THE BROWSING IMPACT AND ABUNDANCE OF EUROPEAN BROWN HARES (*Lepus europaeus*) IN THE CENTRAL NORTH ISLAND, NEW ZEALAND

A thesis presented in partial fulfilment of the requirements for the degree of
Masters of Science in Ecology at Massey University,
Palmerston North, New Zealand

Michael Edmund Perry
October 2003

Abstract

The browsing impact and abundance of hares were investigated at several sites in the Central North Island, New Zealand. The traditional view has been that hares have a relatively minor effect on the vegetation when compared to larger ungulates due to their low, stable densities. However in some areas large grazing mammals have been controlled yet the vegetation continues to degrade, consequently attention is now being shifted towards the problems created by ongoing herbivory by smaller mammals. While the impact of hares on high altitude vegetation has generally been considered to be an issue of low conservation priority, they are now considered to be the main grazers in many alpine systems and there is a large shortfall in knowledge.

The suitability of the cleared plot pellet count method for assessing hare abundance, habitat use, and biomass consumption was investigated and was found to produce precise, easily obtainable results. It was found that hare numbers fluctuated over the course of a year, with a decrease in winter, followed by an increase in spring. Hare abundance was thought to primarily relate to habitat quality, with competition and anthropogenic influences also playing a role.

Hare impact was assessed using a variety of techniques including the utilization of existing exclosures, the construction of new exclosures, and selected monitoring of preferred browse species. The long-term exclosure plots indicated that hares were having no effect on any aspect of vegetation condition, either native or exotic in the Moawhango region. Conversely hares were having a significant effect upon the vegetation in the Manson region of the Kaweka ranges. Where hare browsing appeared to be benefiting native species through the suppression of exotics grass species. However, targeted monitoring of preferred browse species showed that hares browse heavily upon a range of native plant species.

While these results appear contradictory, when the results are considered collectively, and with knowledge of hare density a proposed feeding strategy was formulated. I suggest that the degree to which hares impact native vegetation is dependent upon the level of exotic species present. Where exotic species are present (particularly grasses), they are the preferred browse species. Where exotic species are not readily available, or

competition is high, hares then subsist at lower densities by browsing native vegetation. However if a native species occurs that fulfils hare nutritional requirements, then it will be preferentially targeted by hares resulting in significant detrimental effects.

Acknowledgements

During the course of this thesis I received help and encouragement from many people that are to numerous to name, so I would like to thank everyone who helped in any way, even if it was just a cup of tea at the hut, I appreciated it!

First up I would like to say a big thank you to my chief supervisor, Alastair Robertson, for his advice and guidance, expert photography skills, assistance in the field, and for aiding me at all stages throughout the course of this thesis in his sometimes hectic schedule. I also thank Robin Fordham for acting as my co-supervisor, giving me his advice and encouragement, and for his detailed editing of my drafts.

I would like to thank the Miss E. L. Hellaby Indigenous Grassland Research Trust for funding a large portion of this project, also the trustees who freely provided their advice on the experimental design of the project.

The Department of Conservation was instrumental in several aspects of this thesis. I would firstly like to thank the East Coast Conservancy for funding the construction of the Manson exclosures, helicopter flights and helping wherever they could. I would especially like to thank Eddie Te Kahika and Colin Taylor for their invaluable help on numerous occasions, and Chris Ward for his help with experimental design and recognizing the need for this project. From the Tongariro/Taupo Conservancy I thank Nick Singers, Steve Deverell, and Sean Husheer, for help along the way in both the plentiful amounts of advice and encouragement, and for fieldwork assistance. Also for permission to work in the National Park.

For access into the Moawhango region I thank the New Zealand Army for allowing access into Army training area, in particular John Mangos for his assistance. Bill Fleury and Geoff Rogers for their help in trying to find the historic data from the Moawhango plots. Also Tama Wipaki and for access into Motuamati, and Tony Batley for allowing me to use his families hut, this was greatly appreciated especially when it started to snow!

I would also like to thank all those individuals, and the Ecology discussion group who helped by reading over my sometimes confusing drafts and for gave me plenty of

helpful advice. Also I thank Ian Henderson for his all-knowing statistical expertise and for patiently answering my endless questions, and Jill Rapson for helping me identify many of the plant species.

And finally the field assistants upon whom I inflicted numerous blisters, cold, heat, and often boredom; Kyle Blenkhorn, Rob Fraser, Lesley Pearce, Katie Perry, Mortz Piripi, and Clelland Wallace, your help was invaluable. I would especially like to thank Mortz and Lesley who came back into the field several times, even when they knew what to expect.

Last but not least I would like to thank the support I received from my family, Kate, Rachel and Danny, my parents, Bill and Anne, for your encouragement, support and monetary contributions, I thank you. Finally I would especially like to thank Lesley, for her understanding of my frequent absences, support during all stages of the thesis, and for helping wherever she could.

Table of Contents

Chapter 1

General Introduction

Two Kaimanawa Wild Horses on a Unimog track looking from the Upper Argo Rd exclosure towards Mt Ruapehu.

1.1 BACKGROUND

There is no such thing as a typical pattern of plant-herbivore dynamics (Crawley 1983), but the general mechanisms by which herbivores influence plant communities do not differ fundamentally for terrestrial, aquatic, and marine ecosystems (Huntly 1991). Herbivores can significantly affect the structure, composition, and dynamics of plant communities by altering the numbers, varieties, and relative abundances of plant species (Huntly 1991). This can occur through several conceptually distinct mechanisms that are not mutually exclusive (Huntly 1991) and there is no clear consensus about the importance of herbivores in a community as their impacts vary from biome to biome, and from community to community (Crawley 1997). Therefore given the vast variety and complexity of plants, herbivores, and their interactions, it is easy to conclude that a general understanding of how herbivores affect communities and ecosystems is not possible (Huntly 1991). Nevertheless the literature on plant-herbivore interactions is extensive and a variety of well developed theories exist to understand herbivory in a general way (Huntly 1991).

Herbivory can alter community composition and productivity in all ecosystems (Huntly 1991), with the impact dependent upon the characteristics of herbivore/plant community in question. Selective grazing can have a marked impact on plant diversity (Huntly 1991) and can either depress and increase diversity depending upon the community in which it occurs (e.g. Wilson 1994). Herbivores that disproportionately damage the more common species in a community tend to increase plant diversity (Huntly 1991). While browsing can affect the composition by favouring an increase in unpalatable species (Bryant *et al.* 1991), selective feeding can modify competitive relationships between plant species and allow a normally uncompetitive species to replace its more palatable competitors (Crawley 1983).

Even when rates of defoliation are low, and signs of browsing are minimal, herbivores are capable of changing the identity of the plant species that attains dominance (Crawley 1997). The impact of herbivory on an individual plant species depends upon its timing, location, intensity, and frequency (Crawley 1997). In addition to affecting composition and diversity, grazing may also influence reproductive output (Crawley 1997), survival (Mark 1965b), growth (Lee *et al.* 2000), and physical boundary of a species i.e. altitudinal limits (Wilson 1994). The degree to which a herbivore affects a community is dependent not only on the characteristics of the ecosystem, but the individual species relationships. Specialised herbivores are usually restricted by the distribution and abundance of their selected plant species, while generalist herbivores have more effect on the distribution of their preferred food plants than vice versa (Crawley 1997). Additionally large mobile herbivores, like ungulates, tend to have a greater impact on plant communities than small sessile, specialist herbivores (Crawley 1997). The degree to which a herbivore will affect a community varies and ecosystem level herbivore effects are more likely to be observed in low-productivity and open communities, than in productive, closed systems. However plant populations are usually buffered against over-exploitation by herbivores through various refugia such as long lived seed banks, ungrazable reserves, and spatial refuges (Crawley 1983). This is especially so with native herbivore and native host plants interaction where relationships have evolved over time and plants dynamics are not driven by herbivore feeding (Crawley 1983), but this may not be the case with "foreigner" interactions (ie. introduced pests).

There is a widespread perception that New Zealand biota is especially vulnerable to introduced mammals as a consequence of its separation from Gondwanaland 80 million years ago (Forsyth *et al.* 2002). However there is not universally the case, with many tree and shrub species avoided by introduced herbivores (Forsyth *et al.* 2002). The New Zealand flora evolved alongside a range of indigenous herbivores including a range of insect and moa species (Greenwood and Atkinson 1977), possibly resulting in a range of defensive secondary chemicals evolving that also confer resistance to introduced herbivores (Forsyth *et al.* 2002). Additionally plants need not have evolved in the presence of herbivores to have properties that confer resistance to herbivory, as neutral resistance can develop in response to other selection pressure that incidentally make a plant resistant to herbivores (Forsyth *et al.* 2002). However in saying this there appears to be several species that are highly susceptible to browsing by introduced mammals and in many regions the New Zealand flora has been strongly modified (e.g. Forsyth *et al.* 2002, Rose and Platt 1987, Sweetapple *et al.* 2002). Forest dwelling browsing mammals, notably feral goats and deer, have wide-ranging effects at both the community and ecosystem levels of resolution, with particularly adverse effects for indigenous plant communities (Wardle *et al.* 2001). While it has been suggested that mammals in forest ecosystems are simply filling the ecological niche left with the extinction of the moa (Greenwood and Atkinson 1977), the browsing of mammals is a completely new influence on New Zealand's alpine vegetation (Greenwood and Atkinson 1977). With almost no New Zealand grassland having escaped the indirect effect of human settlement of grazing by feral animals (Wardle 2002). Previous to European settlement, the alpine grasslands of New Zealand were browsed only by invertebrates and a selection of indigenous birds (Rose and Platt 1987). Consequently many alpine grasslands have been strongly modified with the introduction of mammals such as chamois (Yockney and Hickling 2000), deer (Rose and Platt 1987), and thar (Parkes and Thomson 1995). These herbivores can strongly modify grassland composition and structure (Rose and Platt 1987), but in many alpine regions their numbers have been controlled yet the vegetation continues to degrade (Wong & Hickling, 1999). Consequently attention is now being shifted towards the problems created by ongoing herbivory by smaller mammals. While the impact of hares on high altitude vegetation has generally been considered to be an issue of low conservation priority, they are now considered to be the main grazers in many alpine systems (Wong & Hickling, 1999).

1.1.2 HARES IN NEW ZEALAND

Hares were first introduced into New Zealand in 1851 and by the late 1800s they were found throughout most of New Zealand alpine grasslands (Flux 1990). The traditional view has been that hares have a relatively minor effect on the vegetation when compared to larger ungulates due to their low, stable densities (Wong and Hickling 1999). In 1995, five Department of Conservation conservancies documented their concerns that hares may be causing unacceptable damage to high altitude vegetation, particularly alpine grasslands, and conservation staff suggested there was a need for more research into the issues (Wong and Hickling 1999). The Department of Conservation commissioned a review in response to the concerns raised by these Conservancies, and this resulted in a report on "Assessment and management of hare impact on high altitude vegetation" (Wong and Hickling 1999). The aim was to review the known effects of hares on high altitude vegetation, and identify the shortfalls in this knowledge. The review made the following recommendations for hare research in areas of high conservation value (p35).

1. Development and validation of a suitable cleared plot technique for assessing hare population density and determining habitat use.
2. Diet composition and selection studies, using stomach contents or faecal pellet analyses, that can be related to vegetation availability data obtained by field survey.
3. Investigation of long-term hare impact using exclosure-plot and population reduction techniques.
4. Integration of data about hares and other herbivores into an integrated pest management framework for a selected catchment, as a case study of the 'priority place-critical pest' approach.

1.1.3 IMPACTS ON VEGETATION

Hares are generally thought to have minimal impact on vegetation (Wong and Hickling 1999) as they live at relatively low densities, hedge palatable plants without killing them, graze a few leaves from many plants over a wide area, and do not dig burrows (Flux 1990). However in some parts of their range, hare populations are likely to be consuming more forage per hectare than possums, chamois, thar, or deer, while elsewhere, the impact of other grazers is probably far more significant (Wong and Hickling 1999). To date there have only been three studies quantifying hare impact on high altitude vegetation.

Rose and Platt (1992) examined the effects of hare browse on snow tussock regeneration by comparing the vegetation in a single 10-year old exclosure that excluded hares, with vegetation browsed by hares. On the unfenced control plot, browsing pressure was high with 97% of all *Chionocloa macra* individuals showing browsing damage. Although the study block had been retired from sheep grazing since 1955, *C. macra* tussocks were almost as short as the adjacent block still grazed by sheep, with 17% of tussocks senescent. In contrast, C. *macra* inside the exclosure showed pronounced vegetative recovery after ten years protection: only 2% were senescent and tussocks > 5cm diameter were twice as tall as those on the control plot. However protection from hares had not yet resulted in seedling establishment inside the exclosure. On both the exclosure and control plot seedlings were absent and juvenile tussocks made up <10% of each population. They concluded that hare browse alone was capable of inhibiting tussock recovery, reducing seedling densities and resulted in an overall lowering of plant basal area and vigour. Rogers (1994) examined the impact of hares at three sites in the central North Island in conjunction with examining the impact of the Kaimanawa wild horses. In a wetland exclosure, hare browse appeared to slow the recovery of native and exotic sedges, native herbs and exotic grasses. In a hard tussock (*Festuca novae-zealandiae*) and red tussock (*Chionochloa rubra*) grassland exclosure, hares and rabbits were having a substantial dampening effect on the rate of recovery of red and hard tussocks, along with exotic grasses. In another two hard tussock and red tussock grasslands, exclusion of hares from the exclosures did not affect the biomass, stature, or recruitment of either hard tussock or red tussock as hares were thought to feed mainly on exotic grasses. In an unpublished masters thesis, Blay (1989) reported 18.5 % and 19.9% more plant material inside exclosures when compared to hare affected plots.

1.2 GENERAL ECOLOGY OF HARES IN NEW ZEALAND

The general ecology of hares in New Zealand is reasonably well known with many factors such as reproduction (Flux 1967b), habitat size (Parkes 1984) and diet (Flux 1967a; Horne 1979; Blay 1989) having been worked on in the past. Hares in New Zealand are the British subspecies *Lepus europaeus occidentalis* de Winton, 1898. They are darker and smaller than European subspecies living at the same latitude. Males are known as "jacks" or "bucks"; females are "jills" or "does"; young are "leverets". (Flux 1990)

Habitat

Hares in New Zealand are now spread throughout both main islands from sea level to 2000m, wherever suitable habitat occurs. The only regions where they are not found are parts of South Westland, most of Fiordland, and Auckland (Flux 1990). In New Zealand, hares occupy practically all kinds of grassland or open country from coastal sand dunes, cropland, pasture, to forest clearings, marshes and moorlands. In alpine tussock grassland, they occur from the treeline, right to the upper limit of vegetation (even in winter) (Flux 1990). However they are known to make little use of forest environment, Parkes (1984) reported that radio tagged hares avoided the beech forest habitat and spent only 2% of their time there. The home range of hares varies in size from 30ha to 70ha; however most time is spent in less than 10% of the range around one or more focal areas (Parkes 1984).

Population dynamics

Populations in New Zealand are thought to be relatively stable (Douglas 1970), and do not appear to undergo the population fluctuations that are reported in some *Lepus europaeus* populations overseas (Keith 1986), and in the genus *Lepus* in general (Keith 1986; Krebs 1986). Nor did they undergo the eruptions seen when rabbit were introduced to New Zealand (Flux 1990). However, no long term population studies have been reported for New Zealand. Over the whole country the density of hares is approximately 0.1 hares/ha (Flux 1990) and is comparable with European populations. Populations in New Zealand do not appear to exceed three hares/hectare and appear to be self-regulated through some unknown behavioural mechanism (Flux 1990). Previous estimates of hare density in favourable areas range from one hare/ha (Douglas 1970) to two-three hares/hectare (Parkes 1984).

The sex ratio is slightly skewed at birth with approximately 55% being males. However this ratio changes with age as 45% of adult hares are males and only 33% of older hares are male, suggesting that females live longer than males (Flux 1967b).

Breeding

Breeding begins soon after the shortest day and in New Zealand over 90% of females are pregnant from August to February. The average litter size for New Zealand hares is 2.14 with the number of successful litters averaging 4.59 per year. This results in each female producing an average of 9.8 leverets per year (Flux 1967b). The proportion of juveniles in the population changes over time, with the lowest proportion of juveniles found in August (7% of the population being juvenile). This rises to a peak of 56% of the population in March with the average proportion being 29% (Flux 1967b).

Predators

Adult hares have few predators, but there are reports of stoats (Douglas 1970), cats and groups of harriers (Carroll 1968) killing adult hares. Predation of leverets is more prevalent with all of the above, plus weasels (Douglas 1970), responsible. Hares (presumably young) can compose significant portions of these predators diet. On average, 18% of a stoats diet is composed of lagomorphs, with a peak in summer, coinciding with the availability of young rabbits and leverets (King and Moody 1982). Harrier diet has been reported to be composed of as much as 78% from hares (Douglas 1970). However this study was done in an area undergoing a hare control operation, providing large amounts of carrion. In the Manawatu, lagomorphs were the most consistently dominant food group through out the year, comprising 21.3% of the total harrier diet (Wong 2002).

Diet

There have been two studies done on the diet of hares in alpine grasslands in New Zealand. In Cupola Basin, Nelson Lakes National Park, Flux (1967a) showed that hares undergo a dramatic seasonal change in diet composition from *Poa colensoi* in summer to *Chionochloa* and *Celmisia* species in winter. Over the course of one year the diet averaged, 31% *Poa* colensoi, 26% *Chionochloa* spp., and 11% *Celmisia* spp. Horne (1979) also reported seasonal fluctuations in diet on Mt Ruapehu. Although not as pronounced as Flux (1967b), an increase in *Chionochloa rubra* and moss (*Rhacomitrium languginosum*) consumption was observed during winter and spring. The average annual diet for that study was 44% *C. rubra,* 24% *Celmisia spectabilis,* 15% *Brachyglottis bidwillii,* 7% moss, 4% *P. colensoi,* 2% seeds, and 2% grass. Horne (1979) also estimated biomass consumption of hares in feeding trials and average consumption estimate varied for each trial from 94.3, 197.2, to 219.0 g (wet weight)/hare/day.

Blay (1989) investigated the diet of hares in a fescue (*Festuca novae-zelandiae*) grassland in Canturbury. While diet varied for males, females, and juveniles, it largely reflected the availability of food items in the habitat. Up to 94% of the diet was made up of three food groups, *Hieracium pilosella*, grasses, and tussocks; with *H. pilosella* was the major food group. This diet was thought to reflect the plant availability as the major dietary items were the dominant plants in the study area. Therefore, all the above studies suggested that differences in hare diet resulted from the differential availability of plants between habitats and season.

1.3 STUDY SITES

1.3.1 KAWEKAS

The Kaweka Forest Park covers approximately 67,000 hectares in the central North Island east of Napier. The park has undergone a series of modifications in the past. In pre-European times, Maori burnt much of the forest in the eastern and southern portions of the range (Jenkins 1982). Frequent fire also occurred when European settlers arrived and stocked the area with sheep in the later 19th century. Most were lit to clear forest or scrub and to burn off native grasses unpalatable to stock. Large areas of the park were leased to two large sheep stations that ran stock over the entire range. However farming on much of the range was eventually abandoned due to the difficult climate and the spread of rabbits. This was followed by the spread of other introduced wild animals such as deer, pigs, goats, possums and hares (Jenkins 1982; Parkmap 1990). Located to the south-west of the park is the Manson region. The exact history of the Manson area is uncertain. However it underwent similar burnings as the rest of the park and was part of Ngamatea station until at least 1950 (Lethbridge 1971), with wild sheep being reported in the Manson stream in 1981/82 (Jenkins 1982). In a survey of wild animal distribution over the entire park, Jenkins (1982) reported that the highest densities of hares were found in Manson/Kiwi Creek block of the study (hare densities were found to be increasing from a previous survey in 1960). This was attributed to the high proportion of grasslands present in the area. The region contains large areas of what appear to be artificially induced grasslands. Evidence for this is found in the burnt tree stumps present in the region, and the fact that the majority of the area is below the altitudinal limit for Mountain beech.

At total of five study sites were used in the Manson region. Hare densities were assessed at all sites, and new exclosures were established at three of these sites to assess the sampling protocol developed and determine and short term vegetation changes with the removal of browsing pressure.

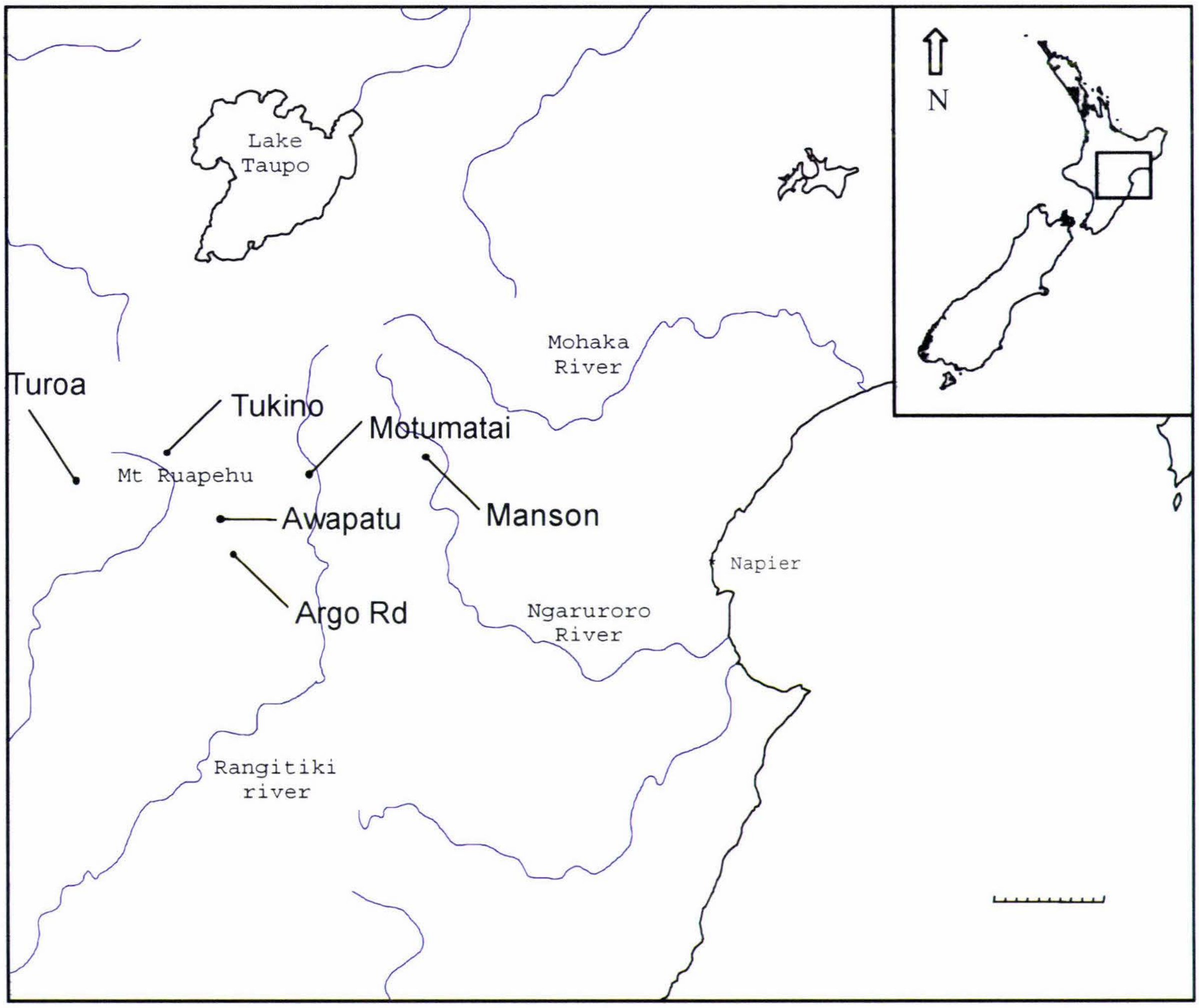

Figure 1.1: Location of the study sites situated throughout the Central North Island, New Zealand.

1.3.2 MOAWHANGO

The Moawhango ecological district is a distinctive, upland plateau and basin floor landscape that comprises 139,500ha of the central North Island (Department of Conservation 1997). The vegetation of the area has undergone an interesting and sometimes complex history. Most of the region was once forested and deforestation was initiated by pre-human fires approximately 3000 yrs ago (Rogers and McGlone 1989). However most of the clearance is attributed to more recent burning by early Maori that resulted in 660 000ha of seral tussock grasslands throughout the Volcanic Plateau (Rogers 1994). While most of the grassland has completely disappeared (only 10% remains), the largest remnant of the Volcanic Plateau grassland is found in the Moawhango ecological district (Rogers 1994). However, other parts of the region have been without trees for thousands of years. These non-forest sites result from cold air inversions, high water tables and frequent geomorphic disturbance (Rogers 1994). This history has resulted in the district having a unique and unusually large range of approximately 750 native plants along with the largest remnant of the red tussockland which once stretched from the Ruahine ranges northwards to Taupo and Rotorua (Department of Conservation 1997). The survival of the region is, in part, because the Moawhango area has never been intensively farmed. However, wild horses have been present in the area since 1876 (Rogers 1991) and until recently were doing considerable damage. Rogers (1991, 1994) found that horses were having a significant detrimental effect on a range of tussock grasslands and oligotrophic bogs through trampling and grazing. However horse impact has been reduced as horses have now been removed from large areas through mustering (Department of Conservation 1995). In these studies hares were reported as having an additional effect on some of the plant communities present. Large areas of land in the Army training area are currently subject to ongoing hare/rabbit control. In 1995 a poisoning operation was initiated over 10,000ha using 1080 (J. Mangos *pers comm.*). Initially the control was for rabbits as populations were as high as 200/ha (J. Mangos *pers comm.*). Originally hare control was a secondary component to the rabbit control; contractors have subsequently been instructed to control hares (J. Mangos *pers. comm.*). Currently a secondary control program is in place for hares and rabbits over 30,000ha (secondary control has been through helicopter shooting for hares and ground poisoning for rabbits). Since 1998 lagomorph populations have been static. In the Argo valley, hare populations are estimated at 0.03/ha and rabbits are now 1/km^2 (J. Mangos *pers comm.*).

A series of hare/horse exclosure plots have been established on land administered by the Army, and private land. The exclosures are divided so that they exclude all herbivores (except possums) from one side, and large herbivores from the other (i.e. horses, deer). A selection of these plots were used in this study in an attempt to assess the long-term impacts of hares on vegetation composition. The study sites in this region are divided into three main regions, Motumatai, Awapatu, and Argo Rd (Table 1.1). The Argo Rd region is further divided through the Upper and Lower Argo Rd exclosure plots which are located relatively close to one another.

1.3.3 TONGARIRO NATIONAL PARK

Tongariro National Park had its beginning in 1887 when the Ngati Tuwharetoa people gifted the nucleus area to the Crown "as a gift for a National Park". The periodic addition of land through Government purchases has increased the size of the park so that it now covers an area of 79,598 hectares (Parkmap 2000). The landscape is dominated by the three volcanic peaks of Tongariro (1968m), Ngauruhoe (2290m), and Ruapehu (2796m) (Tongariro National Park Board 1981). Modification of the indigenous vegetation within the park by man and grazing and browsing mammals is relatively slight when compared with other mountain areas within New Zealand (Horne 1979). There are an estimated 530 species of plants in the Park, excluding mosses, liverworts, lichens and fungi. Mountain Beech (*Nothofagus solandri* var. *cliffortioides*) is the dominant forest type in the park, however the largest part of the park is occupied by various types of alpine vegetation (Esler 1965).

Calluna vulgaris dominates virtually all of the area previously covered in *Chionochloa rubra* tussock grassland below 1200 m over 52 km^2 on the northern ringplain. Only on basin floors, and the even frostier or poorly drained hollows, does *C. rubra* persist as a conspicuous species, but at generally less than 10% crown cover (Rogers and Leathwick 1996). At higher altitudes, the alpine gravelfields and fellfields occupy most of the upper slopes of all three mountains above 1372m. However, on the eastern slopes of Ruapehu, in the region of the Rangipo Desert, a large region of gravelfields extends down to 1067m. The region is not a true desert as annual rainfall is not lower than 1016mm. However, the loose sandy and gravelly substrate, combine with strong winds to dry the soil and make plant survival difficult (Esler 1965).

Hares are the major browser above the treeline within the Tongariro National Park as deer are uncommon and possums, though abundant, are confined to the forest (Horne 1979). A previous Masters thesis also used Tongariro National Park to investigate the diet and abundances of hares. This thesis by Horne (1979) investigated the seasonal diet fluctuation and attempted to assess abundances of hares in the region.

I will be using the park to assess the impact of hares browsing on low productivity/high altitude sites at two main sites, Turoa and Tukino (Table 1.1). A subsidiary site is also located in the Whakapapaiti valley where browsing observations were conducted.

Table 1.1: Summary of the regional characteristics for each region in this study. Question marks denote uncertainty of effect.

Site	Grid reference NZMS T260	Altitude	Degrees from north	Average slope	Exclosures present	Hare control vectors	Other Herbivores
Manson 1	U20 908095	1280m	66°	25°	Yes	Recreational hunting	possums, deer
Manson 2	U20 921085	1350m	43°	20°	Yes	Recreational hunting	possums, deer
Manson 3	U20 913079	1240m	105°	15°	Yes	Recreational hunting	possums, deer
Manson 4	U20 905070	1230m	116°	12°	No	Recreational hunting	possums, deer
Manson 5	U20 916054	1180m	157°	23°	No	Recreational hunting	possums, deer
Awapatu	T20 528976	900m	NA	0°	Yes	Helicopter shooting?	rabbits, horses
Argo Road	T20 551 909	1070m	132°	2°	Yes	Helicopter shooting	rabbits, horses
Motumatai	T20 689062	1300m	74°	2°	Yes	None	rabbits?, horses, deer, possums
Tukino	T20 429103	1120m	NA	0°	No	None	rabbits?,
Turoa	S20 277074	1550m	161°	6°	No	None	None
Whakapapaiti	S20 284151	1400m	NA	NA	No	None	None

1.3 THESIS OBJECTIVES

The previous hare impact studies show that hares have the potential to have a significant detrimental impact on high altitude vegetation when they are present in sufficient numbers. However each study has been limited in scope and all were undertaken as minor components of a larger study. Consequently there are still many unanswered questions with regard to hare impacts on vegetation structure, species composition and abundances (Wong & Hickling 1999). Therefore to further understand the impact of hares and as part of the requirements to obtain my Masters degree at Massey University, I decided to assess the browsing impact of hares on subalpine vegetation for my thesis. With the broad objectives of this thesis being:

1. Assess the suitability of the cleared plot pellet counts for assessing hare abundance, habitat use, and biomass consumption

2. Investigate the long term effect of hare browse on species composition and vegetation structure through the use of existing exclosure plots

3. Design and development of an integrated monitoring program to investigate the effects of hare browse on general species composition and vegetation structure.

4. Investigate the impacts of hare browse on selected, highly preferred browse species.

Through the integration of several different approaches, along with investigations of hare density, a more complete picture of hare browsing impact will be obtained. This work will also address recommendations one and three in the Wong and Hickling (1999) Science for Conservation Report "Assessment and management of hare impact on high altitude vegetation".

Chapter 2

The use of cleared plot pellet counts to assess hare populations in alpine vegetation

Early morning view from the Manson tops looking towards the Kaimanawas

2.1 INTRODUCTION

A wide variety of techniques have been developed for assessing the number of individuals in free-ranging mammalian populations (Horne 1979). These techniques take several approaches and generally involve either the direct observation of animals, trapping, or the observation of an animals sign (Wong and Hickling 1999). Several of these techniques have been used in attempts to quantify hare abundance in New Zealand's alpine grasslands (Flux 1967a; Horne 1979). However they have met with limited success, and no accurate density estimates are available for hares in New Zealand alpine grasslands. Therefore, there is a need for a precise and efficient method that will allow for accurate estimation of hare population densities. Before any attempt to census a population is made all available methods must be evaluated for their suitability (outlined below). After such a review, Wong and Hickling (1999) recommended that the cleared plot pellet technique be developed for assessing population density and determining habitat use of hares in New Zealand conditions. The cleared plot pellet method was also recommended by (Parkes 2001) for assessing hare abundances in all New Zealand habitats. The aim of this chapter is to test the precision and robustness of the cleared plot pellet technique in a series of alpine grasslands at various locations in the Central North Island, New Zealand.

2.1.1 POPULATION CENSUS TECHNIQUES

Sampling techniques used to census populations can provide either relative or absolute estimates of density, depending on the monitoring regime initiated. Complex techniques can provide precise information on density, however they are often costly and labour intensive. While less powerful techniques can provide perfectly adequate data for relative comparisons, and can be validated against detailed studies to provide estimates of absolute numbers. Therefore the sampling program initiated will depend upon the resources available and the accuracy required from the data.

Observation methods can be used to obtain both absolute and relative density estimates, but it is seldom possible to obtain total counts of hares over an entire study area using observational information (Wong and Hickling 1999). Observation data can be gathered directly or indirectly. For example, recording the number of animals encountered during routine fieldwork (encounter rates), can provide an index of population size.

Encounter rates have been shown to provide a reasonable index of population variation for several species in the Yukon Territory, such as Harlan's hawks, spruce grouse, ravens, and coyotes (Hochachka *et al.* 2000). While direct observations can provide absolute estimates of density, results are often variable depending upon weather, time, behaviour, age of animal, and season (Flux 1967a). Direct observations from a hide were used by Flux (1967a) to estimate hare numbers in Cupola basin, Nelson Lakes National Park. Results were found to vary daily, and between each morning and evening. While the final estimate obtained was consistent with other methods, the effort required was high and does not ensure a precise estimate.

Counting the number of hares seen along a transect can also provide an index of density. Ideally hares are counted by spotlight, along a set route over successive nights, in similar weather. A spotlight census is useful when relative population estimates are required (Horne 1979). For accurate results the area should be flat, free from high vegetation (Horne 1979), and preferably accessible by vehicle (Parkes 2001). The spotlight method can also be adapted slightly to obtain estimates of absolute hare density. This can be achieved by counting, along with total numbers, the angle and distance to the each hare seen. Computer programs can then be used to give a density estimate. While spotlight counts were described as having the most potential for assessing hare abundances in Britain (Langbein *et al.* 1999), hare densities in New Zealand are generally too low for this method to provide anything other than large-scale changes over time (Parkes 2001).

Trapping and shooting indices can provide detailed information on hare numbers and involve both the live release, and death, of the study animal. Trapping and hunting indices involve capture without release (i.e. death). Complete removal methods can provide absolute estimates of abundance and density since the total number of animals killed can be directly counted. Kill rate data, such as time to shoot one hare can provide indices of relative abundance (Flux 1969). Mark-recapture methods involve the live trapping, and subsequent release of the study animal. They have been used extensively overseas and can produce reliable estimates of hare numbers (Krebs *et al.* 1987; Krebs *et al.* 2001). These methods can provide very sound and reliable estimates, but the method is very labour intensive and generally not deemed as suitable for New Zealand conditions due to lower hare densities, indistinct runs, and difficulty in trapping (Wong and Hickling 1999).

Less obvious, but simple methods have also been developed as indices of abundance. If mortality data for a population is known, the number of dead hares found in a season can give an indication of the live population. Flux (1967a) used the number of dead hares found in Nelson Lakes National Park to obtain a population estimate. The estimate obtained was consistent with estimates by other methods (faecal pellets counts, snow tracking and hide observations). Hare tracks in the snow were also used by Flux (1967a) to estimate hare abundance. The estimate obtained was consistent with results obtained using other methods and was thought to provide the best estimate of abundance of all methods trialed in the study. However, this method has the obvious disadvantage of requiring snow, a feature not always present in all New Zealand grasslands.

2.1.2 FAECAL PELLET COUNTS

Pellet counts can be used to calculate both absolute and relative population estimates (Parkes 1981; Krebs *et al.* 1987; Krebs *et al.* 2001), habitat and range use (Rao *et al.* 2003), biomass consumption (Hansen 1972), and even sex structure and population biomass (Putman 1984). In New Zealand, pellet counts are commonly used for monitoring long-term trends in densities of wild animal populations. Originally used as a tool to measure changes in relative numbers of browsing and grazing animals (Riney 1957), more complex theoretical models have been developed for assessing absolute density (Batcheler 1973) and calculation of probable errors (Batcheler 1975b).

