Potential conservation impacts of high-altitude small mammals: a field study and literature review

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ABSTRACT

Every few years, the dominant tussock grasses (*Chionochloa* spp.) in the alpine grasslands of New Zealand produce large numbers of flowers and later set seeds. This may be associated with pulses in the abundance of introduced mammals in alpine habitats, which may in turn increase the risks to native biota. The alpine mammals most likely to fluctuate in this way are house mice (*Mus musculus*), brown hares (*Lepus europaeus*) and stoats (*Mustela erminea*), which may also respond directly or indirectly to periodic heavy seedfall in nearby montane beech forest. We assessed the relative abundance of these mammalian species and the diet of mice in alpine grasslands and adjacent high-altitude beech forest in the Borland Valley, Southland, from February 2003 to November 2004. At the same time, we measured the flowering intensity of alpine tussock grasses and other alpine plants, and the production of beech seed. Mice (based on live-trapping) and hares (based on pellet counts) were more abundant at alpine than at forest sites, but numbers of stoats (based on tracking tunnels) were similar in the two habitats. In both habitats, the diet of mice was dominated by invertebrates, especially weta (Orthoptera), spiders (Araneae), caterpillars (Lepidoptera) and grasshoppers (Orthoptera). There was an inverse correlation between capture rates of mice and ground weta (*Hemiandrus* spp.) in snap traps at alpine sites, suggesting that predation by mice may reduce the abundance of these insects. Neither profuse tussock flowering nor heavy beech seedfall occurred during this study; therefore, we do not know how alpine populations of mice, hares or stoats respond to these events. Continued study of these relationships is recommended. Abundance or predation mortality of alpine species likely to be at risk, such as ground weta and rock wrens (*Xenicus gilviventris*), should also be assessed in relation to periodic tussock flowering and beech seedfall events.

Keywords: house mouse, brown hare, stoat, *Chionochloa*, snow tussock, alpine grassland, masting, beech forest, diet, herbivore, weta

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1. Introduction

Alpine snow tussock grasses (*Chionochloa* spp.) periodically produce large quantities of flowers and seed in response to high temperatures during the previous summer (Kelly et al. 2000). Mammalian pests in the alpine zone may respond numerically to the increased availability of food resulting from these flowering events by breeding at increased rates. House mice (*Mus musculus*) and possibly brown hares (*Lepus europaeus*) are the alpine mammals most likely to follow this pattern (rats (*Rattus* spp.) are uncommon at high altitude); stoats (*Mustela erminea*) may also respond indirectly, as a result of the increased abundance of mice or other prey species. It has been shown that mice and stoats increase in abundance after heavy seeding of southern beech (*Nothofagus* spp.) trees (King 1983), which tends to occur synchronously with *Chionochloa* seeding events (Schauber et al. 2002). If mammals move from lower altitude beech forests to alpine grasslands, populations in the latter may be affected by the availability of food in the former (Lavers & Mills 1978).

An increase in the abundance of alpine mammals is likely to threaten their native prey. The numerical response of predators to a plentiful food source may be accompanied by an increased per capita intake of that food (a functional response; Solomon 1949). However, the predators may continue to take alternative prey, which may therefore be at increased risk simply as a result of the rise in mammal numbers. In beech forests, for example, bird and invertebrate remains have been found in a similar proportion of stoat stomachs, whether or not mice were abundant (King 1983; Murphy & Dowding 1995). Mouse diet has not been compared between periods of high and low beech seedfall, but the stomachs of most mice in New Zealand habitats contain both invertebrate and plant remains (Ruscoe & Murphy 2005). Finally, a rise in mammal numbers could have a delayed impact on native prey. If mammals are abundant when the supply of plentiful food is exhausted, they may be forced to increase their consumption of other prey.

In this study, we assessed the abundance of mice, hares and stoats, and the diet of mice in alpine grassland and adjacent high-altitude beech forest in the Borland Valley, Southland, New Zealand. We also measured the rate of flowering and fruiting of alpine plants and of beech seedfall in this region. Flower and seed production were assessed during two consecutive summer–autumn seasons, and mammal population responses were estimated in the following spring. Because of the short duration of the study, detecting temporal relationships between these variables was likely to be contingent upon profuse tussock flowering or heavy beech seedfall occurring, and neither did so. Therefore, we predicted potential threats to native species in the alpine zone based not only on our results, but also on known diets, impacts and population dynamics of introduced alpine mammals.

2. Background

Grasslands dominated by snow tussocks are widespread above the treeline in New Zealand (Wardle 1991: 216). These alpine grasslands are populated by introduced mammals, including herbivores (hares, Himalayan thar *Hemitragus jemlahicus*, chamois *Rupicapra rupicapra*, feral goats *Capra hircus*, and the deer *Cervus* spp. and *Dama dama*), omnivores (mice, and brushtail possums *Trichosurus vulpecula*), and predators (stoats, and feral cats *Felis catus*) (King 2005). Although rats, European rabbits (*Oryctolagus cuniculus*), ferrets (*Mustela furo*) and European hedgehogs (*Erinaceus europaeus*) can occur above the treeline, they are uncommon there (King 2005).

Hares are widespread in New Zealand, with the exception of most of Fiordland and parts of Westland and Northland (Parkes et al. 1978; Wong & Hickling 1999; Norbury & Flux 2005). Chamois and thar occur only in the South Island, thar having a more limited distribution, and goats are patchily distributed within the North and South Islands. Red deer (*Cervus elaphus scoticus*) are widespread, whereas the other deer using alpine habitats (wapiti *C. e. nelsoni*, sika deer *C. nippon*, fallow deer *D. dama*, and white-tailed deer *Odocoileus virginianus*) have more restricted distributions (Forsyth et al. 2003; RPH, pers. obs.); since the advent of helicopter hunting, deer have become relatively uncommon in alpine grasslands (Nugent et al. 1987; Nugent 1990). Mice, possums, stoats and cats occur in alpine habitats throughout the New Zealand mainland, but little is known about their abundance or diet in the alpine zone. It is thought that cats may prefer forest habitat to exposed areas above the treeline, especially in wet weather (Harper 2004).

Small mammals that have the potential to reproduce rapidly, i.e. mice, hares and stoats, are most likely to respond at the population level to inter-annual pulses in food supply resulting from the periodic production of large crops of *Chionochloa* flowers or seeds. It is not known whether mice eat snow tussock seed, but it is likely, given that they are omnivorous, opportunistic feeders (Ruscoe & Murphy 2005); furthermore, their well-documented population growth after heavy seedfall in beech forests (e.g. King 1983) may in part be due to the increased supplies of flowers and of insects feeding on flowers or seeds (Fitzgerald et al. 1996). Hares eat *Chionochloa* leaves (Flux 1967; Horne 1979), but these grasses have not been recorded in the diet of possums (J.P. Parkes, Landcare Research, unpubl. data). Alpine stoats may increase in number if mice, birds, insects and perhaps hares reach a sufficiently high density, as has been found to occur in beech forest (Murphy & Dowding 1995). Larger mammals could respond behaviourally to increased food in the alpine zone by moving into the area. Although the diets of hares and the larger alpine mammals rarely include seeds (Flux 1967; Horne 1979; Cochrane & Norton 2003; J.P. Parkes, unpubl. data), the leaf bases of flowering tussock tillers are higher in nutrients than the non-flowering tillers, and have been shown to be selected by takahe (*Porphyrio mantelli*) (Mills et al. 1991).

This research was conducted in the same area and at the same time as an intensive study of the movements, diet and abundance of stoats in alpine habitat (Smith 2006). More detailed conclusions about stoats in alpine habitats will be available in the PhD thesis and publications resulting from that companion study.

3. Objectives

- To determine the abundance of mice, stoats and hares in alpine grasslands and adjacent high-altitude beech forest in summer, autumn and spring from February 2002 to November 2004.
- To measure changes in some of the food resources available to mice and hares in these habitats, by quantifying the intensity of flowering of alpine tussock grasses, the flowering or fruiting of alpine shrubs, and the production of beech seed during summer 2002 and 2003.
- To assess the relationship between temporal variation in the abundance of mice, hares and stoats, and temporal variation in flowering of alpine tussock grasses, flowering or fruiting of alpine shrubs, or production of beech seed. Detecting these relationships was likely to be contingent upon profuse tussock flowering or heavy beech seedfall occurring during the study.
- To predict periods of potential heightened threat to native species in the alpine zone, based on any relationship detected between mammalian pest abundance and seed production, and the known diets, impacts and population dynamics of these and other alpine mammals.

4. Methods

4.1 STUDY SITES

This research was conducted on the lower western slopes of Mount Burns near the Borland Saddle (45°44' S, 167°23' E) and in the valley of the Borland Burn (South Branch) (45°43' S, 167°25' E), Southland, New Zealand (Fig. 1). The entire study area is referred to below as the Borland Valley. This site was chosen because it is within the relatively undisturbed Fiordland National Park, and because the alpine zone was readily accessible from a road that rises to 900 m a.s.l. at the Borland Saddle and 740 m a.s.l. in the Borland Burn valley bottom. Below the treeline (c. 1000 m a.s.l.), the forest is dominated by mountain beech (*Nothofagus solandri* var. *cliffortioides*) and silver beech (*N. menziesii*), with *Coprosma cuneata*, *C. pseudocuneata*, *Phyllocladus alpinus* and *Astelia nervosa*. Above the treeline, there is alpine grassland dominated by the snow tussock species *Chionochloa crassiuscula*, *C. rigida*, *C. pallens* and *C. teretifolia*, with scattered shrubs including *Coprosma cheesemanii*, *Dracophyllum longifolium*, *D. uniflorum* and *Hebe odora*, and large herbs including *Astelia nervosa*, *Celmisia coriacea* and *C. lyallii*. A narrow band of mixed snow tussock and shrub vegetation separates the two communities. The terrain and vegetation near the Borland Saddle have been described in more detail by Solly (1998).

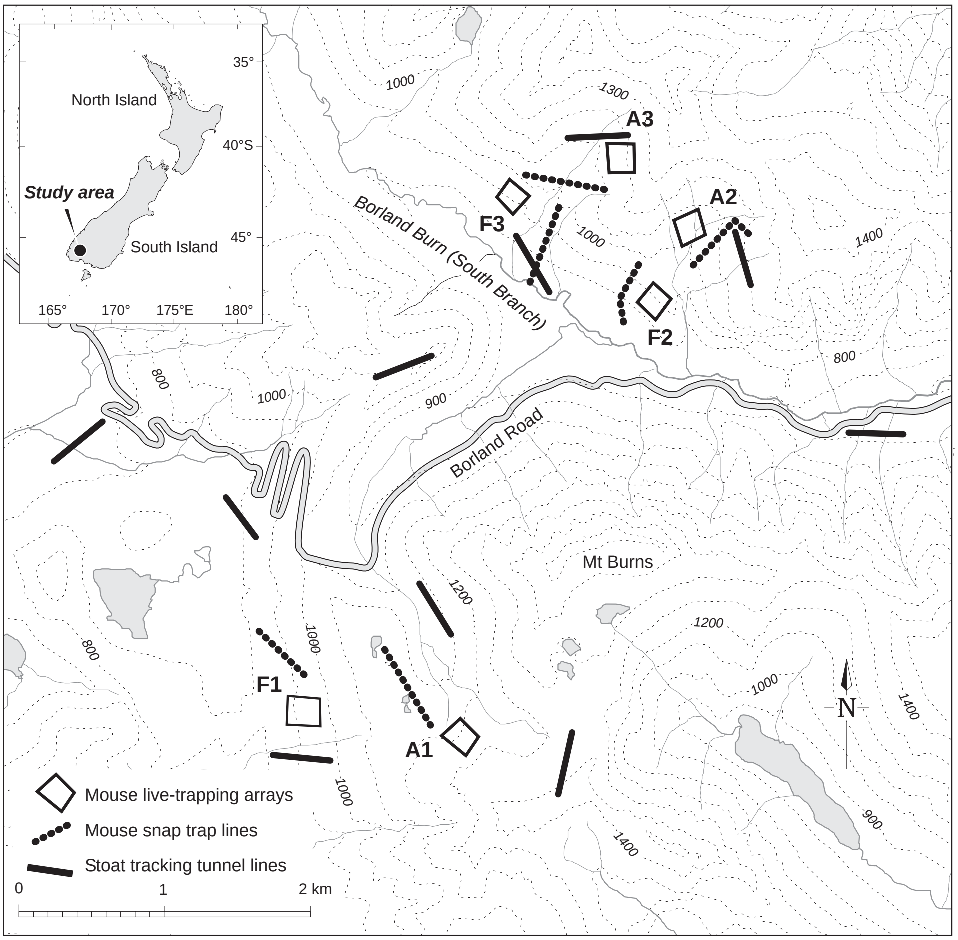


Figure 1. Map of three paired alpine (A1–A3) and beech (*Nothofagus* spp.) forest (F1–F3) study sites on the western slopes of Mount Burns and in the valley of the Borland Burn (South Branch) showing arrays for live-trapping mice (*Mus musculus*), lines of mouse snap traps and stoat (*Mustela erminea*) tracking tunnel lines.

We selected three pairs of study sites above and below the treeline, one pair on the lower slopes of Mount Burns and the others in two adjacent basins in the South Borland Valley (Fig. 1). Alpine sites were separated from each other by at least a ridge, and beech forest sites were separated from each other by at least a deep stream-bed. At each site we laid out live traps and kill traps for mice, plots for counting hare droppings (Fig. 2), transects for assessing flowering and fruiting of alpine plants (alpine sites only), and seed trays for collecting beech seeds (forest sites only), as described below. All trap locations and transects were permanently marked and were used throughout the study. Sites were established in January 2003, and the abundance of mice, hares and stoats was assessed in February, May and November 2003 and in February and November 2004. Falling beech seed was collected in the forest on the same occasions and in May 2004. Flowering and fruiting of alpine plants was recorded in March 2003 and March 2004. Dates of these key field activities are outlined in Table 1.

Figure 2. Map showing transects of plots for counting hare (*Lepus europaeus*) pellets in three paired alpine (A1–A3) and beech (*Nothofagus* spp.) forest (F1–F3) sites on the western slopes of Mount Burns and in the valley of the Borland Burn (South Branch).

