and chamois calculated (number/km<sup>2</sup>).

Deer were occasionally sighted but were excluded from our analyses as, relative to thar, few were observed. Chamois and thar densities were log-transformed to equalise the variances; we then used one-tailed *t*-tests to test three hypotheses regarding the densities of thar and chamois:

1. Chamois density was lower than thar density at sites where only one species occurred.
2. Chamois density was lower at sites with thar compared to those without thar.
3. Thar density was higher at sites without chamois compared to those with chamois.

#### 4.1.2 Long-Term Changes in the Densities of Sympatric Thar and Chamois

Experimental manipulation of density is required to prove competitive effects (Schoener 1983). Differential rates of hunting between sites between 1978 and 1991-1996 were treated as manipulations of thar density at sites where thar and chamois were sympatric in 1978. We used the methods outlined above to recount 16 of the 17 sites between 1991 and 1996. All counts were made during the spring to autumn period, in an identical manner to the 1978 counts. Although different observers made the 1991-1996 counts, all observers were experienced ex-government or recreational hunters. We assumed that the effects of observer differences in sightability and search effort were negligible.

We used one-tailed paired-comparisons *t*-tests (Sokal and Rohlf 1981) to evaluate changes in the densities of thar and chamois between the two surveys. Our hypotheses were:

1. Thar density had increased between the two counts.
2. Chamois density had decreased between the two counts.

## 4.2 How Do Thar Exclude chamois?

### 4.2.1 Study Area and Populations

Carneys Creek (43° 30' S, 170° 40' E; see Fig. 3) drains northward from the Two Thumb Range into the Havelock River, a tributary of the Rangitata River. The 19.1 km<sup>2</sup> catchment is steeply dissected, rising from the valley floor at 800 m to >2000 m peaks in the headwaters. Extensive areas of rock bluff and scree intergrade into patches of tussock and, at lower altitudes, shrubland. Annual precipitation is 4000-5000 mm, with rain or snow occurring on two days in three (Canterbury Regional Council, unpublished data). There is snow on all but the steepest slopes from June until August. Seasonal changes in habitat availability are described in detail below.

Chamois colonised Carneys Creek in the mid 1920s (Davidson 1965) and were probably close to peak density when government hunters observed *ca.* 100 animals of mixed age and sex in the catchment in 1939 (L. Pracy, unpublished data). These hunters also observed 10 thar in Carneys Creek; Caughley (1970c) considers these to have been males, with breeding females not arriving until about 1950.

In the mid 1960s Carneys Creek was closed to all hunting. A census in summer 1965, when the thar population was at peak density, recorded 710 thar (670 females and juveniles, and 40 males  $\geq 2$  years) (Tustin and Challies 1978). Intensive commercial helicopter-based shooting of thar during the 1970s and early 1980s reduced the population dramatically, with just 26 thar censused in Carneys Creek during February 1984 (Forsyth 1997). Aerial hunting of thar was prohibited in the study area from 1983 and annual summer censuses from 1984-1996 revealed an increase in the Carneys Creek thar population of *ca.* 20% per annum (Forsyth 1997). Long-term changes in the density and sex ratio of thar in Carneys Creek are described in Forsyth (1997). Briefly, from 1990-1994 recreational hunting reduced the number of female thar resident in Carneys Creek. An annual spring influx of sub-adult male (2-4 years old) thar, which leaves the catchment again each autumn, resulted in a summer population that since 1991 has been significantly male-biased ( $P < 0.05$ ) relative to the estimated population sex ratio of 1 male : 1.53 females ( $\geq 2$  years) (Forsyth 1997).

Although red deer were once common in the study area intensive commercial helicopter-based hunting has reduced their density and they are now restricted to low altitude forest patches (Guest and Wilkinson 1976). No deer were seen during this study. Introduced brushtail possums were common in low altitude shrubland, and brown hares were present in low densities throughout the catchment.

Intensive hunting has been shown to modify the behaviour of chamois (Douglas 1971) and thar (Tustin and Challies 1978), making surviving animals difficult to observe. Hunting was therefore prohibited in Carneys Creek during this study to maximise observations of undisturbed animals.

#### 4.2.2 Ground-Based Observations

From December 1993 to February 1996 habitat use was observed monthly from five sites in periods of good visibility. Sites were approximately midway between the valley floor and ridges, and gave clear views of discrete sectors in the headwaters of Carneys Creek (Figure 4).

All observations were made by the senior author, eliminating possible inter-observer bias. Binoculars (10 X 40) were used to search the sector in the 3 h post-dawn or pre-dusk, when chamois and thar are most active. During spring and summer, heat shimmer prevented observation outside this 3 h period, and in winter thar are known to spend most daylight hours in non-feeding behaviours (Tustin and Parkes 1988). Each site was visited either once or twice per month, except for two months when adverse weather prevented access to Carneys Creek.

A 20 X spotting scope was used to classify groups ( $\geq 1$  individual) into five thar and two chamois age-sex classes according to physical, behavioural and habitat cues (see Appendix). We defined a group for all species-age-sex classes as consisting of individuals exhibiting collective behaviour (Martin and Bateson 1986), but on the basis of previous work (Clarke and Frampton 1991) arbitrarily defined the maximum distance between two group members as being 100 m.

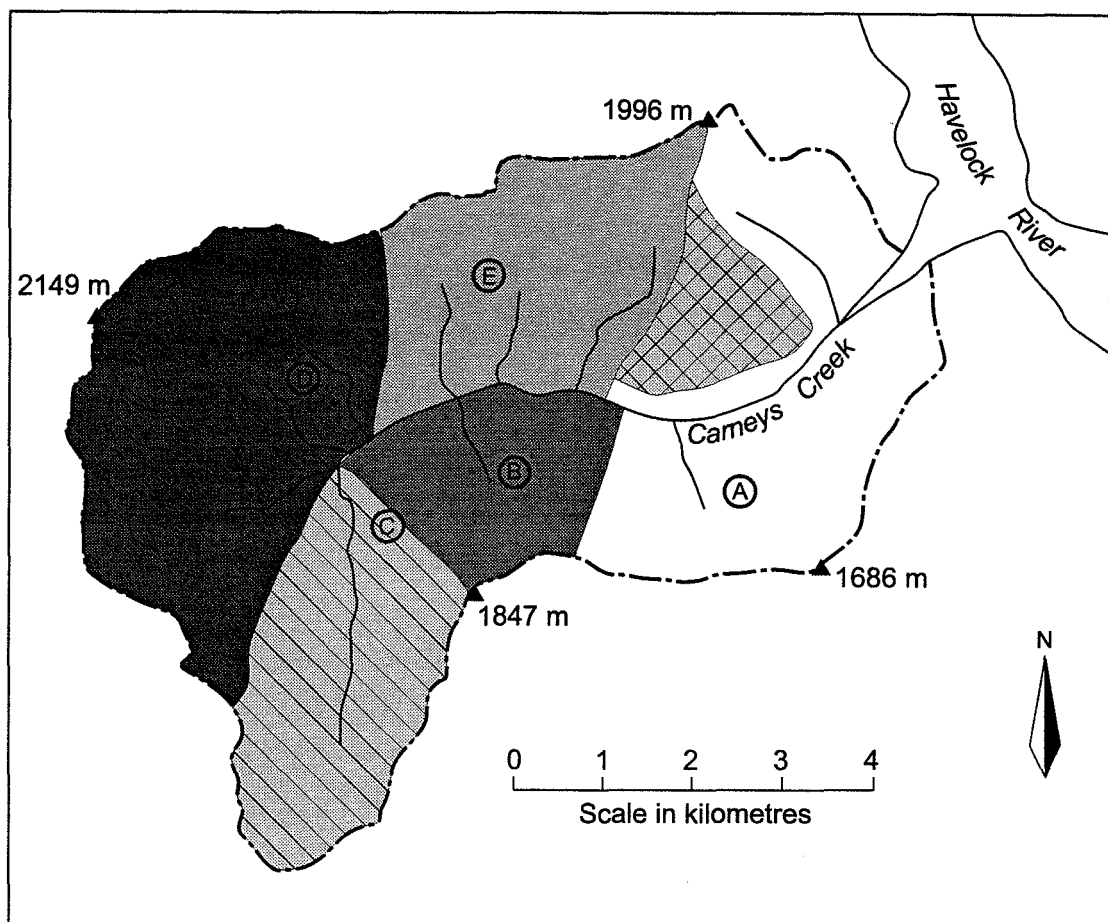


Figure 4. Observation sites (○) used to observe thar and chamois from December 1993-February 1996 in Carneys Creek, New Zealand. Shading indicates the five different areas searched monthly from the lettered observation sites across the valley.

The altitude ( $\pm 10$  m) and location (1 ha) of each individual within a group was estimated from an enlarged 1 : 50 000 scale map (NZMS260, I35). Six vegetation classes that were easily-identifiable (using binoculars and aerial photographs) were assigned: grassland, grass bluff, rock bluff, shrubland, scree, and snow (Table 1). Neither thar nor chamois could be sighted within the low-altitude forest patches present in the lower portion of the study area, so these were not searched.