Examples of the use of faecal pellet counts to assess wild mammals in New Zealand are extensive and too numerous to describe in detail. Faecal pellet counts have been used to assess density fluctuations and habitat preferences of possums along the north bank of the Taramakau catchment (Pekelharing 1979). For deer they have been used to assess relative densities (Riney 1957), compare habitat utilization (Jenkins 1982), and to estimate absolute densities (Batcheler 1975a). Pellet counts were used to show the inverse relationship between hunter pressure and deer density in the Kaimanawa recreational hunting area (Fraser and Sweetapple 1992). They have also been used to show relationships between white-tailed deer densities on Stewart Island, and the resulting vegetation composition (Bellingham and Allan 2003). Several large scale studies have been undertaken to assess the distribution of a range of herbivores in a region. The flexibility of the method means that simultaneous density evaluations of deer, pigs, possums, goats/sheep and lagomorphs can occur (e.g. Riney 1957; Jenkins 1982; Pekelharing and Reynolds 1983; Davis and Orwin 1985)

While faecal pellet counts have been used extensively in New Zealand on other mammals, they have had little use on hare populations in the New Zealand environment (e.g. Flux 1967a; Horne 1979; Parkes 1981). However there is a large body of overseas literature proving the suitability of the method (Krebs *et al.* 1987; Krebs *et al.* 2001; McKelvey *et al.* 2002; Murray *et al.* 2002). Compared to other population census techniques, faecal pellet counts have the advantage that they are not labour intensive and are able to be completed by a single fieldworker (Horne 1979). Pellet counts can be based on standing crop or cleared plot methodology. Standing pellet crop values are a measure of the density of pellets present in the environments at any one time (i.e. pellets/m^2). Cleared pellet plots involve clearing all pellets within a relocatable area, then recounting the area after a period of time to obtain the number of pellets recruited over time (recruitment rates).

Standing pellet crop values can be combined with pellet decay and hare defecation rates to obtain density estimates. The method has been used in New Zealand with imprecise results (Wong & Hickling, 1999). Horne (1979) used the method when assessing hare abundances on Mt Ruapehu. Density estimates were obtained that varied from 0.15 to 36.57 hares per hectare. Flux (1967a) obtained estimates ranging from 2 to 109 hares per hectare in the Cupola Basin, Nelson Lakes National Park. One of the major confounding factors when using standing crop levels is the decay rate of the pellets. Decay rate estimates can vary from site to site depending on altitude, type of food, microsite, climate and breakdown agents such as invertebrates, fungi and bacteria (Flux, 1967). Decay rate estimates for New Zealand conditions vary from one month (Horne 1979) up to 4.5 years (Flux 1967). Horne (1979) obtained decay rates varying from one to 4.5 months, while Flux (1967a) obtained estimates of 1.5 to 4.5 years. Krebs *et. al.* (2001) reported that in North American boreal-forest environments, hare faecal pellets may last 20 years before disintegrating. Therefore reliable interpretation of standing crop data require an accurate estimate of decay rates, an estimate which is often highly variable.

Cleared pellet plots are free from errors introduced by variable decay rates. They have been used in many studies and found to produce precise density estimates. Krebs *et al* (1987, 2001) compared hare density estimates between the Jolly-Seber mark-recapture method and cleared pellet counts. Fifty rectangular quadrats (0.155 m^2) were cleared annually from 1977 to 1983, with optimal plot size determined by sampling five different size quadrats and selecting the one with the lowest variance. The estimates obtained from pellet counts were highly correlated with estimates obtained from the Jolly-Seber mark-recapture method ($r = 0.94$). However the error produced by the data meant pellet estimates were ± 30% of the mean obtained, resulting in a density estimate range from 4.0 hares/ha to 3.2 hares/ha. Krebs *et. al.* (1987) recommended increasing the sample size for improved accuracy, with number of plots required for accurate sampling being dependent on estimated hare densities. It was recommended that 500 quadrats be used at densities of 0.5 hares/ha, and 150 quadrats be used at densities of 3.0 hares/ha. Implementation of these sample regimes would reportedly reduce the error to ± 20% of the mean. Krebs *et al* (2001) used 80 quadrats of 0.155 m^2 and obtained a relationship of $r = 0.76$ between pellet counts and population density.

Both Krebs *et al.* (1987) and Krebs *et al.* (2001) used regression equations to predict absolute hare densities from the recruitment rate data obtained. Krebs *et al.* (1987) proposed a regression equation based on a linear relationship for converting pellet densities to hare densities. This equation was modified by Krebs *et al.* (2001) to a log-log regression equation that improved predictive power, particularly at low densities. However (McKelvey *et al.* 2002) caution against the use of these regression equations if plot dimensions are different, as varying plot size affects the density estimate obtained. Additionally the regression relationships cannot be used in New Zealand due to the significant confounding factors of different vegetation types (boreal forest vs. alpine grassland), and the different hare species involved.

Cleared pellets plots have only been reported once in the literature for hares in New Zealand habitats. Parkes (1981) used the cleared plot pellet technique to successfully show a reduction in pellet recruitment after a poisoning operation. Relocatable circular plots of $0.09m^2$ were measured at 60-day intervals. This plot size was chosen after a field trial to determine which size produced the lowest variance (J. Parkes *pers. comm.*). The method was able to show a substantial reduction in pellet recruitment rates after a poisoning operation, along with a subsequent hare population recovery. However no attempt to assess absolute population numbers was made. However, the general suitability of the pellet counts has been shown, and a similar technique was used to estimate rabbit populations in Hawkes Bay and the Wairarapa (Taylor and Williams 1956). Inside a 24-acre rabbit proof fence, a population of 265 rabbits was sampled using a pellet count technique incorporating standing crop and recruitment rate values, an estimate of 301 rabbits was obtained. Despite the apparent lack of use of the cleared plot method in New Zealand, it is the recommended method for estimating density. Wong and Hickling (1999) recommended that a cleared plot technique be developed for assessing hare population density and determining habitat use for New Zealand conditions. Parkes (2001) also recommended the cleared plot pellet for assessing hare abundances in all habitats.

In this chapter I aim to use the cleared plot pellet technique to obtain pellet recruitment rate of hares at six locations in the Central North Island, New Zealand. Recruitment rates will be used to determine habitat use, compare relative densities between regions and seasons, and to assess biomass consumption and absolute abundance of hares in the regions studied. This chapter will address one of the four recommendations in the Wong and Hickling (1999) Science for Conservation Report "Assessment and management of hare impact on high altitude vegetation": - The development and validation of a suitable cleared plot technique for assessing hare population density and determining habitat use.

2.2 METHODS

A total of ten cleared plot pellet sites were installed in the various regions covered by this thesis (Chapter 1, Table 1.1). Five sites were installed in the Manson region of the Kaweka Ranges. Three more sites were located in the Moawhango ecological zone, one each at Awapatu, Argo Road (Upper), and Motumatai. With the remaining two in Tongariro National Park at Tukino and Turoa.

2.2.1 EXPERIMENTAL DESIGN

At each pellet site, five transects were run with 20 circular sampling points of 0.1 m^2 (r = 17.8 cm) in size. Transect origins were spaced 40 m apart and also permanently marked using aluminium poles and permolat. Sampling points were spaced at 5 m intervals along each transect and permanently marked using an aluminium tree tag pegged to the ground using high tensile fencing wire. The plot size of 0.1 m^2 was selected as it is the size recommended for use in New Zealand conditions (Parkes 2001), and is consistent with the only size reported in the New Zealand literature (0.09 m^2 in Parkes 1984) Where the terrain was flat, transects were run parallel using a compass bearing. Where transects occurred on a slope, transects followed the contour of the slope. At four pellet sites in the Manson, one transect was run 10m inside the bush edge to assess use of the forest habitat. During the initial measurement, each individual plot had aspect, slope, physiography, and vegetation type recorded, with all pellets present counted and then removed. Deer and possum pellets were also recorded at each plot. At each remeasure of the site, pellets were counted and cleared from each sample point.

In the Manson region, habitats were classified by the dominant vegetation type in a 1m radius around the plot. Habitat was divided into five categories:

Herbfield (H): Habitat dominated by species such as *Racomitrium lanuginosum*, *Celmisia spectabilis*, *Poa colensoi*, and *Leucopogon fraseri*

Grasses (G): habitat dominated by both introduced and native grasses such as *Anthoxantum odoratum*, *Holcus lanatus*, along with *Rytidosperma* and *Poa* species

Herbfield /Grasses (H/G): Mixture of the above two habitat types

Mountain Beech (MB): Where transects occurred in *Nothofagus solandri* var. *cliffortioides* dominated forest

Scree (Sc): Where pellet plots occurred on scree and gravel areas.

The most detailed use of the method was in the Manson region with multiple sites and numerous sampling periods. This was to enable detailed testing of the methods general suitability. Sampling at the other regions was less detailed and intended to test the method in varying habitats, and allow for regional comparisons of density. Monitoring of the Manson sites began in March 2002 and the sites were measured five times until March 2003. The first remeasure was in April 2002 (day 65), followed by June (day 128), October (day 251), December (day 308). The final measure was in March 2003 (day 388). While I endeavoured to measure the pellet lines as close to a 60 day interval as possible (Parkes 1981; Parkes 2001), practicalities such as access and snow cover prevented this from occurring. Monitoring occurred for the other sites at various times between November 2002 and May 2003. The number of remeasures varied for the other regions from one to three occasions.

2.2.2 ANALYSIS

Numbers of pellets recruited at each measurement were divided by the number of days between measurements to obtain a daily recruitment rate. This value was then multiplied to obtain estimates per m^2 and per hectare. Recruitment rate values were tested for normality using Ryan-Joiner normality test. Log data transformations were conducted but the large proportion of zeros present in the data prevented conversion to normality. The Manson region was analysed for variations in recruitment rates over season, site, and habitat types. The data from Manson were analyzed using a repeated measures ANOVA in SYSTAT 8.0 (SPSS Inc. 1998). Metric values were adjusted to compensate for variable time intervals. Due to not all combinations of variables being present at each site, several analyses were run using different combinations of variables. Habitat was always the factor; with covariates being aspect, slope and site being. The models using slope & aspect, and site & aspect as covariates are reported here. Aspect was converted to degrees from north to avoid the complications of it being a circular statistic, but will still be referred to as aspect.

Due to the variation in measurement periods for the non Manson regions, recruitment rates were averaged, and used only to determine whether there were differences in the recruitment rates at the regional scale. Since the five sites in the Kaimanawa and Tongariro areas were monitored only over the summer period, the winter values were excluded from the Manson data when calculating the average recruitment rates for regional comparisons. Regional comparison were conducted using a ANOVA performed using S plus v4.5 (MathSoft Inc. 1998) on the summer recruitment rates for the six different regions. A *posteriori* Tukey-Kramey multiple comparison method was used to test which regions were significantly different. Coefficients of variation (Quinn and Keough 2002), initial standing crop values, and the proportion of plots that recruited pellets were calculated for each region. Unless otherwise stated, significance level was $P < 0.05$.

2.3 RESULTS

2.3.1 REGIONAL VARIATION IN RECRUITMENT RATES

The results from the ANOVA show that there was a significant difference in pellet recruitment rates at the regional scale ($F_{5, 878} = 9.34$, $P < 0.001$). A *posteriori* Tukey-Kramey multiple comparison method showed that of the six sites, there was a grouping of sites with high and low pellet recruitment rates. There were no significant differences between the Tukino, Manson and Awapatu regions (high pellet recruitment). There was also no significant difference between the Awapatu, Argo Rd, Motumatai, and Turoa sites (low pellet recruitment) (Figure 2.1). The Awapatu region had a pellet recruitment rate intermediate between the two groups. The coefficient of variation, initial standing crop values, along with the proportion of plots that recruited pellets varied for each region (Table 2.1). Those plots that had higher recruitment rates also had higher standing crops and percentage of plots with pellets, and lower coefficients of variation. However Tukino was the exception to this trend.

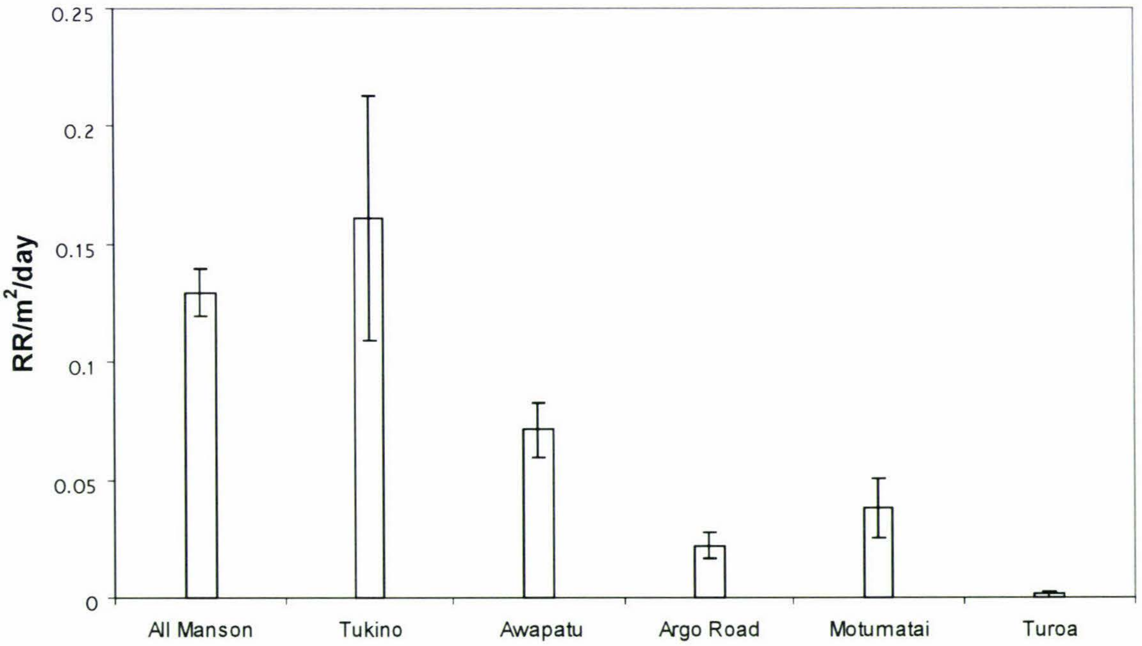

Figure 2.1: Comparison of average summer recruitment rates (pellets/m^2/day) among the six different regions. Letters above the graph indicate significance; sites that have the same letters are not significantly different. Error bars represent the standard error for each sample.

Table 2.1: Summary of the cleared plot pellet data obtained from each region, including total number of plots analysed, initial standing crop (SE), summer recruitment rates (SE), the coefficient of variation and the percent of plots that recruited pellets over the summer period.

Site	N	Standing crop (pellets/m^2)	Recruitment rate (pellets/m^2/day)	Coefficient of variation	% of plots recruiting pellets
Manson	376	25 (1.8)	0.13 (0.01)	1.5	63
Tukino	100	44 (13.6)	0.16 (0.05)	3.2	33
Awapatu	100	15 (2.3)	0.07 (0.01)	1.7	48
Argo Road	100	8 (1.8)	0.02 (0.01)	2.5	20
Motumatai	100	7 (2.3)	0.04 (0.01)	3.4	27
Turoa	100	0 (0)	0.001 (0.001)	10.2	1

2.3.2 VARIATION IN RECRUITMENT RATES FOR THE MANSON REGION

2.3.2.1 Seasonal variation at Manson

The repeated measures ANOVA showed significant variation in pellet recruitment rates over the period of the study ($F_{4, 1840} = 2.88$, $P = 0.022$, Table 2.2). The relationship was significant for a fourth order polynomial (Table 2.2), as several fluctuations were observed throughout the year (Figure 2.2). The first sampling period showed a slight decrease in pellet recruitment from April to June. A larger reduction in pellet recruitment was then observed from June to October. The October to December period then showed a large increase in recruitment. Another decrease was then observed over the summer period from December to March (Figure 2.2). Recruitment rate estimates increased when the data from Mountain Beech and Scree habitat types were removed (Figure 2.2).

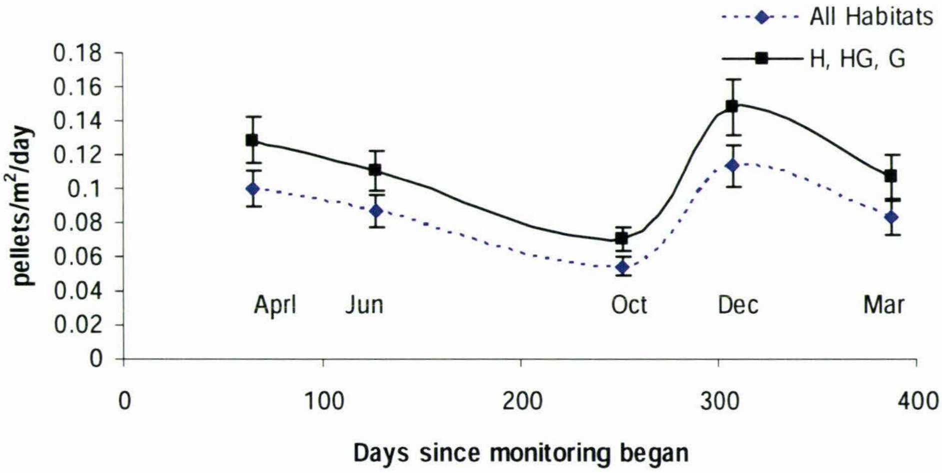

Figure 2.2: Change in average recruitment rate over season for all habitat types, and with Mountain Beech and Scree removed. Months are those in which monitoring occurred. Error bars represent the standard error for each sample. H = Herbfield: G = Grasses: H/G Herbfield /Grasses.

Table 2.2: Significance levels for the repeated measures ANOVA models used in the analysis of Manson recruitment rates. Dependent variable = recruitment rates. Significant results in bold.

	Effect	Between Subject Effects (overall)			Within Subject Effects (season) Univariate Repeated Measure F-test			Single degree of freedom Polynomial contrasts			
		DF	F	P	DF	F	P	1	2	3	4
Overall	(Constant)				4,1840	2.88	**0.022**	0.858	0.993	0.370	**0.001**
Factor =	Habitat	4,460	24.32	**<0.001**	16,1840	3.05	**<0.001**	0.076	0.468	**0.001**	**0.005**
Covariates =	Slope	1,460	4.19	0.660	4,1840	1.27	0.280	0.199	0.077	0.982	0.355
	Aspect	1,460	11.22	**0.001**	4,1840	1.61	0.170	0.152	0.258	0.948	0.073
Overall	(Constant)				4,182	3.41	**0.009**	0.858	0.661	0.837	**<0.001**
Factor =	Habitat	4,457	9.11	**<0.001**	16,18	3.65	**<0.001**	**0.046**	0.117	**<0.001**	**0.001**
Covariates =	Aspect	1,457	9.14	**0.003**	4,182	1.51	0.196	0.923	0.947	0.485	0.170
	Site	1,457	1.95	0.101	4,182	1.87	**0.019**	0.305	0.106	0.132	**0.029**

2.3.2.2 Spatial variation at Manson

Data analyzed for the Manson region showed that pellet recruitment rates changed significantly with habitat type, and by season for each habitat type (Table 2.2). The average recruitment rates over the entire period varied depending on habitat type, with the Grasses habitat category having the highest recruitment rates, followed by Herbfield/Grass, then Herbfield. The Mountain beech and Scree habitat types had the lowest recruitment rates. The interaction between habitats also varied over the season. All habitats (except Scree) fluctuated seasonally, with a decrease in recruitment rates in winter and an increase in the spring period (Figure 2.3). The grasses habitat showed a particularly large increase in recruitment rates during the spring period from October to December (Figure 2.3).

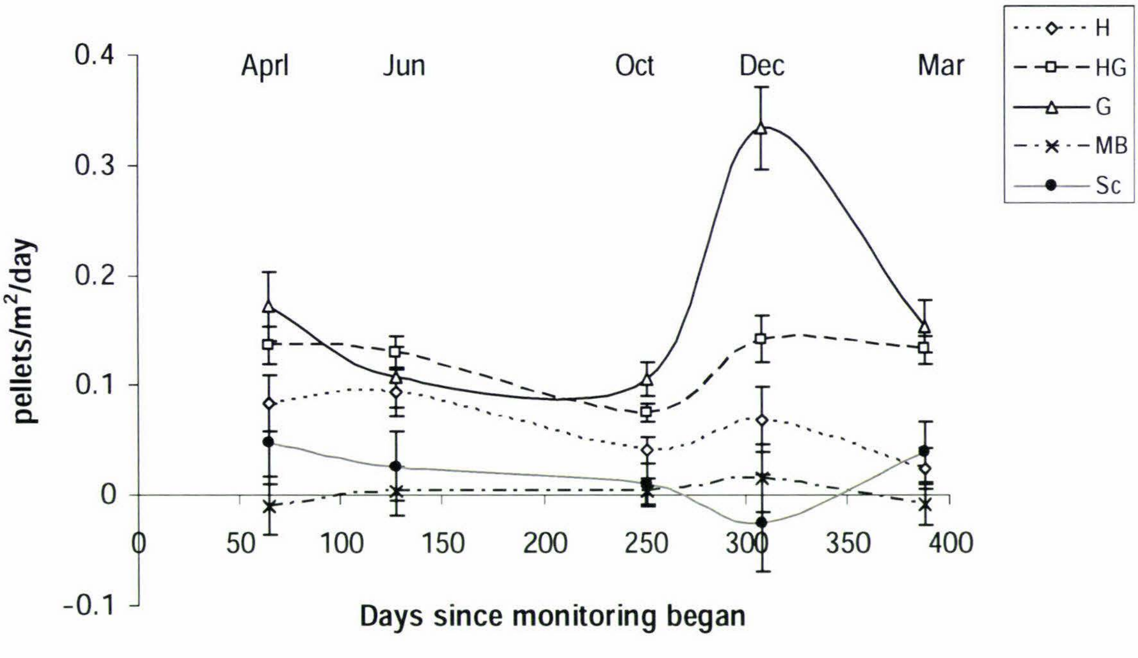

Figure 2.3: Changes in recruitment rates for different the habitats present at Manson. Error bars represent the standard error for each sample. Months are those in which monitoring occurred. Error bars represent the standard error for each sample. H = herbfield: G = grasses: H/G herbfield /grass: MB = Mountain Beech: Sc = scree.

Overall there was no variation between the recruitment rates for the five sites in Manson, indicating a uniform population distribution. However, there was a significant interaction between season and site (within subject effect), indicating that recruitment rate changed with season at the different sites (Figure 2.4). There was a peak in recruitment rates in the spring period for sites two, four and five. While sites one and three showed no increase in production. Aspect was also found to have a significant effect on pellet recruitment, with recruitment rates decreasing away from north (due to aspect being converted to degrees from north, differentiation between east and west cannot be made). Slope was found to have no effect (Table 2.2).

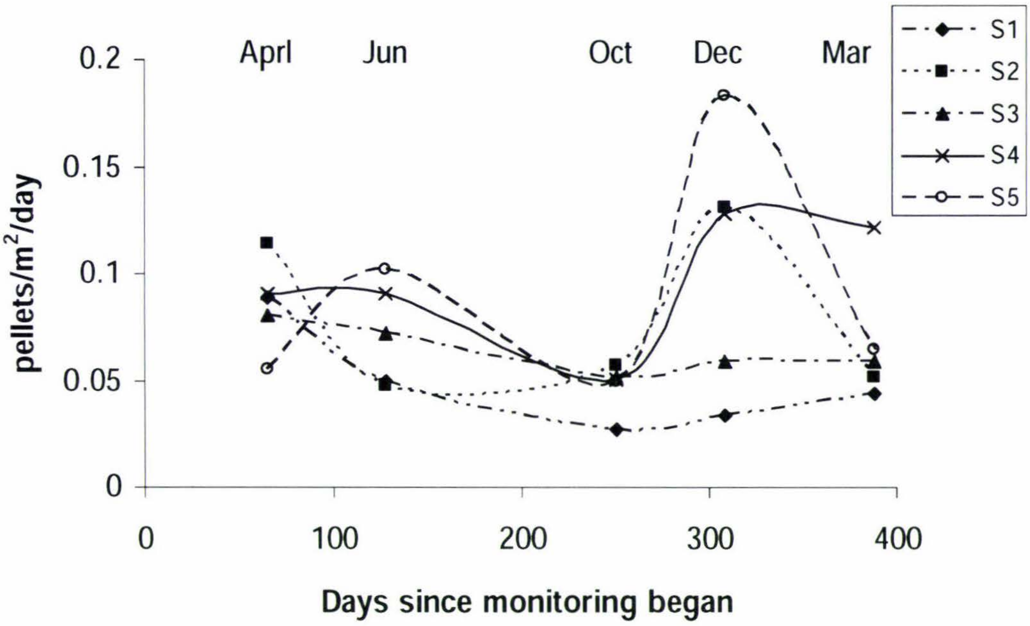

Figure 2.4: Variation in recruitment rates for all habitat types at the different sites at Manson. Months are those in which monitoring occurred.

2.3.3 STANDING CROP: RECRUITMENT RATES CORRELATION

Standing pellet crop data obtained at the initiation of the cleared plot monitoring program showed a significant positive correlation to the recruitment rates subsequently obtained in each plot (Table 2.3). The relationship was significant overall, and for three of the five habitat types. A regression for the Mountain beech habitat type could not be performed due to all the predictor values being zero. The regression equation predicted that the minimum period for all plots to have recruited one pellet was 96 days (Table 2.4). And as habitat preference declined (i.e. preferred = Grass > Herbfield/Grass > Herbfield > Scree), the minimum time for recruitment increased. Meaning the predicted time for all plots in the grass habitat type to contain pellets was 57 days, and 230 days for Scree (Table 2.4). The varying measurement periods in this study showed relatively little change the number of plots containing pellets. The intervals of 64, 63 and 57 days had 33%, 31%, and 34% of plots with pellets, while the longer intervals of 80 and 124 days had 36% and 34% of plots with pellets. If values are averaged over the entire season the number of plots with pellets rises to 75%.

Table 2.3: Regression relationships between initial standing pellet crop values and recruitment rates obtained for the Manson region.

Site	Habitat	P	R^2 (adj)	Regression equation				
1	Herbfield	**0.003**	7.50%	Average RR =	0.00415	+	0.000713	Standing crop
2	Herbfield /Grasses	**< 0.001**	14.50%	Average RR =	0.007641	+	0.001458	Standing crop
3	Grasses	**< 0.001**	30.50%	Average RR =	0.0113	+	0.00214	Standing crop
4	Mountain Beech	NA	NA		NA			
5	Scree	0.166	2.30%	Average RR =	0.00243	+	0.000642	Standing crop
	1 & 2 & 3 Combined	**< 0.001**	19.90%	Average RR =	0.00699	+	0.00173	Standing crop
	Total	**< 0.001**	23.30%	Average RR =	0.004496	+	0.001959	Standing crop

Table 2.4: Calculation of predicted minimum period for all plots to have one pellet recruited in the Manson region given an arbitrary standing crop value of 3 pellets/plot. Standing pellet crop values and predicted recruitment rates are calculated from plots of area 0.1m^2.

Site		Minimum period (days)	Predicted RR/plot	Arbitrary Standing crop/plot value
1	Herbfield	159.0	0.006	3
2	Herbfield /Grasses	83.2	0.012	3
3	Grasses	56.4	0.018	3
4	Mountain Beech	NA	NA	NA
5	Scree	229.6	0.004	3
	1 & 2 & 3 Combined	82.1	0.012	3
	Total	96.4	0.010	3

2.4 DISCUSSION

2.4.1 FURTHER INTERPRETATIONS USING RECRUITMENT RATE DATA

The recruitment rates obtained from the cleared plot pellets counts can be further utilised when the data are combined with information gathered from the literature. Recruitment rates can be converted to absolute hare densities with knowledge of pellet production. Along with estimates of biomass consumption when forage: pellet ratios are known.

2.4.1.1 Population estimation

The recruitment rates obtained from the cleared plot pellet method can be converted to hare densities with knowledge of pellet production. There are two reported pellet production rates for hares in New Zealand. Flux (1967a) tracked five hares in the snow over one night in the Nelson Lakes National Park and counted the number of pellets produced. The average per hare was 434 pellets with extremes of 296 to 671 pellets per hare, with 410 pellets per hare being reported as the best available estimate. From a study of three captive hares fed a mixture of New Zealand alpine vegetation and rabbit pellets, Horne (1979) produced a remarkably similar daily pellet production rate of 409 pellets/hare/day. Therefore, using the estimate of 410 pellets/hare/day, combined with recruitment rates obtained from this study, I estimated population density for the regions in this study.

Since population estimations are derived from recruitment rates, the population estimates for the different regions follow the trends observed in the recruitment rate data. Therefore the summer population estimates range from 3.9 hares/ha at Tukino, to 0.03 hares/ha at Turoa (Table 2.5). As the error associated with the daily pellet production rate is not known, an associated error cannot be given to these values. Therefore the values presented are estimated means with the variation being unknown

Region	hares/ha
Tukino	3.93
Manson	3.15
Awapatu	1.73
Motumatai	0.91
Argo Road	0.53
Turoa	0.03

Table 2.5: Summer population estimates for all regions. Values were calculated using a daily pellet production rate of 410 pellets/hare. The values presented are estimated means with the variation being unknown

Population estimates in the Manson region also follow the seasonal and habitat trends observed from the recruitment rates. Population estimates based upon a production rates of 410 pellets/hare/day (with Mountain Beech and Scree data removed) suggest hare densities varied throughout the year from 3.1 hares/ha originally, dropping to 1.7 hares/ha in winter, and then peaking at 3.6 hares/ha in spring (Figure 2.5). Since the estimates of pellet production are highly variable, both the upper and lower estimates (Parkes 2001) were also used in order to determine the possible variation in population estimates. The yearly population estimate for the Manson region began at 1.9 hares/ha for the highest pellet production rate (600 pellets/day/hare), 2.8 hares/ha for the average rate (410 pellets/day/hare), and 3.8 hares/ha for the lower estimate (300 pellets/day/hare).

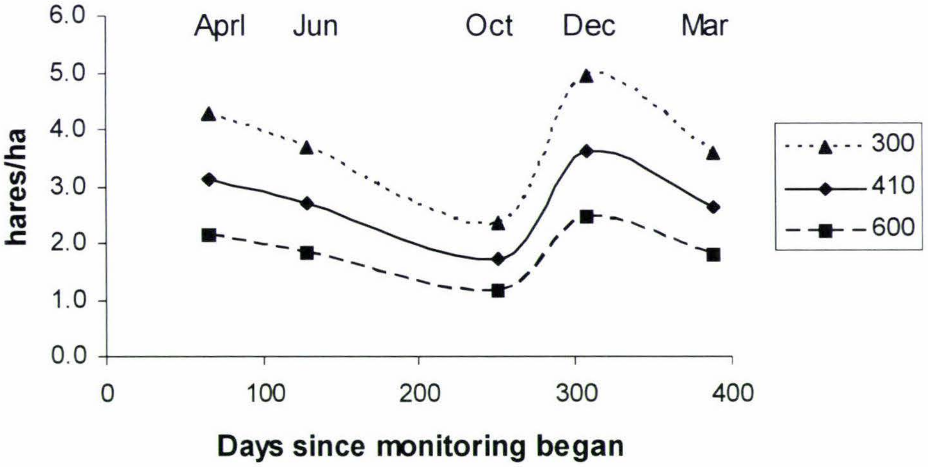

Figure 2.5: Range in population estimation for the combined recruitment rates from the Manson region over the course of one year. Estimates were made using upper (600), lower (300) and average (410) estimates of daily pellet production by hares.

Flux (1990) believes that hare populations in New Zealand self regulate through some behavioural mechanism, and their populations stay below about three hares/ha. However the density estimates obtained for Tukino (3.9 hares/ha) and Manson (3.15 hares/ha) are above this level. These estimates are calculated using the summer recruitment rates, and I have shown in this study that recruitment rates peak in summer. The data from the Manson showed that the average all year population estimate is approximately 88% of the summer estimate. Resulting in the yearly estimate for

Manson being below the limitation level (2.8 hares/ha), however if the Tukino estimate is also reduced, it does not fall below the level (3.4 hares/ha). However with the lack of published hare population studies in New Zealand, the statement by Flux (1990) that hares densities do not exceed of three/ha is questionable.

2.4.4.2 Biomass Consumption

Recruitment rates can also be used to obtain estimates of biomass consumption by hares. An application that appears to have had little utilization in New Zealand, or overseas. In northeastern Colorado, pellet counts were used to obtain estimates of vegetation consumed by jackrabbits in pasture (Hansen, 1972). Jackrabbit defecation rates were calculated for grazed (by cattle) and ungrazed paired plots by counting pellets collected from plots 11 times at approximately three month intervals. By combining the pellet data with the digestion estimate, biomass consumption was estimated. The digestion index is the proportion of dry matter digested by a herbivore, and Jackrabbits have an approximate digestion index of 45%. Therefore, using the formula:

$$\frac{\text{dry weight of pellets produced/hectare/day}}{\text{1 - digestion index.}}$$

It was found that Jackrabbits consume on average 389g dry weight of vegetation/ha/day. The digestion index for hares in New Zealand conditions is unknown. Accordingly for the present study, estimates of vegetation consumption will be obtained by using the data presented in Horne (1979). From these I calculated that one hare pellet is equivalent to 0.44g (wet weight) of vegetation consumed. I then used this value to obtain estimates of vegetation consumed by hares. However as the error associated with this consumption estimate is not known, an associated error cannot be given to these values.

Again, trends follow those of recruitment rates and at the regional scale, biomass consumption varied from 708 g/ha/day for the Tukino site, to 5.28 g/ha/day for Turoa (Table 2.6). The average daily consumption rate across all habitat types at Manson was 378 g/ha/day, this equates to 138kg of live vegetation consumed per hectare per year The estimates of biomass consumed in the Manson region differed across the habitat types as per recruitment rates. The highest amount of biomass consumed (wet weight) was grass at 841 g/ha/day, followed by the herbfield/grasses at 541.73 g/ha/day, then herbfield at 274.03 g/ha/day.

Table 2.6: Estimates of biomass consumed (wet weight) over summer for the regions studied The values presented are estimated means with the variation being unknown

	g/ha/day	kg/ha/yr
Tukino	708.40	258.57
All Manson	568.92	207.66
Awapatu	311.96	113.87
Motumatai	165.00	60.23
Argo Road	95.48	34.85
Turoa	5.28	1.93

To put these values in perspective, weight measurements of 20 *Celmisia spectabilis* and *Chioncochloa rubra* leaves were undertaken. On average, one *C. spectabilis* leaf (~ 9.5 cm in length) weighs approximately 0.70g (SE = 0.005). Additionally a one metre length of *C. rubra* leaf weights approximately 1.81g (SE = 0.81). Further comparison can be made with primary production estimates for alpine vegetation. Above ground biomass production in high alpine environments of Central Otago was estimated for two herbfields of 1390m and 1220m altitude to be 3.3 and 2.7 t/ha (Bliss and Mark 1974). Primary production for a selection of tussock species occurring from 900m to 1400m in Central Otago ranged from 2.7 t/ha for *Poa colensoi,* 5.5 t/ha for *Chionochloa rigida,* to 7.6 and 8.3 t/ha for *Chionochloa macra* (Meurk 1978). If the herbfield primary production values are applied to the Tukino consumption estimates (as these are corresponding habitats) it indicates that hares consume approximately 10% of annual primary production. If the *Poa colensoi* estimate is applied to the Manson region (again similar situations), 8% of primary production is estimated to be consumed.

Comparative to hares, invertebrate impact in New Zealand alpine grasslands is minor. Grasshopper consumption in alpine tussock grasslands averages only 2.7 kg/ha (dry weight) of plant material annually (White 1974). However where other mammalian browsers are present, hare consumption may be significantly overshadowed. With the biomass requirements of Kaimanawa wild horses estimated to be 10 kg (dry matter)/horse/day (Franklin 1995), comparative densities of hares would have to be exceedingly high to surpass horse consumption. Additionally Flux (1967a) surmised that the damage caused by the 6-7 hares in the Cupola Basin, could be offset by shooting one deer.