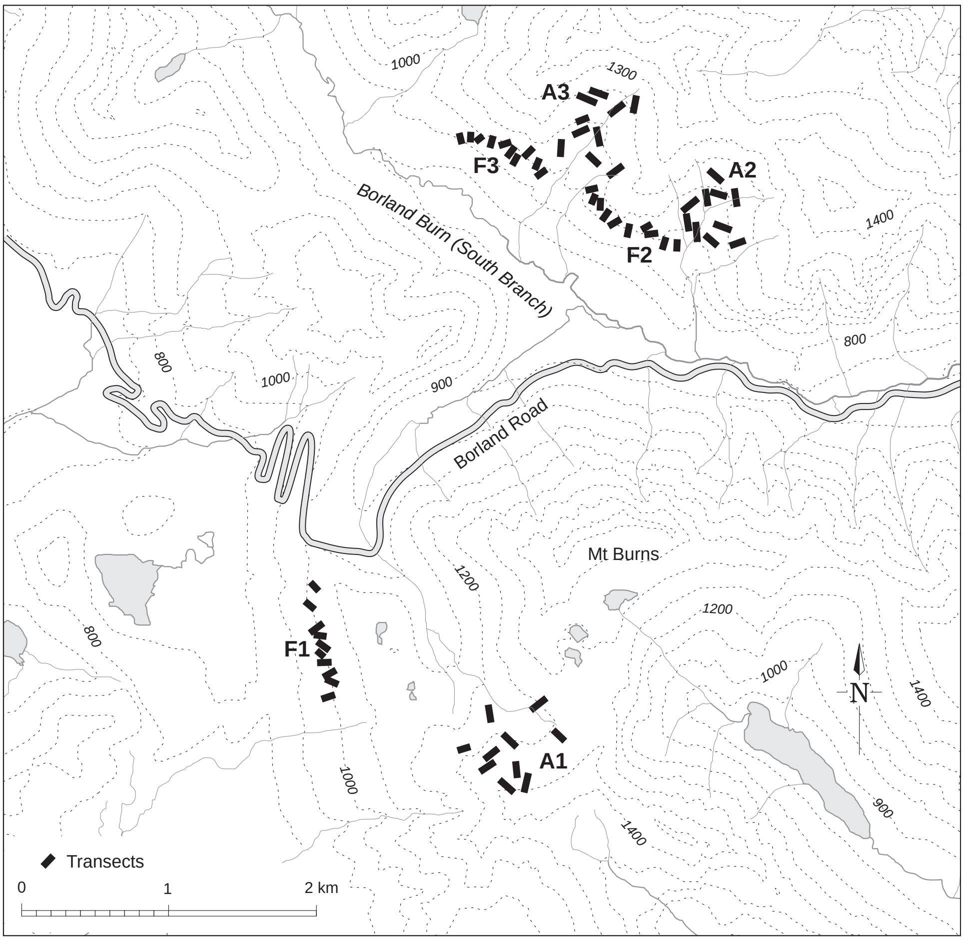


TABLE 1. DATES OF KEY FIELD ACTIVITIES.

DATE	ACTIVITY
23–24 October 2002	Selected study sites in alpine grassland and beech forest
15–24 January 2003	Established live-trapping arrays, snap trap lines, tunnel lines, hare pellet plots, and seed traps
10–17 February 2003	Live-trapped and snap-trapped mice, ran stoat tracking tunnels, counted hare pellets, and collected beech seed
19–21 March 2003	Established tussock flowering transects and assessed flowering and fruiting of alpine plants
7–15 May 2003	Live-trapped and snap-trapped mice, ran stoat tracking tunnels, counted hare pellets, and collected beech seed
4–10 November 2003	Live-trapped and snap-trapped mice, ran stoat tracking tunnels, counted hare pellets, and collected beech seed
9–15 February 2004	Live-trapped and snap-trapped mice, ran stoat tracking tunnels (1 night for rodents and 3 nights for stoats), counted hare pellets, and collected beech seed
17–18 March 2004	Assessed flowering and fruiting of alpine plants
29–30 May 2004	Collected beech seed
1–7 November 2004	Live-trapped and snap-trapped mice, ran stoat tracking tunnels, counted hare pellets, and collected beech seed

4.2 ABUNDANCE OF MICE

4.2.1 Field methods

The abundance of mice was estimated by capture-mark-recapture at each of the three alpine and three forest sites. We expected the density of mice to be relatively low in both alpine grassland and high-altitude forest, based on data from Mount Misery, Nelson Lakes National Park, which showed a decrease in the capture rate of mice in snap traps with increasing altitude (R.H. Taylor & P.R. Wilson, Landcare Research, unpubl. data). Therefore, the trapping array was designed to increase the number of captures relative to a traditional grid layout, while minimising trapping effort and attempting to maintain the rate of recaptures and the precision of the population estimate. The design was tested by using the program DENSITY (Efford 2004; Efford et al. 2004) to simulate captures of randomly located animals with traps laid in a grid, a single open square, or two concentric squares. We simulated mouse populations with moderate v. low density, high v. low trappability, and large v. small home ranges, based on data from previous live-trapping studies (Pickard 1984; Ruscoe et al. 2001, 2004; Davidson 2004). Increasing the total area sampled and the number of traps had the greatest effect on predicted captures, tending to increase both the total number of animals caught and the precision of population estimates. For the three trap layouts, recapture rates were highest with the grid and lowest with the open square; reducing trap spacing from 20 m to 15 m also increased recapture rates. Based on these results, we decided to lay traps in two concentric squares. This configuration covered a much larger area and was quicker to survey and check compared with a grid with the same number of traps, and was predicted to yield an intermediate recapture rate.

At each site (Fig. 1), Elliott live traps were laid out 15 m apart in an outer square of 48 traps and an inner square of 16 traps. This trap layout covered 3.2 ha, compared with 1.1 ha for a grid of 64 traps with 15-m spacing. Traps were baited with peanut butter and oats, contained polyester batting for warmth, and were enclosed in a plastic sleeve to protect them from rain. Traps were checked each morning for 4 consecutive days. Captured mice were marked with numbered metal ear-tags and were released after their weight, head–body length, and reproductive status were recorded.

Trapping arrays were placed more than 350 m apart, measured as walking distance along the ground, i.e. combining both horizontal distance and the vertical distance resulting from any change in altitude. Alpine trapping arrays were placed at 1020–1280 m a.s.l in locations where *Chionochloa pallens* was present. *C. pallens* is widely distributed in high-rainfall mountains in both the South and North Islands, occupying moist, relatively fertile sites (Wardle 1991: 217). We considered that selecting sites with this species present would increase the study's relevance to other New Zealand locations. We also considered that the chance of catching mice might be maximised at relatively fertile sites, and assumed that the presence of *C. pallens* indicated fertility. The forest was dominated by mountain beech on the lower slopes and silver beech on the upper slopes. Trapping arrays in beech forest were placed at 820–960 m a.s.l., where both beech species were present, in order to sample populations of mice that would benefit from abundant seed production by either species.

4.2.2 Analysis of capture-mark-recapture data using the program DENSITY

To estimate the abundance of mice, the following parameters were calculated from the data collected during each trapping session:

M_{t+1}	Number of individuals caught (notation of Otis et al. 1978)
$\hat{N}$	Closed-capture estimate of population size
$\hat{D}$	Estimated density of population (mice/ha)

In this study, the number of individual mice caught during a trapping session (M_{t+1}) was equivalent to the minimum number known to be alive (MNA; Krebs 1966). The calculation of MNA at time t takes into account animals that were not caught at time t but were marked before time t and recaptured after time t (e.g. were caught at times $t-1$ and $t+1$) and therefore must have been alive at time t also. Since no such gaps occurred in the capture histories of mice in our study, it was never necessary to infer that mice not caught had nevertheless been alive.

The population size ($\hat{N}$) of mice on each live-trapping array was estimated during each trapping occasion using the program Density (Efford 2004). This estimate was based on standard closed-population estimators, which assume that no reproduction, mortality, immigration or emigration occur during a trapping session (i.e. over 4 consecutive days). Since only small numbers of mice were captured and recaptured on most trapping arrays, it was necessary to group data for analysis. We pooled data from the sites within each habitat (alpine and forest) during each trapping session, ignoring sites where no mice were caught in that session; this procedure meant that data from two sites were pooled each time (with the exception of one occasion when data from three sites were pooled). The results of three estimators were compared (Otis et al. 1978; Lee & Chao 1994):

- The maximum likelihood estimator for the null model M_0, which assumes that the probability of capturing an animal is constant between individuals and between different trap-nights.
- The jackknife estimator for model M_h ('h' refers to heterogeneity), which assumes that capture probability differs between animals but is constant for each animal through time.
- Chao's second coverage estimator for model M_{th} ('t' refers to time and 'h' to heterogeneity), which allows for both individual and temporal heterogeneity.

To estimate density ($\hat{D}$) from $\hat{N}$, assumptions need to be made about animals' home ranges, so that a spatially explicit model can be fitted. We used the program Density to base these calculations on $\hat{N}$, as well as the capture probabilities ($\hat{p}$) and the mean distances moved between traps ($\bar{d}$), which were estimated from the same trapping data (Efford 2004). The spatial position of home range centres was assumed to follow a Poisson distribution, and simulation and inverse prediction were used to fit half-normal spatial detection functions to the capture data. In these simulations, the population of potentially trappable individuals was considered within a buffer of 150 m around the trapping array. When pooling data from more than one site, traps were modelled as multiple capture devices. Initial parameter values were determined as described in Efford et al. (2004). The factorial design in parameter space spanned ± 20% of the initial values; statistics were averaged from 2000 simulations, which included each combination of parameter values. The variance-covariance matrix was estimated by conducting 1000 further simulations at the fitted values. The precision of the population size and density estimates was expressed as CV(estimate) = SE(estimate)/estimate.

Methods for selecting the best closed-capture model for estimating $\hat{N}$, in the context of the spatial estimation process used in the program DENSITY, are not yet developed (Efford 2004; Efford et al. 2004). However, model selection may not be critical, since biased $\hat{N}$ may yield precise and nearly unbiased $\hat{D}$ (Efford et al. 2004). We expected M_{th} to be the most appropriate model because of the likely heterogeneity of capture probabilities between different sexes and ages of mice and between days experiencing different weather conditions. However, because this model required the most parameters, it was expected to yield the least biased but also the least precise estimates. We decided to compare the results of the three models, because maximising precision might be more important than minimising bias when 95% confidence intervals are being used to compare population parameters over time and between habitats (cf. Davis et al. 2003).

4.3 COLLECTION OF MICE FOR ANALYSIS OF THEIR DIET

4.3.1 Snap trapping

Mice were collected with standard snap traps along a trap-line that was at least 150 m in a random direction from each live-trapping array (Fig. 1). Each line contained 25 pairs of Supreme mouse traps, which were 25 m apart, baited with peanut butter and oats, and covered with wire mesh to exclude birds. Traps were set for 3 nights and checked each morning (Cunningham & Moors 1996). Some lines were laid in a dog-leg shape to avoid steep gullies.

Capture indices were calculated as the number of mice caught per 100 trap-nights corrected for sprung traps, abbreviated as mice/100TN. In calculating corrected trap-nights, 0.5 trap-nights were subtracted for each capture or sprung trap, on the assumption that these traps were not available to catch the target species for half a night, on average (Nelson & Clark 1973). Binomial 95% confidence intervals were estimated as shown in Krebs (1989). Similarly, capture indices of ground weta (*Hemiandrus* spp.), which were often caught at alpine sites, were expressed as weta/100TN. Pearson's correlation coefficient was used to test for relationships between these indices or between alternative estimates of mouse abundance. Data were square-root transformed prior to these analyses, to improve the linearity of the relationships between variables and make the error distributions homogeneous (Zar 1996). All entire weta found in snap traps were identified to species by Anthony Harris, Otago Museum.

4.3.2 Analysis of stomach contents of mice

Each stomach was removed, weighed and emptied into a Petri dish. The stomach contents were mixed with 70% ethanol and examined under a binocular microscope to identify plant and animal remains. Remains were separated as follows:

- Arthropods
- Plants
  —Fruit or seed
  —Shoot (green or woody) material
- Bait
- Other (mouse hair or soil)
- Unidentifiable

We noted recognisable taxa, but did not attempt to identify all invertebrate remains; it was not generally possible to identify plant taxa. The relative volume of each dietary component was estimated visually as 0%, 1%, 5%, or to the nearest 10%. Results were expressed as both frequency of occurrence of food types and percent volume of food types (Hansson 1970). Stomach contents were stored in ethanol for future analysis.

4.4 RELATIVE ABUNDANCE OF STOATS

Stoat tracks were recorded using five lines of standard tracking tunnels (Gillies & Williams 2002) in alpine habitat and five in beech forest (Fig. 1). Tunnel lines were at least 1 km apart and were oriented in a random direction; each line had five tunnels 100 m apart (Gillies & Williams 2002). Tunnels were baited with rabbit meat and checked for footprints after 3 days.

4.5 RELATIVE ABUNDANCE OF RATS

Although rats are thought to be scarce at high altitudes (Atkinson & Towns 2005; Innes 2005a,b), we tested this assumption in February 2004 using four of the five tracking tunnel lines in each of the alpine and forest habitats. These tunnels were baited with peanut butter to attract rodents, and checked the following day, before rebaiting them with meat to attract stoats (Gillies & Williams 2002).

4.6 RELATIVE ABUNDANCE OF HARES

Hare pellets were counted and then removed from small plots in January 2003 and on each trapping trip, following the methodology of Parkes (1999). At each alpine site, ten transects were established within a 0.25-km^2 area, each with a random starting point and direction (Fig. 2). Along each transect there were 20 permanently marked circular plots (area 0.1 m^2), 5 m apart, marked in the centre with a bicycle spoke that had been pressed well into the soil and labelled with a numbered metal tag (larger, above-ground pegs may attract hares and be used as latrine sites; Parkes 1999). Because we expected that hares would not penetrate far into the beech forest (Parkes 1984), the ten forest transects started at the treeline and followed a random bearing down the slope (Fig. 2). These transects were placed at random positions along c. 1 km of the treeline above each forest site, and were half as long as the alpine transects (ten plots each).

The time between pellet counts varied from 3 months (November 2003 – February 2004) to 9 months (February 2004 – November 2004). This difference could have resulted in bias in the counts, due to the decay of hare pellets. However, hare pellets decay very slowly: more than 90% lasted more than 1 year at 1280 m in Nelson Lakes National Park (Flux 1967). Although decay rates were higher in Tongariro National Park (Horne 1979), higher rates were positively related to rainfall, temperature and vegetation height and may have depended on species in the diet, with snow tussock decomposing slowly and *Celmisia* rapidly (Flux 1967; Horne 1979). Therefore, pellets probably decayed quite slowly at 1000–1200 m altitude in the Borland Valley, which is at a more southerly latitude than either of the aforementioned sites, is snow-covered for much of the year, and has roughly similar rainfall to the Nelson Lakes and Tongariro (based on NIWA data of annual rainfall at Manapouri, Nelson and Taupo). The bias associated with differential pellet decay between pellet counts is therefore likely to be small.

Along each transect, the number of pellets per square metre was standardised as the number that had accumulated on average over 100 days, based on the number of days between counts. Generalised linear mixed models with Poisson errors were fitted to these data to test for differences between dates and sites (procedure GLMM; GenStat Committee 2002). Habitat and Site were included as nested random factors, and Date was included as a fixed factor. Procedure GLMM estimates the variance components associated with random effects, and the magnitudes of fixed effects. Variation between habitats or sites was considered unimportant if the estimated variance component due to the factor was not large relative to the standard error of the estimate. Wald chi-square tests were used to test for statistically significant date effects.