Female thar exhibit a consistent daily altitudinal movement (Tustin and Parkes 1988), so we attempted to incorporate resultant changes in habitat selection by re-locating all thar and chamois groups at 30 minute intervals. A maximum of five minutes was spent attempting to relocate sighted groups. Between re-locating sighted groups, the sector was continuously searched to locate new groups.

#### 4.2.3 Accuracy of Observed Age-Sex Classes

Chamois and thar were shot throughout the Southern Alps by the senior author to obtain rumens for an associated diet study (Parkes and Thomson 1995). To check the methods described above, the age-sex class was estimated when first sighted and the actual age-sex class was recorded during necropsy. Chamois were aged as adult or kid by body

Table 1. Physiognomic and floristic description of the six habitat types delineated in Carneys Creek, New Zealand. Descriptions are based on 20 vegetation monitoring plots (J.P. Parkes and C. Thomson, unpublished data), diet analysis of thar (n=31) and chamois (n=2) rumens from Carneys Creek (Parkes and Thomson 1995), Burrows (1977), Wardle (1991), Mark and Adams (1995), and Wilson (1996). Floristic lists are indicative rather than exhaustive. For taxonomic authorities see Allan (1961), Zotov (1963) and Connor and Edgar (1987).

Habitat	Description
Grassland	The dominant tall (>0.3 m) vegetation is tussock (principally <i>Chionochloa pallens</i> , <i>C. flavescens</i> , <i>C. crassiuscula</i> , <i>Poa colensoi</i> , and <i>Rytidosperma setifolium</i> ), with <i>Aciphylla</i> spp. and <i>Dracophyllum</i> spp. at lower altitudes. Lower tiers dominated by <i>Celmisia</i> spp., <i>Ranunculus lyallii</i> , <i>Dolichoglottis scorzoneroides</i> , <i>Luzula</i> spp., <i>Uncinia</i> spp., <i>Gaultheria depressa</i> , <i>G. crassa</i> , <i>Raoulia grandiflora</i> , <i>Schoenus pauciflorus</i> , <i>Anisotome</i> spp., and <i>Hieracium</i> spp. This habitat typically occurs on moderate slopes (<30°) and in basins >1200 m. Some adventive species (e.g., <i>Trifolium repens</i> and <i>Agrostis capillaris</i> ) may occur on low altitude disturbed sites.
Grass bluff	Steeper (≥30°) grasslands intergrading into rock bluff, typically at higher altitude than grassland. Floristic characteristics of both grassland and rock bluff habitats.
Rock bluff	Predominantly greywacke rock. Some herbs ( <i>Anisotome</i> spp. and <i>Epilobium</i> spp., <i>Gingidia montana</i> , <i>Geum parviflorum</i> , <i>Leucogenes grandiceps</i> , <i>Uncinia divaricata</i> , <i>Schoenus pauciflorus</i> , <i>Luzula</i> spp., <i>Ranunculus sericophyllus</i> , <i>R. grahamii</i> , <i>Schizeilema haastii</i> , and <i>Hebe haastii</i> ), mosses and lichens present. <i>Poa novae-zelandiae</i> also common.
Shrubland	Woody plants (principally <i>Hebe</i> spp., <i>Coriaria</i> spp., <i>Carmichaelia</i> spp., <i>Dracophyllum</i> spp., <i>Myrsine nummularia</i> , <i>Podocarpus nivalis</i> , <i>Coprosma</i> spp., <i>Muehlenbeckia australis</i> , <i>Pseudopanax colensoi</i> var. <i>ternatus</i> , <i>Phyllocladus alpinus</i> , and <i>Podocarpus hallii</i> ) occupying stable sites from the valley floor to ca. 1300 m. Dwarf form of <i>Gaultheria crassa</i> common. In mesic sites, herb species (e.g., <i>Ranunculus lyalli</i> , <i>Anisotome</i> spp., and <i>Celmisia</i> spp.), ferns ( <i>Blechnum</i> spp.) and mosses are often abundant. At upper altitudinal limit transitional into grassland or grass bluff.
Scree	Steep, shingle-dominated slopes (usually >30°), and creekbeds. Occurs extensively in higher altitude (>1300 m) basins. Specialised herbs ( <i>Hectorella caespitosa</i> , <i>Epilobium glabellum</i> , <i>Anisotome pilifera</i> , various <i>Aciphylla</i> spp., <i>Leucogenes grandiceps</i> , and <i>Raoulia</i> spp.) and lichens present in low abundance on stable sites.
Snow	Snow and permanent ice. Some tall grassland and shrubland species may be emergent during winter.

size and horn length, and thar of both sexes were aged according to the number of horn rings (Caughley 1965).

#### 4.2.4 Group Sizes

We used Jarman's (1982:336) method of calculating group size rather than mean group size because the former gives an animal-centred assessment of sociality. If  $N$  is the number of sampled groups and  $g_i$  is the size of each group, individuals experience a group size on average of

$$\bar{g} = \frac{\sum_{i=1}^N g_i^2}{\sum_{i=1}^N g_i},$$

with variance

$$\text{var}(\bar{g}) = \frac{\sum g_i^3 - (\sum g_i^2)^2}{\sum g_i} \times \frac{1}{(\sum g_i) - 1}.$$

Re-sighted groups were excluded from this analysis. Mean group size,  $\bar{g}$ , was calculated for each 3 h observation period; if no groups were seen then that observation period was omitted from that species-age-sex class analysis. We tested the null hypothesis that group sizes were independent of season for each species-age-sex class using non-parametric ANOVA and Bonferroni-adjusted Mann-Whitney tests for the individual contrasts. We also tested the null hypothesis that thar and chamois group sizes were not different within each season; to reduce the number of comparisons we used  $\bar{g}$  calculated for all thar groups (i.e., males, females and mixed-sex groups pooled) within each 3 h period.

#### 4.2.5 Altitudinal Movements

We calculated mean morning and evening altitudinal changes (positive or negative metres minute<sup>-1</sup>) for re-sighted thar and chamois groups. When a group divided during observation the largest sub-group was followed. Since a discrete, non-overlapping area was searched from each observation site, the mean for each of the five sites was used as a replicate for each season. Sample sizes were insufficient to test for a year effect. We used repeated measures ANOVA to investigate species, seasonal, and morning and evening changes in altitude.

#### 4.2.6 Habitat Availability

Habitat availability is the quantity of habitat accessible to the study population (Manly *et al.* 1993). Given the agility and mobility of both chamois and thar (see Clarke 1990 and Tustin 1990, respectively), we assumed that all habitats in Carneys Creek were potentially available to all age-sex classes.

We evaluated habitat selection in four seasons; spring (Sept.-Nov.), summer (Dec.-Feb.), autumn (Mar.-May), and winter (Jun.-Aug.). There was *a priori* reason to believe that this classification had biological significance. Indices of abundance showed sub-adult male thar in Carneys Creek (Forsyth 1997) and marked chamois in the nearby Birdwood Range (Clarke and Frampton 1991) to be seasonally mobile in these seasons.

Aerial photographs were taken in winter (1 August 1995), spring (13 November 1995) and autumn (25 March 1996) from a fixed-wing aircraft using a 55 mm lens at 4000 m altitude. The same flightpath was flown on each occasion. Snow conditions on these dates were considered representative of the particular season; because snow was not permanent until June (i.e., winter) the autumn habitat estimates were also used for summer. The area of each habitat was digitised using the ARC/INFO<sup>TM</sup> GIS (Environmental Systems Research Institute, Inc. 1991). Although there will have been

error in assuming that habitat availability was constant within each season (due to monthly changes in snow cover), this error was assumed to be small.

#### 4.2.7 Habitat Selection

Our habitat selection data collection conformed to the Design I format (Thomas and Taylor 1990) with sampling protocol A (Manly *et al.* 1993). That is, individual animals were not identified and were assumed to be randomly sampled, and the proportion of available habitat types was measured rather than estimated (Manly *et al.* 1993).

The assumption that observations for one animal are independent of observations for other animals is violated if animals exhibit territorial behaviour for selected habitats with limited availability, or if animals exhibit grouping behaviour (Allredge and Ratti 1992). In both thar and chamois the former appears weak (see Schaller 1977; Clarke 1990; Tustin 1990). However, male and female thar are gregarious, with female-juvenile groups of >30 common in populations near peak density (Tustin and Challies 1978). To minimise dependency we randomly selected one individual from each sampled group (Allredge and Ratti 1992) for all species-age-sex classes. Re-sighted groups were included in our estimates of habitat selection. Yearling thar and kids of both species, when associated with females, were excluded from our analyses because they select the same habitats as their mother.

The assumption that each observation is independent of every other observation is often impractical in terms of data collection (McNay *et al.* 1994). Although we included re-sighted groups in our estimates of habitat selection, dependency was minimised by the long period over which sampling occurred (see Manly *et al.* 1993).

