NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

Stable isotope analysis reveals variable diets of stoats (*Mustela erminea*) in the alpine zone of New Zealand

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Published online: 22 July 2020

Abstract: The alpine zone of New Zealand covers c. 30% of public conservation land and is home to a high diversity of endemic species. Predation by introduced stoats (*Mustela erminea*) is identified as a major threat to alpine fauna. However, a lack of biological information, such as what stoats eat in different settings, hinders efforts to focus control measures in time and space in order to achieve the greatest conservation gains. We used a biochemical tool, stable isotope analysis, to estimate stoat diet across three time-periods in the alpine zone of three national parks. We then assessed possible drivers of dietary variation that could lead to greater per capita consumption of native species by stoats. Our models indicate that mammal prey items formed the largest contribution to the metabolic requirements of stoats in long-term estimates (47–90%), but the mid-term (spring and summer) estimates show a greater reliance on insects. The estimated proportions of prey consumed did not differ with elevation, sex, or age, but were significantly different between sites and seasons. Both stoat and ship rat (*Rattus rattus*) abundance were significant in explaining the proportion of mammals consumed. Higher stoat trap-catch and an absence of ship rats at one site (Nelson Lakes National Park) coincided with a greater range of prey being regularly consumed by stoats; this was the only site to record substantial proportions of birds (26%) and skinks (33%) in stoat diet. Conservation managers should be aware of the potential for marked differences in per capita rates of consumption of threatened alpine species by stoats, possibly linked to differences in abundance of mammalian prey. While this study confirms that stable isotope analysis can be useful to assess the diet of stoats, further research is needed to determine specific isotope enrichment values and to confirm the accuracy of these results.

Keywords: alpine, diet, invasive species, *Mustela erminea*, predation, SIA, stoat, stable isotope analysis

Introduction

Native taxa inhabiting alpine areas are threatened globally by a range of largely anthropogenic threats (Nagy 1997; Pauli et al. 2003; Dirnböck et al. 2011; Franzén & Molander 2012; Chamberlain et al. 2016). Despite being well represented in the proportion of land under legal protection globally (Kollmair et al. 2005), alpine areas lag behind in terms of realised action to prevent biodiversity loss. The alpine zone of New Zealand reflects these trends: c. 11% of New Zealand and over 30% of its public conservation land is above the natural timberline (Ministry for the Environment 2010; O'Donnell et al. 2017). This area contains a high diversity of endemic species and accordingly 700 000 hectares of land in 14 different alpine ecosystem types has been highlighted for priority conservation management (Department of Conservation 2018a).

In New Zealand's forest, river, coastal, and wetland habitats, introduced mammalian predators pose significant risks to native fauna (King et al. 2010). Alpine ecosystems have been assumed to be relatively safe from the effects of introduced predators (Lavers & Mills 1978). However, stoats (*Mustela erminea*) have been identified as the primary agents in the decline of rock wren (*Xenicus gilviventris*), and are predators of takahē (*Porphyrio hochstetteri*), kea (*Nestor notabalis*), kiwi (*Apteryx* spp), and kākāpō (*Strigops habroptilus*) in the alpine zone, as well as consuming large numbers of alpine invertebrates (O'Donnell et al. 2017; Weston et al. 2018). Despite this, there is limited understanding of the drivers of predation risk in alpine New Zealand, and no best practice tools exist for management of invasive species threatening alpine fauna (O'Donnell et al. 2017). This lack of biological knowledge confounds efforts to assess or to mitigate extinction risks faced by alpine species (Franzén & Molander 2012).

Likelihood of predation can be understood as a combination of the numerical and functional responses of predators to their environment, i.e. predator abundance and the per capita rate at which they eat a given prey type (Murphy et al. 1998; Joly & Patterson 2003). Work is underway to understand drivers of

DOI: https://dx.doi.org/10.20417/nzjecol.44.16

numerical fluctuations in small mammals in the New Zealand alpine zone (Department of Conservation, unpubl. data). In order to fully assess the threat posed by predation, managers also require reliable information on the functional response of stoats in alpine environments, including diet and factors that mediate dietary variation.