4.7 BEECH SEED COLLECTION

Nine seed traps were established at each beech forest site. Each seed trap consisted of a net suspended from a circle (0.28 m^2) of thick wire (Wardle 1970), which was supported 1 m above the ground on three wooden posts. Eight seed traps were spaced evenly around the outer square of the mouse-trapping array and an additional trap was located on the inner square. Seeds were collected during each trapping trip and in May 2004, and were sorted and counted by species. Beech seedfall at each site was converted to total number of seeds m^{-2} $year^{-1}$ and transformed logarithmically prior to statistical analysis. This transformation is commonly used to linearise the relationship between the abundance of mice and beech seeds in New Zealand (e.g. King 1983; Choquenot & Ruscoe 2000), because the scale of variation in seedfall is generally much greater than that of variation in capture indices. Linear regression was used to test whether beech seedfall (transformed data, both species combined) in each year predicted the number of mice caught in live traps (M_{t+1}) or the capture index in snap traps (mice/100TN) at the different forest sites in November of that year. Seedfall of the two beech species was combined for this analysis, because the seeds are of similar size and mass (Wardle 1984). Different authors have related seedfall to mouse abundance pooled annually (August–May) (King 1983), in November (Fitzgerald et al. 1996) or in February (Ruscoe et al. 2004). We were restricted to using data from November, because we did not have data from August 2004 or February 2005.

4.8 FLOWERING AND FRUITING OF ALPINE PLANTS

4.8.1 Snow tussock grasses

The flowering intensity (inflorescences per tussock; Kelly et al. 2000) of *Chionochloa* was assessed at each alpine site in March 2003 and March 2004. Transects were established for each of three tussock species: *C. pallens* and *C. teretifolia* at all sites, and a third abundant species at each site (*C. crassiuscula* at site A1, and *C. rigida* at A2 and A3). The locations of the first 100 distinct tussocks with canopies intersecting the transect line were recorded, and the number of flowering tillers on these plants were counted each year. The coefficient of variation (CV) between the 2 years of the mean numbers of flowering tillers of each species and of all species combined was calculated. CV may not be very informative for only 2 years of data, but is presented for comparison with future results and other studies (e.g. Kelly et al. 2000).

A generalised linear mixed model with Poisson errors was fitted to the data of mean number of flowering tillers at each site, to test for differences between species, years and sites (procedure GLMM; GenStat Committee 2002). Site was included as a random factor, and Species and Year were included as fixed factors. Statistical tests were conducted as outlined in section 4.6.

4.8.2 Flowering shrubs and herbs

In March 2003 and March 2004, at each alpine site, we haphazardly chose c. 100 individuals of each of two common large herbs (*Celmisia coriacea* and *C. petriei*) and three woody shrubs (*Coprosma cheesemanii*, *Dracophyllum uniflorum* and *Hebe odora*) and recorded whether each plant had flowers (or fruits). As these plants were not permanently marked, a different set of individuals was observed each year. A generalised linear mixed model with binomial errors was fitted, to test whether the probability of flowering differed significantly between species, years and sites (procedure GLMM; Genstat Committee 2002). A binomial error structure was assumed; this model resembled a logistic regression, but with Site included as a random factor, and Species and Year included as fixed factors. Statistical tests were conducted as outlined in section 4.6. When there was a significant interaction between Species and Year, differences between years were tested separately for each species. Linear regression was used to test whether the total percentage flowering of all species in each year predicted the number of mice caught in live traps (M_{t+1}) or the capture index in snap traps (mice/100TN) at the different forest sites in November of that year.

4.9 INFERENCES ABOUT TUSSOCK FLOWERING AND BEECH SEEDFALL FROM OTHER LOCATIONS

The flowering intensity of snow tussock is recorded annually at Takahe Valley, about 60 km from the Borland Valley (Kelly et al. 2000; W.G. Lee, Landcare Research, unpubl. data), and the amount of beech seedfall is recorded annually at several nearby locations (Department of Conservation (DOC), Te Anau, unpubl. data). Since snow tussock and beech seeding events are synchronised over large geographic areas (Kelly et al. 2000; Schauber et al. 2002), we expected that at least extreme events of flowering and seedfall in the Borland Valley would be apparent in the same species at nearby locations. In Takahe Valley, the most recent high flowering event was in autumn 2000; another high flowering event was forecast for 2003 during the period of our study, following above-average summer temperatures in 2001–2002 (W.G. Lee, unpubl. data). In autumn 2002, there was no flowering of *Chionochloa* (*C. pallens, C. teretifolia*, *C. crassiuscula* and *C. rigida*) at Takahe Valley. Therefore, we did not expect an irruption of mice at our alpine sites during 2003, the first year of our study.

Similarly, we expected that beech seedfall in the Borland Valley in 2002 would be similar to that at nearby sites. In 2002, mountain beech at Takahe Valley produced 1719 seeds/m^2 and silver beech at Princhester Creek (also within 60 km of the Borland Valley) produced only 17 seeds/m^2 (DOC, Te Anau, unpubl. data); combined, this was equivalent to a 'partial' mast year (500–4000 seeds/m^2; Wardle 1984). Because periods of high mouse abundance have been observed in partial mast years for beech (King 1983; Choquenot & Ruscoe 2000; Fitzgerald et al. 2004), we considered it possible that an outbreak of mice might occur at our forest sites in 2003.

4.10 LITERATURE REVIEW

We reviewed published and unpublished data of diets of mammalian herbivores and predators in alpine habitats in New Zealand. Although house mouse diet has not previously been studied in alpine areas, we reviewed published and unpublished records of the diets and impacts of mice in other habitats, in order to document the types of foods eaten.

5. Results

5.1 ABUNDANCE OF MICE

5.1.1 Live trapping

At both alpine and forest sites, the abundance of mice tended to peak in summer (February) and/or autumn (May), and declined during winter each year (Fig. 3). Between 0 and 28 individual mice (M_{t+1}) were caught at each alpine site, and between 0 and 14 individuals were caught at each forest site, during the 4-day trapping sessions. On each trapping occasion, data from alpine sites A2 and A3 were combined for analysis (mice were never caught at site A1) (Appendix 1). Data from the forest sites where mice were caught on each occasion were also combined, i.e. data from sites F1 and F2, F2 and F3, or in May 2003 from all three forest sites (Appendix 1). Therefore, each estimate of population size ($\hat{N}$) refers to numbers of mice at pairs of sites (with the exception of May 2003) within either alpine or forest habitats.

On average, estimates of $\hat{N}$ from the three closed-captures models were within 30% of each other, and estimates of $\hat{D}$ were within 4% of each other (Appendix 1). This result supports the expectation that biased $\hat{N}$ may yield relatively unbiased $\hat{D}$ (Efford et al. 2004). In most instances, the jackknife (M_h) and Chao (M_{th}) estimates were similar to each other: estimates of $\hat{N}$ were within 5% of each other and estimates of $\hat{D}$ within 0.5%, on average. The precision of $\hat{N}$ was similar whether estimated from M_0 or M_h (CV($\hat{N}$) = 18%, on average), but was much poorer when estimated from M_{th} (CV($\hat{N}$) = 34%). In contrast, the precision of $\hat{D}$ was intermediate when estimated from M_h (CV($\hat{D}$) = 45%). Therefore, M_h appeared to provide a reasonable compromise between precision and bias of $\hat{D}$, and because estimates from M_h and M_{th} were so similar, any bias was likely to be minimal. This model (M_h) has also been used in other studies of mouse density in New Zealand (Ruscoe et al. 2001, 2004). Therefore, the results presented below are based on M_h. Abundance and movement parameters estimated by the program DENSITY are summarised in Appendix 2.

The estimated density ($\hat{D}$) of mice ranged from 0.51 ± 0.20 per hectare at forest sites and 0.90 ± 0.35 per hectare at alpine sites in November 2003, to 5.11 ± 1.53 per hectare at alpine sites in February 2003 (Fig. 3; density estimates could not be calculated for forest sites in February 2003 nor for alpine sites in May 2003 because there were too few data for spatial models to be fitted). In February 2004, the density of mice was significantly higher at alpine sites than at forest sites (based on non-overlapping 95% confidence intervals), whereas there was no difference in November 2003; these were the only trapping occasions where density estimates were available from both habitats (Appendix 2).

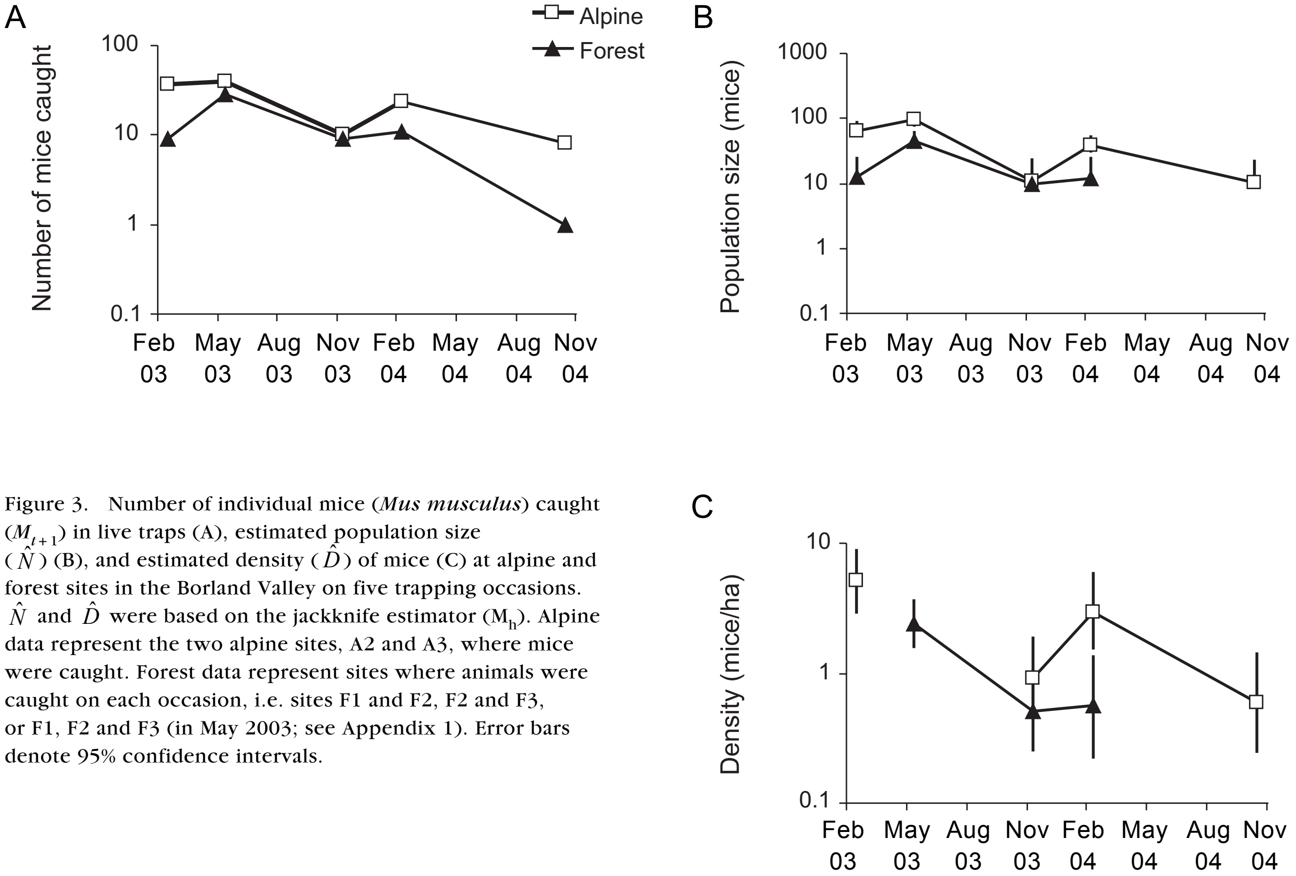


Figure 3. Number of individual mice (*Mus musculus*) caught (M_{t+1}) in live traps (A), estimated population size ($\hat{N}$) (B), and estimated density ($\hat{D}$) of mice (C) at alpine and forest sites in the Borland Valley on five trapping occasions. $\hat{N}$ and $\hat{D}$ were based on the jackknife estimator (M_h). Alpine data represent the two alpine sites, A2 and A3, where mice were caught. Forest data represent sites where animals were caught on each occasion, i.e. sites F1 and F2, F2 and F3, or F1, F2 and F3 (in May 2003; see Appendix 1). Error bars denote 95% confidence intervals.

The estimated population size ($\hat{N}$) of mice was also significantly larger at pooled alpine sites (explained in section 4.2.2) than at pooled forest sites on three of the five trapping occasions: February 2003, May 2003 and February 2004 (Fig. 3; the difference during May 2003 is particularly large, because data from three combined forest sites were compared with only two combined alpine sites). In November 2003, there was no significant difference in population size between alpine and forest sites; in November 2004, population size could not be estimated at forest sites, because only one mouse was caught (eight individuals were caught at alpine sites).

Seven stoats and nine ground weta (*Hemiandrus* spp.) were also caught in live traps. At least one stoat was caught on each trapping occasion. Weta were caught on only three occasions, mostly in November 2004 at site A1, where no mice were caught. However, weta did not always spring the traps, and trappers may not have always noticed weta within the polyester batting inside sprung traps.

5.1.2 Snap trapping

The capture indices of mice caught in snap traps ranged from 0.7 mice/100TN at all alpine sites combined and 0.5 mice/100TN at all forest sites combined in November 2004, to 4.8 mice/100TN at alpine sites and 8.9 mice/100TN at forest sites in May 2003 (Table 2). Capture rates did not differ significantly between the habitats ($t = 0.6$, df = 21, $P = 0.56$, based on indices calculated separately for each site and each trapping session). Capture indices at each site during each trapping session were positively related to M_{t+1} from live trapping ($r = 0.65$, df = 30, $P < 0.001$; all correlation coefficients reported in this section were based on square-root transformed data), but this relationship was not significant when the indices were calculated for each habitat during each trapping session ($r = 0.51$, df = 10, $P = 0.13$). The number of corrected trap-nights was low in May and November 2003, due to heavy rain or snow that set off traps. In May 2003, snow covered traps on sites A1 and A2 on the last night of trapping and may have made some traps inaccessible to mice for at least part of the night, resulting in fewer trap-nights at these sites and negatively biasing the capture indices.