Two independent comparisons of habitat selection were made. We firstly compared habitat selection between thar (male and female observations pooled) and chamois. Our null hypothesis was that thar and chamois do not select habitats differently. When male and female thar are spatially segregated during spring, summer and autumn (Forsyth 1997), differences in habitat selection can be expected (see Main, Weckerly and Bleich 1996). We then compared habitat selection between male and female thar. Our second null hypothesis was that male and female thar do not select habitats differently within each season.

We calculated selection ratios and Bonferroni-adjusted 95% confidence intervals (Manly *et al.* 1993:40-47) for the habitats available in each of the four seasons separately for the two independent comparisons. A habitat was *selected* (i.e., used selectively) if the confidence interval did not include 1. If selected, a habitat was *preferred* if the interval was >1, and *avoided* if <1 (Manly *et al.* 1993).

We adopted the notation used by Manly *et al.* (1993) in our analyses:  $u_{jk}$  = the total number of observations in season  $j$  for species  $k$ ;  $o_{ijk}$  = the proportion of observations in habitat  $i$  in season  $j$  for species  $k$ ;  $\pi_{ij}$  = the proportion of habitat  $i$  available in season  $j$ . The selection ratio,  $w_{ijk}$ , was calculated as

$$\hat{w}_{ijk} = \frac{o_{ijk}}{\pi_{ij}},$$

and the 95% confidence interval

$$\hat{w}_{ijk} \pm Z_{\alpha/2n} \text{se}(\hat{w}_{ijk}),$$



where  $n$  is the total number of comparisons being made within each season  $j$ . The standard error of a selection indice was

$$se(\hat{w}_{ijk}) = \sqrt{\frac{O_{ijk}(1 - O_{ijk})}{U_{jk}T_{ij}^2}}$$

Standardised selection ratios ( $B_{ijk}$ ), which enabled direct comparison between selection ratios within each season, were calculated according to Manly *et al.* (1993:40). Comparisons of habitat selection by thar and chamois, and male and female thar (in which case sex was substituted for species), were explored within each season using a chi-square test of independence. When the expected values for seldom-used habitats (scree and snow) were  $<1$  then these habitats were pooled. If the chi-square test indicated significant differences in selection ( $P < 0.1$ ) then the pairwise comparisons were calculated using the binomial proportion

$$\frac{\hat{p}_{ijt} - \hat{p}_{ijc}}{\sqrt{p_{ij}^* (1 - p_{ij}^*)} \sqrt{\frac{1}{n_{ijt}} + \frac{1}{n_{ijc}}}}$$

where

$$p_{ij}^* = \frac{U_{ijt} + U_{ijc}}{T_{jt} + T_{jc}}$$

and  $T_{jk}$  is the total observations for species  $k$  in season  $j$ .

When making multiple contrasts the probability of making a Type I error,  $\alpha$ , increases such that the  $P$  value for each contrast needs to be adjusted if  $\alpha$  is to be correct. We used Holm's method (Wright 1992:1008; see also Arthur *et al.* 1996) for these pairwise comparisons. Briefly,  $P$  for the individual contrasts were calculated as  $P(\text{adjusted}) = P(\text{unadjusted}) (H - r + 1)$ , where  $H$  was the number of contrasts and  $r$  is the rank of  $P(\text{unadjusted})$  for a particular contrast, ranked from smallest to largest within each season. Testing ends with the first non-significant result ( $P \geq 0.1$ ) and all contrasts with larger  $P(\text{unadjusted})$  are assumed to be non-significant.

#### 4.2.8 Relative Niche Breadth

We calculated Simpsons equitability index ( $E$ ; Begon *et al.* 1986:595) as a measure of niche breadth for thar and chamois in each season using the standardised selection index ( $B_{ijk}$ ).  $E$  approaches 1 with increasing equitability of selection among the habitat types. Grassland and scree were considered unavailable during winter for this analysis. We also calculated the Bonferroni-adjusted probability that the resource utilisation curve of thar or chamois could be drawn from the resource utilisation curve of chamois or thar, respectively, within each season (see Ludwig and Reynolds 1988:115-6).

#### 4.2.9 Interspecific Behavioural Interactions

Behavioural interactions between thar and chamois were recorded in Carneys Creek as part of the observations described above. Additionally, one interaction was observed in the North East Gorge, *ca.* 10 km from Carneys Creek, during an associated study.

An interaction was defined as occurring when groups ( $\geq 1$ ) of thar and chamois were within 100 m and could see each other. Clarke and Frampton (1991) defined 100 m as the maximum distance between two members of a chamois group, and that classification was also used in this study (see above). It proved difficult to determine the cause of a change in group behaviour at distances  $>100$  m because of the mountainous terrain. *Ad libitum*

sampling (Martin and Bateson 1986) was used to record each interaction. All interactions were observed by the senior author.

Because of the small number of interactions observed we classified observations into four outcomes on the basis of group movement and behaviour;

1. *Neither displaced.* Neither group markedly changed behaviour nor moved away from the other.
- 2/3. *Thar displaced/Chamois displaced.* One group moved away from the other in a manner indicative of an active response. (This was usually accompanied by a dramatic change in behaviour by the displaced species; e.g., from feeding to running).
4. *Both displaced.* Both groups changed direction and behaviour in response to the other.

## 5. RESULTS

### 5.1 Do Thar Exclude Chamois?

#### 5.1.1 Densities of Thar and Chamois in 1978

Mean thar density in thar-only sites was greater than the mean chamois density in chamois-only sites (Table 2; one-tailed  $t_{34} = 1.92$ ,  $P = 0.032$ ). Thar density was lower in sites containing chamois compared to sites without chamois (one-tailed  $t_{42} = 1.88$ ,  $P = 0.033$ ). Chamois density was lower in sites with thar than without thar (one-tailed  $t_{24} = 2.42$ ,  $P = 0.012$ ).

The likelihood of both species being seen was positively associated with the size of the area searched. Mixed sites were significantly larger than sites containing only thar or chamois ( $10.6 \pm 1.5$  (SE)  $\text{km}^2$  and  $5.9 \pm 0.8$   $\text{km}^2$ , respectively; normal approximation to a Mann-Whitney  $Z = 3.06$ ,  $P = 0.002$ ).

Table 2. Mean density index (number  $\text{km}^{-2}$ ) of thar and chamois in 53 sites during November 1978-April 1979 in the eastern Southern Alps, New Zealand.

Site status	Species	No. of sites	Mean density $\pm$ SE
Both species present	Thar	17	$1.87 \pm 0.46$
	Chamois	17	$0.53 \pm 0.12$
One species present	Thar	27	$3.52 \pm 0.67$
	Chamois	9	$1.44 \pm 1.43$

#### 5.1.2 Effect of Increasing Thar Densities 1978-1996

High densities of domestic sheep were recorded in two sites during 1991-1996; these were excluded from our analyses leaving 14 sympatric sites. There was a six-fold increase in the mean density of thar between the two counts (Fig. 5; one-tailed paired  $t_{13} = 3.73$ ,  $P = 0.001$ ), whereas chamois density declined at all but one site (one-tailed paired

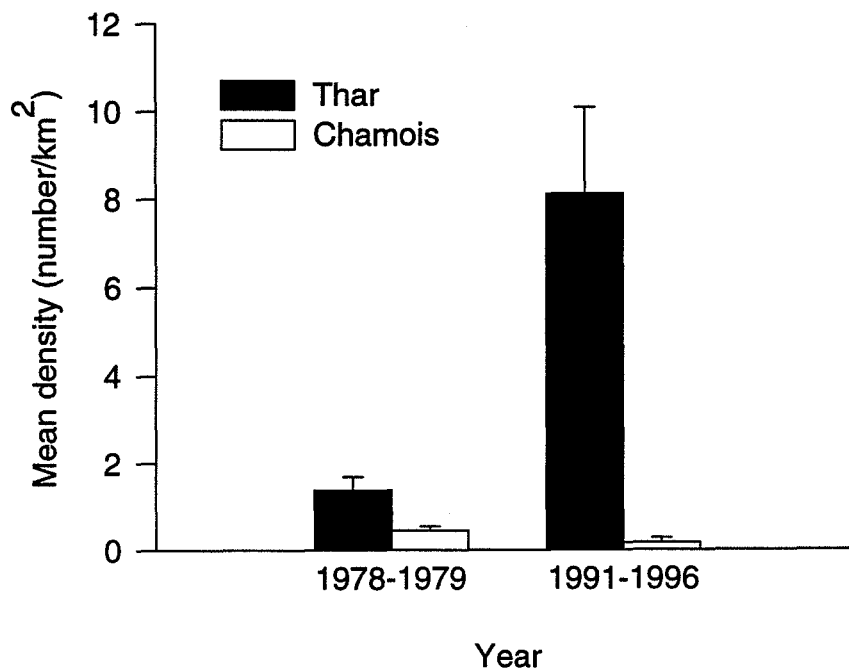


Figure 5. Mean densities (+ SE) of sympatric Himalayan thar and chamois at 14 sites in the eastern Southern Alps, New Zealand, during 1978-1979 and 1991-1996. All commercial and most government hunting of thar was prohibited by government order in 1983.