Previous data on stoat diet in the New Zealand alpine zone can be extracted from four published studies: one in the Kaikōura Ranges in Marlborough (Cuthbert et al. 2000), and three in Fiordland National Park (Lavers & Mills 1978; Smith et al. 2005; Smith et al. 2008). The Fiordland work shows a strong reliance by stoats on alpine invertebrates, especially ground wētā *Hemiandrus* spp. However, this and previous data are from summer periods (Smith et al. 2005), during which invertebrates are more active, emergent, and potentially available to stoats; these data might not be reflective of stoat diet during other seasons. The Kaikōura Range study (Cuthbert et al. 2000) covers some seasonal variation (spring to autumn) and is focussed on a large shearwater (*Puffinus huttoni*) colony (> 100 000 birds) in the Kaikōura Ranges. This abundant food source drives a 'hyperabundance' of predators at that site, limiting the applicability to other alpine areas.

In non-alpine environments in southern New Zealand low abundance of small mammals has been associated with high rates of invertebrate consumption by stoats (Murphy et al. 1995), with invertebrates present in up to 90% of stoat stomachs sampled (Murphy et al. 2016). However, preliminary unpublished data, from a sample of 20 stoats collected by community trapping organisations in the northern South Island, show a different stoat diet composition. Invertebrates were present in just 5% of stomach samples collected (n = 20) in the alpine area of Kahurangi National Park (M. Milne, Friends of the Cobb, unpubl. data). The timberline ecotone in the southern South Island is around 500 metres lower than the same ecotone in northern South Island. The abundance of ship rats (*Rattus rattus*), an important stoat prey item, may decrease with elevation (Christie et al. 2017), but it's unknown how this might vary with latitude, or how changes in rat abundance might affect stoat diet.

Stoat diet is also highly variable within their native range in the Northern Hemisphere. Several studies in alpine areas record substantial proportions of stoat prey items not reported in other systems, including fruit (Martinoli et al. 2001) and beetles (Hernández & Zaldívar 2016). In one study, fruit and invertebrates replaced small mammals in stoat diet at higher elevation; stoats in the upper valleys of Cantabria, Spain, consumed a far smaller proportion of small mammals compared with stoats at lower elevations (12% frequency of occurrence, compared to 56% and 77% in the middle and lower valley, respectively) (Hernández & Zaldívar 2016). Yet, at similar or greater elevations in the nearby Pyrenees mountains, stoats do not commonly prey on insects. Instead small mammals constitute 98% of their diet (Leconte 1984, cited in Hernández & Zaldívar 2016). Stoat diet has also been shown to vary with age class and sex (King et al. 2010), but it's uncertain how these data apply to stoats in the alpine zone of New Zealand.

The cryptic biology and low densities of stoats, which severely limit sample sizes (Smith 2006), means no study has yet been able to provide spatial and temporal replication of dietary data from the alpine zone. This lack of information about spatial and temporal variation inhibits the ability of conservation managers to apply their findings to wider areas, or to examine common factors correlated to stoat diet. Collection of such data allows estimation of the per capita rate of consumption of native species under differing ecological settings. Our study uses a biochemical tool, stable isotope analysis (SIA), to greatly expand our ability to assess the diet of alpine stoats, examining diet at three sites across three time-periods. We aimed to document how the diet of stoats varies across the alpine zone, and to examine drivers of variation, including season, latitude, and availability of ship rats as prey.

Methods

Study sites and stoat collection

This study was conducted in the alpine zone (above the natural timberline) of Nelson Lakes National Park, Mt Aspiring National Park and Fiordland National Park across the South Island of New Zealand (Fig. 1). Sites range from 750 to 2053 m above sea level, and are a mix of alpine grasslands, sub-alpine scrub, rock, scree, and herb and cushion field vegetation, located above large tracts of beech forest (Nothofagaceae). Each site has an existing network of mustelid kill-traps run by the Department of Conservation (DOC), and/or local community groups, for the protection of alpine fauna. Trapping effort and intensity vary between each site (Table 1).