Nineteen ground weta were caught in snap traps at the alpine sites, mostly at site A1. All of the individuals identified were *Hemiandrus maculifrons*. The capture index of weta at all alpine sites combined ranged from 0.3 weta/100TN in May 2003 to 1.4 weta/100TN in November 2004 (Table 3). Captures of weta at alpine sites were inversely related to captures of mice at the same sites, both when indices were calculated separately for each site × date combination ($r = -0.69$, df = 15, $P = 0.005$; Fig. 4A) and when indices were calculated for all alpine sites on each date ($r = -0.95$, df = 5, $P = 0.014$; Fig. 4B). These correlations were unlikely to be due to competition for traps between mice and weta,

TABLE 2. CAPTURE INDICES OF MICE (*Mus musculus*) (MICE/100TN; 95% CI IN PARENTHESES) IN SNAP TRAPS AND NUMBER OF CORRECTED TRAP-NIGHTS (TN) AT ALPINE (A) AND FOREST (F) SITES IN THE BORLAND VALLEY DURING FIVE TRAPPING OCCASIONS.

	ALPINE SITES					FOREST SITES				
		INDIVIDUAL		ALL			INDIVIDUAL		ALL	
DATE	SITE	TN	MOUSE INDEX	TN	MOUSE INDEX	SITE	TN	MOUSE INDEX	TN	MOUSE INDEX
Feb 03	A1	133	0.0 (0.0–2.2)	410	0.7 (0.2–1.9)	F1	119	0.8 (0.0–3.9)	369	1.6 (0.7–3.2)
	A2	142	1.4 (0.3–4.4)			F2	121	3.3 (1.1–7.4)		
	A3	136	0.7 (0.0–3.5)			F3	129	0.8 (0.0–3.6)		
May 03	A1	124	0.0 (0.0–2.4)	378	4.8 (3.1–7.0)	F1	90	1.1 (0.1–5.2)	215	8.9 (5.9–12.7)
	A2	116	3.4 (1.2–7.7)			F2	66	19.7 (12.1–29.5)		
	A3	138	10.1 (6.2–15.4)			F3	59	8.5 (3.4–17.1)		
Nov 03	A1	73	0.0 (0.0–4.0)	237	3.0 (1.4–5.5)	F1	81	0.0 (0.0–3.6)	294	1.0 (0.3–2.6)
	A2	87	3.4 (0.9–8.7)			F2	93	3.2 (0.9–8.1)		
	A3	77	5.2 (1.8–11.6)			F3	120	0.0 (0.0–2.5)		
Feb 04	A1	139	0.0 (0.0–2.1)	423	1.2 (0.5–2.5)	F1	102	0.0 (0.0–2.9)	332	1.5 (0.6–3.1)
	A2	140	2.1 (0.6–5.4)			F2	117	3.4 (1.2–7.7)		
	A3	145	1.4 (0.2–4.3)			F3	114	0.9 (0.0–4.1)		
Nov 04	A1	134	0.7 (0.0–3.5)	426	0.7 (0.2–1.8)	F1	135	0.7 (0.0–3.5)	394	0.5 (0.1–1.6)
	A2	148	0.7 (0.0–3.2)			F2	139	0.0 (0.0–2.1)		
	A3	145	0.7 (0.0–3.2)			F3	121	0.8 (0.0–3.9)		

because the indices had been corrected for each sprung trap to remove this bias. Furthermore, at these low capture rates (< 20 captures/100TN) competition for traps is expected to have little effect on the number of animals caught, and the relationship between capture rate and density should be almost linear (Caughley 1977: 18). Another indication that weta or other invertebrates were present at a site was that bait had often been removed from unsprung traps at alpine sites, especially at site A1. No other non-target species were caught in snap traps, although the traps were disturbed by possums and perhaps stoats, particularly at forest sites.

TABLE 3. CAPTURE INDICES OF GROUND WETA (*Hemiandrus* spp.) (WETA/100TN; 95% CI IN PARENTHESES) IN SNAP TRAPS AND NUMBER OF CORRECTED TRAP-NIGHTS (TN) AT ALPINE SITES IN THE BORLAND VALLEY ON FIVE TRAPPING OCCASIONS.

		INDIVIDUAL SITES		ALL SITES	
DATE	SITE	TN	WETA INDEX	TN	WETA INDEX
Feb 03	A1	133	2.3 (0.6–5.7)	410	1.2 (0.5–2.5)
	A2	142	0.7 (0.0–3.3)		
	A3	136	0.7 (0.0–3.5)		
May 03	A1	124	0.8 (0.0–3.8)	378	0.3 (0.0–1.2)
	A2	116	0.0 (0.0–2.5)		
	A3	138	0.0 (0.0–2.1)		
Nov 03	A1	73	2.7 (0.5–8.4)	237	0.8 (0.2–2.6)
	A2	87	0.0 (0.0–3.4)		
	A3	77	0.0 (0.0–3.8)		
Feb 04	A1	139	2.9 (1.0–6.5)	423	1.2 (0.5–2.5)
	A2	140	0.0 (0.0–2.1)		
	A3	145	0.7 (0.0–3.2)		
Nov 04	A1	134	4.5 (2.0–8.6)	426	1.4 (0.6–2.8)
	A2	148	0.0 (0.0–2.0)		
	A3	145	0.0 (0.0–2.1)		

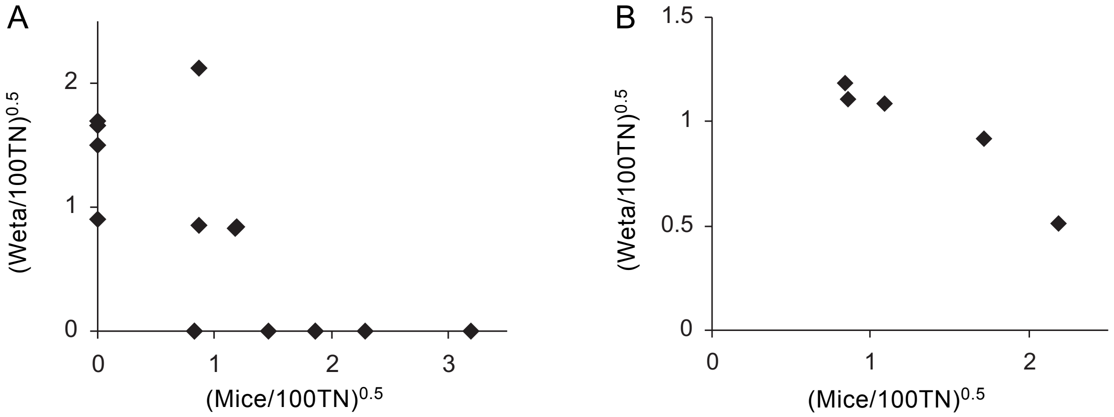


Figure 4. Relationship between the square roots of the capture indices of ground weta (*Hemiandrus* spp.) and mice (*Mus musculus*) caught in snap traps at three alpine sites in the Borland Valley. A. Indices calculated separately for each alpine site and each trapping session, and B. indices calculated for all alpine sites combined during each trapping session.

5.1.3 Mouse tracks in tracking tunnels

In tracking tunnels baited with meat to attract stoats, the tracking rate of mice, i.e. the mean percentage of tunnels tracked per line, varied from 20 ± 8.9% to 0.0 ± 0.0% (mean ± SEM; Fig. 5A) between sampling sessions. No mouse tracks were found on the single night when the tunnels were baited with peanut butter. Based on the magnitude of the standard errors (Fig. 5A), the tracking rate of mice did not differ significantly between the habitats. We also present the percentage of lines tracked by mice (Fig. 5B) for comparison with the stoat data (section 5.3, Fig. 7B). Up to 40% of lines (three of five lines) were tracked by mice in beech forest, and up to 60% were tracked in alpine habitats on different occasions. The percentages of lines tracked by mice did not differ significantly between the habitats either on any one occasion (Fisher exact test, $P > 0.52$) or when all samples were combined (logistic regression, $\chi^2 = 0.1$, df = 1, $P = 0.768$).

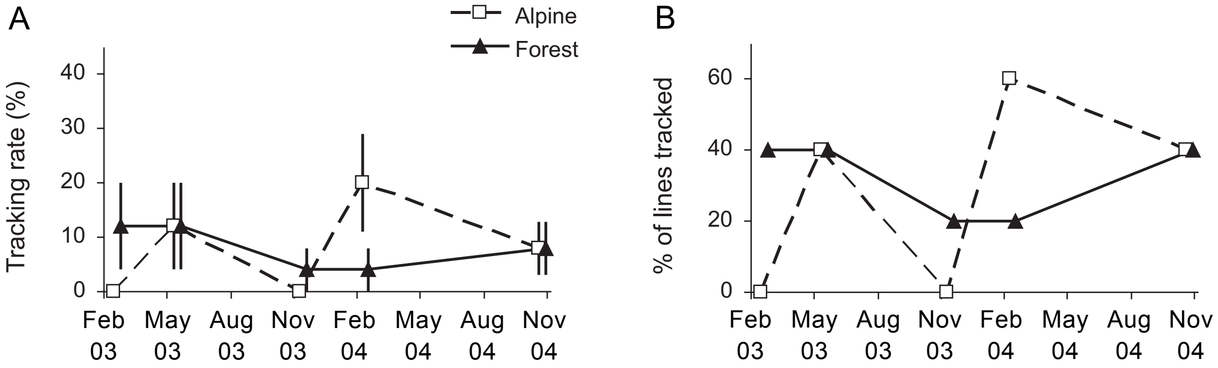


Figure 5. Tracking rate (mean (± SEM) percentage of tunnels tracked per line of five tunnels) (A), and percentage of tunnel lines tracked (B) by mice (*Mus musculus*) on five occasions. Binomial confidence intervals for B. span up to 75% (Krebs 1989) and are not shown. Tunnels were baited with meat (not peanut butter) and checked after 3 days.

5.2 DIET OF MICE

The contents of the mouse stomachs were finely masticated. All stomachs contained some unidentifiable fragments, which were excluded from the subsequent data analysis. It should also be noted that bait, which was present in 58% of stomachs, may have masked the presence of small quantities of seed material. Of 67 stomachs analysed, 97% contained arthropod remains and only 13% contained plant material (Table 4), which was seed in all but two instances (leaf or twig fragments). These frequencies of occurrence were similar across all trapping sessions and both habitats (Table 4). On average, arthropod remains accounted for an estimated 61% by volume of the stomach contents, with bait making up the bulk of the remainder (Table 5).

TABLE 4. FREQUENCY OF OCCURRENCE (%) OF DIFFERENT FOOD TYPES IN STOMACHS OF MICE (*Mus musculus*) CAUGHT IN SNAP TRAPS DURING FIVE TRAPPING SESSIONS, IN ALPINE AND FOREST HABITATS IN THE BORLAND VALLEY.

'Other' includes unidentifiable material when it was present in large amounts; all stomachs contained some unidentifiable fragments that were excluded from this analysis.

HABITAT	FOOD CATEGORY	FEB 03	MAY 03	NOV 03	FEB 04	NOV 04	ALL SAMPLES
Alpine	*n*	6	17	3	5	2	33
	Arthropod	100.0	100.0	100.0	80.0	100.0	97.0
	Plant	16.7	17.6	0.0	20.0	50.0	18.2
	Bait	66.7	47.1	33.3	80.0	100.0	57.6
	Other	0.0	11.8	0.0	20.0	0.0	9.1
Forest	*n*	3	16	7	5	3	34
	Arthropod	100.0	93.8	100.0	100.0	100.0	97.1
	Plant	0.0	18.8	0.0	0.0	0.0	8.8
	Bait	0.0	56.3	57.1	100.0	66.7	58.8
	Other	0.0	12.5	0.0	0.0	0.0	5.9

TABLE 5. ESTIMATED VOLUME (%) OF DIFFERENT FOOD TYPES IN STOMACHS OF MICE (*Mus musculus*) CAUGHT IN SNAP TRAPS DURING FIVE TRAPPING SESSIONS, IN ALPINE AND FOREST HABITATS IN THE BORLAND VALLEY.

'Other' includes unidentifiable material when it was present in large amounts; all stomachs contained some unidentifiable fragments that were excluded from this analysis.

HABITAT	FOOD CATEGORY	FEB 03	MAY 03	NOV 03	FEB 04	NOV 04	ALL SAMPLES
Alpine	*n*	6	17	3	5	2	33
	Arthropod	53.3	75.8	86.7	53.0	45.0	67.4
	Plant	6.7	5.1	0.0	1.0	20.0	5.2
	Bait	37.2	10.3	10.0	45.2	30.0	21.6
	Other	0.0	0.7	0.0	2.0	0.0	0.7
Forest	*n*	3	16	7	5	3	34
	Arthropod	98.3	41.2	57.9	72.0	56.0	55.5
	Plant	0.0	5.9	0.0	0.0	0.0	2.8
	Bait	0.0	41.1	39.7	25.0	36.7	34.4
	Other	0.0	3.1	0.0	0.0	0.0	1.4

The invertebrate groups commonly present in the diet of mice were weta (Orthoptera, Stenopelmatidae) (in 36% of stomachs), spiders (Araneae) (34%), caterpillars (Lepidoptera) (22%) and grasshoppers (Orthoptera) (13%) (Fig. 6). Although grasshoppers were more commonly found in the diet of mice in alpine than in forest habitats, and caterpillars and spiders were eaten more frequently in forest than alpine habitats, these differences were not statistically significant (Fisher exact tests, $P > 0.2$).

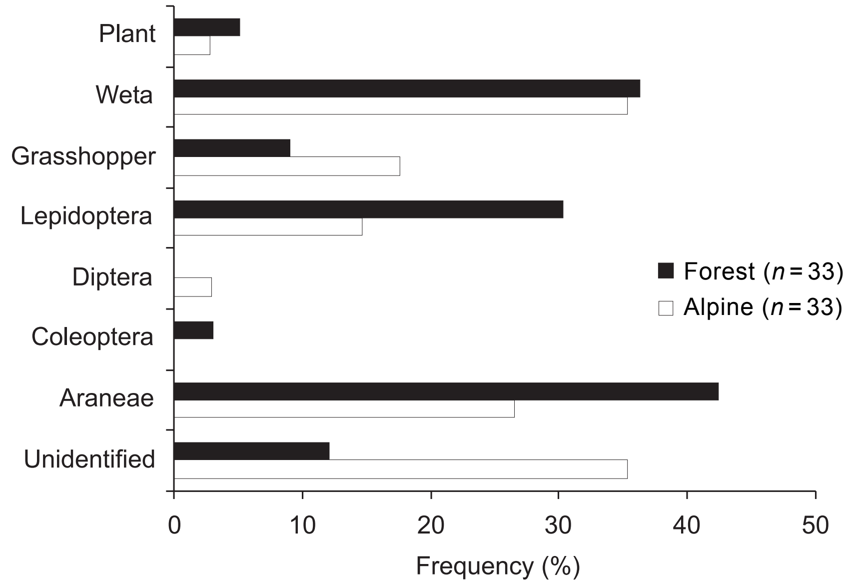


Figure 6. Frequency (%) of plant material and different groups of arthropods in stomachs of mice (*Mus musculus*) collected from forest and alpine habitats in the Borland Valley throughout the study. Weta and grasshoppers are both in order Orthoptera. The category 'unidentified' refers to unidentified arthropods.

