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ECOLOGY AND MANAGEMENT OF  
HIMALAYAN THAR AND SYMPATRIC CHAMOIS  
IN THE SOUTHERN ALPS, NEW ZEALAND

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A thesis  
submitted in partial fulfilment  
of the requirements for the Degree of  
Doctor of Philosophy  
at  
Lincoln University  
by  
David M. Forsyth

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Lincoln University

1997

## Frontispiece



A female (left) and adult male thar during winter in the Southern Alps (G. Roberts).



An adult chamois in summer pelage (G. Roberts).

**This thesis is dedicated to the late Julie Alley**

(11.03.68 - 8.10.96)

Here dead we lie because we did not choose  
To live and shame the land from which we sprung.  
Life, to be sure, is nothing much to lose;  
But young men think it is, and we were young.

A. E. Housman

... there is no such thing as lasting happiness on earth,  
but moments of happiness occur now and then if you  
are quick enough to seize them before they vanish.

Peter Bamm

*The Invisible Flag*, Faber and Faber, 1956.

Abstract of a thesis submitted in partial fulfilment of the  
requirements for the Degree of Ph.D.

## Ecology and management of Himalayan thar and sympatric chamois in the Southern Alps, New Zealand

by David M. Forsyth

This thesis investigated aspects of the ecology and management of Himalayan thar (*Hemitragus jemlahicus*) and sympatric chamois (*Rupicapra rupicapra*) in the eastern Southern Alps of New Zealand.

The hypothesis that increasing densities of thar are associated with declining densities of chamois was investigated. Counts of thar and chamois at 53 sites within their sympatric range during 1978 revealed chamois densities to be significantly higher at sites without thar compared with those sites with thar. Although this result is consistent with the occurrence of interspecific competition, differential habitat selection could also explain the observed segregation of the species. Hence, 16 of 17 sites at which chamois and thar co-existed in 1978 were recounted during 1991-1996 to test predictions about the numerical response of chamois to increasing densities of thar. There was a six-fold increase in mean thar density between the two counts, whereas chamois density declined significantly. Chamois persisted at only three sites, two of which had the highest chamois densities in 1978. This is reliable evidence that increasing densities of thar exclude chamois from all but the most favoured habitats.

Monthly observations of habitat selection by sympatric thar and chamois in Carneys Creek during 1993-1996 showed significant interspecific differences in selection of some habitat types. These differences were most pronounced in spring and summer, and least in autumn. It is concluded that chamois can co-exist with the low-density population of thar in Carneys Creek due to differential habitat selection. Thar selected a broader range of habitats than chamois in Carneys Creek in all seasons, suggesting that thar have a broader niche than chamois in the eastern Southern Alps.

Nevertheless, there was strong overlap in the preference of thar and chamois for

grassland and shrubland, suggesting a high potential for interspecific competition when thar densities increase.

Observations of 24 interspecific interactions in the Two Thumb Range showed that chamois moved away from thar groups significantly more often than *vice versa*. I 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 and density-dependent mechanism that best explains the recent (1978-1996) decline of chamois in the eastern Southern Alps.

Long-term trends in the summer adult male : female ratio of thar in the Two Thumb Range are described. Annual summer censuses were made in two catchments subject to different harvest strategies from 1984-1996. Densities in both catchments increased during the study. In Carneys Creek, subjected to unrestricted harvest, the summer population sex ratio was approximately equivalent to the estimated wider Southern Alps adult sex ratio during 1984-1991, but thereafter became increasingly male-biased. In North Branch, subjected to a small harvest of adult (trophy-size) males, the summer population was significantly female-biased in every year. A postal and telephone survey of recreational hunters who hunted in Carneys Creek during 1993 revealed the thar harvest to be strongly male-biased. Monthly counts of adult male (>4 years), sub-adult male (2-4 years) and female thar (>2 years) in Carneys Creek during 1993-1996 revealed an influx of sub-adult males during spring. Censuses of thar at six adjacent sites during summer 1996 indicated the likely source of these males to be an adjacent hunting reserve. High densities of females in the hunting reserve are postulated to have produced large numbers of sub-adult males that migrated to the northern Two Thumb Range because of a combination of preferred habitats and low overall density.

Given the interspecific and intersexual differences in habitat selection, diet and mobility evident in sympatric thar and chamois, managers face a difficult task attempting to mitigate the deleterious impacts of these pests on conservation resources. This is compounded by the presence of hares (*Lepus europaeus occidentalis*), red deer (*Cervus elaphus scoticus*), and possums (*Trichosurus vulpecula*), all of which are

likely to overlap in their habitat use and diet. Some ideas for the integrated management of the central Southern Alps herbivore pest community are presented. The need to understand competitive interactions between pests, as well as pest-resource dynamics, is highlighted.

**Key words:** alpine, behaviour, chamois, competition, control, density, diet, habitat selection, harvesting, *Hemitragus jemlahicus*, Himalayan thar, hunting, interspecific competition, *Rupicapra rupicapra*, sexual segregation, Southern Alps, wildlife management, New Zealand.

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Despite the help that these people gave me, all errors are entirely my responsibility. So, comfortable reader, sit back and enjoy my toils!

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# Chapter 1

## General Introduction

New Zealand has been the recipient of two 'waves' of human colonisation. Polynesian settlers arrived *ca.* 850 AD (but possibly considerably earlier; Holdaway 1996), introducing kiore (Polynesian rat; *Rattus exulans*) and kuri (Polynesian dog; *Canis familiaris*) (Davidson 1984). The second wave began in 1769 with the arrival of Europeans who liberated domestic species such as goats (*Capra hircus*), pigs (*Sus scrofa*) and sheep (*Ovis aries*) to establish feral populations.

Following annexation by Great Britain in 1840, the pace of New Zealand's human settlement increased. Predominantly European colonists introduced a plethora of animals (and plants) to their new homeland for a variety of reasons (Wodzicki 1950; Druett 1983; King 1990). At least 52 mammal species were liberated by Europeans, 23 of which were ungulates (King 1990). Some, such as the zebra (*Equus zebra*), gnu (*Connochaetes gnou*) and alpaca (*Lama pacos*), never established. But many did. Presently there are at least 14 ungulate species in New Zealand with one or more feral populations (King 1990; Coleman 1993).

Feral mammals on land administered by the New Zealand Department of Conservation are classified as 'pests' for a variety of reasons (Holloway 1993). Parkes (1991) summarised the Department of Conservation's statutory obligation:

"Among the Department's functions is an obligation to manage, for conservation purposes, all land and all other natural and historic resources held under the Conservation Act and other tenures with the agreement of the land owner and Minister. Conservation is defined as the 'preservation and protection' of these natural resources for the 'purposes of maintaining their intrinsic values'... Indigenous natural resources are deemed to have more intrinsic value than introduced natural resources. This interpretation is supported by the implied or actual definitions of introduced animals as pests in other acts administered by the Department."

This thesis investigates aspects of the ecology and management of two introduced ungulates, Himalayan thar (*Hemitragus jemlahicus*) and chamois (*Rupicapra rupicapra*). These species co-exist (termed sympatric) in the alpine and sub-alpine zones of the

central Southern Alps, South Island, New Zealand, and both are managed by the Department of Conservation as pests. The questions that this thesis seeks to answer were generated, directly or indirectly, by the Himalayan Thar Control Plan (Department of Conservation 1993). That document summarised the state of knowledge regarding the biology and impacts of thar, and highlighted major gaps in knowledge required for the long-term management of thar.

Recent authors (e.g., Hone 1995; Parkes and Nugent 1995) have emphasised the need to manage the impacts of a pest, rather than the pest *per se*. Because the breeding range of thar entirely overlaps with chamois, and because casual observations indicate that they use similar habitats (Department of Conservation 1993), the impacts of thar and chamois on conservation resources (indigenous plant and animal populations, species, communities, and ecosystems) are likely to be largely cumulative.

A study of the contents of sympatric thar and chamois *rumens* by Parkes and Thomson (1995) indicated that chamois and thar eat the same species, albeit in different proportions. Although this was not conclusive evidence that their impacts overlap (for instance, different habitats within their sympatric range might be utilised), it suggested that they do. Management of thar and chamois should therefore be *integrated* (*sensu* Parkes and Nugent 1995); that is, there is a need to at least consider both species in any management action aimed at protecting indigenous flora within their sympatric range. In particular, the Department of Conservation has already recognised the potential for competitive interactions between thar and chamois (Department of Conservation 1993). Holloway (1993:290) said that "no protection (of indigenous flora) will be achieved if chamois or sheep replace thar as the damaging agent".

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## OBJECTIVES

This thesis addresses the following objectives:

1. To evaluate whether increasing densities of Himalayan thar are associated with decreasing densities of chamois, and if so, to outline possible causal mechanisms.
2. To describe seasonal habitat selection by Himalayan thar and chamois in a catchment representative of their sympatric range, and to discuss its implications for the co-existence of these species.
3. To investigate mechanisms underlying long-term changes in the summer adult sex ratio of thar in two catchments in the Two Thumb Range.
4. To discuss the management implications of the answers to the preceding objectives.

## STRUCTURE OF THESIS

This thesis represents work that commenced in July 1993 under the supervision of Drs Graham Hickling and Adrian Paterson. The thesis is structured as a series of interconnecting, yet self-contained, chapters. These chapters, excluding the General Introduction, Literature Review and General Conclusions, have been prepared for submission to various journals, and so are not entirely consistent in their layout and style. Throughout this thesis I have adopted the spelling 'thar' rather than 'tahr'. The former is most commonly used within New Zealand whereas the latter is used internationally. The observant reader will note that in some figures the spelling 'tahr' is used; this is because it is intended to publish that chapter in an international journal.

The order of the chapters is:

- **Chapter one**, *General introduction*, describes the background to, and structure of, the thesis. The objectives of the thesis are outlined.
- **Chapter two**, *Literature review: ecology and management of thar, chamois and other introduced ungulates*, discusses the ecology and management of introduced ungulates. A biological, economic and political account of Himalayan thar and chamois in New Zealand is given.

- **Chapter three**, *Increasing Himalayan thar and decreasing chamois densities in the eastern Southern Alps, New Zealand: evidence for interspecific competition*, uses long-term data on changes in the densities of sympatric thar and chamois to test the hypothesis that increasing densities of thar are associated with decreasing densities of chamois.
- **Chapter four**, *A mechanism for the competitive exclusion of chamois by Himalayan thar in the eastern Southern Alps, New Zealand*, describes seasonal habitat selection by thar and chamois within one catchment representative of their sympatric range. The implications of these results for the exclusion of chamois by thar are discussed.
- **Chapter five**, *Harvesting and sexual segregation in a New Zealand population of Himalayan thar*, describes long-term spatio-temporal trends in the summer adult sex ratio of thar in the Two Thumb Range, and hypothesises these to be a consequence of different harvest strategies in adjacent catchments. Possible ultimate mechanisms for sexual segregation in thar are briefly discussed, as are the management implications of this phenomenon.
- **Chapter six**, *A case for integrated management of sympatric herbivore pest impacts in the central Southern Alps, New Zealand*, uses the example of sympatric thar and chamois to illustrate why integrated management of the central Southern Alps alpine pest community will give improved conservation benefit relative to the current single-species management approach.
- **Chapter seven**, *General conclusions*, highlights the key findings of the previous chapters and outlines important questions arising from the thesis.

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# Chapter 2

## Literature Review:

### Ecology and Management of Thar, Chamois and Other Introduced Ungulates

#### SCOPE

This literature review critically evaluates aspects of the ecology and management of introduced ungulates that are conservation pests. The management of introduced ungulates as a hunting resource is beyond the scope of this review. A precis of the biology of Himalayan thar and chamois that is required by the reader, to comprehend this thesis is presented. Information presented in detail in subsequent chapters is, for the reader's sake, only outlined briefly in this review. The political, social and technological factors that have shaped (and will continue to shape) management of thar and chamois in New Zealand are emphasised.

#### ECOLOGY OF INTRODUCED UNGULATES

##### Establishment

Animals may establish new populations in a variety of ways, either aided or unaided by humans. I consider how introduced (sometimes termed non-native) ungulates establish such populations, and how the need for management by humans arises. In contrast to smaller mammals such as rats (*Rattus* spp.), ungulates are seldom introduced unintentionally by humans. Domestic livestock, however, do escape and sometimes establish feral populations; examples include feral goats *Capra hircus* (Parkes 1990) and cattle *Bos taurus* (Taylor 1990) in New Zealand, and camels *Camelus dromedarius* in central Australia (Lever 1985).

Where ungulates have disappeared from their indigenous range, re-introductions are often made with the aim of re-establishing the species (e.g., alpine ibex *Capra ibex*; Schröder and Kofler 1984, and Prezewalski horse *Equus ferus przewalskii*; Van Dierendonck and De Vries 1996). Furthermore, since ungulates are highly valued by humans (see below), they have commonly been introduced deliberately outside their

native range with the intention of establishing feral populations (Lever 1985; Putman 1989). In New Zealand, for example, 23 ungulate species have been introduced, most deliberately (King 1990).

The study of animal invasion has in recent decades been re-kindled by conservation biologists who wish to maximise the success of establishing new populations, often with small numbers of individuals (Griffith *et al.* 1989). Additionally, the characteristics and ecological impacts of exotic species can provide insight into the processes that structure communities (Lodge 1993).

*Invasion* has been defined as the successful founding of a population where none previously existed, followed by an expansion of the invading species (Barrett and Richardson 1986). *Colonisation* has been defined as the process of immigrants arriving and establishing a population such that the extinction probability of the population is no longer dependent on its initial state (Ebenhard 1991). Factors influencing the establishment of an invasion have been the subject of considerable debate (see, for example, Crawley 1987; Drake *et al.* 1989; Pimm 1991). Although general patterns can be described from differential success and failure (e.g., Elton 1958; Diamond and Case 1986), quantitative analysis is often difficult (Brown 1989). Certain intrinsic characteristics, however, do appear to predispose some species to be successful invaders while their close relatives are less successful (Ehrlich 1989; Lodge 1993). For mammals the most important factors appear to be body size, fecundity and diet (Ehrlich 1986; 1989; Crawley 1987).

Increasing body size is negatively correlated with intrinsic rate of increase but positively correlated with longevity (Caughley and Krebs 1983). Crawley (1989) suggested that larger mammals are more buffered against environmental extremes, are more polyphagous, have fewer predators, and may be able to disperse over greater distances relative to smaller mammals. Pimm (1991) proposed that established populations of large animals exhibit relatively little variation in population size, which may reduce the probability of a small population going extinct. Conversely, low intrinsic rate of increase means that invading populations of large animals would take longer to attain a population size that makes unlikely their extinction from environmental disturbances or stochastic processes (Pimm 1991). The difficulties of

conducting critical tests of these hypotheses mean that we can only surmise as to the relative importance of each factor.

Initial propagule size will influence the rate at which the colony can grow beyond the size at which stochastic and environmental processes can make the population extinct. Recent quantitative analysis of early bird introductions into New Zealand by Acclimatisation Societies has shown initial propagule size and the number of introductions (collectively termed *introduction effort*) to be the prime determinants of success (establishment or not) (Veltman *et al.* 1996). This mirrors results of insect biocontrol, where establishment rates increased with the number of individuals released (Crawley 1987).

The role of community invasibility (termed 'biotic resistance' by Simberloff 1989) in determining invasion success has been much debated. Island communities such as New Zealand and Hawaii have been particularly invulnerable, presumably because of their long periods of evolutionary isolation and resulting high proportion of endemic biota, and their vulnerability to predatory and competitive effects of invading species (Moller *et al.* 1993). The extraordinary effort put into introducing many species to these islands is also likely to have been important.

The role of interspecific competition in establishment is unclear. Among New Zealand birds, patterns of success were consistent with both competition (number of introduced species present) and introduction effort effects, but the two variables are confounded (R. P. Duncan, *pers. comm.*). Both empirical and theoretical studies indicate that species-poor communities are more invulnerable than species-rich communities (Vermeij 1991), suggesting that interspecific competition is important. More case studies describing the mechanisms why species fail to establish are required to improve our understanding of the role of interspecific competition in invasion success.

The absence of native terrestrial mammals apparently made New Zealand particularly invulnerable for introduced mammals. For example, 33 mammals successfully invaded New Zealand, in stark contrast to mammals' lack of invasion success of New Guinea, which already had a species-rich indigenous mammalian fauna (Moller *et al.* 1993). In

addition, extinctions and habitat alterations by Maori probably acted to make New Zealand more invulnerable to European biota (Moller *et al.* 1993).

Most invasions, however, do not succeed. Many species probably do not possess the appropriate adaptations to the new physical environment. This may explain why widespread species are more successful invaders than species with small geographical ranges (Moulton and Pimm 1986; Crawley 1987; Lawton 1993). Widespread species may be able to tolerate a wider range of ecological conditions than restricted species, and they may also be better able to cope with predators and competitors than restricted species.

The conditions needed for successful introductions may be scarce in both space and time. Rare events (e.g., fire) may well be the cause of major change to a community enabling a species to successfully invade (Crawley 1989). This may explain why the number of introductions was a significant predictor of the establishment of exotic bird species in New Zealand (Veltman *et al.* 1996).

Dispersal also appears to influence establishment. For birds introduced to New Zealand, species from a migratory population were significantly less likely to establish than non-migratory species (Veltman *et al.* 1996). Animals that disperse far are less likely to find a mate, but species that do not disperse widely may not establish due to the effects of intraspecific competition. Consequently, the role of dispersal is also likely to be closely related to species gregariousness, diet-breadth and mate-finding ability.

Moller *et al.* (1993) considered New Zealand to have been particularly prone to invasion. That is, many species successfully invaded New Zealand that might not be expected to succeed elsewhere. Although a wide variety of animals have established in New Zealand (e.g., chamois, brushtail possum, *Trichosurus vulpecula*, and several species of wallaby, *Macropus* spp.), many of these species have not been liberated elsewhere (or if liberated, their fate has not been recorded) so their *relative* success in New Zealand cannot be quantified.

Caughley (1989) divided the recent history of New Zealand's biota into three phases. From BC 5000 to AD 850 was a period of relative stasis. Following the arrival of

Polynesians *ca.* AD 850, hunting, habitat modification (principally through fire), and the impacts of their two introduced mammals, kiore (Polynesian rat) and kuri (Polynesian dog), massively changed the principal plant-vertebrate herbivore relationships. In AD 1800, when European colonisation began, New Zealand's 'biotic resistance' to invasions was probably very weak. Early extinctions due to predation and hunting may have facilitated the success of new species, which in turn could have lead to further extinctions of endemics (Moller *et al.* 1993). In many cases we cannot be certain whether introductions were responsible for extinctions in New Zealand, or whether extinctions permitted introductions (Diamond & Veitch 1981).

The factors influencing the success of ungulate introductions into New Zealand are unknown (and would make a fascinating study), but introduction effort can be expected to have been important. Some ungulates introduced into New Zealand established only due to the great enthusiasm (and expenditure) of their liberators. For example, from 1851-1922, five strains of red deer *Cervus elaphus scoticus* were liberated 32 times in the northern South Island. Only one liberation, of two hinds and a stag, was successful (Clarke 1971).

### Effects of introduced ungulates

There is a large body of literature describing the impacts of animal invaders on communities. Ebenhard (1988) reviewed the effects of >800 mammal introductions. He defined an *effect* to occur where the invader caused extinctions and/or altered the abundance of species in the receiving community. Herbivorous mammals introduced to continents had measureable effects in 26% of 84 cases. On oceanic islands 49% of 188 introductions showed effects. It is, however, very difficult to predict the effects of introducing a herbivorous mammal with a generalized diet into a community. The consequence of species introductions, if they are successful, is likely to depend upon the complexity of the food web (Pimm 1991).

Pimm (1987) considered that species introductions are likely to be severe when:

1. Species are introduced where predators are absent.
2. Highly polyphagous species are introduced.
3. Species are introduced into relatively simple communities where the removal of a few plant species will collapse the food chain.

Most ungulates are polyphagous (see Belovsky 1986) and those that did establish in New Zealand have generally had profound and pervasive effects on the distribution and abundance of indigenous biota (Elton 1958; Veblen and Stewart 1982). However, since communities are spatially and temporally complex, changes to date are more commonly major shifts in composition rather than complete community collapse.

Following liberation, introduced ungulates in New Zealand are inferred to have undergone an irruptive cycle (Riney 1964; Caughley 1970a; Clarke 1971). Caughley (1980) summarised the cycle as follows. For a period after establishment densities increase to a peak, but as the food supply is depleted the densities decline to lower levels. This decline is followed by long-term adjustments of the vegetation to browsing. Caughley (1980) considered these fluctuations to be relatively small around a constant carrying capacity. Such cycles have been observed in ungulates elsewhere (e.g., reindeer *Rangifer tarandus* on South Georgia; Leader-Williams 1988).

Due to the complete absence of non-human predators, ungulate populations in New Zealand are food limited. Ungulates can also be thought of as *K*-strategists, characterised by low intrinsic rates of increase, generally low rates of dispersal, and restricted habitat requirements relative to *r*-strategists. Populations of *K*-strategist species are also typically more stable than those of *r*-strategists, so that impacts on vegetation are chronic rather than periodic (Parkes 1993a).

There are likely to be fundamental differences between herbivore-vegetation interactions in grassland and in forest (Parkes and Nugent 1995). In the former, herbivores will have access to all above-ground foliage all of the time (except in montane systems where snow may seasonally make some vegetation types unavailable), whereas in forests much foliage is unavailable to ungulates until it falls to the ground (Nugent 1990). Because of the shorter generation time of grasses relative to trees, herbivore-vegetation equilibriums in grassland communities should be reached more quickly than in forests. In the latter it may take hundreds of years to attain equilibrium (Nugent and Challies 1988).

Parkes (1993b) compared the diets of two populations of feral goats living in North Island forest. The rumens of recently-established goats contained more understorey species and herbs and less canopy species than the longer-established population.

Unfortunately the available forage was not measured (e.g., Nugent 1990), but the inference is that the abundance of most understorey species and herbs is decreased by sustained browsing by feral goats. After favoured species become rare the goats must eat more of the less-favoured canopy foliage.

Despite the considerable body of theory that has developed about the impact of exotic herbivores on receiving communities, field-studies have frequently struggled to differentiate natural from animal-induced vegetation change (Veblen and Stewart 1982). Studies in New Zealand have either been descriptive, comparative, or what I term 'quasi-experimental'. All three approaches are problematic. Descriptive studies (e.g., Mark and Baylis 1982) involve using transects or plots to measure the distribution and abundance of plant species. Inferences about the effects of ungulates are made in association with observations of browsing. For example, the absence of seedlings of highly-favoured (from browsing observations) species is cited as evidence for the removal of that species by the ungulate(s) present. Because there is no unbrowsed vegetation to directly compare the browsed vegetation with, inferences are essentially guesses. Additionally, because the stage of ungulate population growth (irruption, stabilisation, decline, or post-decline) is seldom known with any certainty the knowledge gained from this approach is unreliable (*sensu* Romesburg 1981).