2.4.2 REGIONAL VARIATION

The detection of significant differences in recruitment rates between regions was possible only when there were large scale differences in recruitment rates - sites that were significantly different were those that had the largest differences in recruitment rates. Each region also had varying errors which can be partly attributed to the sampling design and vegetation present. In general sites with higher recruitment rates had a higher proportion of plots with pellets, and had lower coefficients of variation (Table 2.1). However the Tukino site is an exception to this observation. This is possibly an effect of the clumped vegetation at the site leading to a non-random pellet distribution. At this site hares appeared to have preferred areas in which pellet density was extremely high (Plate 2.1). One plot had 94 pellets on set up with 28, then 16 pellets on subsequent measures; however the majority of plots contained no pellets. The high error at the Turoa site is because in all 100 plots, only one pellet was found.

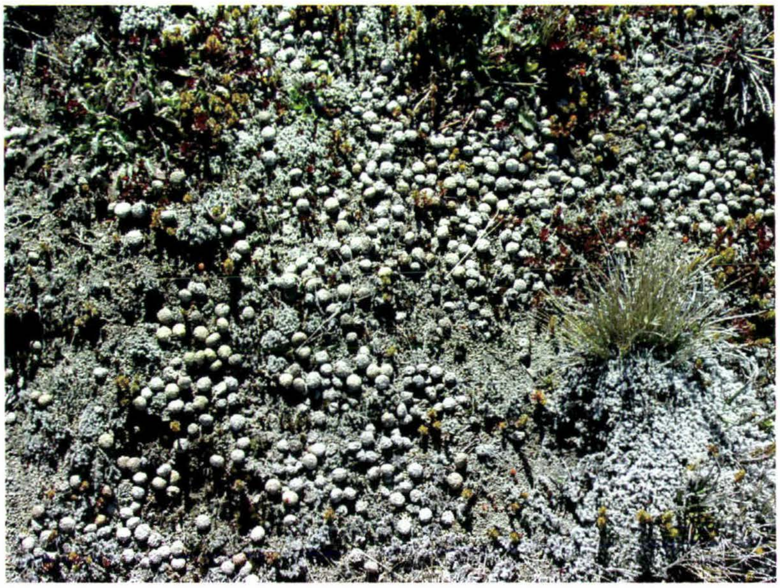

Plate 2.1: Example of the clumped distribution of pellets at the Tukino Site.

Variation in recruitment rates evident at the regional scale occur as each region has limiting factors such competition, suitability of resources and targeted lagomorph control programs. Food will be a limiting factor to all herbivores some of the time, but it will be especially important to those species with low levels of disease, scarce natural enemies, with plentiful cover and breeding sites (Crawley 1983). Therefore the population densities observed will directly relate to the quality of the habitat present. The Manson region has large areas of herbaceous vegetation that appear ideal hare habitat. However there are several factors that might affect densities. While no direct control of hares occurs, the region is extensively hunted by deerstalkers. Several of whom have reported frustration at shooting no deer, and have shot hares instead (up to 5 hares in one evening). This behaviour may not be an effective means of hare control, but it suggests that hares in the Manson do suffer hunting pressure much of the year. The presence of deer suggests that competition for resources could also be occurring. In the Moawhango region, the Awapatu and Argo Road regions are subject to ongoing hare and rabbit control by the New Zealand Army. Control levels are higher at the Argo Road site (*pers. obs.*), and the highest concentration of Kaimanawa wild horses are present in this locality (Rogers 1994; Franklin 1995). While evidence of wild horses was seen at the Awapatu site, it is within the zero density horse area (Department of Conservation 1995) and subsequently horses should not have a competitive effect on hare densities. In the Motumatai region, there is no apparent control of any means. It is not frequently hunted, and no control programs are in place. However there are high numbers of wild horses present (Rogers 1994; Franklin 1995) that could be suppressing the hare population through competition for resources. At the Turoa and Tukino site I observed no limiting factors other than constraints imposed resources limitation. Consequently, only at two of the pellet sites (Awapatu, Upper Argo Rd) were anthropogenic factors thought to be affecting hare density, therefore all other variations can be attributed to natural population processes.

2.4.3 SEASONAL AND SPATIAL VARIATION AT MANSON

More subtle trends in recruitment rates were observed at Manson as extensive data were available. The cleared pellet plot technique showed significant differences in recruitment rates between habitats and sites, and the interactions with these variables over season. The results showed that there was an apparent reduction in recruitment rates over the winter period, and that habitat use changes with season. Seasonal shifts in habitat preferences by hares have been reported before in overseas studies (Hulbert *et al.* 1996; Rodgers and Sinclair 1997; Rao *et al.* 2003) and in the New Zealand literature (Flux 1967a; Horne 1979). Use of the grassland habitat showed the largest fluctuation of all habitats with a high peak in spring. This increase could likely coincide with a flush of spring growth in this vegetation type. While the other vegetation types did not undergo large absolute fluctuations in pellet recruitment, during winter pellet recruitment in the Herbfield and Herbfield/Grass habitats increased relative to the grass habitat type. Indicating that use of these habitats was relatively higher in winter. Hare use of the Mountain Beech habitat was consistently low, with the average recruitment only 0.3% of the total for the region. This agrees with Parkes (1984) who reported that radio tagged hares in the Craigieburn State Forest Park avoided the beech forest habitat, and spent only 2% of their time there. Horne (1979) suggests that hares only use the forest habitat as shelter during periods of stormy weather, or as a route from one grassland area to another.

While the five sites in Manson showed no overall difference in recruitment rates (indicating a uniform population), subtle seasonal changes in site usage were detected. Sites one and three did not show the peak in recruitment rate during the spring period as sites two, four, and five did. All sites were fairly similar in vegetation, therefore the difference cannot easily be explained by habitat differentiation. One factor that could possibly have an effect is that grasses present at sites one and three, tended to be native. While the difference did not seem significant during my observations, it could be a tentative explanation. Therefore in future, differentiation should be made between introduced and native grasses in habitat classification.

2.4.4.1 Confounding issues for interpreting Manson data

While the cleared plot pellet line avoids many of the confounding issues associated with other census techniques, it is not without complications. Seasonal change in habitat use in not an uncommon occurrence for hares (Horne 1979), but it introduces the compounding factors of differential pellet decay and defecation rates. Defecation rates have been shown to vary with season and habitat for other herbivores, and is considered a significant confounding factor in the analysis of pellet numbers (Riney 1957; Davis and Orwin 1985). For example, because of a diet shift to high fiber forage, white-tailed deer in Minnesota were shown to have a seasonal variation in defecation rates with a peak in autumn and a low in winter (Rogers 1987). However studies of other lagomorphs have shown that defecation rates do not change with diet or season. For instance in jackrabbits (*Lepus californicus* and *L. alleni*), the average daily pellet count remains constant irrespective of the daily weight of green forage consumed (Arnold and Reynolds 1943). Therefore differential defecation rates are not considered to be a significant confounding factor in this study. However a shift in diet can alter the decay rates of pellets.

Diet composition reportedly affects pellet decomposition as diets composed of *Celmisia* produce pellets that disintegrate rapidly (Wong and Hickling 1999). Pellets with a high composition of pubescent *Celmisia spectabilis* break down after the first rain, as the hairy surface readily absorbs moisture and explodes (Horne 1979). If the decay rate shortened to below that of the measurement period, the recruitment rate would be erroneous. Minimum pellet decay estimates for New Zealand conditions vary from one month (Horne 1979) to six months (Flux 1967). As the measurement period for the winter period was 124 days (due to snow cover), the chance of pellet decay increased. Indicating that the decrease in recruitment rates perceived over the winter period could be attributed to a change in diet composition and hence faster pellet decay. However I do not consider pellet decay to be significant factor. When sampling hare pellets, no differentiation is made between "valid" and "invalid" pellets as for deer pellet counts (Baddeley 1985). Therefore a pellet only needs to be recognisable as "hare" to be counted, and the likelihood of a pellet completely disappearing during the sample periods of this study was unlikely.

I suggest that natural population cycles are responsible for the variation in hare numbers seen over the year at Manson. In winter the population may fall naturally through the deaths of older/weaker individuals. In the Nelson Lakes National Park, Flux (1967a) reported that most adult hares died during winter, presumably of starvation because there are no predators of adult hares in New Zealand. Additionally the fluctuation observed can be linked to known biological processes. The peak observed in pellet production during spring, coincides with the commencement of the hare breeding season. Breeding begins soon after the shortest day and, in New Zealand, over 90% of females are pregnant from August to February (Flux 1967b). It takes approximately two months from conception for leverets to begin consuming vegetation (Flux 1967b). Therefore the earliest individuals would be recruited into the population is early October, after which leveret numbers increase to a peak in March (Flux 1967b). The subsequent drop in numbers after December has two possible explanations, population regulation or predation. Flux (1990) believes populations of hares in New Zealand self regulate through some behavioural mechanism, consequently the perceived drop in population could be due to this unidentified regulatory agent. However, I suggest that predation is responsible for the drop in hare numbers observed after the December sample. Leverets are preyed upon readily by stoats (King and Moody 1982) and harriers (Wong 2002), two predators known to be present at Manson (personal observation). The breeding seasons of these predators is slightly later than hares with the breeding season for stoats from September to October in the North Island; with the juveniles becoming independent from November onwards (King 1990). Harriers also have a similar breeding season, with female beginning to nest from October to November, and chicks fledging from December to February (Wong 2002). The timing of these breeding seasons suggests that an increase in predation pressure could occur from November onwards and result in a reduction of juvenile hare numbers. This predation could occur through either adult predators feeding juveniles, or from the juvenile predators themselves. Therefore I suggest the peak hare densities observed from October to December result from the breeding season of the hare beginning earlier than that of the predators, after which, an abundance of predators acts to reduce the leveret population.

2.4.4 STANDING CROP: RECRUITMENT RATE CORRELATION

While the standing crop method (Flux 1967a) was not considered suitable for population estimation in this study, standing crop information is collected at the initiation of a cleared plot monitoring program. This information can be used to provide valuable information for the management of the cleared plot pellet sampling. A significant relationship between the standing crop and subsequent recruitment rates was shown, and this enabled prediction of minimum remeasurement times. These equations may be of use in the future when setting up similar monitoring programs. The predicated minimum measurement time for Manson was 96 days. However, the time periods for remeasurement in this study varied, but the number of plots with pellets remained relatively constant, even with an interval of 123 days. While this interval was during the winter period, when recruitment rates were perceived to be lower, an interval of 80 days occurred during the summer period with no perceived change in the number of plots with pellets. This lack of change could be attributed to hares showing ongoing preference for certain plots over time. If plots occur in preferred habitat, then they will show higher standing crops and subsequently, recruitment rates. Some plots will occur in the least favourable sites at which pellet recruitment will almost always be zero. Therefore simply increasing the measurement time will not ensure these least preferred plots will receive pellets. Consequently increasing the measurement period will not guarantee recruitment in every plot, merely increase the probability.

2.4.5 EVALUATION OF METHOD

It is difficult to draw comparisons between the present study and the only other published study on the cleared plot pellet technique in New Zealand (Parkes 1981). Parkes (1981) showed a fluctuation in recruitment rates in the Craigeburn State Forest Park. In that study, remeasurement times appear relatively constant with a homogeneous grassland habitat, hence reducing many of the compounding factors outlined above. The recruitment rates obtained fluctuated from approximately 5-13 pellets/m^2 over the 60 day periods. This indicates the population in that study was slightly higher than in the regions of this study. The summer recruitment rate of the Manson would produce 7.8 pellets/m^2 over a 60 day period. However, the population in the Craigeburn State Forest Park could have been artificially high as the fluctuations were artificially induced through the application of fertiliser and sowing of clover in the area during winter.

While the direct comparison to overseas studies using the cleared plot sampling technique are not relevant, evaluation of error rates provides interesting information. Krebs *et. al.* (1987) obtained estimates that, using 95% confidence intervals, were $\pm$ 30% of the mean. These recruitment rates produced density estimates highly correlated ($r = 0.94$) with actual density. The Manson data produced estimates that, using 95% confidence intervals, were $\pm$ 15% of the mean, indicating that the density estimates obtained in this study are accurate. However, while the population estimates obtained are the best available for New Zealand, a validation program needs to be run to confirm the accuracy of the method. This could occur through a detailed mark-recapture program, however I suggest validation through sampling a know population size inside a large exclosure as done by Taylor and Williams (1956). This way the population can be experimentally altered and the subsequent effect on population estimates assessed.

To test the sampling power of the sample sizes used, and to produce an indication of appropriate samples size, statistical power analysis was undertaken using the online power calculator from the University of California Statistics Department (http://calculators.stat.ucla.edu/powercalc/). The number of plots required to enable significant detection of a recruitment rate reduction was tested for each region. Variable reductions in recruitment rates of 25, 50, and 75% were used to simulate initiation of a hare control regime. The number of plots required related to the recruitment rate of the region and the variability of the data from that region (Table 2.7). The power analysis showed that at Manson (using summer only estimates), where recruitment rates are high and error low, that 103 plots would be required to significantly detect a reduction in recruitment rates of 50%. While at Tukino, where recruitment rates are also high, but so is the error, 460 plots would be required to significantly detect a 50% reduction.

The number of plots required at each site to detect significant regional differences was also investigated (Table 2.8). As would be expected those regions that showed significant differences in recruitment rates (Figure 2.1) had plot number estimates lower than those used in this study. The power analysis indicated that the addition of a further 20 plots at the Awapatu site would have enabled the detection of a significance difference in recruitment rates between this site, and the Manson and Argo Rd sites. Apart from this site, most other regions would require a substantial increase in sample size to enable significant detection of regional differences. However when the data from the two power analyses are combined, an indication of appropriate sample size can be obtained.

Table 2.7: Power analysis of the number of plots required for each region to significantly detect a change in recruitment rates 95% of the time if a one-tailed test with significance level of $P < 0.05$ is used.

	Actual	Plots required to detect a reduction of :		
Site	N	75%	50%	25%
Manson	376	46	103	406
Tukino	100	203	460	1835
Awapatu	100	56	118	465
Argo Road	100	111	262	874
Motumatai	100	205	476	1710
Turoa	100	3181	9713	155633

Table 2.8: Power analysis of the number of plots required to significantly detect regional differences in recruitment rates 95% of the time if a one-tailed test with significance level of $P < 0.05$ is used. There was insufficient data at the Turoa site to undertake power analysis. Shown in bold are those regions that were significantly different in recruitment rate analysis (Figure 2.1).

	Tukino	Awapatu	Argo Road	Motumatai
Manson	Manson = 1494 Tukino = 3979	Manson = 198 Awapatu = 120	Manson = **14** Argo Road = **44**	Manson = **84** Motumatai = **54**
Tukino		Tukino = 535 Awapatu = 121	Tukino = **204** Argo Road = **22**	Tukino = **293** Motumatai = **71**
Awapatu			Awapatu = 111 Argo Road = 51	Awapatu = 346 Motumatai = 369
Argo Road				Argo Road = 494 Motumatai = 1151

The appropriate sample size will vary depending upon heterogeneity of the habitat and population size. Larger populations will require fewer plots as the data produced is likely to have a low error, and therefore estimates will be more precise. For a high density hare population in homogenous habitat, a sample size of 100 plots would be the minimum number of plots required. This plot size would be appropriate to detect a 50% reduction in hare numbers, and allow for detection in large scale regional differences in recruitment rates. However in heterogeneous habitat, or where population sizes are low, this sample size would generally be too small. In these habitats a sample size of 200-300 plots would be the minimum. However it appears from these results that if detailed sampling of all habitats is required, 500 plots would be the minimum to be able to significantly detect most differences and fluctuations in recruitment rate data. While this number is substantially higher than that used in this study, the number of plots is not unpractical.

During this study the sample times for remeasurement of a pellet site of 100 plots averaged a minimum of two hours. This time varied depending mainly upon the vegetation present at each site which affects the ease of plot relocation. In herbfield vegetation, plot relocation is generally simple, however in dense grass and tussock swards plot relocation can be problematic. The maximum number of pellet sites I was able to complete in a single day was three. This was at Manson where travel time between the sites was approximately an hour and plot relocation generally simple. In most of the regions the most time consuming aspect of the pellet site was travel time. Therefore addition of an extra 100-200 plots would enable more precise sampling of recruitment rates but not increase sampling time dramatically. Pellet plots are relatively simple to measure and only require a single fieldworker, therefore two competent observers could measure plots separately meaning up to 300 plots could be easily sampled in a day. If the area was easily accessible, then 500 plots a day would be possible in low stature vegetation. Above this number of plots, sampling becomes unpractical.

2.4.5.2 Improvements to sampling design

A measurement period of 60 days with a plot size of 0.1 m^2 was recommended by Parkes (2001) as being suitable for the cleared pellet plot technique in New Zealand. These criteria were used in this study to maintain a consistent methodology for New Zealand. But they significantly influenced the analysis due to the non normal distribution of the data, as a large proportion of pellet plots recruited no pellets. Consequently the data were skewed towards zero at all sites (Figure 2.6). Even when the Manson values were summarized to represent one sample period of 380 days, a non-normal distribution was found (Ryan-Joiner normality test $p < 0.01$). Log data transformations were conducted, but the large proportion of zeros present in the data prevented conversion to normality.

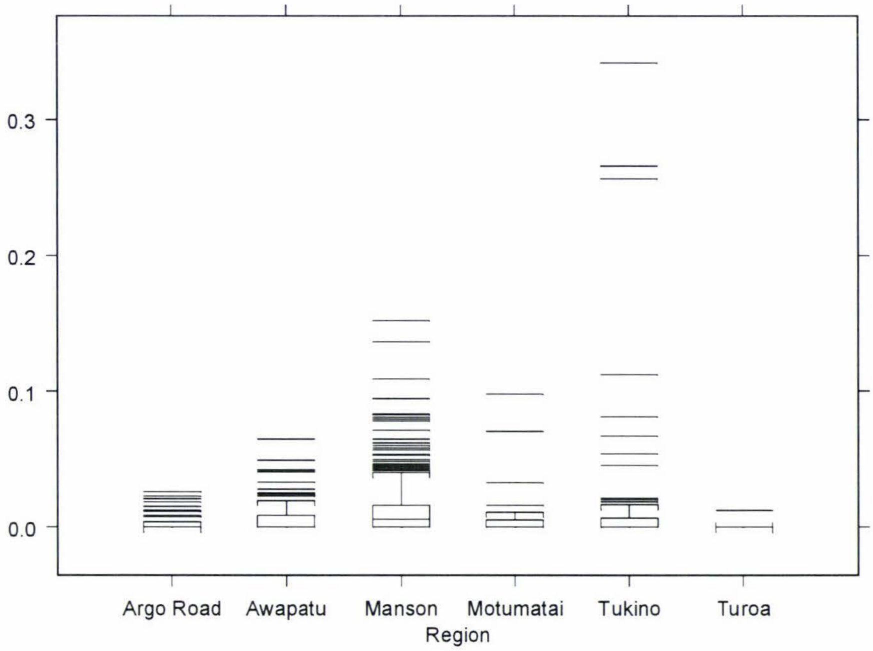

Figure 2.6: Non-normal distribution of summer recruitment rate data from all regions. Recruitment rates are in pellets/m^2/day

While provisions for the avoidance of this situation can be made, each suffers drawbacks in the method. Remeasurement periods can be increased, but possibility of pellet decay occurring also increases. But as we have seen the number of plots with pellets does not necessarily increase with longer sample periods. Alternatively plot size could be increased to cover a large area to increase the chance of pellet recruitment. However, differing plot areas can produce different estimates of recruitment rates and density (McKelvey *et al.* 2002; Murray *et al.* 2002). McKelvey *et al.* (2002) investigated the effect of plot size and shape on pellet density estimates at two locations in the Rocky Mountains. It was found that size and shape affected the pellet density result. Using long thin rectangles (e.g. Krebs *et al.* 1987, 2001) produced pellet densities approximately twice as high as those calculated using large circular plots. Small plots of similar shape also produced higher estimates than their larger counterparts. The reasons proposed by McKelvey *et al.* (2002) for these differences were that either, pellets were missed in the larger plots or, for the small and particularly the rectangular plots, there was an inclusion bias due to the high edge-to-area ratios. McKelvey *et al.* (2002) concluded that large circular plots are preferable for low density populations. These plots were easier to lay out, plot boundaries are more precisely defined, and their wide use making comparisons easier. That study highlighted that comparisons of pellet densities between studies is not reliable unless similar plot designs are used. Therefore, while increasing plot size might improve the distribution of the data, it would add complications for comparisons of different studies. Increasing plot size also reduces the sampling accuracy. Searching effort decreases with increasing plot size resulting in pellets being missed (McKelvey *et al.* 2002). I concur with this view, due to the complex structural nature of many of New Zealand's subalpine environments, a plot size larger than that used here would significantly increase search time, and reduce searching efficiency. Indeed, whether or not the sampling design requires alteration at all is something that can not be determined until after sampling has already occurred. Therefore modifications to the basic sampling design should be made only after careful consideration. Sampling periods should be lengthened only after an investigation into the decay rates at each specific site, and how altering plot sizes will affect comparison between studies.

2.4.6 CONCLUSIONS

The cleared pellet plot technique is a viable sampling tool for examining hare habitat use and providing estimates of hare densities, both relative and absolute. Hares undergo dramatic fluctuations in habitat usage with season; they consume large amounts of vegetation, and appear to undergo seasonal population fluctuations. While the sampling design produced non-normal data, the results were able to show minor changes in habitat and site use when adequate sample sizes were available. The precision of the method was reduced during the regional comparisons stage, due to less available data when the sampling periods were clumped. However relative density trends between the regions were shown after minimal sampling. However, this method needs to be validated for New Zealand conditions. While accurate estimates of hare density have been obtained overseas (Krebs *et al.* 2001; Murray *et al.* 2002), a validation study (such as mark-recapture) should be conducted in New Zealand. The sampling design used here provides precise information and would provide a starting point for future studies. Modifications to the basic design should be made only after careful consideration.

Chapter 3

Long term effect of hare browse on species composition and vegetation structure

Abandoned truck in the Awapatu valley

3.1 INTRODUCTION

Historically the browsing impact of hares in New Zealand has been thought of as minimal (Flux 1967a). This is especially so when compared to the severe impacts occurring with the introduction and subsequent population explosions of numerous other herbivores in New Zealand, for example several species of deer (Forsyth *et al.* 2002), thar (Levine 1985), goats (Parkes 1993), and rabbits (Norbury 1996). But the reality is the relative importance of hare impact on New Zealand vegetation is unknown. They have been present in many parts of their range for decades but the full effects of their browsing may not yet be apparent due to long lived nature of many browse species (Wong and Hickling 1999). Previous investigations into impact of hare browsing have been relatively short-term and limited in terms of replication. However the previous studies were sufficient to show that hares have the potential to have a significant detrimental impact on high altitude vegetation (e.g. Rose and Platt 1992; Rogers 1994). In this chapter I aim to begin addressing this shortfall in knowledge by investigating the long term browsing impacts of hares on subalpine vegetation through the examination of a series of existing exclosure plots.

At present there have only been three studies done to quantify the effects of hare browse on high altitude vegetation (detailed in the general introduction). Rose and Platt (1992) examined the effects of hare browse on snow tussock regeneration. Rogers (1994) examined the impact of hares at three sites in the central North Island in conjunction with examining the impact of the Kaimanawa wild horses. In an unpublished masters thesis, Blay (1989) investigated food preferences of hares in fescue grassland. These studies began to address the shortfall in knowledge, but there are still many unanswered questions with regard to long-term vegetation impacts of hare browsing such as the effects on community composition, structure, and abundance. This study used an existing network of permanent grassland exclosure plots established in the Moawhango region to determine the long-term browsing impact of hares. This will begin to address one of the four recommendations in the Wong and Hickling (1999) Science for Conservation Report "Assessment and management of hare impact on high altitude vegetation": Namely the investigation of long-term hare impact using exclosure-plot and population reduction techniques.

3.2 METHODS

3.2.1 STUDY SITES

There are a total of ten exclosure plots in the Moawhango region that are potentially suitable for assessing the long term browsing impact of hares. These exclosures are of a split plot design with an exterior 20m x 20m fence to exclude large grazers. The plots are divided further by a hare-proof fence running through the middle to create a 10m x 20m area in which hares are excluded. This design allows the browsing impact of hares to be assessed in the absence of horses, and other large grazers. Some of the exclosure plots are located on private land and others in the Wairoru Army Training Area. Initially all ten were planned to be measured; however fence degradation and insufficient hare numbers meant that of these sites, only four were deemed suitable for remeasurement in this study (detailed below). Full site descriptions and history of the sites is detailed in Chapter 1.

Motumatai: Two exclosure plots (established in 1979) are located on private land in the Moawhango catchment. Of the two plots, only one was suitable for measurement and this was situated on a plateau of red tussock-hard tussock grassland, adjacent to a stand of Mountain Beech (Rogers 1994)(referred to as Motumatai). The other plot was located a short distance away inside a stand of Mountain Beech. However the dividing fence had suffered several treefalls and was no longer hare-proof. The remaining eight plots occur on land administered by the Army, but only three of these eight plots were deemed suitable for measurement.

Awapatu: Three exclosure plots (established in 1990) are located in the Awapatu subcatchment. Two of these plots have suffered fence degradation resulting in only one exclosure being suitable for measurement. The wetland exclosure plot and the hillslope red tussock and hard tussock exclosure plot as described by Rogers (1994) had suffered fence degradation. Leaving only the Basin floor, hard tussock grassland exclosure suitable for measurement (referred to as Awapatu).

Argo Rd: Five exclosure plots were established in 1993-1994 by the Army along the Argo Road. Two of these exclosure plots are located in the Argo Valley but were deemed unsuitable due to lack of hare presence. One other high altitude plot was located adjacent to the Argo road, in the vicinity of the Three Kings, and had suffered fence degradation. The remaining two exclosure plots that were suitable for measurement were located in relatively close spatially proximity (< 1 km) adjacent to the Argo Rd, in the locality of Westlawn Hut (referred to as Upper Argo Rd, and Lower Argo Rd).

Some of the plots have been measured at various times in the past using a variety of methods. It was originally hoped to replicate these historic measurements to allow temporal comparisons to be made. However after extensive searching, it appears that the previous data has been lost. Rogers (1991, 1994) contains summaries of the vegetation trends, but as the actual data was not available, reliable temporal comparisons could not be made. Therefore the method was modified slightly to suit this study. The sampling design of Rogers (1991; 1994) used sampling transects run on the overall diagonals of the exclosure, i.e. each transect inside the exclosure ran through both the horse and horse/hare exclosure. While a differentiation in data appears to have been made, the predominant focus of Rogers (1994) was the impact of horses. I examined each plot individually for herbivore impacts.

3.2.2 VEGETATION ASSESSMENT

Vegetation was assessed using 80 Scott (1965) height frequency sampling points per plot (horse exclosure, hare/horse exclosure, and unfenced control). Two 20m transects with sampling points every 0.5m were run on the diagonals of each plot. For each sampling point, a continuous sampling column occurred from the ground, to the maximum height of vegetation through the incision of a rod marked at 5 cm intervals. An open-ended frame measuring 5 cm (vertical) x 5 cm (horizontal depth) x 4 cm (horizontal width) was then inserted at each 5cm height tier, and all plant species present within the confines of this space were recorded (total area of each frame = 100 cm^3). When data from the sampling points were combined, each species had the number of occurrences in each height tier summed across the plot. Additionally, by summing the number of occurrences of a species in all height tiers, a summed height frequency value was obtained that represented the total abundance of that species in the plot (biomass index).

3.2.3 STATISTICAL ANALYSIS

Variations in vegetation composition and structure were compared between the four sites in general, and between each of the three treatment plots present at each site. Scott height frequency diagrams were drawn using the graphing program MAC Juno (courtesy of Stephen Marshall, Victoria University, Wellington) to allow visual comparisons of the SHF data for each plot. Species names in SHF graphs were abbreviated to the first three letters of the genus (uppercase) followed by the first three letters of species (lowercase). A list of full species names for these abbreviations can be found in Appendix 1. All further analyses were run on the summed Scott height frequency values.

Nonmetric Multidimensional Scaling (NMS) ordinations were carried out in PC-ORD 4.0 (McCune and Mefford 1999) on the summed Scott height frequency (SHF) values from each of the three treatment plots over the four sites. Distance measure used was Sorenson (Bray-Curtis) as suggested by McCune and Grace (2002) for analysis of community data. Random starting configurations were used with six axes initially assessed using 40 runs of real data, 50 with randomized data and 400 iterations. Autopilot mode within PC-ORD was used to select optimal dimensionality. A Pearson correlation was run on ordination outputs to determine which species were strongly correlated with each axis. A strong correlation was regarded as r = +/- 0.5. Cluster Analysis was run in PC-ORD 4.0 on the summed Scott height frequency (SHF) values from each plot over the four sites. Sorenson (Bray- Curtis) distance measure was used along with Flexible beta group linkage method (beta = -0.250).

3.3 RESULTS

3.3.1 VEGETATION CONDITION AND HERBIVORE IMPACTS

There was no evidence from any of the established exclosure plots in the Moawhango region to indicate that hares are having a long-term impact on overall vegetation condition. When the Scott height frequency (SHF) graphs are examined, it is apparent that horses and not hares, are having a major browsing impact in the Moawhango region (Figure 3.1). At the Awapatu site, where horse presence was negligible, there was no apparent difference in vegetation composition and structure between any of the three treatment plots (Figure 3.1). At the remaining three sites where horses are present in reasonable numbers, unmistakable vegetation differences occur in the unfenced control plots.

At both the Upper and Lower Argo Rd sites, the horse and hare/horse exclosure plots showed little apparent difference both visually and after examination of the SHF data. But clearly identifiable differences in vegetation composition were apparent in the unfenced control plots at both sites. At the Upper Argo Rd site the abundances of *Festuca rubra*, *Anthoxantum* odoratum, and *Poa cita* were all considerably lower in the unfenced control plot. With *Holcus lanatus* and *Chionochloa rubra* showing increased abundances in the unfenced control. In the Lower Argo Rd unfenced control plot, general vegetation stature was suppressed with *Festuca rubra* and *Microlaena avenacea* being notably reduced. There was also a notable increase in several prostrate species such as *Hieracium pilosella, Pernettya macrostigma,* and *Leucopogon fraseri*.

Sizeable differences were observed between all three plots at the Motumatai site where horses are more common. Unlike the other sites in the region, differences were observed between the horse and hare/horse exclosure plots. This can be seen especially in the differing abundances of *Chionochloa rubra*. The summed SHF values for *C. rubra* were 728 in hare/horse exclosure, 253 in the horse exclosure, and 30 in the unfenced control. There were also large differences between the two exclosure plots, when compared to the unfenced control. Several grass species present in the exclosure had reduced abundances in the unfenced control. These included *F. rubra*, *F. novae-zelandiae*, and *F. ovina*. Additionally, *Hieracium pilosella, Aceana microphylla, Wahlenbergia pygmaea,* and *Leucopogon fraseri* were all major components of the unfenced control plot, but only represented a small proportion in both exclosure plots.

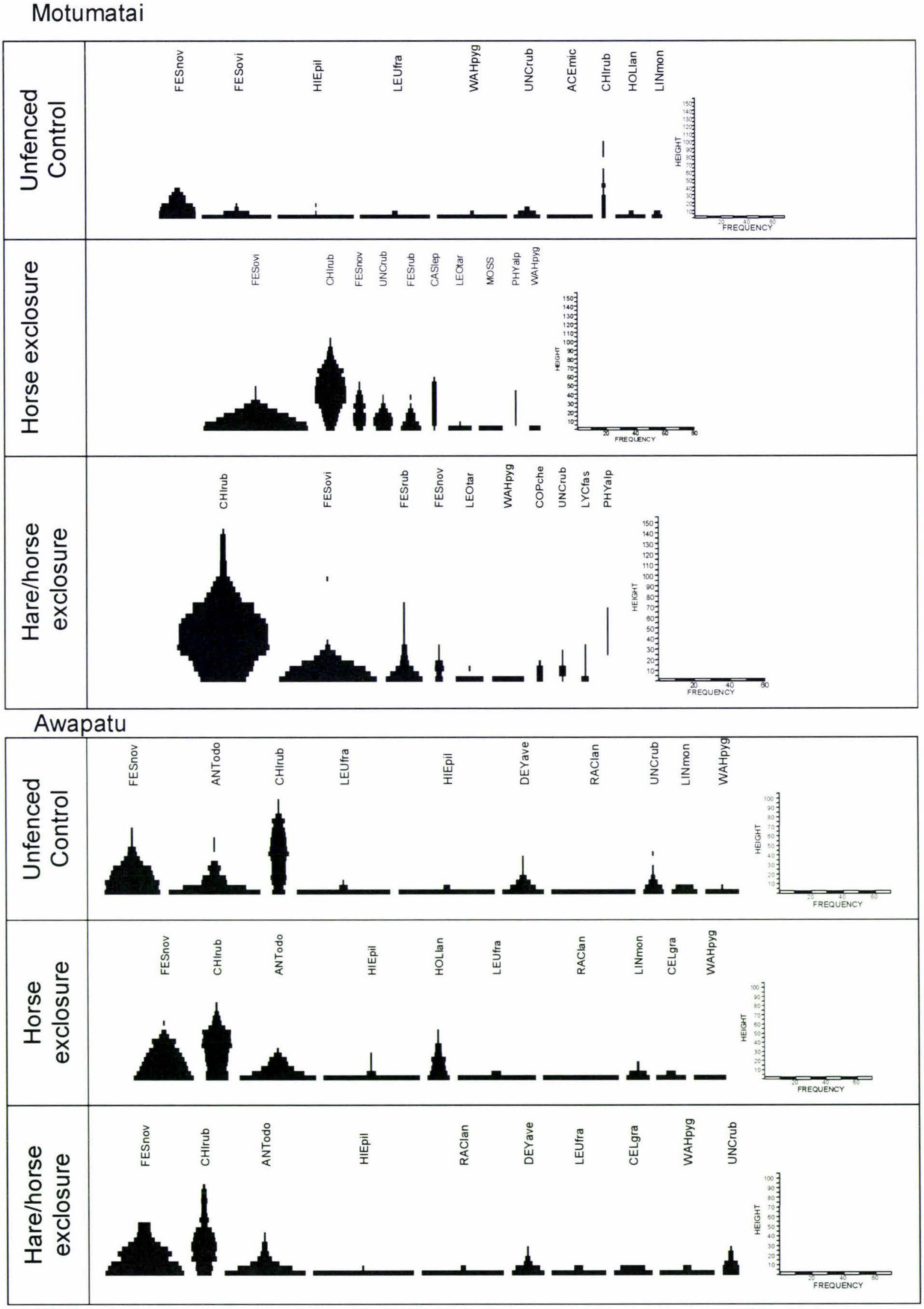

Figure 3.1: Scott Height Frequency diagrams for each of the three treatments plots in the four exclosure sites measured in the Moawhango region.

