

## Stoat density, diet and survival compared between alpine grassland and beech forest habitats

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**Abstract:** In New Zealand, alpine grasslands occur above the treeline of beech forest. Historically stoat control paradigms in New Zealand's montane natural areas have assumed alpine grassland is a marginal habitat that limits dispersal between beech forest stoat populations. We compared the summer-to-autumn (January–April) density, weight, diet and winter survival of stoats between these two habitats during years of low beech seedfall. Stoats were live-trapped, marked and released in alpine grassland and low-altitude beech forest in the Borland Valley, Fiordland National Park, during 2003 and 2004, and were caught and euthanased for necropsy in 2005. Stoat density was estimated using spatially explicit capture–recapture (SECR). The proportion of stoats marked in one year but recaptured in the next was used as a measure of ‘observed survival’. Prey remains were identified from scats collected during 2003 and 2004 and stomachs from stoats killed in 2005. Stoat density was similar in both habitats over the two years, about one stoat per square kilometre. Observed survival from 2003–2004 was also similar, but survival from 2004–2005 was higher in alpine grassland than in beech forest. In 2003, male stoats were on average heavier in alpine grassland than in beech forest, although average weights were similar in the other years. Diet differed significantly between the two habitats, with stoats in alpine grasslands eating mainly ground weta (a large invertebrate) (72%) and hares (23%), while stoats in beech forest ate mainly birds (31%) and mice (19%). Collectively these results suggest that alpine grasslands are not a poor quality habitat for stoats. Traditionally it has been thought that stoats cannot survive on invertebrate prey alone. This research demonstrates that stoats relying largely on invertebrate prey can occur at similar densities and with equivalent survival to stoats relying on vertebrate prey.

**Keywords:** *Chionochloa*; *Mustela erminea*; New Zealand; snow tussock

## Introduction

Stoats (*Mustela erminea*) are small mammalian carnivores that are widespread throughout the Northern Hemisphere (King & Powell 2007). Stoats were introduced to New Zealand in the 1880s (King et al. 2001) and have since been implicated in the decline of many native fauna (Elliott 1996; Elliott et al. 1996; McLennan et al. 1996; Wilson et al. 1998). Stoats are the most widespread introduced predators in forests dominated by southern beech (*Nothofagus* spp.) (King & McMillan 1982; King 1983; Murphy & Dowding 1995), where their populations increase dramatically in abundance every 4–6 years (King & McMillan 1982; Dilks et al. 2003). It is hypothesised that these increases are numerical responses to increased densities of mice (*Mus musculus*) (King 1983), birds

(Murphy & Dowding 1995) and invertebrates (Alley et al. 2001; Fitzgerald & Gibb 2001) that result from irregular heavy beech seedfall events. This relationship has been the dominant theme of stoat research in New Zealand since 1972 and is a major focus of conservation management (King & McMillan 1982; King 1983; Murphy & Dowding 1994, 1995; O'Donnell & Phillipson 1996; O'Donnell et al. 1996; Powell & King 1997; King 2002; Dilks et al. 2003; King et al. 2003; Purdey et al. 2004). However, 70–80% of years are not preceded by heavy beech seedfall and less is known about the population biology of stoats during these ‘normal’ years.

Most protected areas in New Zealand's South Island are montane, with alpine grasslands dominated by snow tussock (*Chionochloa* spp.) occurring above a beech forest treeline. Few studies have looked at stoats in alpine

grasslands. Radio tracking has shown that stoats captured near valley bottoms have tended to remain close to the valley floor (Murphy & Dowding 1994; Lawrence & Dilks 2000; Purdey et al. 2004). It has been assumed that the movement of stoats between forested valleys is restricted by intervening alpine areas (Lavers & Mills 1978; Dilks et al. 2003). This may be because alpine areas are generally impassable for stoats and lack the food resources to be a good quality habitat. However, more recently it has been shown that stoats have summer ranges in alpine grassland (Smith & Jamieson 2005) and stoats live-trapped and radio-tagged above treeline in the Borland Valley appeared to select alpine grasslands over adjacent beech forest (Smith et al. 2007). These results suggest that alpine grasslands are unlikely to limit stoat dispersal between valleys but could potentially be inhabited by source populations for stoats that disperse into beech forest valley floors.

The hypothesis that alpine grassland is a poorer quality habitat than beech forest predicts that the density and survival of stoats should be lower there than in beech forest, because there are fewer resources, leading to a lower carrying capacity. Also, the average weight (and therefore condition) of alpine stoats should be lower compared with forest stoats, because they may have to forage more for fewer prey resources. To test these predictions we compared density, survival, mean body weight, and age structure between stoat populations in alpine grassland and adjacent low-altitude forest dominated by mountain beech (*Nothofagus solandri* var. *cliffortioides*). We also compared the diet of stoat populations between the habitats. It was thought that diet analysis might help in developing hypotheses about differences in density and survival, perhaps by identifying key prey resources utilised by beech forest stoats but missing from the diet of stoats in alpine habitats.