Comparative studies (e.g., Stewart and Burrows 1989) involve comparing vegetation on browsed areas with similar unbrowsed areas (usually islands). The major potential flaw in this method is that the unbrowsed area is normally some distance from the browsed area, and often subject to different environmental gradients (e.g., small islands) resulting in different vegetation between the sites in the absence of browsing. The ungulate population density, or stage of population growth, is again usually unknown.

The 'quasi-experimental' approach (e.g., Allen *et al.* 1984) uses fenced exclosures to exclude ungulates. After some years the vegetation within exclosures is compared to nearby unfenced plots. Although this method gives the most reliable inferences of the three approaches, exclosures are always established when ungulates are already present, so the vegetation is almost certain to have been modified. Patterns resulting from removal of ungulates therefore may not resemble the pre-ungulate vegetation (Allen *et al.* 1984). Another problem with the quasi-experimental approach is that the

fenced exclosures are usually of small size and number, and spread over a small spatial scale, further limiting the inferences that can be made.

Patterns of ungulate modification are also confounded by the presence of other introduced mammalian herbivores. For example, possums are widespread in New Zealand's forests and shrublands (Cowan 1990). The use of exclosures that exclude ungulates but not possums overcomes this problem. Nevertheless, there are often two or more species of ungulate co-existing, making inferences about the impacts of each species difficult.

Reliable evidence for the impacts of introduced ungulates on indigenous ecosystems can only be gained by long-term and adequately replicated experiments that compare densities of ungulates (within enclosures) with a control (zero density within enclosures). Model examples of such experiments are provided by Tilghman (1989) and deCalesta (1994). The latter even showed that both the diversity and abundance of intermediate canopy-nesting songbirds declined with increasing densities of white-tailed deer in managed forests in Pennsylvania, U.S.A. The experiment was run for 10 years with four densities (3.7-24.9 deer km<sup>-2</sup>) of deer. Of course, the impacts of ungulates on *unmodified* ecosystems can only be ascertained by performing such experiments in unmodified ecosystems.

The effects of introduced ungulates on the New Zealand vegetation have been widely interpreted as catastrophic (e.g., Elton 1958). Because the specific effects of ungulates depend on the ecosystem and herbivore characteristics (Huntly 1991; Hobbs 1996), here I present only a general account of ungulate impacts. There is always a decrease in the distribution and abundance of palatable food species, and usually a subsequent increase in the distribution and abundance of unpalatable species following release from interspecific competition and/or a change in environmental conditions (e.g., Caughley 1970a; Stewart and Burrows 1989). There is sometimes an increase in the proportion of bare ground, especially as populations begin to decline after attaining peak density (e.g., Caughley 1970a). Because plant community composition, ungulate population density and ungulate behaviour are spatially heterogeneous (Huntly 1991), the effects of ungulates will be highly variable in both space and time (e.g., see Hone 1995). There is a growing body of evidence that indirect interactions (e.g., changes in nitrogen cycling through ungulate excretion) may be just as important as direct

herbivory in the modification of some ecosystems by ungulates (see Hobbs 1996). I know of no New Zealand studies that have examined such indirect interactions between introduced ungulates and the ecosystem; clearly this is an area for future research.

Until the 1980s there was a common perception in New Zealand that introduced herbivores caused erosion of mountain lands and silting of rivers (Caughley and Sinclair 1994). Subsequent studies have shown the contribution of these animals to erosion to be negligible relative to abiotic processes (Grant 1989). Trampling effects may sometimes cause local compaction on well-used tracks, but this effect is usually considered insignificant relative to other impacts (Hobbs 1996).

In summary, the impacts of introduced ungulates are likely to depend on the characteristics of the receiving ecosystem. One generality is that the distribution and abundance of favoured plant species will decrease, with a concomitant increase in less favoured species following release from direct or indirect interspecific competition. Indirect interactions, for example through excretion-mediated changes to the nitrogen cycle, are also likely to be important, but hitherto there has been little research into these processes. Replicated field experiments (with different ungulate densities the 'treatments') are required to reliably determine the impacts of introduced ungulates.

## MANAGEMENT OF INTRODUCED UNGULATES

### Why control introduced ungulates?

Ungulates may be considered too numerous for several reasons (Caughley 1981). First, because few people enjoy all species equally, there is often a general desire to increase the abundance of favoured organisms. An example is the browsing of aspen (*Populus tremuloides*) by elk (*Cervus elaphus nelsoni*) in Yellowstone National Park. People who enjoy aspen favour the reduction of elk, which browse the trees, to low densities (Caughley 1981). Second, the equilibrium density itself may be considered to be deleterious (Caughley 1981). This reasoning often relies on popular misconceptions of herbivore-vegetation interaction, natural regulation of animal populations, and ecosystem stability (Porter 1992). It has been realised that in most areas various forms of large-scale disturbance are indigenous (Sprugel 1991), effectively making the

concept of 'equilibrium' redundant at the spatial and temporal scales considered by scientists (Porter 1992).

The function of wildlife managers is to satisfy both positive and negative social aspirations assigned to wildlife (Wagner and Seal 1992; Caughley and Sinclair 1994). The term "pest" applies to populations whose actions are considered by some in society to have negative value. With regard to mitigating the modification of indigenous ecosystems by introduced ungulates in New Zealand, these goals have been framed by legislation (Parkes 1991; Holloway 1993; Parkes 1993b) that appears to reflect public attitudes to introduced animals (see Fraser 1995). The Conservation Act 1987 obliges the Department of Conservation to preserve and protect natural resources that have intrinsic values. The intrinsic values of indigenous biota, ecosystems and processes are emphasised in the Conservation Law Reform Act 1990, and defined as "those aspects of ecosystems and their constituent parts which have value in their own right...". In practice, the intrinsic values are the attributes of species (e.g., rare, distinct), ecosystems (e.g., rare, representative) or processes (e.g. stable, dynamic) (Parkes 1993b).

Introduced ungulates have undoubtedly modified the ecological processes and species composition of most of New Zealand's remaining grasslands, shrublands and forests, and the need to manage these impacts has been officially recognised since the 1930s (Holloway 1991). Traditional control methods (principally ground-based hunting) did not prove successful and it is only since the development of markets for wild venison in the late 1950s that extensive and sustained reductions in introduced ungulate numbers have occurred.

Historically, control of ungulates in New Zealand has suffered from a lack of clearly defined objectives, resulting in the means (killing pests) becoming the end (Caughley and Sinclair 1994). For example, the National Parks Act 1980 required managers to "exterminate introduced plants and animals as far as possible" unless the National Parks and Reserves Authority declared otherwise. The policy in National Parks is therefore eradication, despite this being unobtainable in most instances (Bomford and O'Brien 1995); this was rightly criticized by Williams (1979) as "high sounding, poorly conceived and biologically not very sensible".

Pest control (including control of ungulates) to protect conservation resources is a major function of the Department of Conservation. For example, in 1993 *ca.* 16 percent of its budget was spent managing weed and animal pests (Parkes and Nugent 1995). The Department of Conservation is currently preparing a series of national control plans for introduced mammalian pests that specify actual management objectives. A national control plan exists for Himalayan thar (Department of Conservation 1993), and similar plans are being prepared for feral goats and red deer.

### **Strategies for managing introduced ungulates**

A variety of management strategies are available to managers, each of which can be distinguished on the basis of the stability of outcome and the need for continued control (Parkes 1993a). Management *strategies* are distinct from management *techniques*; the latter is a method of control (e.g., shooting, poisoning) that can be used under different strategies.

Parkes (1993a) outlined three strategies for dealing with mammal pests. One strategy is to do nothing. This strategy is valid where the costs outweigh the benefits of control, but for ungulates that are conservation pests, determining the financial benefits of control is difficult. In some other cases there may be no effective control technology available. This strategy has no ongoing costs, but stability of outcome depends entirely on the characteristics of the particular herbivore-vegetation system.

A one-off strategy is a single management action that has no ongoing cost. An example is the eradication of goats from Raoul Island (Parkes 1984a). Eradication is the permanent removal of the entire population within a specified time period, and must also involve the prevention of subsequent immigration or introductions. The success or failure of eradication is relatively simple to monitor, although the conditions required for eradication to occur (see Bomford and O'Brien 1995) are often not present. Sustained control requires ongoing control action, the aim of which should be to maintain the pest below a threshold at which the resource is unacceptably modified (Parkes 1993a). This strategy requires an understanding of the relationship between pest density and the resource being protected. For ungulates, the outcome of sustained control is likely to be stable, simply because a new pest-resource equilibrium will be achieved. This new equilibrium should be such that the resource is not unacceptably modified. For most ungulates managed by the New Zealand Department of

Conservation, changing fiscal and political pressures have seldom resulted in the ongoing effort required for this strategy to achieve the desired protection of conservation resources (Parkes 1993a).

Control will be inappropriate where the pest is not responsible for the resource modification, or where the control has an unacceptable effect on non-target species (Caughley and Sinclair 1994).

### **HIMALAYAN THAR AND CHAMOIS IN NEW ZEALAND**

Himalayan thar and chamois were introduced by the New Zealand Government with the aim of establishing a hunting resource for local and overseas sportsmen (Donne 1924). Their subsequent biological, political and economic history mirrors that of many of the other feral ungulates in New Zealand.

#### **Liberation and dispersal**

The New Zealand thar population originates from a captive herd held at Woburn Park, England. The Woburn Park herd was itself descended from only 23 animals (Caughley 1970b). In 1904 three females and two males, gifted by the Duke of Bedford, were liberated near Mount Cook by the Tourist and Health Resorts Department (Donne 1924). A further gift from the Duke of Bedford in 1909 resulted in six males and two females being released in the vicinity of the original liberation (Donne 1924). Four more thar (sex unknown) from the Wellington Zoo were added in 1919 (Anderson and Henderson 1961).

Two other liberations are known to have failed. Two females and one male were released near Rotorua (central North Island) in 1909 and two females and one male were liberated at Franz Josef Glacier (western South Island) in 1913 (Thomson 1922; Donne 1924).

The Mount Cook population apparently began breeding soon after liberation (Graham 1965). A group of 13 was observed near the original liberation site in 1915 (Thomson 1922), 18-20 in 1916 and one group of 50 in 1918 (Donne 1924). By the early 1920s the herd exceeded 100 animals (Donne 1924).

Ten chamois (three males and seven females), gifted from the Emperor of Austria, were also released at Mount Cook during 1907-1914 (Donne 1924). There is confusion about the origin of the chamois, but a recent investigation (Schasching 1995) suggests that at least some of the chamois were captured at Ebensee, Austria. Both herds were fully or partially protected until 1930.

The dispersal of both thar and chamois in New Zealand has been well documented. Chamois dispersed faster and further than any other ungulate introduced into New Zealand (Caughley 1963). Dispersal was apparently initiated by yearlings, and at first chamois moved north-east along the Southern Alps, subsequently colonising the lateral ranges (Clarke 1990). Chamois dispersal southward of Mount Cook was considerably slower.

Chamois had colonised most of the mountain ranges along the Southern Alps by the 1960s, and at that time were spreading into Fiordland and North West Nelson (Clarke 1990). Today, chamois are still colonising parts of Fiordland, Southland and eastern Otago (Parkes and Clarke 1993).

Caughley (1970b) reconstructed the distribution of thar in 1936, 1946 and 1956 through interviews with government hunters, and in 1966 by field surveys during the previous four years. In contrast to previous workers (Wodzicki 1950; 1961; Anderson and Henderson 1961; Christie and Andrews 1964), Caughley differentiated between breeding range (the area containing female thar) and gross range (the range containing both sexes). This distinction is important because male thar have frequently been recorded many kilometres from known female groups (e.g., Anderson and Henderson 1961; Caughley 1970b). Knowing the breeding range is of primary importance because the density of thar will be far greater than in the male-only periphery of the gross range.

Caughley inferred the dispersal sequence of thar from temporal changes in the breeding range. Dispersal occurred at a maximum of 3 miles per year with northward dispersal approximately twice the southward speed (Caughley 1970b). Dispersal from the liberation site was north-east and south-west along the eastern Southern Alps. By the mid-1930s females were in the headwaters of the Murchison and Dobson Valleys. Thar probably colonised the western Southern Alps via low passes in the headwaters

of the Godley and Hopkins Rivers during the 1940s (Caughley 1970b). In the mid-1950s thar populations were well established in Westland (in the headwaters of the Perth, Copland and Karangarua Rivers).

Thar achieved their greatest range in the early 1970s. In the eastern Southern Alps breeding populations extended from the Wilberforce River headwaters (Cronin Stream) in the north to the Hunter River in the south. In the west, thar were present from the Arahura to the Callery River, and from the Cook River to the south bank of the Landsborough River. Along the central Southern Alps there is a band of bare rock, snow and ice (generally  $>2000$  m) from which female thar have always been absent.

Caughley (1967; 1970b) tested two models of dispersal using breeding range area calculated from his distribution maps. His analyses indicated that a diffusion model (in which thar dispersed independently of population density) rather than a density-dependent model best described dispersal of female thar. Caughley (1977), however, did acknowledge that dispersal from 1904-1936 must have been non-linear. Re-analysis of these data by Parkes and Tustin (1985) showed errors in Caughley's calculations, but there is no evidence to suggest that his original maps were wrong. Parkes and Tustin (1985) showed that an exponential curve best fitted the re-calculated breeding areas for the entire 1904-1966 period. Density-dependent dispersal suggests a threshold group size at which females permanently emigrate. If managers can control female-juvenile groups below this threshold the implication is that further dispersal would not occur (Parkes and Tustin 1985).

### Population dynamics

The first attempt at understanding the ecology and population dynamics of thar was made by an organised group of sportsmen, the New Zealand Deerstalkers' Association (Inc.) Big Game Research Group. This group summarised seven years of field observations and post-mortem data in a lengthy monograph (Anderson and Henderson 1961). The monograph was extensive in its analysis of thar ecology and biology, but was essentially descriptive in nature.

Ideas presented by Anderson and Henderson (1961) were later developed by Graeme Caughley. Caughley tested whether differences in the period of colonisation of thar were also evident in population parameters (such as birth and death rates and body

condition). It was hypothesised (Caughley 1967) that such differences would reflect the irruptive stages of the population proposed by Riney (1964). Caughley's data were collected by ground-based hunters shooting in four areas hypothesised to reflect the different stages of the irruptive cycle; increasing, stationary, declining, and post-decline.

Life tables for female thar showed that fecundity was 90% in adults from both increasing and stationary populations, but 75% in post-peak and declining populations. In increasing populations 67% of young females gave birth at two years compared to just 27% in the stationary population (Caughley 1970a). It was mortality rate, however, particularly in the first year of life, that governed rate of increase. In the increasing population 37% of juveniles died, compared with 53% in the stationary and 59% in the decline phases (Caughley 1970a). Trends in median age at death and kidney fat (an index of condition) also conformed to Caughley's predictions (Caughley 1970a; 1970c).

Caughley (1970d) proposed that chamois underwent an irruptive cycle similar to thar. A long-term study of a post-peak population showed numerical stability within the range of 3.2-5.0 chamois km<sup>2</sup> (Clarke 1990; Clarke and Frampton 1991). Monthly observations of individually-marked chamois showed many individuals to be highly mobile, migrating across the Main Divide between summer and winter ranges (Clarke 1986; Clarke and Frampton 1991). Clarke and Frampton (1991) concluded that this population was regulated by social interactions rather than decreasing survival or fecundity. Unfortunately there are no data on peak population densities of chamois (cf. thar; see Chapters 3 and 5) so there is uncertainty as to whether chamois underwent an irruptive cycle regulated by food supply; Clarke and Frampton's data suggest not.

### **Management of thar and chamois**

Both thar and chamois were listed as game animals in the Animals Protection and Game Act 1921-1922. This enabled the Department of Internal Affairs and Acclimatisation Societies to regulate hunting through the sale of permits and closed seasons.

During the 1920s public concern about competition between thar, chamois and domestic sheep increased. This resulted in all protection being lifted in 1930. The Department of Internal Affairs employed hunters to shoot chamois and thar from 1936 to 1955. At least 24 000 thar and 68 000 chamois were killed during this period although the number shot by recreational hunters is unknown. Responsibility for wild animal control shifted to the New Zealand Forest Service (NZFS) in 1956, and from 1956 to 1976 both species were treated as pests under the Noxious Animals Act 1956. From the late 1960s wild ungulates came to be viewed as a commercial resource by some people, and this eventually forced legislative change. The Wild Animal Control Act 1977 aimed to control introduced ungulates by regulating harvesters through a system of permits.

The NZFS was replaced by the Department of Conservation in 1987. The Conservation Act 1987 superseded the Wild Animal Control Act, relegating introduced animals to pest status (Parkes and Clarke 1993). The legislative status of chamois and thar as game or as a commercial resource was reduced.

Ground-based government and recreational hunting had no noticeable impact on the speed or direction of thar (Caughley 1970b) or chamois (Clarke 1990) dispersal. Although some authors (e.g., Douglas 1984) claimed that hunting accelerated dispersal by scaring animals into new range, there is no evidence to support this contention.

Following the establishment of a commercial market for venison and associated by-products in the 1960s, helicopters began to be used for hunting. Helicopters were originally used to transport hunters and carcasses, but later became shooting platforms (see Challies 1974). The NZFS began to use helicopters to shoot, but not recover (termed 'search-and-destroy'), deer and chamois in the mid 1960s (W. R. Forsyth, *pers. comm.*). In September 1967 shooting thar from a helicopter was trialed in the Rangitata Valley; 400 thar and 25 chamois were shot in 4 hours (Boyd 1968, cited in Tustin and Challies 1978). This trial established helicopter-based search-and-destroy as the principal means of thar control. Ground-based culling became limited to 'mopping-up' high-density pockets (D. C. Anderson, *pers. comm.*).

The development of a commercial market for thar and chamois meat led to intensive helicopter-based commercial harvest from the early 1970s. The record was 174 thar

shot and recovered in one day (Tustin 1990); tallies of >200 chamois were common (Clarke 1990). The commercial harvest of thar peaked in 1974 with *ca.* 10 000 carcasses recovered. Helicopter-hunters switched to thar and chamois in the winter months (June-October) when red deer were relatively unavailable and the alpine species could be easily located and shot after a heavy snowfall (Parkes *et al.* 1996). Tallies of >100 thar shot and recovered per day were common in the early years of thar recovery (Tustin 1980). Commercial exploitation of thar, however, followed a 'boom and bust' pattern (Parkes *et al.* 1996). By the early 1980s densities of thar had been dramatically reduced, with <300 carcasses recovered by commercial hunters in 1983 (Parkes and Tustin 1985).

The 1976 breeding range was estimated by Ken Tustin, a Forest Research Institute scientist, in consultation with commercial helicopter crews who hunted thar in the winters of 1972-1976. The 1984 breeding range was determined by John Parkes in consultation with land-owners (in the eastern Southern Alps), commercial hunters and NZFS staff involved with thar control. Female thar expanded their range from 1966 to 1976, particularly in the north and south, but also colonised parts of central Westland (Parkes and Tustin 1985). After 1976 female thar were apparently eliminated from peripheral areas of the 1976 range by commercial helicopter-based hunting, although several new areas were colonised in the eastern Southern Alps where lease-holders could limit hunting operations (Parkes and Tustin 1985).

There is some uncertainty as to the extent of the range retraction described by Parkes and Tustin (1985). Not all thar encountered by helicopter-based hunters can be shot (New Zealand Forest Service, unpublished data) and there is considerable anecdotal evidence that survivors became 'helicopter-shy' (e.g., stood motionless or hid in rock bluffs and scrub) following intensive helicopter-hunting (Tustin 1990). Survivors probably utilised habitats offering protection from aerial hunters (see Tustin and Challies 1978), and thar in these habitats would also be difficult for ground-based observers to count (Parkes 1984b). Although thar densities were undoubtedly dramatically reduced throughout the Southern Alps by helicopter-based hunters (Tustin and Challies 1978; Tustin 1980), some areas mapped as containing no females in 1984 may actually have contained low density populations (Parkes 1984b; Parkes and Tustin 1985; Levine 1985; Tustin 1990). The 1984 distribution estimates should therefore be interpreted with caution.

Since 1984 there have been several extensions to the breeding range of thar (Department of Conservation 1993). Most significantly, females are now present south of the Haast Pass highway, which had been considered a barrier to southern dispersal. These thar, however, are believed to have originated from an illegal captive herd, and efforts are being made to eradicate this population (P. Hondelink, *pers. comm.*). Females have also closed gaps in their distribution within the Ben McLeod Range (D. C. Anderson, *pers. comm.*).

Following the large reductions in the thar population achieved by commercial helicopter hunting during the 1970s and early 1980s, recreational hunters became concerned that thar might be eradicated from the Southern Alps. The New Zealand Deerstalkers' Association (Inc.) petitioned Parliament in 1983, and in August of that year the Minister of Forests approved a moratorium on all commercial carcass recovery and live capture (for stocking game reserves and zoos) of thar, except within National Parks and at the southern and northern perimeters of their range (Parkes 1984b). The stated objective of the moratorium was to enable an assessment of the 1983 thar range and population size to be conducted.

Fifteen catchments spread throughout the 1976 thar breeding range were censused in March 1984 (Parkes 1984b). Two teams of observers used 8-10 X binoculars and 20 X spotting scopes to search for thar in the early mornings and late evenings. The results indicated generally low but variable densities of thar. Based on these data, Parkes (1984b) guessed the total feral population to be 1 000 - 2 000.

### **Thar management 1984-1993**

In 1984 the NZFS asked for public submissions on how it should manage thar. Of the 72 submissions 75% favoured managing thar for hunting (Hughey and Parkes 1995). A policy proposing to establish a Recreational Hunting Area (where thar would be managed by recreational hunting to balance their environmental impacts) was drafted (New Zealand Forest Service 1985). This proposal was eventually curtailed by the restructuring of the Government's environmental agencies (primarily the Wildlife Service, Protection Forestry Division of the NZFS and the Department of Lands and Survey) to form the Department of Conservation in 1987.

The legislation under which the Department of Conservation operates defines animals such as thar and chamois as pests more clearly than did the legislation guiding the New Zealand Forest Service (Hughey and Parkes 1995). The Department of Conservation commissioned John Parkes (Forest Research Institute) to review options for managing thar. His review (Parkes 1988) identified the three management possibilities discussed previously in this chapter (i.e., *eradication*, *sustained control*, or *passive management*). Parkes thought it "debatable" as to whether current control methods could eradicate thar from the Southern Alps, a point supported by Ken Tustin (Tustin 1990). Any eradication attempt would cost >NZ\$5 million over 10 years (Parkes 1989). Passive management would involve the Department of Conservation determining where, how and by whom thar are harvested, but it itself would not control thar. Sustained and active control would involve killing thar in perpetuity to achieve management objectives (Parkes 1989).