DOC staff, local contractors, and volunteers returned stoat carcasses caught within the study areas. Stoat and rat trap-catch data are expressed as catch per 100 trap nights of all traps above the timberline, after correcting for sprung

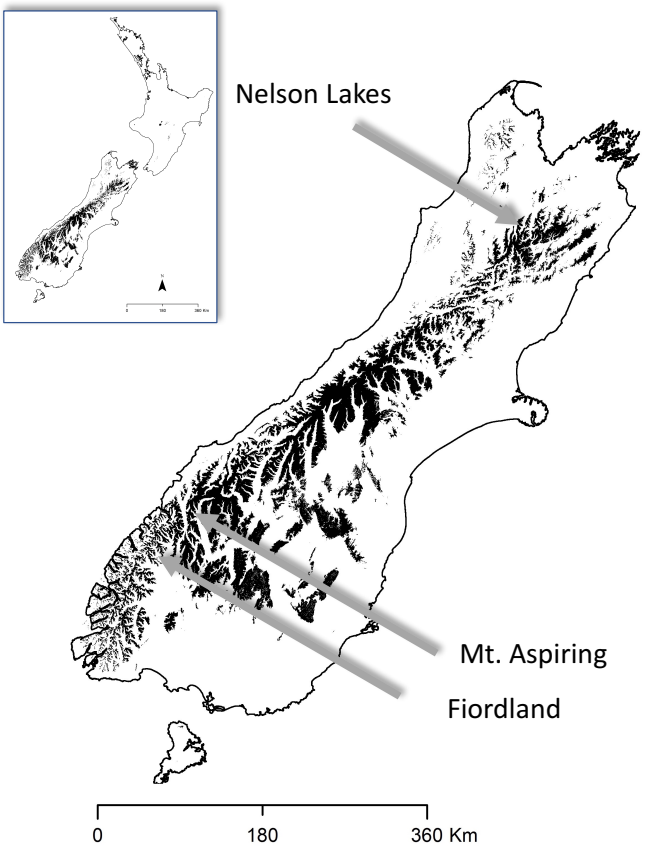

Figure 1. Locations where stoats were caught for use in this study. Nelson Lakes, Mt Aspiring and Fiordland National Parks. Shading shows the estimated extent of the alpine zone, modified with permission from O'Donnell et al. (2017).

Table 1. Detail of trapping regime at Study Sites.

Site Name	Description	Elevation (m a.s.l)	Traps checked	Bait	Prey sampling location
Nelson Lakes National Park	171 single set DOC 200[1] traps along St Arnaud Range and spurs ~1–3 kms apart. Covering of 901 hectares	1350–1880	Monthly December to May	Single chicken[2] egg or Erayz™ block[3]	Rainbow Ski field Lat: −41.16910; Long: 172.62246
Mt Aspiring National Park[4]	446 double-set DOC 150 and 200 traps across ridges, spurs and tracks along the Routeburn track covering 2901 hectares	958–1760	Monthly October to May, avalanche dependant	3 cm cube of fresh rabbit[5] meat or an Erayz™ block and a single chicken egg	Harris Basin Lat −44.727314; Long168.173389
Fiordland National Park	348 double-set DOC 150 traps along alpine areas of Murchison Mountains special takahē area, covering 5237 hectares	950–1680	May, November & February only	3cm cube of fresh rabbit meat and a single chicken egg	Plateau Creek Lat: −45.24064; Long: 167.53034

[1]Trap design: Peters & Waddington 2004
[2]*Gallus gallus domesticus*
[3]Connovation Ltd, Auckland, New Zealand
[4]Site straddles park boundary for both Mt Aspiring and Fiordland National Parks, for similicity is hereafter Mt Aspiring NP
[5]*Oryctolagus cuniculus*

traps (c $100CTN^{-1}$) (Nelson & Clark 1973). We used ArcGIS (Esri 2011) to apply a 25 m resolution digital elevation model (Columbus et al. 2011) to GPS points for all trap locations to determine trap elevation for each capture. Areas covered by trapping operations were calculated as the area of alpine terrain (as defined by the Land Information New Zealand Landcover Database) within 200 m of a stoat trap.

Beech and Tussock Masting

Beech forests adjacent to all study sites produced seed in the study period. DOC data shows beech masting was widespread, yet variable, throughout the South Island in autumn 2016 (Department of Conservation 2018b). A full mast (> 4000 seeds m^{-2}; Wardle 1984) was recorded at beech forest adjacent to the Fiordland NP site, while sites adjacent to the Nelson Lakes and Mt Aspiring NP sites recorded a partial mast (500–4000 seeds m^{-2}: Wardle 1984). It is unknown how increased stoat or rodent densities in beech forests might affect densities in adjacent alpine areas.