$t_{13} = 2.92, P = 0.006$ ). Chamois were recorded at only 3 of the 14 sites during 1991-1996. Two of these sites had the highest densities of chamois recorded during 1978. The third was the only site where the density of thar declined between the two counts.

## 5.2 How Do Thar Exclude Chamois?

### 5.2.1 Accuracy of Observed Thar and Chamois Classification

All 12 chamois shot were accurately classified (Table 3). Of 29 thar shot during spring and summer only one individual was wrongly identified; a kid (*ca.* 5 months old) was misclassified as a yearling.

### 5.2.2 Group Sizes

Male thar groups were significantly smaller in winter than in other seasons (Table 4). Chamois groups were smaller in summer than in autumn, but female thar and mixed-sex thar group sizes were similar throughout the seasons. Pooled thar groups were larger than chamois groups in spring ( $z = 4.54, P < 0.0001$ ) and summer ( $z = 6.54, P < 0.0001$ ), but not in autumn ( $z = 1.41, P = 0.64$ ) and winter ( $z = 0.71, P = 1.00$ ).

Table 3. Age-sex classes of thar and chamois shot by the senior author between December 1993 and March 1996 in the Southern Alps, New Zealand.

	Season			
	Spring	Summer	Autumn	Winter
<b>Thar</b>				
Adult males	1	5	2	-
Sub-adult males	-	4	-	-
Females	1	10	1	-
Yearlings	-	7	-	-
Kids	-	1	1	-
Total	2	27	4	0
<b>Chamois</b>				
Adults	-	7	1	2
Kids	-	1	-	1
Total	0	8	1	3

Table 4. Mean seasonal group sizes [ $\bar{g} \pm SD (n)$ ] of chamois, male-only thar, female-only thar, and mixed-sex thar groups in Carneys Creek, New Zealand, December 1993-February 1996. Refer to text for group and season definitions.

Group	Season			
	Spring	Summer	Autumn	Winter
Male thar <sup>a</sup>	4.88 ± 2.20 (27)	6.03 ± 3.50 (42)	4.51 ± 2.42 (30)	1.59 ± 0.59 (16)
Female thar <sup>b</sup>	1.69 ± 0.55 (11)	4.23 ± 1.84 (23)	4.24 ± 1.86 (11)	1.36 ± 0.46 (7)
Mixed thar <sup>c</sup>	4.38 ± 1.92 (13)	6.00 (1)	5.75 ± 1.81 (8)	7.44 ± 3.70 (12)
All thar <sup>d</sup>	4.41 ± 1.85 (35)	5.62 ± 3.13 (51)	4.78 ± 2.17 (38)	5.76 ± 3.57 (19)
Chamois <sup>e</sup>	1.86 ± 0.79 (25)	1.75 ± 0.84 (36)	2.85 ± 0.91 (19)	2.73 ± 1.02 (10)

<sup>a</sup> Winter group size was smaller than spring ( $z = 3.26$ , Bonferroni-adjusted  $P = 0.03$ ), summer ( $z = 4.97$ ,  $P = 0.0003$ ), and autumn ( $z = 3.06$ ,  $P = 0.002$ ).

<sup>b</sup> Seasonal differences were not significant ( $z \leq 2.77$ ,  $P \geq 0.14$ ).

<sup>c</sup> Seasonal differences were not significant ( $z \leq 1.45$ ,  $P = 1.00$ ).

<sup>d</sup> Seasonal differences were not significant ( $z \leq 2.15$ ,  $P \geq 0.94$ ).

<sup>e</sup> Summer group size was smaller than autumn ( $z = 3.22$ ,  $P = 0.03$ ).

### 5.2.3 Altitudinal Changes

Surprisingly, there was no significant seasonal difference in mean morning or evening altitudinal change for thar ( $F_{3,9} \leq 0.548$ ,  $P \geq 0.67$ ; Figure 6). This was most likely to have been a consequence of large between-site variation in altitude and habitat availability that appeared to influence the rate of daily altitudinal movement for thar (D.M. Forsyth, personal observation); this was reflected in the large standard errors for that species. There was also no significant seasonal difference in mean morning or evening altitudinal change for chamois ( $F_{3,5} \leq 2.00$ ,  $P \geq 0.22$ ; Figure 6). When the data were averaged over all seasons, thar did move significantly faster than chamois (thar =  $0.34 \text{ m min}^{-1}$ , chamois =  $0.04 \text{ m min}^{-1}$ , Wilcoxon normal approximation  $z = 2.02$ ,  $P = 0.04$ ). As anticipated, thar moved upslope in the morning and downslope in the evening ( $z = 1.75$ , one-tailed  $P = 0.04$ ).

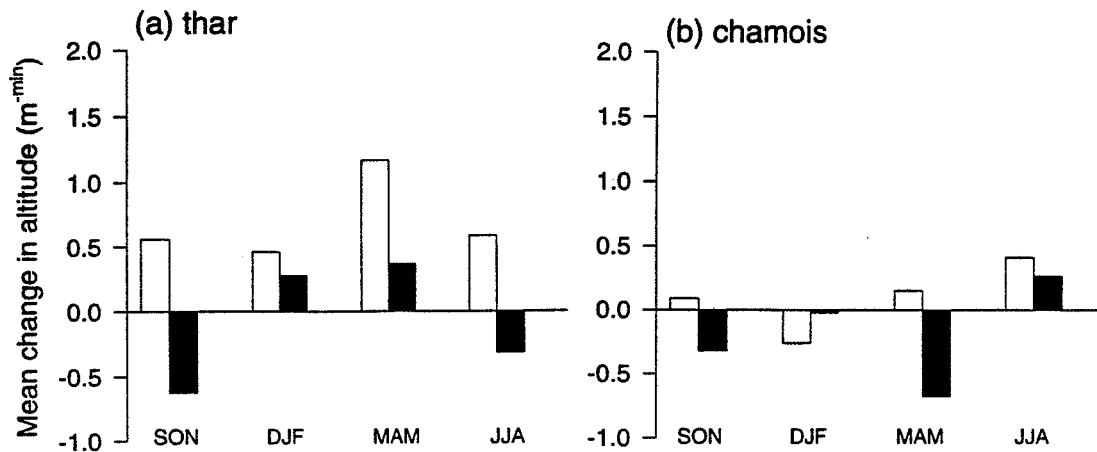


Figure 6. Seasonal mean altitudinal movement of thar (male and female pooled) and chamois during 3 h observation periods in the morning (open bars) and evening (solid bars) in Carneys Creek, New Zealand. SON, spring; DJF, summer; MAM, autumn; JJA, winter.

#### 5.2.4 Seasonal Habitat Availability

Snow dominated the landscape in winter (85% cover) and spring (49%) (Figure 7). same (see text). During winter the only available vegetated habitats were shrubland, grass bluff and rock bluff. In summer and autumn, scree (44%) was the commonest habitat, followed by rock bluff (24%), grassland (13%), and grass bluff (12%). Shrubland only constituted 4% of summer habitat.

#### 5.2.5 Habitat Selection

A total of 897 observations of thar (653 males and 244 females) and 431 of chamois were made during 177 observation periods (*ca.* 531 hours) and used in our analyses (Table 5; Table 6). Observations of thar were significantly male-biased in all seasons relative to the estimated Southern Alps adult population sex ratio of 1 male : 1.53 females ( $G \geq 26.76$ ;  $P < 0.001$ ).

##### 5.2.5.1 Thar and Chamois

Scree and snow were generally avoided by both thar and chamois in the seasons in which they were available (Table 5). In the other seasons there were insufficient observations (*i.e.*,  $u_i < 5$ ) to make reliable inferences about the selection of these habitats.

In every season, grassland (except winter, when it was unavailable), grass bluff, rock bluff, and shrubland were either used in approximate proportion to their availability (*i.e.*, not selected) or preferred by thar. Chamois exhibited a similar pattern of habitat selection, except that grass bluff was avoided in spring and summer, and rock bluff avoided during summer. Chamois and thar both preferred shrubland and grassland during spring and summer.