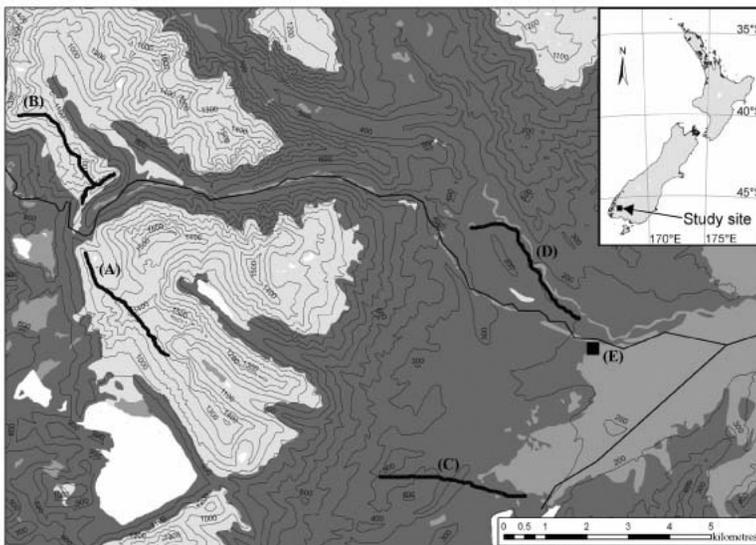
## Methods

### Study site

The Borland Valley (45°40'S, 167°20'E) is 63 km south of Te Anau, New Zealand, in the south-eastern part of Fiordland National Park. The area consists of rugged mountains rising from sea level to >1600 m separated by U-shaped, glacially formed valleys. The most distinctive ecotone is the beech forest treeline at 900–1000 m a.s.l. above which alpine grasslands dominate. A shingle road for power line maintenance crosses the Borland Saddle at 990 m a.s.l., providing the easiest access to alpine grasslands in the national park. There were no heavy beech seedfall events in the Borland Valley during the time frame of this research (Smith 2006).

### Live-trapping

Four 4-km live-trap lines were set up, two in alpine grassland and two in low-altitude beech forest (Fig. 1). Each line consisted of 20 live traps set at 200-m intervals. The two live-trap lines in alpine grassland were set up on either side of the Borland Saddle, and were separated by a distance of 2 km. This distance was based on the mean home-range size of stoats observed in a similar habitat (Smith & Jamieson 2005), and was intended to provide some spatial independence between the two lines. Because of logistical limitations the line at alpine site 2 was only 2 km long (10 traps) in 2003 but was extended to 4 km in 2004. The two beech-forest lines were placed at the start of two hiking trails, and were 4 km apart at their closest point. The first trap on each line was a minimum of 500 m from the road. The closest distance between any beech forest line and any alpine grassland line was



**Figure 1.** Borland Valley study area. A = alpine grassland live-trap-line 1; B = alpine grassland live-trap-line 2; C = beech forest live-trap-line 1; D = beech forest live-trap-line 2; E = Borland Lodge. White = lakes/water; light grey (where A & B are) = alpine grassland; dark grey = beech forest; mid-grey (to the right of the figure) = farmland.

6 km. Previous research in the Borland Valley has found mouse populations there to reach unusually high densities following heavy beech seedfall (King 1982, 1983; King et al. 2003; Purdey et al. 2004), but all of these studies were undertaken along the Borland Road. In this study we deliberately chose sites away from the road to try and prevent any confounding effects from unusually high mouse densities near the road.

The alpine grassland lines were between 1100 and 1475 m a.s.l. and the beech forest lines were between 200 and 335 m a.s.l. The alpine grassland lines traversed continuous snow tussock, while the beech forest lines traversed tall mountain beech forest (with the exception of part of beech forest line 1, which passed through kānuka (*Kunzea ericoides*) bog for 300 m). The beech forest understorey was generally dominated by densely growing shield fern (*Polystichum vestitum*), crown fern (*Blechnum discolor*), *Coprosma* spp. and other shrubs, or open mossy areas.

The two types of live trap used were aluminium Elliott B traps (Elliott Scientific Equipment™) with wooden nest boxes, and wooden Edgar traps (King & Edgar 1977). Each line contained 15 Elliott traps and 5 Edgar traps. Edgar traps were at positions 1, 5, 10, 15 and 20 in each line. Traps were baited with a chicken egg and a 3-cm-square chunk of fresh rabbit meat. Trap lines were checked on foot.

This research was conducted over three consecutive summers (2003–2005). All lines were run for 5 nights during January 2003, March 2003, January 2004, April 2004 and January 2005. However, because the alpine grassland lines were part of a more intensive study (Smith et al. 2007), they were also run for 2 nights each fortnight during February 2003, February 2004 and March 2004. Captured stoats were ear-tagged, weighed, sexed, and released, except in January 2005 when all stoats caught were euthanased for further dissection.

### Density

Stoat density was estimated by spatially explicit capture–recapture (SECR) in program DENSITY (Efford et al. 2004). This method estimates the number of animals per unit area by fitting a spatially explicit detection model to the capture data, incorporating information about capture locations (Efford 2004). Because sample sizes from each line during each trapping session were small it was necessary to group data for analysis. Data were pooled across lines within the same habitat and across sessions within the same year. This allowed us to estimate stoat density in alpine grassland (sites combined) and for beech forest (sites combined) in both 2003 and 2004. Coefficients of variation (CV, the standard error of an estimate divided by the estimate) were used to measure the precision of each estimate of  $D$  (density),  $g_0$  (probability of capture if trap location and home range centre are equal) and  $\sigma$  (the spatial scale over which probability of capture declines

with distance from the home range centre);  $g_0$  and  $\sigma$  are parameters used in the spatial modelling process. Where 95% confidence intervals are reported, they are log-normal confidence intervals.

### Survival

Computer-intensive mark–recapture modelling to estimate survival of open populations requires large sample sizes (Pollock et al. 1990). Stoats occur at densities that are too low to generate sufficient sample sizes for these types of analyses, even with the trap lines used in this research. Therefore, the survival of stoats in the two habitats was compared based on the percentage of stoats marked in 2003 reappearing in 2004 and the percentage of stoats marked in 2003 and 2004 reappearing in 2005. These estimates are referred to as ‘observed survival’ and exclude pre-independence mortality of juveniles. These percentages were compared between alpine grassland and beech forest sites using Fisher’s exact tests. Data from sites within each habitat were combined.