Parkes' review was released for public submissions in 1989. Of 470 submissions received, 14% favoured eradication, 11% wanted control to low densities and the remaining 75% expressed a wish for thar to be managed as a hunting resource (Hughey and Parkes 1995). The Minister of Conservation published the Himalayan Thar Management Policy in 1991 (Marshall 1991). This policy combined the *passive management* and *sustained and active control* options recommended by Parkes. Both recreational and commercial hunting were to be used to maintain thar below densities at which indigenous flora may be unacceptably modified; Department of Conservation control would occur if densities exceeded the specified threshold density. Threshold densities would vary in different parts of the range according to "ecologically acceptable vegetation and estate condition"; these threshold densities would be reviewed on the basis of monitoring (Marshall 1991:7). The policy was also to prevent further northward or southward dispersal of females. The document indicated how the policy would be implemented. Target populations (termed thresholds) for each management unit would be specified as the number of animals  $\text{km}^{-2}$ , which would vary according to the protection needs of each area. The policy stated that a maximum allowable population of 10 000 "should not cause unacceptable impacts on vegetation and other natural values, but will provide reasonable hunting opportunities". No public consultation was requested, or legally required, on the policy (Hughey and Parkes 1995).

Research needs were also identified in the Himalayan Thar Management Policy.

Information was specifically required on:

- diet of thar
- vegetation responses to thar
- rates of increase and population size for thar
- improved control techniques
- impacts of other introduced herbivores living in the thar range

A private consultant was commissioned to write a draft thar control plan in 1992. The plan aimed to provide the operational definitions so that the policy could be enacted by Department of Conservation staff. A Thar Management Advisory Group (TMAG) was also established to advise the consultant during the drafting of the plan. This group contained representatives of the New Zealand Conservation Authority and the four regional conservation boards that contained thar. The North Canterbury and West Coast boards opposed the fundamental objectives of the plan, whereas the Aoraki Conservation Board generally supported the way the plan defined the policy (Hughey and Parkes 1995).

The Draft Himalayan Thar Control Plan (Department of Conservation 1992) partitioned the thar range into nine units with threshold densities ranging from zero (northern and southern exclusion zones) to 2.5 thar km<sup>-2</sup>. Public submissions generally supported the draft plan (71%), but some (17%) fundamentally opposed the plan. The remainder (12%) accepted the plan but favoured lower threshold densities (Hughey and Parkes 1995). Many critics complained that the plan lacked detail on the environmental impacts of thar. Hughey and Parkes (1995) thought that the proper place for such debate is in peer-reviewed science journals.

The New Zealand Conservation Authority and the four regional Conservation Boards were invited by the Minister of Conservation to comment on the draft plan. Dr Graham Hickling (Department of Entomology and Animal Ecology, Lincoln University) was commissioned by the New Zealand Conservation Authority to independently comment on the Boards' submissions. Hickling's (1993) report supported the direction of the draft plan. Comments made in the public submissions, board submissions and by Hickling (1993) resulted in several major changes to the draft plan (Hughey and Parkes 1995). Perhaps the most important were the decisions

not to introduce a permit fee for overseas thar hunters using a hunting guide (set at \$500 in the draft), and to bring forward the plan's review date from 2003 to 1998.

It is interesting to speculate on the name change in the Himalayan Thar *Management* policy to Himalayan Thar *Control* Plan. This was probably the result of conservation lobbyists' concerns that *management* implied recognition of thar as a game resource (Hickling 1993). The Himalayan Thar Management Policy, however, recognises the potential of thar "to provide recreation hunting opportunities for New Zealand hunters... (and) employment and economic development opportunities, in attracting overseas visitors to hunt in New Zealand, and in the commercial harvesting of thar and thar products" (Marshall 1991:7) and then details how these harvesters will be managed (Marshall 1991:9). These changes in wording (and actual implementation) from the policy to the plan may at least partly explain misunderstanding about the status of thar among the various stakeholder groups.

The final Himalayan Thar Control Plan (Department of Conservation 1993) was approved by the Minister of Conservation in late 1993. As noted by Hughey and Parkes (1995), the Minister of Conservation emphasised the pest status of thar in stating "if it was possible eradication would be the preferred option" (Department of Conservation 1993:1). This was the first national control plan to specify actual target densities rather than general ideals such as "the lowest practicable density" or similar (Hughey and Parkes 1995).

### **Implementing the Himalayan Thar Control Plan, 1993-present**

Densities of thar are monitored annually or biennially in more than 20 catchments spread throughout the seven management units. These catchments are assumed to be representative of trends throughout the remainder of the management unit. Thar are counted by ground-based observers in the early evenings and mornings, when thar are active. Recreational hunters are issued permits free-of-charge with no restrictions on the number of thar that can be harvested. The recreational hunting harvest is monitored through the return of hunting diaries, although compliance both in obtaining permits and returning completed diaries is low (D. C. Anderson, *pers. comm.*). The plan attempts to prevent expansion of the breeding range by restricting "female-kid groups... to 10 or less per group" (Department of Conservation 1993:32).

Vegetation monitoring was also emphasised in the plan. Photo-points have been established in some catchments where thar are regularly monitored (J. Andrew, *pers. comm.*), but this technique offers only a general indication as to the 'health' of tussock communities. To evaluate how known densities of thar impact on vegetation, 70 permanent vegetation plots were established during 1991-1994 in five of the catchments where thar are regularly counted.

Variable-area permanently marked plots were sited in areas of palatable species of snow tussock (primarily *Chionochloa flavescens*, *C. pallens* and *C. rigida*). These species figured predominantly in the rumens of thar shot throughout the Southern Alps (Parkes and Thomson 1995). The number, basal area, height, and percent crown death were measured for all live snow tussocks (Parkes and Thomson 1995). The first plots established were remeasured during the 1995-1996 summer and are currently being analysed (C. Thomson, *pers. comm.*).

The above methodology has several flaws. First, any changes in tussock 'health' is assumed attributable to the densities of thar counted in the annual (or biennial) summer censuses. Second, other introduced herbivores (such as brown hare *Lepus europaeus occidentalis*, red deer, domestic sheep, and chamois) do also eat tussock. Third, densities of thar are not normally stable from year to year due to a high intrinsic rate of increase ( $r_m \approx 0.25$ ; Parkes and Thomson 1995) and strong yearly variation in hunting harvest. Since plots will be remeasured at three to four year intervals (C. Thomson, *pers. comm.*) it will be difficult to know what densities of thar (and other herbivores) were actually present.

Manipulative experiments are the most reliable method of determining the impacts of animals on communities (see above). Large-scale replicated field experiments to determine the relationship between thar densities and vegetation impacts are possible in eastern Southern Alps tussocklands. Here road access exists to high altitudes on some pastoral leases enabling construction and maintenance of enclosures. Such an experiment should use at least two replicates of the different thar densities; the densities should span between zero (a control) and *ca.* 20 thar km<sup>-2</sup>. (Impacts of thar on vegetation are almost certain to be unacceptable at the latter density.) The number of different densities used in the experiment would depend on the level of knowledge desired and financial constraints. Such an experiment would provide an opportunity

to examine the indirect impacts of thar on non-vegetative components (e.g., indigenous moth diversity and abundance; see White 1991) of the community.

### **Current management of chamois**

Unlike thar there is no one management plan pertaining to chamois. Current management is stipulated by a series of land and wild animal control plans produced by the New Zealand Forest Service and Department of Lands and Survey, and inherited by the Department of Conservation (Parkes and Clarke 1993). These plans do not specify target densities, so there is little 'active management' by the Department of Conservation. Most (53%) of the *ca.* 50 000 km<sup>2</sup> breeding range is on leasehold or freehold land (Parkes and Clarke 1993).

Because chamois are yet to colonise southern Fiordland (Clarke 1990), official helicopter-based shooting is conducted annually to prevent dispersal into this area (Parkes and Clarke 1993). Otherwise there is currently no official control against chamois. Commercial helicopter-based hunters shoot several hundred chamois during the winter months in the western Southern Alps (Parkes and Clarke 1993), and recreational hunters shot an estimated 1800 chamois in 1988 (Nugent 1992). Densities of chamois in forest habitats are unknown, so any estimate of total population size should be interpreted with caution. Parkes and Clarke (1993) guessed the total population to be >15 000. Counting chamois is difficult because of the mobile nature of individuals (Clarke 1990) and because many animals use semi-forested and forested areas (Yockney 1997). There is also no standard methodology for estimating abundance of chamois. Chamois are counted when observed during regular monitoring of thar, but there is no monitoring programme in the remainder of the chamois range. Anecdotal observations suggest that densities are highest in the semi-forested and forested habitats of the central western Southern Alps (J. Mead, *pers. comm.*).

Options for the management of chamois were described by Parkes and Clarke (1993). Given that chamois cannot be eradicated with current technology, sustained control of chamois at densities below which conservation values are modified is necessary. There is, however, no published information describing the relationship between chamois densities and their impacts on indigenous resources; nor would such

information be easy to collect given the overlap of chamois with various other ungulates.

### Concluding remarks

Managing the effects of introduced ungulates that cannot be eradicated requires an understanding of their impacts on conservation resources. There is scant information on the relationship between densities and impacts for any ungulate in New Zealand. For thar (which are restricted in their distribution relative to chamois) such knowledge can be gained from *in situ* monitoring of vegetation and thar densities, but the most reliable way of determining impacts is to use rigorous experimental design and enclosed densities of thar. In contrast to thar, chamois are outnumbered by other ungulates through much of their range. Consequently, determining the impacts of chamois alone will be very difficult.

Only in recent years have attempts been made to estimate the costs and benefits of ungulate control in New Zealand; the benefits of past control operations for conservation resources are unknown. For example, about 90 000 chamois have been shot by government hunters since 1930 (Clarke 1990) but there is no indication as to the conservation value of this action. Both thar and chamois (except within forest habitats) can now be controlled to low densities by helicopter-based hunting. The impacts of these species, once known, can thus be relatively easily managed.

The remainder of this thesis investigates aspects of the ecology (Chapters 3-5) and management (Chapter 6) of thar and sympatric chamois in the eastern Southern Alps. The problems that I investigated were posed by conservation managers rather than academics, but I have sought to provide answers of value to both groups.

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## Chapter 3

# Increasing Himalayan Thar 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 thar (*Hemitragus jemlahicus*) are associated with declining densities of chamois (*Rupicapra rupicapra*) in the Southern Alps, New Zealand. To examine this phenomenon, densities of thar 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, thar density was significantly higher than chamois density ( $P=0.032$ ), probably reflecting species differences in sociality. Chamois density was higher in catchments without thar than in those with thar ( $P=0.012$ ). Similarly, thar density was significantly higher at sites without chamois than at those with chamois ( $P=0.033$ ). Sites with both species present (sympatric) were significantly larger than those with only chamois or thar ( $P<0.001$ ). Following the prohibition of aerial hunting of thar in 1983, 16 of the 17 sites where thar and chamois were sympatric during 1978-1979 were recounted during 1991-1996. There was a six-fold increase in the mean density of thar 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 thar exclude chamois from all but the 'best' habitats. We conclude that intensive aerial hunting of thar during 1967-1983 reduced thar densities such that chamois could co-exist with thar. Possible mechanisms for the exclusion of chamois by thar are discussed.

**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 not 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 thar (*Hemitragus jemlahicus*) and chamois (*Rupicapra rupicapra*) in the eastern Southern Alps, New Zealand, following the abrupt cessation of commercial and most government hunting of thar 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 thar.

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  $\text{km}^{-2}$  (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

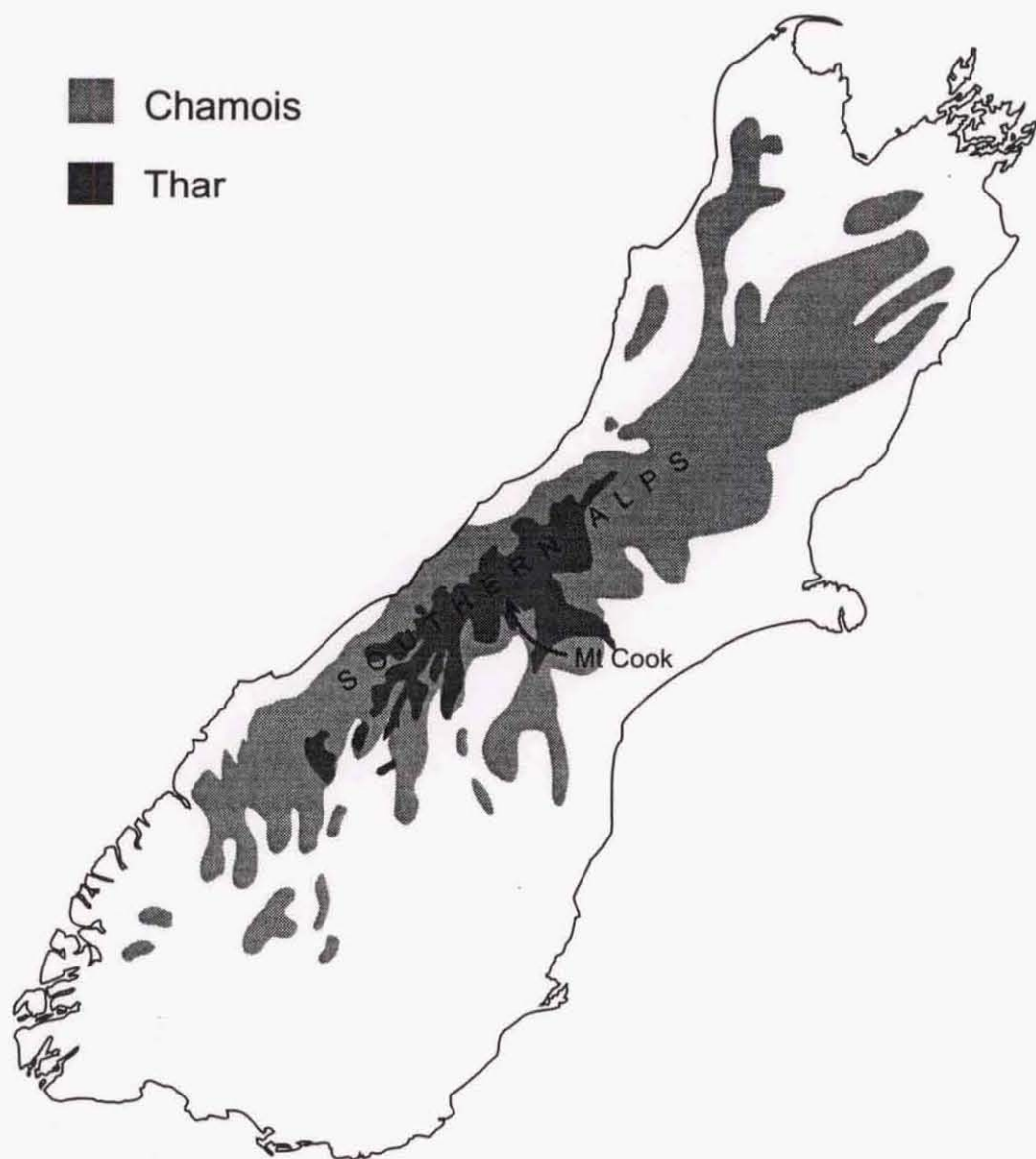


Figure 1. Liberation site (Mt. Cook) and 1996 distributions of Himalayan thar and chamois in the South Island of New Zealand (updated from Department of Conservation 1993 and Parkes and Clarke 1993).

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).

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,

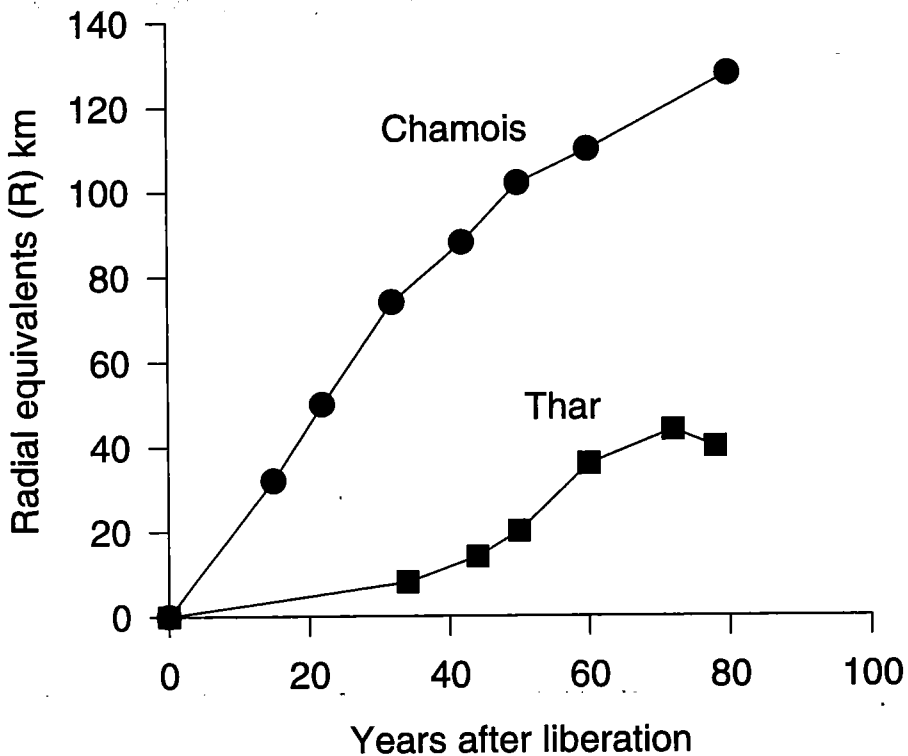


Figure 2. Dispersal of Himalayan thar and chamois liberated at Mt. Cook, New Zealand (after Parkes and Clarke 1993). The size of the breeding range is expressed as the radius of a circle of equivalent area to the observed range. Parkes and Clarke (1993) suggested that a linear model ( $y=12.76 + 1.51x$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

McIlbraith 1929). Government hunters, employed to cull thar and chamois from 1937, recorded similar observations. E. B. Davison (1946, unpublished report) 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.

Female thar are gregarious and sedentary on rock bluffs throughout the year (Tustin and Parkes 1988). 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 unhunted populations (Clarke and Frampton 1991). In both species the sexes segregate outside the April-July rut (Shank 1985; Clarke 1986; Chapter 5). Thorough accounts of the ecology of thar and chamois in New Zealand are given by Tustin (1990) and Clarke (1990) respectively.

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).

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

## METHODS

### Densities of sympatric thar and chamois in 1978

Between November 1978 and April 1979 (hereinafter termed '1978') government 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 (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 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.

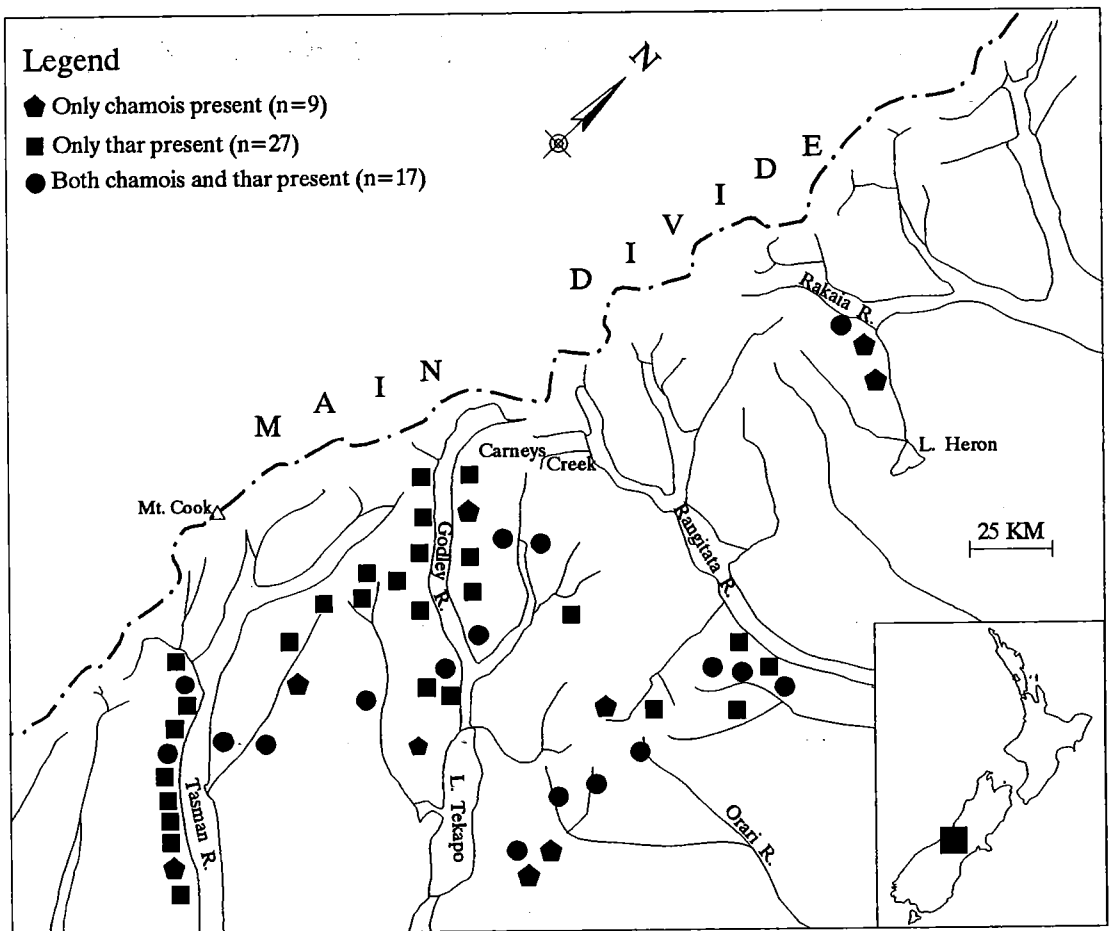


Figure 3. Location of 53 sites in the eastern Southern Alps, New Zealand, in which Himalayan thar and/or chamois were observed during November 1978-April 1979.

The area hunted 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 the Appendix.) 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 (see Appendix) 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.

#### **Long-term changes in the densities of sympatric thar and chamois 1978-1996**

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.

## RESULTS

### 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 1; one-tailed  $t_{34}=1.92$ ,  $P=0.032$ ). Thar density was lower in sites containing chamois compared with 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 1. 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	$1.44 \pm 1.43$

### 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. 4; one-tailed paired  $t_{13}=3.73$ ,  $P=0.001$ ), whereas chamois density declined at all but one site (one-tailed paired  $t_{13}=2.92$ ,  $P=0.006$ ). 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.