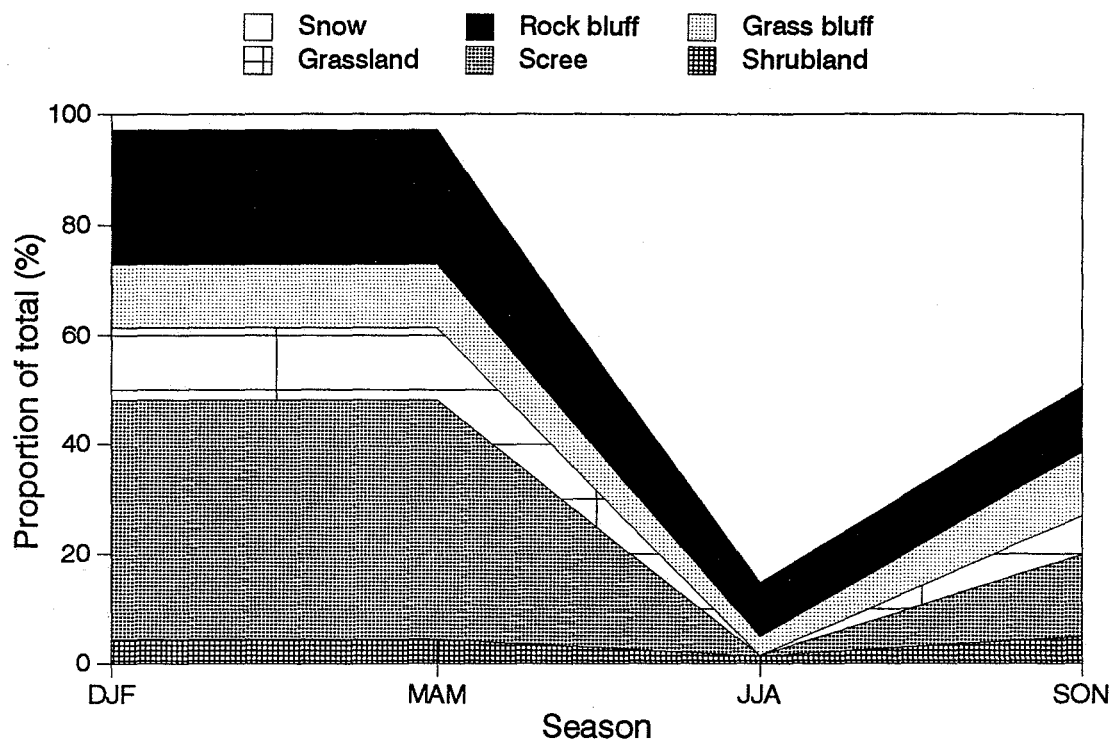


Figure 7. Seasonal changes in the availability of six habitats in Carneys Creek, New Zealand. The area of each habitat was estimated from aerial photographs taken in winter, spring and autumn; summer and autumn habitat availability is assumed to be equal (see text).

Standardised selection ratios ( $B_i$ ) indicated that shrubland in winter was the most preferred habitat among all seasons for both chamois and thar. Thar selected grassland, grass bluff, rock bluff, and shrubland more similarly in spring, summer and autumn compared to winter. Chamois preferred shrubland more than any habitat in all seasons except autumn, when grassland was more preferred.

Habitat selection by the two species differed significantly in spring ( $\chi^2_5 = 65.70$ ,  $P < 0.0001$ ), summer ( $\chi^2_4 = 67.28$ ,  $P < 0.0001$ ) and winter ( $\chi^2_3 = 10.89$ ,  $P = 0.01$ ), but not in autumn ( $\chi^2_4 = 5.33$ ,  $P = 0.38$ ). Chamois and thar selection ratios were significantly different ( $P < 0.1$ ) in 10 paired comparisons. During spring chamois selected grassland, shrubland, scree, and snow significantly more than thar, but selected grass bluff and rock bluff significantly less. There was a similar pattern in summer, but thar and chamois selected grassland similarly. Although shrubland was highly preferred by both species in winter, chamois preferred this habitat significantly more than thar.

Fewer observations of chamois and thar were recorded in autumn and winter compared to spring and summer, so the probability of Type II errors increased in these seasons.

Table 5. Seasonal habitat selection indices for Himalayan thar and chamois in Carneys Creek, New Zealand, 1993-1996 (continued overleaf).

Habitat	$\pi_i$	$u_i$	Thar				Chamois					z	$P_{\text{Holm}}$
			$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$	$u_i$	$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$		
<b>Spring</b>													
Grassland	0.071	76	3.811	2.822	4.802	0.331	49	8.154	6.554	9.754	0.363	-2.09	0.095
Grass bluff	0.116	47	1.436	0.929	1.942	0.125	3 <sup>c</sup>	0.304	0.000	0.668	0.013	2.15	0.095
Rock bluff	0.121	95	2.770	2.157	3.384	0.241	12	1.161	0.506	1.817	0.052	3.64	0.002
Scree	0.150	9	0.213	0.028	0.398	0.018	13	1.020	0.471	1.570	0.045	-2.92	0.01
Shrubland	0.049	44	3.204	2.028	4.380	0.278	48	11.596	9.265	13.926	0.517	-4.96	<0.0001
Snow	0.493	11	0.079	0.017	0.141	0.007	9	0.215	0.072	0.358	0.010	-1.34	0.095
Total	1.000	282	11.513			1.000	134	22.450			1.000		
<b>Summer</b>													
Grassland	0.132	150	3.043	2.535	3.552	0.371	81	3.513	2.757	4.270	0.301	-1.41	NS
Grass bluff	0.116	65	1.512	1.060	1.963	0.184	10	0.497	0.093	0.902	0.043	2.71	0.02
Rock bluff	0.242	86	0.956	0.716	1.195	0.116	9	0.214	0.030	0.398	0.018	3.24	0.005
Scree	0.437	31	0.191	0.104	0.277	0.023	19	0.250	0.106	0.393	0.022	-1.02	NS
Shrubland	0.044	38	2.322	1.376	3.267	0.283	55	7.184	5.061	9.307	0.616	-6.54	<0.0001
Snow	0.029	2 <sup>c</sup>	0.187	0.000	0.537	0.023	0 <sup>c</sup>	0.000	0.000	0.000	0.000		
Total	1.000	372	8.211			1.000	174	11.658			1.000		

<sup>a</sup> Lower Bonferroni confidence limits

<sup>b</sup> Upper Bonferroni confidence limits

<sup>c</sup> Inferences for these habitats are unreliable due to low observations ( $u_i < 5$ )

Table 5 (continued). Seasonal habitat selection indices for Himalayan thar and chamois in Carneys Creek, New Zealand, 1993-1996.

Habitat	$\pi_i$	$u_i$	Thar				Chamois					$z$	$P_{Holm}$
			$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$	$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$			
<b>Autumn<sup>c</sup></b>													
Grassland	0.132	47	2.728	1.886	3.571	0.352	30	2.830	1.748	3.913	0.359		
Grass bluff	0.116	16	1.065	0.404	1.725	0.137	14	1.514	0.540	2.488	0.192		
Rock bluff	0.242	39	1.240	0.780	1.681	0.160	14	0.723	0.258	1.189	0.091		
Scree	0.437	15	0.264	0.094	0.434	0.034	14	0.400	0.143	0.658	0.051		
Shrubland	0.044	11	1.923	0.453	3.393	0.248	7	1.989	0.086	3.891	0.252		
Snow	0.029	2 <sup>d</sup>	0.536	0.000	1.533	0.069	1 <sup>d</sup>	0.436	0.000	1.583	0.055		
Total	1.000	130	7.756			1.000	80	7.892			1.000		
<b>Winter</b>													
Grassland	0.000												
Grass bluff	0.034	17	4.425	1.878	6.972	0.208	5	3.587	0.000	7.457	0.104	0.42	NS
Rock bluff	0.099	47	4.210	3.001	5.418	0.197	8	1.975	0.362	3.588	0.057	2.02	NS
Scree	0.001	0 <sup>d</sup>	0.000	0.000	0.000	0.000	0 <sup>d</sup>	0.000	0.000	0.000	0.000		
Shrubland	0.014	19	12.363	5.702	19.025	0.580	16	28.694	14.270	43.119	0.829	-3.28	0.004
Snow	0.852	30	0.311	0.186	0.437	0.015	12	0.343	0.129	0.558	0.010	-0.34	NS
Total	1.000	113	21.309			1.000	41	34.599			1.000		

<sup>a</sup> Lower Bonferroni confidence limits

<sup>b</sup> Upper Bonferroni confidence limits

<sup>c</sup> Habitat selection by thar and chamois was not significantly different in this month ( $\chi^2_3 = 0.38$ )

<sup>d</sup> Inferences for these habitats are unreliable due to low numbers of observations ( $u_i < 5$ )



Table 6. Seasonal habitat selection indices for male and female thar in Carneys Creek, New Zealand, 1993-1996 (continued overleaf).

