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## Increasing Himalayan tahr and decreasing chamois densities in the eastern Southern Alps, New Zealand: evidence for interspecific competition

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**Abstract** There is anecdotal evidence that increasing densities of Himalayan tahr (*Hemitragus jemlahicus*) are associated with declining densities of chamois (*Rupicapra rupicapra*) in the Southern Alps, New Zealand. To examine this phenomenon, densities of tahr and chamois were measured at 53 sites within their sympatric range in the eastern Southern Alps during 1978–1979. In sites where only one species was present, tahr density was significantly higher than chamois density ( $P = 0.032$ ), probably reflecting species differences in sociality. Chamois density was higher in catchments without tahr than in those with tahr ( $P = 0.012$ ). Similarly, tahr density was significantly higher at sites without chamois than at those with chamois ( $P = 0.033$ ). Sites with both species present (termed sympatric) were significantly larger than those with only chamois or tahr ( $P < 0.001$ ). Following the prohibition of aerial hunting of tahr in 1983, 16 of the 17 sites where tahr and chamois were sympatric during 1978–1979 were recounted during 1991–1996. There was a 6-fold increase in the mean density of tahr between the two counts ( $P = 0.001$ ), whereas chamois density had declined significantly ( $P = 0.006$ ). Chamois persisted at only three sites, two of which had the highest chamois densities in 1978–1979. This is evidence that increasing densities of tahr exclude chamois from all but the ‘best’ habitats. We conclude that intensive aerial hunting of tahr during 1967–1983 reduced tahr densities such that chamois could co-exist with tahr.

**Key words** Density · Hunting · Interspecific competition · Southern Alps · Ungulates

### Introduction

The importance of interspecific competition in structuring ungulate communities is unclear. For example, long-term monitoring of the Serengeti ungulate community has provided equivocal evidence for interspecific competition between wildebeest (*Connochaetes taurinus*) and Thomson’s gazelle (*Gazella thomsoni*) (Dublin et al. 1990 and references therein).

Although reliable evidence (*sensu* Romesburg 1981) for interspecific competition is best provided by removal experiments (e.g., Redfield et al. 1977), such experiments have seldom been performed with ungulates for practical reasons (Caughley and Sinclair 1994). For example, chamois (*Rupicapra rupicapra*) 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).

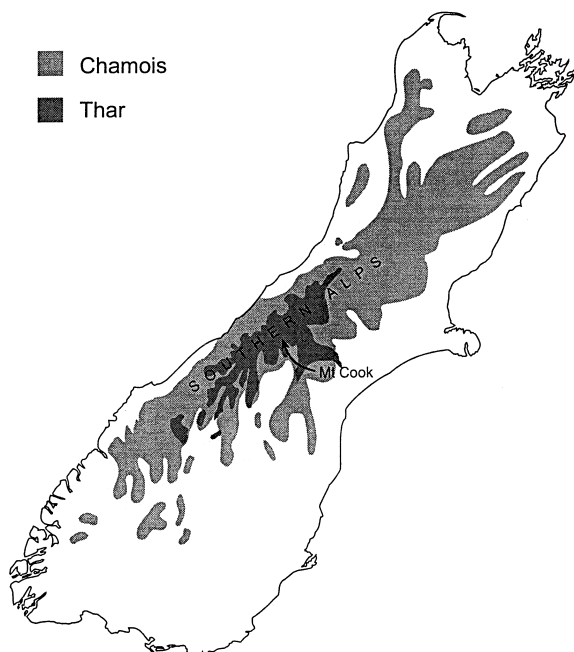
In this paper we describe long-term changes in the densities of sympatric Himalayan tahr (*Hemitragus jemlahicus*) and chamois (*Rupicapra rupicapra*) in the eastern Southern Alps, New Zealand, following the abrupt cessation of commercial and most government hunting of tahr in 1983 (Hughey and Parkes 1995). These circumstances presented a unique opportunity to test hypotheses about the numerical response of chamois to increasing densities of tahr.