In 2016 DOC monitored tussock grass (*Chionochloa* spp.) flowering at seven sites around the South Island. Tussock flowering in 2016 was widespread, with some flowering recorded at all monitored sites except South Westland. Average flowering tillers per tussock (of 100 plants per species, spread over five transects) ranged from 0 to 4.7 (mean = 2.0) (DOC, unpubl. data). These levels fall well below the peak mean flowering of 57 flowers per tussock observed by Wilson & Lee (2010) and below strong mast years reported for four long running datasets of *Chionochloa pallens* (Kelly et al. 2000). Data are not available for the Nelson Lakes and Mt Aspiring NP sites, but as the intensity of tussock flowering is synchronous among sites several hundred kilometres apart (Kelly et al. 2008), we can infer that tussock at these sites also likely flowered to some extent.

Prey collection

We visited one locality within each study site (Table 1) to collect samples of the potential prey species available to stoats. Prey were selected based on previous research on the diet of alpine stoats, both in New Zealand (Smith et al. 2005), and abroad (King et al. 2010). We caught house mice (*Mus musculus*) in lines of Victor snap traps (Woodstream Corporation, 69 N. Locust St. Lititz, PA, USA) baited with peanut butter and rolled oats, laid at 20 m intervals in alpine grasslands, and collected carcasses of ship rats opportunistically from the networks of mustelid traps described above. We caught a representative selection of local alpine passerines (for species see Appendix S1 in Supplementary Materials) and sampled < 1 ml of whole blood from each bird by brachial venepuncture. We then smeared blood on cleaned glass microscope slides for air drying (as Hobson et al. 1997).

We hand-collected insects, chiefly wētā (*Hemiandrus* and *Hemideina* spp) and grasshoppers (*Sigaus* spp.) from tussock, scree and herb cushion fields. We hand-collected tussock grass seeds and the fruit of alpine plants based on their availability during field visits. Samples of beech seed were obtained from DOC beech seed-monitoring funnels in beech forest adjacent to each study site. Feathers dropped by ground birds were collected opportunistically in the study area, except those of takahē. Short sections of wing covert were provided by the DOC takahē recovery programme from dead takahē recovered from the Fiordland National Park study area between 2013 and 2016. We engaged a professional contract hunter (Huntsman Ltd, Te Anau) to shoot European hares (*Lepus europaeus*), in the alpine zone of Mt Aspiring NP only. Hare samples from Mt Aspiring were also used as a proxy for other sites with hares present. We stored mouse, rat, hare and insect samples on ice then frozen for transport and storage. We stored fruit, seed, dried blood and feathers in paper envelopes and slide cases.

Stoat dissection

In the laboratory, we determined the sex of mustelids by the presence of a baculum or visible nipples (King & Moody 1982). Stomach, gut, and rectum (hereafter: stomach contents) were examined visually and under a binocular microscope (10–40×). For each stomach, different prey types were recorded as present or absent, and as the proportion of the total contents using a petri dish marked into sections. We used prey categories described in Smith et al. (2008) and included empty stomachs where no prey remains were present. It was beyond the scope

of this study to differentiate hare, rat, and mouse hair within the stomachs of stoats caught; all were recorded as mammal.

We determined the age of stoats by counting annular cementum rings of mandibular canine teeth and compared these to a reference collection of known-age stoats (Grue & King 1984). One canine from each individual was immersed in fixative (2 days) and de-calcifying fluid (2-4 days until no calcium residue was seen in the solution). Teeth were then washed in distilled water, embedded in a cryomatrix mould, and frozen at −80°C. Twelve micron slices were cut by running samples through a cryotome (temperatures = cryobar −50°C, chamber −25ºC, specimen −16ºC). Sections were air dried on microscope slides then immersed in distilled water (two minutes) and stained with haemotoxin (three minutes). Haemotoxin stain was then washed out with distilled water, and slides were dehydrated in 95% ethanol (two minutes), 100% ethanol (two minutes), and put through three xylene washes (two minutes/wash). Samples were then set with Entellan® mounting medium and a coverslip and dried overnight before observation. A nominal birth date of 1 October was assigned to all stoats. Cementum annuli were then scored visually at 100× and 400× magnifications by an independent observer and compared with the known-age stoat teeth obtained by Grue and King (1984).