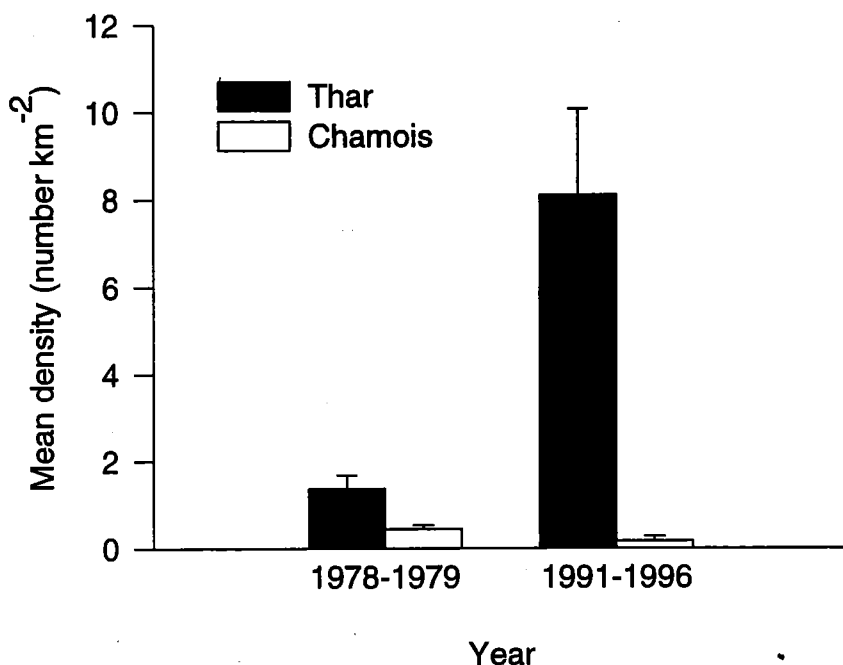


Figure 4. Mean densities (+ SE) of sympatric Himalayan thar and chamois at 14 sites in the eastern Southern Alps, New Zealand, during 1978-1979 and 1991-1996. All commercial and most government hunting of thar was prohibited by government order in 1983.

## DISCUSSION

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 (Chapter 5). In contrast, chamois in New Zealand are typically solitary (Clarke 1990; Clarke and Frampton 1991).

Changes in the density of thar 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 in the eastern Southern Alps. In 1965, when the Carneys Creek population was at peak density, a summer census counted 710 thar (>30 km<sup>2</sup>). 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 (Chapter 5). Despite intensive recreational hunting, annual censuses since 1984 have

showed a population increase of *ca.* 20% per annum (see Chapter 5). 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 km<sup>-2</sup>). Current management policy, however, is to control thar to densities  $\leq 2.5$  thar km<sup>-2</sup> (Department of Conservation 1993). By the 1990s, when thar exceeded *ca.* 3 thar km<sup>-2</sup> 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  $\geq 3$  km<sup>-2</sup>, but would be seen in sites where thar densities were  $< 3$  km<sup>-2</sup>. 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).

Despite animal density not being a reliable indicator of habitat 'quality' (Van Horne 1983), the almost total exclusion of chamois recorded in this study makes other measures (e.g., reproductive status of females) redundant. Indeed, few studies have presented such evidence for interspecific competition between ungulates. Corbett (1995) recorded

a doubling of a feral pig (*Sus scrofa*) population following the experimental removal of swamp buffalo (*Bubalus bubalis*) in northern Australia; buffalo apparently trampled the pigs' food source. This and Corbett's study illustrate the opportunities provided by control operations for experimentally investigating competition between ungulates (*sensu* Sinclair 1991).

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.

Understanding the mechanism(s) responsible for interspecific competition is important (Tilman 1987). At least three mechanisms might explain the decline of chamois in the eastern Southern Alps during 1978-1996:

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

Daniel and Christie (1963) summarised accounts of thar and chamois infected with kerato-conjunctivitis (*Rickettsia conjunctivae*) and contagious ecthyma in the Southern Alps. Kerato-conjunctivitis caused high mortality in a number of chamois populations at high density but not in thar (Daniel and Christie 1963; Christie 1965). Contagious ecthyma caused one "severe outbreak" in thar but was normally of low virulence in both species (Daniel and Christie 1963). There is no evidence that either disease resulted in consistent mortality of chamois relative to thar. No thar or chamois shot during the 1978 control operation showed signs of either disease and there were no reports of diseased animals in the 1978-1996 period (D. C. Anderson, personal communication).

Chamois and thar in New Zealand are host to a range of parasites (Andrews 1973; Clark and Clarke 1981; Tenquist and Charleston 1981; Henderson and Clarke 1986). Sikó and Nagus (1988) recorded high parasite overlap between chamois (*Rupicapra rupicapra capratica*) and domestic sheep in the Cantabrian range, Romania. In both cases it is unknown how parasites interact with disease to affect an individual's fitness or habitat selection (see a recent review by McCallum and Dobson 1995). In a post-peak chamois population outside the thar breeding range, increasing *Pastuerella* infection was negatively correlated with body condition; this infection causes acute pneumonia and bronchitis (Henderson and Clarke 1986). In contrast, lungworm (principally *Muellerius* spp.) infestation did not strongly impair physical condition (Henderson and Clarke 1986). The high densities of thar relative to chamois that were observed in both surveys could be expected to make thar more susceptible to both parasites and disease than chamois. Therefore, like Schröder and Kofler (1985), we believe that mechanisms other than disease and parasites are of greater relevance to the observed decline of chamois.

Belovsky (1986) showed that competition between food-limited generalist herbivores, such as chamois and thar, depends upon the fractions of shared and exclusive resources. Schröder and Kofler (1984) concluded that ibex excluded chamois because the former grazed forage such that the food quality became insufficient to support chamois.

An unpublished diet study has shown that sympatric chamois and thar 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 thar, but less tussock (J. P. Parkes *et al.*, unpublished data).

Historically, food competition may have been an important factor in the decline of chamois. Thar attained very high densities prior to the advent of helicopter-based hunting (Tustin and Challies 1978), and the four stages of thar population irruption, stabilisation, decline, and post-decline described by Caughley (1970a) were causally related to a decline in snow tussock (*Chionochloa* spp.) biomass. High densities of thar apparently eliminated *Ranunculus lyallii* and, by inference, some of the other herb species that are eaten by both thar and chamois, around Mount Cook (Fisher 1965; Wilson 1976). There are several descriptive accounts of thar modifying alpine grassland and sub-alpine shrublands, culminating in a greater abundance of bare ground and less-palatable plant species (Burrows 1974; Douglas 1977; Wardle 1979). Such dramatic changes in the flora have not been described in catchments colonised only by chamois, although the irruptive oscillation postulated for chamois by Caughley (1970b) and Clarke and Frampton (1991)

was presumably related to a decline in the quality and quantity of food. We consider the potential for diet competition between thar and chamois to be high.

Berducou (1984) suggested that chamois in the Pyrenees underutilised some habitats during winter because of over-grazing by domestic sheep during summer. However, chamois apparently also benefitted from the vigorous growth where livestock had deposited nitrogen (Berducou 1984). In the Maritime Alps, habitat use and diet of chamois and Corsican sheep overlapped strongly through all seasons but was only considered important during winter, when food resources were non-renewable and individuals of both species were physiologically stressed (Pfeffer and Settimo 1973). A Swiss population of chamois apparently declined following the liberation and subsequent increase of ibex; this decline was attributed to ibex grazing vegetation so closely that insufficient forage was available for chamois to survive the winter (Schröder and Kofler 1984). In the Southern Alps of New Zealand, possible differences in rumen morphology between thar and chamois may allow the former to feed on lower quality forage, thus conferring a competitive advantage to thar over chamois (*sensu* Fraser 1996; K. W. Fraser, personal communication).

The third mechanism - behavioural intolerance - was suggested by C. M. H. Clarke (personal communication) as the 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). When population density was high in the Bavarian Alps, adult male chamois sought solitude due to "social intolerance and irritableness" (Shank 1985). In contrast, thar are highly social with female-juvenile groups of >30 common at high population density (Caughley 1967; Tustin and Challies 1978). Aggressive behaviour within these female-juvenile groups is apparently uncommon (Schaller 1977; Tustin and Parkes 1988). Miller (1967) proposed that intraspecific behaviours could govern interspecific interactions between mammal species; more social and territorial species could be expected to dominate less social species. Hamr (1988) noted that female chamois in Austria avoided areas with high livestock densities. The mobility of most chamois relative to the strong philopatry of female thar 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 thar are difficult to test experimentally because (i) they are not mutually exclusive; (ii) some effects may take many years to become evident, and (iii) 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 thar at low densities (Department of Conservation 1993) may give further insight into the mechanism(s) of interspecific competition.

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Appendix. Numbers of Himalayan thar and chamois counted at 53 sites in the eastern Southern Alps, New Zealand, by government hunters during spring 1978-autumn 1979. Of the 17 sites containing both thar and chamois, 16 were recounted during 1991-1996. Domestic sheep were not seen during 1978-1979 but were seen in 1991-1996. No other ungulates were observed in the 1991-1996 counts.

Site	Location <sup>a</sup>	Area <sup>b</sup>	Number observed					
			1978-1979			1991-1996		
			Thar	Chamois	Others <sup>c</sup>	Thar	Chamois	Sheep
1	J35, 510 650	7.2	1	1	0	33	0	0
2	J36, 470 160	9.4	23	5	0	195	0	7
3	J36, 495 170	3.0	2	1	0	50	0	33
4	J36, 435 145	14.7	9	2	0	114	0	5
5	J37, 360 080	10.5	6	6	0	48	0	0
6	I37, 275 995	9.8	4	3	0	23	0	0
7	I37, 230 960	14.4	1	4	1 F.D.	24	0	0
8	I37, 200 940	25.5	7	8	6 R.D.	52	0	0
9	I36, 180 330	10.1	12	11	0	192	15	0
10	I36, 165 310	11.1	28	13	4 R.D.	226	5	0
11	I36, 090 280	9.3	18	1	3 R.D.	87	0	0
12	I36, 070 205	6.1	28	2	0	17	0	71
13	I36, 995 155	4.5	18	2	0	64	0	0
14	H37, 870 070	23.8	30	20	0	84	0	0
15	H36, 820 120	10.6	14	2	0	24	0	0
16	H37, 760 050	9.0	23	1	10 R.D.	13	4	0
17	H36, 750 140	1.9	14	4	0			
18	I37, 215 910	15.6	0	14	2 F.D.			
19	I37, 220 865	9.0	0	39	5 F.D.			
20	H37, 780 810	5.1	0	1	0			
21	I36, 040 115	4.8	0	3	0			
22	I36, 100 395	6.2	0	5	0			
23	I36, 910 155	2.4	0	1	0			
24	J35, 540 630	3.8	0	14	0			
25	J35, 570 560	10.0	0	5	1 R.D.			
26	J36, 340 145	1.4	0	2	0			
27	I36, 000 270	3.8	4	0	0			
28	I35, 105 425	3.5	3	0	0			
29	I36, 045 375	3.0	10	0	0			
30	I36, 040 340	6.3	11	0	0			

(Continued overleaf)

## Appendix (Continued).

31	I36, 040 310	7.6	16	0	0
32	I36, 055 245	3.3	3	0	0
33	I36, 080 185	1.3	6	0	0
34	I36, 015 260	5.7	24	0	0
35	I36, 970 235	3.0	39	0	0
36	I36, 900 155	3.8	2	0	0
37	I36, 915 195	3.2	7	0	0
38	H36, 745 150	1.0	11	0	0
39	I36, 090 375	10.3	11	0	0
40	I36, 240 280	11.8	25	0	0
41	J36, 355 165	5.2	3	0	0
42	I36, 090 175	8.3	24	0	0
43	H36, 760 115	6.5	32	0	0
44	H36, 760 080	4.3	18	0	0
45	H37, 760 010	8.6	31	0	0
46	H37, 750 950	1.9	22	0	0
47	H37, 750 920	10.1	19	0	0
48	H37, 750 890	9.0	65	0	0
49	H37, 890 100	1.3	1	0	0
50	H38, 720 760	27.2	1	0	6 R.D.
51	J36, 490 200	1.1	2	0	0
52	J36, 510 140	2.9	12	0	0
53	J36, 445 190	3.5	8	0	0

<sup>a</sup> NZMS 1 : 50 000 map, 6 figure grid reference

<sup>b</sup> km<sup>2</sup>

<sup>c</sup> Other ungulates were fallow deer (*Dama dama*) (F.D.) and red deer (*Cervus elaphus scoticus*) (R.D.)

## Chapter 4

# A Mechanism for the Competitive Exclusion of Chamois by Himalayan Thar in the Eastern Southern Alps, New Zealand

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### SUMMARY

1. Increasing densities of Himalayan thar are associated with decreasing densities of chamois in the eastern Southern Alps, New Zealand. Two mechanisms, diet competition and behavioural avoidance, have been proposed to account for this phenomenon: both mechanisms require habitat selection by thar and chamois to overlap. We tested the hypothesis that differential habitat selection permits chamois to co-exist with low density thar populations.
2. Seasonal habitat selection by sympatric thar and chamois was estimated by observing unmarked male thar, female thar and chamois monthly for 25 months in a catchment representative of their sympatric range. To calculate habitat selection ratios the proportional availability of six habitats (grassland, grass bluff, rock bluff, shrubland, scree, and snow) was measured from aerial photographs taken in each of the four seasons.
3. The null hypothesis that thar and chamois select habitats similarly was rejected; thar and chamois selected habitats differently ( $P \leq 0.01$ ) in three of the four seasons. However, there was overlap in preference for some habitats (grassland and shrubland) and avoidance of others (scree and snow), suggesting a strong potential for interspecific competition when thar densities increase. Overlap in habitat selection was greatest during winter when snow dominated (85% cover) the landscape, reducing the availability of vegetated habitats.
4. Simpson's equitability index ( $E$ ) indicated that thar used available habitats more

evenly than chamois in every season, suggesting that thar have a broader niche than chamois. Significant differences in habitat selection by male and female thar when segregated outside winter, and their daily altitudinal movements, probably contributed to this broader habitat selection.

5. Observations of 24 interspecific encounters indicated that chamois moved away from thar more often than vice versa ( $P < 0.005$ ). Our results suggest that behavioural interactions with thar regulate chamois densities in a similar manner to their intraspecific behavioural interactions.

6. We propose that as thar populations grow and disperse more thar select habitats preferred by chamois, thereby increasing both behavioural interactions and dietary competition. Since these mechanisms will operate at different time scales, behavioural intolerance of thar by chamois is the most likely explanation for the recent decline of chamois in the eastern Southern Alps.

**Key words:** behaviour, habitat selection, interspecific competition, niche, ungulates.

## INTRODUCTION

The role of interspecific competition in limiting ungulate populations has been the subject of debate (e.g., Sinclair and Norton-Griffiths 1982; Sinclair 1985; Dublin *et al.* 1990). Introduced ungulates offer opportunities to study competitive processes that may be less apparent in co-evolved communities (Sinclair 1989; 1991). In the eastern Southern Alps of New Zealand, increasing densities of introduced Himalayan thar (*Hemitragus jemlahicus* Smith) have in recent decades replaced earlier-introduced and faster-dispersing chamois (*Rupicapra rupicapra* L.) (Chapter 3). Counts during 1991-1996 revealed that when helicopter-based hunting of thar ceased in 1983, chamois disappeared from sites where thar increased to above *ca.* 3 km<sup>2</sup> (Chapter 3). These findings reinforced anecdotal accounts of chamois being replaced by domestic sheep (*Ovis aries*), alpine ibex (*Capra ibex*) and moufflon (*Ovis musimon*) in Europe (Rebollo *et al.* 1993; Schröder and Kofler 1984; Gonzalez 1985).

Both chamois and thar are considered to have undergone irruptive fluctuations following colonisation of catchments within New Zealand (Caughley 1970a; Caughley 1970b; Clarke and Frampton 1991). Nevertheless, the two species have distinct social systems resulting in different post-decline densities. Densities of 3.2-5.0 chamois km<sup>-2</sup> were reported for an eastern Southern Alps chamois population (in the absence of thar but not red deer, *Cervus elaphus scoticus* Lönnberg) some 50 years after colonisation (Clarke and Frampton 1991). Thar peaked at densities >30 km<sup>-2</sup> ca. 15 years after colonising an area (Tustin and Challies 1978) but intensive commercial harvesting has confounded subsequent estimates of post-decline densities (Parkes, Nugent and Warburton 1996). Thar are highly social with female-juvenile groups of >30 common, and aggressive interactions are uncommon (Tustin and Parkes 1988; Tustin 1990). Consequently, the post-decline density of thar is likely to be higher than that of chamois. The sexes of both species are segregated outside of the April-July rut (Clarke 1990; Chapter 5).

Chapter 3 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, brown hare (*Lepus europaeus occidentalis* de Winton), brushtail possum (*Trichosurus vulpecula* Kerr), and chamois. Sustained grazing by these species reduces the distribution and abundance of preferred plant species (see, for example, Caughley 1970b). 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). Sympatric thar and chamois in the eastern Southern Alps feed on the same species, albeit in different proportions according to season (J. P. Parkes *et al.* unpublished data). Chamois may have been excluded by thar through scramble competition for food (see also Schröder and Kofler 1984).
- (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 of these 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). In this paper we propose that such a process is responsible for the exclusion of chamois by increasing densities of thar in parts of the eastern Southern Alps, New Zealand. We hypothesise that chamois can co-exist with low densities of thar due to differential habitat selection. However, as thar populations grow and disperse, their use of habitats preferred by chamois increases until chamois avoid those areas.

The objectives of this study were consequently to describe seasonal habitat selection by sympatric populations of thar and chamois in a catchment representative of their eastern Southern Alps range, and to test whether chamois behaviourally avoid thar.

## METHODS

### Study area and populations

Carneys Creek (43° 30' S, 170° 40' E; Plate 1) 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, liberated near Mount Cook, 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 (Chapter 5). 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 (Chapter 5). Long-term changes in the density and sex ratio of thar in Carneys Creek are described in Chapter 5. 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 leave 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) (Chapter 5).



Plate 1. The headwaters of Carneys Creek, March 1995 (D. M. Forsyth).

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.

### **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 1).

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 (Christie 1963; Tustin and Parkes 1988; Clarke 1990). 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.

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.

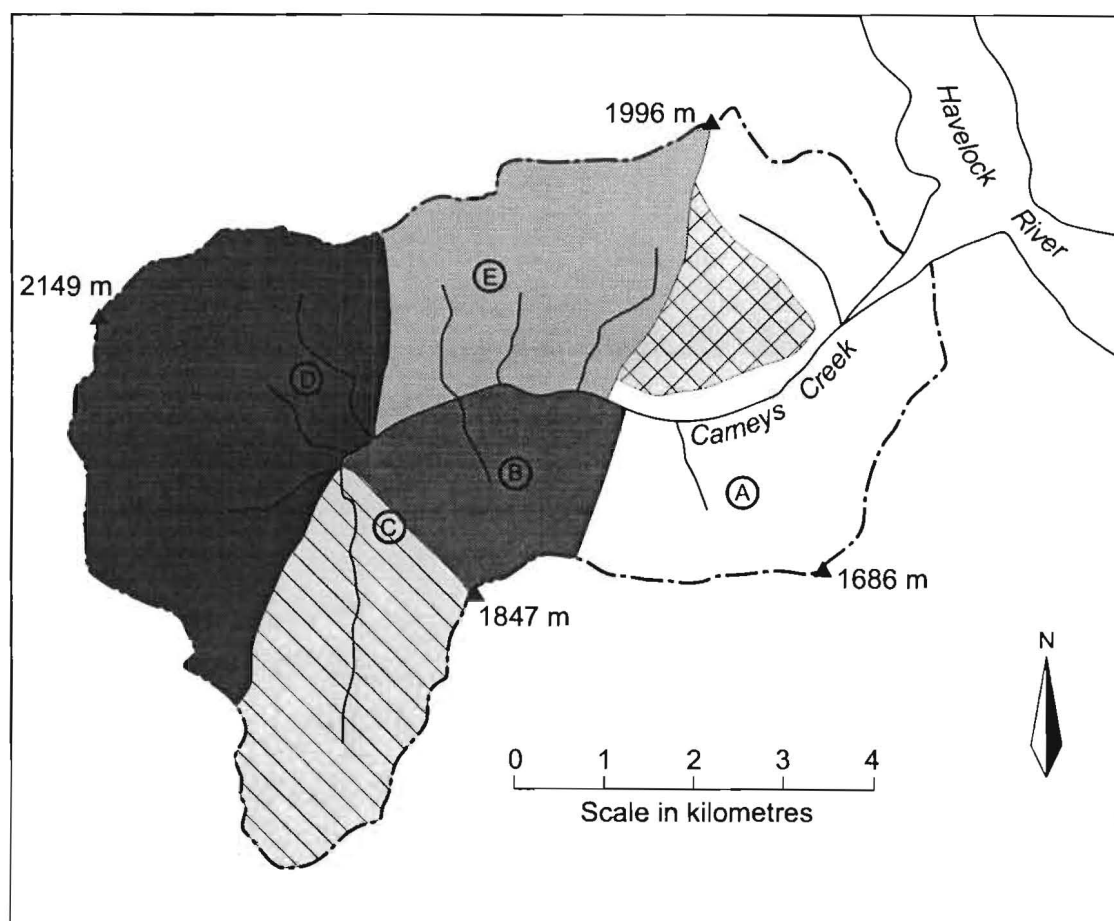


Figure 1. Observation sites (○) used to observe thar and chamois from December 1993–February 1996 in Carneys Creek, New Zealand. Shading indicates the five different areas searched monthly from the lettered observation sites across the valley.

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 (J. P. Parkes *et al.* unpublished data), 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>

(Continued overleaf)

Table 1 (Continued).

Shrubland	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.

### 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 (J. P. Parkes *et al.* unpublished data). 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 size and horn length and thar of both sexes were aged according to the number of horn rings (Caughley 1965).

### 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.

### Altitudinal movements

A previous study of female thar in the eastern Southern Alps recorded a daily pattern of movement that varied seasonally (Tustin and Parkes 1988). 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.

### Habitat availability

Habitat availability is the quantity of habitat accessible to the study population (Manly, McDonald and Thomas 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 (Chapter 5) 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™ 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.

### 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 (Alldredge 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 (Alldredge 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, Jorgan and Bunnell 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 (Chapter 5), 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

$$\text{se}(\hat{w}_{ijk}) = \sqrt{\frac{o_{ijk}(1 - o_{ijk})}{u_{jk}\pi_{ij}^2}}.$$

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.

### Relative niche breadth

We calculated Simpson's equitability index ( $E$ ; Begon, Harper and Townsend 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).

## 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.

## RESULTS

### Accuracy of observed thar and chamois classification

All 12 chamois shot were accurately classified (Table 2). 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.

### Group sizes

Male thar groups were significantly smaller in winter than in other seasons (Table 3). 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

Table 2. Age-sex classes of thar and chamois shot by the senior author during December 1993-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 3. Mean seasonal group sizes [ $\bar{g} \pm \text{SD} (n)$ ] 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 ( $z = 3.22$ ,  $P = 0.03$ ).

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 ( $z = 0.71, P = 1.00$ ).