### Age structure and recruitment

Cementum lines in upper canine teeth, confirmed as annual by Grue and King (1984), were used to classify ages of dead stoats. The upper canine teeth were removed from all stoats collected in January 2005 and sent to Matson’s Laboratory (PO Box 308, Milltown, Montana, USA) for cementum age analysis. Using October as a standardised birthday (Powell & King 1997), the age (in years) of each stoat was determined. Plots of the age classes were then used to determine whether the frequencies of different age classes varied between the two habitats.

Recruitment was estimated as the proportion of the sample population that was juvenile in each habitat in each year. In 2003 and 2004, live young of the year (juveniles) were distinguished from adults by visual assessment. Juvenile males are easily distinguished from adult males because they lack swollen testes; juvenile females were distinguished from adult females by the absence of exposed nipples. This classification system is less reliable for females than males (Grue & King 1984). Cementum sections taken from the same individuals in 2005 showed that of five females from the alpine grassland sites classified when alive as juveniles in 2004, four had been correctly classified while one had not.

### Weight

Mean weight of adult males was compared between the two habitats in each year, but because the visual distinction between juvenile and adult females is unreliable weight of adult females was compared between the two habitats in 2005 only, when cementum aging could be used. We assumed that mean weights differed significantly between habitats in a particular year when their 95% confidence intervals did not overlap (Johnson 1999), making this a

two-tailed analysis. No further analyses were undertaken because of the small, unbalanced sample sizes and because some stoats used in the analysis were present in more than one year but others were not.

### Diet

Diet samples came from scats and stomachs. Most scats were collected from trap sites when setting traps, as stoats had often excreted on top of the traps. Scats were also collected from within the trap after a stoat was caught. Stoat scats were also found by chance throughout the study site. Most stomach samples were collected from stoats killed in January 2005, and some were removed from stoats unintentionally killed during handling in 2003 and 2004. Twenty-seven scats collected from alpine site 1 between 24 February and 19 April 2004 were excluded from analysis because diet was experimentally manipulated at this site during this period (Smith 2006). It was thought that such a short manipulation would have minimal impact on winter survival, although it may have temporarily impacted on mass.

Samples were stored in 70% ethanol and then partitioned under a dissecting microscope into the prey categories bird, mammal, invertebrate, lizard and other. Only invertebrates and mammals were identified further. Invertebrates were identified as either ground weta (large flightless Orthoptera, Family: Anostomatidae, Genus: *Hemiandrus*) or as 'invertebrate other'. Hair samples were taken from mammal remains and used to identify them to genus or species level. This was done in two ways. First, the length, colour and structure of hair samples were compared with a reference collection created from known specimens. Second, guard hairs were cast in a 50:50 solution of polyvinyl acetate (PVA) and distilled water (Day 1966; Brunner & Coman 1974). Scale patterns left in the casts were compared with the plates in Brunner & Coman (1974) and with additional slide casts created using the reference collection.

The minimum number of ground weta in each sample was estimated by counting the number of left and right mandibles in each scat or stomach. No regularly occurring morphological features of birds and mice were found in the scats and stomachs to allow estimation of

the minimum number of individuals. We considered that hares were so large that each diet sample must contain remains from only a single individual. Previous studies have shown differences in the diet of male and female stoats (King & Moody 1982; Murphy & Dowding 1995); however, the number of scats in this study that could be linked to individual stoats was insufficient to make such a comparison.

Each prey category was quantified by calculating its percentage frequency of occurrence (Day 1966; King & Moody 1982; Reynolds & Aebischer 1991) in the diet samples. Logistic regression was used to test for the effects of habitat and year on the probability of the five most common prey categories appearing in the stoat diet. Habitat and year were regressed together (as independent variables), with a separate regression for each prey type identified. For these analyses it was assumed that each scat was independent, i.e. that each represented a single meal. Ninety-five-percent binomial confidence intervals were calculated for these percentages using the formulae for 'confidence limits for population proportions' described in Zar (1996, p. 524).

## Results

### Density

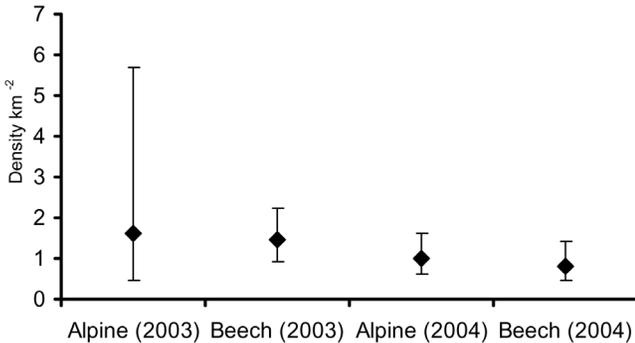
The data used to estimate stoat density are summarised in Table 1. Estimated density was similar between the two habitats during both years (2003: alpine grassland = 1.6 km<sup>-2</sup>, beech forest = 1.46 km<sup>-2</sup>; 2004: alpine grassland = 1.0 km<sup>-2</sup>, beech forest = 0.82 km<sup>-2</sup>), with 95% confidence intervals overlapping all four estimates (Fig. 2). The density estimate for alpine grassland in 2003 was very imprecise (CV 73%), but the estimates for alpine grassland in 2004 (CV 26%) and for beech forest in 2003 (CV 23%) and 2004 (CV 29%) were reasonably precise given the large scale of stoat movements indicated by estimated  $\sigma$  (Table 2).