Stoat tissue

Trophic Enrichment Factors

As different tissue types metabolise isotopes at different speeds, simultaneous analysis of several tissue types allows comparison of the diet of one individual between different time periods (Dalerum & Angerbjörn 2005). We selected suitable tissues based on the unique time periods of interest they represented, and the availability of trophic enrichment factors (TEFs; see below). Collagen represents the long-term diet (over many months), whereas liver is indicative of diet over a short-term period of only days (Dalerum & Angerbjörn 2005). Claw represents a mid-term dietary estimate. Although the growth of nail or claw tissue is a linear process (Orentreich et al. 1979), the exact growth rate of stoat claws (and therefore the period of diet represented by claw tissue) is not known. Claws of captive ferrets (*Mustela pustoria*) grow at between 4–10% of their length per day (Bleavins et al. 1982); beaver (*Castor canadensis*) claws at 0.12 mm day^{-1} (summer mean) (Severud 2011), and domestic cat (*Felis catus*) claws at 0.27 mm day^{-1} (Homberger et al. 2009). The 2 mm claw sections sampled here represent the period of diet shortly before the animal's death, likely between 1–10 weeks.

A TEF or discrimination value is a species- and tissue-specific value indicating the rate at which a given species metabolises isotopes into different tissues. We applied these values to stable isotope mixing models (below) to correct for this variable fractionation rate. Experimental work has not yet been conducted to determine TEFs for stoat tissues. We therefore used TEFs from another small-bodied mammalian hyper-carnivore, arctic fox (*Vulpes lagopus*). Liver C^{13} 0.57 ± 0.19 ‰, N^{15} 2.40 ± 0.47 ‰; Claw C^{13} 2.19 ± 0.06 ‰, N^{15} 3.60 ± 0.73 ‰. For collagen, no such suitable alternatives were identified and we instead took estimate values from the SIDER (Stable Isotope Discrimination Estimate in R, Healy et al. 2017) package for program R (R Core Team 2017), giving C^{13} 1.7 ± 1.8, N^{15} 3.6 ± 1.4. The 'isospace', or isotopic mixing space, is the two-dimensional space defined by the $\delta^{13}C$ and $\delta^{15}N$ ratios of potential prey categories. Stoat values using proposed TEFs were visually checked to ensure the consumer values fell within the prey values in this isospace, as failure of this test can indicate an incorrect TEF or important prey category missing from the sample. Incorrect or inappropriate TEF values can lead to substantial error in mixing model results (Bond & Diamond 2011). While all care was taken to choose biologically appropriate surrogate values, the inclusion of surrogate TEFs incorporates an unknown amount of error into these results, and they should be treated as indicative until pen trials can confirm accurate TEFs for this species. A full appraisal of relative benefits of available tissue types and available enrichment values is given in McAulay (2019).

Bone Collagen

After dissecting the left ulna, radius, and humerus, we extracted bone collagen (hereafter: collagen) using a modified Longin method (Longin 1971). In the Longin method an 'ultrafiltration' step is used to remove very small particles for radiocarbon dating studies, or for isotope samples with very high collagen lipid content. As the lipid content of small mammals is not high (Guiry et al. 2016) we found no *a priori* reason to invoke this step for this study.

Claw

We removed and boiled the two front paws of each stoat to extract the external claw sheath from the dermis of the basal matrix of the nail. We washed this keratin sheath in an ultrasonic water bath with a 2:1 mixture of chloroform:methanol to remove contaminants. Any remaining soft tissue was scraped away with a scalpel and 0.7 mm dental tool (Kohler Medical Products). Using marked, straight-edged nail clippers and magnifying glass, we cut a one mm section from the proximal edge of the claw. The thickened dorsal ridge of this cross section was then removed (and discarded) leaving two slices of lateral wall (blade horn) keratin from the proximal edges of each claw (Fig. 2). This excludes the dorsal ridge which can complicate time-series comparisons as additional keratin layers are deposited along its top edge, and also avoids the keratin-homogenisation complications of using distal claw tips (Ethier et al. 2010). Lateral wall samples from between three to five claws of the front paws (depending on size and availability on the carcass) were pooled, and segments totalling 0.8 mg were weighed into tin cups for mass spectrometry.

Liver

We extracted 10 mm sections of the sinister-caudal lobe of liver from carcasses which were not heavily degraded (as per Gennard 2007). We dried liver for 48 hours at 40°C and ground to a powder, then chemically removed lipids by washing repeatedly in 5 ml of 2:1 chloroform:methanol solution in an ultrasonic water bath until the solution ran clear of lipids.

This study was conducted under Otago University Animal Ethics Committee approved protocol number ET27/2016, and under the Department of Conservation Alpine Research Project.