Tahr 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,

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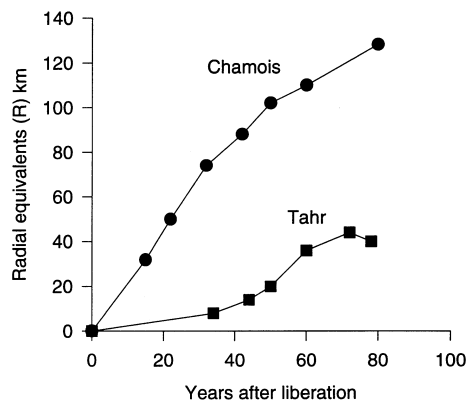
**Fig. 1** Liberation site (Mt Cook) and 1996 distributions of Himalayan tahr and chamois in the South Island of New Zealand (updated from Department of Conservation 1993 and Parkes and Clarke 1993)

also to establish a hunting resource. Both species flourished (Donne 1924). Tahr underwent an irruptive oscillation (Caughley 1970a), increasing to peak densities of  $> 30$  tahr  $\text{km}^{-2}$  (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 tahr (see Clarke and Frampton 1991).

Rapid dispersal of chamois relative to tahr (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). Tahr 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 tahr seldom formed mixed groups, despite living in similar habitats when apart (see, for example, McIlbraith 1929). Government hunters, employed to cull tahr and chamois from 1937, recorded similar observations. Davison (1946) observed that "where tahr 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 tahr... now tahr are numerous on both sides and few chamois are seen." More recent workers (e.g., K. Tustin in Schaller 1977) have reported similar observations.

Female tahr are gregarious and sedentary on rock bluffs throughout the year (Tustin and Parkes 1988). At



**Fig. 2** Dispersal of Himalayan tahr 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 tahr dispersal ( $r^2 = 0.99$ )

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 tahr, 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 tahr and chamois in New Zealand are given by Tustin (1990) and Clarke (1990) respectively.

Government-funded ground-based hunting of tahr continued until the early 1980s. The advent of helicopter-based hunting for the control of tahr in 1967, and the establishment of an overseas market for carcasses in 1970, dramatically reduced the density and distribution of tahr in the Southern Alps (Tustin 1980; Parkes and Tustin 1985). Annual commercial harvests of tahr peaked at *c.* 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 tahr 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 tahr control, and densities of tahr have steadily increased in regularly monitored catchments (Department of Conservation 1993).

We studied spatial and temporal patterns in the densities of sympatric Himalayan tahr and chamois in the eastern Southern Alps to determine whether there is evidence that increasing densities of tahr are causally linked to decreasing chamois densities.

## Methods

### Densities of sympatric tahr and chamois in 1978

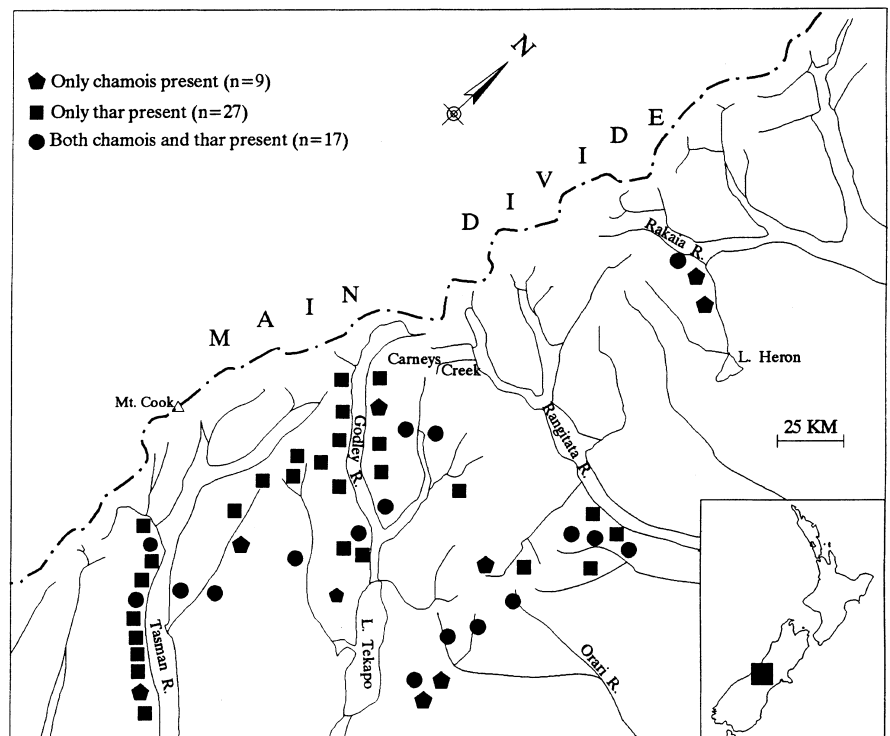
Between November 1978 and April 1979 (hereinafter termed "1978") government hunters visited 53 sites within the then breeding range of tahr (Parkes and Tustin 1985) and chamois (Clarke 1990) in the eastern Southern Alps (Fig. 3). The hunters aimed to reduce the densities of tahr and chamois within these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