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 2). 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 2). When the data

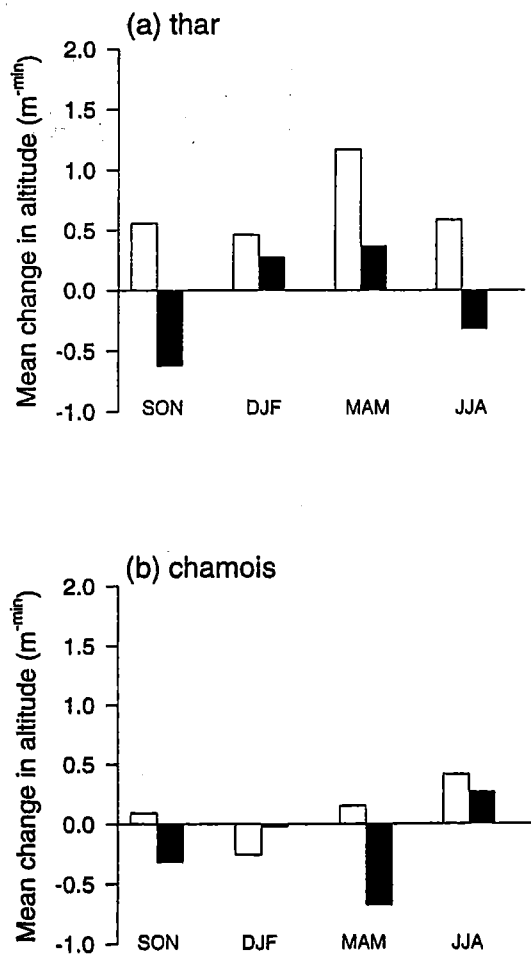


Figure 2. Seasonal mean altitudinal movement of thar (male and female pooled) and chamois during 3 h observation periods in the morning (open bars) and evening (solid bars) in Carneys Creek, New Zealand. SON, spring; DJF, summer; MAM, autumn; JJA, winter.

were averaged over all seasons, thar did move significantly faster than chamois (thar = 0.34 m min<sup>-1</sup>, chamois = 0.04 m min<sup>-1</sup>, 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  $P = 0.04$ ).

Seasonal habitat availability

Snow dominated the landscape in winter (85% cover) and spring (49%) (Figure 3). 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%), grass bluff (12%). Shrubland only constituted 4% of summer habitat.

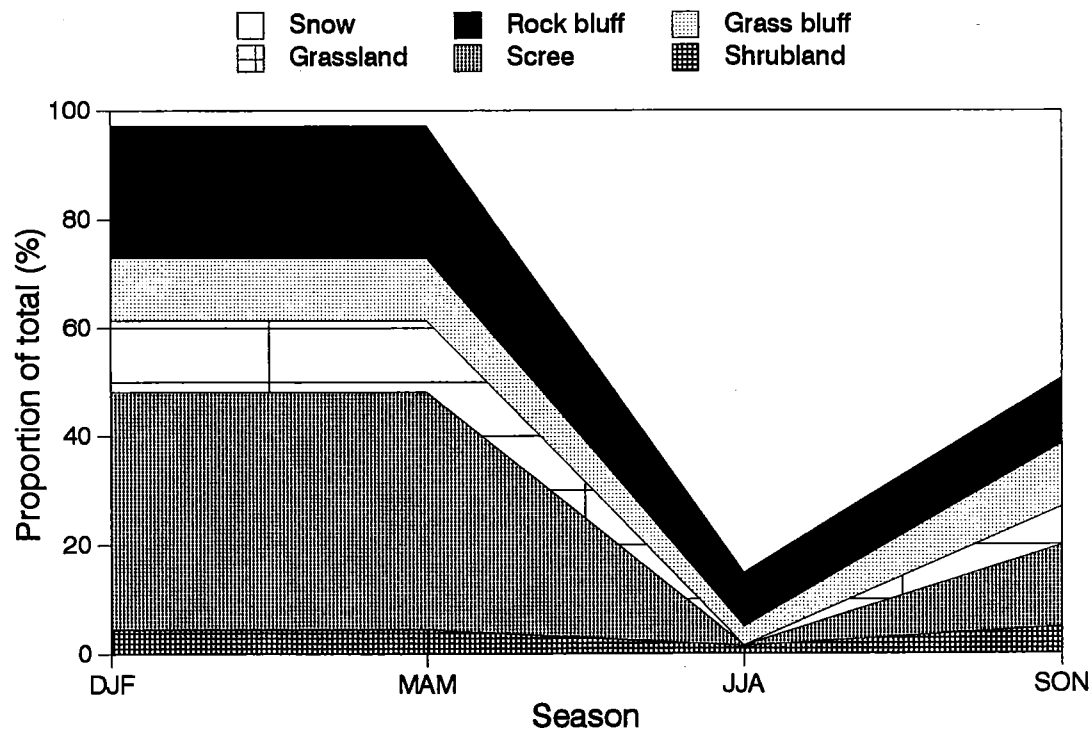


Figure 3. Seasonal changes in the availability of six habitats in Carneys Creek, New Zealand. The area of each habitat was estimated from aerial photographs taken in winter, spring and autumn; summer and autumn habitat availability is assumed to be the same (see text).

## 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 4; Table 5). 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 ( $G \geq 26.76$ ;  $P < 0.001$ ).

### (i) Thar and chamois

Scree and snow were generally avoided by both thar and chamois in the seasons in which they were available (Table 4). In the other seasons there were insufficient observations (i.e.,  $n_i < 5$ ) 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.

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.

Table 4. Seasonal habitat selection indices for Himalayan thar and chamois in Carneys Creek, New Zealand, 1993-1996.

Habitat	$\pi_i$	$u_i$	Thar				$B_i$	$u_i$	Chamois				$B_i$	$z$	$P_{\text{Holm}}$
			$\hat{W}_i$	$\hat{W}_{\text{lower}}^a$	$\hat{W}_{\text{upper}}^b$	$\hat{W}_i$			$\hat{W}_{\text{lower}}^a$	$\hat{W}_{\text{upper}}^b$					
Spring															
Grassland	0.071	76	3.811	2.822	4.802	0.331	49	8.154	6.554	9.754	0.363	-2.09	0.09		
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	0.09		
Rock bluff	0.121	95	2.770	2.157	3.384	0.241	12	1.161	0.506	1.817	0.052	3.64	0.00		
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	<0.00		
Snow	0.493	11	0.079	0.017	0.141	0.007	9	0.215	0.072	0.358	0.010	-1.34	0.09		
Total	1.000	282	11.513			1.000	134	22.450			1.000				
Summer															
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	0.00		
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	<0.00		
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 ( $u_i < 5$ )

(Continued overleaf)

Table 4 (Continued). Seasonal habitat selection indices for Himalayan thar and chamois in Carneys Creek, New Zealand, 1993-1996.

Habitat	$\pi_i$	$u_i$	Thar				$u_i$	Chamois				$z$	$P_{Helm}$
			$\hat{W}_i$	$\hat{W}_{ilower}^a$	$\hat{W}_{iupper}^b$	$B_i$		$\hat{W}_i$	$\hat{W}_{ilower}^a$	$\hat{W}_{iupper}^b$	$B_i$		
Autumn <sup>c</sup>													
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		
Winter													
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 ( $u_i < 5$ )

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

### (ii) Male and female thar

Male and female thar avoided scree and snow in all the seasons during which these habitats were available (Table 5). 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.

### Relative niche breadth of thar and chamois

Thar selected habitats more equally than did chamois (Table 6) 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  $P > 0.05$ ). [Statistical tests for niche overlap indices incorporating resource abundance are unavailable (Ludwig and Reynolds 1988) so these comparisons did not account for differences in resource availability.]

Table 6. 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

Table 5. Seasonal habitat selection indices for male and female thar in Carneys Creek, New Zealand, 1993-1996.

Habitat	$\pi_i$	$u_i$	Male				$B_i$	$u_i$	Female				$z$	$P_{Holt}$
			$\hat{W}_i$	$\hat{W}_{lower}^a$	$\hat{W}_{upper}^b$	$\hat{W}_i$			$\hat{W}_{lower}^a$	$\hat{W}_{upper}^b$	$B_i$			
Spring														
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			
Summer														
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	0.00	
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 ( $u_i < 5$ )

(Continued overleaf)

Table 5 (Continued). Seasonal habitat selection indices for male and female thar in Carneys Creek, New Zealand, 1993-1996.

Habitat	$\pi_i$	$u_i$	Male				$B_i$	$u_i$	Female				$z$	$P_{Helm}$
			$\hat{W}_i$	$\hat{W}_{ilower}^a$	$\hat{W}_{iupper}^b$	$\hat{W}_i$			$\hat{W}_{ilower}^a$	$\hat{W}_{iupper}^b$	$B_i$			
Autumn														
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			
Winter <sup>d</sup>														
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 ( $\chi^2_3 = 0.52$ )

## 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 7; McNemar  $G = 10.7$ ,  $P < 0.005$ ). Chamois were displaced in 54% of encounters and thar in only 8%.

Table 7. 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.

## DISCUSSION

Group size data (Table 3) 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  $\text{km}^{-2}$ ) 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 (Chapter 3) must also have been important.

Spatial segregation of male and female thar outside rut (Chapter 5) was associated with significant differences in habitat selection between the sexes in this study (Table 5). 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 groups (i.e., male-only, female-only and mixed) 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 (Chapter 3; Rosenzweig 1981). Third, the seasonal migration of male thar (Chapter 5) 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 Chapter 5).

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' (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 (Chapter 3). Moreover, Chapter 3 indicated 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; Clarke and Henderson 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  $\text{km}^{-2}$ , as required by a government management plan, could provide tests of hypotheses arising from this conclusion (see Chapter 3). More information is also required on the role of dominance relationships (Clarke and Henderson 1981; Clarke and Henderson 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 (Chapter 5) which increased the probability of chamois encountering male rather than female thar. Second, inspection of Tables 4 and 5 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 (1970b) 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 1970b: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  $\text{km}^{-2}$ ; 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 (J. P. Parkes *et al.* unpublished data). 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 1970b). 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* Temminck) 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 (but see Gordon and Illius 1996).

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 eastern Southern Alps chamois population (Clarke 1990), chamois will recolonise preferred sites (see Chapter 3).

## CONCLUSIONS

Many factors can limit ungulate populations (Sinclair 1989); interspecific competition may only be important in certain circumstances. Release of ungulate populations from predators (e.g., Smuts 1978; Sinclair 1985), disease (e.g., Dublin *et al.* 1990), or hunting

(Chapter 3) may result in the density of one species increasing such that interspecific competition does become important. Although controlled manipulative experiments are possible in some situations (e.g., Hobbs *et al.* 1996), in most circumstances they are impractical (Caughley and Sinclair 1994). Hence, understanding the mechanisms responsible for competition between wild ungulates is likely to rely on largely descriptive and circumstantial evidence.

Sympatric Himalayan thar and chamois in the eastern Southern Alps of New Zealand provide insight into mechanisms of interspecific competition between ungulates. In the absence of hunting thar will attain densities that are seldom attained by non-introduced ungulates. Following the cessation of all commercial and most government hunting of thar in 1983, densities of thar increased six-fold between 1978 and 1996, resulting in the almost complete exclusion of chamois from previously used sites (Chapter 3). When sympatric at low densities both species select similar habitats (this study) and have overlapping diets (J. P. Parkes *et al.* unpublished data), and chamois behaviourally avoid thar groups. We propose that as thar populations grow, increasing densities of both sexes must utilise less thar-preferred habitats, inevitably overlapping with chamois-preferred habitats. Our results suggest that interspecific behavioural interactions regulate chamois densities similarly to intraspecific interactions. Behavioural avoidance of thar is an instantaneous and density-dependent mechanism that best explains the recent (1978-1996) decline of chamois in the eastern Southern Alps.

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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

(Continued overleaf)

Appendix (Continued).

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Kid thar	Small body size relative to adult females
(<1 year)	Adult females present
(sex indeterminate)	Suckling behaviour
	Horns small
Adult chamois	Body size $\geq 2 \times$ kid
( $\geq 1$ year)	Horns visible
Kid chamois	Small body size
(<1 year)	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).

## Chapter 5

# Harvesting and Sexual Segregation in a New Zealand Population of Himalayan Thar

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### ABSTRACT

Distribution of Himalayan thar in the Southern Alps of New Zealand is characterised by segregation of the sexes outside winter. Annual summer censuses of thar were made from 1984-1996 in two catchments subject to different harvest regimes within the Two Thumb Range. Summer populations in the two catchments increased at similar rates over this period ( $r = 0.15$  and  $0.17$ ), but their adult ( $\geq 2$  years old) sex ratios diverged markedly in the late 1980s. In Carneys Creek, which was subject to unrestricted hunting, the summer adult sex ratio was initially equivalent to the estimated population sex ratio, but from 1991 was male-biased ( $P < 0.001$ ). This change was due to both a decline in the number of females and an increase in males. In North Branch, only 10 km from Carneys Creek but subject to an adult (trophy) male harvest, the summer population was significantly female-biased in all years. To investigate these changes, I estimated hunter harvest within Carneys Creek during 1993 and made monthly counts of adult male ( $> 4$  years old), sub-adult male (2-4 years) and female ( $\geq 2$  years) thar over a 27 month period in 1993-1996. These counts were used to construct a seasonal index of abundance. I recorded a strongly male-biased harvest in Carneys Creek, with nearly all males harvested whilst sexually segregated. In both years, there was a consistent seasonal change in abundance of sub-adult males ( $P = 0.001$ ) and perhaps adult males ( $P = 0.08$ ), but not of females ( $P = 0.47$ ). Sub-adult males immigrated during spring, increasing to a summer maximum before emigrating during autumn; few sub-adult males were present in Carneys Creek during winter. This pattern was more pronounced in the two sites without females than in those with females ( $P = 0.05$ ). The number of females present in

Carneys Creek was insufficient to recruit the number of sub-adult males observed during summer or recorded shot by hunters. Censuses of thar at seven nearby sites in summer indicated that the likely source of these males was an adjacent hunting reserve containing a moderate female density ( $3\text{--}12\text{ km}^{-2}$ ) and female-biased population in summer. Few adult or sub-adult males were observed in this hunting reserve, suggesting that male thar used Carneys Creek when sexually segregated because it contained preferred habitats and had a low female density. Management of ungulates that exhibit sexual segregation, particularly those that are harvested or controlled, requires consideration of the landscape-level interactions of intersexual differences in density, mobility and resource selection.

**Key words:** alpine, habitat, *Hemitragus jemlahicus*, Himalayan thar, hunting, migration, New Zealand, sexual segregation, Southern Alps, spatial harvesting.

## INTRODUCTION

Sexual segregation is common among north temperate ungulates and a variety of hypotheses have been proposed to account for this phenomenon (see reviews by Main and Coblentz 1990, Miquelle *et al.* 1992, Main *et al.* 1996, and Bleich *et al.* 1997).

Segregation of the sexes can lead to extreme differences in habitat use at a variety of spatial and temporal scales (Bowyer *et al.* 1996). For example, male and female mountain sheep (*Ovis canadensis nelsoni*) use different mountain ranges outside the rut (Bleich *et al.* 1997).

Various ultimate and proximate factors determine the extent of sexual segregation in an ungulate population. Sexual differences in habitat and diet preferences, and the spatial distribution of these resources, are important (Bowyer 1984; McCullough *et al.* 1989; Bleich *et al.* 1997). Differences in sociality (Shank 1985) and predation-risk (Jakimchuk *et al.* 1987; Miquelle *et al.* 1992; Bleich *et al.* 1997) between age-sex classes also affect spatial distribution, and density effects may interact with these factors directly or indirectly (Clutton-Brock *et al.* 1987).

Many ungulates that exhibit sexual segregation are intensively harvested, so it is important to understand how such exploitation can affect patterns of sexual segregation.

In this paper I describe landscape-level effects of two harvest strategies in a population of Himalayan thar (*Hemitragus jemlahicus*) in the Two Thumb Range, New Zealand (Figure 1).

Himalayan thar were liberated into New Zealand's Southern Alps to provide a hunting resource (Donne 1924) and have dispersed throughout the central Southern Alps (Caughley 1970a; Parkes and Tustin 1985). Following colonisation, thar apparently underwent an irruptive oscillation, increasing to peak densities of  $>30$  thar  $\text{km}^{-2}$  within 15 years (Caughley 1970b; Tustin and Challies 1978). The post-peak decline to lower densities predicted by Riney (1964) and Caughley (1970b) was obscured by intensive commercial helicopter-based hunting from 1971 (Parkes *et al.* 1996). Caughley (1970b) showed that the irruptive cycle was primarily influenced by yearling mortality in winter, with only a small decline in adult fecundity in high density populations.

The sexes are strongly dimorphic, with adult males weighing up to 125 kg and adult females averaging 36 kg (Tustin 1990). The season of conceptions is centred in May and the median birth date of thar in the eastern Southern Alps is 30 November (Caughley 1971).

Habitats utilised by thar in New Zealand are considered "identical" to those used in central Nepal (Caughley 1970c). Female thar in New Zealand are sedentary on rock bluffs (Tustin and Parkes 1988) with home ranges of *ca.* 2  $\text{km}^2$  (Tustin 1990). The limited female dispersal that occurs appears to be density-dependent (Parkes and Tustin 1985). In contrast, adult males are frequently recorded many kilometres from the nearest female group (Anderson and Henderson 1961; Caughley 1970a). The sexes aggregate on snow-free bluffs during winter for the rut (Tustin and Parkes 1988; Chapter 4), but are segregated outside this period (Caughley 1967; Tustin 1990; Chapter 4). Adult and sub-adult males form loose groups in late winter, and move into "summer habitat" which may be well separated from, or interspersed between, habitat used by female groups (Caughley 1967).

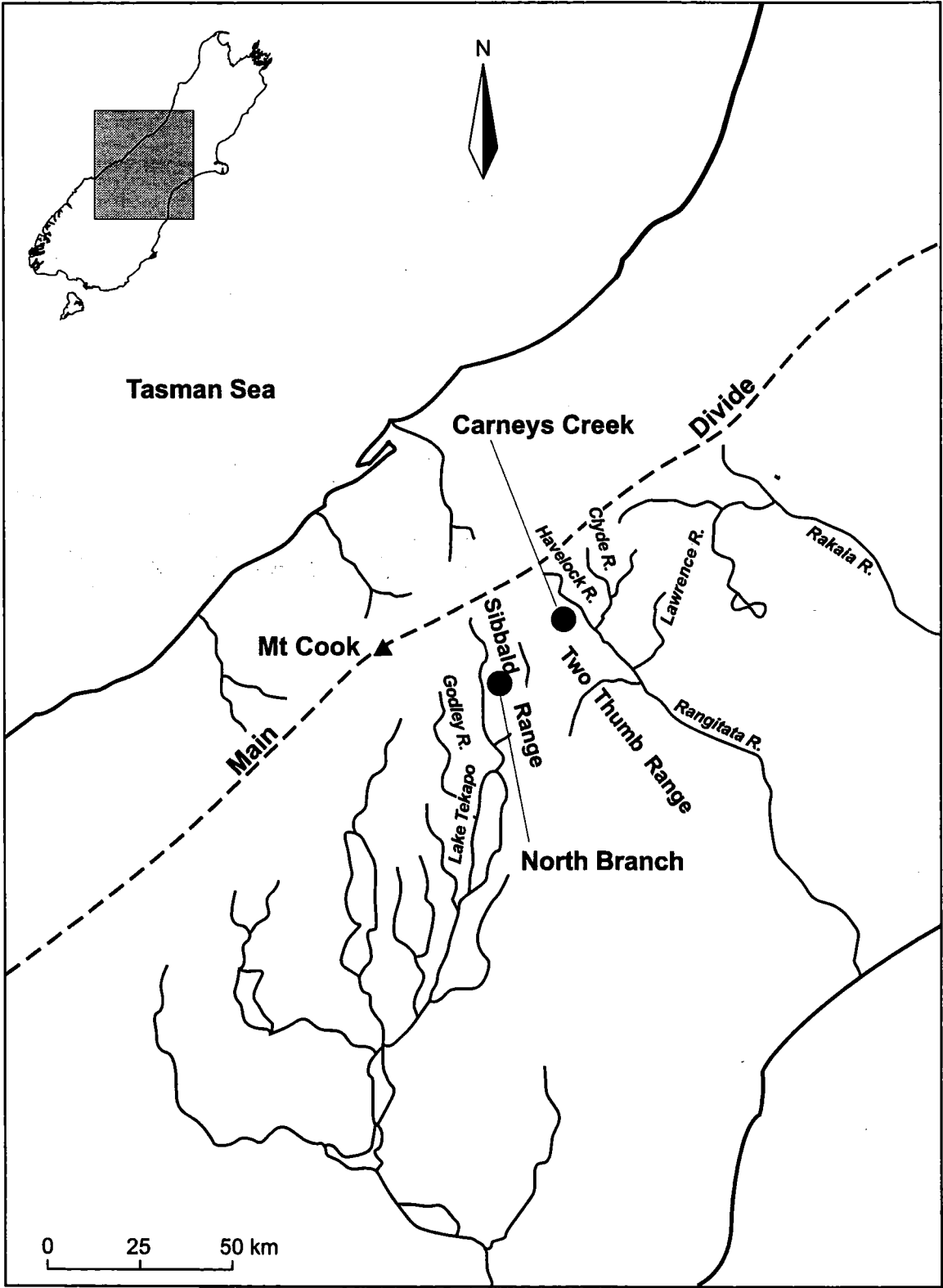


Figure 1. Location of study areas (●) where thar were censused annually in the Two Thumb and Sibbald Ranges, South Island, New Zealand, during 1984-1996.

## STUDY AREA AND POPULATION

The Two Thumb Range extends eastward from the central Southern Alps and is drained by the Godley and Macaulay Rivers in the south, and by the Havelock and Rangitata Rivers in the north (Figure 1). Elevations range from 500 m a.s.l. to > 2500 m peaks near the Main Divide. The terrain is typical of thar habitat in the eastern Southern Alps (Tustin and Challies 1978) with extensive areas of scree and tussock intergrading with rock bluffs and, at lower altitudes, subalpine shrubland and small patches of podocarp forest (Chapter 4). The region receives 4000-5000 mm of precipitation annually, with rain or snow recorded on two days in three (Canterbury Regional Council, unpubl. data).

Female thar, dispersing northward from the liberation site at Mount Cook, colonised the Two Thumb Range in the early 1940s (Caughley 1970a). Although thar were seen in Carneys Creek in 1939 (Davidson 1965), these likely were males and breeding females probably did not arrive until *ca.* 1949 (Caughley 1970a).