Prey sample preparation

We scraped whole dried passerine blood into glass vials and homogenised. We cut bird feather vane into fine segments (> 1 mm) and homogenised, excluding the rachis. We removed quadriceps muscles of both anterior legs of mice, wētā and grasshoppers and dried at 40°C for >48 hours, then homogenised with a 0.7 mm dental tool (Kohler Medical Products). For the hare samples, we dissected a 20 mm distal segment of the right

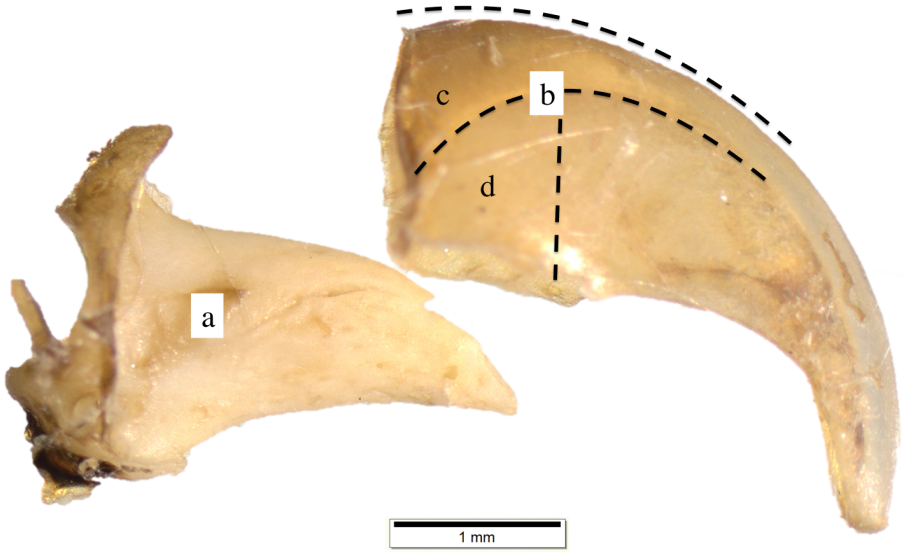

Figure 2. Distal phalanx [a] and external claw sheath (nail) [b] of a stoat. Thickened dorsal ridge [c] was excluded leaving two 1-mm wall sections [d] of blade horn keratin for use in the analysis.

quadricep muscle, dried, and homogenised with a ball-mill grinder (MM 200, Retsch Scientific, Haan, Germany). We then removed lipids from mice and hare muscle, and feather samples by washing three times in ultrasonic water bath with 5 ml of 2:1 chloroform:methanol. Other insects, fruits, and seeds were oven dried (as above) and homogenised with the bug grinder. We extracted collagen from rat bones using the modified Longin method described above for stoats.

Effects of ethanol on skink samples trial

An unexpected prevalence of skink (Scincidae family) in stoat stomach contents necessitated inclusion of skink tissue in prey sampling. As no skink tissue was available from wild capture, we used undigested skink pieces extracted from stoat stomachs as prey samples for mass spectrometry. These pieces had been stored in ethanol, which might (Hobson et al. 1997; Kim & Koch 2011; Sarakinos et al. 2002) or might not (Edwards et al. 2002; Kelly et al. 2006) affect $\delta^{13}C$ and $\delta^{15}N$ ratios. To measure the effect (if any) of this ethanol treatment on New Zealand skinks, three skink samples (two plague skinks *Lampropholis delicata,* and one southern grass skink *Oligosoma polychroma*) were obtained from DOC; the skinks had been either found dead (grass skink) or euthanised by freezing as part of biosecurity control (plague skinks).We split each skink sagittally into two equal portions. One random portion we dried and ground immediately, the other we stored in ethanol (of the same batch as used for skinks from stoat stomachs) for 60 days. We then evaporated off the alcohol and dried and ground the skinks. To measure the effect (if any) of ethanol on $\delta^{13}C$ and $\delta^{15}N$ ratios, the two sets of samples (with and without ethanol, n = 3 per treatment) were processed by mass spectrometer and the $\delta^{13}C$ and $\delta^{15}N$ ratios were compared using *t*-tests assuming equal variance. Plague and common skink samples were not used as inputs for mixing models, but only to obtain any necessary correction factor for ethanol treatment. Samples of the unidentified skinks extracted from stoat stomachs were processed in the same way and utilised in mixing model dietary estimates.