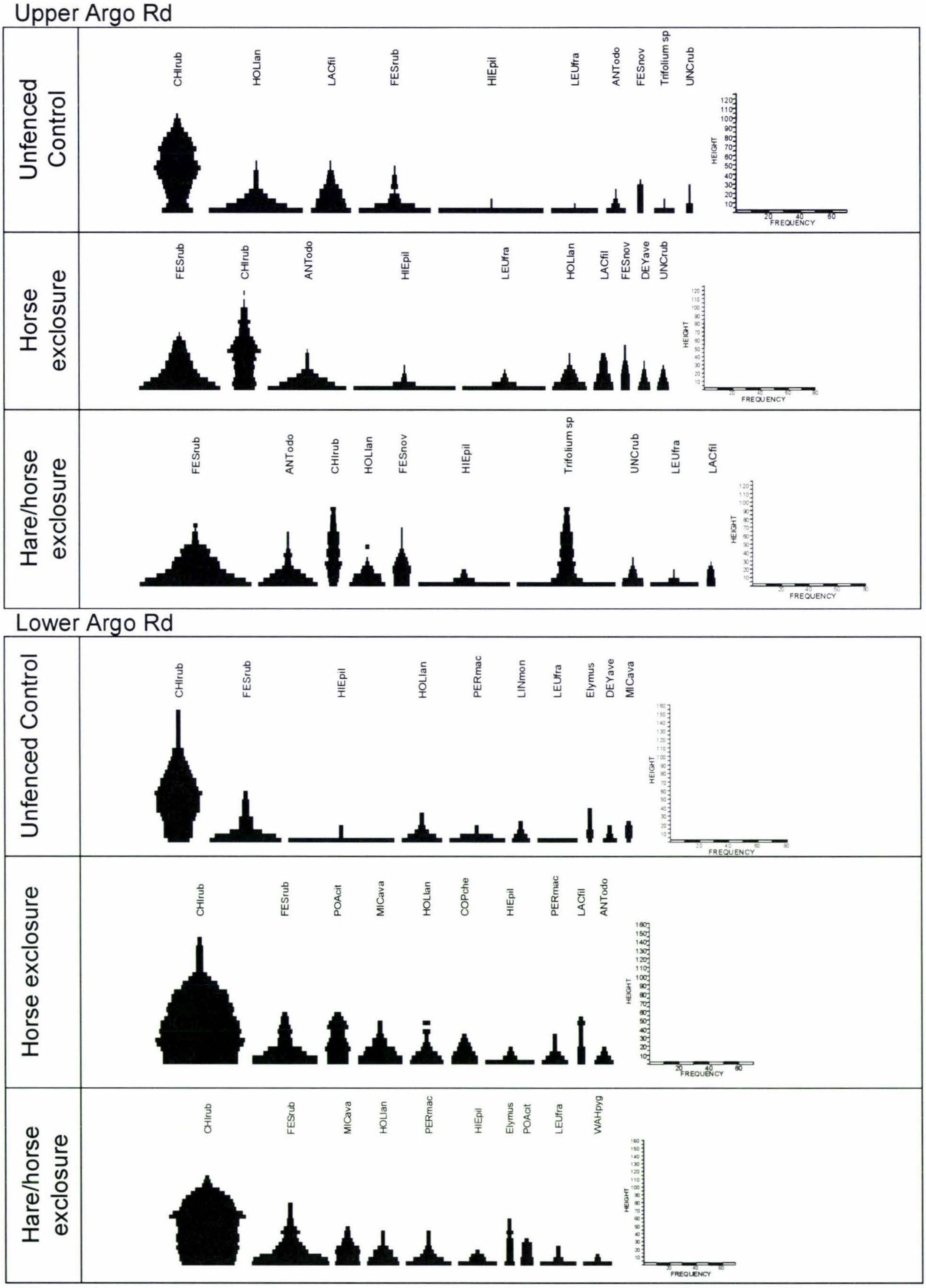

Figure 3.1: continued

3.3.2 NONMETRIC MULTIDIMENSIONAL SCALING

The Nonmetric Multidimensional Scaling (NMS) ordination was run using two dimensions with 42 iterations in the final solution (Appendix 2 for Monte Carlo test). The resulting final stress was 7.25. The stress value is a measure of the departure in plot distances required to fit original distances in ordination space, to a 2-D ordination graph (McCune and Grace 2002). The stress value obtained in this study, using Clarkes (1993) rule of thumb, indicates "a good ordination with no real risk of drawing false inferences". The proportion of variance represented by each axis based on the r^2 distances was 0.510 for Axis 1 and 0.388 for Axis 2. The cumulative r^2 for both axes was 0.898. The NMS ordination clearly differentiated three of the four regions (Figure 3.2) by regional clustering of plots. The Awapatu and Lower Argo Rd plots showed as a distinct cluster of plots for each site. The Upper Argo Rd site was not as clearly differentiated with between plot ordination distances being slightly higher. The ordination distance between the Upper and Lower Argo Rd unfenced control plots was similar to the among plot distances at the Upper Argo Rd site. No clear grouping was evident for the Motumatai plots with among plot ordination distances being similar or greater than between site distances.

Correlations of species with the ordination axes showed the species most highly correlated with Axis 1 were *Chionochloa rubra* (positively) and *Poa cita* (negatively). The species most highly correlated with Axis 2 were *Festuca ovina* (positively) and *Hieracium pilosella* (negatively) (Table 3.2).

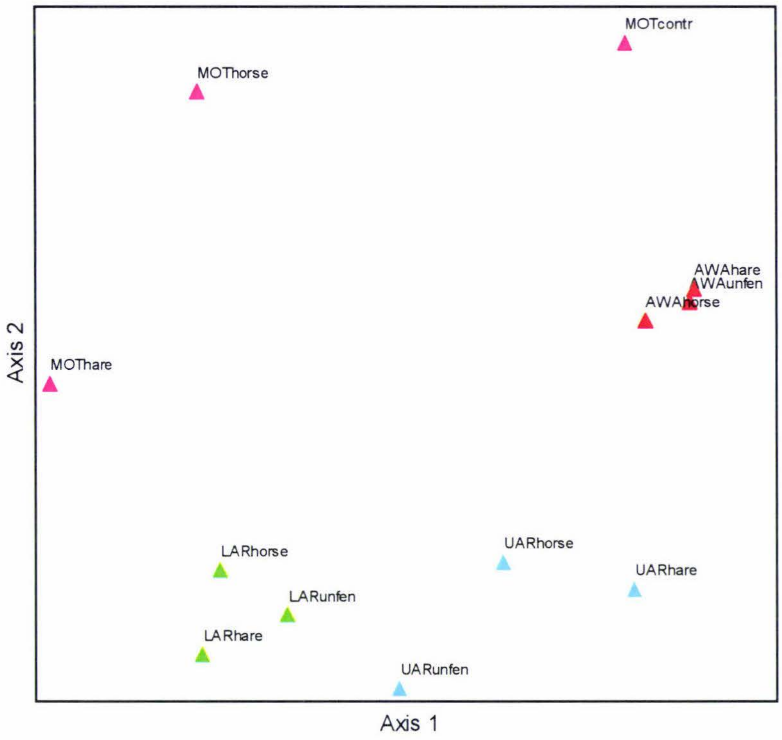

Figure 3.2: Nonmetric Multidimensional Scaling ordination graph of the summed SHF data for each treatment (unfen = unfenced control, horse = horse exclusion, hare = hare/horse exclusion) at the four exclosure sites measured in the Moawhango region (MOT = Motumatai, AWA = Awapatu, LAR = Lower Argo Rd, UAR = Upper Argo Rd).

Table 3.2: Species showing strong Pearson correlations (r = +/- 0.5) with ordination axes for the Nonmetric Multidimensional Scaling ordination run on the summed SHF values for each treatment (unfenced control, horse exclusion, hare/horse exclusion) at the four exclosure sites measured in the Moawhango region.

Direction of	Axis 1		Axis 2	
correlation	Species	r	Species	r
Positive	*Chionochloa rubra*	0.853	*Festuca ovina*	0.914
	Pernettya macrostigma	0.62	*Leontodon taraxacoides*	0.899
	Anaphalioides bellidioides	0.572	*Phyllocladus alpinus*	0.865
	Microlaena avenacea	0.564	*Leucanthemem vulgare*	0.85
	Elymus sp.	0.553	*Muehlenbeckia axillaris*	0.829
	Festuca rubra	0.53	*Poa colensoi*	0.729
			Anisotome aromatica	0.639
Negative	*Poa cita*	-0.748	*Hieracium pilosella*	-0.907
	Racomitrium lanuginosum	-0.648	*Luzula migrata*	-0.751
	Euchiton traversii	-0.626	*Trifolium* sp.	-0.732
	Pimelea oreophila	-0.61	*Anthoxantum odoratum*	-0.707
	Uncinia rubra	-0.592	*Leucopogon fraseri*	-0.672
	Ranunculus sp.	-0.539	*Holcus lanatus*	-0.575
			Hydrocotyle sp.	-0.56

3.3.3 CLUSTER ANALYSIS

Cluster Analysis of the summed SHF data grouped the Moawhango plots into two main clusters (Figure 3.3). One group was composed of the three plots from the Awapatu site (showing a close relationship), clustered with the Motumatai unfenced control. A second group comprised the Upper and Lower Argo Rd sites, with the remaining two plots from Motumatai. The Motumatai plots were clustered separately from the Argo Rd sites. At the Argo Rd sites, the unfenced control plots were grouped together, but were separate from the horse and hare/horse exclosure. These plots were clustered together by site (Figure 3.3)

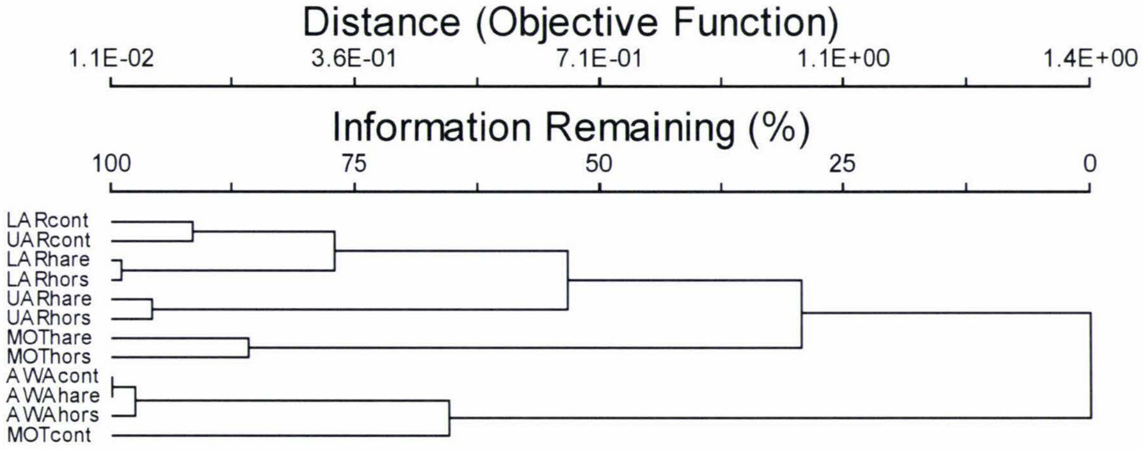

Figure 3.3: Cluster analysis dendrogram of the summed SHF data for each treatment (unfen = unfenced control, horse = horse exclusion, hare = hare/horse exclusion) at the four exclosure sites measured in the Moawhango region (MOT = Motumatai, AWA = Awapatu, LAR = Lower Argo Rd, UAR = Upper Argo Rd).

3.4 DISCUSSION

3.4.1 VEGETATION CONDITION AND HERBIVORE IMPACTS

The results from the exclosure measurements in the Moawhango region indicate that it is horses, not hares, which are predominantly effecting vegetation composition in the region. Impacts of long term herbivory on general vegetation composition and structure by hares were not observed at any of the sites. However herbivory impacts by horses were observed at three out of the four sites. In general horse browsing suppressed the overall height structure of several grass species and encouraged the growth of prostrate species (Figure 3.1). The most heavily impacted species by horses were exotics grasses such as *Festuca rubra, Anthoxantum odoratum,* and *Holcus lanatus.* The native grasses *Poa cita, Microlaena avenacea,* and *Festuca ovina* also showed signs of suppression. The most severe suppression of any species in the region was observed on the latter two species. A large amount of variation was also observed in *Chionochloa rubra* in the Moawhango region. I attribute this variation to natural vegetation patterns, as opposed to the influence of herbivores. While it has been shown in this region (Rogers 1991) and others throughout New Zealand (Walker and Lee 2002) that *C. rubra* has the potential to be impacted by herbivory. No evidence of widespread suppression through herbivory was observed, although some individuals of *C. rubra* did show browsing impacts (which are examined further in Chapter 5). While no statistical analyses were run utilizing the height tier information sampled in the Scott height frequency method. The NMS ordination, along with the cluster analysis, iterated further the observational trends outlined in the SHF diagrams.

The NMS ordination separated the majority of the plots into regional clusters. A large proportion of the dissimilarity observed between the plots was observed on Axis 1. The strong positive correlation of *Chionochloa rubra* with Axis 1 indicates that this species was partially responsible for differentiation of the sites on this axis, with the plots situated on the left of Axis 1 in the NMS ordination graph (Figure 3.2) generally having lower proportions of *C. rubra.* The variation observed on Axis 2 was less for three of the four sites, with a strong separation of Motumatai from the other sites. When the species correlated with Axis 2 are examined (Table 3.2), it becomes apparent that the primary determinate of this separation is the high abundance of *Festuca ovina* at Motumatai (Table 3.2). Additionally there are several highly correlated species present at Motumatai that are not present elsewhere (*Leontodon taraxacoides, Phyllocladus alpinus, Anisotome aromatica*).

The cluster analysis further supported the observation made on the SHF diagrams, and the regional clustering observed in the NMS ordination. While cluster analysis was not intended for investigations into herbivory impacts, it permits the regional relationships of the plots to be analysed in further detail. The tight clustering of the Awapatu plots in the NMS ordination was supported by the low separation distances observed in the cluster analysis. Of all the sites measured in the Moawhango region, the three Awapatu plots had the closest grouping observed. The association of the highly impacted Motumatai unfenced control with the Awapatu group indicated that the vegetation was similar between the two areas (Plates 3.1 and 3.2). Since I have stated the vegetation in the Motumatai control is highly modified, the similarity could indicate that the Awapatu site is itself highly modified. However, if the site was highly impacted by herbivores, then a difference in vegetation composition between the individual plots at Awapatu would be expected (as seen at Motumatai). Since the Awapatu site evidenced no clear differentiation, even after 13 years of exclusion, I do not consider the similarities between the Awapatu site and Motumatai unfenced control plot to be as a result of similar herbivory. I suggest that historical herbivory by wild horses, rabbits, and hares, along with disturbance (i.e. fire) at the Awapatu site are the cause of the present similarities in composition and structure, not that present herbivory is impacting the site. However the structure and composition at the Motumatai unfenced control is induced by the strong browsing pressure exerted by horses in the region.

Plate 3.1: Photo of the unfenced control plot at Motumatai in the Moawhango region, with the exclosure at the rear.

Plate 3.2: Photo of the unfenced control plot at Awapatu exclosure site in the Moawhango region.

Visual inspection at the Motumatai site indicated abundance of several grass species in the unfenced control plot was severely reduced through obvious browsing by horses. This observation was supported by the SHF data obtained showing *F. rubra*, *F. novae-zelandiae*, and *F. ovina* having reduced abundances. Suppression of grass species in the unfenced control plot by horses seemed to enable enhanced growth of several prostrate species. This was in evidence most at the Motumatai unfenced control site. *Hieracium pilosella, Aceana microphylla, Wahlenbergia pygmaea, Leucopogon fraseri* were all major components of the unfenced control plot, but only represented a small proportion in both exclosure plots. While the abundances of the above species are related to horse browsing, I do not attribute the difference seen in *Chionochloa rubra* between the two exclosure plots at Motumatai to hare browsing. Hare presence in the exclosure plot was negligible with few faecal pellets observed. Furthermore, with no accurate historical data, differences prior to fencing can not be ruled out. The separation of the Motumatai horse and hare/horse exclosure plots is not as pronounced in the cluster analysis as in the NMS ordination. The primary separation of the two plots in the NMS ordination is partially due to the variation in *C. rubra* abundance, with the separation of the two plots on Axis 2 being minimal. And while appearing highly dissimilar in the NMS ordination, the grouping of the cluster analysis indicates that they are in fact more similar to each other than to the plots in the region. I also attribute the high presence of *C. rubra* for the apparent similarity of the Motumatai exclosure plots to the Argo Rd plots.

Both the Argo Rd sites showed a similar composition of modified grassland species, to that seen at Motumatai. Furthermore the close grouping of the Lower and Upper Argo Rd sites is indicative of their close spatial proximity. The cluster analysis of the horse and hare/horse plots for both sites showed a close within site relationship. But the between site distance was comparatively distant. However strong similarities were observed between the unfenced control plots of the Upper and Lower Rd sites. I suggest this similarity is an artefact of horse browsing modifying the vegetation present. As these sites are within the Kaimanawa wild horse area (Department of Conservation 1995) browsing by horses would be expected.

3.4.2 IMPLICATIONS AND RECOMMENDATIONS FOR MANAGEMENT

In the case of the plots measured in the Moawhango region, a certain level of browsing might be desirable to reduce the invasion of exotic weeds. As seen in three of the exclosures measured here, the complete removal of horse browsing resulted in domination of the plots by exotic grasses. However, high levels of horse browsing also resulted in the vegetation being dominated by exotic broadleaf weeds. Additionally, if the dense grass swards observed in the exclosures were to occur over the entire region, they would pose a considerable fire risk. Therefore it appears a moderate level of browsing might be required in some areas. The topic of horse presence in the Moawhango region is a volatile one, and not relevant to the aims of my study. However, the Kaimanawa Wild Horses Plan (Department of Conservation 1995) recognises that "Horses are not compatible with ecological values in the northern Moawhango District. Its fragile ecosystems make it very difficult to accurately manage horse impacts simply by manipulating horse numbers. As we cannot gamble with at-risk species the only long term solution is to remove all horses from the specified northern area". With the impacts of horses being well documented elsewhere (Rogers 1991; Rogers 1994), the full implications of their presence are not detailed here. This study simply further iterates the finding that horses are having a detrimental impact on the vegetation in the region. However it would appear horse impact has lessened since studies by Rogers (1991; 1994).

Two of the exclosure plots utilised in my study (Awapatu & Motumatai) were measured in a previous study on horse/hare impacts in the region (Rogers 1994). No evidence of hare impact was reported for the exclosures at that time. Unfortunately the two exclosure plots in the Awapatu valley in which Rogers (1994) noted hare/rabbit impact, were those that had suffered fence degradation and could not be used in my study. Vegetation condition in the Awapatu valley seems to have improved considerably, with none of the degradations described by Rogers (1994) being evident. Visual inspection of the other two exclosure plots in the Awapatu valley also indicated that their vegetation condition had improved markedly, although differences were still perceivable. The vegetation conditions observed at Motumatai in this study were consistent with those reported by Rogers (1991; 1994), and there was no perceivable improvement in vegetation condition in the unfenced control plot. These observations are consistent with the current management practises at each site. At Motumatai there has been no control of horses or hares since Rogers (1991; 1994), hence no improvement in the vegetation. Whereas the Awapatu site is now within the zero horse density area (Department of Conservation 1995), and undergoes ongoing rabbit and hare control (J. Mangos *pers. comm.*). This appears to have allowed the vegetation to "recover" since Rogers (1991; 1994). Since no estimates of hare/rabbit densities are available from the 1991/94 period, no direct comparison can be made. However the results from Chapter 2 show that hare densities in Awapatu are 1.7 hares/ha, which were the highest in the Moawhango region. Fortunately it appears that the Awapatu site has not become dominated by exotic species, which can occur if browsing is suppressing exotic weeds (Meurk *et al.* 2002; Walker and Lee 2002).

The extensive network of hare exclosure plots in the Moawhango region suggested an opportunity to provide major insights into the long-term browsing impacts of hares. However the power of this study was significantly reduced through the loss of original data and degradation of the exclosure fences. While data will inevitably be lost with the passage of time and personnel turnover, every effort should be made to preserve all data to ensure it is available for future research. Hopefully the creation of the National Vegetation Database by Landcare Research will prevent this occurring in the future. Additionally a prime opportunity was missed to assess the vegetation recovery trends for a wide range of vegetation types represented in the exclosures as no vegetation measurements were completed immediately after the construction of the Argo Rd exclosures. A significant opportunity to investigate lagamorph impacts was again lost with the fence degradation observed at several of the exclosures. However these exclosures were primarily intended to investigate the impacts of horses in the region, to which they remained effective. The degradation observed can primarily be attributed to snowfall damage and construction materials sagging over time. The netting used for the construction of the hare proof portion of the exclosures was unsuitable for long-term exclosure plots. It was of a soft chicken wire construction with little strength and so sagged easily with time, further to this it appears to corrode easily. Fully galvanised diamond mesh netting of 900 mm in height should be used in the construction of hare exclosures.

3.4.3 CONCLUSIONS

At their current densities, hares are having no perceivable effect on the long-term general composition and structure of vegetation present in the Moawhango region. In contrast, horses appear to be having a considerable impact on vegetation structure and composition where present. This is particularly true at Motumatai where no horse management is undertaken. Horse impacts appear to have been reduced since the study of Rogers (1991) for the Awapatu site but not at Motumatai. I recommend that horse management be undertaken at Motumatai to prevent further degradation of the vegetation. Our power to detect hare impacts has been reduced through the loss of data and fence degradation. In spite of the results from this chapter, I suggest caution in dismissing hare impacts with the limited data available here.

Chapter 4

Development of a monitoring protocol to assess hare browsing impacts

Construction of exclosure site 1 at Manson

4.1 INTRODUCTION

The assessment of hare (*Lepus europaeus*) browsing impact in alpine vegetation has been the subject of much speculation, and while several studies have been attempted in the past for New Zealand, little is actually known and there is a shortfall in knowledge in many areas. Each of the three studies completed on hare impacts (Blay 1989; Rose and Platt 1992; Rogers 1994) has taken a different approach, using differing experimental designs and sampling protocols (Table 4.1). Furthermore, at the initiation of this study, there were no guidelines for assessing hare impacts in alpine grasslands. Therefore there is a need for a monitoring protocol designed specifically to assess hare browsing impact in New Zealand alpine grasslands. Browsing can influence the species richness, relative abundance, and physical structure of a vegetation community (Huntly 1991). Therefore experimental design will be dependent upon the specific impact of interest and the shortfall of knowledge regarding hare impacts leaves many avenues open for research. I aimed to develop, implement, and test a monitoring protocol for assessing the impact of hare browsing on species composition and vegetation structure. And use this protocol to assess short-term vegetation responses to the removal of hare browsing pressure.

Traditionally herbivore impact studies in New Zealand have been based upon the use of exclosure plots (e.g. McIntosh *et al.* 1997; Bellingham and Allan 2003). However, other methods must be considered when initiating a monitoring program. Observational surveys can provide information on plant species susceptible to browsing. But for comprehensive monitoring, browsing pressure needs to be reduced or removed so the length and degree of recovery can be assessed. Preferably this would occur over a period of time relevant to the potential recovery abilities of the ecosystem of interest. For example, *Chionochloa pallens* can take up to 30 years to fully recover from severe browsing (Lee *et al.* 2000). However, the extended time periods involved in alpine grassland recovery mean that reliance is often placed upon historical studies. For that reason, any investigation should consider the potential value of their research for future studies and incorporate a degree of permanency into the monitoring.

Table 4.1: Experimental design and vegetation sampling methods used in previous investigations into hare browsing impact in New Zealand.

Study	Experimental design	Vegetation sampling
Blay (1989)	-Six 1.4 x 1.4m exclosure plots and controls -3 sample periods Initial + 8 mo + 5mo = 1.1yr	-Biomass calculations through vegetation clipping, drying and weighing of 300 x 300 mm areas
Rose and Platt (1992)	-One exclosure plot and control - 900m^2 -1 sample	-Mapping and measurement of all *Chionochloa* individuals -Visual estimation of cover
Rogers (1994)	-Four split plot exclosures of 20 x 20m -2 samples, 7 yrs apart	-100 modified Scott (1965) sampling points -Randomly located 2m^2 quadrats recording tussock density, size class, and stature

One approach is to initiate a control program to reduce herbivore densities over a large study area. Resulting changes in the vegetation can then be assessed, and compared with non-treatment areas (Wong and Hickling 1999). Complete removal of hares is unlikely to occur during a control program, with a reduction in hare numbers more likely. For example Parkes (1981) assessed hare population recovery following a control program in inland Canterbury where, after an initial reduction of 60%, hare numbers recovered substantially in the subsequent breeding season. This result emphasises that maintenance of hare populations at low densities, requires an ongoing commitment to control. This type of study would provide information on vegetation responses to a reduction in numbers, which is more likely to be of use to managers, as opposed to complete removal data provided by exclosure plots (Wong and Hickling 1999).

Exclosure plots have been used extensively in New Zealand to assess herbivore damage. For instance they have been used to assess damage by rats (Campbell and Atkinson 2002), goats (Bellingham and Allan 2003), deer (Bellingham and Allan 2003; Husheer 2003), horses (Rogers 1991), rabbits (McIntosh and Allen 1998), and hares (Rose and Platt 1992; Rogers 1994). Exclosure plots have the advantage that they allow for the exclusion of different herbivores in close spatial proximity. Split plot exclosures as used by Rogers (1991; 1994) excluded all grazers from half of the exclosure, but allowed hares to access the other. This system allows for the different grazing impacts of large vs. small herbivores to be determined. Exclosure plots have the advantage of providing information on grazing impacts with little ongoing commitment after the initial set-up. When remeasuring established exclosure plots, if accurate historical data are available, temporal comparisons can be made. However if data are not available, differences observed could be due herbivore pressure, or to random variation in the vegetation. Several studies have used established exclosure plots to assess long term trends in vegetation composition induced by herbivores (e.g. Husheer 2003). In other cases, small, short-term exclosures have been used to assess herbivore impacts (Blay 1989). However short-term investigations ignore the potential long-term vegetation impacts of herbivory. In any case, the above methods need not be used singularly, and an integrated approach can give a comprehensive view into herbivore impacts and responses to management practices.

An example of how various methods can be combined to improve understanding of herbivore impacts can be seen in the extensive study of the impacts of deer on Kaimanawa and Kaweka beech forests by Husheer (2003). Combinations of established and new exclosure plots were used, along with differing control practices, to assess deer impacts forest composition and seedling regeneration. Established plots were used to determine compositional changes that had occurred in the forest over the last two decades. New exclosures were established in areas of differing control practices to determine impacts of deer on Mountain beech (*Nothofagus solandri* var. *cliffortioides*) seedling growth responses under varying management practises. By integrating these approaches, it was demonstrated that 1) intensive aerial culling of deer increased seedling growth to a level comparable to exclosure plots. And 2) that deer control through enhanced recreational hunting did not increase seedling growth.

While an intergrated approach may be desirable, many agencies interested in implementing a monitoring program for hares will not have the resources available for a comprehensive exclosure/management policy. Additionally, the time period over which a study occurs should be relevant to the potential recovery abilities of the ecosystem of interest. Making the use of short-term exclosures and control regimes unsuitable. Therefore, I developed a monitoring protocol based around the use of permanent exclosure plots. Ideally any research will attempt to answer as many questions as possible. And while the main aim of this chapter is to investigate the impact of hare browsing on species composition and vegetation structure, this does not exclude the incorporation of additional sampling to address knowledge gaps (Chapter 5).

Three exclosure plots were established in the Manson region of the Kaweka ranges in order to test the monitoring protocol developed, and assess the short-term vegetation responses to the removal of hare browsing pressure.

4.2 METHODS

4.2.1 SELECTION OF MONITORING PROTOCOL

4.2.1.1 Experimental design

The monitoring protocol developed consisted of a three-way split plot exclosure with four vegetation monitoring plots. The treatments consisted of a deer exclusion - hare/deer exclusion (plot A), hare access plot (plot B), unfenced control (plot C), hare exclusion - deer access (plot D). Each treatment consisted of a 6 m x 6m exclosure, in which a 4 m x 4m vegetation sampling plot was located. Split plot exclosures as used by Rogers (1994) consisted of a two-way split plot exclosure, which excluded all grazers from half of the exclosure, but allowed hares to access the other. The addition of the extra treatment (hare exclusion - deer access) in this study allowed for a further region of comparison between the herbivores. Difference in large vs. small herbivores can be inferred by simply excluding the large herbivores and allowing access by hares. However by allowing deer to access without hares, the relationship between the two browsers can be examined more rigorously.

The vegetation sampling plots were arranged adjacent to each other, forming a block of four squares. Since the control plot was unfenced, it created an L shaped fenced area (Plate 4.1). Exclosures were setup so as each plot had equal access opportunities. Both hares and deer had three sides of the exclosure to access the plots. Hares had access to plot B through the holes present in the deer netting used. Deer had access to plot D by jumping the netting.

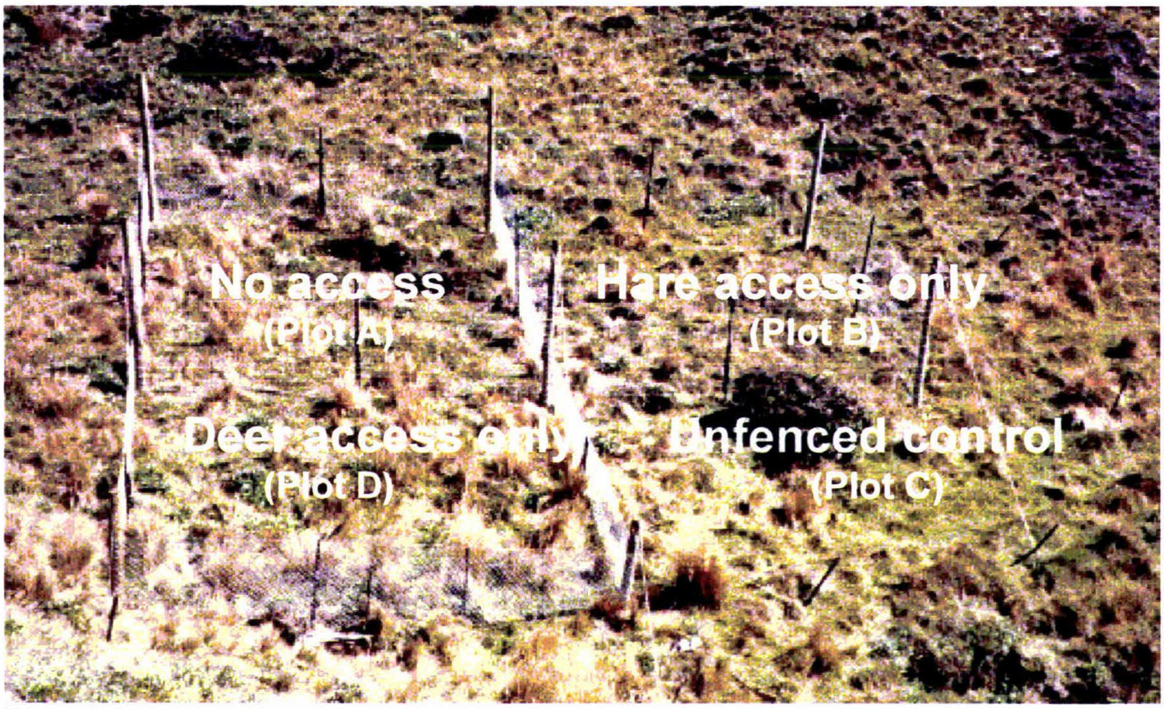

Plate 4.1: Photo of the split plot exclosure design at one of the three sites in the Manson region. Each fenced segment is 6 m x 6 m in size. The layout of the four treatments is also shown.

4.2.1.2 Vegetation sampling:

Of the many methods available for assessing alpine vegetation, Dickinson *et al.* (1992) advocate the Scott (1965) height frequency (SHF) method as a multipurpose vegetation monitoring tool to assess vegetation structure and floristic composition. The method has been used to show spatial and temporal changes in a wide range of vegetation including cushionfields, herbfields, tussocklands, wetlands, and shrubland up to 1.5m tall (Dickinson *et al.* 1992). It has also been used to show seasonal changes in the semi-arid vegetation of Central Otago (Walker *et al.* 1999), and the impact of horses on tussock grasslands in the Central North Island (Rogers 1991). After a review of methods available for monitoring alpine vegetation, and an evaluation of the Scott height frequency method, Perry (2003) concurred with Dickinson *et al.* (1992) as to the value of the method as a vegetation monitoring tool. However several areas of weakness were raised. It was found that the method did not accurately detect all species present in the vegetation plots. Nevertheless it provided detailed information on the structure and dominance relationships of the major species. Common species were detected accurately at low sample sizes with precision of frequency results remaining high even when sample sizes were halved. However uncommon species were highly variable in species detection and precision of frequency results, even at large sample sizes. Therefore it was suggested that presence/absence quadrats be used when implementing a monitoring program to allow for improved sampling of rare species. This suggestion was employed here and presence/absence quadrats incorporated in the sampling design. Furthermore, it was suggested that for low stature, homogenous vegetation, the number of sampling points could be reduced and accurate result still be obtained for the common species. This would allow for smaller exclosure plots and increased replication when limited resources were available. For that reason 45 sampling points were used for each plot in my study. This number is lower than the traditional 100 sampling points used for this method. The data obtained using 45 points should be within 5% of the values from 100 sampling points for the dominant species (Dickinson *et al.* 1992; Perry 2003).

4.2.2 FIELD PROCEDURE

4.2.2.1 Site Selection

Sites for the Manson exclosures were selected on a restricted random basis. A ground survey of the Manson tops was carried out and areas that met selection criteria were marked onto a map. Selection criteria were: within 40 m of a bush area, generally suitable for fencing, vegetation indicative of the general area. Three sites were then randomly selected from this information. Exact plot placement was subjective to ensure the area was suitable for exclosure construction.

4.2.2.2 Vegetation description

The vegetation in each plot was assessed using a combination of Scott height frequency (1965) sampling points (SHF), and presence/absence quadrats. A total of 32 presence/absence quadrats of 0.5 x 0.5 m were sampled in each vegetation plot, along with 45 SHF sampling points. Five transects of four metres in length were run with SHF sampling points every 0.5 m (see Figure 4.1 for layout). For each sampling point, a continuous sampling column occurred from the ground, to the maximum height of vegetation though the incision of a rod marked at 5 cm intervals. An open-ended frame measuring 5 cm (vertical) x 5 cm (horizontal depth) x 4 cm (horizontal width) was then inserted at each 5cm height tier, and all plant species present within the confines of this space were recorded (total area of each frame = 100 cm^3). When data from the sampling points were combined, each species had the number of occurrences in each height tier summed across the plot. Additionally, by summing the number of occurrences of a species in all height tiers, a summed height frequency value was obtained that represented the total abundance of that species in the plot (biomass index).

Exclosures were constructed in late February–early March 2002. Vegetation sampling occurred at least 2 weeks after construction to allow vegetation recovery. Vegetation sampling occurred during March 2002, and was repeated in March 2003.

Herbivore use of the exclosure plots was assessed by counting and removing all faecal pellets. Pellets were initially cleared after exclosure constructions in March 2002, the first remeasure was in April 2002 (day 23), followed by May (day 53), June (day 88), October (day 213), December (day 270). The final measure was in March 2003 (day 350).

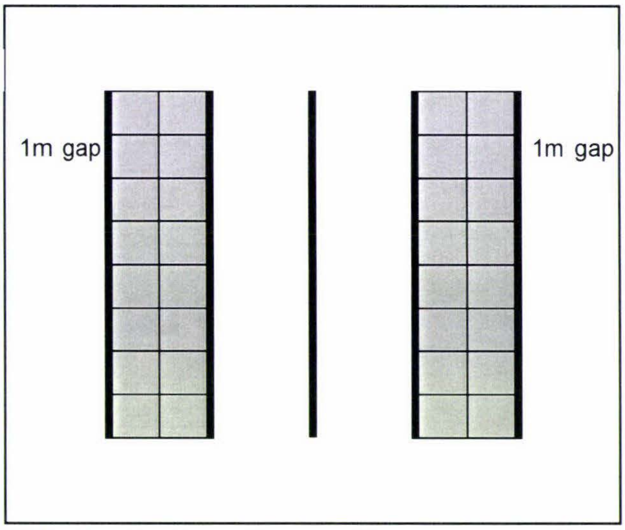

Figure 4.1: Layout of the interior 4 m x 4 m sampling area present in each of the four treatments found in one exclosure site in the Manson region. The presence/absence quadrats were placed as shown by the shaded squares, with the Scott height transects run on the bold vertical lines. The 1m gaps in the middle and along the fence are to allow for the measurement of the plot without trampling the sample area.