Habitat	$\pi_i$	$u_i$	Male				Female					$z$	$P_{\text{Holm}}$
			$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$	$u_i$	$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$		
<b>Spring</b>													
Grassland	0.071	65	4.667	3.411	5.923	0.416	11	1.830	0.466	3.195	0.150	2.67	0.02
Grass bluff	0.116	25	1.093	0.552	1.634	0.097	22	2.229	1.145	3.314	0.183	-2.97	0.01
Rock bluff	0.121	66	2.755	2.022	3.488	0.246	29	2.806	1.685	3.926	0.230	-0.10	NS
Scree	0.150	9	0.305	0.042	0.568	0.027	0 <sup>c</sup>	0.000	0.000	0.000	0.000		
Shrubland	0.049	22	2.293	1.072	3.514	0.205	22	5.315	2.730	7.900	0.435	-3.41	0.003
Snow	0.493	10	0.103	0.019	0.187	0.009	1 <sup>c</sup>	0.024	0.000	0.087	0.002	0.97	NS
Total	1.000	197	11.216			1.000	85	12.204			1.000		
<b>Summer</b>													
Grassland	0.132	131	3.363	2.783	3.943	0.433	19	1.838	0.866	2.811	0.186	2.64	0.04
Grass bluff	0.116	48	1.412	0.918	1.907	0.182	17	1.885	0.814	2.957	0.191	-1.22	NS
Rock bluff	0.242	62	0.872	0.611	1.132	0.112	24	1.272	0.700	1.845	0.129	-1.99	NS
Scree	0.437	29	0.226	0.120	0.331	0.029	2 <sup>c</sup>	0.059	0.000	0.167	0.006	1.25	NS
Shrubland	0.044	23	1.778	0.835	2.721	0.229	15	4.371	1.683	7.058	0.443	-3.55	0.002
Snow	0.029	1 <sup>c</sup>	0.119	0.000	0.432	0.015	1 <sup>c</sup>	0.447	0.000	1.623	0.045	-1.24	NS
Total	1.000	294	7.770			1.000	78	9.872			1.000		

<sup>a</sup> Lower Bonferroni confidence limits

<sup>b</sup> Upper Bonferroni confidence limits

<sup>c</sup> Inferences for these habitats are unreliable due to low observations ( $u_i < 5$ )

Table 6 (continued). Seasonal habitat selection indices for male and female thar in Carneys Creek, New Zealand, 1993-1996.

Habitat	$\pi_i$	$u_i$	Male				Female					$z$	$P_{Holm}$
			$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$	$u_i$	$\hat{W}_i$	$\hat{W}_{i\text{lower}}^a$	$\hat{W}_{i\text{upper}}^b$	$B_i$		
<b>Autumn</b>													
Grassland	0.132	31	2.600	1.598	3.601	0.332	16	3.019	1.470	4.568	0.397	-0.63	NS
Grass bluff	0.116	7	0.673	0.026	1.320	0.086	9	1.946	0.433	3.460	0.256	-2.54	0.07
Rock bluff	0.242	29	1.332	0.792	1.872	0.170	10	1.034	0.284	1.784	0.136	0.79	NS
Scree	0.437	12	0.305	0.088	0.522	0.039	3 <sup>c</sup>	0.172	0.000	0.424	0.022	0.83	NS
Shrubland	0.044	10	2.525	0.530	4.520	0.323	1 <sup>c</sup>	0.568	0.000	2.055	0.075	1.01	NS
Snow	0.029	1 <sup>c</sup>	0.387	0.000	1.407	0.050	1 <sup>c</sup>	0.871	0.000	3.150	0.114	-0.64	NS
Total	1.000	90	7.822			1.000	40	7.610			1.000		
<b>Winter<sup>d</sup></b>													
Grassland	0.000												
Grass bluff	0.034	11	4.494	1.376	7.611	0.208	6	4.304	0.245	8.363	0.208		
Rock bluff	0.099	33	4.639	3.153	6.125	0.214	14	3.456	1.582	5.330	0.167		
Scree	0.001	0 <sup>c</sup>	0.000	0.000	0.000	0.000	0 <sup>c</sup>	0.000	0.000	0.000	0.000		
Shrubland	0.014	12	12.255	4.181	20.329	0.566	7	12.554	1.752	23.356	0.606		
Snow	0.852	16	0.261	0.117	0.404	0.012	14	0.401	0.183	0.618	0.019		
Total	1.000	72	21.649			1.000	41	20.715			1.000		

<sup>a</sup> Lower Bonferroni confidence limits

<sup>b</sup> Upper Bonferroni confidence limits

<sup>c</sup> Inferences for these habitats are unreliable due to low observations ( $u_i < 5$ )

<sup>d</sup> Habitat selection by thar and chamois in this season was not significantly different ( $\chi^2_3 = 0.52$ )

### 5.2.5.2 Male and Female Thar

Male and female thar avoided scree and snow in all the seasons during which these habitats were available (Table 6). In every season grassland (except winter, when it was unavailable), grass bluff, rock bluff, and shrubland were either not selected or preferred by both sexes.

Habitat selection by the two sexes differed significantly in spring ( $\chi^2_5 = 29.51$ ,  $P < 0.0001$ ), summer ( $\chi^2_4 = 20.45$ ,  $P = 0.0004$ ) and autumn ( $\chi^2_4 = 8.44$ ,  $P = 0.077$ ), but not in winter ( $\chi^2_3 = 2.27$ ,  $P = 0.52$ ). During both spring and summer male thar preferred grassland significantly more, and shrubland significantly less, than females. In spring and autumn females selected grass bluff significantly more than males. During autumn and winter there were few observations of both male and female thar so the probability of Type II errors increased in these seasons.

### 5.2.6 Relative Niche Breadth of Thar and Chamois

Thar selected habitats more equally than did chamois (Table 7) and in no season was the resource utilisation curve of thar similar to that of chamois ( $G_5 \geq 14.90$ , Bonferroni-adjusted  $P < 0.05$ ). However, in autumn the utilisation curve of chamois was similar to thar ( $G_5 = 8.69$ , Bonferroni-adjusted  $P > 0.05$ ).

Table 7. Simpson's equitability index ( $E$ ) for standardised habitat selection indices of Himalayan thar and chamois in Carneys Creek, New Zealand, December 1993-February 1996. Four habitats were assumed available in winter, six in the other seasons (see text).  $E$  approaches 1 with increasing equitability of selection among the habitat types.

Species	Season			
	Spring	Summer	Autumn	Winter
Thar	0.64	0.63	0.71	0.60
Chamois	0.41	0.35	0.69	0.36

### 5.2.7 Behavioural Interactions

All interspecific interactions involved male thar, and only one interaction was observed in winter. There was a significant difference in the response of chamois and thar during interspecific encounters (Table 8; McNemar  $G = 10.7$ ,  $P < 0.005$ ). Chamois were displaced in 54% of encounters and thar in only 8%.

Table 8. Outcomes of 24 interspecific interactions between thar and chamois in the Two Thumb Range, New Zealand. Refer to methods for explanation of categories.

		Thar	
		Displaced	Not displaced
Chamois	displaced	1	12
	not displaced	1	10

The effect of these encounters on chamois was sometimes pronounced. An adult female chamois and kid were observed to run >2 km and leave Carneys Creek following an encounter. More usually, displaced chamois would stop feeding, move 100-200 m and subsequently spend additional time in an alert posture. The behaviour of thar groups towards chamois was never interpreted as overtly aggressive, but more inquisitive. On seeing chamois nearby (<100 m) thar would often move towards the chamois, sometimes running. This behaviour seemed different from that exhibited between thar groups. In the latter situation agonistic behaviours were also uncommon, but thar seldom ran towards other groups.

## 6. DISCUSSION

### 6.1 Do Thar Exclude Chamois?

The high density of thar relative to chamois at single-species sites in 1978 reflects species' differences in sociality. Studies of un hunted populations have recorded densities of thar considerably higher than chamois (see Tustin and Challies 1978; Clarke and Frampton 1991). Female-juvenile groups of thar are gregarious (Tustin and Parkes 1988), as are males outside rut (Forsyth 1997). In contrast, chamois in New Zealand are typically solitary (Clarke 1990; Clarke and Frampton 1991).

Changes in the density of thar in Carneys Creek following the advent of helicopter-based hunting have been described by Tustin and Challies (1978) and are considered representative of trends in the eastern Southern Alps. In 1965, when the Carneys Creek population was at peak density, a summer census counted 710 thar ( $>30/\text{km}^2$ ). A repeat census in 1977 counted 48 thar; this 93% reduction was attributed to government and commercial helicopter-based hunting after 1967 and 1971, respectively (Tustin and Challies 1978). All commercial and most government hunting was prohibited in 1983; a census in summer 1984 recorded just 26 thar in Carneys Creek (Forsyth 1997). Despite intensive recreational hunting, annual censuses since 1984 have showed a population increase of *ca.* 20% per annum (Forsyth 1997). The decline of chamois since the cessation of intensive hunting of thar in 1983 suggests that commercial and government helicopter-based hunting had enabled chamois to co-exist with low densities of thar during the 1970s.

Given that the thar densities recorded during 1991-1996 were only moderate by historical standards, we predict that chamois would be completely excluded if thar ever increased to peak densities (i.e.,  $\geq 30$  thar/ $\text{km}^2$ ). Current management policy, however, is to control thar to densities  $\leq 2.5$  thar/ $\text{km}^2$  (Department of Conservation 1993). By the 1990s, when thar exceeded *ca.* 3 thar/ $\text{km}^2$  in our study sites, chamois were absent from all but the 'best' sites. This suggests a threshold density at which chamois are excluded by thar. In the one site where both species increased, the chamois were observed in an area with very few thar. The spatial scale of habitat use by thar and chamois at each site will affect the frequency and outcome of competitive interactions (Morris 1987). It would be instructive to learn whether or not chamois have persisted at the sites in which thar were not present in 1978; casual observation suggests that thar now inhabit many of those sites. We predict that chamois would not be observed in sites where thar increased to  $\geq 3/\text{km}^2$ , but would be seen in sites where thar densities were  $< 3/\text{km}^2$ . The large-scale decline in chamois densities in the eastern Southern Alps recorded in this study may confound the prediction.