The area hunted and the number of tahr, chamois and other ungulates seen at each site were recorded on a 1:63 360 scale map. For each site the area searched was digitised using ARC/INFO (Environmental Systems Research Institute 1991) and the density of tahr and chamois calculated (number km<sup>-2</sup>).

Red deer (*Cervus elaphus scoticus*) and fallow deer (*Dama dama*) were occasionally sighted but were excluded from our analyses as, relative to tahr, very few were observed. Chamois and tahr densities were log-transformed to equalise the variances; we then used one-tailed *t*-tests to test three a priori hypotheses regarding the densities of tahr and chamois:

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

**Fig. 3** Location of 53 sites in the eastern Southern Alps, New Zealand, in which Himalayan tahr and/or chamois were observed during November 1978–April 1979



### Long-term changes in the densities of sympatric tahr and chamois 1978–1996

Experimental manipulation of density is required to prove competitive effects (Schoener 1983). Differential rates of hunting among sites between 1978 and 1991–1996 were treated as manipulations of tahr density in sites where tahr 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–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 predicted changes in the densities of tahr and chamois between the two surveys. Our hypotheses were:

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

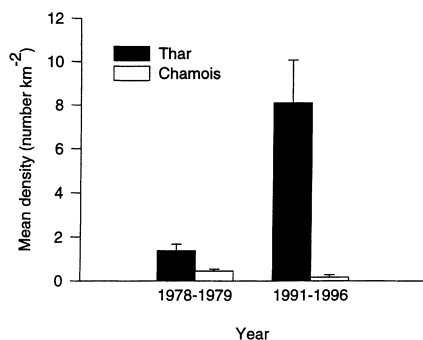
## Results

### Densities of tahr and chamois in 1978

Mean tahr density in tahr-only sites was greater than the mean chamois density in chamois-only sites (Table 1; one-tailed  $t = 1.92$ ,  $df = 34$ ,  $P = 0.032$ ). Tahr density was lower in sites containing chamois compared to sites without chamois (one-tailed  $t = 1.88$ ,  $df = 42$ ,  $P = 0.033$ ). Chamois density was lower in sites with tahr than without tahr (one-tailed  $t = 2.42$ ,  $df = 24$ ,  $P = 0.012$ ).

**Table 1** Mean density index (number km<sup>-2</sup>) of tahr 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 ± SE
Both species present	Tahr	17	1.87 ± 0.46
	Chamois	17	0.53 ± 0.12
One species present	Tahr	27	3.52 ± 0.67
	Chamois	9	1.44 ± 1.43



**Fig. 4** Mean densities (+SE) of sympatric Himalayan tahr 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 tahr was prohibited by government order in 1983

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 tahr or chamois [ $10.6 \pm 1.5$  (SE) km<sup>2</sup> and  $5.9 \pm 0.8$  km<sup>2</sup>, respectively; normal approximation to a Mann-Whitney  $Z = 3.06$ ,  $P = 0.002$ ].

#### Effect of increasing tahr densities on chamois densities

High densities of domestic sheep were recorded in two sites during 1991–1996; these were excluded from our analyses, leaving 14 sympatric sites. Within these 14 sites, there was a 6-fold increase in the mean density of tahr between the two counts (Fig. 4; one-tailed paired  $t = 3.73$ ,  $df = 13$ ,  $P = 0.001$ ), whereas mean chamois density declined significantly (one-tailed paired  $t = 2.92$ ,  $df = 13$ ,  $P = 0.006$ ).

Chamois were recorded in only 3 of the 14 sites during 1991–1996. Two of these sites had the highest densities of chamois recorded during 1978. The third site, one of the two at which chamois had increased between the two counts, was the only site where the density of tahr declined between the two counts.