5.3 RELATIVE ABUNDANCE OF STOATS

The tracking rate of stoats, i.e. the mean percentage of tunnels tracked per line, varied from 28 ± 13.6% to 0 ± 0% (mean ± SEM) between sampling sessions, and did not differ significantly between the habitats (based on the size of the standard errors) (Fig. 7A). Because individual tunnels were only 100 m apart, they were not independent measures of stoat activity. The percentage of lines tracked (Fig. 7B) may better match the scale of stoat movements (Gillies & Williams 2002), although the lines may also not be independent, as individual stoats may range farther than 1 km (Murphy & Dowding 1994, 1995; Smith & Jamieson 2005). Up to 60% of lines (three of five lines) were tracked in beech forest, and up to 40% were tracked in alpine habitats on different occasions. There was no significant difference in tracking rate between the habitats on any one occasion (Fisher exact test, $P > 0.16$) or when all samples were combined (logistic regression, $\chi^2 = 3.37$, df = 1, $P = 0.066$).

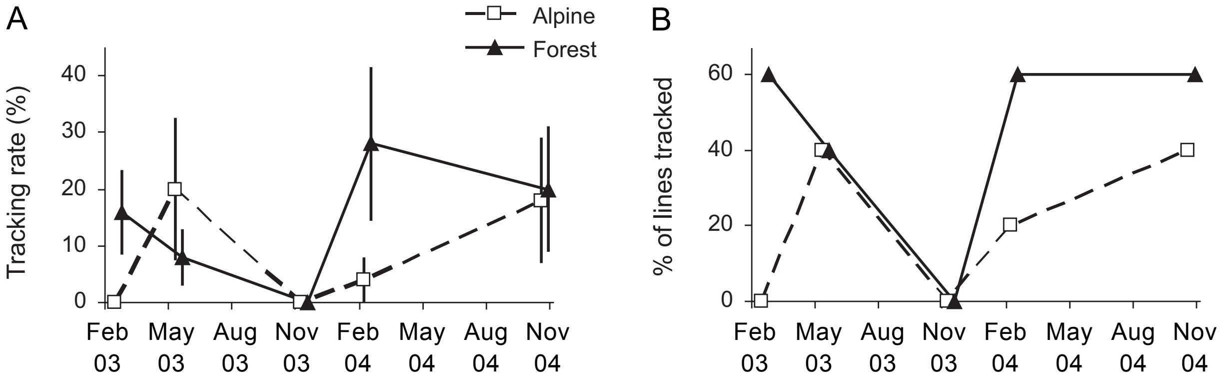


Figure 7. Tracking rate (mean (± SEM) percentage of tunnels tracked per line of five tunnels) (A), and percentage of tunnel lines tracked (B) by stoats (*Mustela erminea*) on five occasions. Binomial confidence intervals for B. span up to 75% (Krebs 1989) and are not shown.

5.4 RELATIVE ABUNDANCE OF RATS

No rat tracks were found in tunnels, whether peanut butter or meat was used as bait.

5.5 RELATIVE ABUNDANCE OF HARES

Before the hare plots were first cleared in January 2003, there were on average 7.9 pellets/m^2 along alpine transects (mean ± SEM = 5.9–10.7, calculated based on log-transformed data and then back-transformed). No pellets were found along forest transects in January 2003.

Subsequent counts of pellets recruited to the plots per 100 days were usually greater than zero along alpine transects but almost always zero along forest transects (with only two exceptions, in February 2004 and November 2004). When the data from both habitats were combined, the fit of the model was poor, due to the large number of zeroes in the forest data. Therefore, we fitted separate generalised linear mixed models to the data from the two habitats. At alpine sites, there was evidence of significant variation between dates in the number of pellets that had accumulated per 100 days ($\chi^2 = 7.7$, df = 3, $P = 0.052$). The rate of accumulation tended to be higher between May and November 2003 (c. 3 pellets/m^2 per 100 days; Fig. 8) compared with the other periods (1–2 pellets/m^2 per 100 days). However, since the longest period between pellet counts was February–November 2004, the rate of accumulation during this period may have been negatively biased as a result of decomposition (see section 4.6). At forest sites, the mean rate of accumulation was only 0.06 pellets/m^2 per 100 days (mean ± SEM = 0.03–0.11), with no significant difference between sites ($\chi^2 = 2.3$, df = 3, $P = 0.52$). No significant variation could be ascribed to Site in either habitat (estimated variance components ± SE: 0.0 ± 0.03 at alpine sites in January 2003; subsequently, 0.0 ± 0.09 at alpine sites, 0.5 ± 1.1 at forest sites).

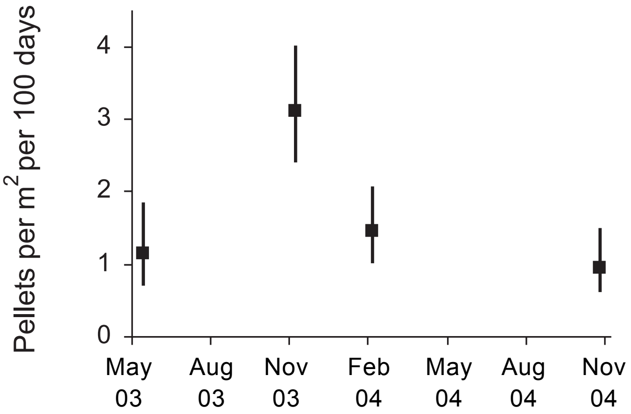


Figure 8. Mean (± SEM) number of hare (*Lepus europaeus*) pellets per m^2 per 100 days that accumulated at three alpine sites combined in the Borland Valley, during four different periods from January 2003 to November 2004.

5.6 BEECH SEEDFALL

Mountain beech seeded at a low rate in 2003 but at a moderately high rate in 2004, whereas silver beech seeded at low rates in both years (Fig. 9). In 2004, there was considerable variation in the seedfall of mountain beech between sites (Fig. 9); this may reflect different relative abundances of the two beech species between sites. Combining both species, the 2003 seeding was equivalent to a 'poor' mast year (< 500 seeds/m^2; Wardle 1984: 257) and the 2004 seeding to a 'partial' mast year (500–4000 seeds/m^2; Wardle 1984). The only other seeds in our seed traps were *Coprosma* spp. and a few unidentified seeds. Mountain beech and silver beech seedfall in 2003 and 2004 were highly correlated with the corresponding seedfall of mountain beech at Takahe Valley and silver beech at Princhester Creek in autumn (March–May) ($r = 0.98$, df = 4, $P = 0.018$) (DOC, Te Anau, unpubl. data). This relationship supported our assumption of regional synchrony of beech seedfall.

Neither the number of mice caught in live traps (M_{t+1}) in November 2003 ($F = 1.6$, df = 1, 4, $P = 0.27$; Fig. 10) nor the November snap-trap index ($F = 0.9$, df = 1, 4, $P = 0.40$) at the three forest sites was significantly related to the number of beech seeds/m^2 (log-transformed data) that fell in the preceding year.

In both years, fewer seeds were collected in May (i.e. seed that fell since the previous collection in February) than in November (i.e. seed that fell since May). It should be noted that seeds collected in February 2003 represent seedfall during the preceding month only, whereas seeds collected in February 2004 represent seedfall during the preceding quarter. However, the error introduced by this difference will be small because little seedfall occurs in summer (fewer than 30 beech seeds/m^2 were collected in February 2004).

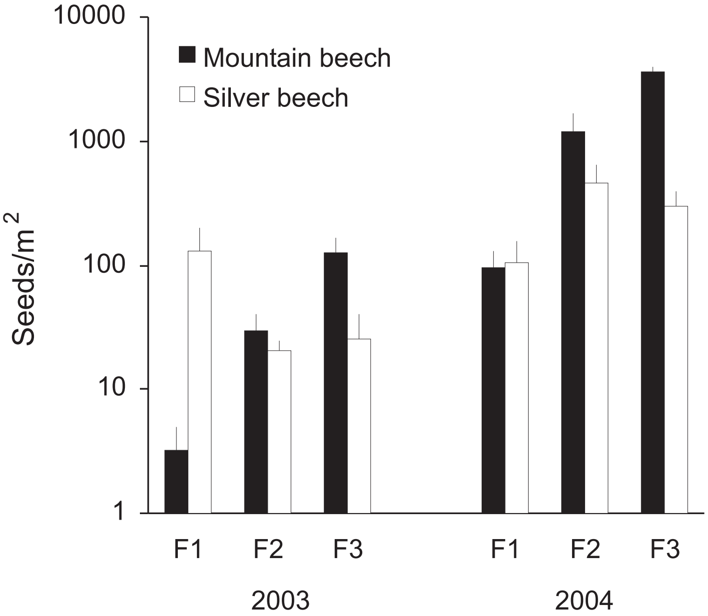


Figure 9. Annual seedfall (February–November) of mountain beech (*Nothofagus solandri* var. *cliffortioides*) and silver beech (*N. menziesii*) at three forest sites (F1–F3) in the Borland Valley during 2003 and 2004.

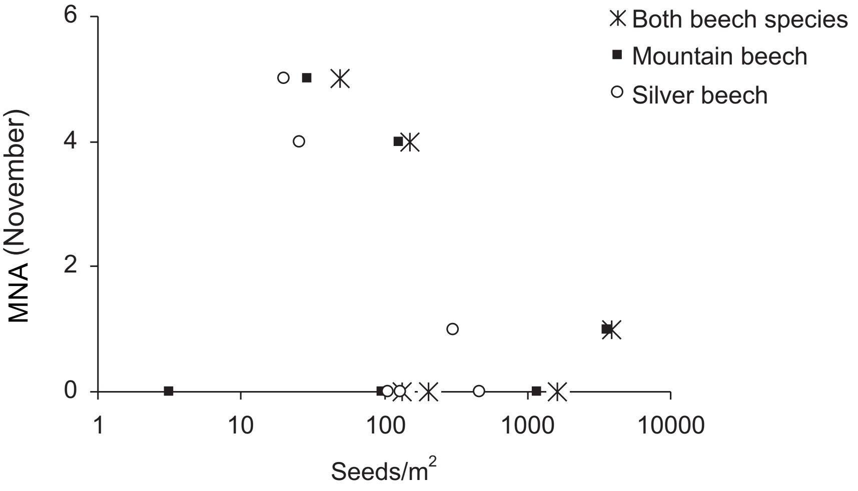


Figure 10. Number of mice (*Mus musculus*) caught (M_{t+1}) in live traps at three beech (*Nothofagus* spp.) forest sites in the Borland Valley during November 2003 and November 2004 as a function of seedfall of mountain beech (*Nothofagus solandri* var. *cliffortioides*), silver beech (*N. menziesii*) and of both species combined in November of the preceding year. Numbers are presented as the minimum number alive (MNA).

5.7 FLOWERING AND FRUITING OF ALPINE PLANTS

5.7.1 Snow tussock flowering

All four species of snow tussock that were monitored flowered at moderate intensity in 2003 and at very low intensity in 2004. In March 2003, 25%–80% of tussocks of all species monitored had at least one flowering tiller at all three alpine sites. In contrast, in March 2004, at most 2 of the 100 tussocks of *C. teretifolia* and none of the other tussock species monitored at each site were flowering. The average flowering intensity across all species and sites was 4.63 ± 0.45 inflorescences per tussock (mean ± SEM) in 2003 and 0.00 ± 0.00 inflorescences per tussock in 2004 (untransformed data; Kelly et al. 2000). The coefficient of variation of mean flowering intensity between the 2 years was 0.993 for all species combined and either 0.999 or 1.000 for individual species. Flowering of *C. pallens*, *C. teretifolia*, *C. crassiuscula* and *C. rigida* at the Borland sites in 2003 and 2004 was correlated with flowering of the same species in Takahe Valley ($r = 0.74$, df = 8, $P = 0.037$) (W.G. Lee, unpubl. data). This relationship supports our assumption of flowering synchrony between the two locations.

There was a significant difference in flowering intensity between years ($\chi^2 = 4.6$, df = 1, $P = 0.032$; Fig. 11A) and species ($\chi^2 = 57.1$, df = 3, $P < 0.001$; Fig 11B). The interaction between these terms was not significant ($\chi^2 = 0.0$, df = 3, $P = 1.0$) and was removed from the model. On average, *C. pallens* had the highest number of flowering tillers per tussock (7.8 in 2003, based on a model fitted to the 2003 data only; Fig. 11B) followed by *C. teretifolia* (2.3), *C. rigida* (1.9) and *C. crassiuscula* (0.8). Because the estimated variance component due to Site was of a magnitude similar to that of its standard error, we concluded that no significant variation could be ascribed to differences between sites. Nevertheless, total flowering intensity at site A1 far exceeded that at the other sites, due to particularly strong flowering of *C. pallens* there (Fig. 11B), although the difference between sites was not consistent for the other species.

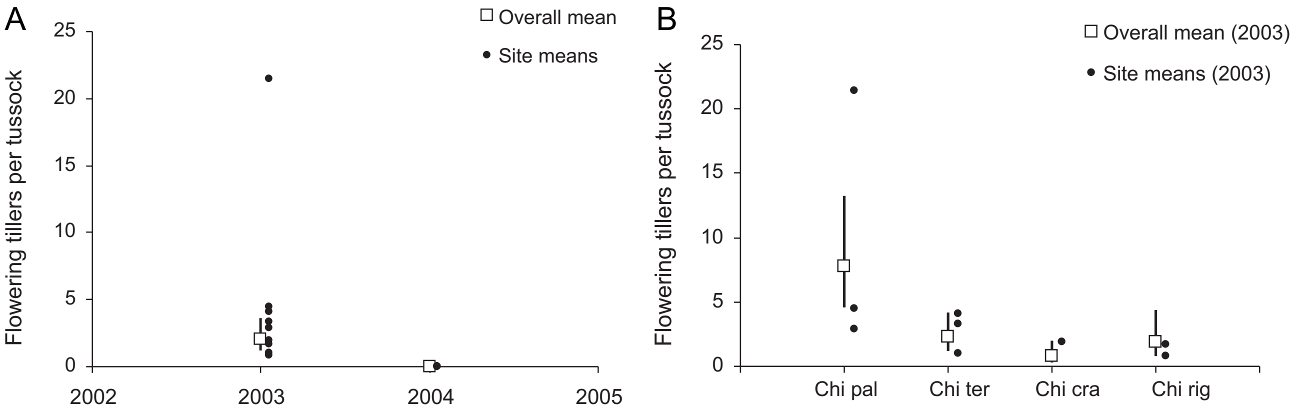


Figure 11. Number of flowering tillers per *Chionochloa* tussock at three alpine sites. Open squares denote mean (± SEM) number of flowering tillers per tussock at all sites combined, closed circles denote mean (± SEM) number of flowering tillers on 100 tussocks of each species at each site. A. All species combined in March 2003 and March 2004, and B. each species in March 2003 only. Species names are abbreviated as follows: Chi pal—*C. pallens* (all sites); Chi ter—*C. teretifolia* (all sites); Chi cra—*C. crassiuscula* (site A1); and Chi rig—*C. rigida* (sites A2 and A3).