There is also no evidence to suggest that during the 1978-1996 period chamois were subject to relatively greater harvest by recreational hunters than thar in the eastern Southern Alps. The chamois population had been established for >50 years and would have been in the numerically stable post-peak phase of population growth (Clarke and Frampton 1991). Although the spatial segregation of thar and chamois evident in the 1978 surveys could be caused by differential habitat preferences of the two species (large sites are likely to contain more habitat types than small sites [Krebs 1989]), the decline of chamois following the six-fold increase in thar is evidence for interspecific competition (Schoener 1983).

In New Zealand, chamois are sympatric with a variety of ungulates throughout their range and there is anecdotal evidence of competition with these ungulates. For example, Fokerd (1962) observed an increase in chamois following intensive control of red deer in the Waimakariri catchment, and chamois are in high densities where there are few red deer in the lowland forests of central Westland (Yockney 1997). It is clear that understanding the distribution and densities of chamois throughout the South Island of New Zealand will require consideration of competitive interactions with other ungulates.

## **6.2 How Do Thar Exclude Chamois?**

Group size data (Table 4) confirmed, according to Christie and Andrews' (1964) criteria, that this was a low-density population of thar (i.e., 1-5 animals per group). Summer counts during 1994-1996 (D.M. Forsyth, unpublished data) indicated that the Carneys Creek chamois population density was considerably lower than the post-decline population studied by Clarke and Frampton (1991), but intensive hunting in adjacent catchments may have killed migrant animals that utilised Carneys Creek (see Clarke 1986).

Simpson's equitability index showed thar to have a broader niche than chamois in Carneys Creek during three of the four seasons; chamois may have used habitats more equally in autumn due to rut activities. This result was unexpected because chamois occupy a broader range of habitats than thar within the South Island of New Zealand. Chamois live year-round within the low-altitude forests of central Westland (Yockney 1997) through to the high-altitude basins of the central Southern Alps (this study). In contrast, thar are restricted to the high-altitude mountain ranges of the central Southern Alps (Tustin 1990). These broad-scale differences may simply reflect the effectiveness of intensive government and commercial helicopter-based hunting in limiting the dispersal of thar (see Parkes and Tustin 1985). Our results suggest that thar attained far higher peak densities (>30 thar/km<sup>2</sup>) in the Southern Alps compared to chamois due, at least in part, to an ability to exploit a broader range of habitats. Innate differences in sociality, as recorded in this study (Table 3) and during 1978-1979 in the eastern Southern Alps must also have been important.

Spatial segregation of male and female thar outside rut (Forsyth 1997) was associated with significant differences in habitat selection between the sexes in this study (Table 6). Males preferred grassland significantly more, and shrubland significantly less, than females during spring and summer. During autumn and winter the sexes utilised habitats more similarly. These intersexual differences in habitat selection when

segregated must at least partly explain the broader niche of thar relative to chamois in Carneys Creek. Sexual segregation has been documented in a European population of chamois (Shank 1985), and is also likely to result in differential habitat selection by male and female chamois in New Zealand (Clarke 1986). However, chamois are less sexually dimorphic than thar, so such behaviours would be expected to be less extreme than those observed in thar (see Main *et al.* 1996).

The daily altitudinal movement of thar recorded in this study and in a previous study (Tustin and Parkes 1988) may also explain the less pronounced habitat selection exhibited by thar relative to chamois, because habitat is correlated with altitude (Table 1). In spring, summer and autumn, all (i.e., male-only, female-only and mixed) groups of thar typically fed to lower altitude grassland and shrubland in the evening and to higher altitude grass bluff and rock bluff in the morning, where they rested until evening. This daily movement was greatest in spring, a result also recorded by Tustin and Parkes (1988), with some groups descending >400 m in the evening to feed in shrubland and grassland. Daily altitudinal movements of this kind have not been recorded for chamois in any New Zealand study.

Although many studies have documented resource overlap between sympatric ungulates (e.g., Dunbar 1978; Jarman and Sinclair 1979; Schröder and Kofler 1984; Spowart and Hobbs 1985; Wydeven and Dahlgren 1985; Jenkins and Wright 1988; Gordon and Illius 1989), interpreting the implications of these studies for interspecific competition is problematic (Colwell and Futuyma 1971; Hobbs *et al.* 1996). Because the principle of competitive exclusion (Gause 1934) is tautological, competition cannot automatically be inferred from resource overlap (Caughley and Sinclair 1994). Thus, although our results refuted the null hypothesis that thar and chamois within Carneys Creek selected similar habitats in three of four seasons, the biological significance of this result is unclear.

Both species generally preferred grassland and shrubland and avoided scree and snow in the seasons that they were available. This indicates a strong potential for interspecific competition as densities of thar increase. Our data suggest that the potential for habitat overlap between thar and chamois is greatest during winter, when deep snow forces animals to congregate on snow-free rock bluff, grass bluff and shrubland. This behaviour has been reported previously for both chamois (Christie 1963; Clarke and Henderson 1984; Clarke 1986; Clarke 1990) and thar (Tustin and Parkes 1988; Tustin 1990) in New Zealand. However, many of the chamois that summer in the eastern Southern Alps apparently migrate to lower-altitude forests during winter (Clarke 1986), and a similar trend was recorded in Carneys Creek (D.M. Forsyth, unpublished data). This probably explains why few chamois were observed in Carneys Creek during winter. Such migration would reduce both behavioural interactions and dietary competition between thar and chamois during winter.

Inferences about habitat selection by sympatric thar and chamois within Carneys Creek can be extrapolated to the remainder of the sympatric thar and chamois range with caution. First, patterns of habitat distribution vary between catchments and mountain ranges, as well as from west to east with the dominant climatic gradient (see Clarke 1986; Wardle 1991). Habitat selection is likely to depend on the relative frequencies of the available habitats (Manly *et al.* 1993) and on the plant species within each habitat. Second, habitat selection will vary according to the density of thar and chamois, and that

of other sympatric ungulates such as red deer (Rosenzweig 1981). Third, the seasonal migration of male thar (Forsyth 1997) and some chamois (Clarke 1986; Clarke and Frampton 1991) results in seasonal changes in the density of each species' age-sex classes. For example, in this study our observations of thar were significantly male-biased in all seasons due to immigration of sub-adult males into Carneys Creek as a consequence of long-term population trends in the Two Thumb Range (see Forsyth 1997).

There is evidence to suggest that the results of this study can be applied to the remainder of the eastern Southern Alps sympatric range. Analysis of thar and chamois rumens collected from this area during 1989-1996 indicated significant species and seasonal differences in diet. Overall, chamois rumens contained greater proportions of 'woody plant' and 'herbs' species than thar, and lesser proportions of 'grasses' (Parkes and Thomson 1995; J.P. Parkes *et al.* unpublished data). In Carneys Creek, 'woody plants' were restricted to the shrubland habitat, and this habitat type was most preferred by chamois in three of the four seasons, and preferred significantly more by chamois compared to thar in two seasons. Similarly, 'grasses' were most commonly associated with grassland and grass bluff habitats; thar selected or preferred these habitats in every season that they were available. Thus, there appears to be broad agreement between these two studies, but a quantitative description of the vegetation within the six habitats in Carneys Creek would be required to confirm this.

When chamois and thar groups interact, chamois are likely to leave the immediate vicinity. This phenomena could account for the spatial segregation of thar and chamois observed during an extensive ground-based hunting programme conducted between November 1978 and April 1979. Moreover, our data indicate a threshold density (*ca.* 3 thar/km<sup>2</sup>) above which chamois are excluded from sites by thar. This threshold is within the long-term post-peak density of 3.2-5.0 chamois/km<sup>2</sup> described by Clarke and Frampton (1991) for a population just outside the breeding range of thar. In that population chamois were regulated by a combination of social and spatial factors, and food availability (Clarke and Henderson 1981, 1984; Clarke 1990; Clarke and Frampton 1991). Our results imply that interspecific interactions with thar regulate population density in a manner similar to intraspecific interactions; chamois avoid both thar and other chamois by behavioural avoidance. Long-term monitoring of the numerical response of chamois to sustained control of thar at densities  $\leq 2.5$  thar/km<sup>2</sup>, as required by the Himalayan Thar Control Plan, could provide tests of hypotheses arising from this conclusion. More information is also required on the role of dominance relationships (Clarke and Henderson 1981, 1984; Locati and Lovari 1991) in the behavioural avoidance of both conspecifics and other ungulates by chamois in the Southern Alps of New Zealand.

There are two reasons why all observed interspecific interactions involved male thar. First, Carneys Creek contained a significantly male-biased thar population (Forsyth 1997) which increased the probability of chamois encountering male rather than female thar. Second, inspection of Tables 5 and 6 suggests that in the spring, summer and autumn seasons there is greater overlap in habitat selection between male thar and chamois than there is between female thar and chamois.

There is anecdotal support for Rosenzweig's (1981) prediction that chamois should contract their habitat selection to reduce competition with increasing densities of thar.