4.2.2.3 Statistical Analysis

Height tier data was utilised by visually inspecting Scott height frequency (SHF) diagrams drawn using the graphing program MAC Juno (courtesy of Stephen Marshall, Victoria University, Wellington). This allowed compositional and structural differences to be interpreted between sites, plots, and years. Species names were abbreviated in these diagrams to the first three letters of the genus (uppercase) followed by the first three letters of species (lowercase). A list of full species names for these abbreviations can be found in Appendix 1. All further analyses used summed Scott height frequency values and were run using PC-ORD 4.0 (McCune and Mefford 1999). Blocked Multi-Response Permutation Procedures (MRBP) were run to test for significant changes between years for the entire region, and each site. Nonmetric Multidimensional Scaling (NMS) ordinations were carried out on the summed SHF values from each plot over the three sites. The distance measured used was Sorenson (Bray-Curtis) as suggested by McCune and Grace (2002) for analysis of community data. Random starting configurations were used with six axes initially assessed using 40 runs of real data, 50 with randomized data and 400 iterations. Autopilot mode was used to select optimal dimensionality. Cluster Analysis was run on the summed SHF values from each plot over the four sites. Sorenson (Bray- Curtis) distance measure was used along with Flexible beta group linkage method (beta = -0.250). Species data were also grouped into guilds for detection of general trends and species were assigned as into native grasses, native herbs, exotic grasses, or exotic herbs. Unless otherwise stated significance level was $P < 0.05$.

4.3 RESULTS

4.3.1 VEGETATION DESCRIPTION

A total of 69 species were detected over the three sites at Manson. The two sampling methods emphasised different aspects of the dominance relationship at each site. The summed SHF data indicated that the taller grass species were dominant (see Appendix 3 for plot by plot rankings), whereas the quadrat data placed a high emphasis on herbaceous, spreading species which are more frequent, but lesser stature than the taller shrubs and tussocks (see Appendix 4 for plot by plot rankings).

Site 1: The two methods were relatively consistent with regard to dominance at Site 1. *Celmisia spectabilis* was dominant for both methods with *Leucopogon fraseri, Poa colensoi,* and *Racomitrium lanuginosun* also ranking highly.

Site 2: Out of the three sites, the highest proportion of exotics species present was found at this site. Both methods showed five of the top ten species to be exotics. The community was comprised of grasses and herbs, with lower proportions of herbfield species present. The quadrat data for Site 2 listed a high proportion of herbs to be dominant. *Trifolium* spp. were the most dominant, with *Blechnum penna-marina*, *Holcus lanatus*, and *Viola cunninghamii* also conspicuous. The summed SHF data indicated that grasses rated highly in terms of dominance. *Holcus lanatus* was dominant with *Poa cita*, *Anthoxantum odoratum*, and *B. penna-marina* also being ranking highly.

Site 3: The dominant species at this site were the native grasses. The summed SHF data showed *Rytidosperma setifolium* as dominant along with *Poa colensoi*, *Deyeuxia avenoides*, and *Anthoxantum odoratum*. The quadrat information placed *Hypochoeris radicata* as dominant with *P. colensoi*, *R. setifolium* and *C. spectabilis* also important.

4.3.2 NONMETRIC MULTIDIMENSIONAL SCALING (NMS)

The Nonmetric Multidimensional Scaling (NMS) ordination was run using two dimensions (Appendix 5 for Monte Carlo test). There were 71 iterations in the final solution, with a resulting stress of 7.53. The stress value is a measure of departure in plot distances required to fit original distances in ordination space, to a 2-D ordination graph (McCune and Grace 2002). The stress value obtained in this study, using Clarkes

(1993) rule of thumb, indicates "a good ordination with no real risk of drawing false inferences". The proportion of variance represented by each axis based on the r^2 distances was 0.826 for Axis 1 and 0.115 for Axis 2. The cumulative r^2 for both axes was 0.942. The NMS ordination grouped the vegetation plots into three distinct clusters corresponding to each site, with no overlap (Figure 4.2). The ordination distances were less between sites 1 and 3, than between these sites and site 2, indicating that those sites are more similar in composition. The directional shift observed between the plots at sites 1 and 2, indicate that a change in vegetation occurred at those sites between 2002 and 2003. Further observations using the NMS ordinations are discussed below.

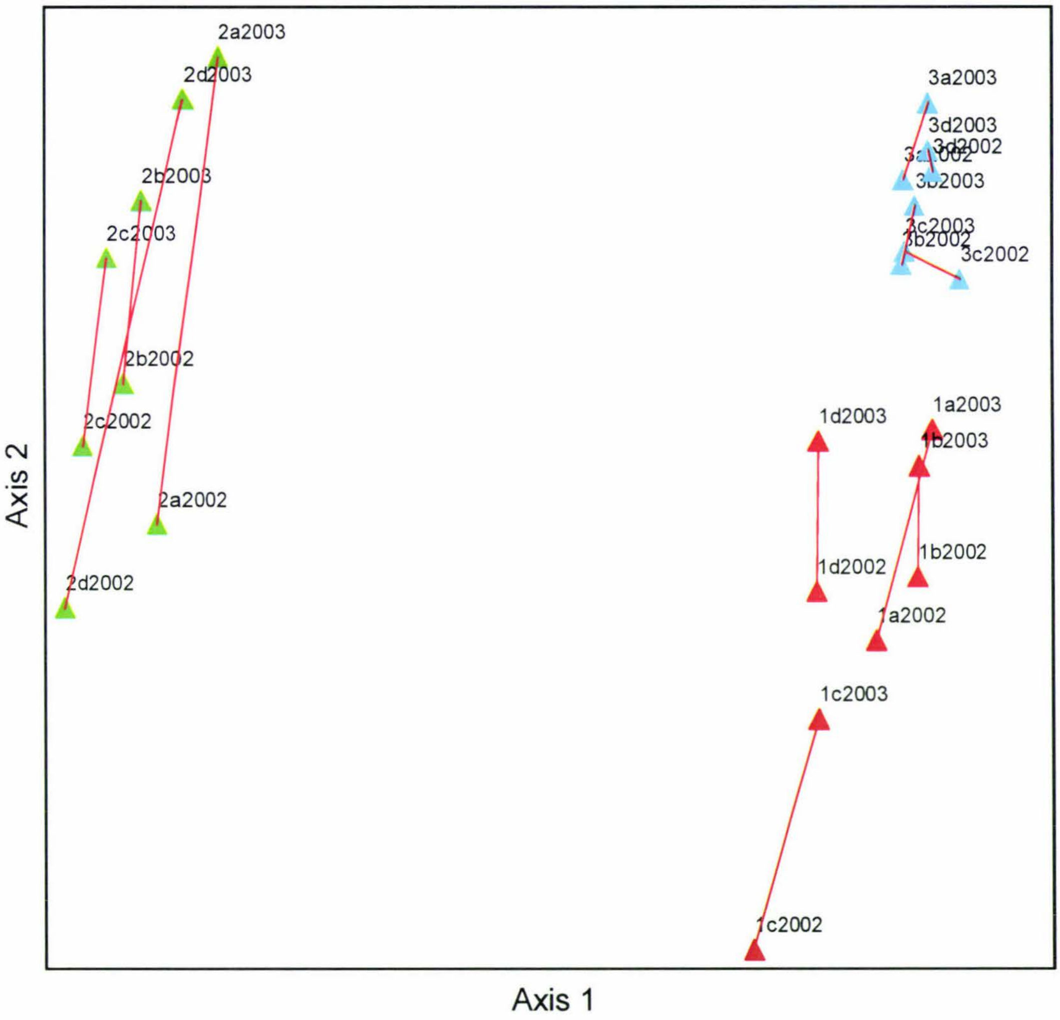

Figure 4.2: Graph of the Nonmetric Multidimensional Scaling (NMS) ordination run on the 2002 and 2003 summed Scott height frequency data for each plot at the three exclosure sites present in the Manson region. Each plot is coded so the first character = site, second character = plot, followed by year e.g. 1a2002 = site 1, plot A, measured in 2002. Plot A: hare/deer exclusion, plot B: hare access – deer exclusion, plot C: unfenced control, plot D: hare exclusion - deer access.

4.3.3 TEMPORAL CHANGES

4.3.3.1 General Region

Visual inspection of the SHF diagrams indicated that there was a general increase in vegetation abundance across the region (Figures 4.3a, 4.3b, 4.3c). This was indicative of the increased growth and flowering observed for most species over the entire region (not just the exclosure sites). This confounded the interpretation of results as changes occurred in the vegetation that could not solely be attributed to exclusion of browsing. Yet several trends were observed that could be attributed to browsing (Plate 4.2). Visual inspection of the summed SHF guild data confirmed the general pattern with increases observed for most guilds and sites (Figure 4.3c). With the Blocked Multiple Response Permutation Procedure (MRBP) run on the SHF and quadrat data showing that the increases observed over the entire region were statistically significant (Table 4.2).

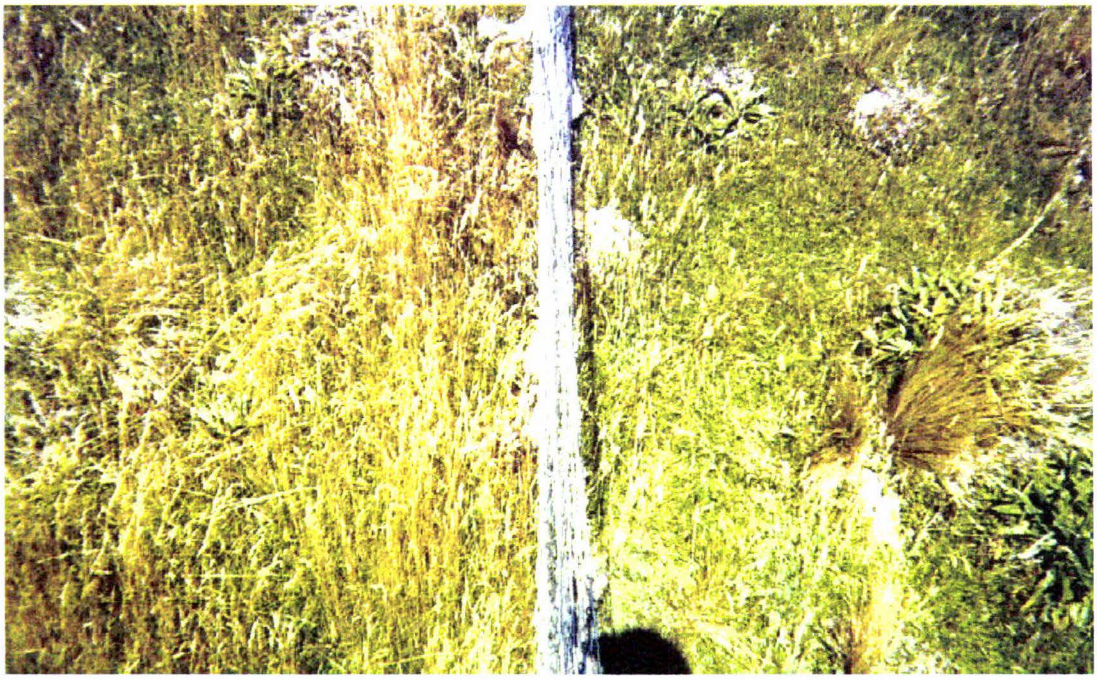

Plate 4.2: Photo of exclosure Site 2 in the Manson region taken one year after exclosure construction. Photo is taken from above looking down on dividing fence. Both hares and deer are excluded from the left hand side (plot A), hares only (no deer) have access to the right hand side (plot B).

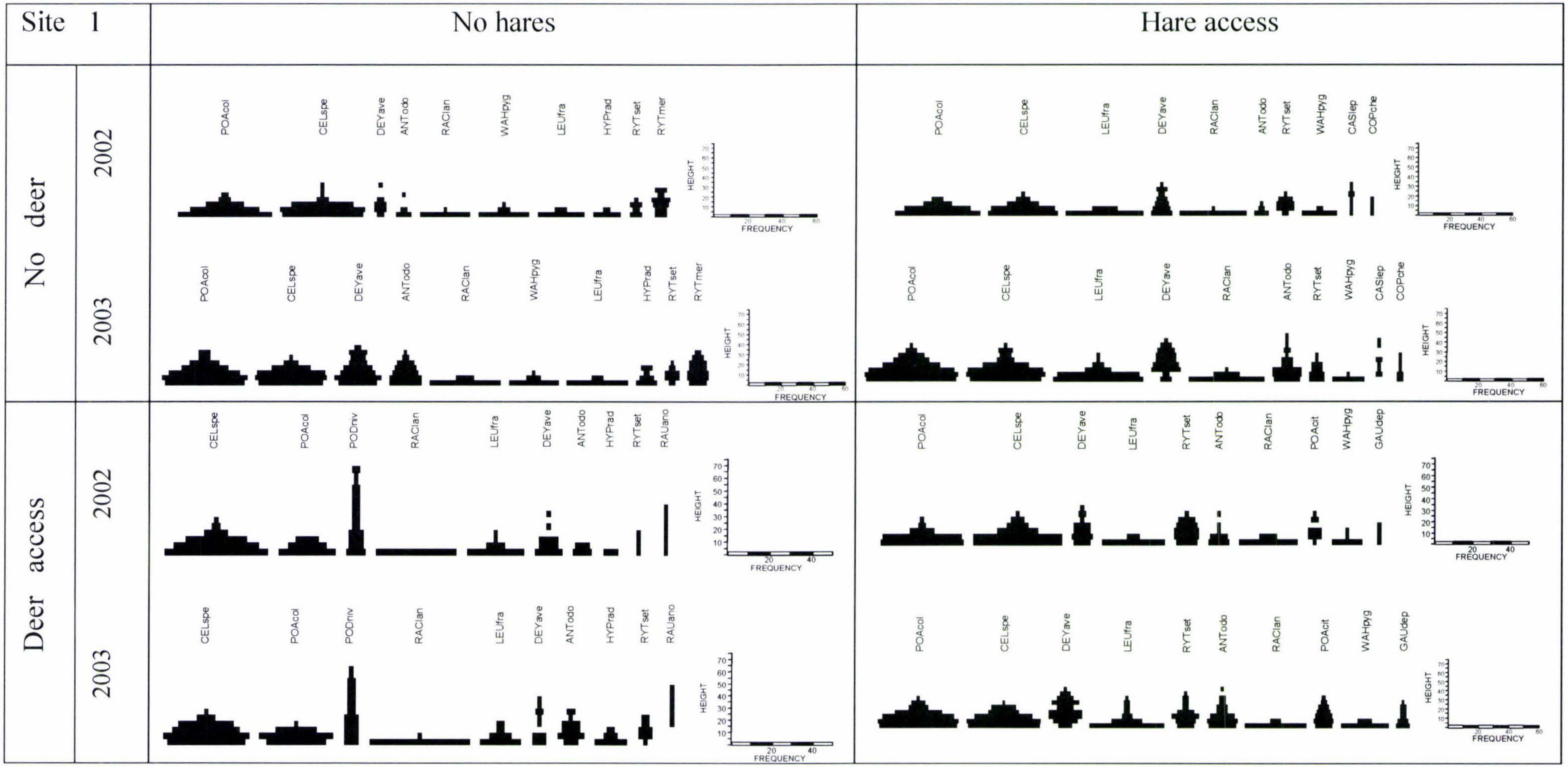

Figure 4.3a: Scott height frequency diagrams of the top 10 ranked species in each plot (for 2002 & 2003) for the vegetation measured at Site 1 of the Manson exclosures.

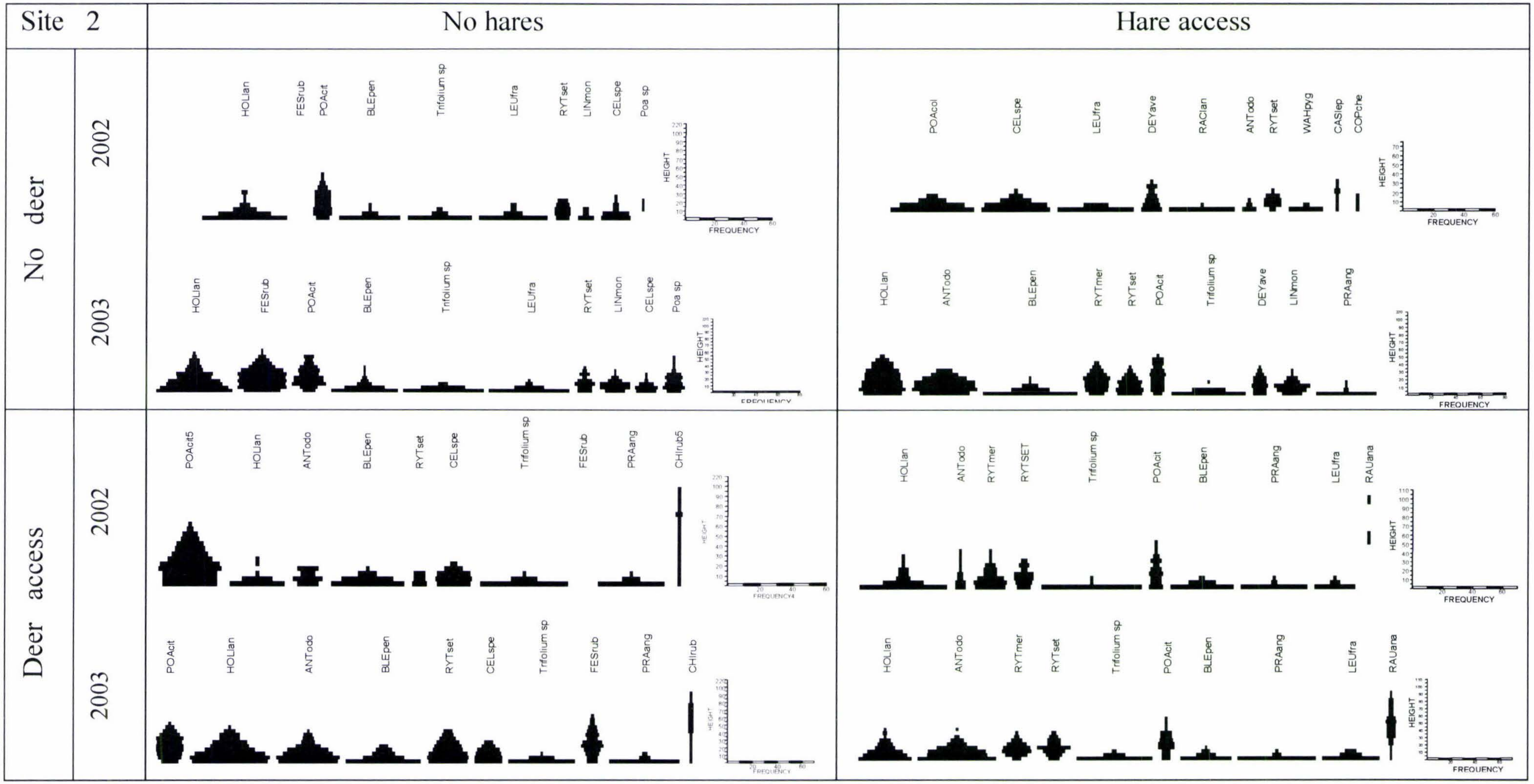

Figure 4.3b: Scott height frequency diagrams of the top 10 ranked species in each plot (for 2002 & 2003) for the vegetation measured at Site 2 of the Manson exclosures.

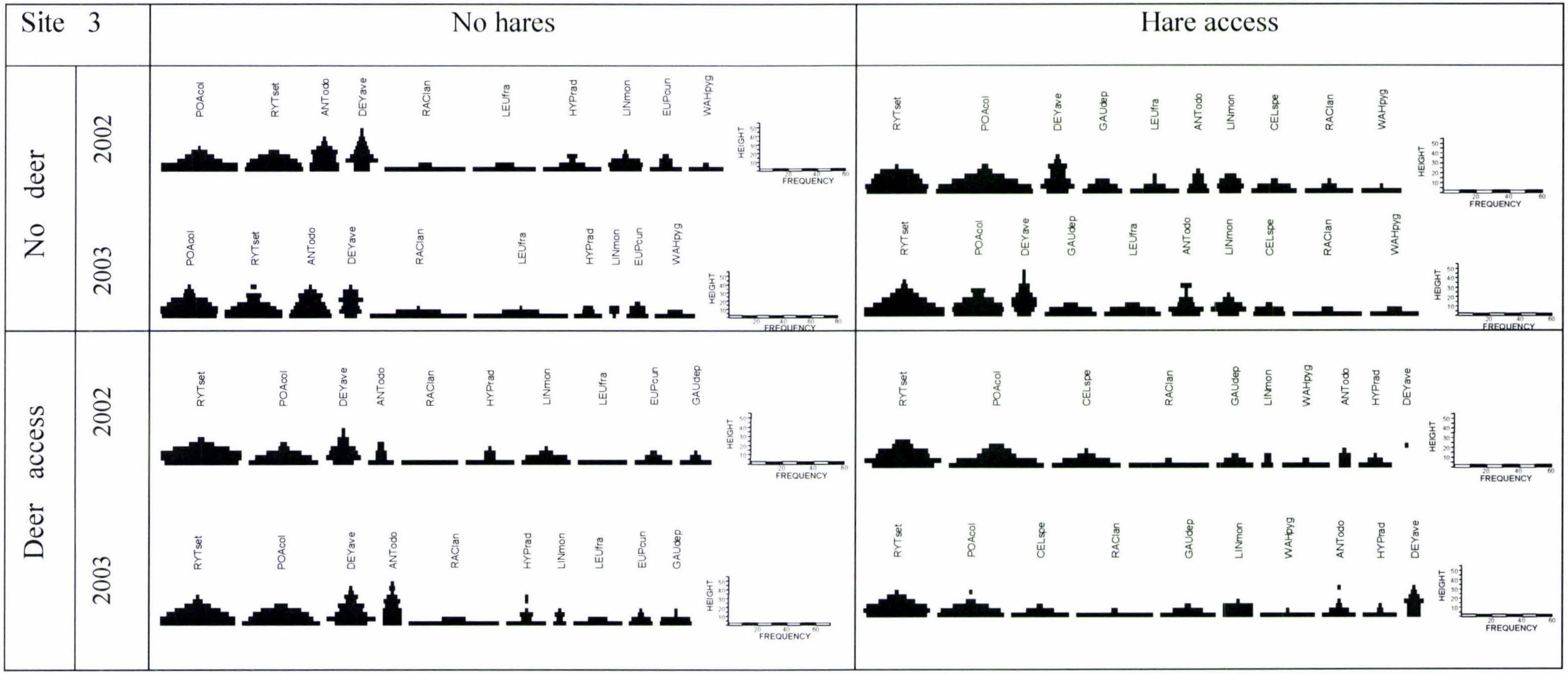

Figure 4.3c: Scott height frequency diagrams of the top 10 ranked species in each plot (for 2002 & 2003) for the vegetation measured at Site 3 of the Manson exclosures.

Table 4.2: Blocked Multiple Response Permutation Procedure results comparing the initial and final measurements of the three exclosures sites present in the Manson region. *A* = Chance-correlated within-group agreement. Significant result in bold.

	Sample Method	Data type	groups	blocks	P	*A*
All sites	SHF	species	2	12	**<0.001**	0.268
	SHF	guilds	2	12	**<0.001**	0.268
	Quadrats	species	2	12	**0.007**	0.058
	Quadrats	guilds	2	12	**0.005**	0.170
Site 1	SHF	species	2	4	**0.036**	0.370
Site 2	SHF	species	2	4	**0.030**	0.302
Site 3	SHF	species	2	4	0.066	0.133

4.3.3.2 Site specific temporal changes

Site 1: General increases were observed in most species (Figure 4.3a) and guilds (Figure 4.4) at Site 1, with MRBP showing the increase to be statistically significant (Table 4.2). The increases were universal across the plots for most species and guilds, with no difference between the four plots. However an anomalous observation occurred in plot C for the native grasses guild. This plot showed little increase when compared to the remainder of plots at this site. The general change in abundance at the site was reflected in the NMS ordination graph with a consistent shift in one direction for all plots (Figure 4.2). While plot C showed a similar change in direction and distance as the other plots, the NMS ordination separated both measurements of plot C from the other three plots. Both years were clearly distant from the other plots for both years.

Site 2: The most obvious increase in vegetation of the three exclosure sites occurred at Site 2, with the MRBP showing this change to be significant (Table 4.2). The most notable increase occurred in the exotic grasses guild (Figure 4.4). While all plots showed a marked increase in this guild, in the two plots that had had hare browsing pressure removed (plots A & D), the increase was over double that observed in the hare access plots (plots B and C) (Figure 4.4). Although not as pronounced, this trend was also observed in the exotic weeds and native grasses guilds. The native herbs guild showed a general increase at this site but no trends could be discerned. When the above trends are examined in detail using the SHF diagrams (Figure 4.3b), several species stand out as responsible for the differential changes observed. The site is dominated by exotic grass species such as *Holcus lanatus* and *Anthoxantum odoratum*, and while a large increase was observed in these species, it could not be solely attributed to the removal of hare browse. However one species that increased disproportionately at the site was *Festuca rubra*. It was not detected at all in the initial 2002 measure, but constituted a significant proportion of the plot in the 2003 measure. In 2003 it was detected in the hare access plots, but only in low numbers (summed SHF values, plot B = 8, plot C = 16 occurrences). However in the hare exclosure plots it became one of the dominate species, ranked third in plot A, and seventh in plot D.

Site 3: The NMS ordination shows that there was little or no change in the vegetation composition at site 3. This was supported by the MRBP showing no significant change between the two sampling periods (Table 4.2). Even so, some changes occurred in the guilds that were possibly due to browsing pressure. The exotic weeds guild decreased in abundance for the two hare exclosure plot (plots A and D), while staying relatively constant in the hare access plots (plots B and C). Conversely the native grasses guild increased in the hare exclosure plots, but stayed constant in the hare access plots (Figure 4.4).

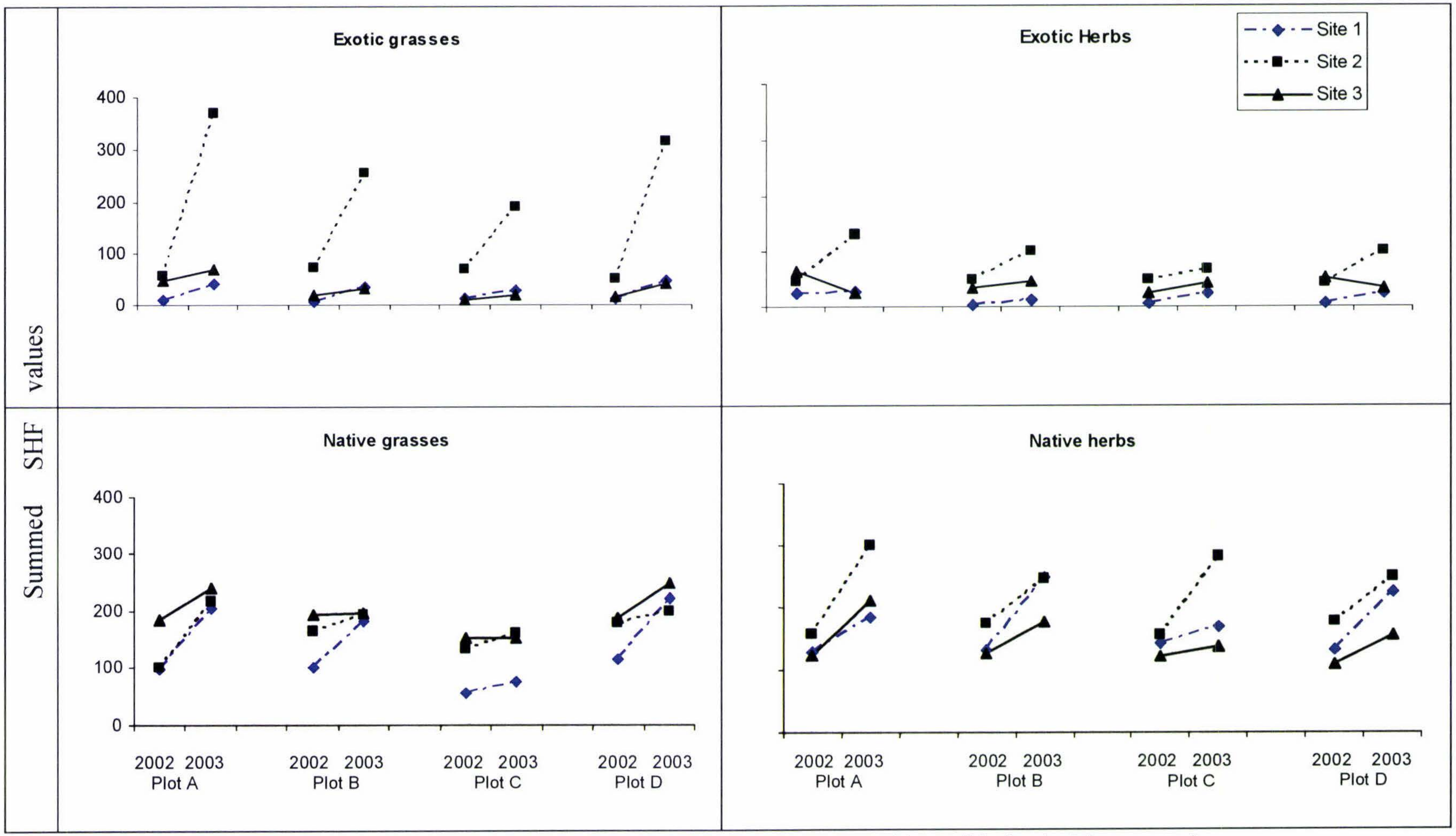

Figure 4.4: Changes over one year in the summed Scott height frequency values grouped by guilds for the Manson region.
Plot A: hare/deer exclusion, plot B: hare access – deer exclusion, plot C: unfenced control, plot D: hare exclusion - deer access.

4.3.4 CLUSTER ANALYSIS

When the summed SHF data was run through cluster analysis, the three sites were clearly differentiated (Figure 4.5). The first differentiation made by the cluster analysis was the separation of sites 1 and 3 from site 2. Site 1 showed a differentiation between years for three of the four treatments. For both years the control plot was grouped separately from the other three plots. The remaining three plots showed a clear differentiation between the years. At Site 2 there was a clear differentiation between the years for all plots at site 2, with no clear pattern to the plot groupings in 2002. However in 2003, the cluster analysis grouping resulted in the hare exclusion plots (A with D) being grouped together, with the hare access plots (B with C) clearly separated. However at Site 3 there was no evidence of any grouping either by year or treatment.

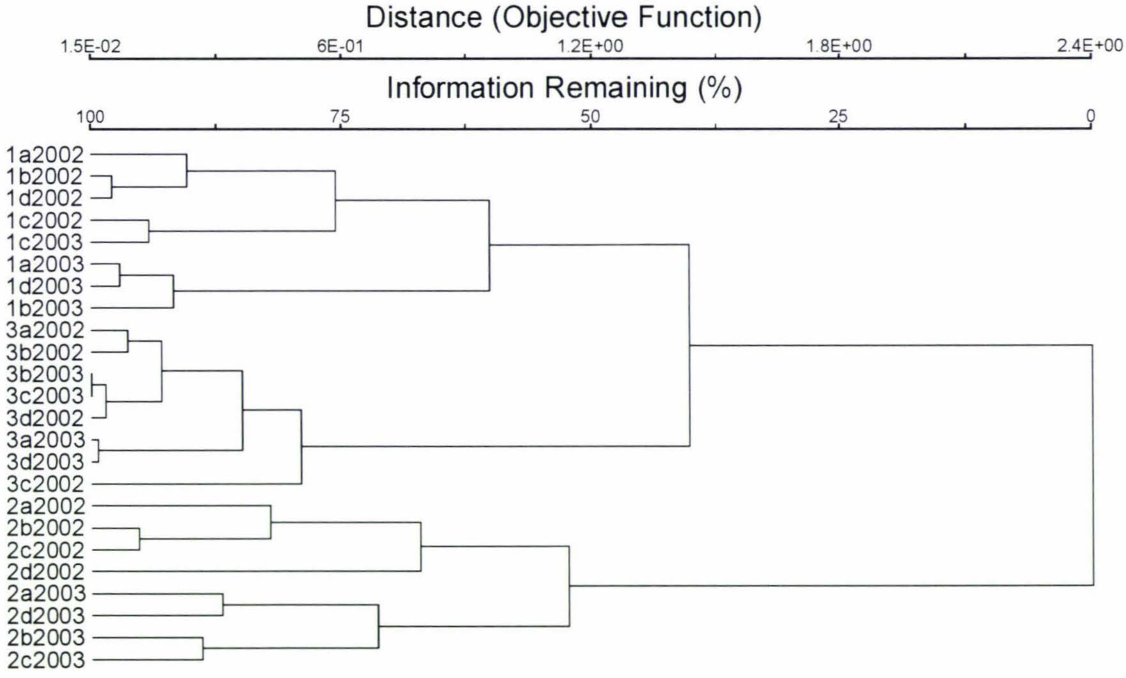

Figure 4.5: Cluster analysis dendrogram on the 2002 and 2003 summed Scott height frequency data for each plot at the three exclosure sites present in the Manson region. Each plot is coded so the first character = site, second character = plot, followed by year e.g. 1a2002 = site 1, plot A, measured in 2002.

4.3.5 HERBIVORE USE OF EXCLOSURE PLOTS

Use of the exclosure plots by hares was highly variable over the year (Figure 4.6). In mid autumn (April), the initial hare use of the plots was low, however there was then a large peak in recruitment rates at the next sampling period in late autumn (May). This was followed by a drop in recruitment over winter, and an increase in spring (October). There was then a large decrease in December at the final remeasurement of the plots. The average recruitment rate over the course of one year for all sites was 0.55 pellets/m^2/day. With the average for sites 1, 2, and 3 being 0.5, 0.5, and 0.6 pellets/m^2/day respectively. Deer pellets were present in the exclosure plots at construction, but no pellets were observed in any of the plots during any of the pellet counts. Possum pellet recruitment in the exclosures was relatively constant, with a slight drop in autumn. The average recruitment rate over the year being 0.03 pellets/m^2/day. Over the total period of the study 454 possum pellets were cleared for site 1, 671 from site 2, and 545 from site 3.

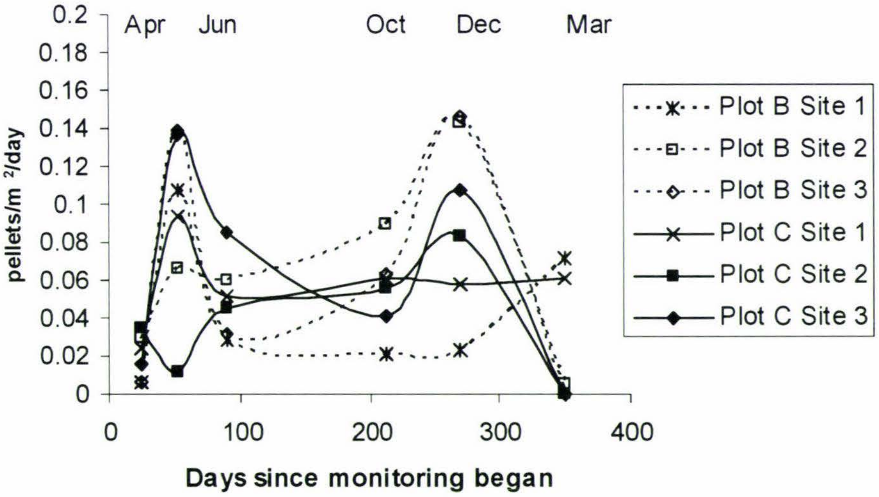

Figure 4.6: Recruitment rates of hare pellets cleared off the hare access plots (plots B & C) at the three exclosure sites located in the Manson region. Months are those in which monitoring occurred.

4.4 DISCUSSION

4.4.1 VEGETATION CHANGES

The increased growth and flowering observed for most plant species over the entire region significantly complicated interpretation of the results. However the exclosure plot monitoring design used in this study showed that hares in the Manson region have minimal effect upon native vegetation in the exclosure plots, at least in the short-term. But they do appear to be having a significant dampening effect upon several introduced grass species in the region. Both the NMS ordination and the cluster analysis indicated similar trends in the vegetation composition. With sites 1 and 3 being clearly differentiated from site 2, and the vegetation at sites 1 and 2 being significantly different between 2002 and 2003. Vegetation at Sites 1 and 3 was comprised primarily of native species. Overall abundance of species at Site 1 increased significantly over the year, and no trends attributable to browsing were observed. Whereas the vegetation at Site 3 did not change significantly, although removal of browsing resulted in a slight increase in native grasses and a decrease in exotic weeds. The vegetation at Site 2 showed a significant change in vegetation over one year, with exotic grasses, exotic herbs, and native grasses all increasing disproportionately in the hare exclusion plots at this site.