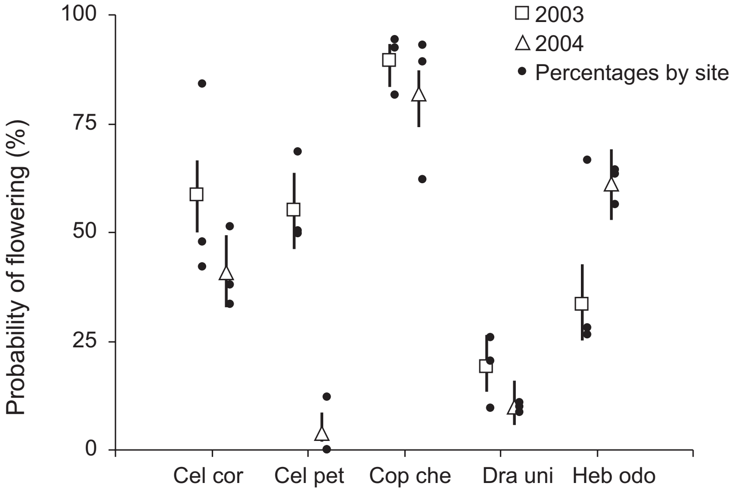
Of the three alpine sites, by far the fewest mice were caught at A1 (none in live traps and only one in a snap trap), where total flowering intensity was highest in both years (substantially so in 2003); therefore, there was clearly no positive spatial relationship between mouse density at alpine sites and tussock flowering intensity.

5.7.2 Shrub and herb flowering

The probability that a shrub or large herb was flowering differed greatly between species ($\chi^2 = 60$, df = 4, $P < 0.001$; Fig. 12). Of the five species tested, *Coprosma cheesemanii* had the highest probability of flowering in both years. There was a significant interaction between Species and Year ($\chi^2 = 23$, df = 4, $P < 0.001$), indicating that differences between years varied by species. Most species flowered at a lower rate in 2004 than in 2003, with the exception of *Hebe odora*, which followed the opposite pattern at two of the three sites. When the effect of year was tested separately for each species, it was statistically significant in each instance ($\chi^2 = 4.1$, 8.2, 6.5, 5.3, 4.9; df = 1; $P = 0.043$, 0.004, 0.011, 0.021, 0.027, for *Celmisia coriacea*, *C. petriei*, *Coprosma cheesemanii*, *D. uniflorum* and *Hebe odora*, respectively). However, because Wald chi-square tests tend to give significant results too frequently when sample sizes are small (GenStat Committee 2002) (in the single-species models there were data from only 3 sites × 2 years), the marginally significant result for *C. coriacea* should be interpreted with caution. In each model, the variance component was of a magnitude similar to that of its standard error; we therefore concluded that no significant variation could be ascribed to differences between sites.

Neither the number of mice caught in live traps (M_{t+1}) in November 2003 nor the November snap-trap index at the three alpine sites was predicted by the sum of the percentages of flowering plants of all species combined in the previous year ($F < 0.9$, df = 1, 4, $P \geq 0.40$).

Figure 12. Estimated probability that a large herb or woody shrub of each of five species was flowering in March 2003 and March 2004 (open symbols), and percentage of shrubs flowering at each site in each year (closed symbols). Error bars represent standard errors of the mean. Species names are abbreviated as follows: Cel cor—*Celmisia coriacea*; Cel pet—*C. petriei*; Cop che—*Coprosma cheesemanii*; Dra uni—*Dracophyllum uniflorum*; and Heb odo—*Hebe odora*.



5.8 DIETS OF ALPINE MAMMALS

Of the 63 datasets of diets of introduced mammalian herbivores that were reviewed and analysed by Cochrane & Norton (2003), nine originated from alpine habitats (Table 6). We also cite unpublished data of thar, chamois and possum diets (J.P. Parkes, unpubl. data).

The ordination analysis (detrended correspondence analysis based on the presence or absence of different plant genera in diets) of Cochrane & Norton (2003) showed similarities between the diets of different mammalian herbivores within alpine habitats and within forest habitats (Fig. 13). This conclusion was based on the first two axes of the ordination, which together explained only 11% of the total variation in the diets (Cochrane & Norton 2003). Most of this variation was probably due to the presence of different plant genera in each habitat. Inspection of the alpine data on Cochrane & Norton's (2003) ordination plot (Fig. 13) reveals a gradient in diet composition, from hares, thar and chamois at one end to possums, deer and goats at the other. This gradient cannot be interpreted without further analysis of the data.

TABLE 6. DATASETS OF DIETS OF INTRODUCED MAMMALIAN HERBIVORES IN ALPINE HABITATS, REVIEWED BY COCHRANE & NORTON (2003).

SPECIES		LOCATION OF STUDY	REFERENCE
Red deer	(*Cervus elaphus scoticus*)	Murchison Mountains	Lavers 1978
Wapiti	(*C. e. nelsoni*)	Fiordland west of Lake Te Anau; data from tops	Poole 1951
Feral goat	(*Capra hircus*)	Data from Red Hills, Marlborough	Asher 1979
Chamois	(*Rupicapra rupicapra*)	Southern Alps	Parkes & Thomson 1995
Thar	(*Hemitragus jemlahicus*)	Macaulay River, Southern Alps	Parkes 1988
		Southern Alps	Parkes & Thomson 1995
Possum	(*Trichosurus vulpecula*)	Rangitata catchment, Southern Alps	Parkes & Thomson 1995
Hare	(*Lepus europaeus*)	Nelson Lakes National Park	Flux 1967
		Tongariro National Park	Horne 1979

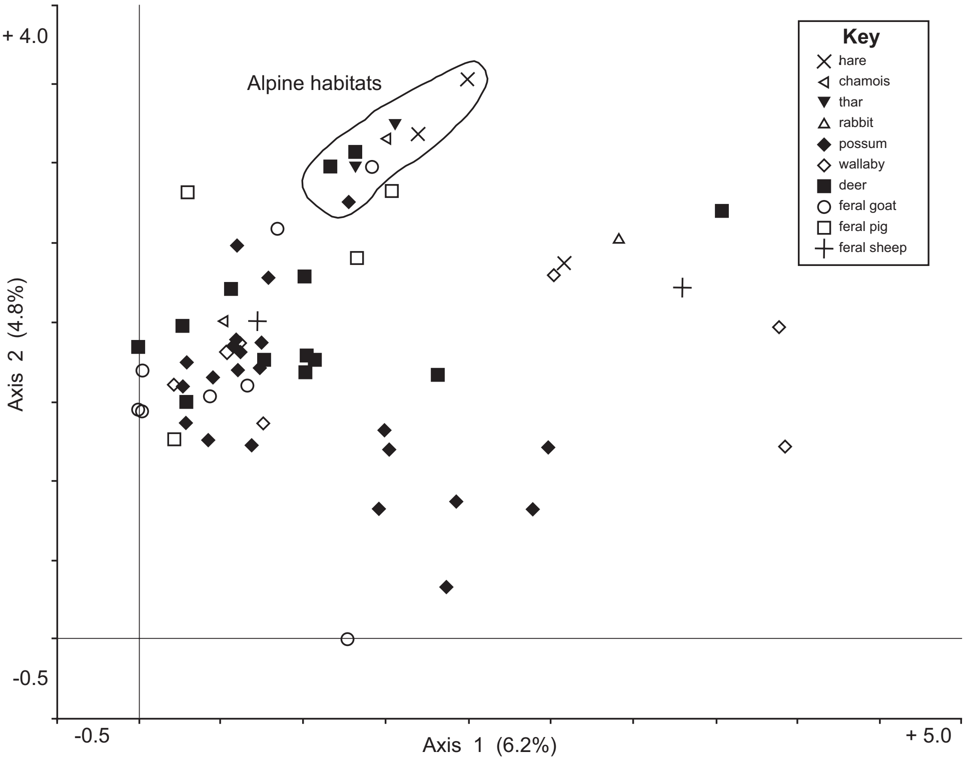


Figure 13. Ordination of 63 studies of diets of introduced herbivorous mammals in New Zealand, redrawn from Cochrane & Norton (2003: figs 8 and 9). The following species are represented: hare (*Lepus europaeus*), chamois (*Rupicapra rupicapra*), thar (*Hemitragus jemlahicus*), rabbit (*Oryctolagus cuniculus*), possum (*Trichosurus vulpecula*), wallaby (*Macropus* spp.), deer (Cervidae), feral pig (*Sus scrofa*), feral goat (*Capra hircus*) and feral sheep (*Ovis aries*). Sources of the 'Alpine' group of data are Poole (1951: data from tops); Flux (1967); Lavers (1978); Horne (1979); Asher (1979: Red Hills data); Parkes (1988); and Parkes & Thomson (1995: three datasets). In fig. 8 of Cochrane & Norton (2003), the 'Alpine/Sub-antarctic Islands' group included four studies from subantarctic islands and two studies (forest data in Poole 1951; Sweetapple 2003) from predominantly forested habitats (H.C. Cochrane, University of Canterbury, pers. comm.). These studies are not included in the Alpine group shown here.

Habitats within the alpine zone are to some extent partitioned between herbivores: thar use grassland, shrubland and bluffs; chamois and deer use grassland and shrubland; hares use primarily grassland; and possums use primarily shrubland (Forsyth et al. 2000). Goats in alpine areas tended to feed in open grassland and to shelter in subalpine shrubland or at the forest edge at night (Asher 1979).

5.8.1 Thar and chamois

The diet of thar in the Southern Alps consisted of more than 50% grasses (primarily snow tussock), c. 25% shrubs and less than 20% herbs, based on mean percentage dried weight in stomachs (Parkes & Thomson 1995). Snow tussock made up over 90% of the diet in the Macaulay River area of the Southern Alps (Parkes 1988), although most stomachs also contained shrub (particularly *Podocarpus nivalis* and *Dracophyllum* spp.) and herb (*Celmisia* spp.) remains. In contrast, only 15% of the diet of chamois consisted of grasses (less than 2% was snow tussock); more than 50% was woody plants and less than 30% was herbs. Thar and chamois ate few seeds of any species (J.P. Parkes, unpubl. data).

The condition (basal area, height and density) of snow tussocks (*Chionochloa pallens*, *C. flavescens* and *C. rigida*) was inversely related to thar density (Parkes et al. 2004). The condition of mature tussocks has improved since massive reductions in thar density in the 1970s (Parkes et al. 2004), but it may take several decades for *Chionochloa* tussocks to reach their former size after heavy grazing (Lee et al. 2000). In the last decade, there has also been an increase in the frequency of occurrence of some herbs that are eaten by thar (Parkes et al. 2004).

5.8.2 Possums

Possum diet in an alpine area (Rangitata Catchment) of the Southern Alps in autumn comprised 52% fruit, 28% woody plants, 18% herbs and less than 1% grasses, ($n = 11$ stomachs). In contrast, possum diet in the same area in spring comprised no fruit, 37% woody plants, 52% herbs and 3% grasses, ($n = 28$ stomachs; Parkes & Thomson 1995). Possums did not eat *Chionochloa* species (J.P. Parkes, unpubl. data).

Sympatric thar, chamois and possums partitioned their food resources: thar ate mainly grass, chamois ate mainly shrubs and herbs, and possums ate fruit when available, and different species of shrubs and more herbs than chamois (Parkes & Thomson 1995).

Possums are opportunistic feeders; being monogastric (unlike ungulates), they require additional sources of protein and energy than are available from foliage (Nugent et al. 2000). They commonly eat invertebrates, usually (but not always) in small quantities (Nugent et al. 2000; Cochrane et al. 2003), and they also eat birds and their eggs (Nugent et al. 2000; Parkes & Thomson 1995).

5.8.3 Hares

In an alpine area of Nelson Lakes National Park, hares fed primarily on snow tussock in winter and the grass *Poa colensoi* in summer (Flux 1967). Hares also ate herbs, including *Celmisia* spp., and, to a smaller degree, shrubs such as *Aristotelia fruticosa* and *Coprosma* spp., especially in winter (Flux 1967). In many instances, the species eaten reflected their availability, particularly in winter (Flux 1967; Horne 1979). In Tongariro National Park, hare diet was dominated by snow tussock (*Chionochloa rubra*), herbs (predominantly *Brachyglottis bidwillii* and *Celmisia spectabilis*), moss and *Poa colensoi*, although the proportions of the different foods in the diet depended on altitude and season (Horne 1979). Hares ate few seeds in either study, although at Tongariro seed consumption increased in autumn (Horne 1979). Whether seed consumption by hares changes in relation to seed production by snow tussock species has not been investigated, although Horne (1979) noted that *Poa colensoi* tended to be consumed in autumn when its seed heads were ripe.

Hares may affect the condition (basal area, height and density) of *Chionochloa* tussocks (Parkes et al. 2004), and intensive browsing by hares may be enough to prevent the recovery or re-establishment of tussocks (*C. macra*), even many years after the removal of sheep (Rose & Platt 1992).

5.8.4 Deer

At alpine sites in the Murchison Mountains, the main foods of red deer were snow tussock (*Chionochloa pallens* and *C. flavescens*), the large herbs *Anisotome haastii, Aciphylla takahea*, *Celmisia* spp., *Dolichoglottis lyallii* and *Ranunculus lyallii*, and to a lesser degree the shrubs *Gaultheria* spp., *Myrsine* spp. and *Coprosma* spp. (Lavers 1978). Grasses accounted for 34% of the total rumen contents, large herbs 31%, and woody species only 10% (Lavers 1978). At alpine sites in Fiordland, wapiti (possibly including some red deer and wapiti-red deer crosses) primarily ate the grasses *Rytidosperma* spp., the shrubs *Coprosma serrulata* and *Gaultheria* spp., and the herb *Phormium cookianum* (based on frequency of occurrence and volume in nine stomachs; Poole 1951). *Celmisia* spp., *Hebe* spp. and *Astelia cockaynei* were also present in at least five of the nine stomachs (Poole 1951).

These dietary data are supported by observed impacts of alpine deer. In mountainous areas of Fiordland north of the Murchison Mountains, deer chose relatively fertile habitats dominated by *Chionochloa pallens*, *C. flavescens* and large-leaved herbs, and these species showed the greatest recovery after deer control (Rose & Platt 1987).

5.8.5 Feral goats

Goats in alpine habitats in Red Hills, Marlborough, primarily ate grasses (*Chionochloa* and *Poa* spp.; present in all 16 stomachs analysed, and the most or second most abundant food type by volume in all 16) (Asher 1979). The remainder of the diet was primarily woody shrubs, especially *Aristotelia fruticosa* (present in 12 stomachs, and most or second most abundant in four) and *Hebe* spp. (present in eight, and second most abundant in three), and *Phormium cookianum* (present in eight, and most or second most abundant in five) (Asher 1979). *Griselinia littoralis*, a forest and subalpine species (Wilson 1996), was also often eaten (present in six stomachs, and second most abundant in two) (Asher 1979).