### Survival

Over the three years 25 individual stoats were caught in alpine grasslands and 39 individuals in beech forest. Ten of these died during the study for reasons other than

**Table 1.** Number of stoats caught each year, number of recaptures achieved within the same year, and trap-nights in alpine grassland and beech forest sites in the Borland Valley. Tallies of individual stoats in 2004 and 2005 include some animals marked in the previous year.

Year	Alpine grassland			Beech forest		
	Individuals	Recaptures	Trap-nights	Individuals	Recaptures	Trap-nights
2003	9	5	10	15	21	10
2004	17	42	15	16	23	10
2005	11	0	5	18	0	5



**Figure 2.** Estimates of stoat density in alpine grassland and beech forest in the Borland Valley in 2003 and 2004. Vertical bars are 95% confidence intervals.

**Table 2.** Estimates of  $D$ ,  $g_0$ , and  $\sigma$ , and their associated standard errors and coefficients of variation.

Year	Habitat	$D$ (km <sup>-2</sup> )	SE	CV (%)	$g_0$	SE	CV (%)	$\sigma$ (m)	SE	CV (%)
2003	Alpine grassland	1.6	1.2	73	0.017	0.002	9	521	263	51
	Beech forest	1.5	0.3	23	0.077	0.022	29	429	72	17
2004	Alpine grassland	1.0	0.3	26	0.047	0.014	30	726	105	15
	Beech forest	0.8	0.2	29	0.040	0.009	22	891	176	20

natural causes (i.e. becoming 'known fates'). In the alpine grassland sites one stoat died during handling and two died when they were caught in the mouse live traps of Wilson et al. (2006). In the beech forest three stoats died during handling, one stoat was caught in a Department of Conservation (DOC) trap line (which was subsequently decommissioned to prevent any further interference with our research), and three were caught on the Borland Lodge grounds during the winter.

The number of stoats marked in 2003 that were still unaccounted for when the 2004 field season commenced (i.e. after removing non-natural mortalities, above) was nine in beech forest and eight in alpine grassland. Five marked beech forest stoats were recaptured in beech forest in 2004 (56%) and five marked stoats in alpine grassland were recaptured in alpine grassland in 2004 (63%). These percentages did not differ significantly between beech forest and alpine grassland (Fisher's exact test,  $P=0.6$ ). The number of marked stoats unaccounted for before trapping in 2005 was 14 in beech forest and 15 in alpine grassland. In 2005 one marked stoat was recaptured in the beech forest (7%) and nine marked stoats were recaptured in alpine grassland (64%). These percentages were significantly different (Fisher's exact test,  $P=0.03$ ).

#### Age structure and recruitment

None of the stoats collected from alpine grassland in 2005 were young of the year, 34% were one-year-olds and 66% were  $\geq 2$  years old ( $n=11$ ; Fig. 3a). Sixty-one percent of

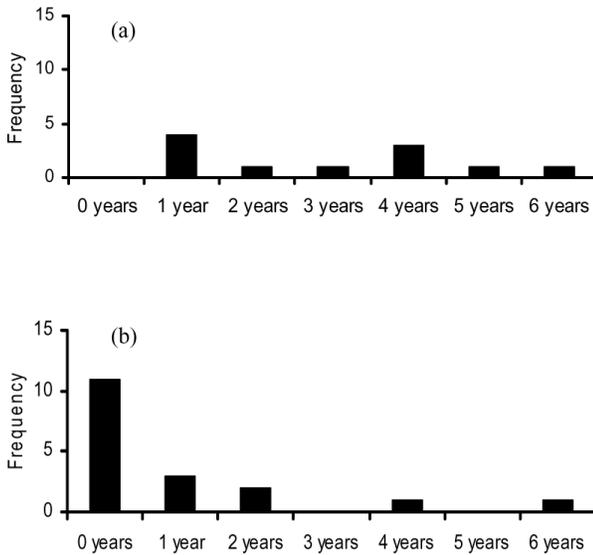
stoats collected in beech forest were young of the year, 16% were one-year-olds, and 22% were  $\geq 2$  years old ( $n=18$ ; Fig. 3b).

The percentages of the alpine grassland sample population classified as juvenile was 44% in 2003 (4 of 9), 47% in 2004 (8 of 17) and 0% in January 2005 (0 of 12). In beech forest the percentages were 38% in 2003 (6 of 15), 40% in 2004 (6 of 15) and 61% in January 2005 (11 of 18). The January 2005 field season consisted of just 5 days of trapping in each habitat, meaning that these values are not directly comparable with the other years (where trapping went on for  $>10$  days in each habitat).

#### Weight

The only year that 95% confidence intervals on adult male weights did not overlap between habitats was 2003, when the weight of adult male stoats in alpine grassland sites was on average higher than in beech forest sites (Table 3). Two male stoats in alpine grassland weighed  $>400$  g that year, making them the heaviest stoats observed during this study. Confidence intervals were often large in 2004 and 2005, which is likely a result of the small sample sizes. The mean weights observed for adult male stoats exceeded the Fiordland average of  $303 \pm 10.11$  g but were consistent with the New Zealand average of  $324 \pm 2.63$  g (King & Murphy 2005).

The mean weight of adult female stoats in 2005 did not differ significantly between the two habitats, based on overlapping 95% confidence intervals. The heaviest



**Figure 3.** Ages of stoats (derived from cementum analysis) collected in 2005: (a) in alpine grasslands ( $n = 11$ ), (b) in beech forest ( $n = 18$ ).

**Table 3.** Mean weights (g) of adult stoats live-trapped in the Borland Valley between 2003 and 2004. Beech = beech forest, Alpine = alpine grassland.