Rogers (1994) concluded at two of the sites studied, that hares had no effect on native vegetation because the animals were thought to feed mainly on exotic grasses. In my study I suggest that hares are not only having no effect on native species composition, they may in fact be beneficial to the retention of native vegetation due to their selective suppression of exotic species. Three prominent invasive weed species identified by Walker and Lee (2002) in modified grasslands were *Hieracium pilosella, Festuca rubra,* and *Agrostis capillaris*, all of which were present in the Manson exclosures. In particular, *F. rubra* showed a substantial increase with the cessation of hare browsing. The large increase in this species following hare exclusion indicates that hares are having a significant suppression effect upon this species. While no other obvious changes occurred in abundance or composition for other species, the short time frame means that any further adverse or beneficial effects may not yet be apparent. However the general results obtained in this study are consistent with the current literature regarding vegetation trends after the removal of browsing (e.g. Lord 1990; Duncan *et al.* 2001; Meurk *et al.* 2002; Walker and Lee 2002).

It is well documented that substantial vegetation changes have occurred in New Zealand tussock grasslands over the past 150 years (Meurk *et al.* 2002). Currently there appears to be a widespread decline in species richness throughout New Zealand's tussock grasslands, particularly those of Otago and Canterbury (Duncan *et al.* 2001). With climate change, burning, grazing, introduction of exotic species, and soil type being cited as probable causes (Lord 1990; Duncan *et al.* 2001; Meurk *et al.* 2002; Walker and Lee 2002). Of particular concern is the collective effect of the browsing removal and subsequent invasion of exotic species. The removal of grazing is not always beneficial to native vegetation and does not guarantee reversion to a "natural" state. It appears that vegetation transformations after grazing removal are dependent on the both the native and exotic species present, historical grazing, and site characteristics. In many grasslands, grazing serves to maintain high species diversity through suppression of exotic species (Duncan *et al.* 2001). With the cessation of grazing exotic species appear to increase in dominance and competitively exclude native species. The tall tussock (*Chionochloa* spp.) grasslands appear more resistant to this invasion, as the dense canopies and thick litter layers confer the greatest resistance to invasive species such as *Hieracium pilosella*. However short tussock (e.g. *Festuca novae-zealandiae, Poa cita*) grasslands are more susceptible to invasion and loss of intertussock herbs (and in some cases the tussocks themselves) occur regardless of whether grazing is removed (Meurk 1978). *Poa cita* cover decreases substantially where there is competition from exotic species following grazing removal (Meurk *et al.* 2002), and it appears that low-intensity grazing may be the best management option for strongly modified short tussock grassland (Lord 1990). The presence or absence of native tussock grasses at the time of exclosure may be critical for retention or recovery of native biomass. Since invasion of native tussock grasses into dense exotic swards following exclosure is unlikely (Walker and Lee 2002).

4.4.2 FUTURE COMPOSITION SHIFTS

When knowledge gained from the existing literature is applied to the exclosure plots in the Manson region, it becomes possible to hypothesise as to future vegetation changes. While the Manson region has been heavily impacted in the past by anthropogenic influences, specifically extensive burning and grazing, two of the sites were found to be primarily composed of native herbfield species. Exclosure sites 1 and 3 were dominated by a variety of native species, which appeared to increase slightly in abundance with the removal of browsing. These changes, plus evidence from the literature (e.g. Lord 1990; Meurk *et al.* 2002) suggest that exclosure Sites 1 and 3, will remain static in composition, or undergo "natural" successional processes. In contrast the vegetation at site 2 had high levels of exotic species initially, which increased after just one year of browsing exclusion. This suggests that the vegetation present will become increasingly dominated by exotic species, and that native species abundances will be considerably reduced and possibly eliminated at this site. While *Poa cita* composed a major portion of the site, it has been clearly shown that it cannot compete with adventive grasses (Lord 1990; Meurk *et al.* 2002). Therefore continued browsing would be necessary at site 2 to maintain species richness and ensure the existence of native species.

4.4.3 HERBIVORE USE OF EXCLOSURE PLOTS

Following the initial pellet clearance from the exclosure plots, it appeared that hares took relatively little time to become accustomed to the exclosure setup. Recruitment rates in the first month were the lowest observed, but there was a substantial increase in the next period. This suggests that hares initially avoided the exclosure, then became accustomed to the plots and usage increased substantially. Resulting in usage during the initial period being disproportionate to the general area, firstly lower, then substantially higher. Hare use after this period appeared to stabilise as recruitment rates followed a pattern similar to that observed in Chapter 2 for the cleared pellet plots. However the reason for the sudden decrease observed in the final period is unclear. In terms of exclosure use relative to the general area, hare use of the exclosure plots appears to be slightly lower than that of the general region. While the recruitment rate estimates from the exclosure plots were highly variable, the average was 0.55 pellets/m^2/day, compared to 1.1 pellets/m^2/day for the general area. Whether or not the lower recruitment rate is an artefact of the different sampling techniques used, or a real difference in recruitment rates is uncertain. It would be expected that hare use would be higher in the exclosure plots as large pegs that remain above the ground attract hares and are used as latrine sites (Parkes 2001). Furthermore densities of hare pellets (*Lepus granatensis*) on plots centred around stakes, were higher than on plots not centred on stakes for open grassland in Spain (Lazo *et al.* 1992).

The usage patterns of possums and deer could potentially effect the interpretation of the vegetation responses. Deer made no use of the exclosure plot area, which makes interpretation of their browsing impact difficult (discussed below). The recruitment of possum pellets was relatively stable over all sites and plots throughout the course of the study. This suggests that possums were using the exclosures constantly over the course of the study, and whether or not the use was "normal" is uncertain. However use by possums of the exclosure set-up indicates that they are potentially affecting vegetation condition. While possums are thought to have minimal impact in alpine vegetation, as they are generally confined to the forest (Horne 1979), these results contradict that view and indicate that possum impacts should be taken into account in future alpine grassland research.

4.4.4 IMPROVEMENTS

4.4.4.1 Exclosure design

While the exclosure setup was successful in isolating the browsing effect of hares, several improvements could be made. In particular the utility of the hare exclusion/deer access treatment plot is uncertain. At initiation I was unsure as to whether deer use of this plot would be "normal". Theoretically the addition of the treatment would have helped in the interpretation of the different herbivore impacts. However, practically this did not happen. No evidence was found that deer were using the plot and indeed they seemed to avoid the exclosure area in general. While deer pellets were observed within 5m of the exclosure, no pellets were recorded in the plots. This also causes problems in the interpretation of the results from the unfenced control plots, as they would have been primarily browsed by hares. During the experimental design of this project it was thought that exclosure construction could result in abnormal use of the site through the creation of runs along fence lines and the attraction/repulsion of animals from the site. This turned out to be the case with the lack of use by deer of the exclosure setup. In the design phase placement of the control plot some distance away from the site was considered. However since animals had access to certain parts of the exclosure set up, if abnormal patterns were observed they would affect treatments plots as well. Therefore the control plot was placed in alignment with the treatments so any abnormal behaviour also affected the control plot. However with the abnormal usage patterns observed, modification of plot setup needs to be considered. Relocation of the unfenced plot further from the exclosure would solve this issue. Unfortunately if use by hares of the hare access/deer exclosure plot was also disproportionately higher, then a disjunct unfenced control plot would not undergo the same bias. Therefore the optimal solution would be two unfenced control plots, one located as in this study, and another located some distance away. But it is also possible that hare and deer use of the exclosure sites will stabilise over time, to an approximation of normal browsing. At this stage the addition of the extra deer access provided no additional information, other than a pseudo-replicate of the hare exclosure. It also provided complications in the exclosure construction due to the interlacing of the differing materials and tensioning of the fences. While the L shape design allowed for compact placement of plots, it complicated construction and a rectangular setup would have been simpler. In general however, the exclosure setup worked well and the permanent nature of these exclosures should be able to provide information on hare impacts for a considerable period.

4.4.4.2 Sampling design

The height tier information gathered using the Scott height frequency method is under-utilised due to complications it causes in statistical analysis. While the data enable construction of height frequency diagrams that are useful for visual inspection of vegetation composition and structure, their use statistically, is limited. The lack of independence between each height tier makes the application of statistical tests difficult. Previous papers have used tests such as the Chi-squared, but the test assumes independence between each row and column. For that reason no statistical tests of the height tier data were undertaken. And while the summed SHF data provide useful indexes, large amounts of information are not utilised when data are summed to a single value for each species. While the value provides a biomass index for that species in the plot, it makes no utilisation of the height information. Changes in a plants growth habit would be missed and no statistical test can reliably be used to test for significant changes in habit.

While the quadrat data had little utilization in the current study, it was intended to provide information on the rarer species that might be present. For examination of the dominance relationships, I believe the SHF data is more useful, because quadrat data will not differentiate between a small herbaceous plant and a large tussock or shrub.

The advantage of quadrats is that they enable the detection of several smaller species not detected using the SHF sampling. For example, *Euphrasia zelandica*, *Stackhousia minima*, and *Uncinia rubra* were detected several times in the quadrat sampling, but not the SHF. The short time frame of this study was insufficient for subtle compositional changes to be identified, but in the future quadrats will be a valuable tool for identifying compositional changes.

4.4.5 RECOMMENDATIONS

This study indicates that hares are potentially having a beneficial influence in the Manson region through there apparent suppression of exotic grasses. Therefore at this stage hares appear to be no threat to the general vegetation of the region. However the time period of this study was relatively short and in future, changes may occur in the exclosure plots that reveal this is not the case. While it appears that the vegetation at Site 2 will become dominated by exotic species, the futures of Sites 1 and 3 are less certain. At this stage I recommend a wait-and-see approach as to the vegetation responses. I also suggest that the exclosures be remeasured in 2004, as the fluctuations observed in vegetation conditions did not make it possible for the establishment of the "normal" vegetation condition. After this period ongoing measurement should occur with no more than a five year interval between measurements. This will allow assessment of ongoing vegetation responses to the removal of hare browsing.

4.4.6 CONCLUSIONS

Split plot exclosures are an effective way of determining hare impacts in New Zealand alpine grasslands. While refinements to both the exclosure design, and sampling method might be desirable, overall the method was effective at determining the effect of hare browse on vegetation composition and structure. The exclosures will be able to provide long-term information on hare browse not possible using population reduction, and temporary exclosure techniques.

Hares in the Manson region appear to be having minimal effect upon the composition and structure of the native plant species present, but they appear to be suppressing several exotic grasses. Without grazing pressure these grasses increase in abundance and evidence from the literature suggests that they will dominate and exclude less aggressive native species. Therefore hare impact in the Manson region appears to be slightly beneficial to native composition and structure in the short-term, but monitoring should be continued in the future.

Chapter 5

Impact of hare browsing on highly preferred plant species

Hare pellets scattered on a clump of vegetation at the Tukino study site

5.1 INTRODUCTION

Hares in New Zealand are generally thought to have minimal impact on alpine vegetation (Wong and Hickling 1999). Their grazing patterns result in impacts being spread over the wider environment, as they graze few leaves from many plants over a wide area. In addition, hare browsing on a palatable plant will not kill, but hedge the individual (Flux 1990). While hares are thought to have minimal impact on alpine plant communities, hare browsing is capable of having severe detrimental impacts upon other vegetation. In farmland hares cause significant damage to fruit trees, pine plantations, and horticultural crops (Flux 1990). In alpine vegetation, hares prefer particular plants species (Horne 1979), and to even prefer particular parts of plants (Wong and Hickling 1999). Rose and Platt (1992) investigated the effect of hare browse on Snow tussock (*Chionochloa macra* and *C. flavescens* ssp. *brevis*) population structure, but there is no report in the literature investigating the wider effect of browsing preference on native plant species. Therefore there was a need for a study into the impacts of hare browsing on their preferred plant species. Preferential browsing of native plants by introduced herbivores has been noted on several occasions in New Zealand (e.g. Mitchell *et al.* 1987), and can lead to increased damage, reproductive inhibition, and even population decline in the target species.

In a study of possum diet in podocarp-hardwood forest in the Central North Island, possums (*Trichosurus vulpecula*) were shown to selectively browse mistletoe (*Tupeia Antarctica*)(Sweetapple *et al.* 2002). Mistletoe comprised 1.2% of the total possum diet, but represented only 0.003% of the estimated total foliage biomass. Most mistletoe plants were estimated to have established more than 20 years ago, and the current potential for recruitment of new individuals into the population was severely limited by possum browsing (Sweetapple *et al.* 2002). On Mt Taranaki, goats (*Capra hircus*) selected or rejected different plant species largely independently of plant availability (Mitchell *et al.* 1987). For instance *Schefflera digitata* was relatively scarce in the environment but was possibly the most preferred food as it represented a high proportion of the diet. Several species (e.g. *Pseudopanax arboreus, S. digitata)* declined markedly in the presence of goats which ate the foliage and then barked and killed the trees. While previous research indicated that hares do prefer particular plant species, it was not known what the impact of this preference had on the plants. In this chapter I investigate which plants species are preferred by hares, and examine the level of impact this preference has on these plant species.

The two studies on hare diet in the alpine grasslands of New Zealand indicate that the dominant food groups are relatively consistent (detailed in general introduction). In Cupola Basin, Nelson Lakes National Park, Flux (1967a) showed that over one year, a hare's diet averaged 31% *Poa colensoi*, 26% *Chionochloa* spp., and 11% *Celmisia* spp. On Mt Ruapehu, the average annual diet was 44% *C. rubra,* 24% *Celmisia spectabilis,* 15% *Brachyglottis bidwillii,* 7% moss, 4% *P. colensoi,* 2% seeds, and 2% grass (Horne 1979). While these species appear to be the major contributors to a hare's diet, feeding trials showed that they are not necessarily the most preferred. Horne (1979) conducted feeding trials on captive hares fed a selection of alpine plant species and found *Aciphylla squarrosa, C. rubra* and *Calluna vulgaris,* were the most preferred species. While preferences of penned animals cannot be assumed to be those of wild animals (Flux 1967a), they can be used to identify possible preferred and targeted species. *Chionochloa rubra* features as a dominant food group in free ranging hare populations of Mt Ruapehu, which reflects its abundance in the diet and prevalence in the environment. However the other two species do not feature as a major proportion of the diet. *Calluna vulgaris* was major component of the vegetation at several of the sites studied; therefore availability would not restrict diet and the reason it is not heavily consumed is unclear. However *A. squarrosa* was not a prevalent species, but showed distinct signs of hare browsing, indicating it is potentially a preferred species. Horne (1979) found no relationship between diet choice and nutritional components of the plant species consumed. But even though the exact mechanisms for diet preference in herbivores are unclear, selection of preferred plant species can be related to the plant chemistry. In a review of 19 studies of ungulate diet preferences, Forsyth *et al.* (2002) found that of the 379 plant species recorded as eaten in New Zealand, five species are always preferred, with preference being for woody species with low foliar lignin. However diet selection of hares is less certain and does not appear to be directly related to a single chemical property (Schmitz *et al.* 1992).

The mechanisms governing diet choice for hares has been studied extensively overseas. Energy content, protein quality and plant secondary chemicals have all been proposed as important factors effecting the browsing preferences of hare species (Sinclair and Smith 1984; Rodgers and Sinclair 1997). Preference has been related to defensive chemistry of plants (Bryant *et al.* 1994), but it appears that hares do not exclusively select twigs to avoid plant secondary compounds, or to maximise the intake of a limiting nutrient. Browsing preference by mountain hares (*L. timidus*) in Scandinavia was strongly related to nitrogen concentration and, to some degree, digestibility (Hjalten 1992). Digestibility, but not calorific value, was found by Blay (1989) to influence food choice for hares in Canterbury. While Horne (1979) found that diet selection by hares on Mt Ruapehu was not determined by the nutrient content of the plant species. Even if diet selection criteria could be isolated, the exact process of diet selection for hares is not as simple as identifying preferred species. Hares cannot subsist by eating a single species of high-quality browse, nor are they able to meet their metabolic requirements by increasing consumption of poor-quality food (Rodgers and Sinclair 1997). Preference is conditional upon the relative nutritional, physical and chemical attributes of highly defended and less defended plant species available in the habitat (Schmitz *et al.* 1992). Development of a set of criteria that would diagnose preferred species based upon absolute nutritional criteria would be confounded and complicated. Preference in any given area will be conditional upon the species available for consumption. To accurately demonstrate preference the abundance of a plant species must be compared to its availability in the environment (e.g. Sweetapple *et al.* 2002). Preferred species will be disproportionately more abundant the diet relative to their availability. However without any definitive guidelines available to predict the preferred species in a region, simple observational studies provide the best solution for a preliminary determination of preference.

Along with further investigations to complement existing literature on which plant species are preferred by hares, the aim of this chapter is to investigate the impact hare browse has on plant species that are highly preferred. To accomplish this a range of vegetation surveys and measurement were undertaken at several sites in the Central North Island, New Zealand.

5.2 METHODS

5.2.1 STUDY AREAS AND SPECIES

In order to determine which native plant species had the potential to be preferentially browsed, the existing literature was consulted (Flux 1967a; Horne 1979; Blay 1989), along with recommendations from Department of Conservation staff, and observations made onsite. Where preferred species occurred within the exclosure plots used in Chapters 2 and 3, measurements were incorporated into the monitoring design for those sites (outlined below). During the background work for this study it became apparent that hares could also be having a significant effect on additional species in areas where there were no exclosure plots. Therefore additional monitoring was implemented outside the main exclosure plots to assess hare impacts on these species.

Monitoring outside exclosure sites was initiated at three sites situated in Tongariro National Park. Hares are the major browser above the treeline in Tongariro National Park since deer are uncommon and possums, though abundant, are confined to forest (Horne 1979). Horne (1979) studied the diet of hares on Mt Ruapehu, but did not assess the browsing impact of hares on the vegetation. On Mt Ruapehu most of the browsing damage in the region appears to be isolated to particular sensitive/palatable plants. Browsing is relatively minor on a landscape scale as most plants are unbrowsed, however the damage to sensitive plants can be quite intense or extreme (N. Singers, Department of Conservation, *pers. comm.)*.

At two high altitude sites on the western side of Mt Ruapehu, the impact of hares was investigated for several plant species thought to be heavily browsed by hares. One site was at 1550m a.s.l. directly below the Turoa Skifield car park. The other was in the Whakapapaiti Valley, upstream from the Whakapapaiti hut at approximately 1450m a.s.l. Horne (1979) showed that a major component of a hare's diet in the region was comprised of *Chionochloa* species and casual observation also suggested that hares were causing significant damage to *Chionochloa* species in the region (Plate 5.1). There are two *Chionochloa* species present that are of interest, *C. rubra* and *C. pallens. Chionochloa rubra* is present in large tracts throughout the region (Rogers and Leathwick 1994; Rogers and Leathwick 1996), and is known to be a major component of hare diet (as well as being a preferred species) (Flux 1967a; Horne 1979).

Chionochloa pallens is present at lower frequencies (*pers. obs.*) and is restricted to relatively high fertility soils associated with alluvial and colluvial soils in the wet regions (referred to flush zones) of the alpine zone (Williams *et al.* 1976). Additionally, these species interbreed and produce hybrids in the region (Conner 1991), and it appeared that the level of hybridization was effecting the occurrence of browsing on these species. Leading me to hypothesize that *C. pallens* individuals were suffering increased browsing damage from hares and consequently I sought a way to test this. While the degree of hybridization was apparent when plants were visually inspected, a quantitative measure was sought. The width of the flattened leaf was used as it appeared to be a measurable physical attribute that was related to the degree of hybridization. Pure *C. rubra* plants appear to average 2-3 mm in width, while pure *C. pallens* were approximately 6-8 mm in width. With the hybrid individuals varying in leaf width between these values.

Plate 5.1: Example of *Chionochloa pallens* showing browsing damage at the Turoa site. Note the hare pellets present throughout the photo.

A species of prostrate broom, *Carmichaelia nana*, was also identified as a potential preferred species. *Carmichaelia nana* usually forms a dense mat of cladodes approximately 20-60mm x 0.5m in size and usually occurs on stable but unconsolidated alluvial river beds and braid islands, river terraces, moraines and shingle slopes (Heenan 1995). This species was investigated at a study site adjacent to the Tukino ski field access road on the eastern flanks of Mt Ruapehu. It is a common species in the region and is often browsed to small cushions by hares (N. Singers, Department of Conservation, *pers. comm.*).

5.2.2 SAMPLING PROTOCOLS

5.2.2.1 Tongariro National Park

5.2.2.1.1 Turoa and Whakapapaiti

Hare abundance: In addition to the randomly located pellet line installed at the Turoa site to assess hare abundance (see chapter 1); I selectively placed ten cleared pellet plots at the Turoa site to compare the use of the flush zones (where *Chionochloa pallens* primarily occurs) with the adjacent area.

Plant distribution and browsing levels: The cleared pellet plots were also used to determine the distribution and impact of hares on species thought to be preferred by hares. Selected species that occurred within the cleared pellet plot were counted and browse scores assigned. The browse scores ranged from 0 to 3; 0 = no browsing evident, 1 = light browsing (0-25%), 2 = moderate browsing (26-75%), 3 = heavy browsing (76 -100%). Total percent cover of all vascular and nonvascular plant species were also recorded for each plot.

Distribution and browsing estimates were obtained for species described by Horne (1979) as being preferred by hares; *Brachyglottis bidwillii, Celmisia gracilenta, Celmisia spectabilis, Chionochloa spp., Dracophyllum recurvum, Poa colensoi, Rytidosperma setifolium, Schoenus pauciflorus*. No differentiation was made between *C. rubra* and *C. pallens* because of the difficulty created by the presence of hybrids (additional measurements were taken to address this issue, outlined below). In recognition of the scarcity of the vegetation at both Turoa and Whakapapaiti plot size was enlarged for vegetation measurements from that used in the cleared pellet plots from $r = 17.8$ cm, to $r = 60$ cm,

Chionochloa measurements: At the Turoa site, all tussocks present within a 60 cm radius of the cleared pellet plots had measurements taken of extended leaf length, leaf width, and browse score. The sampling pattern utilising the cleared pellet plots did not produce sufficient sample sizes, therefore additional tussocks were randomly selected. At the Whakapapaiti site, plots of radius 60 cm were selected on a restricted random basis in which tussock measurement occurred. When encountered, flush zones were recorded separately from hillslope tussock populations. A total of 33 tussocks were measured in total at the Whakapapaiti site, with 46 tussocks measured at the Turoa site. Measurements were made in January 2003. Data were analysed using two sample t tests in MINITAB v13.1 (Minitab Inc. 2000). Significance level was set at $P < 0.05$ for statistical testing in this chapter.

5.2.2.1.2 Tukino

Estimates of distribution of *Carmichaelia nana*, and *Celmisia gracilenta* were obtained at the Tukino site from the cleared plot pellet line (plot size was not enlarged as at Turoa). Further monitoring was initiated for *C. nana*. Twenty plants were tagged and measured to assess the level of browsing damage. Ten of these plants were caged to assess potential for recovery from browsing over one growing season. Cages were constructed of open wire mesh that would have minimal effect on environmental conditions. The remaining ten plants were left unmanipulated as controls. The total number, and number of cladodes browsed were counted, along with the length of the longest cladode. Basal size was also measured by recording the maximum length of the plant along two perpendicular axes (north/south (x) & east/west (y)). Plants were chosen by randomly selecting cleared plot pellet markers and finding the closest plant to that point suitable for caging. Individuals were then randomly assigned as either treatment (caged) or control (uncaged). Data were analysed for both year and treatment effect using a repeated measures ANOVA in SYSTAT 8.0 (SPSS Inc. 1998).

5.2.2.2 Moawhango exclosures

Where present, *Chionochloa rubra, Festuca novae-zelandiae,* and *Dracophyllum subulatum* were measured at each of the exclosure plots located within the Moawhango region (Motumatai, Awapatu, Upper and Lower Argo Rd). A maximum of ten randomly selected individuals were measured in each of the three treatment plots found at each exclosure site (horse exclosure, horse/hare exclosure, and unfenced control). For *C. rubra* and *F. novae-zelandiae,* basal diameter, maximum extended leaf/flower length and browse score were recorded. *Chionochloa rubra* was measured at all exclosure sites. Due to insufficient numbers, *F. novae-zelandiae* was not recorded at the Lower Argo Rd site. *Dracophyllum subulatum* had height and browse scores recorded, along with an estimate of basal size (as for *C. nana* above). Basal proportion was measured by recording the maximum length of the plant along two perpendicular axes (north/south (x) & east/west (y)). Height: basal area ratio (height/(x+y)) as then calculated as a measure of form. *Dracophyllum subulatum* was measured only at the Awapatu and Upper Argo Rd sites. Only one measurement was made on these species in Moawhango during May 2003. Data were analysed for both site and plot (treatment) effect using a General linear model ANOVA run in MINITAB v13.1.

5.2.2.3 Manson exclosures

Species measurements were completed at the exclosure sites constructed in the Manson region. Species recorded at Manson included *Chionochloa rubra, Ozothamnus leptophyllus, Poa cita,* and *Raukaua anomalus.* These plants were measured at the initial set-up of the exclosures (March 2002), and again one year later (March 2003).
All individuals of *C. rubra, Ozothamnus leptophyllus,* and *Raukaua anomalus* were recorded at each site, but *Poa cita* was recorded only at Site 2. For each individual of every species, basal diameter, height, and browse score were recorded. Data were analysed for both year and treatment effect using a repeated measures ANOVA in SYSTAT v8.0.

5.3 RESULTS

5.3.2 TONGARIRO NATIONAL PARK

5.3.2.1 Turoa and Whakapapaiti

Pellet distribution: The selectively placed pellet plots from the Turoa site showed a significant difference in recruitment rates between the flush zones and the randomly placed cleared plots (two sample t test, $P = 0.026$). Only one pellet was recruited in the 100 sample plots for the hillslope plots, compared to 21 pellets recruited in the ten flush zone plots. Recruitment rates for the flush zones were 0.285 pellets/m^2/day (SE = 0.104) and compared to 0.0012 (SE = 0.0012) pellets/m^2/day for the general area. Use of these data to compute population density provides an estimate of 6.95 hares/ha in the flush zones, and 0.03 hares/ha in the hillslope environment.

Plant distribution of hillslope vs. flush zones plots: Hillslope distribution data from the Turoa site showed that the average number of vascular plants per plot was higher in the hillslope plots at 12.2 (SE = 2.8) plants/plots, while the flush zones averaged 7.2 (SE = 0.2) plants/plots. However, vegetation cover in the flush zones was significantly higher than the hillslope plots (two sample t test, $P < 0.001$). Percent vegetation cover in the flush zones averaged 94.4% (SE = 3.8), compared to 31.6% (SE = 2.6) in the hillslope plots.

Browsing levels - Turoa: Of the species recorded in the hillslope vegetation plots, *Chionochloa* spp., *Dracophyllum recurvum,* and *Schoenus pauciflorus* were those most heavily browsed by hares (Table 5.1). *Dracophyllum recurvum* was present in low numbers and showed signs of light browsing on all plants. Of the *S. pauciflorus* plants measured, 50% suffered light to moderate browsing damage, with 13% severely damaged. For *Chionochloa* spp. the majority (61%) of plants showed no damage, with 39% of showing signs of light browsing. Species showing evidence of browsing in the flush zones, were similar to those on the hillslope. *Schoenus pauciflorus* again showed signs of browsing, though no heavily browsed plants were detected in the sampling area (although they were observed elsewhere). *Chionochloa* spp. and *Poa colensoi* also showed signs of heavy browse in the flush zones (Table 5.1).

Browsing levels - Whakapapaiti: Several species were found in common at both sites, but overall, browsing damage was higher at the Whakapapaiti site than at Turoa.

Evidence of browsing was found on all species except *Rytidosperma setifolium* in the hillslope plots (Table 5.1). All species measured in the flush zones had individuals showing browsing damage to at least the moderate level. *Schoenus pauciflorus* was the most heavily impacted with the majority (67%) of plants showing severe browse damage.

Table 5.1: Results from plant distribution plots showing the percentage of plants present in each browse category for species thought to be preferred by hares. Numbers in brackets represent raw counts. Browse score ranges from 0 - 3; 0 = no browsing evident, 1 = light browsing (0-25%), 2 = moderate browsing (25-75%), 3 = heavy browsing (76 -100%).

Site	Species	Browse score			
		0	1	2	3
Turoa - hillslope (100 plots)	*Brachyglottis bidwillii*	100% (3)			
	Celmisia gracilenta	100% (33)			
	Celmisia spectabilis	99.6% (263)	0.37% (1)		
	Chionochloa spp.	61.5% (8)	30.7% (4)	7.69% (1)	
	Dracophyllum recurvum		100% (6)		
	Poa colensoi	100% (452)			
	Rytidosperma setifolium	100% (614)			
	Schoenus pauciflorus	37.5% (6)	43.7% (7)	6.25% (1)	12.5% (2)
Turoa-flushes (9 plots)	*Celmisia spectabilis*	97.3% (37)	2.63% (1)		
	Chionochloa spp.	31.5% (6)	21.0% (4)	10.5% (2)	36.8% (7)
	Poa colensoi			75% (3)	25% (1)
	Schoenus pauciflorus	50% (2)	50% (2)		
Whakapapaiti -hillslope (30 plots)	*Chionochloa* spp.	35.7% (10)	25% (7)	17.8% (5)	21.4% (6)
	Celmisia spectabilis	87.0% (27)	12.9% (4)		
	Poa colensoi	50% (10)	50% (10)		
	Schoenus pauciflorus	5.26% (1)	15.7% (3)	21.0% (4)	57.8% (11)
	Rytidosperma setifolium	100% (26)			
Whakapapaiti - flushes (30 plots)	*Chionochloa* spp.	55.5% (10)	27.7% (5)	16.6% (3)	
	Celmisia spectabilis	58.9% (23)	17.9% (7)	15.3% (6)	7.69% (3)
	Poa colensoi		28.5% (2)	28.5% (2)	42.8% (3)
	Schoenus pauciflorus		11.1% (9)	22.2% (18)	66.6% (54)
	Rytidosperma setifolium		76.1% (16)	9.52% (2)	14.2% (3)

Turoa/Whakapapaiti tussock measurements: Leaf width in *Chionochloa* plants was significantly higher in the flush zones plots for both the Turoa (two sample t test, P <0.001) and Whakapapaiti sites (two sample t test, P = 0.016). The average width of tussock leafs in the Turoa flushes was 6.1 mm (SE = 0.5), with the hillslope average being 3.4 mm (SE = 0.2). *Chionochloa* spp. plants located in the Whakapapaiti flushes were not as severely browsed as the Turoa flushes plants, and leaf widths at Whakapapaiti were significantly smaller (two sample t test, P= 0.001). The average leaf width for the Whakapapiti flushes was 4.0 mm (SE = 0.3), and 3.0 mm (SE = 0.2) for the hillslope plants. The tussock measurements from Turoa and Whakapapaiti show a significant relationship between leaf width and the level of browsing (Ordinal Logistic Regression, P < 0.001) (Figure 5.1). As the width of the tussock leaf increased, browse scores also increased significantly.

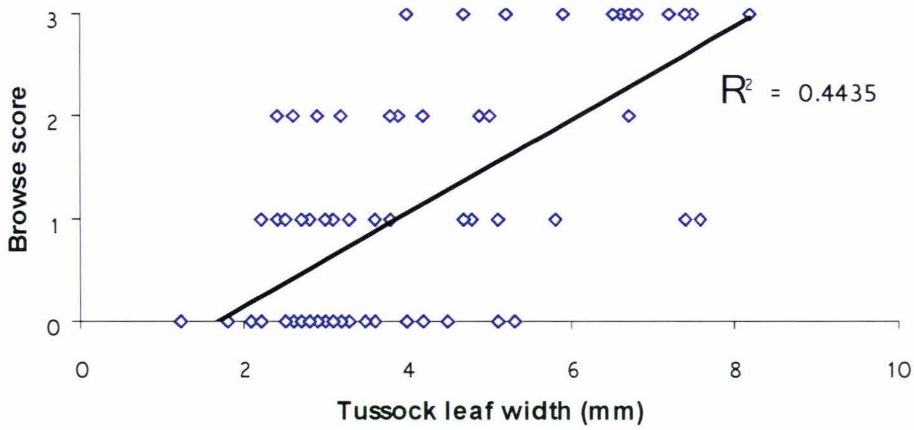

Figure 5.1: Ordinal Logistic Regression showing the significant relationship (P < 0.001) of leaf width and browse score for the *Chionochloa* spp. individuals measured at the Turoa and Whakapapaiti sites.

5.3.2.2 Tukino

The distribution and browsing data obtained from the cleared pellet plots showed both *Carmichaelia nana* and *Celmisia gracilenta* were browsed. For *C. gracilenta*, 84% of the plants showed no signs of browsing, with 11, 4, and 1% of plants showing light, moderate, and heavy signs of browsing. Browsing damage on *C. nana* was higher with 72% of the plants were browsed to some extent: 40% were severely damaged, 12% moderate, and 20% with light damage (see Plate 5.2 for example of severe browsing). Leaving only 28% of plants showing no browsing damage.

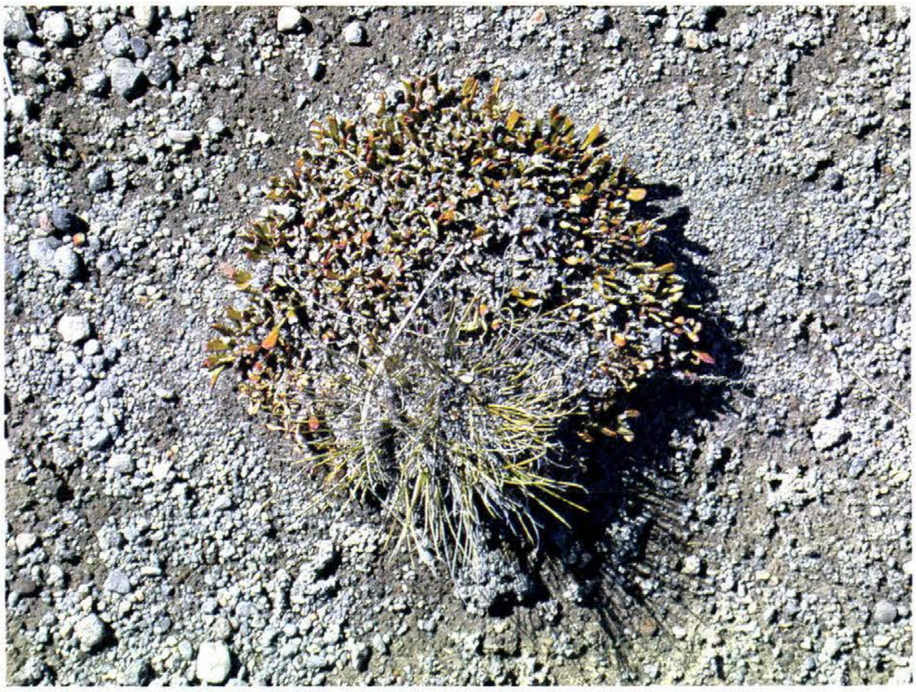

Plate 5.2: Example of a heavily browsed *Carmiachaelia nana* plant found at the Tukino site. The basal proportions of this individual were 11 cm (x) and 14 cm (y).

The total number of *C. nana* leaves counted, along with basal size increased significantly for both the caged and uncaged plants over the period of one growing season (Table 5.2). There was no significant change in the level of browse in terms of both absolute and relative measures; however, levels of browsing did show interesting trends (Table 5.2). Browsing percentages for the uncaged individuals stayed relatively constant between 2002 (38%) and 2003 (36%). However browsing percentages in the caged plants reduced from 31% in 2002, to 17% in 2003. There was no significant change in maximum leaf length, although both caged and uncaged values increased slightly.

Table 5.2: Summary table of all the variables measured on *Carmichaelia nana* at the Tukino site showing the mean scores and ANOVA significance values for each variable.