Mass Spectrometry

We prepared samples for carbon and nitrogen isotope analysis by weighing 0.8 mg (± 0.08) samples of homogenised material into tin foil capsules and drying under vacuum overnight. Samples were processed at the Isotrace lab at the University of Otago, Dunedin, New Zealand. Nitrogen and carbon isotopes were assayed by combusting whole material to N_2 and CO_2 gas in a Carlo Erba NC2500 elemental analyser (CE Instruments, Milan), using helium carrier gas enriched with oxygen. The gases were separated on a packed Porapak QS GC column and sent sequentially to the inlet of a '20/20 Hydra' (Europa Scientific, UK) isotope ratio mass spectrometer (IRMS), in continuous flow mode. Raw isotope ratios were normalised by three-point calibration to international scales using two IAEA (International Atomic Energy Agency) reference materials (USGS-40 and USGS-41) and a laboratory standard (EDTA–OAS; Elemental Microanalysis Ltd, UK), assayed with the unknown samples. $\delta^{13}C$ and $\delta^{15}N$ values of these standards are given in McAulay (2019).

The laboratory standard, EDTA-OAS (Elemental Microanalysis Ltd, UK) has multi-year and multi-laboratory calibration records against IAEA reference materials. EDTA-OAS was also used as a drift control material by assaying a pair of aliquots after every twelve samples of a batch. Instrumental drift corrections were calculated from regression of the EDTA-OAS against time. Precision was assessed from the RMS difference between sequential duplicates (IANZ 2004) of every 10th sample by random inclusion of three true control materials chosen to mimic the nature of the sample materials. Expected precision for analysis of control materials is typically ± 0.2 ‰ for $\delta^{15}N$ and ± 0.1 ‰ for $\delta^{13}C$. Isotopic ratios are then expressed as parts per thousand using the formula:

$$\delta X(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \quad (1)$$

where δX is $\delta^{15}N$ or $\delta^{13}C$, and R is the respective $^{15}N/^{14}N$ or $^{13}C/12C$ ratio of the sample being measured. Table 2 shows delta values of reference materials and laboratory standards.

Mixing models

Mixing models take isotopic data to produce estimates of the relative contribution of various prey items to the total metabolic requirement of the consumer. We analysed data using Bayesian mixing model package MixSIAR (Stock & Semmens 2016) in program R (R Core Team 2017). We created separate models for each tissue at each study site

Table 2. Delta values of International Atomic Energy Agency reference materials (USGS-40 and USGS-41) and a laboratory standard (EDTA –OAS) These values are used in three-point calibration to the international scales as a laboratory reference for mass spectrometry.

Material	$\delta^{13}C$	$\delta^{15}N$
USGS-40	−4.52	−26.24
USGS-41	−47.57	−37.76
EDTA-OAS	−0.73	−38.52

using informative priors; uninformative priors were not used in this study. Informative priors improve the accuracy of mixing models and reduce confidence intervals of dietary estimates, especially where prey categories are closely spaced or linearly aligned within the isospace (Moore & Semmens 2008). We based informative priors on percentage frequency of occurrence of each prey category in stomach contents of stoats at each site (including only stoats with intact stomachs). To avoid an overly-informative alpha prior based on a small sample size (number of stoat stomachs per site), we scaled informed priors to the weight of an uninformative prior, using the following formula:

$$\alpha = \frac{\text{proportion of diet from prey category} * \text{number of prey categories}}{\text{total number of samples from all categories}} \quad (2)$$

Mixing models produce the most reliable results when prey are clumped into broad categories of easily identified items within the stomach contents (Phillips et al. 2014). This 'lumping' means loss of some resolution to distinguish between prey items (e.g. between different groups of mammals), but yields far greater certainty from model estimates and narrower confidence intervals (Phillips 2012). Ground birds (kiwi, takahē, and weka) did not fall into one obvious prey grouping within the isospace plots. Because we expected these to be in stoat diet at only a very low frequency, they were dropped from prey data in order to simplify the model.

We chose to use raw mix (prey) data in models, with no fixed, nested or random factors, and a residual:process interaction error term (Parnell et al. 2010). We ran another model for each site, using claw values with individuals as fixed factors in the model, creating a dietary estimate for each individual stoat. We used the same site level informative priors as above, with separate priors for each site.