	Adult males 2003		Adult males 2004		Adult males 2005		Adult females 2005	
	Beech ( $n = 4$ )	Alpine ( $n = 3$ )	Beech ( $n = 3$ )	Alpine ( $n = 5$ )	Beech ( $n = 2$ )	Alpine ( $n = 3$ )	Beech ( $n = 3$ )	Alpine ( $n = 7$ )
Mean	310.0	406.7	369.3	334.6	360	307.5	240.8	218.9
SD	60.6	30.6	24.8	45.0	17.7	69.3	11.6	29.3
95% CI	250–369	376–437	341–397	295–374	336–385	229–386	227–255	197–241

female (272.5 g) observed during this study was caught in alpine grassland). Mean adult female weights in both alpine grassland and beech forest in 2005 (Table 3) exceeded both the Fiordland ( $200 \pm 3.32$  g) and New Zealand ( $207 \pm 1.52$  g) averages.

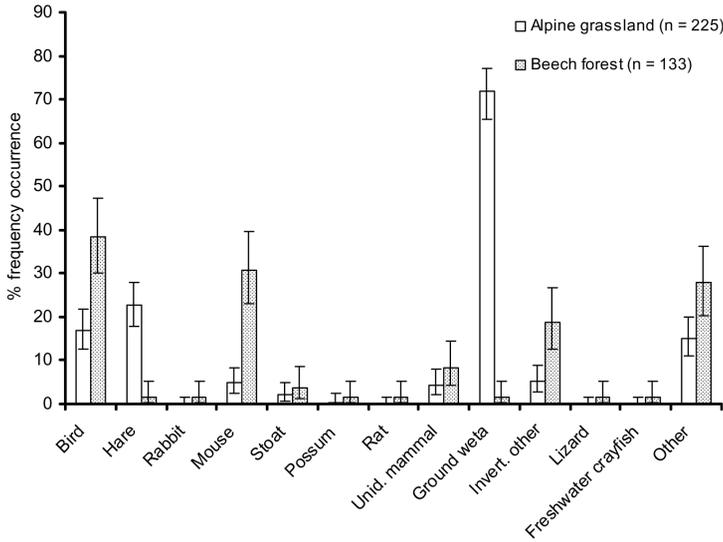
### Diet

Over the three summers 225 diet samples were collected from the alpine grassland sites (213 scats and 12 stomachs) and 133 from the beech forest sites (111 scats and 22 stomachs). The sample size of scats was much larger in alpine grasslands because more fieldworker hours were spent in that habitat and more live trapping was undertaken there (see Methods).

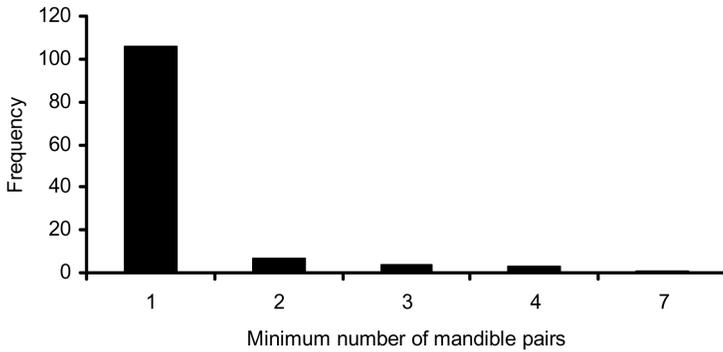
The percentage frequency occurrence of the different prey categories indicate that the diet of stoats inhabiting alpine grassland sites differed substantially from that of stoats in the beech forest sites (Fig. 4). The five most common prey types in the diet were ground weta, birds,

mice, hares and 'invertebrate other'. Ground weta occurred in 72% of samples from alpine grasslands, but in only 1.5% of beech forest samples. Hares occurred in 23% of samples from alpine grasslands, but in only 1.5% of beech forest samples. Birds, mice and 'invertebrate other' were more common in beech forest samples, occurring in 39%, 31% and 19% of samples respectively, compared with 17%, 5% and 5% in alpine grassland samples. Prey items allocated to the 'invertebrate other' category included the following orders: Orthoptera (grasshoppers), Coleoptera, Lepidoptera, Hymenoptera, Diptera and Arachnida. Another notable difference was the 'other' category, which was recorded in 28% of beech forest samples but only in 15% of alpine grassland samples. Items recorded as 'other' included leaves, wood, seed, moss, sand, grass and stones.

Habitat was a significant predictor of frequency of occurrence of ground weta, birds and mice ( $P < 0.05$ ; Table 4). Habitat was not a significant predictor of hare



**Figure 4.** Diet of stoats in alpine grasslands and beech forest. Data are combined for sites within each habitat, across all years (2003, 2004 and 2005). Vertical bars are 95% binomial confidence intervals.



**Figure 5.** Minimum frequency of ground weta in stoat scats and stomachs, as estimated by counting mandible pairs.

**Table 4.** Logistic regressions relating the probability of the five most common prey types identified in stoat diet to the independent variables habitat and year. Each prey type was regressed separately (all regressions had 356 d.f.). Significant values are in bold.