Changes in thar numbers have been described in Carneys Creek by Tustin and Challies (1978) and are considered representative of the Two Thumb Range population. Sporadic government-funded and recreational ground-based hunting in previous decades had only localised impact, and thar increased rapidly during the 1950s and 1960s (Tustin and Challies 1978; Tustin 1980). In February 1965, 710 thar were censused in Carneys Creek; 40 of these were males ( $\geq 2$  years) with the remainder females ( $\geq 2$  years), yearlings and kids (Tustin and Challies 1978). Following the establishment of an overseas market for thar meat in 1970, government and commercial helicopter-based shooting coupled with recreational hunting dramatically reduced thar densities throughout the Southern Alps (Tustin 1980; Parkes *et al.* 1996). During February 1977 just 48 thar were censused in Carneys Creek, a 93% reduction from 1965 (Tustin and Challies 1978). Helicopter-based hunting continued in the Two Thumb Range until 1983 (W. R. Forsyth, New Zealand Forest Service, *pers. comm.*) when a government moratorium prohibited the practice in this area (Hughey and Parkes 1995). The moratorium was removed in 1992.

Annual monitoring (see Methods) of thar densities in the Two Thumb Range began in Carneys Creek and North Branch in 1984. These two catchments occupied different land tenures subject to contrasting harvest strategies and were considered to be representative of thar habitat in the Two Thumb Range. North Branch was in an area of pastoral lease (hereinafter referred to as the Godley Hunting Reserve) that the leaseholders managed as

a safari-style hunting reserve until 1996. Only adult male thar ( $\geq 5$  years old; see Parkes and Tustin 1988) were harvested by sport hunters from North Branch during 1984-1992 (G. Joll, NZ Trophy Guide Ltd., *pers. comm.*) but, beginning in 1993 a new leaseholder conducted some helicopter-based control of females and juveniles (N. Bolton, Department of Conservation, *pers. comm.*). In 1995 the lease was surrendered to the Crown and from early 1996 the Godley Hunting Reserve was subject to unrestricted recreational hunting (N. Bolton, Department of Conservation, *pers. comm.*).

The upper Havelock River, and Carneys Creek in particular, has traditionally been a popular area for recreational thar hunting (Challies and Thomson 1989a, unpubl. report). During 1984-1996 recreational hunting was actively encouraged as a means of controlling thar by the New Zealand Forest Service (1984-1987) and the Department of Conservation (1987-1996). Hunting permits were issued free-of-charge to recreational hunters with no restrictions on the number, age or sex of thar that could be harvested. The area east of Carneys Creek, in the northern Two Thumb Range, is pastoral lease. In contrast to North Branch, recreational hunters have had virtually unlimited access to this lease (L. Prouting, Mesopotamia Station, *pers. comm.*). For simplicity the northern Two Thumb Range that was subject to unrestricted recreational hunting is called the Rangitata Hunting Area.

North Branch and Carneys Creek, *ca.* 10 km apart, are of similar size (20.4 and 19.1 km<sup>2</sup>, respectively) and habitat. Seasonal habitat selection by thar (and chamois *Rupicapra rupicapra*) was evaluated in Carneys Creek in an associated study (Chapter 4). Habitat availability was estimated in 1995-1996 by digitising aerial photographs in three seasons (spring, summer-autumn, and winter). In winter only the steepest rock and grass bluffs were free of snow but in spring grasslands and sub-alpine shrublands became available at lower altitudes on north-facing slopes. During summer and autumn only a few small areas of permanent snow and ice remained.

A 1988 survey of recreational hunting recorded a male-biased harvest that was greater than the number of adult (i.e., breeding) females living in Carneys Creek (Challies and Thomson 1989b, unpubl. report). However, illegal hunting was not estimated so the actual harvest was probably considerably greater (see below). These findings raised questions about long-term trends in the abundance and sex ratio of thar within Carneys Creek and North Branch, and in the wider Two Thumb Range. Hence, the objectives of

this study were to describe long-term and seasonal trends in the Two Thumb Range thar population, and to determine the cause of the male-biased harvest recorded in Carneys Creek.

## METHODS

### Annual trends in Carneys Creek and North Branch

An annual census of thar was undertaken in Carneys Creek and North Branch during February, March or April 1984-1996. (Failure to gain permission from the leaseholder resulted in North Branch not being censused every year). Each year, hunting was prohibited in Carneys Creek from early January until the census was completed so that the thar would be undisturbed and more easily counted.

Thar were counted by experienced observers based at observation sites located midway to the ridgeline (Tustin and Challies 1978; Challies 1992, unpubl. report). The same sites were used each year; they provided complementary and overlapping views of each catchment. Counts were usually made on two different days by different observers, although at least one person was the same from year to year. All counts were made during the 3 h post-dawn and pre-dusk when thar were most active (see Tustin and Parkes 1988).

Thar were located with 8-10 X binoculars and then classified using 20-60 X spotting scopes into one of five age-sex classes using a variety of physical, behavioural and habitat cues (see Appendix). The age-sex classes, based on Caughley (1967) and Tustin (1990), were adult males ( $> 4$  years), sub-adult males (2-4 years), females ( $\geq 2$  years), yearlings (1-2 years), and kids ( $< 1$  year). The location, time observed and composition of each thar group were plotted on enlarged aerial photographs. This enabled observers to cross-reference after each count, and the largest and most accurate counts for all groups were summed to give the census total (Tustin and Challies 1978; Challies 1992, unpubl. report). Although not all thar present were likely to have been counted using this technique (see Forsyth and Hickling in press), for the purposes of this paper I assumed that the method was a census adequate for detecting population trends. Yearlings and kids were excluded from subsequent analyses because it proved difficult to accurately differentiate between the two classes (see below), and because sex could not be determined even with spotting scopes.

Log-linear regression was used to calculate the rate of increase for the thar in the two catchments (Eberhardt and Simmons 1992). I compared trends in the adult sex ratio using logistic regression (McCullagh and Nelder 1989); the dependent variable in the logistic model was the proportion of males (adult and sub-adult pooled) censused.

### **Testing for biased sex ratios**

Because I did not know the true adult (i.e.,  $\geq 2$  years old) sex ratio of the Two Thumb Range population, I estimated the ratio from a sample of 2775 adult thar shot in the eastern Southern Alps from helicopters during winter 1972-1975 (K. G. Tustin and J. P. Parkes, unpubl. data). These thar were shot during months when the sexes were aggregated (May-September), and were aged by counting horn rings (Caughley 1965). I assumed that there was no sex bias in the harvested sample. I tested for departure of the censused sex ratios from this population estimate using a G-test for Goodness of Fit with Williams' correction for  $n < 200$  (Sokal and Rohlf 1981:705).

### **Carneys Creek recreational hunter harvest**

In order to estimate the number of thar harvested in Carneys Creek during 1993 I used a mail and telephone survey to determine the legal harvest. I also used the mail survey and an additional non-systematic telephone survey to measure illegal harvest. These data were important because the harvest by recreational hunters in Carneys Creek was suspected to have increased since the 1988 survey by Challies and Thomson (1989b, unpubl. report). The size and age-sex class ratio of the harvest could also be useful in making inferences about the seasonal movements of thar in the Two Thumb Range.

A list of all hunters who obtained permits to hunt within the Rangitata Conservation Area (which includes Carneys Creek) during the 1993 calendar year was obtained from the Department of Conservation, Canterbury. I used a mail survey, followed up by a telephone survey of all non-respondents six weeks later, to determine who hunted in Carneys Creek and how many thar they harvested. Both surveys asked identical questions.

Because many hunters do not gain permits before hunting (D. C. Anderson, Department of Conservation, *pers. comm.*) I also attempted to measure the total illegal harvest. I asked legal hunters to list other party members so that I could cross-check whether they had held hunting permits. I also measured illegal harvest by telephoning people who had

entered their names in hut books in and around Carneys Creek and specified the purpose of their visit as "hunting".

I used the Total Design Method (Dillman 1978) for formatting the mail survey; this involved asking questions that were easily understood and could be answered with minimal effort (Gray and Kaminski 1993). I asked respondents to list separately their monthly harvests and those of other members of their party. Many hunters could not accurately differentiate between adults and sub-adults of either sex (D. M. Forsyth, *pers. obs.*), so I used four classes to measure harvest; 'males' (> 12 months), 'females' (> 12 months), 'kids' ( $\leq$  12 months), and 'unknown' (i.e., shot animals that were not recovered).

### Seasonal index of abundance in Carneys Creek

Seasonal changes in the abundance (i.e., migration) of adult male, sub-adult male and female thar may have been responsible for long-term changes in the abundance and sex ratio of thar recorded in Carneys Creek. To examine this possibility I visited five observation sites (Figure 2) in the headwaters of Carneys Creek in 25 months from December 1993 to February 1996 as part of a study of seasonal habitat selection by sympatric thar and chamois (Chapter 4). These five sites encompassed the habitat of 99.7% of adult and sub-adult male thar and 65.6% of female thar observed in the annual censuses during 1993-1996. Extreme weather prevented access to the study area during two months. Carneys Creek was closed to all hunting from January 1994 until the study ended, and although some illegal hunting occurred I considered it insufficient to have influenced the trends reported here.

A discrete non-overlapping area was searched from each site with binoculars (10 X 40) for 3 h post-dawn or pre-dusk (Figure 2) during periods with good visibility. All searching was done by the author using a 20 X spotting scope to classify thar into one of the five age-sex classes. Although sighted animals were resighted at 0.5 h intervals to quantify daily patterns of habitat use, this paper considers only the numbers of different individuals sighted within each 3 h count.

I differentiated between sites where female thar were (A, C and E; Figure 2) and were not (B and D) observed during winter because males formed mixed groups with females in winter (Chapter 4) but tend to avoid female habitat when segregated (Caughley 1967).

Each year was divided into four 3-month seasons: spring (Sep.-Nov.); summer (Dec.-Feb.); autumn (Mar.-May); and winter (Jun.-Aug.). These seasons have biological meaning in the Southern Alps; Clarke and Frampton (1991) recorded significant seasonal changes in the abundance of marked chamois in Basin Creek (70 km north-east of Carneys Creek) using these pooled months. Additionally, habitat selection by male and female thar differed significantly according to this seasonal classification (Chapter 4).

The counts were ln-transformed and pooled into seasons, giving 3 replicate counts per season per year. We tested for differences in abundance between (a) years, (b) seasons and (c) site \* season interactions using repeated measures ANOVA in the SYSTAT package (Wilkinson 1990). Interaction effects are not reported unless significant ( $P < 0.1$ ).

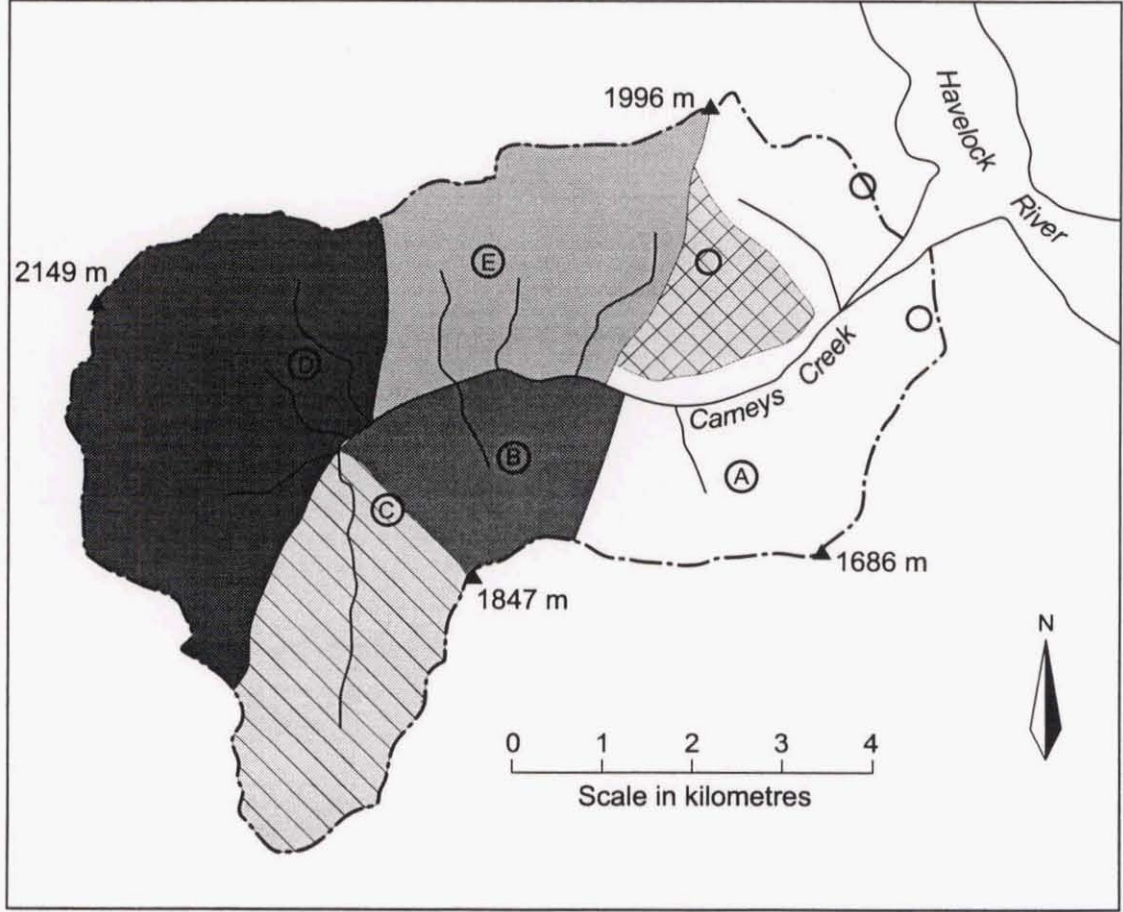


Figure 2. Observation sites (O) used to count thar annually in summer from 1984-1996 and monthly from December 1993-February 1996 in Carneys Creek, New Zealand. Shading indicates the five areas searched monthly from the lettered observation sites across the valley.

## Densities in adjacent catchments

The summer densities and age-sex class ratio of thar in catchments between Carneys Creek and North Branch were unknown but may have been one of the sources of males recorded shot in Carneys Creek during 1988. Consequently, I used the largest-count method (outlined above) to census thar at seven sites in the Two Thumb and Sibbald Ranges during January-March 1996. Density was assessed as the number of thar sighted divided by the area of the catchment. Site area was calculated from 1 : 50 000 scale Department of Survey and Land Information maps using ARC/INFO GIS (Environmental Systems Research Institute, Inc. 1991).

## RESULTS

### Reliability of age-sex classes

Of 33 thar shot by the author during the study period for an associated diet study (J. P. Parkes *et al.* unpubl. data), only one kid was misclassified (as a yearling) when first sighted (Chapter 4). Observers in annual censuses were experienced government or recreational hunters, and their classifications were assumed to be similarly accurate.

### Annual trends 1984-1996

The Carneys Creek and North Branch summer populations increased at similar rates (Figure 3;  $r = 0.15$  and  $0.17$ , respectively). The North Branch summer population was female-biased in every year, whereas in Carneys Creek there was a change from equivalence with the estimated population adult sex ratio of 1 adult male : 1.53 adult females to an increasingly male-biased ratio from 1991. Logistic regression confirmed the location and time effects to be significant, but the time and location interaction was not (Table 1). Thus, although the proportion of males increased in both catchments, the adult sex ratios were significantly different. The large residual deviance indicates lack of fit ( $\chi^2 = 44.32$ ; 17 df;  $P < 0.0001$ ); the most likely explanation for this is that thar were observed in single-sex groups during summer and the assumption of independence may have been violated. Under the assumption that the model structure is correct but that variance is  $kp(1 - p)$  rather than  $np(1 - p)$ , where  $k$  is an arbitrary variance-scaling constant, the  $F$  values should be approximately correct (see McCullagh and Nelder 1989:125).

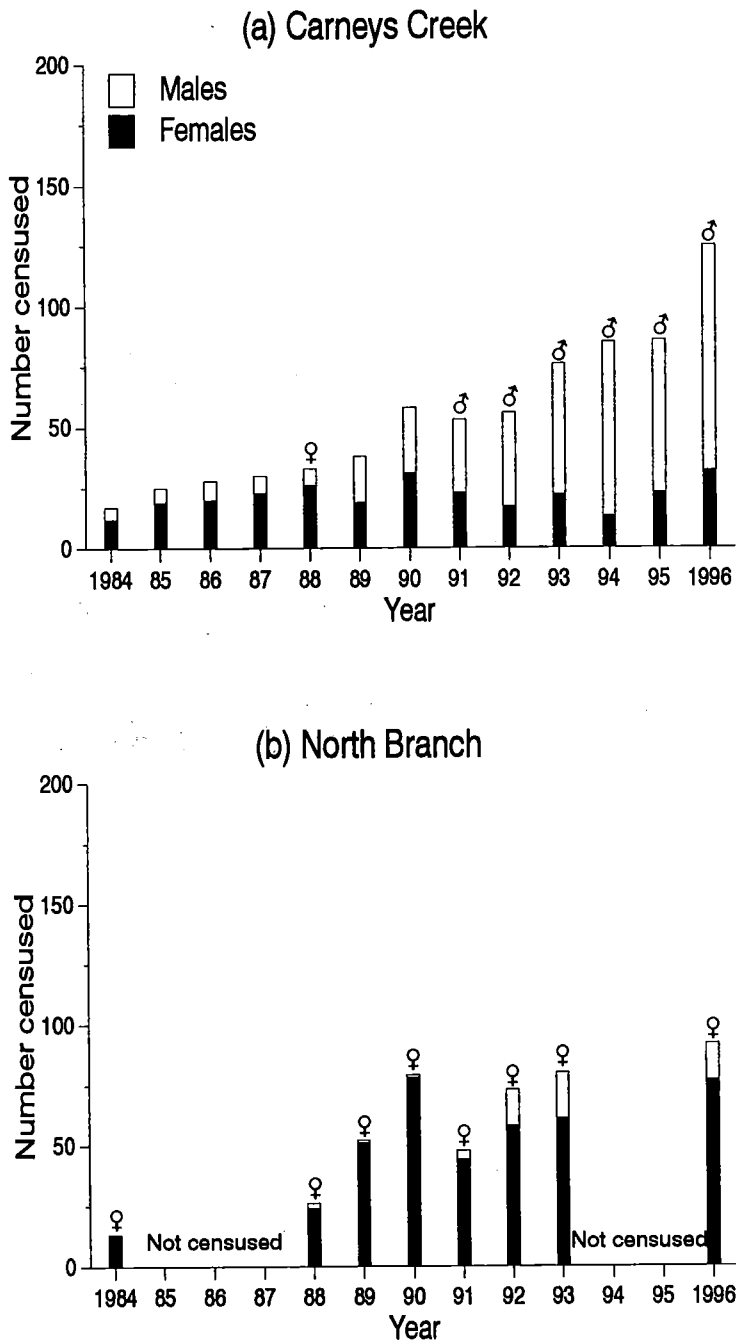


Figure 3. Number of male (adult and sub-adult pooled) and female thar censused in (a) Carneys Creek and (b) North Branch, Two Thumb Range, New Zealand, during summer 1984-1996. Recreational hunting in Carneys Creek was permitted during March-December from 1984-1993, but thereafter hunting was prohibited in all months. North Branch was subject only to adult male harvest (see text). The symbol above each bar indicates that the sex ratio in that year was significantly ( $P < 0.05$ ) male- (♂) or female-biased (♀) relative to the population estimate of 1 male : 1.53 females (see text for details). Bars without symbols indicate years in which there was no significant sex bias.

Table 1. Logistic regression analysis of changing adult thar sex ratios in Carneys Creek and North Branch, Two Thumb Range, New Zealand, 1984-1996.

Variable	df	Deviance	F	P
Location	1	294.39	12.91	< 0.0001
Time	1	118.61	45.49	< 0.0001
Time * Location	1	0.21	0.08	0.78
Residual	17	44.32		
Total	20	457.53		

From 1990-1994 the number of females in Carneys Creek declined, but increased again in 1995 and 1996 following the local prohibition of hunting.

#### Hunter harvest in Carneys Creek during 1993

Of 181 legal hunters, 164 (85%) were surveyed. The remainder had either provided insufficient addresses and could not be traced, or had moved with no forwarding address. Hence, the harvest presented here is conservative. Out of the 164 legal hunters contacted, 37 had hunted in Carneys Creek during the 9 months (mid-March to December) in which hunting was permitted. An additional 27 hunters were sampled who hunted in Carneys Creek without a permit (i.e., illegally).

Hunters shot more thar than were present in Carneys Creek during March 1993 (see Table 2), when a total of 84 thar were censused (22 females, 8 kids, 45 sub-adult males, and 9 adult males). There was a strong seasonal bias in the sex ratio of the harvest, with few males being shot during winter when the sexes were aggregated.

#### Yearly and seasonal patterns of abundance in Carneys Creek

The abundance of sub-adult males and females did not increase in Carneys Creek over the two years that monthly observations were made ( $F = 3.82$ ; 1, 3 df;  $P = 0.15$  and  $F = 0.37$ ; 1, 3 df;  $P = 0.59$ , respectively), but adult male abundance did ( $F = 24.98$ ; 1, 3 df;  $P =$

Table 2. Seasonal harvest of recreational hunters in Carneys Creek, New Zealand, during March-December 1993. Male and female thar are segregated during spring (SON), summer (DJF) and autumn (MAM).

Age-sex class (see methods)	Season				Total
	DJF	MAM	JJA	SON	
Males	34	21	2	8	65
Females	10	7	-	5	22
Yearlings/kids	2	3	-	-	5
Unknown	-	3	-	-	3
Total	46	34	2	13	95
Proportion of annual harvest (%)	(48)	(36)	(2)	(14)	(100)

0.02). There were no seasonal differences in the abundance of females (Figure 4a;  $F = 0.92$ ; 3, 9 df;  $P = 0.47$ ), but there was a suggestion of a seasonal trend in adult males (Figure 4b;  $F = 3.06$ ; 3, 9 df;  $P = 0.08$ ), although the numbers of thar observed in these two age-sex classes were small.

Sub-adult males displayed a strong seasonal trend in abundance (Figure 4c;  $F = 16.64$ ; 3, 9 df;  $P = 0.001$ ) that varied according to whether or not the site had females ( $F = 3.84$ ; 3, 9 df;  $P = 0.05$ ). There were significantly fewer sub-adult males present in winter compared to the other three seasons ( $F \geq 15.31$ ; 1, 3 df;  $P \leq 0.03$ ), and fewer sub-adult males in autumn compared to summer ( $F = 15.31$ ; 1, 3 df;  $P = 0.03$ ). These changes were significantly greater in the sites without females from summer to winter ( $F = 12.53$ ; 1, 3 df;  $P = 0.04$ ) and from autumn to winter ( $F = 15.67$ ; 1, 3 df;  $P = 0.03$ ).

### Population structure in adjacent catchments

Murphy Stream and Camp Creek, both adjacent to Carneys Creek and within the Rangitata Hunting Area, contained low density and male-biased populations of thar (Table 3; Figure 5). In contrast, the four sites within the Godley Hunting Reserve were of moderate (by historical standards) female density, and composed almost exclusively of females.