5.8.6 Overlap between diets of different herbivorous alpine mammals

In summary, hares, thar and goats in the alpine zone depended primarily on grasses, chamois on shrubs and herbs, deer on grasses and large herbs, and possums on fruit, shrubs and herbs. Few, if any, plant genera were preferred by all these mammals. Although there was considerable overlap between ungulates in the shrub and herb genera eaten, diets of possums and hares were relatively distinct. It is difficult to compare plant genera eaten between mammal species that were studied separately, since the measures used and the availability of different forage species varied between studies. The only alpine studies in which diets of sympatric mammals were compared were those of Parkes & Thomson (1995) and J.P. Parkes (unpubl. data). However, some overall similarities and differences between the diets of different mammals emerge from the other studies cited above.

Grasses

Snow tussocks (*Chionochloa* spp.) or other grasses were important foods for thar, chamois, goats, deer and hares.

Herbs

The large herbs that formed a major component of the diet of alpine red deer and wapiti (section 5.8.4) seemed much less important to the other alpine herbivores. These herbs appeared in the diets of thar and chamois, but at less than 12% mean dry weight (Parkes & Thomson 1995; J.P. Parkes, unpubl. data). *Aciphylla*, *Astelia* and *Dolichoglottis* were absent or <2% dry weight in the diet of alpine possums (Parkes & Thomson 1995; J.P. Parkes unpubl. data). Although *Celmisia* formed a major component of the diet of hares (Flux 1967; Horne 1979) and hares preferred *Aciphylla* in feeding trials (Horne 1979), *Anisotome* and *Astelia* appeared to be of little importance (Flux 1967), and *Ranunculus lyallii* was barely touched by hares at Mount Cook (Wilson 1986). None of these large herbs were reported in the diet of alpine goats, although *R. verticillatus* occurred in 3 of 16 stomachs and was the second most abundant species in 1 stomach (Asher 1979).

Phormium cookianum was an important food of deer and goats only (Poole 1951; Asher 1979).

Shrubs

Gaultheria and *Coprosma*, which were important foods of deer and wapiti, were much less prominent in the diets of the other herbivores. These shrubs were eaten by thar and chamois, but at less than 6% mean dry weight (Parkes & Thomson 1995; J.P. Parkes, unpubl. data). Foliage of these species made up less than 2% of possum diet (Parkes & Thomson 1995; J.P. Parkes, unpubl. data), but possums ate the fruit of both species (J.P. Parkes, unpubl. data). Of 16 goat stomachs sampled, *Coprosma* was found in 5 and *Gaultheria* in 1, but these species did not rank highly in relative volume in these stomachs (Asher 1979).

Carmichaelia was a key food of chamois (17% mean dry weight; Parkes & Thomson 1995) and to a lesser degree of thar (8%; Parkes & Thomson 1995) but was not eaten by sympatric possums (Parkes & Thomson 1995; J.P. Parkes, unpubl. data). *Carmichaelia* was eaten by hares in Mount Cook National Park (Wilson 1986).

Podocarpus nivalis foliage and fruits were main foods of possums only (J.P. Parkes, unpubl. data). Hares did not eat this species or *Phyllocladus alpinus*. Shrubs formed a very small component of the diet of hares: <1% mean volume of droppings sampled (Horne 1979) and <5% of bites recorded in winter and <1% in summer (Flux 1967).

Seeds and fruits

With the exception of possums, seeds and fruits were not a large component of the diets of any of the mammals reviewed above.

5.8.7 Mice

We are not aware of any previous studies of the diet of mice in alpine habitats. Elsewhere in New Zealand, wild mice have been shown to eat both invertebrates and plant material (primarily seeds) (Pickard 1984; Badan 1986; Miller & Miller 1995; Fitzgerald et al. 1996; Miller & Webb 2001). Diet appeared to be determined by both food availability (Badan 1986) and preference, both of which may vary seasonally (Pickard 1984; Craddock 1997; Miller & Webb 2001). However, as it may be impossible to calculate the relative availability of different food items for such a flexible omnivore, it is difficult to determine food preferences. Elsewhere in the world, invertebrates also predominated in the diet in many habitats (Berry & Tricker 1969; Watts & Braithwaite 1978; Copson 1986), but seeds predominated in desert (Watts 1970), grassland (Tomich et al. 1968; Borchert & Jain 1978), and agricultural areas (Whitaker 1966; Houtcooper 1978; Bomford 1987; Tann et al. 1991).

In New Zealand, the most common invertebrate group eaten by mice is caterpillars (Lepidoptera), followed by spiders (Araneae), beetles (Coleoptera) and weta (Orthoptera) (Ruscoe & Murphy 2005). Mice choose some prey on the basis of size, preferring spiders > 10 mm (Dugdale 1996) or 3–12 mm (Craddock 1997) in different studies, but eat caterpillars of different sizes in proportion to their availability (Craddock 1997).

In some circumstances, mice may prey on small eggs and nestlings. For the New Zealand robin (*Petroica australis*), which lays 25-mm eggs (Heather & Robertson 1996), mouse tracks were found in association with predation in 1 of 39 nests near Kaikoura (Moors 1978); however, there was no evidence of mouse predation on 16 robin nests on Allports Island, where mice were common (Flack & Lloyd 1978). In laboratory trials, captive mice did eat small (30-mm) eggs and nestlings (Moors 1978). Predation on several rock wren (*Xenicus gilviventris*) eggs (20 mm; Heather & Robertson 1996) in an alpine area of the Murchison Mountains was attributed to mice, based on the pattern of damage to the shells: the shells were opened and either the yolk was gone or the embryo had been partly eaten; serrations on broken shells matched the small teeth of mice (Heath 1989). Nest predation was also attributed to introduced house mice on Gough Island in the south Atlantic Ocean (Cuthbert & Hilton 2004). Mice may also kill lizards (Whitaker 1978; Newman 1994): capture rates of skinks (*Cyclodina macgregori*) and geckos (*Hoplodactylus maculatus*) increased after mice were eradicated from Mana Island (Newman 1994).

5.8.8 Stoats

Small mammals (mostly mice) and insects (mostly weta) were the most common prey items in stoat scats in an alpine area of the Murchison Mountains, followed by birds (mostly passerines) (Lavers & Mills 1978). In the year 1999–2000, following heavy flowering of tussock species and a full beech mast in this region, birds (mostly passerines), mice and invertebrates (mostly ground weta) occurred at similar frequencies in the diet of stoats (Smith 2001).

5.8.9 Feral cats

The diet of feral cats in alpine areas has not been reported. Elsewhere on the New Zealand mainland, the diet of feral cats is dominated by small mammals, including rabbits, rats and mice; birds, lizards and invertebrates (especially Orthoptera and Coleoptera) were also common prey (Gillies 2001). Although it has not been demonstrated experimentally, in some instances cats may benefit the native species eaten by rabbits or rodents by limiting populations of these smaller pests (Fitzgerald & Gibb 2001; Gillies 2001).

6. Discussion and conclusions

6.1 ABUNDANCE OF MICE IN ALPINE GRASSLAND AND HIGH-ALTITUDE BEECH FOREST

The observed pattern of summer and autumn peaks in mouse density followed by winter declines is typical of beech forests during low seeding years and in habitats without periodic seeding events, as mice respond to the increased availability of both invertebrates and seeds during summer (Ruscoe & Murphy 2005). Mouse populations in both alpine and high-altitude forest habitats may have the potential to attain the peak densities observed in lowland beech forest following a pulse in the food supply (up to 50/ha; Ruscoe et al. 2001), as the densities (based on live trapping) and the capture indices (based on snap trapping) in both habitats were typical of those found in beech forests during low seeding years (reviewed by Ruscoe & Murphy 2005). However, capture rates of mice in subalpine shrubland at Mount Misery, Nelson Lakes National Park, reached a maximum of only 8 mice/100TN (P.R. Wilson, Landcare Research, & M.G. Efford, University of Otago, unpubl. data), i.e. a lower number than found in beech forest after mast years (10–30 mice/100TN; Ruscoe & Murphy 2005).

6.2 POPULATION DYNAMICS OF ALPINE MICE

Whether a mouse population outbreak occurs in response to a high snow tussock-flowering year depends in part on the amount and accessibility of food produced. Mice eat seeds of both wild and cultivated grasses (e.g. Whitaker 1966; Pickard 1984; Bomford 1987; Tann et al. 1991), and their ability to adjust their diet according to the availability of different foods (e.g. Badan 1986; Bomford 1987) suggests that they will eat snow tussock seed when it is plentiful. The flowering intensity of *Chionochloa* can vary more than 5000-fold between years (Kelly et al. 2000), an amplitude similar to that of beech seed production (Wardle 1984: 257–259). Snow tussock seed production is not usually reported as seeds/m^2, but at Mount Hutt there were up to 46.8 inflorescences of *C. pallens*/m^2 (Kelly et al. 2000), with 62 034 seeds/m^2 on average (Kelly et al. 1992). In contrast, the highest mountain beech seedfall recorded at Takahe Valley was only 11 300 viable seeds/m^2 (seed containing endosperm)

(DOC, Te Anau, unpubl. data). However, the average mass of a mountain beech seed (4.1 mg) is about four times that of a *C. pallens* seed (1.0 mg) (Lee & Fenner 1989; Ruscoe et al. 2004). (Seed masses of the other species of *Chionochloa* present in the Borland Valley are similar to *C. pallens*; Lee & Fenner 1989.) Since the seeds of *C. pallens* and mountain beech both contain c. 5% nitrogen (Lee & Fenner 1989; Ruscoe et al. 2004), the energy and protein available from snow tussock seeds during a high flowering year may be equivalent to that available from beech seeds during a full beech mast year. However, a mouse would have to husk and eat four times as many tussock seeds as beech seeds to access as much food. A mouse requires at least 736 mountain beech seeds per day, and can eat as many as 1100 (Ruscoe et al. 2004), but we do not know whether a mouse can eat 2944 (4 × 736) grass seeds in 1 day.

An increase in seed availability may not be the only factor necessary to stimulate a population increase of mice. The population response of mice to beech seedfall may also in part be due to an increased availability of arthropod food, such as lepidopteran larvae, which feed on fallen beech flowers (Fitzgerald et al. 1996). When *Chionochloa* seeds are abundant, the density of some species of invertebrates may also increase (Kelly et al. 2000; McKone et al. 2001), further augmenting the supply of food for mice. However, little is known about these dynamics in either ecosystem.

6.3 POPULATION DYNAMICS OF MICE IN BEECH FOREST

Following heavy beech seedfall, peak mouse numbers have occurred in the winter, spring or summer (August, November or February, in quarterly trapping sessions), although in most instances high mouse numbers were first detected in August or November (King 1983; Murphy 1992; Fitzgerald et al. 1996; Wilson et al. 1998; Choquenot & Ruscoe 2000; Ruscoe et al. 2001, 2003; Fitzgerald et al. 2004). In spite of the moderately high beech seedfall at our forest sites in 2004, very few mice were captured in November 2004. There are several possible interrelated explanations for these low numbers: the density fell to such low levels in autumn or winter 2004 that subsequent rapid population growth was inadequate to raise it to a measurable level; the quantity of beech seed was insufficient to sustain a long period of rapid breeding, when combined with other factors, such as weather or availability of invertebrate foods; and/or because more than half of the seed fell after May 2004, the expected mouse outbreak was delayed and may instead have been detectable in February 2005. Although most beech seed falls between March and May (Wardle 1984: 259), it may be delayed at high altitude, and/or an additional burst of spring seedfall may occur (Wardle 1984).

Seedfall of silver and mountain beech tends to be maximal at intermediate altitudes; both the quantity and quality of seed decreases at higher and lower altitudes (Wardle 1984: 261). Seedfall and possibly mouse density may, therefore, have been higher downhill from our forest sites; in support of this, capture rates of mice were much higher in the Borland Valley bottom (Smith 2006). The middle of our arrays of seed traps corresponded to the highest altitude silver beech site cited by Wardle (1984)—at 905 m a.s.l., 100 m below the treeline, in the Takitimu Range east of the Borland Valley. Our lowest seed traps were at c. 840 m a.s.l., which is also a higher altitude than where peak seedfall occurred in the data cited by Wardle (1984).

6.4 DENSITY OF HARE PELLETS

Before plots were cleared, hare pellet density (7.9 pellets/m^2) was similar to that recorded in an alpine basin in Nelson Lakes National Park (4.7–7.3 pellets/m^2; Flux 1967). Lower densities of 1.8 pellets/m^2 and 2.6 pellets/m^2 were found at alpine sites in the Blue Mountains and Mount Bee, Otago, respectively (Solly 1998), whereas pellet density has been found to exceed 100 pellets/m^2 on river flats in Canterbury (Parkes 1999). Flux (1967) estimated an average density of 9.5 hares over 120 ha (0.07 hares/ha), based on pellet counts, but cautioned that because of various uncertainties the actual number could be anything between 2 and 109. Therefore, there is no evidence that average hare density in the Borland Valley differed from mean densities in the Nelson Lakes, the Blue Mountains or on Mount Bee.

The relatively high accumulation of hare pellets that we recorded between May and November 2003 is difficult to explain. It could indicate that hares spent more time feeding at altitudes where flowering *Chionochloa* tussocks were plentiful in autumn 2003. Not only would such a response lead to more pellets at these altitudes, but a diet high in *Chionochloa* leaves would tend to produce pellets that decayed slowly (Flux 1967). It is also possible that there was a reproductive response to tussock flowering, since hares produce multiple litters and can breed throughout most of the year, with young being weaned after c. 60 days (Norbury & Flux 2005). In either case, the hares may have been eating the bases of flowering tillers rather than seeds: in spring and summer, flowering tillers may be higher in nutrients than non-flowering tillers (Mills et al. 1991); however, it is not known whether this difference continues into autumn. A final possibility is that the high level of pellet accumulation may simply have been due to slow pellet decomposition in winter, whereas during the second winter sampled, the average monthly accumulation may have been reduced because of the long period between pellet counts. To fully interpret this result, a longer time series of data is required, in order to test whether pellet numbers increase in association with flowering events.

6.5 POTENTIAL IMPACTS OF MICE ON WETA

The inverse relationship between captures of ground weta and mice suggests that mice, even at low densities, may limit the abundance of weta through predation. Weta were the most common invertebrate prey in the stomachs of mice, and mice can significantly depress populations of their insect prey and may have extirpated some species from islands (Crafford 1990; Chown & Smith 1993; Marris 2000). We caught most weta at site A1, where the tussocks and shrubs were smaller than at the other alpine sites (pers. obs.) and may have provided less cover for mice. The capture rates at this site of up to 4.5 weta/100TN were similar to those in alpine habitat in the Murchison Mountains, where up to

5 weta/100TN and no mice were caught (Smith 2001). Alpine habitats that are suboptimal for mice, perhaps because of poor cover or a shortage of nest sites, may afford relatively predator-free space for native invertebrates.