Dependent variable	Model	Estimate	SE	Z value	P
Ground weta	Habitat	-7.6	2.8	-2.7	0.00
	Year	-1.0	1.2	-0.9	0.38
	Habitat:Year	1.1	1.1	1.0	0.31
Mouse	Habitat	2.0	1.0	2.1	0.04
	Year	-0.7	0.9	-0.8	0.45
	Habitat:Year	0.0	0.5	0.1	0.94
Hare	Habitat	-3.6	2.0	-1.8	0.07
	Year	-0.4	1.0	-0.4	0.67
	Habitat:Year	0.4	0.9	0.4	0.71
Bird	Habitat	1.7	0.7	2.3	0.02
	Year	0.5	0.5	0.8	0.40
	Habitat:Year	-0.3	0.3	-0.8	0.41
Invertebrate other	Habitat	2.5	1.5	1.7	0.09
	Year	1.6	1.1	1.5	0.14
	Habitat:Year	-0.4	0.6	-0.6	0.55

or 'invertebrate other' ( $P = 0.07$  and  $0.09$  respectively). Neither year nor the interaction between habitat and year were significant predictors of frequency of occurrence of these five common prey types (Table 4).

Seven individual ground weta were found in each of two diet samples, but only one individual was identified in most samples (Fig. 4). Although stoat scats often contain more than one prey item, notably, 44% of all alpine grassland diet samples contained only ground weta remains and 31% of all beech forest diet samples contained only bird remains (Table 5). 'Invertebrate other' was the only prey category never to occur by itself in a single sample.

## Discussion

Our observations do not support the hypothesis that alpine grassland at the Borland Valley is an inferior habitat for stoats compared with adjacent beech forest. Stoat density was similar in both habitats, and observed survival was similar in both habitats during winter 2003 but was higher in alpine grassland than in forest during winter 2004. Because probability of capture was not estimated, we are cautious about interpreting this as meaning survival was lower in the beech forest in winter 2004, as the probability of recapture may have been lower in beech forest for unknown reasons. However, three stoats marked in 2003 in our alpine grassland sites were recaptured in 2005, whereas no stoats marked at our beech forest sites in 2003 were recaptured in 2005. Although sample sizes are small, cementum analysis showed a reasonably even cross section of age classes in the alpine grassland population, whereas the beech forest population seemed to be more strongly represented by the younger age classes (Fig. 3); this result also suggests adults survived longer in alpine

grassland compared with beech forest. In addition, stoats in alpine grasslands were often large, weighing near or above mean weights observed for stoats elsewhere in Fiordland; suggesting that they were not in poor condition. The use of alpine areas by stoats is not surprising, given that in Europe and North America stoats are widespread in arctic tundra habitats (Aspšov & Popov 1940; Simms 1979; Debrot & Mermod 1983).

The proportion of juveniles captured was similar in the two habitats in 2003 and 2004 suggesting similar summer recruitment. The zero catch of juveniles in 2005 is difficult to interpret because trapping was done only during 5 days in January, and it is possible that juveniles may have been caught in alpine grassland had trapping been continued throughout the remainder of the summer).

### Diet of stoats in alpine grassland

The frequency of ground weta observed in the diet of stoats in alpine grasslands at the Borland Valley is the highest occurrence of invertebrates recorded in any published stoat diet study (King & Powell 2007, pp. 97–112). Weta occurred far more often in the stoat diet compared with hare, the second most frequent prey. Ground weta are relatively large (15–22 mm) and are widespread but patchily distributed throughout New Zealand (Johns 2001). At the Borland Valley they appear to be a staple prey for stoats inhabiting alpine grasslands, not just because of the high frequency with which they occurred in diet samples, but also because nearly half of all the samples from alpine grasslands contained solely ground weta (Table 5). As many as seven ground weta were observed in some samples. Although one might expect hares (or leverets) to provide a better meal for stoats, compared with weta, only 9% of diet samples contained solely hare. Hares are certainly less abundant than ground weta in alpine grasslands at the Borland Valley, and adult hares

**Table 5.** Frequency of prey in stoat diet. Also showing for each prey type, the percentage of diet samples that contained only that prey type (Only this prey) and percentage of all samples containing this prey type that contained only this prey type (All samples with this prey).

Prey Type	Frequency of occurrence (%)	Only this prey (%)	All samples with this prey (%)
Alpine grassland	( $n = 225$ )		
Ground weta	72	44	60
Hare	23	9	41
Bird	17	5	29
Mouse	5	3	63
Beech forest	( $n = 133$ )		
Bird	39	31	80
Mouse	31	23	73
Invertebrate other	19	0	0

may be difficult for stoats to kill, although a single hare might provide multiple meals.

King and Powell (2007, p. 135) have suggested the high energy requirements of stoats means that stoat populations cannot be maintained on insects, which are an inadequate substitute for the small mammals that are common prey for stoats in the Northern Hemisphere. Our results suggest that in alpine grasslands at the Borland Valley large invertebrates are a key prey resource, enabling stoats to persist in this habitat at densities similar to those in adjacent beech forest, where they eat vertebrate prey. Smaller invertebrates may be less important than weta in stoat diet, as 'invertebrate other' never occurred by itself in a diet sample. This persistence on invertebrates does not seem to have compromised the body weight of stoats, as the average weights of both males and female exceeded the Fiordland National Park average, and some individual males weighed more than the New Zealand average. However, we measured the frequency of prey remains in scats and stomachs, and further research will be needed to assess the relative biomass of each prey species consumed. This will require an understanding of (1) how many meals a stoat typically takes from a hare (2) how many weta a stoat typically consumes in a single foraging session (3) and how long these different prey species persist in the stomach.

Ground weta were prominent in stoat diet in two other alpine studies (Lavers & Mills 1978; Smith et al. 2005). The two species of ground weta identified from stoat stomachs in the Murchison Mountains were *Hemiandrus focalis* and *H. madisylvestris* (Smith et al. 2005), whereas *H. maculifrons* were the predominant species of ground weta in alpine grasslands at the Borland Valley (Smith 2006). It would be interesting to explore the distribution of different species of ground weta and whether they define stoat distribution in alpine areas. One major difference between the Borland Valley and the Murchison Mountains is that no hares have been recorded in the Murchison Mountains (D. Crouchley pers. comm.). Further research will be necessary to determine whether stoat survival and abundance differs in alpine grassland sites with and without hares.