Caughley (1970a) observed chamois co-existing with peak densities of thar in the Rangitata River Valley during the 1960s. He observed that the "habitat requirements" of chamois differed sufficiently from thar "to suggest that there is little interaction between the two species, either socially or in the utilization of forage" (Caughley 1970a:59). Interestingly, no chamois were observed within the Carneys Creek study area during the February 1965 census (C.N. Challies, personal communication) when thar were at, or near to, peak density ( $>30$  thar/km<sup>2</sup>; Tustin and Challies 1978). During this study we observed 24 interspecific behavioural interactions and have documented overlap in habitat selection, and an associated study has demonstrated dietary overlap (Parkes and Thomson 1995). We speculate that Caughley's observations were of chamois that had contracted their habitat selection, and thus could co-exist with high densities of thar. Only quantification of the niche breadth of chamois co-existing with different densities of thar could properly test this inference.

Although the results presented here do not enable us to differentiate between the behavioural intolerance and dietary mechanisms of replacement, we believe that the weight of evidence supports the former. Dietary competition would likely require a significant depletion of preferred plant species, a process that would require at least 10 years of colonisation by thar (see Caughley 1970a). It is significant that during the recent (1978-1996) decline of chamois there has been only localised modification of tussock communities attributable to thar, which we consider has been insufficient for scramble competition to occur. We note, however, that recent models of ungulate nutrition suggest that only small reductions in browse biomass and quality can have potentially large nutritional impacts (Illius and Gordon 1992; Gordon and Illius 1996). Schröder and Kofler (1984) proposed that ibex excluded chamois due to an ability to better utilise lower quality forage. Fraser (1996) concluded that a similar mechanism enabled sika deer (*Cervus nippon*) to exclude the closely-related and earlier-introduced red deer in the central North Island, New Zealand. The broader niche of thar relative to chamois recorded in this study suggests that thar may similarly be better able to utilise lower-quality forage.

In contrast, behavioural intolerance is an instantaneous mechanism dependent only upon the frequency of interspecific interactions (which are increased by the daily altitudinal movements of thar). Despite the two mechanisms not being mutually-exclusive, we propose that the increasing frequency of behavioural interactions is the proximate cause of chamois abandoning their home range. In Carneys Creek, significant differences in habitat selection, particularly during spring and summer, apparently permitted chamois to co-exist with low densities of thar. Thar are more social than chamois, and chamois behaviourally avoid thar. As a thar population grows, increasing densities of thar will utilise less preferred habitats within a catchment, thereby increasing both behavioural and dietary interactions with chamois.

Behavioural avoidance of thar appears to regulate chamois densities in a density-dependent fashion similar to intraspecific behavioural interactions. We predict that when thar densities are reduced below 3 thar/km<sup>2</sup>, the minimum post-decline density recorded in an un hunted eastern Southern Alps chamois population (Clarke 1990), chamois will recolonise preferred sites.



## 7. MANAGEMENT IMPLICATIONS

This study has provided evidence that increasing densities of thar exclude chamois from some habitats. The corollary of this result is that controlling thar to  $\leq 2.5$  thar/km<sup>2</sup>, as required by the Himalayan Thar Control Plan, is likely to result in increased use of some sites by chamois. However, because the *in situ* impacts of thar and chamois on conservation resources are unknown, it is unclear what the conservation implications of such increased use might be.

Given that there is no management plan concerning chamois, we can only discuss the implications of our results with regard to the Himalayan Thar Control Plan. For the six management units within the plan for which conservation objectives are defined, all centre on “maintain(ing) healthy plant cover, species diversity and regenerative capacity of plant communities in thar habitat”. Maximum allowable densities of thar are being determined by *in situ* monitoring of snow tussocks in five catchments throughout the thar breeding range (Parkes and Thomson 1995). Since (i) thar attain far higher densities compared to chamois, and (ii) the rumens of thar contained a significantly greater proportion of tussock than sympatric chamois (Parkes and Thomson 1995), it is unlikely that chamois will modify snow tussocks. Consequently, any increase in chamois following reduction of thar to densities  $< 2.5$  thar/km<sup>2</sup> is unlikely to impact on snow tussocks. However, both chamois and thar have the potential to modify other vegetation types (e.g., shrublands and herbfields; Parkes and Thomson 1995; this study), and as knowledge of impacts increases, the conservation importance of any increase in chamois following thar control may increase. Managers need to ask: “are chamois likely to impact on the conservation resource that we seek to protect from thar?”

Although national eradication of thar is not current policy (Marshall 1991), such a strategy may be reconsidered at some future time. If thar are eradicated (i.e., reduced to 0 thar/km<sup>2</sup> across the entire range) but chamois are not, then chamois populations are likely to increase in some catchments. Depending on the relative conservation impacts of chamois and thar, the value of eradicating only thar may well be diminished. Certainly, managers would need to allocate increased resources to monitoring and perhaps controlling chamois following the eradication of thar.

Like Parkes and Thomson (1995), we believe that the current single-species approach to the protection of conservation resources in the central Southern Alps alpine zone (i.e., the Himalayan Thar Control Plan) does not maximise conservation benefits in this area. That is, controlling just thar (and not other sympatric introduced herbivores, including chamois) may result in only partial protection of conservation resources that are also modified by the other pests. The theoretical and practical issues surrounding this concept are discussed in detail in Forsyth (1997). We suggest that the current single-species approach should be replaced by an integrated management plan that better accommodates the spatial and temporal variation in the distribution of conservation resources and pest impacts.

## 8. RECOMMENDATIONS

- The Department of Conservation should consider the consequences for sympatric chamois of reducing thar densities.
- The Department of Conservation should integrate its management of alpine herbivores if it wishes to maximise protection of conservation resources.
- The Department of Conservation should monitor densities of thar and chamois at the 53 sites in which these species were present during 1978 at approximately 10 year intervals. Such monitoring would provide further insight into the numerical relationship between densities of thar and chamois in the eastern Southern Alps.

## 9. ACKNOWLEDGEMENTS

The senior author gratefully acknowledges the ideas, enthusiasm and support of the late Julie Alley in this study. We thank the New Zealand Forest Service hunters who carefully recorded their observations, and the leaseholders who gave their permission for sites to be recounted during 1991-1996. D.C. Anderson and N. Bolton (Department of Conservation, Canterbury) assisted with transport and liaised with leaseholders. A. Jepson, S. Harraway and K. Lange helped with the 1991-1996 surveys, and A. Harrington assisted with mapping. We thank L. Prouting for periodic aerial transport into Carneys Creek and for permission to use tracks and huts belonging to Mesopotamia Station. The efforts of K.F.D. Hughey, J. Andrew and D.C. Anderson in prohibiting hunting in Carneys Creek during the study were greatly appreciated. Kelvin Nicolle and pilot Ray French conducted aerial photography in difficult conditions. B.F.J. Manly kindly suggested trying Holm's method. R. Breejart translated several European papers and C.M. Frampton gave statistical advice. We also thank J.P. Parkes for permission to use unpublished data in Figure 2. J.P. Parkes, A.M. Paterson, R.J. Barker, M. Alley, and K. Schöps made helpful comments on the draft manuscript. Additional funding was received from Lincoln University, New Zealand Lottery Grants Board and the New Zealand Deerstalker's Association (Inc.).

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## 11. APPENDIX

Morphological, behavioural and habitat features used to classify thar and chamois into age-sex classes in Carneys Creek, New Zealand, in descending order of importance (after Caughley 1967 and Tustin 1990).

Age-sex class	Cues
Adult male thar (>4 years)	Body size 2 X adult female; 1.5 X sub-adult male Knee-length mane; black autumn/winter, otherwise blonde Horns long ( $\geq 25$ cm), thick and tapering to behind ears Black face One per female group in winter, otherwise solitary or small groups
Sub-adult male thar (2-4 years)	Body size less than adult males, 1.5 X adult females Short mane present; brown in autumn/winter, otherwise blonde Horns thin and tapering to ears, <25 cm long Light brown/black in winter Same-sex groups spring-summer, mixed-sex groups in winter
Female thar (>2 years)	Kid and/or yearling present Body size < sub-adult and adult males Mane absent On rock bluffs <sup>b</sup> /known female range
Yearling thar (1-2 years)	0.5 - 0.75 X body size of adult females Small ruff Part of, or close to female groups Outside winter mixed-sex groups Horns small
Kid thar (<1 year) (sex indeterminate)	Small body size relative to adult females Adult females present Suckling behaviour Horns small
Adult chamois ( $\geq 1$ year)	Body size $\geq 2$ X kid Horns visible

(Continued overleaf)

Appendix (Continued).

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Kid chamois (<1 year)	Small body size Adult chamois present Suckling behaviour Horns not visible
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<sup>a</sup> Tests of observed sex to actual (shot) sex indicated the sex of yearlings could not be determined.

<sup>b</sup> Females are sedentary on rock bluffs with home ranges of *ca.* 2 km<sup>2</sup> (Tustin and Parkes 1988; Tustin 1990).