## Discussion

Although the spatial segregation of tahr 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 6-fold increase in tahr is evidence for interspecific competition. The almost total exclusion of chamois recorded in this study makes other measures of fitness (e.g., reproductive status of females) redundant.

The high density of tahr relative to chamois at single-species sites in 1978 reflects species differences in sociality. Studies of un hunted populations have recorded densities of tahr considerably higher than chamois (see Tustin and Challies 1978; Clarke and Frampton 1991). Female-juvenile groups of tahr 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 tahr in Carneys Creek (see Fig. 3) following the advent of helicopter-based hunting have been described by Tustin and Challies (1978) and are considered representative of trends elsewhere in the eastern Southern Alps. In 1965, when the Carneys Creek population was at peak density, a summer census counted 710 tahr ( $> 30$  km<sup>-2</sup>). A repeat census in 1977 counted 48 tahr; 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 of tahr was prohibited in 1983, and a census in summer 1984 recorded just 26 tahr in Carneys Creek (Forsyth 1997). Despite intensive recreational hunting, annual censuses of tahr in Carneys Creek since 1984 have showed a population increase of *c.* 20% per annum (Forsyth 1997). The widespread decline of chamois recorded in this study suggests that intensive commercial and government helicopter-based hunting of tahr enabled chamois to co-exist with low densities of tahr during the late 1970s.

There is no evidence to suggest that chamois in the eastern Southern Alps were subject to relatively greater harvest by recreational or commercial hunters compared to tahr. Monitoring of hunted chamois populations outside the tahr breeding range during 1991–1993 recorded densities similar to those recorded in this study during 1978–1979 (Parkes and Clarke 1993), indicating that hunting is unlikely to be responsible for the disappearance of chamois from 11 of the 14 sympatric sites.

At least three mechanisms might explain the decline of chamois in the eastern Southern Alps between 1978 and 1991–1996:

1. Differential susceptibility of chamois to disease and/or parasites that they share with tahr (*sensu* Schröder and Kofler 1985) may have reduced the fitness of chamois.
2. High densities of tahr may have modified plant communities such that sites were no longer preferred by chamois.
3. Behavioural intolerance of tahr by chamois may have resulted in chamois moving away from sites containing high densities of tahr.

Diseases and/or parasites are unlikely to have resulted in consistently greater mortality of chamois relative to tahr during this study (Forsyth 1997). No tahr or chamois shot during the 1978 control operation showed signs of disease, and there were no reports of diseased animals in the 1978–1996 period (D.C. Anderson, personal communication).

An unpublished diet study has shown that sympatric chamois and tahr in the eastern Southern Alps feed on the same plant species, but in different proportions according to season. In general, chamois rumens contained greater amounts of shrub and herb species than those of tahr, but less tussock (J.P. Parkes et al., unpublished work). Because competition between food-limited generalist herbivores depends upon the fractions of shared and exclusive resources (Belovsky 1986), we consider the potential for dietary competition between chamois and tahr to be high.

The third mechanism – behavioural intolerance – was suggested by C.M.H. Clarke (personal communication) as an explanation for the decline of chamois. Chamois in New Zealand are antisocial and space themselves by “mutual avoidance” (Clarke and Frampton 1991). New Zealand chamois are also highly mobile, with some individuals migrating long distances between summer and winter ranges (Clarke 1986). In contrast, tahr are highly social with female-juvenile groups of >30 common at high population density (Caughley 1967; Tustin and Challies 1978), and aggressive behaviour within these female-juvenile groups is apparently uncommon (Tustin and Parkes 1988). Miller (1967) proposed that intra-specific behaviours could govern interspecific interactions between mammal species; more social and territorial species could be expected to dominate less social species. The mobility of most chamois relative to the strong philopatry of female tahr offers a proximate mechanism for the movement of chamois from previously favoured sites.

All three mechanisms proposed to account for the decline of chamois associated with increasing densities of tahr are difficult to test experimentally because (1) they are not mutually exclusive; (2) some effects may take many years to become evident, and (3) the mobility of many chamois makes long-term study of individuals difficult, particularly in hunted populations. Nevertheless, continued monitoring of chamois densities in response to sustained control of tahr at low densities (Department of Conservation 1993) may provide insight into the mechanism(s) of interspecific competition.

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