Predation of ground weta by stoats in alpine grasslands in the Borland Valley appears to be frequent, and ground weta are also eaten by mice in alpine grasslands in the Borland Valley (Wilson et al. 2006). We do not know what fraction of the population is taken, as ground weta density in alpine grassland is unknown. Whether the life-history strategy of species such as *Hemiandrus maculifrons* enables their populations to sustain such predation needs to be urgently assessed.

### Diet of stoats in beech forest

We found that birds were a common prey of beech forest stoats. Others have also shown that birds are common prey of stoats in beech forests outside of heavy beech seedfall

years (King & Moody 1982; Murphy & Dowding 1994, 1995). Mice were also common in the diet of forest stoats in all three summers. This result contrasts with that of Murphy & Dowding (1995), who did not detect mice in the stomachs ( $n=26$ ) and scats ( $n=44$ ) of stoats collected from a beech forest site in northern Fiordland between October 1991 and May 1992. It therefore appears that in years without heavy beech seedfall the presence of mice in the diet of beech forest stoats is highly variable between sites.

Purdey et al. (2004) also found that birds were the most frequent prey in the stomach contents of 63 stoats caught in January 2001 along the Borland Road verge, but otherwise their results differed from ours. In particular, in that study possum remains were more common than rodents in the stomachs, and rats were more common than mice. Remarkably, Coleoptera occurred in 35% of the stomach samples in that study; we grouped these in 'invertebrate other'. There may be a temporal explanation for these differences, e.g. seasonally fluctuating food supplies, or they may be site specific. In particular, possums are poisoned regularly along the Borland Road, and are also common as roadkill (D. Smith, pers. obs.) so their carcasses may have been more readily available there than in the areas we sampled, which were well away from the road.

### Stoat diet in alpine grassland vs beech forest

These results show clear differences in stoat diet between alpine grasslands and low-altitude mountain beech forest in the Borland Valley. During this study, mice were less abundant in alpine grasslands than in low-altitude beech forest (Smith 2006; Wilson et al. 2006). The most common birds in the Borland area are native and introduced Passeriformes, which were seen more often in the beech forest than in alpine grassland (D. Smith, pers. obs.). Thus it is likely there were fewer mice and birds available as prey for stoats in alpine grasslands than in the low-altitude beech forest. But stoats in alpine grasslands had two additional prey types available to them, ground weta and hares, that were not available to beech forest stoats (Smith 2006).

Stoats in alpine grassland at the Borland Valley appeared to select that habitat over adjacent beech forest (Smith et al. 2007). Perhaps these stoats deliberately selected alpine grasslands in order to feed on ground weta and hares, and not because they were forced out of beech forest by other stoats and had to eat what was available. Because this study was confined to the Borland Valley, further research is needed to see whether these patterns occur in other alpine areas in New Zealand.

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## References

- Alley JC, Berben PH, Dugdale JS, Fitzgerald BM, Knightbridge PI, Meads MJ, Webster RA 2001. Responses of litter-dwelling arthropods and house mice to beech seeding in the Orongorongo Valley, New Zealand. *Journal of the Royal Society of New Zealand* 31: 425–452.
- Aspisov DI, Popov VA 1940. Factors determining fluctuations in the numbers of ermines. Reprinted in: King CM ed. 1980. *Biology of mustelids: some Soviet research*. DSIR Bulletin 227 (Vol. 2): 109–131.
- Brunner H, Coman BJ 1974. *The identification of mammalian hair*. Australia, Inkata Press. 176 p.
- Day MG 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Journal of Zoology* 148: 201–217.
- Debrot S, Mermod C 1983. The spatial and temporal distribution pattern of the stoat (*Mustela erminea* L.). *Oecologia* 59: 69–73.
- Dilks P, Willans M, Pryde M, Fraser I 2003. Large scale stoat control to protect mohua (*Mohoua ochrocephala*) and kaka (*Nestor meridionalis*) in the Eglinton Valley, Fiordland, New Zealand. *New Zealand Journal of Ecology* 27: 1–9.
- Efford M 2004. Density estimation in live-trapping studies. *Oikos* 106: 598–610.
- Efford MG, Dawson DK, Robbins CS 2004. DENSITY: software for analysing capture–recapture data from passive detector arrays. *Animal Biodiversity and Conservation* 27(1): 217–228.
- Elliott GP 1996. Productivity and mortality of mohua (*Mohoua ochrocephala*). *New Zealand Journal of Zoology* 23: 229–237.
- Elliott GP, Dilks PJ, O'Donnell CFJ 1996. The ecology of yellow-crowned parakeets (*Cyanoramphus anriceps*) in *Nothofagus* forest in Fiordland, New Zealand. *New Zealand Journal of Zoology* 23: 249–265.
- Fitzgerald BM, Gibb JA 2001. Introduced mammals in a New Zealand forest: long-term research in the Orongorongo Valley. *Biological Conservation* 99: 97–108.
- Grue HE, King CM 1984. Evaluation of age criteria in New Zealand stoats (*Mustela erminea*) of known age. *New Zealand Journal of Zoology* 11: 437–443.
- Johns PM 2001. Distribution and conservation status of ground weta, *Hemiandrus* species (Orthoptera: Anostomatidae). *Science for Conservation* 180. Wellington, Department of Conservation. 25 p.
- Johnson DH 1999. The insignificance of statistical significance testing. *Journal of wildlife management* 63: 763–772.
- King CM 1983. The relationship between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52: 141–166.
- King CM 2002. Cohort variation in the life-history parameters of stoats *Mustela erminea* in relation to fluctuating food resources: a challenge to boreal ecologists. *Acta Theriologica* 47: 225–244.
- King CM, Edgar RL 1977. Techniques for trapping and tracking stoats (*Mustela erminea*); a review, and a new system. *New Zealand Journal of Zoology* 4: 193–212.
- King CM, McMillan CD 1982. Population structure and dispersal of peak-year cohorts of stoats (*Mustela erminea*) in two New Zealand forests, with especial reference to control. *New Zealand Journal of Ecology* 5: 59–66.
- King CM, Moody JE 1982. The biology of the stoat (*Mustela erminea*) in the National Parks of New Zealand II: Food habits. *New Zealand Journal of Zoology* 9: 57–80.
- King CM, Murphy EC 2005. Stoat. In: King CM ed. *New Zealand handbook of mammals*, 2nd edn. Melbourne, Oxford University Press. Pp. 261–287.
- King CM, Powell RA 2007. The natural history of weasels and stoats: ecology, behaviour and management. 2nd edn. New York, Oxford University Press. 446 p.
- King CM, Griffiths K, Murphy EC 2001. Advances in New Zealand mammalogy 1990–2000: Stoat and weasel. *Journal of the Royal Society of New Zealand* 31: 165–183.
- King CM, White PCL, Purdey DC, Lawrence B 2003. Matching productivity to resource availability in a small predator, the stoat (*Mustela erminea*). *Canadian Journal of Zoology* 81: 662–669.
- Lavers RB, Mills JA 1978. Stoat studies in the Murchison Mountains, Fiordland. In: *Seminar on the takahe and its habitat*. Wildlife Service, Department of Internal Affairs, Invercargill.
- Lawrence BL, Dilks PJ 2000. Effectiveness of diphacinone to control stoat populations. *Conservation Advisory Science Notes* No. 306. Wellington, Department of