Four widespread species of ground weta may be present in the Borland Valley: *Hemiandrus focalis*, *H. fiordensis*, *H. maculifrons* (the only species that was identified in this study), and *H.* 'madisylvestris' (Johns 2001). No other genera of true weta (Stenopelmatidae) have been reported in southern Fiordland, although cave weta (Rhaphidophoridae) are found throughout New Zealand (Gibbs 1998). Ground weta burrow in moss or soil and may be confined to burrows for days or weeks (Johns 2001). Eggs, which are also laid in moss or soil, hatch 2–18 months later, and nymphs take 2 or even 3 years to develop into adults (Johns 2001). These burrowing species are probably vulnerable to mouse predation at all life stages, and, because they mature slowly, predators may have a considerable impact on their abundance.

6.6 EXPECTED IMPACTS OF ALPINE MAMMALS AFTER A TUSSOCK FLOWERING EVENT

Since neither a high tussock-flowering year nor a full beech mast occurred during this study, we can only speculate about how the impacts of introduced mammals would change in response to one of these events. Most of the following discussion focuses on mice, because their potential to respond to a pulse in the food supply at the population level is well documented.

6.6.1 Mice

Mice need 91 kJ/day of energy on average; this is the equivalent of 4.4 g (dry mass) of invertebrates daily (Miller 1999). Mice at a density of 50/ha, as recorded in beech forest after a year of high beech seed production (Ruscoe et al. 2001), could therefore eat up to 6.6 kg ha^{-1} $month^{-1}$ of invertebrates (dry mass). The number of individuals killed to satisfy this energy requirement is magnified if mice eat only parts of an individual invertebrate and discard the remainder. Since mice prey selectively on invertebrates of certain sizes (Chown & Smith 1993; Dugdale 1996; Craddock 1997), some species and age classes of alpine invertebrates may be significantly reduced in numbers when mice are at high density. Based on our diet data, weta, spiders, grasshoppers and lepidopterans are the alpine arthropods most likely to be affected, although diet composition may differ during high flowering years if the availability of invertebrates changes in response to food availability or predation. Mice may also eat snails, including *Powelliphanta* spp., which occur in alpine habitats (Walker 2003); these may not be detectable in their stomachs.

Modelling has shown that mice are unlikely to eat all the beech seed that falls during a full mast year because the seed is only available to predators until the following spring, when the majority germinates (Ruscoe et al. 2005). Most viable seed of *Chionochloa macra* also germinated in spring or early summer, and this was considered to also be the case for *C. pallens* and other alpine tussock species (Spence 1990). Therefore, as with beech seed, mice are unlikely to consume enough *Chionochloa* seed (see section 6.2) to threaten the reproduction of snow tussock. We did not detect an increase in plant material in the diet of alpine mice in February or May 2003, when tussock flowers or seed were most likely to have been available, but bait in the stomachs may have partially hidden this material. It is possible that at peak density mice could destroy a substantial proportion of the seed produced by other alpine plants, and simultaneously kill or compete with native seed- or fruit-eating invertebrates.

Finally, alpine mice at high density may be important predators of rock wren eggs (Heath 1989). Since these birds are classified as nationally vulnerable (Hitchmough 2002; Molloy et al. 2002), this interaction warrants further investigation. The impacts of mice on alpine skinks and geckos are unknown (R. Hitchmough, DOC, pers. comm.).

6.6.2 Herbivorous mammals

Based on the characteristic diets of the different species of mammalian herbivores, we can predict the groups of plants that would be impacted if one or more of these mammalian species increased in abundance in response to tussock flowering or other events. However, it should be noted that large increases in density of a single species or of multiple species of herbivore with overlapping diets may also impact less favoured forage plants, as preferred forage becomes increasingly scarce.

Seeds and invertebrates are infrequent in the diets of deer, thar, chamois, goats or hares. However, it is possible that during high *Chionochloa*-flowering years these herbivores alter their diets and foraging behaviours to feed on the relatively nutrient-rich leaf bases of the flowering tillers (Mills et al. 1991). Possums rely heavily on fruits, seeds and, in some circumstances, invertebrates (Nugent et al. 2000), and eat large quantities of beech flowers and seeds (Sweetapple 2003), which are dry-fruited like grass seeds. Since *Chionochloa* has not been recorded in possum diets (J.P. Parkes, unpubl. data), and possums prefer subalpine shrub to alpine grasslands (Forsyth et al. 2000), they may not eat this species even when it is flowering or fruiting. This assumption could be tested by studying the stomach contents of alpine possums during a high tussock-flowering year. It has been suggested that a population response of possums to beech seedfall events could occur, especially after two consecutive beech mast years (Sweetapple 2003); if possums eat tussock flowers or seeds, a similar response to tussock flowering is possible. However, since possums usually have only one and a maximum of two young per year (Fletcher & Selwood 2000), the population increase would be relatively small.

6.6.3 Stoats and cats

In beech forest, stoats increase in numbers following heavy seeding as a result of the increased abundance of mice, birds and possibly invertebrates (King 1983; Murphy & Dowding 1995); this increase impacts on forest birds (O'Donnell & Phillipson 1996; Wilson et al. 1998). Some stoats spend most of their time in alpine areas (Smith & Jamieson 2003). If the population dynamics of alpine mice after high tussock flowering mirrors those after heavy beech seedfall, a similar parallel is likely between stoat population dynamics in alpine and beech habitats. Furthermore, since the home ranges of stoats often encompass both forest and alpine habitats (Smith 2006), the number of stoats in the alpine zone may also increase following a beech mast. An outbreak of stoats in alpine habitats would be almost certain to affect their alpine prey, i.e. birds and invertebrates, particularly weta (Lavers & Mills 1978; Smith 2001). Takahe (Maxwell 2001; Smith & Jamieson 2003) and rock wrens are acutely threatened (Molloy et al. 2002; Hitchmough 2002) alpine birds that are likely to be particularly vulnerable to such periodic increases in predator density.

Feral cats responded to low densities of rats on Stewart Island/Rakiura by moving away from their home ranges; their survival also decreased at these times (Harper 2004). Similarly, when mice are abundant in alpine grasslands, cats may move there and have greater survival rates, especially if mice are simultaneously scarce in montane forest. Such behavioural and demographic responses by cats are likely to have consequent impacts on other alpine prey, notably birds and invertebrates.

7. Recommendations

The authors recommend continued research in the following areas:

- The abundance of mice, hares and stoats should continue to be assessed annually at alpine sites in the Borland Valley, along with tussock flowering and beech seedfall. Since neither a high tussock-flowering year nor a full beech mast occurred during this study, we still do not know how alpine populations of these mammals respond to these events.
- Tussock flowering should continue to be measured annually at Takahe Valley in the Murchison Mountains in order to predict likely outbreaks of mice and stoats in alpine zones. Because of the very high synchrony in tussock flowering between widely separated sites, between species at a site, and between plants in a population (Kelly et al. 2000), not many sites need to be monitored. The Murchison Mountains are of interest because of the presence of the endangered takahe (Maxwell 2001). If species at distant alpine sites (e.g. on the east coast of the South Island or in the North Island) are threatened by potential outbreaks of mice, stoats or hares, similar monitoring should be introduced at those sites.
- Beech seed production should continue to be monitored at various locations, including those near Te Anau. Heavy beech seedfall may also be a predictor of outbreaks of mice in alpine habitats.
- Once the relationship between the population dynamics of mice, hares and stoats in alpine environments and either tussock flowering or beech seedfall has been determined, it may not be necessary to continue to monitor these introduced mammals. Instead, it may be possible to predict periods of risk to native species based on the flowering and seedfall data, and to increase the level of pest management as required at these times.

- To test predictions of heightened risk that have been made based on flowering and seedfall data, the abundance of native alpine plants or animals that are considered to be at risk, or indices of herbivory or predation on these species, should be assessed before and after flowering or seedfall events. Ground weta and rock wrens are possible candidates for such monitoring.
- The relationship between the abundance of alpine mice and ground weta should be studied further. Standard tracking tunnels could be used to compare the relative abundance of weta between sites, altitudes and periods of high and low mouse density. A more detailed investigation of the relationship between mouse density and the size distribution of weta would help to show how predation affects the population dynamics of weta. Manipulating mouse density with exclosures or intensive removal might be the most powerful way to approach these studies. Further, assessing the biomass of weta in alpine areas would enable calculation of the potential impact of mice on weta populations.
- The rate of predation by mice on rock wren nests should be investigated by monitoring nests in years of high and low mouse abundance.
- Whether possums eat flowers or seed of snow tussocks should be determined by analysing the stomach contents of possums during a high flowering year.
- Traps used to collect mice for diet studies should be baited with inaccessible bait, such as an oil-based scent on leather tied to the trigger of the trap (Bomford 1987). When it is desirable to identify the taxa of seeds eaten, reference slides should be prepared from the contents of the stomachs of captive mice fed on known seed species (Hansson 1970; Bomford 1987; Tann et al. 1991). Starch granules in the endosperm and/or seed coat fragments can be used to distinguish monocotyledons and dicotyledons, and sometimes to determine the genus or species of the seeds (Bomford 1987).

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Appendix 1

COMPARISON OF POPULATION SIZE AND DENSITY ESTIMATES OF MICE (*Mus musculus*) BASED ON THREE DIFFERENT ESTIMATORS

Population size ($\hat{N}$) and density ($\hat{D}$) of mice in forest (F) and alpine (A) habitats in the Borland Valley during five trapping sessions, estimated with the null model (M_0), the jackknife estimator (M_h) and Chao's second coverage estimator (M_{th}) (details in section 4.2.2). NA means that density could not be estimated.

TRAPPING SESSION	SITES	$\hat{N}$			$\hat{N}$ RELATIVE TO M_0		CV($\hat{N}$)			$\hat{D}$			$\hat{D}$ RELATIVE TO M_0		CV($\hat{D}$)		
		M_0	M_h	M_{th}	M_h	M_{th}	M_0	M_h	M_{th}	M_0	M_h	M_{th}	M_h	M_{th}	M_0	M_h	M_{th}
Feb 03	F1, F2	14.0	12.8	13.5	0.91	0.96	0.37	0.26	0.40	NA	NA	NA	NA	NA	NA	NA	NA
	A2, A3	55.0	65.4	60.0	1.19	1.09	0.16	0.14	0.26	4.61	5.11	4.68	1.11	1.02	0.29	0.32	0.39
May 03	F1, F2, F3	31.0	44.7	40.9	1.44	1.32	0.06	0.15	0.20	1.94	2.43	2.50	1.25	1.29	0.21	0.27	0.29
	A2, A3	207.0	93.8	535.5	0.45	2.59	0.52	0.13	0.76	NA	NA	NA	NA	NA	NA	NA	NA
Nov 03	F2, F3	9.0	9.8	8.4	1.08	0.93	0.05	0.12	NA	0.63	0.51	0.52	0.81	0.82	0.37	0.50	0.50
	A2, A3	10.0	11.1	11.4	1.11	1.14	0.10	0.21	0.25	0.94	0.90	0.94	0.97	1.00	0.37	0.49	0.51
Feb 04	F2, F3	12.0	12.0	11.4	1.00	0.95	0.13	0.20	0.14	0.69	0.57	0.53	0.82	0.77	0.47	0.59	0.68
	A2, A3	30.0	37.7	35.4	1.26	1.18	0.14	0.17	0.28	2.62	2.98	2.83	1.14	1.08	0.33	0.41	0.63
Nov 04	A2, A3	8.0	10.4	12.0	1.30	1.51	0.11	0.28	0.41	0.52	0.59	0.68	1.15	1.33	0.44	0.57	1.12
Mean		41.8	33.1	80.9	1.08	1.30	0.18	0.18	0.34	1.71	1.87	1.81	1.04	1.04	0.35	0.45	0.59

Appendix 2

ESTIMATED CAPTURE, MOVEMENT AND POPULATION SIZE PARAMETERS OF MICE (*Mus musculus*) (USING THE PROGRAM DENSITY)

Key parameters estimated for mice at forest (F) and alpine (A) habitats in the Borland Valley during five trapping sessions; for details see section 4.2.2 and Efford (2004). Standard errors are shown in parentheses. NA means that the parameter could not be estimated.

M_{t+1}	Number of individuals caught
Recaps	Number of animals marked and then recaptured during a session
$\hat{N}$	Closed-capture estimate of population size
$\hat{p}$	Closed-capture estimate of capture probability
$\bar{d}$	Mean distance between successive captures of an individual (m)
RPSV	Root pooled spatial variance, a measure of spatial pattern used in the estimation of $\hat{D}$ (m)
$\hat{g}_0$	Estimated probability of capture when trap is at the centre of home range
$\hat{\sigma}$	A measure of home range width (m)
$\hat{D}$	Estimated density of population (mice/ha)

TRAPPING SESSION	SITES	M_{t+1}	RECAPS	$\hat{N}$	$\hat{p}$	$\bar{d}$	RPSV	$\hat{D}$	$\hat{g}_0$	$\hat{\sigma}$	CV($\hat{N}$)	CV($\hat{D}$)
Feb 03	F1, F2	9	3	12.8 (3.3)	0.23	52.4 (18.8)	50.9	NA	NA	NA	0.26	
	A2, A3	37	16	65.4 (9.4)	0.20	22.6 (5.7)	23.4	5.1 (1.5)	0.09 (0.01)	19.4 (2.9)	0.14	0.30
May 03	F1, F2, F3	29	29	44.7 (6.7)	0.32	18.4 (2.5)	17.5	2.4 (0.5)	0.23 (0.04)	15.6 (1.7)	0.15	0.22
	A2, A3	39	3	93.8 (11.8)	0.11	23.0 (16.1)	28.4	NA	NA	NA	0.13	
Nov 03	F2, F3	9	14	9.8 (1.2)	0.59	27.8 (7.0)	28.2	0.5 (0.2)	0.41 (0.20)	23.6 (5.1)	0.12	0.38
	A2, A3	10	10	11.1 (2.4)	0.45	21.2 (4.7)	17.7	0.9 (0.4)	0.34 (0.11)	15.3 (3.0)	0.21	0.39
Feb 04	F2, F3	11	9	12.0 (2.4)	0.42	33.4 (14.2)	47.4	0.6 (0.3)	0.09 (0.02)	37.8 (11.9)	0.20	0.51
	A2, A3	24	14	37.7 (6.3)	0.25	18.9 (5.9)	21.7	3.0 (1.1)	0.13 (0.02)	18.1 (3.3)	0.17	0.37
Nov 04	F1, F2, F3	1	0	NA								
	A2, A3	8	8	10.4 (2.9)	0.39	32.7 (11.2)	38.4	0.6 (0.3)	0.10 (0.03)	29.1 (8.1)	0.28	0.47