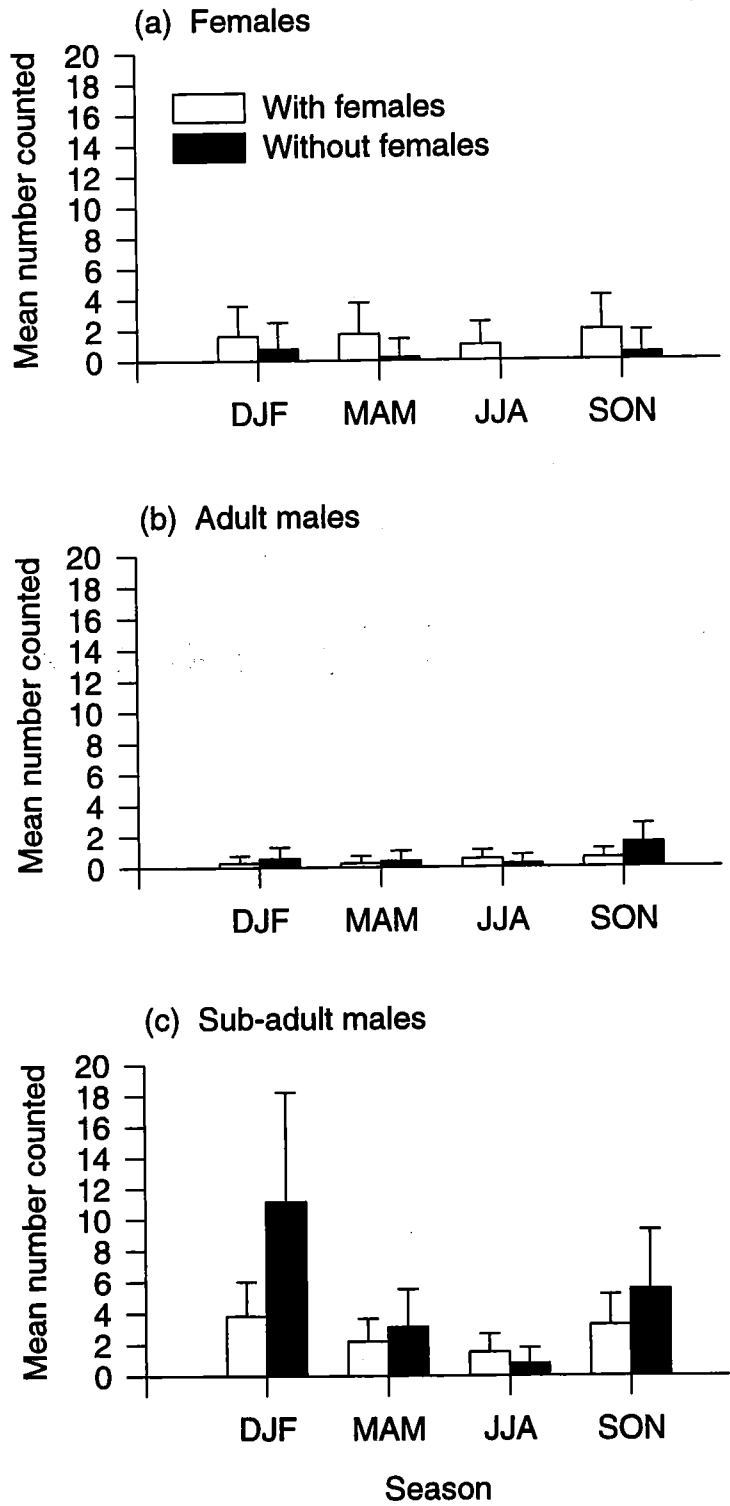


Figure 4. Mean number (+95% C.I.) of thar counted at 3 sites with females and 2 sites without females, in Carneys Creek, New Zealand during 1994-1996. Counts were made monthly from each site, and are presented back-transformed (lower C.I.s would be conservative). Seasonal differences were only statistically significant ( $P < 0.1$ ) for adult and sub-adult males (see text).

Table 3. Number of male (adults and sub-adults pooled) and female ( $\geq 2$  years) thar counted at eight sites in the Two Thumb and Sibbald Ranges, New Zealand, summer 1996.

Site <sup>a</sup>	Area (km <sup>2</sup> )	Males	Females	Female density (number km <sup>-2</sup> )	Sex bias <sup>b</sup> , $G^c$	$P <$
<b>Rangitata Hunting Area</b>						
Carneys Creek	19.1	93	32	1.7	M, 62.38	0.001
Murphy Stream	10.2	32	9	0.9	M, 5.00	0.001
Camp Creek	17.0	31	28	1.7	M, 4.04	0.05
<b>Godley Hunting Reserve</b>						
Toms Stream	11.6	10	61	5.3	F, 43.45	0.001
East Macaulay	10.1	10	67	6.6	F, 44.69	0.001
West Macaulay	11.1	11	130	11.7	F, 73.69	0.001
North Branch	20.4	4	77	3.8	F, 38.11	0.001
Weka Stream	9.3	10	52	5.6	F, 15.96	0.001

<sup>a</sup> Site locations are shown in Figure 5.

<sup>b</sup> Male (M) or female (F) biased.

<sup>c</sup>  $G$ -test (Sokal and Rohlf 1981) for goodness of fit with estimated population ratio (1 male : 1.53 females; see Methods), with Williams' correction (1 df).

### Long-term changes in the summer male : female ratio in Carneys Creek

The sex ratios of thar populations in Carneys Creek during summer were significantly different in 1965 and 1995, with more males and fewer females present in the latter census (Table 4).

Table 4. Ratios and densities of age-sex classes censused within Carneys Creek in summer 1965 and 1995. Compared to the estimated population ratio of 1 male : 3.35 females, juveniles and kids (see Methods) the ratio was female-biased in 1965 and male-biased in 1995 ( $G \geq 57.23$ ; 1 df;  $P < 0.001$ ), and was significantly different between the two years ( $G = 209.51$ ; 1 df;  $P < 0.001$ ).

Year	Males <sup>a</sup> : Females <sup>b</sup>	Female <sup>b</sup> density (number km <sup>-2</sup> )
1965 <sup>c</sup>	40 : 670	32.9
1995	63 : 49	2.3

<sup>a</sup> 'Males' includes adult and sub-adult males

<sup>b</sup> 'Females' includes yearlings and kids pooled

<sup>c</sup> from Tustin and Challies (1978)

## DISCUSSION

Female thar give birth to similar numbers of male and female offspring (Caughley 1966; 1967), so in 1991-1996 the Carneys Creek female population was insufficient to produce the number of sub-adult males present during spring-autumn, when thar are sexually segregated (Figure 3). The most likely source of these males was the Godley Hunting Reserve on the southern flanks of the Two Thumb Range (Figure 5). During the 1993-1996 monthly counts, adult and sub-adult male thar were frequently observed moving in and out of Carneys Creek along the axial ridge of the Two Thumb Range during the spring-autumn period.

The extreme male-biased recreational hunter harvest recorded in Carneys Creek during 1993 (Table 2) is strong circumstantial evidence that seasonal male migration also occurred in that year. Only two (3%) of 65 males were shot during winter, suggesting that substantially fewer males were present in Carneys Creek during winter compared to autumn and spring 1993. The annual censuses (Figure 3) suggest that seasonal migration of male thar born in the Godley Hunting Reserve in Carneys Creek began about 1989. In that year the proportion of males censused in Carneys Creek began to increase and the number of females began to decrease.

In summer 1996 the Godley Hunting Reserve contained, relative to the peak densities of the 1960s, moderate densities of females but few males. From 1981 to 1992, only 30-40 adult trophy males ( $\geq 5$  years) and no females were harvested annually from this area (G. Joll, NZ Trophy Guide Ltd., *pers. comm.*). During the winter of 1995 a commercial helicopter-based harvest was taken from the Godley Hunting Reserve (J. Andrew, Department of Conservation, *pers. comm.*), so the densities of females recorded during summer 1996 were probably lower than during previous years.

Murphy Stream and Camp Creek were very popular with recreational hunters (Challies and Thomson 1989b, unpubl. report; L. Prouting, Mesopotamia Station, *pers. comm.*) so densities of female thar there were low. Although recreational hunters preferentially harvest male thar for their trophy horns and skins (Davys 1996), it seems that sufficient females were harvested to maintain low female densities. As in Carneys Creek, the numbers of females in these catchments were insufficient to produce the males observed there during summer 1996. I suggest that most of the males present in these catchments during spring, summer and autumn are likely to have been born in the Godley Hunting

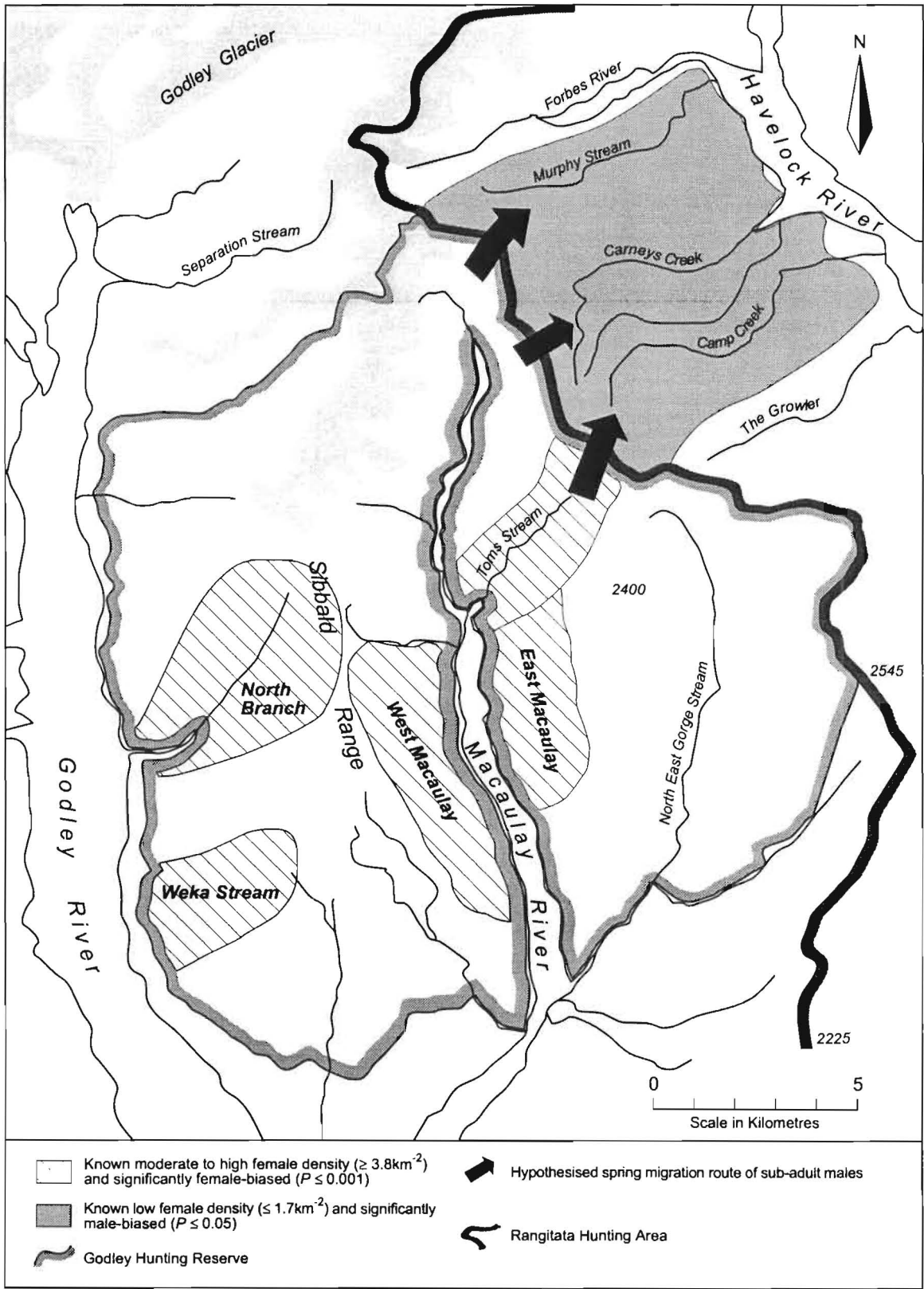


Figure 5. Summer thar densities, and hypothesised spring migration route of sub-adult male thar, in the Two Thumb Range, New Zealand. Sub-adult males born in the moderate female density Godley Hunting Reserve emigrate to the low female density Rangitata Hunting Area in spring and return in autumn (see text for details).

Reserve.

Seasonal migration, defined by McCullough (1991) as "consistent seasonal shifts of the population between different geographic areas in response to seasonal changes in resource availability and quality", has been hypothesised to facilitate temporary exploitation of high quality forage that cannot be occupied year-round (Fryxell and Sinclair 1988). The seasonal migration of sub-adult male thar in the Two Thumb Range appears to be related to changes in the availability of preferred habitats and food species. When sexually segregated, both sub-adult and adult males select lower-altitude grasslands and shrublands for feeding, but in winter snow covers these habitats and the sexes are more-or-less confined to the steep snow-free rock bluffs, where mating also occurs (Tustin 1990; Chapter 4). Associated with these changes in habitat selection is a change in the diet of male thar, reflecting the greater availability of presumed higher quality food species (J. P. Parkes *et al.* unpubl. data). In contrast, the diet of female thar changes less from season to season, reflecting the relatively constant availability of rock and grassland bluff species (J. P. Parkes *et al.* unpubl. data). I hypothesise that Carneys Creek contains relatively large areas of habitat and plant species preferred by male thar when sexually segregated. Seasonal changes in snow cover (Chapter 4) and plant phenology (e.g., Clarke 1968; Mark 1965) create extreme spatial and temporal variability in food quality and quantity in the Southern Alps. By the time the heavy winter snows arrived in Carneys Creek in 1994 and 1995, most of the sub-adult males had emigrated, probably to their natal bluffs.

Female density appears to affect habitat use by male thar while they are sexually segregated. In 1965, when the Two Thumb Range population was considered to be at, or near to, peak density (Caughley 1967; Tustin and Challies 1978), few males summered in Carneys Creek. Interestingly, in February 1965 large female-juvenile groups were observed in the two sites that did not contain females in this study (see Figure 2 in Tustin and Challies 1978). In Carneys Creek the seasonal changes in abundance of sub-adult males were more extreme in the non-female sites than in the female sites during 1993-1996. Furthermore, few sub-adult males were observed within the Godley Hunting Reserve during summer, despite this class not being harvested there. This suggests that sub-adult male thar avoid habitats utilised by females during summer.

Clutton-Brock *et al.* (1987) observed increased sexual segregation in red deer (*Cervus elaphus*) at high population density, probably because stags avoid low-biomass forage induced by sustained female grazing. A similar mechanism may operate in thar. Caughley (1970b) found the density and biomass of preferred tussock species in the eastern Southern Alps to be negatively correlated with the period of female colonisation. Several qualitative studies describe a decrease in palatable species and an increase in unpalatable species and bare ground following sustained grazing by thar (e.g., Burrows 1974; Wardle 1979; Evans 1980). These accounts are almost certainly describing grazing by large female-juvenile groups. The energetic needs of males exceed females because of the greater body size of males', but ingestion rate is unlikely to increase with body size as rapidly as metabolic requirements (Clutton-Brock and Harvey 1983). Large animals are relatively more restricted in bite depth and volume on short swards relative to smaller animals (Illius and Gordon 1987). Thus males may be unable to feed economically where the quality and quantity of forage is low (Clutton-Brock *et al.* 1987; Illius and Gordon 1990). Avoidance of large female-juvenile groups by male thar when sexually segregated may be a proximate mechanism to minimise intersexual food competition at a critical time of year (Geist and Petocz 1977). Alternatively, male thar may simply be avoiding areas of low forage quality and quantity rather than avoiding females, as occurs in mountain sheep (Bleich *et al.* 1997).

Although a detailed discussion of the possible mechanisms underlying sexual segregation in Himalayan thar is beyond the scope of this paper, a brief description of the likely ultimate factors is relevant to understanding patterns of seasonal migration in ungulates (Fryxell and Sinclair 1988; *sensu* Gavin 1991). A literature review by Main *et al.* (1996) concluded that intersexual differences in energetics and predation risk linked to reproductive success best explained sexual segregation in ungulates. They hypothesised that male ungulates seek to optimise body size and condition because both factors are positively correlated with male reproductive success. Female reproductive success, they argued, is primarily determined by offspring survival. Selection should therefore favour female behaviours that increase the survival of offspring, in particular behaviours that reduce predation risk.

There is evidence that segregation of male and female thar in New Zealand conforms to the reproductive-strategy hypothesis of Main *et al.* (1996). Thar of both sexes undergo a distinct seasonal cycle in body condition (Caughley 1970d; Figure 6) typical of other

ungulates (Mautz 1978). Fat reserves are highest mid-winter and lowest in spring, presumably because energy expenditure exceeds energy gained from foraging during late winter. In winter both sexes reduce feeding and movement so as to conserve energy (termed "winter anorexia" by Tustin and Parkes 1988). Female thar feed at low altitudes on the new tussock growth in spring and summer, but always retreat to the safety of rock bluffs during the day, before and after kidding (Tustin and Parkes 1988). Males leave the female groups to form same-sex groups in spring (Tustin 1990; Chapter 4). Both sexes feed intensively during spring and summer (Tustin and Parkes 1988) and kidney fat increases throughout these months, up to a winter maximum (Caughley 1970d). The diets of male and female thar in the eastern Southern Alps have significant seasonal differences; their diet did not differ during May-October, when the sexes are aggregated on rock bluffs, but diverged outside this period (J. P. Parkes *et al.* unpubl. data). Given that male mating success in ungulates (Clutton-Brock *et al.* 1988), and winter survival in thar (Caughley 1970b), are both positively correlated with body condition, it is likely that males segregate from females to feed on high quality forage in non-bluff habitats so as to maximise body growth and fat deposition for the next mating season and winter.

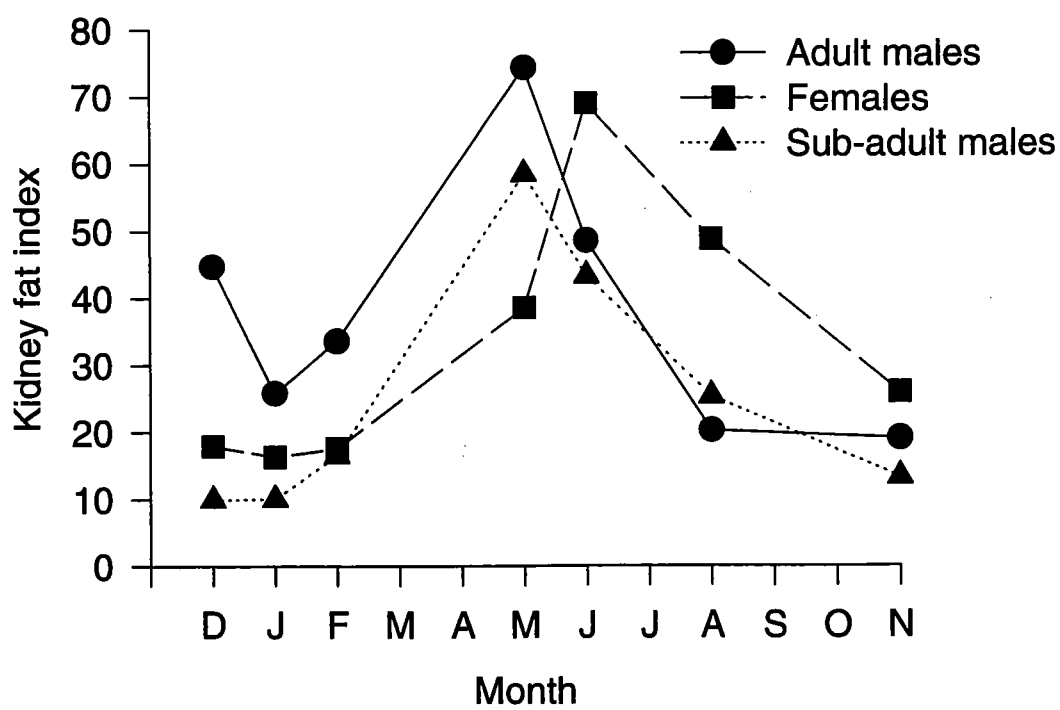


Figure 6. Seasonal changes in the kidney-fat index (100 X weight of fat surrounding the kidney, divided by the weight of the kidney) of thar shot in the Two Thumb and Sibbald Ranges, New Zealand, during 1963-1966 (data from Caughley 1970d).

Females may be sedentary on rock bluffs for several reasons. Steep rock bluffs have been demonstrated to provide escape cover from predators for a variety of mountain ungulates (e.g., Geist and Petocz 1977; Schaller 1977; Berger 1991; Fox *et al.* 1992). Rice (1986) observed nilgiri thar (*Hemitragus hylocrius*) in their native habitat using rock bluffs to escape leopard (*Panthera pardus*) and Dang (1967, cited in Schaller 1977) recorded similar behaviour with Himalayan thar and snow leopard (*Panthera uncia*). Himalayan thar in Nepal could additionally be preyed by wolf (*Canis lupus*), leopard, golden cat (*Felis temmincki*), lynx (*Felis lynx*), Asiatic black bear (*Ursus thibetanus*), and perhaps dhole (*Cuon alpinus*) (G. Schaller, *pers. comm.*). During winter, rock bluff was the second commonest habitat after snow in Carneys Creek (Chapter 4), offering relative warmth, some forage and possible protection from winter storms. In spring-autumn, the risk of predation for females and their offspring may exceed the benefits of presumed forage quality and quantity offered in non-bluff habitats (see Festa-Bianchet 1988; Berger 1991; Bleich *et al.* 1997). In any case, the metabolic costs of a smaller body size *versus* forage intake outlined above may make such habitats less advantageous to females relative to males.

### MANAGEMENT IMPLICATIONS

Many ungulates that exhibit sexual segregation are subject to intensive harvesting, so it is important to understand the likely implications of different harvesting strategies on habitat use as well as population dynamics. Indeed, age-sex class harvests are sometimes manipulated to maximise the number and quality of adult male ungulates harvested from the population (e.g., red deer *Cervus elaphus*, Clutton-Brock and Lonerghan 1994). Such populations will exhibit strong spatial structure when the sexes are segregated (*sensu* McCullough 1996), with the extent of spatial structuring depending on the distribution of preferred habitat types and the mobility of each age-sex class. Density effects, such as those highlighted in this study and in Clutton-Brock *et al.* (1987), may also shape habitat use at the landscape scale.

There is considerable circumstantial evidence that herbivory by females may influence habitat use by males (Clutton-Brock *et al.* 1987; Main and Coblentz 1996). Maintaining high female densities may therefore have a negative effect on both the number and quality of males within a harvest unit.

McCullough (1996) proposed that for continuously-distributed populations, harvest may be regulated through a mosaic of hunted and unhunted areas. In this study the two strategies, unrestricted female and male harvest *versus* no female harvest and limited adult male harvest, created low and high female densities respectively. Migration of male thar born in the moderate density population to the low density population when sexually segregated created a strong bias in male harvest in the low density area. Such outcomes should be considered by managers when designing harvest strategies for ungulates that exhibit sexual segregation.