Variable measured		2002 Mean(SE)	2003 Mean(SE)	Effect tested	$F_{1,18}$	P
Total number of cladodes	Caged	206 (16)	358 (22)	Year effect	37.07	**<0.001**
	Uncaged	197 (18)	314 (21)	Treatment effect	0.62	0.440
Basal area	Caged	27 (1)	34 (1)	Year effect	19.20	**<0.001**
	Uncaged	28 (2)	33 (1)	Treatment effect	0.85	0.369
Max leaf length (cm)	Caged	3.6 (0.2)	4.2 (0.2)	Year effect	3.03	0.099
	Uncaged	2.8 (0.1)	3.3 (0.1)	Treatment effect	0.08	0.785
Number of browsed cladodes	Caged	94 (16)	72 (8)	Year effect	0.08	0.784
	Uncaged	61 (6)	94 (8)	Treatment effect	2.22	0.153
Percent of cladodes browsed	Caged	31 (3)	17 (1)	Year effect	1.40	0.253
	Uncaged	38 (3)	37 (3)	Treatment effect	0.97	0.337

5.3.3 MOAWHANGO EXCLOSURES

Chionochloa rubra varied significantly by site for all the variables measured (Table 5.3). The Lower Argo Rd site contained the largest (height and diameter) individuals, followed by Motumatai, Upper Argo Rd and then Awapatu (Table 5.4). Browse score was the only variable to vary significantly at the plot level. Browse scores were significantly higher in the unfenced control plots, than in the horse and horse/hare exclosures (Figure 5.2). Browsing was observed in all unfenced control plots in the region. No hare browsing on this species was observed at the Lower and Upper Argo road site; however Motumatai and Awapatu showed evidence of hare browsing. The average browse score of 0.6 at Motumatai was obtained through three lightly browsed plants, and one heavily browsed individual in the sample. At Awapatu, only one individual plant showed moderate signs of browse. No browse was observed in the horse/hare exclosure at any of the sites (Figure 5.2).

Table 5.3: General linear model ANOVA table of the significance levels for site and plot effects for each variable measured on the species in the Moawhango region.

Species	Variable	Site effect			Plot effect		
			F	P		F	P
Chionochloa rubra	Height	$F_{3,119}$ =	6.85	**<0.001**	$F_{2,119}$ =	0.96	0.387
(Motumatai, Awapatu, Lower and Upper Argo Rd)	Diameter		7.04	**<0.001**		0.28	0.756
	H:D		3.02	**0.033**		3.75	0.270
	Browse		3.39	**0.020**		12.11	**<0.001**
Festuca novae-zelandiae	Height	$F_{2,86}$ =	4.50	**0.014**	$F_{2,86}$ =	3.98	**0.022**
(Motumatai, Awapatu,	Diameter		3.79	**0.027**		0.93	0.399
Upper Argo Rd)	H:D		3.30	**0.042**		2.18	0.120
	Browse		14.80	**<0.001**		17.50	**<0.001**
Dracophyllum subulatum (Awapatu, Upper Argo Rd)	Height	$F_{1,51}$ =	16.13	**<0.001**	$F_{2,51}$ =	9.80	**<0.001**
	x + y		3.79	0.057		0.54	0.586
	H / (x +y)		13.38	**0.001**		14.90	**<0.001**
	Browse		32.35	**<0.001**		35.66	**<0.001**

Table 5.4: Total site averages (SE) for each of the variables measured on each species at the four exclosure sites in the Moawhango region.

	Variable	Lower Argo Rd	Upper Argo Rd	Awapatu	Motumatai
Chionochloa rubra	Height (cm)	118 (4.3)	95.8 (5.1)	92.2 (4.5)	105.1 (5)
	Diameter (cm)	106.7 (14.8)	61 (6.5)	53 (6.6)	89.5 (9.1)
	H:D	1.8 (0.2)	2.1 (0.2)	2.2 (0.2)	1.5 (0.1)
	Browse	0.07 (0.07)	0.17 (0.01)	0.37 (0.14)	0.5 (0.14)
Festuca novae-zelandiae	Height (cm)	-	53.9 (2.2)	61.5 (1.7)	54.5 (2.5)
	Diameter (cm)	-	24.6 (2.4)	34.1 (2.2)	34.4 (3.4)
	H:D	-	2.7 (0.3)	2 (0.1)	2 (0.2)
	Browse	-	0 (0)	0 (0)	0.63 (0.18)
Dracophyllum subulatum	Height (cm)	-	44.5 (5.1)	26.5 (3.6)	-
	Diameter (cm)	-	0.33 (0.14)	1.42 (0.24)	-
	x+y	-	69 (10.6)	50.8 (4.3)	-
	h/x=y	-	0.7 (0.06)	0.5 (0.05)	-

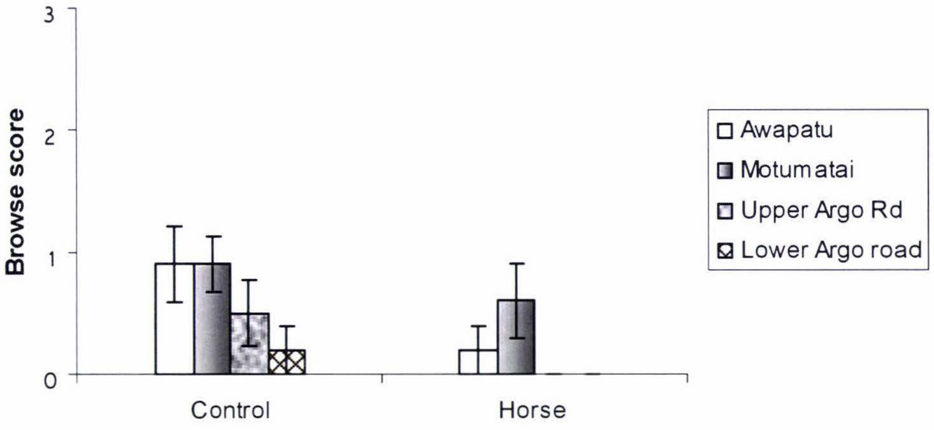

Figure 5.2: Average browse scores for *Chionochloa rubra* measured at the four exclosure plot sites in the Moawhango region. No browse was observed in the hare exclosure plots. Browse score ranges from 0 - 3; 0 = no browsing evident, 1 = light browsing (0-25%), 2 = moderate browsing (26-75%), 3 = heavy browsing (76 -100%). Error bars represent standard error.

Festuca novae-zelandiae also varied significantly by site for all the variables measured (Table 5.3), with the Awapatu site containing the largest individuals (Table 5.4). Both browse scores and height varied significantly by plot for *F. novae-zelandiae* (Table 5.3). The only *F. novae-zelandiae* individuals to show browsing damage were in the Motumatai unfenced control plot. The average browse score there was 1.9 (SE = 0.2). Heights were lower at Motumatai and Upper Argo Rd in the unfenced control plots (Figure 5.3).

Dracophyllum subulatum was only recorded at the Awapatu and Upper Argo Rd sites – there were insufficient numbers elsewhere. There was significant variation for both site and plot interactions for height, height:basal area ratio (H / (x + y)), and browse (Table 5.3). The Upper Argo Rd site had greater heights (Figure 5.4) and basal area ratios (Figure 5.5), along with a lower browse than Awapatu. Browse scores at the Upper Argo Rd site averaged 0.27 (SE = 0.14) for the unfenced control, 1.33 (SE = 0.67) in the horse exclosure, and 0 in the hare exclosure. While browse scores at the Awapatu site averaged higher at 2.67 (SE = 0.17) for the unfenced control, 2.22 (SE = 0.22) in the horse exclosure, and 0 in the hare exclosure.

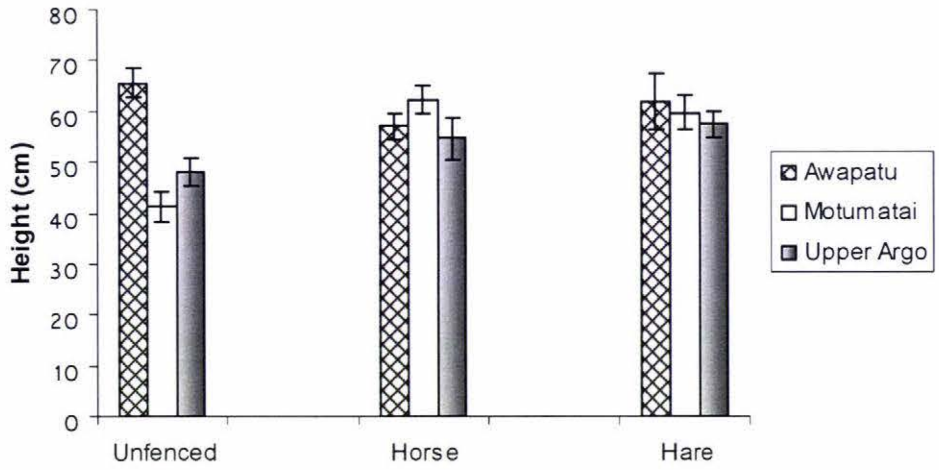

Figure 5.3: Height measurements of *Festuca novae-zelandiae* by plot for each of the three sites where measured in the Moawhango region. Height varied significantly by site (P = 0.014) and plot (P = 0.022). Error bars represent standard errors.

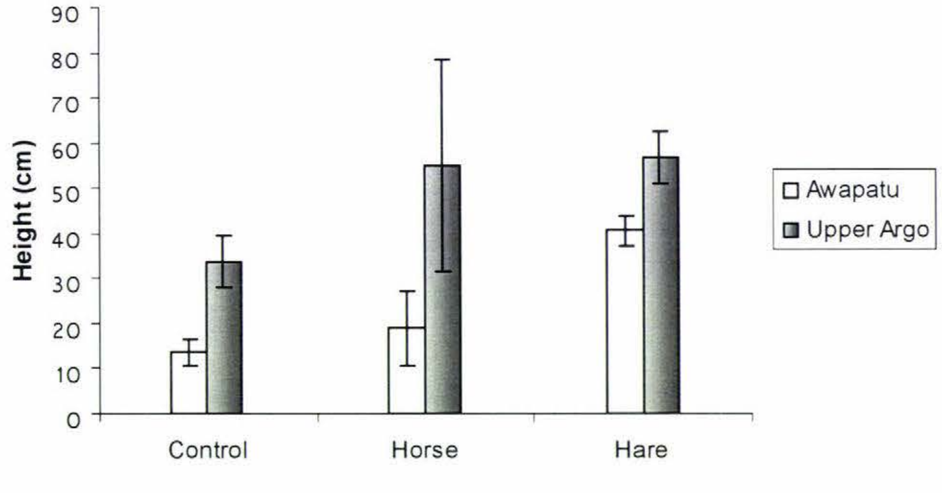

Figure 5.4: Height measurements by plot for *Dracophyllum subulatum* measured at two sites in the Moawhango region. Error bars represent standard error.

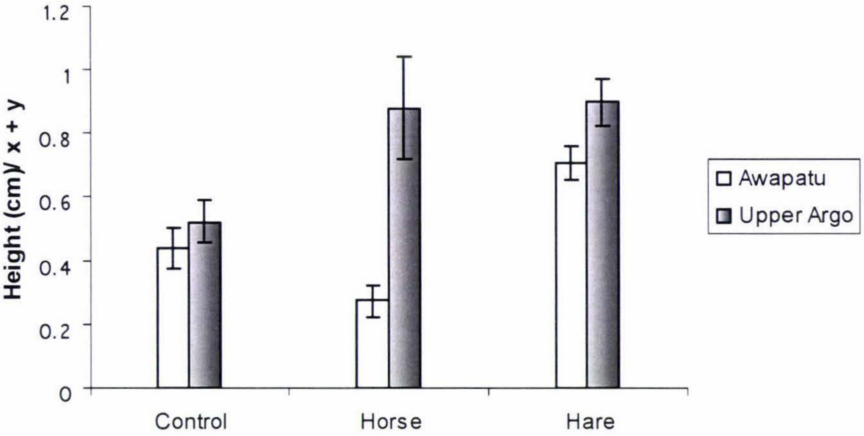

Figure 5.5: Height: basal area ratios by plot for *Dracophyllum subulatum* measured at two sites in the Moawhango region. Error bars represent standard error.

5.3.3 MANSON EXCLOSURES

There were insufficient numbers of *Chionochloa rubra* and *Raukaua anomalus* individuals present in the Manson exclosures for statistical analysis. However some individuals were present allowing limited investigations. The four individuals of *R. anomalus* showed no change in height or diameter over one year. With all individuals showing signs of moderate to heavy browsing at both sample occasions; however the herbivore that caused the damage could not be determined. Three individuals of *C. rubra* were measured in the Manson exclosures, and height increases of 6, 7, and 12 cm were observed, but there was no change in diameter measurements. All individuals showed signs of moderate browsing at initiation, and the two individuals located within the exclosure recovered to show no signs of browsing in one year, while the browse score of the third increased.

Ozothamnus leptophyllus showed no significant change in height or diameter over the year (Table 5.5). Only one plant showed signs of light browsing at initiation. Of the initial 18 plants, only five appeared to be "healthy". Three died during the year and were not included in analysis, the remaining ten plants showed signs of dieback ranging from 60 – 95% of the plant. There was no obvious cause for this observation.

Of the *Poa cita* recorded at site 2, no individuals showed any signs of browsing at any stage. Over the four treatments, there was a significant increase (Table 5.5) in height over the period of one year (Figure 5.6), but no treatment effect on the height increases as observed (Table 5.5). Diameter showed no change over the year (Table 5.5).

Table 5.5: ANOVA table of significance levels for the variables measured over one year on the individual species analysed in the Manson region.

	Ozothamnus leptophyllus			*Poa cita*					
	Height:	F value	P value	Height:	F	P	Diameter:	F	P
Year Effect	$F_{1,11}$ =	0.416	0.532	$F_{1,20}$ =	15.217	**<0.001**	$F_{1,20}$ =	1.532	0.230
Treatment effect	$F_{3,11}$ =	1.644	0.236	$F_{3,20}$ =	2.179	0.122	$F_{3,20}$ =	3.096	0.0501

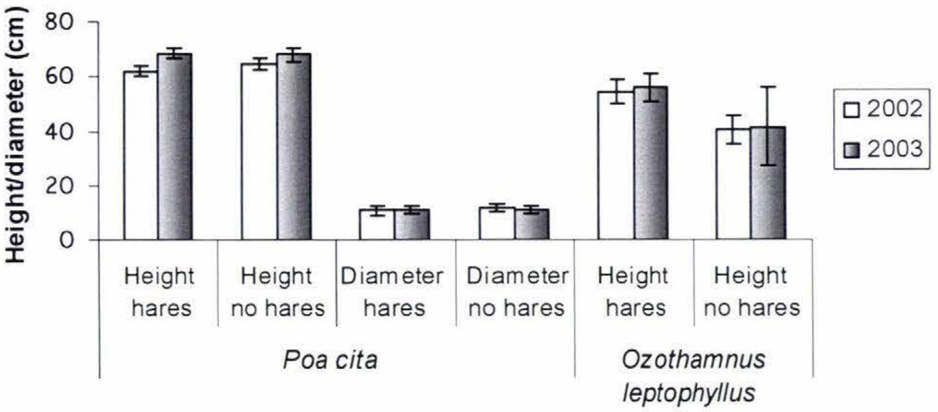

Figure 5.6: Variables measured for species that underwent statistical analysis in the Manson region. Data for this graph has been grouped over the entire regions, and by hare access/exclusion.

5.4 DISCUSSION

5.4.1 TONGARIRO NATIONAL PARK

5.4.1.1 Turoa and Whakapapaiti

Hares in the high altitude sites located on the western slopes of Mt Ruapehu appear to be selectively locating themselves in nutrient rich flush zones where damage to the vegetation is often severe. While the sample size for the flush zone cleared pellet plots was limited, habitat selection by hares was plainly apparent. Browsing damage in the hillslope habitat was generally light to non-existent, with the exception of *Chionochloa* spp. and *Schoenus pauciflorus*. However, the browsing impact in the flush zones was significantly higher. Preference for flush zone plants is evident when the browse scores are compared between the two habitats. Furthermore, if the plants located in the flush zones are subject to a higher input of nutrients, then recovery from browsing impact would presumably be swifter than on the hillslope with faster eradication of browsing evidence. While no quantitative measures were done to assess soil fertility in the flush zones, higher nutrient concentrations can be assumed because of enrichment from water flow, and also inferred from the significantly higher vegetation cover evident in flush zones. Mineral nutrient concentrations for New Zealand tussocks increases with soil fertility (Lee and Fenner 1989) and while there were no guidelines for predicting hare food preference, preference is conditional upon the relative nutritional, physical and chemical attributes of the available species (Schmitz *et al.* 1992). For that reason I suggest that hares are preferentially browsing plants in the flush zones because of their increased nutrients levels. While several plant species showed signs of browsing, it was evident that *Chionochloa* spp. and *Schoenus pauciflorus* were being heavily impacted.

The levels of browsing observed on *S. pauciflorus* indicate that it is a highly preferred species on Mt Ruapehu. *Schoenus pauciflorus* is a food of hares, but only in small proportions (Flux 1967a; Horne 1979; Blay 1989). It was not reported by Flux (1967a) in faecal pellets examined, but was recorded during observations of the number of hare bites on plant species. During summer it represented 0.37% of the total number of bites observed and in winter 11.8%. *Schoenus pauciflorus* has also been reported as a food of chamois (Clarke 1986), horses (Rogers 1994), and thar (Parkes and Thomson 1995). While the chamois and thar ate only small quantities, horses had a significant detrimental impact upon *S. pauciflorus* abundance (Rogers 1994). Little is known about the biology of *S. pauciflorus* in New Zealand, but observations of other members of the genus indicate that it is not a browse tolerant species. For example, observations of *Schoenus nigricans* on coastal dunes in North-Holland showed that seedling growth was very slow, with only two leaves after 3 months. The survival of seedlings was also low during the first year (12%), and flowers were only observed in experimental populations after 3 years (Ernst and Van Der Ham 1988). While infrequent defoliations of *Schoenus* can increase shoot densities and reproductive outputs, detailed mortality studies have shown that shoot death is highest in dense, regularly defoliated swards (Diemer and Pfadenhauer 1987). Therefore the high levels of browse observed on *S. pauciflorus* on Mt Ruapehu represent a serious problem for the continuation of this species in the high altitude environment.

The browsing of *Chionochloa* in both habitat types confirm that it is a preferred food for hares. While all forms of *C. pallens* and *C. rubra* were browsed, the relationship between leaf width and browsing indicate that the *C. pallens* genotype is the most preferred. However, the relationship between leaf width and habitat may confound the issue. Increasing soil fertility has been shown to increase both nutrient levels and tiller weight in *Chionochloa* (Lee and Fenner 1989). Therefore the increase in leaf width in the flush zone could be due to the increasing nutrients, as opposed to parentage. While we have seen in the other species monitored (with no hybridization issues) that browsing increases in the flush zones. I suggest that the genotypic traits of *C. pallens* are the primary determinate of browse in these *Chionochloa*, with habitat determined nutrient levels being of secondary importance. All "pure" members of *C. pallens* showed signs of heavy browsing, and a large body of literature documents herbivore preference for *C. pallens*. For instance it is listed as the second most preferred *Chionochloa* species for red deer in Fiordland (Mills and Mark 1977). It has the highest metabolisable energy, the second highest protein levels, and the fourth highest nutrient mineral content of eleven southern *Chionochloa* species (Fenner *et al.* 1993). *Chionochloa pallens* has also been shown to contain high levels of water-soluble sugars, levels are comparable to the leaves of perennial ryegrass (*Lolium perenne*) grown in high quality pasture (Williams *et al.* 1976). This preference is of concern as the historic absence of mammalian grazers from New Zealand means that *Chionochloa* may be vulnerable to introduced mammalian browsers (Lee *et al.* 2000). Evidence for this vulnerability is seen in the plants elevated apical meristems, slow growth rates, low root:shoot ratios, and low levels of silica. *Chionochloa* species are known to have low levels of silica (SiO_2), which has abrasive and indigestible qualities, thought to be a defensive feature of grazing-adapted grasses (Fenner *et al.* 1993). *Chionochloa* also has a low root:shoot ratio compared to grasses with a long grazing history, defoliated plants are, therefore, dependent upon limited nutrient reserves in roots to produce new foliage (Lee *et al.* 2000). The impact of the browsing observed on *C. pallens* in this study can be put into context, as the levels of browsing observed are similar to the experimental manipulations applied by Mills *et al.* (1989). Severe clipping 10 cm above ground level induced a marked and long-term decrease in the productivity of *C. pallens*, and eight years after cutting, the biomass of cut tussocks remained 64% less than that of uncut tussocks. A further measure of these cut tussocks (Lee *et al.* 2000) showed that even after 20 years recovery was incomplete. Tiller dry weights and size, along with dry weight per unit area remained significantly depressed (by about 30%) in the clipped plots. It was estimated that the effects of a single severe defoliation on biomass will persist for nearly three decades (Lee *et al.* 2000). Mark (1965b) showed that annual spring clipping of *Chionochloa* can eliminate mature healthy plants in four years. This evidence, combined with the low numbers and extremely high defoliation levels, suggest the long term survival of *C. pallens* is severely threatened in the high alpine flushes of Mt Ruapehu.

5.4.1.2 Tukino

The levels of browsing observed on *Carmichaelia nana* at Tukino show that it is a highly preferred species. With 40% of individuals showing signs of browsing, the species appears to be highly impacted. Little is known about the life history, ecology and conservation of most species of *Carmichaelia* in New Zealand (Gruner and Heenan 2001). In New Zealand the genus includes 14 species that are nationally threatened or uncommon (de Lange *et al.* 1999), thus making the genus one of significant concern for conservation biologists (Gruner and Heenan 2001). Wood anatomy indicates that *C. nana* is slow growing species, with plants of 10cm height, and 2cm in diameter being up to 22 years old (Heenan 1997). However with both size measures (total cladodes and basal area) increasing significantly over one growing season, recovery appears possible in a relatively short period of time. This is also suggested by the reduction in the percentage of cladodes browsed in the treatment plants. Fortunately for any conservation efforts it appears that *C. nana* produce viable seed that can last for up to 24 years in storage (Heenan 1997). While no browsing of the intensity observed at Tukino has been found in the literature, *Carmichaelia* has been shown to be a significant component of several herbivores diets. *Carmichaelia* spp. was found to comprise on average 9% of thar, and 19% of chamois diet in the Rangitata/Rakaia catchments (Parkes and Thomson 1995). Samples of *Carmichaelia* were found in 78 % of 40 chamois rumens examined from Westland forests, usually in large quantities. Blay (1989) found that hares consume variable amounts of *Carmichaelia* throughout the year, with composition of *Carmichaelia* peaking at approximately 12% during the winter period.

5.4.2 MOAWHANGO EXCLOSURES

Hare browsing on *Chionochloa rubra* and *Festuca novae-zelandiae* in the Moawhango region was found to be negligible. No impact from hares was observed on *F. novae-zelandiae* at any of the sites. However, hare browsing was evident on *C. rubra* in the region, with light browsing observed at Motumatai and Awapatu. These results indicate that hare browse on these species in the region is negligible, especially when compared to the impact of horses in the region. Horses have been shown to have severe detrimental impacts in the region (Rogers 1991; Rogers 1994), and while their numbers have been reduced in some areas, they appear to be causing more damage on these two species than hares. However the same cannot be said for *Dracophyllum subulatum* in the region.

The results from this study indicate that hare browse can reduce the height, and change the growth form of *D. subulatum* to a prostrate habit (i.e. low height: basal area ratio). High levels of browsing were observed at both sites and as the Awapatu site is within the zero horse density area (Department of Conservation 1995) all browse observed at Awapatu, including in the unfenced control, can be attributed to hares. Also, at the Upper Argo Rd site, browse levels in the horse exclosure were five times higher in the than the unfenced control plot. When these browsing levels are combined with the differences observed in height, and height : basal area ratios, it becomes apparent that these browsing levels are sufficient to alter the growth habit of *D. subulatum*. Lower height and height: basal area ratios solely attributable to hares were only observed at Awapatu. While the unfenced control plot at the Upper Argo Rd site had reduced height and height: basal area ratios, horse presence at the Upper Argo Rd site was also much higher and browsing in the unfenced control could be due to either hares or horses. I suggest that these higher horse densities are responsible for the elevated levels of browse observed in the horse exclosure plot at this site. Competition between hares and horses would presumably be higher at the Upper Argo Rd site, and could result in hares concentrating in the horse exclosure where they had exclusive access. However hares were not effecting the overall composition of the plot (Chapter 3), and no other plant species were obviously impacted by hares. Therefore, I suggest hares are frequenting the plot for the main purpose of browsing on *D. subulatum*. Further evidence to support hare preference for *D. subulatum*, is the population densities obtained from the cleared plot pellet lines reported in Chapter 1. At Awapatu, hare density is higher (1.73 hares/ha) than at Upper Argo Rd (0.53 hares/ha). I suggest this is the reason for the Awapatu browse scores being significantly higher than at the Upper Argo Rd site. This evidence combines to indicate that hares have a strong preference for *D. subulatum* and are capable of altering its growth habit. Whether or not the impact is sufficient to reduce the viability of the species is uncertain and would require further investigation.

Dracophyllum is not a genus typically associated with being impacted by herbivores in New Zealand. *Dracophyllum uniflorum* was listed by Flux (1967a) as a minor species of hare diet in Cupola basin, Nelson Lakes National Park. Furthermore, in a review of ungulate feeding preference, the only member of the genus to be mentioned, *Dracophyllum longifolium*, is listed as being avoided when present (Forsyth *et al.* 2002), although it is browsed by chamois (Clarke 1986). *Dracophyllum subulatum* is a central North Island endemic that often dominates frost flat communities subject to cold-air ponding and unseasonal frosts. Frost flat heathland sites too frosty for manuka (*Leptospermum scoparium*), may have once occupied tens of thousands of hectares of the Eastern Volcanic Plateau (Smale 1990). Dominance of *D. subulatum* appears to be maintained by periodic fire and its prevalence as a frost flat dominant is threatened through a reduction in the fire regime and invasion of exotic weeds (Smale 1990).

Therefore the addition of hare browsing pressure might enhance the decline of this species.

5.4.3 MANSON EXCLOSURES

In the Manson region there was no significant change for any species in any of the variables measured that could be attributed to herbivore impact. The increase in *Poa cita* at Site 2 can be attributed to the increased flowering and growth seen in numerous grass species throughout the region (see Chapter 4). The dieback observed in *Ozothamnus leptophyllus* is concerning and requires further investigation. While the dieback could not be linked to any obvious cause, the state of this species should be monitored to ensure that this is not a widespread phenomenon. While there were not sufficient individuals of *Raukaua anomalus* and *Chionochloa rubra* for statistical evaluation, the results obtained highlight possible areas for further investigation. All four individuals of *R. anomalus* showed signs of moderate too heavy browsing, suggesting that it is a preferred species by a herbivore in the region. The growth habit of this species is one of divarication (Greenwood and Atkinson 1977), therefore possibly inferring some resistance to browsing. But without further investigation the high levels of browsing could be highly impacting the species. While only three individuals of *C. rubra* were measured, all showed signs of browsing at initiation with those having hare browsing pressure removed, recovering in one season. Whilst all three individuals measured showed signs of browsing, this was not the case for all individuals in the region. There are isolated pockets of *C. rubra* scattered throughout the region and the majority of specimens did not show signs of browsing.

5.4.4 GENERAL OBSERVATIONS

The results from this chapter have raised several interesting features of hare browsing preference and me lead to propose several hypotheses concerning feeding strategies of hares. Hare browsing preference is conditional upon the relative nutritional, physical and chemical attributes of the available species (Schmitz *et al.* 1992). Variation in these parameters would be expected to be greater between species. Therefore the primary determinant of browsing preference will be at the species level. However variation in soil fertility also effects nutrient levels in plants (Lee and Fenner 1989). Therefore I suggest the physical location of an individual plant will also effect its predisposition to browse. While no quantitative measures were done to assess soil fertility in the Turoa and Whakapapaiti flush zones, higher nutrient concentrations were assumed through enrichment from water flow and inferred from the significantly higher vegetation cover evident in the flush zones. Therefore while the primary determinant of browsing selection will be species, the secondary determinant will be the micro site location of the individual. Consequently species that occur primarily in flush zones will be particularly predisposed to browsing e.g. *C. pallens*. Further evidence for this theory is found in observations made of *Carmichaelia nana* at Tukino.

The vegetation of the Rangipo desert varies from virtually continuous cover, to scattered clumps situated on recent alluvial fans. The full range of vegetation types was present in the Tukino study site and, from casual observations, it appeared that the specimens of *C. nana* occurring in the alluvial fans suffered higher levels of browsing. I suggest this is related to nutrient enrichment from the alluvial substrate. It appears that *C. nana* is one of the pioneer species that will colonise the alluvial fans. If nutrient levels increase with soil fertility, as seen in *Chionochloa* (Lee and Fenner 1989), then those individuals occurring in the alluvial fans could have comparatively high nutrient levels. This is of concern for the revegetation of the alluvial fans. It appears that *C. nana* will form a distinct clump of vegetation that will stabilise the substrate and allows for invasion by other species. If the revegetation process is inhibited by hare browsing, then a gradual decrease in vegetation could become apparent in the region.

An interesting observation was made across the regions of this study regarding the exposure of *Chionochloa* to browsing. It appeared that the further away an individual plant was from its nearest neighbour, the more browsing it received. This has several credible explanations, and leads into the theoretical relationships between species abundance and herbivore impact. The most plausible explanations for this observation, relate to the chemical properties of *Chionochloa*. If hares obtain from *Chionochloa,* nutrients that cannot be obtained elsewhere, than a larger population of plants has the potential to spread the browsing load. Whereas an isolated plant would be targeted for all nutrient requirements. This observation can also be interpreted through the chemical defences of plants acting to inhibit browsing. When a species is so rare that it's mass of toxins does not exceed the detoxification capacity of the browsing animals, all individuals of that species can be eaten (Bryant *et al.* 1991). However as the biomass of the species exceeds the detoxification capacity of its herbivores, the average browsing intensity decreases (Bryant *et al.* 1991). The level this toxification occurs at is uncertain, but the concept leads onto the application of theoretical herbivore-plant interactions for understanding hare impacts (which will be discussed in Chapter 6). Interestingly, security was not always ensured by being a member of a larger population. Often a single individual was observed to be severely browsed by hares, when other individuals remained untouched. With this could be due to microsite location, defoliation of *Chionochloa* will increase the production of new tillers, along with temporarily raising P, N and K concentrations (Mills *et al.* 1989). This leads me to suggest that when hares target an individual plant, they induce a temporary increase in production and nutrient levels. Whether this selection is ongoing on one individual or rotated once production decreases, would be a fascinating area for investigation.

5.4.5 RECOMMENDATIONS

While this study has provided an insight into the feeding strategies of hares in the alpine environment, it has also opened many avenues in which to pursue further research. While hare browsing impact was shown, this study has only looked at the short term and immediate effects on the species concerned. For a full picture of the true browsing impact, long-term effects on reproductive output, growth, and survival needs to be investigated for every species concerned. Until this is completed, the true impact of browsing cannot be known. In spite of this, many interesting results were obtained that raised avenues for further research. Some of the questions raised are theoretically based with regard to feeding strategies, while others address management issues directly relating to species preservation. It is apparent that hare preference is based firstly upon species, and then habitat location. But many other areas of hare feeding strategies have been alluded to by the data, and opened many areas for future research. These include investigations into the relationship between an individual's isolation and browsing, browsing to stimulate and induce growth in plant species, and if competition with other herbivore effects diet selection. Understanding exactly which nutrients were targeted by hares would be interesting in itself, but would also provide a useful management tool for the identification of potentially vulnerable species.

The long history of hare presence in these regions could mean that many species that were once preferred have declined to the point that they are no longer evident as a food supply. These species would be hard to detect but are perhaps the most critical due to their vulnerability. For example *Aciphylla squarrosa* was listed by Horne (1979) as being highly preferred by hares, yet it was not observed at any of the study sites. Whether it is naturally uncommon in the region or has reduced through the influence of browsing need to be investigated. Additionally several of the highly impacted species on Mt Ruapehu require immediate action. The relationship between *C. pallens* and browsing was clearly evident for the regions in this study. A full scale survey of the high altitude flush zones should be undertaken to assess the status of *C. pallens* on Mt Ruapehu. If the browsing observed here is an isolated case, then the required action will be minimal. However I suspect that it will be a problem encountered for the entire region and substantial action will be required to preserve the species on Mt Ruapehu. A similar issue requires addressing on the eastern slopes of Mt Ruapehu. If hares are inhibiting the revegetation of the alluvial fans by their browsing of *C. nana*, a loss of indigenous biodiversity is possible along with a potential erosion problem for that area. While currently the species did not appear to be at threat, if there is a long term continuation of the browsing that could change.

5.4.6 CONCLUSIONS

The results from this chapter contradict the view that hare browsing impact on alpine vegetation is minimal due to impact being spread over the wider environment (Flux 1990). Varying nutrient levels appear to cause highly selective browsing on preferred plant species, with browsing levels varying depending on species, microsite, and region. Hares on Mt Ruapehu appear to be selectively locating themselves in favourable habitat where nutrient enrichment of plants is higher, and this can result in severe damage to the vegetation. *Chionochloa* spp., *Schoenus pauciflorus*, and *Carmichaelia nana* were identified as highly preferred species that hares appear to be having significant detrimental effects upon. In the Moawhango region hare impact was negligible on most species investigated, with the exception of *Dracophyllum subulatum*. This species appeared highly preferred by hares and growth form was significantly affected by their browsing. The preferential browsing observed by hares is of concern for the ongoing survival of several species.

Chapter 6

General discussion

6.1 SYNOPSIS

No previous study of hare impact in New Zealand has attempted to cover a wide range of vegetation types, and relate vegetation impact to population density. Each chapter in this thesis has provided interesting stand alone results, but at first they may appear somewhat contradictory with no overlying result obvious. From the small number of long term exclosure plots in Chapter 3, it appeared that hares were having no effect on any aspect of vegetation condition, either native or exotic in the Moawhango region. While in Chapter 4 hares were having a significant effect upon the vegetation in Manson over just one season. While here there may have been some detrimental effects to native vegetation as a direct consequence of hare browse, the overriding impression was that hares were benefiting native species through the suppression of exotics. In contrast Chapter 5 showed hares were browsing heavily upon a range of native plant species.

These somewhat paradoxical results do not appear to develop upon the existing knowledge regarding hare impacts in New Zealand. However a better understanding of hare impact can be gained when the results are considered collectively, and with knowledge of hare density.

Chapter 2 showed, along with the viability of the cleared pellet plot technique, that hare populations varied considerably from site to site. Only at two of the pellet sites (Awapatu, Upper Argo Rd) were anthropogenic factors thought to be affecting hare density, therefore all other variations can be attributed to natural population processes.

Food will be a limiting factor to all herbivores some of the time, but it will be especially important to those species with low levels of disease, scarce natural enemies, along with plentiful cover and breeding sites (Crawley 1983). Therefore the population densities observed will directly relate to the quality of the habitat present. In Manson, the habitat quality would be expected to be high due to the large areas of modified grassland present. This was reflected in the high hare densities at this site. While the Moawhango region had large areas of modified grassland present, these areas also had high competition from horses, or targeted hare and rabbit control programs. However the most surprising density result was obtained from the Tukino site. While a high density would be expected at Manson, Tukino is composed of scattered clumps of vegetation amongst alluvial fans. Whilst the high density was unexpected, high levels of browsing on the nitrogen fixing *Carmichaelia nana* in the region (Chapter 5) indicate that this species is highly preferred, and therefore possibly capable of fulfilling the nutritional requirements of hares and thus supporting a high population. Since the high populations were observed in contrasting habitat types, both would appear to be high quality habitat for hares. Consequently, the combination of results leads me to hypothesise as to a general feeding strategy for hares in New Zealand.