- Conservation. 12 p.
- McLennan JA, Potter MA, Robertson HA, Wake GC, Colbourne R, Dew L, Joyce L, McCann AJ, Miles J, Miller PJ, Reid I 1996. Role of predation in the decline of kiwi, *Apteryx* spp., in New Zealand. *New Zealand Journal of Ecology* 20: 27–35.
- Murphy EC, Dowding JE 1994. Range and diet of stoats (*Mustela erminea*) in a New Zealand beech forest. *New Zealand Journal of Ecology* 18: 11–18.
- Murphy EC, Dowding JE 1995. Ecology of the stoat in *Nothofagus* forest: Home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology* 19: 97–109.
- O'Donnell CFJ, Phillipson SM 1996. Predicting the incidence of mohua predation from the seedfall, mouse, and predator fluctuations in beech forests. *New Zealand Journal of Zoology* 23: 287–293.
- O'Donnell CFJ, Dilks PJ, Elliott GP 1996. Control of a stoat (*Mustela erminea*) population irruption to enhance mohua (yellowhead) (*Mohoua ochrocephala*) breeding success in New Zealand. *New Zealand Journal of Zoology* 23: 279–286.
- Pollock KH, Nichols JD, Brownie C, Hines JE 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107: 1–97.
- Powell RA, King CM 1997. Variation in body size, sexual dimorphism and age-specific survival in stoats, *Mustela erminea* (Mammalia: Carnivora), with fluctuating food supplies. *Biological Journal of the Linnean Society* 62: 165–194.
- Purdey DC, King CM, Lawrence B 2004. Age structure, dispersion and diet of a population of stoats (*Mustela erminea*) in southern Fiordland during the decline phase of the beechmast cycle. *New Zealand Journal of Zoology* 31: 205–225.
- Reynolds JC, Aebischer NJ 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review* 21: 97–122.
- Simms DA 1979. North American weasels: resource utilization and distribution. *Canadian Journal of Zoology* 57: 504–520.
- Smith DHV 2006. Movements, population dynamics and predatory behaviour of stoats inhabiting alpine grasslands in Fiordland. Unpublished PhD thesis, University of Otago, Dunedin, New Zealand. 225 p.
- Smith DHV, Jamieson IG 2005. Lack of movement of stoats (*Mustela erminea*) between *Nothofagus* valley floors and alpine grasslands, with implications for the conservation of New Zealand's endangered fauna. *New Zealand Journal of Ecology* 29: 45–52.
- Smith DHV, Jamieson IG, Peach RME 2005. Importance of ground weta (*Hemiandrus* spp.) in stoat (*Mustela erminea*) diet in small montane valleys and alpine grasslands. *New Zealand Journal of Ecology* 29: 207–214.
- Smith DHV, Wilson DJ, Moller H, Murphy EC, van Heezik Y 2007. Selection of alpine grasslands over beech forest by stoats (*Mustela erminea*) in montane southern New Zealand. *New Zealand Journal of Ecology* 31: 88–97.
- Wilson DJ, McElrea GJ, McElrea LM, Heyward RP, Peach RME, Thomson C 2006. Potential conservation impacts of high-altitude small mammals: a field study and literature review. DOC Research & Development Series 248. Department of Conservation, Wellington, New Zealand. 51 p.
- Wilson PR, Karl BJ, Toft RJ, Beggs JR, Taylor RH 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological Conservation* 83: 175–185.
- Zar JH 1996. *Biostatistical analysis*. 3rd edn. New Jersey, Prentice-Hall. 662 p.

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