In situations where ungulates are controlled to protect environmental values, such as thar in the Southern Alps of New Zealand, management will often necessitate large and instantaneous population reductions within management units. These reductions may alter habitat use by segregated males and females in a non-linear fashion relative to the population reduction. The potential for such effects is particularly evident at the border of management units (i.e., areas subject to differing control intensities, as occurred in this study). Managers may need to understand, and perhaps manage, populations in adjacent management units.

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Appendix. Morphological, behavioural and habitat features used to classify thar into five age-sex classes in the Two Thumb Range, New Zealand. Features are listed in decreasing order of importance (after Caughley 1967 and Tustin 1990).

Age-sex class	Cues
Adult males (> 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 ( $\leq 4$ )
Sub-adult males (2-4 years)	Body size less than adult males, 1.5 X 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
Females (> 2 years)	Kid and/or yearling present Body size < sub-adult and adult males Mane absent On rock bluffs <sup>a</sup> /known female range
Yearlings (1-2 years) (sex indeterminate)	0.5 - 0.75 X body size of females Small ruff Part of, or close to, female groups Outside winter mixed-sex groups Horns small
Kids (< 1 year) (sex indeterminate)	Small body size relative to females Females present Suckling behaviour Horns small

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

## Chapter 6

# A Case for Integrated Management of Sympatric Herbivore Pest Impacts in the Central Southern Alps, New Zealand

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Five herbivorous mammalian pests are sympatric in the central Southern Alps. All of these species have the potential to affect conservation values, yet the Department of Conservation at present monitors and mitigates the impacts of only one. We outline some ideas for the integrated management of sympatric herbivore pest impacts and use the two-species system of sympatric thar and chamois to highlight the need for integrated management of the central Southern Alps alpine pest community.

### INTRODUCTION

Five introduced herbivores, Himalayan thar (*Hemitragus jemlahicus* Smith), chamois (*Rupicapra rupicapra* L.), red deer (*Cervus elaphus scoticus* Lönnerberg), possum (*Trichosurus vulpecula* Kerr), and hare (*Lepus europaeus occidentalis* de Winton) presently co-exist (termed sympatric) in the central Southern Alps alpine zone. The Department of Conservation has a statutory obligation to control pests to minimise their impacts on indigenous biota (Holloway, 1993) but actively manages (i.e., monitors and controls) only one of these species (thar).

In this paper we show that because (1) all five species are generalist herbivores with varying degrees of dietary overlap, and (2) habitat use by these species is known to overlap, the *impacts* of these species on conservation resources are likely to be largely cumulative. That is, more than one of these species will modify the distribution and abundance of a particular plant species.

We describe why *integrated* management of these pests is likely to deliver improved conservation benefit relative to the current single-species approach. We also outline the essential elements of an integrated pest management plan for the central Southern Alps alpine zone. For the purposes of this paper we consider this zone to be that area normally covered by winter snow, including shrubland but excluding forest, within the thar breeding range (see Department of Conservation, 1993).

### **The central Southern Alps' alpine pest community**

Current densities and distributions of the five herbivores in the central Southern Alps reflect differences in the carrying capacity of alpine habitats for each species (Table 1) and their different histories of management and harvesting.

The current densities and distributions of the three ungulates have been determined largely by over 60 years of control and harvesting. Recreational hunters have taken variable annual harvests of deer since last century and of thar and chamois since the 1920s. Government-funded control of all three species began in the 1930s, continued until the 1960s for deer and chamois, and remains ongoing for thar. Justifications for this control have changed over time. Early campaigns were widespread and aimed to reduce competition with domestic stock; later campaigns were more focussed and were usually justified to mitigate supposed downstream water and soil quality effects (Caughley and Sinclair, 1994). Current official control of thar aims to halt their dispersal (Department of Conservation, 1993).

In the alpine zone ungulates are highly vulnerable to helicopter-based hunting. Consequently, the advent of commercial harvesting of the ungulates for game meat in the 1960s reduced red deer, thar and chamois populations to very low densities (to

Table 1: *Attributes of five herbivore pests sympatric in the central Southern Alps alpine zone (? indicates unknown).*

Species	Body weight (kg) <sup>a</sup>	Maximum density (number km <sup>-2</sup> ) <sup>b</sup>	Variability in density <sup>c</sup>	Maximum biomass (kg km <sup>-2</sup> ) <sup>d</sup>	Habitat(s) used <sup>e</sup>
Thar	45	>30	High	>1350	g, b, s
Chamois	31	5	High	155	g, s
Red deer	58	10	High	580	g, s
Possum	2.8	?	Low	?	s
Hare	3.5	<1	Low	<3.5	g

<sup>a</sup> Average of female and male (adapted from King, 1990)

<sup>b</sup> Figures based on King (1990), Flux (1967) and personal observations

<sup>c</sup> Relative spatial and temporal variability in density

<sup>d</sup> Product of biomass and maximum density

<sup>e</sup> Habitats are grassland (g), bluff (b) and shrubland (s); information based on Chapter 3, Chapter 4, Christie (1963), Guest and Wilkinson (1976), King (1990), Parkes and Thomson (1995), and personal observations

zero in many places; see Parkes, Nugent and Warburton, 1996). Current national harvests of deer and chamois from the central Southern Alps alpine zone are unknown but probably number only a few hundred each, mostly from the western Alps. After a moratorium imposed in 1983, commercial harvests of thar recommenced in 1995 and totalled *ca.* 1300 in that year (J. Andrew, *pers. comm.*; Department of Conservation, Christchurch).

Possum populations are controlled to protect conservation values over  $\geq 10\,000$  km<sup>2</sup> of New Zealand (Parkes, Baker and Ericksen, 1996) using a large number of control techniques (Cowan, 1990). However, none of the 250 ongoing control programmes occur in the central Southern Alps alpine zone. Fewer techniques are available to control hares (e.g., Parkes, 1984) and none have been tested in alpine habitats (Wong and Hickling, 1996). Hares are not targeted in any control operation for conservation reasons.

### **Current planning procedures**

The Department of Conservation currently has national policies and specific plans for thar (Marshall, 1991; Department of Conservation, 1993) and possums (Department of Conservation, 1994), although as noted the latter has as yet no consequences for possums in the alpine zone.

The planning and consultative process for the thar plan has been summarised by Hughey and Parkes (1995). The plan divides the thar breeding range (*ca.* 7 000 km<sup>2</sup>) into two exclusion zones, which aim for zero thar density, and seven management units. The management units are based on different land tenures and vegetation types. Each management unit has a specified maximum allowable density of thar ( $\leq 2.5$  thar km<sup>-2</sup>), with recreational and commercial hunting encouraged to maintain thar below that density; government-funded control in the seven management units is used only as a 'last resort'. All management units have unique conservation objectives based on maintaining "healthy plant cover, species diversity and regenerative capacity of plant communities" (Department of Conservation, 1993).

Densities of thar are monitored annually or biennially in more than 21 catchments spread throughout the seven management units. Thar are counted using binoculars and spotting scopes; chamois and red deer are also counted, if observed. Densities in these catchments are used to infer population density within each management unit.

Monitoring the impacts of thar on tussock communities is a major feature of the plan. Seventy permanent plots have been established in five catchments to monitor the impacts of different densities of thar on the vegetation; these plots are being remeasured every 2-4 years (Parkes and Thomson, 1995). No other government-funded monitoring of pest impacts in the central Southern Alps alpine zone is being undertaken.

### **The ecological basis for *integrated* pest management**

Niche theory (e.g., Gause, 1934; Diamond, 1978) states that when two or more species co-exist their habitat use and diet, and therefore impact on community structure, will not completely overlap. Indeed, differential resource selection is viewed as a

fundamental process enabling co-evolved species to co-exist (Rosenzweig, 1981). This generality, however, has been derived from studies of natural communities.

Introduced species can be expected to show greater niche overlap than co-evolved species because there has been insufficient time for competitive effects to shape the community (McNaughton, 1986).

Since most large mammalian herbivores are generalist feeders (Belovsky, 1986), there is likely to be considerable dietary overlap when introduced herbivores are sympatric. Thus, their *impacts* on particular indigenous biota can be expected to be largely cumulative. Because plant community composition, herbivore population density and herbivore behaviour are spatially heterogeneous (Huntly, 1991), pest impacts will also be highly variable in space and time (e.g., see Hone, 1995). Control action is likely to amplify the variability of herbivore behaviour (e.g., Douglas, 1971) and population density (e.g., Chapter 3; Chapter 5).

In addition to the strong trophic links typical of herbivore-plant communities (Pimm, 1991) there will be interference competition and mutualistic associations (Moller, 1989). The latter interactions may be direct (e.g., behavioural interactions) or indirect (e.g., via nitrogen cycling altering plant distribution and abundance). There is growing evidence that indirect interactions may be just as important as direct ones in determining patterns and processes in some ecosystems (Hobbs, 1996).

The questions are what and how strong are these ecological interactions when the species in the community have not co-evolved? Competitive interactions between introduced species may be stronger than might be expected in co-evolved communities. Therefore, where two or more species strongly interact the effect of managing one species on the other should be considered (May *et al.*, 1979). Control operations that reduce a population may allow a competitor to increase. For example, a feral pig (*Sus scrofa* L.) population in tropical Australia doubled in numbers following the experimental removal of Asian buffalo (*Bubalus bubalis* Smith) due to release from interspecific competition; buffalo had been trampling the pigs' food supply (Corbett, 1995). Hare densities increased in some alpine grasslands and in

forest following control of chamois and red deer in the Harper-Avoca catchments, Southern Alps (Batcheler and Logan, 1963).

An alternative possibility is that control of one species may lead to a decrease in another. An example would be reducing the density of a pest such that resulting changes in habitat structure make the habitat less suitable for another pest. Red deer preferentially used pasture grazed by cattle on the Isle of Rhum, apparently because cattle grazing (*Bos taurus* L.) encouraged spring grass growth (Gordon, 1988). Hare densities declined in the heavier grasslands that developed in the Harper-Avoca following red deer and chamois control (Batcheler and Logan, 1963).

#### **A simplified system - sympatric thar and chamois**

Observations of seasonal habitat selection by sympatric thar and chamois in Carneys Creek (Chapter 4) showed overlap in habitat selection; grassland and shrubland were generally preferred by both species in the seasons that these habitats were accessible. Thar preferred rock bluff and grass bluff habitats whereas chamois selected them in approximate proportion to their availability in all seasons except during winter (when they were preferred; Chapter 4). Shrubland was especially preferred by both species in winter, when other vegetated habitats were largely unavailable. Scree and snow were generally avoided by both species.

Analysis of the diet of thar and sympatric chamois from the eastern Southern Alps indicated that both ate the same plant species, albeit in different proportions depending upon season. Overall, thar ate significantly more grasses and significantly less shrub and herb species than chamois (Parkes and Thomson, 1995; Parkes *et al.*, in prep.). This suggested either that thar and chamois preferred different *species* within the same habitats, or that different *habitats* were preferred.

Although the results from Carneys Creek can only be extrapolated to the remainder of the sympatric thar-chamois range with caution (Chapter 4), they suggest high seasonal overlap between thar and chamois in the use of some habitats, particularly grassland and shrubland. Finer-scale analysis of habitat use, however, might reveal significant differences in the vegetation communities of habitats used by thar and chamois.

Combined, the diet and habitat selection studies described above are strong evidence that the impacts of thar and chamois on indigenous biota will sometimes be cumulative; both are likely to modify the distribution and abundance of some species. To protect plant species that are highly palatable to thar and chamois (e.g., *Gaultheria crassa* Allan; Parkes and Thomson, 1995) it may be necessary to control both species.

Thar and chamois are both sexually segregated outside of the rut (Clarke, 1986; Chapter 4; Chapter 5), which is a characteristic of many north-temperate ungulates (Main and Coblenz, 1990). When segregated, the habitat selection and diet of male and female thar are significantly different (Chapter 4; Parkes *et al.*, in prep.), and such differences are also likely to be evident between male and female chamois (see the recent review by Main, Weckerly and Bleich, 1996). In addition, male thar are highly mobile during spring, summer and autumn whereas females are sedentary (Chapter 5). These intersexual differences in diet, habitat selection and mobility complicate the management of these species at a variety of spatial scales (see Chapter 5).

There is anecdotal evidence that fast-dispersing chamois populations (Caughley, 1963) were later excluded from favoured habitats by increasing densities of thar. The potential for chamois to increase following thar control has been acknowledged by the Department of Conservation (Holloway, 1993). Chapter 3 presented evidence that increasing densities of thar do exclude chamois from sites they had previously used. Observations of thar-chamois encounters in Carneys Creek indicated that chamois avoided thar by moving away from them when they were encountered (Chapter 4). Sustained grazing by high densities of thar may have also made dietary competition important prior to the advent of helicopter-based hunting (Chapter 3; Chapter 4). These findings have important implications for management strategies. For example, eradicating (Parkes, 1989) or reducing thar to very low densities is likely to result in increased utilisation of *some* sites by chamois. (Although national eradication is not the goal of current management, this debate may well re-surface at some future time). If thar are eradicated or reduced to very low densities managers may then need to allocate resources to monitoring and perhaps controlling chamois.

### **Why *integrated* management is needed**

All five herbivores have the potential to impact on conservation values in the central Southern Alps alpine zone. These impacts are likely to be cumulative for some plant species in some habitats (see Table 1). The particular pest(s) modifying conservation values at any site will depend on which plant species and associations are valued and on the biomass of the different pests (Parkes, 1994). For example, snow tussock is, judging by the proportion in their diet, more likely to be affected by thar (Caughley, 1970; Parkes and Thomson, 1995) and red deer (Lavers *et al.*, 1983; Rose and Platt, 1987) than by hares (Rose and Platt, 1992), chamois (Parkes and Thomson, 1995), or possums (which do not eat it at all; Parkes and Thomson, 1995).

Within the central Southern Alps there is high spatial and temporal variation in pest densities, in particular for the ungulates that are subject to commercial harvest. When combined with variation in the distribution of conservation resources, variation in pest densities will create high spatial and temporal variability in individual pest impacts.

Since many pest control methods are species-specific, managers require flexibility in allocating resources to control the appropriate pest(s). Management actions, like the impacts of different pests, occur at different scales in space and time. For example, there is a simple and affordable technique for widespread control of thar (helicopter-based shooting) but not for hares (because the relevant techniques are too expensive for any large-scale use that might be required; Wong and Hickling, 1996).

Integration of management therefore needs to be 'nested' within at least four levels of variation. The conservation resources that require protection will themselves vary in space, and dietary evidence indicates that the pest impacts will vary by species and perhaps location. The densities of the pest species will also vary in both space and time due to different equilibrium densities and different harvesting regimes by commercial, recreational and/or government hunters. Furthermore, the available pest control techniques may be specific against particular pests and so practically applicable at different scales.

The measure of success in managing the introduced herbivores of the central Southern Alps must be the state of defined conservation goals. We believe that an integrated

management plan will better protect the conservation resources of the Southern Alps than the current practice of preparing multiple single-species control plans. Integrated management would provide greater flexibility for managers to manage the spatially and temporally variable impacts of pests and resulting pest interactions.

We consider that integrated management of herbivorous conservation pests should:

- specifically define the conservation resources to be protected (which species and where) and the level of protection (some measureable attribute of the resource) desired;
- identify the pests that most affect these resources (from dietary studies or by experimental manipulation of the pests);
- incorporate some understanding of (i) the relationships between pest densities and their impacts, and (ii) important between-pest interactions, or an ability to gain these understandings as management proceeds (to set target densities of pests);
- provide sufficient organisational flexibility to sustain control (including management of other harvesters) of the appropriate pest specie(s).

We see three major benefits arising from integrated management relative to the single-species approach. First, there will be improved conservation benefit because, where necessary, multiple species will be controlled (Parkes and Nugent, 1995) to protect defined conservation resources. Such integration is difficult to achieve under multiple single-species plans (Parkes and Nugent, 1995).

The second benefit will be reduced opportunity costs. Single-species plans sometimes result in pests being killed for little or no conservation benefit because another pest is also modifying the resource. An example would be control of thar, with the aim of maintaining tussock health, on leasehold land subject to intensive summer grazing by domestic sheep (*Ovis aries* L.). This action would have little conservation benefit, and should not be undertaken under an integrated management approach unless sheep densities were also reduced.

Third, in the present system only nominated pests receive funding so some control operations are conducted that give less benefit than would control of an 'unfunded'

pest elsewhere. Integrated management aims to control the pest(s) that will give greatest conservation benefit.

### **Anticipated problems with *integrated* management**

Defining conservation values and criteria for monitoring their 'health' is problematic. This is a problem of applying human values to the natural environment (e.g., Wagner and Seal, 1992; Wagner *et al.*, 1995; McNaughton, 1996) rather than a limitation of integrated management. Similarly, there are formidable problems in monitoring complex systems, especially those with inherent timelags (see Heywood, 1995). Consultation with the public and lobby groups could make the definition of conservation resources and associated levels of protection a lengthy process (Hughey and Parkes, 1995), but without it it is difficult to sustain control.

Identifying damaging pests from *in situ* monitoring of conservation resources may also prove difficult. We suggest that basic research into impacts of the pests will help remedy this situation. Improved field techniques for monitoring both conservation resources and pest densities (e.g., Forsyth and Hickling, *in press*) are also required.

## **CONCLUSIONS**

The measure of success for managing the introduced herbivores of the central Southern Alps must be the status of defined conservation resources. Once defined, these resources need to be monitored such that spatial and temporal variation in the pest(s) modifying the resource can be detected. Sufficient organisational flexibility is required so that managers can quickly control the particular pest(s) responsible for modifying the resource at the appropriate spatial scales. 'Control' should be defined as enacting management such that the defined level of protection of conservation resources is achieved.

We believe that an integrated pest management plan offers three advantages over multiple single-species plans. First, conservation resources will be better protected by enabling more than one pest species to be controlled where necessary; single-species plans make this difficult. Second, there will be reduced opportunity costs by avoiding

unnecessarily controlling pests that are not the only ones modifying conservation resources. Third, the political processes that generate funding of nominated pests such that higher-priority pest control cannot be funded will be circumvented.

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## Chapter 7

### General Conclusions

This thesis investigated aspects of the ecology and management of Himalayan thar and sympatric chamois in the eastern Southern Alps of New Zealand. The 'questions' that formed the foci of Chapters 3-6 were posed by managers, rather than academics, but I have sought to provide answers that span the interests of both groups.

The results of this thesis highlight the spatial and temporal complexity of managing thar and chamois in the Southern Alps. Variable harvesting, combined with interspecific and intersexual differences in mobility and resource selection, presents conservation managers with numerous difficulties. These difficulties are amplified by the lack of information on the impacts of thar and chamois, and other sympatric pests, on conservation resources (Chapter 6).

Sustained management of sympatric thar and chamois requires information on competitive interactions. The cessation of aerial hunting of thar in 1983 provided an opportunity to test the hypothesis that increasing densities of Himalayan thar are associated with decreasing densities of chamois (Chapter 3). This natural experiment provided evidence that chamois *are* excluded from previously used sites by increasing densities of thar. Few studies have provided such evidence of interspecific competition between ungulates. 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. On the basis of the results presented in Chapter 3 I predict that chamois would no longer be seen at sites where thar increased to  $> ca. 3 \text{ km}^2$ , but would be seen at sites where thar densities were  $\leq 3 \text{ km}^2$ . Unfortunately, the exclusion of chamois from nearby sites where thar have increased may confound this prediction.

Two mechanisms, both being consequences of interspecific differences in sociality, could explain how chamois are excluded by increasing densities of thar. Thar and chamois populations in New Zealand are both food-limited, but thar are more gregarious than chamois, living in larger groups and attaining higher peak densities. Thar may reduce the distribution and abundance of plant species eaten by chamois

such that chamois are excluded by scramble competition for food (exploitative competition). In Carneys Creek, chamois were observed to move away from groups of thar, indicating that chamois behaviourally avoid thar (interference competition). Although the two mechanisms are not mutually exclusive, because increasing densities of thar in the 1978-1996 period are not considered to have modified vegetation in the eastern Southern Alps, I contend that the behavioural avoidance hypothesis best explains the decline of chamois during that period. Nevertheless, I acknowledge that dietary competition may become increasingly important after sustained grazing by high densities of thar.

Chamois were apparently able to co-exist with a low density population of thar in Carneys Creek through habitat partitioning. In three of four seasons thar exhibited less marked habitat preferences than did chamois, suggesting that thar have a broader niche than chamois. Differential habitat selection by male and female thar outside rut, and a daily altitudinal movement, probably contributed to this broad habitat selection. However, overlap in *preference* for grassland and shrubland by thar and chamois in Carneys Creek indicates potential for both interference and exploitative competition when thar density increases. I propose that as a thar population grows, increasing densities of thar select habitats preferred by chamois, thereby increasing interspecific behavioural interactions. These behavioural interactions result in chamois abandoning their home ranges.

These results suggest that eradicating or reducing thar to very low densities ( $<1 \text{ km}^{-2}$ ) will result in an increase of chamois at some sites. Interspecific differences in sociality will always mean that, in the absence of hunting, thar will attain higher densities than chamois. Although such competitive effects should be considered in strategic decision-making (e.g., whether or not to eradicate thar), maximum allowable densities of thar and chamois must be decided upon by their impacts on defined conservation resources (Chapter 6).

Some long-term landscape-scale consequences of the interaction between harvesting and sexual segregation for a population of thar were described in Chapter 5. Seasonal migration of sub-adult male thar from a high female density area to a low female density area when sexually segregated confounded inferences about the impact of recreational hunters in Carneys Creek. Extreme differences in the summer population

structure were apparently caused by disparate hunting strategies; 'unlimited' harvesting in the northern Two Thumb Range and trophy adult male harvesting in the southern Two Thumb Range. This example highlights the need for wildlife managers to understand the ecological consequences of evolutionary processes (Gavin 1991), as well as population processes in adjacent management units.

Chapter 6 presented a case for the integrated management of sympatric alpine herbivore pests. Spatial and temporal variation in the impacts of the five sympatric pest species in the central Southern Alps is likely to be high. Hence, the financial savings of the integrated management approach are likely to be considerable, principally through reduced opportunity cost (i.e., not controlling pests that do not modify conservation values). Integrated management would give managers the flexibility to protect conservation resources that are modified by more than one pest, something that single-species plans make difficult. The primary requirements of an integrated management approach are to quantify the conservation values to be protected and to enact monitoring programmes to evaluate what pest(s), if any, are modifying the resource(s). There is a need for, and considerable scope for innovation in the design of, field experiments to: (i) describe the impacts of sympatric pests on conservation resources; (ii) investigate the competitive and mutualistic *interactions* between sympatric pests; and (iii) enable managers to monitor the impacts and abundance of sympatric pests.

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