6.2 PROPOSED GENERAL FEEDING STRATEGY

While hare browsing preference of hares is related to nutritional components within plants (Sinclair and Smith 1984; Rodgers and Sinclair 1997), diet selection is dependent mainly upon prevalence of individual plant species in the environment, and partially due to favourability (Blay 1989). In cases where a preferred species is also abundant, hares will consume large quantities, e.g. *Hieracium pilosella* in Canturbury (Blay 1989). While hares in New Zealand adopt a generalist feeding strategy (Flux 1990), they appear to show a preference for exotic species (Blay 1989; Rogers 1994). While they can have significant detrimental effect upon native plants species (this study: Blay 1989; Rose and Platt 1992; Rogers 1994), I suggest that the degree to which hares impact native vegetation is dependent upon the level of exotic species present. Where exotic species are present (particularly grasses), they are the preferred browse species. Indeed it appears that hares can suppress these species to the apparent benefit of the native species present (i.e. Manson). Where exotic species are not readily available, or competition is high, hares then subsist at lower densities by browsing native vegetation (i.e. Awapatu). Hence if nutritionally adequate plant species are lacking in the environment, then hare numbers will be reduced (i.e. Turoa hillslope). However if a native species occurs that fulfils hare nutritional requirements, then it will be preferentially targeted by hares resulting in significant detrimental effects. Evidence for this was clearly seen at Tukino, and in the Turoa flush zones, exotic species were few, but hare densities and vegetation impact was high. Therefore I suggest it is the relationship between exotic and native plant abundance, along with plant nutritional components that will determine the answer to the next question, are hares a pest?

6.3 ARE HARES A PEST?

The biggest problem facing New Zealand pest managers is that the interactions between biological and sociological processes have only begun to be understood, and cannot be used to formulate convincing rules and policy (Parkes 1993). Therefore the exact definition required for a species to be labelled a pest is unclear. However conservation in New Zealand is largely focused on reducing the impacts of introduced mammals on indigenous species (Choquenot and Parkes 2001). This relationship is clouded with hares as interactions between hares and their browse species are confounded by the issues created by invasive exotic species. This is evidenced by the wide range of results obtained in this thesis, resulting in the answer to the question of whether hares are pests, being multifaceted. However the general feeding strategy proposed above helps to answer this question.

I suggest that in modified grasslands, hares will not be a pest due to preference for exotic species. While there may be detrimental impacts on native vegetation, the Manson exclosures, along with evidence from the literature, suggest that hare browsing is beneficial to the retention of native biodiversity. However the role of apparent competition (Huntly 1991) would need to be investigated. If hare populations are maintained at a high level through browsing of the exotic species, they may be having a significant effect by "casual" browsing of native species. I suggest it is in the semi-modified to unmodified alpine ecosystems that hare impact has the potential to be most detrimental. While hare browsing is said to be generalist (Flux 1990), in these systems, hares appear to target certain native species resulting in a significant detrimental impact. Whether or not the apparent impact truly reflects greater feeding preference on these preferred species, or is an artefact of slower growth and recovery times of these species is uncertain. But nevertheless the damage appears to be significant. Additionally it is in these semi-modified to unmodified alpine ecosystems that hares are often the primary browser. In ecosystems where larger mammalian herbivores are present (e.g. horses, deer), hare densities would need to be exceedingly high to overshadow their impact. Further insight into the possible role of hares as a pest can be gathered through application of theoretical pest modelling.

6.4 APPLICATION OF HERBIVORE IMPACT MODELLING

Many characteristics of hares and their relationships with plant species are implicated in the theoretical literature regarding pest modelling. Hares in New Zealand are described as living at relatively low densities, in stable populations, and graze from a wide range of species (Flux 1990). These characteristics place the hare as a *K*-strategist species, which are described as having low intrinsic rates of increase, stable populations, and as poor dispersers (Parkes 1993). Since *K*-strategists do not generally undergo dramatic population cycles, impacts are not periodic, but stable over time and consequently the impacts of these types of pests have the potential to be chronic as they are sustained with no resource recovery period (Parkes 1993). Additionally, the generalist browsing strategy of hares leads to a Type 2 functional response between the pest and resource (Choquenot and Parkes 2001). In a Type 2 response, if the availability of a threatened resource does not limit pest density, then a decline in the resource will not limit the pest population and such systems are prone to resource extinction (Choquenot and Parkes 2001). This would appear to be the case with hares as they are generally not limited by a single resource. If we apply the characteristics of a Type 2 response to herbivore-vegetation interactions, at high resource abundance the impact will be comparatively minor as the effect will stay constant at a level sustainable by the resource. However if the impact is above a threshold that is not sustainable, resources are consumed at a declining rate until exhausted (Choquenot and Parkes 2001). Therefore small populations of preferred plants would be highly vulnerable to the browsing impacts of a generalist herbivore, such as the hare. Additionally there is a well developed field in conservation biology, usually for vertebrates, regarding the effect of small population size on a population's viability. As populations become smaller there are a number of interacting processes that can destabilize small populations such as instability of breeding, genetic effects, and predation (Lacy 2000). Therefore once a population becomes small, it may enter an "extinction vortex", from which deterministic and stochastic factors act to drive the population to extinction (Gilpin and Soule 1986).

If these models are applied to hares, even without the knowledge of the results in this study, it suggests that hares have the potential to significantly affect vegetation. In addition, the results from the present study strongly support many of the modelling predictions. I suggest high levels of impact observed on *Schoenus pauciflorus*, *Chionochloa pallens*, and on the isolated *Chionochloa rubra*, are a result of a Type 2 functional response. Hare numbers are maintained through their generalist browsing, but they are selectively targeting certain species and I suggest these populations are below the sustainability threshold. The Type 2 response is further supported by the low impacts observed in the large *C. rubra* populations, suggesting it is above the sustainability threshold. Whether or not other species such as *Carmichaelia nana* and *Dracophyllum subulatum* are above or below the sustainability threshold require investigation. These results indicate that hare browse will significantly effect small populations of favourable plants, both by causing their decline, and preventing their establishment.

6.5 CONCLUSION

This thesis has contributed to the knowledge of hares in New Zealand by not only studying hare browsing impact in a variety of habitats, but incorporating estimates of density into the interpretation. Hare browsing impact is highly variable depending upon the vegetation present in the habitat. In modified alpine grasslands, hare browsing appears to benefit native species through the suppression of invasive exotic species. But where exotic species are absent, hares can cause significant damage to native plant species. Hare densities varied from site to site in relation to habitat quality, competition, and anthropogenic influences. However relationship between hare density and vegetation impact is confounded. Hares can exist at high densities and have minimal impact on native vegetation (due to browsing exotics), but as the proportion of exotic species decreases, impact on native species increases. Conversely if a highly preferred native species occurs in an otherwise "sparse" environment, then hare impact can be significant.

REFERENCES

Arnold, J. F. and Reynolds, H. G. (1943). "Droppings of Arizona and Antelope Jack rabbits and the "Pellet Census"." Journal of Wildlife Management **7** 322-327.

Baddeley, C. J. (1985). Assessments of wild animal abundance. FRI bulletin No. 106, Forest Research Institute, Christchurch, New Zealand: 46.

Batcheler, C. L. (1973). "Estimating density and dispersion from truncated or unrestricted joint point-ditance nearest neighbour distances." Proceedings of the New Zealand Ecological Society **20** 131-147.

Batcheler, C. L. (1975a). "Development of a distance method for deer census from pellet groups." Journal of Wildlife Management **39** 641-652.

Batcheler, C. L. (1975b). "Probable limit of error of the point distance-neighbour distance estimate of density." Proceedings of the New Zealand Ecological Society **22** 28-33.

Bellingham, P. J. and Allan, C. N. (2003). "Forest regeneration and the influences of white-tailed deer (*Odocoileus virginianus*) in cool temperate New Zealand rain forests." Forest Ecology & Management **175** 71-86.

Blay, G. (1989). Food preferences of the European hare (*Lepus europaeus* Pallas) on a fescue grassland, Unpublished MSc thesis, Zoology Department, University of Canterbury: 104p.

Bliss, L. C. and Mark, A. F. (1974). "High-alpine environments and primary production on the Rock and Pillar Range, Central Otago, New Zealand." New Zealand Journal of Botany **12** 445-483.

Bryant, J. P., Provenza, F. D., Pastor, J., Reichardt, P. B., Clausen, T. P. and du Toit, J. T. (1991). "Interactions between woody plants and browsing mammals mediated by secondary metabolites." Annual Review Ecology and Systematics **22** 431-436.

Bryant, J. P., Swihart, R. K., Reichardt, P. B. and Newton, L. (1994). "Biogeography of woody plant chemical defence against snowshoe hare browsing: Comparison of Alaska and eastern North America." Oikos **70** 385-395.

Campbell, D. J. and Atkinson, I. A. E. (2002). "Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands." Biological Conservation **107** 19-35.

Carroll, A. L. K. (1968). "Foods of the harrier." Notornis **15** 23-28.

Choquenot, D. and Parkes, J. (2001). "Setting thresholds for pest control: how does pest density affect resource viability?" Biological Conservation **99** 29-46.

Clarke, C. M. H. (1986). "Chamois movements and habitat use in the Avoca River area, Canterbury, New Zealand." New Zealand Journal of Zoology **13** 175-198.

Clarke, K. R. (1993). "Non-parametric multivariate analyses of changes in community structure." Australian Journal of Ecology **18** 117-143.

Conner, H. E. (1991). "*Chionochloa* Zotov (Gramineae) in New Zealand." New Zealand Journal of Botany **29** 219-282.

Crawley, M. J. (1983). Herbivory: the dynamics of animal-plant interactions, Blackwell Scientific Publications, Oxford: 437p.

Crawley, M. J. (1997). Plant-herbivore dynamics. Plant ecology. M. J. Crawley, Blackwell Science, Oxford ; Malden, USA**:** pp 401-474.

Davis, M. R. and Orwin, J. (1985). Report on a survey of the proposed Wapiti area, West Nelson. FRI bulletin No.84, Forest Research Institute, Christchurch, New Zealand.**:** 245.

de Lange, P. J., Heenan, P. B., Given, D. R., Norton, D. A., Ogle, C. C., Johnson, P. N. and Cameron, E. K. (1999). "Threatened and uncommon plants of New Zealand." New Zealand Journal of Botany **37** 603-628.

Dickinson, K. J. M., Mark, A. F. and Lee, W. G. (1992). "Long-term monitoring of non-forest communities for biological conservation." New Zealand Journal of Botony **30** 163-179.

Diemer, M. W. and Pfadenhauer, J. (1987). "Effect of differential defoliation on shoot growth density and phytomass of three graminoids in a calcareous fen." Oikos **50** 183-190.

Department of Conservation (1995). Kaimanawa Wild Horses Plan, Department of Conservation, Wanganui Conservancy, Wanganui, New Zealand**:** 93p.

Department of Conservation (1997). Moawhango Ecology: native plants at risk. Wanganui Conservancy, Wanganui, New Zealand.

Douglas, M. J. W. (1970). "Foods of harriers in a high country habitat." Notornis **17** 92-95.

Douglas, M. J. W. (1970). "Movements of hares *Lepus europaeus* Pallas, in high country in New Zealand." New Zealand Journal of Science **13** 287-305.

Duncan, R. P., Webster, R. J. and Jensen, C. A. (2001). "Declining plant species richness in the tussock grasslands of Canturbury and Otago, South Island, New Zealand." New Zealand Journal of Ecology **25** 35-47.

Ernst, W. H. O. and Van Der Ham, N. F. (1988). "Population structure and rejuvenation potential of *Schoenus nigricans* in coastal wet dune slacks." Acta Botanica Neerlandica **37** 451-466.

Esler, A. E. (1965). Tongariro National Park Handbook, Tongariro National Park Board, Wellington. 93p

Fenner, M., Lee, W. G. and Duncan, S. J. (1993). "Chemical features of *Chionochloa* species in relation to grazing by ruminants in South Island, New Zealand." New Zealand Journal of Ecology **17** 35-40.

Flux, J. E. C. (1967a). "Hare numbers and diet in an alpine basin in New Zealand." Proceedings of the New Zealand Ecological Society **14** 27-33.

Flux, J. E. C. (1967b). "Reproduction and body weights of the hare *Lepus europaeus* Pallas, in New Zealand." New Zealand Journal of Science **10** 357-401.

Flux, J. E. C. (1969). "Current work on the reproduction of the African hare, *Lepus capensis* L., in Kenya." Journal of Reproduction and Fertility Supplement **6** 225-227.

Flux, J. E. C. (1990). Brown hare. The handbook of New Zealand mammals. C. M. King, Oxford University Press, Auckland: pp138-174.

Forsyth, D. M., Coomes, D. A., Nugent, G. and Hall, G. M. J. (2002). "Diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand." New Zealand Journal of Zoology **29** 323-343.

Franklin, A. J. (1995). Patterns of dispersion, behaviour, and reproduction in feral horses (*Equus caballus*), and plant growth in Argo Valley, Waiouru. Unpublished MSc thesis. Massey University, New Zealand.

Fraser, W. K. and Sweetapple, P. J. (1992). "Hunters and hunting patterns in part of the Kaimanawa recreational hunting area." New Zealand Journal of Zoology **19** 91/98.

Gilpin, M. E. and Soule, M. E. (1986). Minimum viable populations: Processes of species extinction. Conservation Biology: the science of scarcity and diversity. M. E. Soule, Sianuer Associates Inc. Sunderland, Massachusetts.

Greenwood, R. M. and Atkinson, I. A. E. (1977). "Evolution of divaricating plants in New Zealand in relation to moa browsing." Proceedings of the New Zealand Ecological Society **24** 21-33.

Gruner, I. and Heenan, P. B. (2001). "Viability and germination of seeds of Carmichaelia (Fabaceae) after prolonged storage." New Zealand Journal of Botany **39** 125-131.

Hansen, R. M. (1972). "Estimation of herbage intake from Jackrabbit feces." Journal of Range Management **25** 468-471.

Heenan, P. B. (1995). "A taxonomic revision of Carmichaelia (Fabaceae-Galegae) in New Zealand (part I)." New Zealand Journal of Botany **33** 455-475.

Heenan, P. B. (1997). "Heteroblasty in Carmichaelia, Chordospartium, Corallospartium, and Notospartium (Fabaceae-Galegeae) from New Zealand." New Zealand Journal of Botany **35** 243-249.

Hjalten, J. (1992). "Plant sex and hare feeding preferences." Oecologia, Berlin. **89** 253-256.

Hochachka, W. M., Martin, K., Doyle, F. and Krebs, C. J. (2000). "Monitoring vertebrate populations using observational data." Canadian Journal of Zoology **78** 521-529.

Horne, R. S. C. (1979). Seasonal and altitudinal variations in diet and abundance of the European hare in Tongariro National Park, New Zealand. Unpublished MSc thesis, Massey University. New Zealand.

Hulbert, I. A. R., Glenn, I. R. and Racey, P. A. (1996). "Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies." Journal of Applied Ecology **33**.

Huntly, N. (1991). "Herbivores and the dynamics of communities and ecosystems." Annual Review Ecology and Systematics **22** 477-503.

Husheer, S. W. (2003). Impacts of deer on Kaimanawa beech forests, Unpublished Ph.D thesis, Massey University, Palmerston North.

Jenkins, C. (1982). The animals and vegetation of Kaweka State Forest Park. Palmerston North, N.Z. Forest Service: 60p.

Keith, L., B., (1986). "Role of food in hare population cycles." Oikos **40** 385-395.

King, C. M. (1990). Stoat. The handbook of New Zealand mammals. C. M. King, Oxford University Press, Auckland: pp288-313.

King, C. M. and Moody, J. E. (1982). "The biology of the stoat (*Mustela erminea*) in the national parks of New Zealand. II Food habits." New Zealand Journal of Zoology **9** 57-80.

Krebs, C. J. (1986). "Are lagomorphs similar to other small mammals in their population ecology." Mammal Review **16** 187-194.

Krebs, C. J., Boonstra, R., Nams, V., O'Donoghue, Hodges, K. E. and Boutin, S. (2001). "Estimating snowshoe hare population from pellet plots: a further evaluation." Canadian Journal of Zoology **79** 1-4.

Krebs, C. J., Gilbert S. B., Boutin S. and Boonstra R. (1987). "Estimation of snowshoe hare population density from turd transects." Canadian Journal of Zoology **65** 565-567.

Lacy, R. C. (2000). "Considering threats to the viability of small populations using individual-based models." Ecological Bulletins **48** 39-51.

Langbein, J., Hutchings, M. R., Harris, S., Stoate, C., Tapper, S. C. and Wray, S. (1999). "Techniques for assessing the abundance of Brown Hares, *Lepus europaeus*." Mammal Review **29** 93-116.

Lazo, A., De Le Court, C. and Soriguer, R. C. (1992). "Evaluation of hare abundance allowed by their use of attraction points." Mammalian Biology, Zeitschrift Fuer Saeugetierkunde **57** 373-379 [abstract only].

Lee, W. G. and Fenner, M. (1989). "Mineral nutrient allocation in seeds and shoots on twelve *Chionochloa* species in relation to soil fertility." Journal of Ecology **77** 704-716.

Lee, W. G., Fenner, M., Loughnan, A. and Lloyd, K. M. (2000). "Long-term effects of defoliation: Incomplete recovery of a New Zealand alpine tussock grass, *Chionochloa pallens*, after 20 years." Journal of Applied Ecology **37** 348-355.

Lethbridge, C. (1971). Sunrise on the hills : a musterer's year on Ngamatea--New Zealand's biggest sheep station. Auckland, Hodder and Stoughton 176p.

Levine, M. J. (1985). Himalayan thar in New Zealand : issues in management of an introduced mammal : report presented in partial fulfilment of the degree of Master of Science in Resource Management, Centre for Resource Management, University of Canterbury, Christchurch,New Zealand.

Lord, J. M. (1990). "The maintenance of *Poa cita* grassland by grazing." New Zealand Journal of Ecology **13** 43-49.

Mark, A. F. (1965b). "Effects of management practises on narrow-leaved snow tussock, *Chionochloa rigida*." New Zealand Journal of Botany **3** 300-319.

McCune, B. and Grace, J., B., (2002). Analysis of ecological communities, MjM Software design, USA

McCune, B. and Mefford, M. J. (1999). Multivariate analysis of ecological data, MjM Software, Gleneden Beach, Oregon, U.S.A.

McIntosh, P. D. and Allen, R. B. (1998). "Effect of exclosure on soils, biomass, plant nutrients, and vegetation, on unfertilised steeplands, Upper Waitaki District, South Island, New Zealand." New Zealand Journal of Ecology **22** 209-217.

McIntosh, P. D., Allen, R. B. and Scott, N. (1997). "Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand." Journal of Environmental Management **51** 169-186.

McKelvey, K. S., McDaniel, W., Mills, L., S. and Griffin, P. C. (2002). "Effects of plot size and shape on pellet density estimates for snowshoe hares." Wildlife Society Bulletin **30** 751-755.

Meurk, C. D. (1978). "Alpine phytomass and primary productivity in Central Otago, New Zealand." New Zealand Journal of Ecology **1** 27-50.

Meurk, C. D., Walker, S., Gibson, R. S. and Espie, P. (2002). "Changes in vegetaion states in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990-2000." New Zealand Journal of Ecology **26** 95-106.

Meurk, C. D., Walker, S., Gibson, R. S. and Espie, P. (2002). "Changes in vegetation states in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990-2000." New Zealand Journal of Ecology **26** 95-106.

Mills, J. A., Lee, W. G. and Lavers, R. B. (1989). "Experimental investigations of the effects of takahe and deer grazing on *Chionochloa pallens* grassland, Fiordland New Zealand." Journal of Applied Ecology **26** 397-418.

Mills, J. A. and Mark, A. F. (1977). "Food preference of takahe in Fiordland National Park, New Zealand, and the effect of competition from introduced red deer." Journal of Animal Ecology **46** 939-958.

Mitchell, R. J., Fordham, R. A. and John, A. (1987). "The annual diet of feral goats *Capra hircus* L. in lowland Rimu-Rata-Kamahi forest on eastern Mount Taranaki Mount Egmont New Zealand." New Zealand Journal of Zoology **14** 179-192.

Murray, D. L., Roth, J. D., Ellsworth, E., Wirsing, A. J. and Steury, T. D., q (2002). "Estimating low-density snowshoe hare populations using fecal pellet counts." Canadian Journal of Zoology. **80** 771-781.

Norbury, D. (1996). The effect of rabbits on conservation values. Science for Conservation 34, Department of Conservation, Wellington, New Zealand.

Parkes, J. P. (1981). Hare control in the high country. What's New in Forest Research, Forest Research Institute, Rotorua, New Zealand. **97:** 4.

Parkes, J. P. (1984). "Home ranges of radio-telemetered hares (*Lepus capensis*) in a sub-alpine population in New Zealand: implication for control." Acta Zoologia Fennica **171** 279-281.

Parkes, J. P. (1993). "The ecologigal dynamics of pest-resource systems." New Zealand Journal of Zoology **20** 223-230.

Parkes, J. P. (1993). "Feral goats: designing solutions for a designer pest." New Zealand Journal of Ecology **17** 71-83.

Parkes, J. P. (2001). Methods to monitor the density and impact of hares (*Lepus europaeus*) in grasslands in New Zealand, DOC Science Internal Series 8. Department of Conservation, Wellington**:** 13p.

Parkes, J. P. and Thomson, C. (1995). Management of thar. Science for Conservation 7, Department of Conservation, Wellington, New Zealand**:** 42p.

Parkmap (1990). Kaweka Forest Park, Department of Survey and Land Information. Wellington, New Zealand.

Parkmap (2000). Tongariro National Park, Department of Conservation, Wellington, New Zealand.

Pekelharing, C. J. (1979). "Fluctuation in opossum populations along the north bank of the Taramakau Catchment New-Zealand and its effect on the forest canopy." New Zealand Journal of Forestry Science **9** 212-224.

Pekelharing, C. J. and Reynolds, R. N. (1983). "Distribution and abundance of browsing mammals in Westland National Park New-Zealand in 1978 and some observations on their impact on the vegetation." New Zealand Journal of Forestry Science **13** 247-265.

Perry, M. E. (2003). Utility of the Scott height frequency method as a tool for monitoring alpine vegetation. Unpublished report prepared for Department of Conservation**:** 23p.

Putman, R. J. (1984). "Facts from faeces." Mammal Review **14** 79-97.

Quinn, G. P. and Keough, M. J. (2002). Experimental design and data analysis for biologists, Cambridge University Press. United Kingdom: 537.

Rao, S. J., Iason, G. R., Hulbert, I. A. R., Daniels, M. J. and Racey, P. A. (2003). "Tree browsing by mountain hares (*Lepus timidus*) in young Scots pine (*Pinus sylvestris*) and birch (*Betula pendula*) woodland." Forest Ecology and Management **176** 459-471.

Riney, T. (1957). "The use of faeces counts in studies of several free-ranging mammals in New Zealand." New Zealand Journal of Science and Technology **38B** 507-532.

Rodgers, A. R. and Sinclair, A. R. E. (1997). "Diet choice and nutrition of captive snowshoe hares (*Lepus americanus*): Interactions of energy, protein, and plant secondary compounds." Ecoscience **4** 163-169.

Rogers, G. (1991). "Kaimanawa feral horses and their environmental impacts." New Zealand Journal of Ecology **15** 49-64.

Rogers, G. (1994). Kaimanawa feral horses: recent environmental impacts in their northern range., Conservation Advisory Science Notes No. 105, Department of Conservation, Wellington, New Zealand**:** 11p.

Rogers, G. M. (1994). "North Island seral tussock grasslands: 1. Origins and land-use history." New Zealand Journal of Botany **32** 271-286.

Rogers, G. M. and Leathwick, J. R. (1994). "North Island seral tussock grasslands 2. Autogenic succession: Change of tussock grassland to shrubland." New Zealand Journal of Botany **32** 287-303.

Rogers, G. M. and Leathwick, J. R. (1996). "North Island seral tussock grassland. 3. The influence of heather (*Calluna vulgaris*) on rates of change from tussock grassland to shrubland." New Zealand Journal of Botany **34** 473-487.

Rogers, G. M. and McGlone, M. S. (1989). "A postglacial vegetation history of the southern-central uplands of North Island New Zealand." Journal of the Royal Society of New Zealand **19** 229-248.

Rogers, L. L. (1987). "Seasonal changes in defecation rates of free-ranging White-Tailed Deer." Journal of Wildlife Management **51** 330-333.

Rose, A. B. and Platt, K. H. (1987). "Recovery of northern Fiordland alpine grasslands after reduction in deer population." New Zealand Journal of Ecology **10** 23-33.

Rose, A. B. and Platt, K. H. (1992). "Snow tussock (*Chionochloa*) population responses to removal of sheep and European hares, Canterbury, New Zealand." New Zealand Journal of Botany **30** 373-382.

Schmitz, O. J., Hik, D. S. and Sinclair, A. R. E. (1992). "Plant chemical defense and twig selection by snowshoe hare: An optimal foraging perspective." Oikos **65** 295-300.

Scott, D. (1965). "A height frequency method for sampling tussock and shrub vegetation." New Zealand Journal of Botany **3** 253-260.

Sinclair, A. R. E. and Smith, J. N. M. (1984). "Do plant secondary compounds determine feeding preferences of snowshoe hares, *Lepus americanus*." Oecologia, Berlin. **61** 403-410.

Sinclair, A. R. E. and Smith, J. N. M. (1984). "Do plant secondary compounds determine feeding preferences of snowshoe hares?" Oecologia **61** 403-410.

Smale, M. C. (1990). "Ecology of *Dracophyllum subulatum* dominant heathland on frost flats at Rangitaiki and North Pureora, Central North Island, New Zealand." New Zealand Journal of Botany **28** 225-248.

Sweetapple, P. J., Nugent, G., Whitford, J. and Knightbridge, P. I. (2002). "Mistletoe (*Tupeia antarctica*) recovery and decline following possum control in a New Zealand forest." New Zealand Journal of Ecology **26** 61-71.

Taylor, R. H. and Williams, R. M. (1956). "The use of pellet counts for estimating the density of populations of the wild rabbit, *Oryctolagus cuniculus* (L.)." New Zealand Journal of Science and Technology **38** 237-256.

Tongariro National Park Board (1981). Tongariro National Park management plan.

Walker, S. and Lee, W. G. (2002). "Alluvial grasslands of Canterbury and Marlborough, eastern South Island, New Zealand: Vegetation patterns and long-term change." Journal of the Royal Society of New Zealand **32** 113-147.

Walker, S., Wilson, J. B. and Mark, A. F. (1999). "Seasonal changes in semi-arid vegetation of Central Otago, New Zealand." New Zealand Journal of Botany **37** 479-493.

Wardle, D. A., Barker, G. M., Yeates, G. W., Bonner, K. I. and Ghani, A. (2001). "Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences." Ecological Monographs **71** 587-614.

Wardle, P. (2002). Vegetation of New Zealand, Blackburn Press, Caldwell New Jersey, USA. 672p

White, E. G. (1974). "Grazing pressures of grasshoppers in an alpine tussock grassland." New Zealand Journal of Agricultural Research **17** 357-372.

Williams, P. A., Copper, P., Nes, P. and O'Connor, K. F. (1976). "Chemical composition of tall-tussocks in relation to the diet of the takahe (*Notornis mantelli* Owen), on the Murchison Mountains, Fiordland, New Zealand." New Zealand Journal of Botany **14** 55-61.

Williams, P. A., Grigg, J. L., Nes, P. and O'Connor, K. F. (1976). "Vegetation/soil relationships and the distribution of selected macronutrients within shoots of tall-tussocks on the Murchison Mountains, Fiordland, New Zealand." New Zealand Journal of Botany **14** 29-53.

Wilson, S. D. (1994). "The contribution of grazing to plant diversity in alpine grassland and heath." Australian Journal of Ecology **19** 137-140.

Wong, M. D. (2002). Spacing and ecology of the Australasian Harrier (*Circus approximans*) in the Rangitkei-Manawatu sand country, Unpublished MSc thesis, Massey University. New Zealand: 125p.

Wong, V. and Hickling, G. J. (1999). Assessment and management of hare impact on high altitude vegetation. Science for Conservation 116, Department of Conservation. Wellington, New Zealand: 40p.

Yockney, I. J. and Hickling, G. J. (2000). "Distribution and diet of chamois (*Rupicapra rupicapra*) in Westland forests, South Island, New Zealand." New Zealand Journal of Ecology **24** 31-38.

APPENDICES

Appendix 1: Table of abbreviated species names used in Scott height frequency graphs. Names are abbreviated to the first three letters of the genus (uppercase) followed by the first three letters of species (lowercase).

Abbreviation	Scientific name	Abbreviation	Scientific name
ACEmic	*Aceana microphylla*	LEUfra	*Leucopogon fraseri*
ANTodo	*Anthoxantum odoratum*	LINmon	*Linum catharticum*
BLEpen	*Blechnum penna-marina*	LYCfas	*Lycopodium fastigiatum*
CASlep	*Ozothamnus leptophyllus*	MICava	*Microlaena avenacea*
CELgra	*Celmisia gracilenta*	Moss	Moss
CELspe	*Celmisia spectabilis*	PERmac	*Pentachondra pumila*
CHIrub	*Chionochloa rubra*	PHYalp	Phyllocladus alpinus
COPche	*Coprosma cheesemanii*	Poa sp	*Poa* species
DEYave	*Deyeuxia avenoides*	POAcit	*Poa cita*
Elymus sp.	*Elymus* species	POAcol	*Poa colensoi*
EUPcun	*Euphrasia cuneata*	PODniv	*Podocarpus nivalis*
FESnov	*Festuca novae-zelandiae*	PRAang	*Pratia angulata*
FESovi	*Festuca ovina*	RAClan	*Racomitrium lanuginosum*
FESrub	*Festuca rubra*	RAUano	*Raukaua anomalus*
GAUdep	*Gaultheria depressa*	RYTgra	*Rytidosperma gracile*
HIEpil	*Hieracium pilosella*	RYTmer	*Rytidosperma merum*
HOLlan	*Holcus lanatus*	RYTset	*Rytidosperma setifolium*
HYPrad	*Hypochoeris radicata*	Trifolium sp	*Trifolium* species
LACfil	*Lachnagrostis filiformis*	UNCrub	*Uncinia rubra*
LEOtar	*Leontodon taraxacoides*	WAHpyg	*Wahlenbergia pygmaea*

Appendix 2: Monte Carlo test of stress in relation to dimensionality (Number of Axes) for the Nonmetric Multidimensional Scaling ordination carried out on the summed SHF values for each of the 12 plots over the four sites in the Moawhango region.

	Stress in real data 40 runs			Stress in randomized data Monte Carlo test, 50 runs			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	22.5	38.0	52.5	20.9	44.4	52.7	0.059
2	7.3	8.6	20.6	9.8	16.1	34.7	0.020
3	3.4	4.2	19.8	4.1	7.3	11.8	0.020
4	1.2	1.5	2.4	0.9	3.7	6.3	0.039
5	0.0	0.1	1.6	0.5	1.6	3.2	0.020
6	0.0	0.1	0.4	0.0	0.7	3.6	0.020

p = proportion of randomized runs with stress < or = observed stress
i.e., p = (1 + no. permutations <= observed)/(1 + no. permutations)

Appendix 3: The top 10 ranked species based upon the summed Scott height frequency data for each of the three exclosure plots in Manson Region. Plot A: hare/deer exclusion, plot B: hare access – deer exclusion, plot C: unfenced control, plot D: hare exclusion - deer access.

		Plot A		Plot B		Plot C		Plot D	
		2002	2003	2002	2003	2002	2003	2002	2003
Site 1	*Celmisia spectabilis*	65	73	52	89	61	68	61	77
	Poa colensoi	57	93	54	112	25	39	48	93
	Deyeuxia avenoides	11	58	24	41	16	12	21	53
	Leucopogon fraseri	15	20	29	60	18	18	18	41
	Racomitrium lanuginosum	14	25	20	29	17	23	18	21
	Anthoxantum odoratum	7	39	7	35	7	20	12	35
	Rytidosperma setifolium	9	13	17	16	4	11	27	31
	Wahlenbergia pygmaea	17	19	12	10	1	4	9	18
	Hypochoeris radicata	9	15	2	9	3	12	4	11
	Podocarpus nivalis	0	0	0	0	31	29	0	0
Site 2	*Holcus lanatus*	56	156	58	122	51	70	26	144
	Poa cita	43	85	34	46	27	38	127	78
	Anthoxantum odoratum	0	35	8	118	15	102	24	99
	Blechnum penna-marina	26	57	53	56	30	30	40	59
	Rytidosperma setifolium	21	35	48	49	41	46	10	85
	Trifolium sp	27	55	33	40	32	38	32	34
	Festuca rubra	0	160	0	8	0	16	0	55
	Rytidosperma merum	16	25	40	59	28	45	1	0
	Pratia angulata	16	22	24	26	23	33	24	31
	Linum catharticum	9	43	8	43	6	10	1	34
Site 3	*Rytidosperma setifolium*	63	75	69	93	77	74	92	91
	Poa colensoi	77	91	86	59	71	53	51	77
	Deyeuxia avenoides	43	41	38	38	1	24	39	60
	Anthoxantum odoratum	48	68	18	32	10	20	17	40
	Racomitrium lanuginosum	29	48	18	23	24	25	16	35
	Leucopogon fraseri	26	44	21	33	4	6	14	21
	Linum catharticum	33	7	22	28	7	28	31	10
	Gaultheria depressa	12	16	23	31	18	27	13	21
	Hypochoeris radicata	31	16	11	16	14	13	21	22
	Celmisia spectabilis	9	8	23	19	38	27	10	7

Appendix 4: The top 10 ranked species based upon the Quadrat data for each of the three exclosure plots in Manson. Plot A: hare/deer exclusion, plot B: hare access – deer exclusion, plot C: unfenced control, plot D: hare exclusion - deer access.

		Plot A		Plot B		Plot C		Plot D	
		2002	2003	2002	2003	2002	2003	2002	2003
Site 1	*Celmisia spectabilis*	30	30	32	32	30	32	31	32
	Leucopogon fraseri	28	30	32	30	26	30	28	30
	Poa colensoi	29	32	28	27	26	23	23	29
	Racomitrium lanuginosum	24	29	28	31	26	26	24	29
	Wahlenbergia pygmaea	21	30	22	26	20	23	20	25
	Hypochoeris radicata	26	31	15	20	19	20	17	27
	Deyeuxia avenoides	10	28	15	23	20	19	12	26
	Anthoxantum odoratum	17	25	4	12	8	17	11	18
	Rytidosperma setifolium	15	12	12	14	1	17	20	8
	Gaultheria depressa	16	16	10	9	1	10	11	1
Site 2	*Trifolium sp*	29	30	28	31	29	32	28	30
	Blechnum penna-marina	27	28	30	31	17	24	31	32
	Holcus lanatus	26	29	25	30	30	32	23	21
	Viola cunnighami	26	29	26	30	23	30	18	20
	Hypochoeris radicata	21	29	28	30	23	31	16	22
	Lycopodium	22	31	26	32	15	16	24	29
	Pratia angulata	17	18	27	22	18	30	24	21
	Anthoxantum odoratum	13	24	17	32	16	32	12	22
	Oreomyrrhis colensoi	15	15	25	22	26	24	17	15
	Linum catharticum	18	26	25	32	11	18	9	13
Site 3	*Hypochoeris radicata*	32	32	32	31	28	31	33	32
	Poa colensoi	32	31	31	32	31	30	27	29
	Rytidosperma setifolium	26	29	25	25	30	30	32	32
	Celmisia spectabilis	29	29	30	30	30	31	27	21
	Euphrasia cuneata	30	30	25	26	28	28	29	28
	Racomitrium lanuginosum	29	28	26	23	31	32	31	24
	Leucopogon fraseri	32	30	28	29	12	16	27	25
	Anthoxantum odoratum	20	24	25	21	19	23	26	22
	Linum catharticum	22	19	24	24	22	29	15	16
	Gaultheria depressa	26	19	27	0	26	26	23	13

Appendix 5: Monte Carlo test of stress in relation to dimensionality (Number of Axes) for the Nonmetric Multidimensional Scaling ordination carried out on the summed SHF values for each plot in the Manson region.

	Stress in real data 40 run(s)			Stress in randomized data Monte Carlo test, 50 runs			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	14.7	41.1	55.3	35.6	50.4	55.3	0.020
2	7.5	10.1	38.4	19.9	25.1	32.0	0.020
3	4.5	4.7	5.2	12.4	16.3	18.7	0.020
4	2.9	3.1	3.7	9.3	11.4	14.1	0.020
5	2.1	2.2	2.3	6.3	8.5	10.0	0.020
6	1.5	1.6	1.9	5.0	6.3	7.4	0.020

p = proportion of randomized runs with stress < or = observed stress
i.e., p = (1 + no. permutations <= observed)/(1 + no. permutations)