Seasonal variation

Seasonal variation in the isotopic signature of a consumer can be caused by variation in consumer diet but also by a change in the isotopic signature of that diet (e.g. a dietary shift by a key prey species). To test for this effect, we conducted winter prey sampling in July 2017 at one site (Nelson Lakes NP). We then compared winter samples to summer samples from that site using a K-nearest neighbour randomisation test (Rosing et al. 1998).

Factors affecting diet

Proportional dietary contributions provided by MixSIAR fail to meet the homoscedasticity requirements and other assumptions of generalised linear models (Koenker & Bassett 1982). Instead, beta regressions are commonly used for modelling continuous data restricted to values between zero and one (Schreier & Prügl 2011). We fitted beta regression models to assess the effect of stoat sex, stoat age, catch elevation, and/or study site on the proportions of prey consumed by individual stoats. Due to the large proportion of juveniles caught, we entered age as a two-level categorical variable (juvenile or adult). To measure the effect of age of juveniles, we gave juveniles an age in days from a nominal birthday of 1 October (King & Moody 1982) until the day they were collected by trappers. We ran one model per prey category using the mean prey proportions consumed by individual stoats as the dependent variable. We also included interaction terms sex × age, age × site and elevation × site. As diet was dominated by just two prey categories at some sites, we do not compare directly between diet proportions (e. g. proportions of mammals and insects) because they are inversely related. We used the type II ANOVA function in the package CAR (Fox & Weisberg 2011) with Beta regressions using *betareg* package (Grün et al. 2012) in program R (R Core Team 2017).

To test whether the abundance of rats or stoats at each site would better explain diet variation compared to using 'study site' as a categorical variable, we ran each beta regression twice more using site specific rat abundance then stoat abundance (c $100TN^{-1}$) in place of study site. This procedure provided a set of three beta regressions ('site model', 'rat model' and 'stoat model') for each dietary category (% mammals, % passerines, % insects). We compared each set of three models using Akaike's Information Criterion (AIC; Akaike 1998) to assess which variable best explained variation in stoat diet.

Results

Samples returned

From November 2016 until May 2017 trappers returned 55 stoat carcasses suitable for use in analyses. Of these, eight were adults, 41 juveniles, and four unknown (canines not present/intact). Sex ratios were roughly even between sites (Fig. 3). Degradation of carcasses varied from 'fresh' to 'advanced decay/liquefaction' (Gennard 2012), often affecting the state of liver tissue. A total of 51 claw, 50 collagen and 28

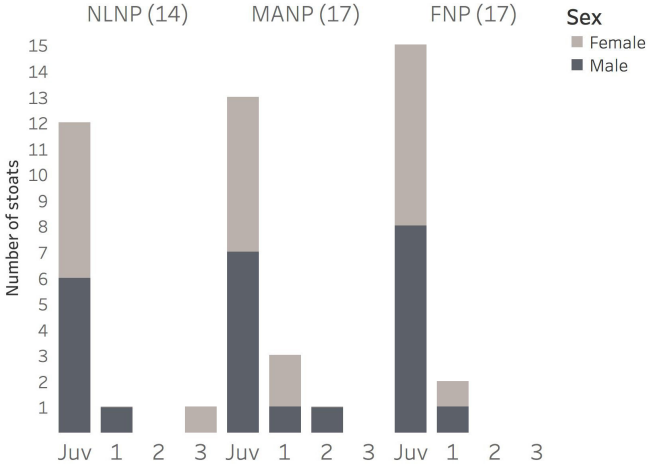

Figure 3. Sex and age of stoats caught in the alpine zone of Nelson Lakes (NLNP), Mt Aspiring (MANP), and Fiordland (FNP) National Parks in the summer of 2016/17. Age classes = Juvenile (Juv), 1, 2, and 3 years assuming a nominal birthday of 1 October. Age class information was not available for every stoat sampled in this study. Sample size for age and sex data in parentheses.

Table 3. Percentage frequency of occurrence of prey items in the stomachs of 35 stoats from the alpine zone of three national parks in New Zealand.

	Mammal	Bird	Insects	Plant	Skink	Sample size
Nelson Lakes NP	50%	19%	37%	19%	37%	11
Mt Aspiring NP	90%	0%	30%	20%	0%	10
Fiordland NP	100%	0%	27%	7%	0%	14

liver samples were analysed and used in mixing models. Rat abundance was 0.007 c $100TN^{-1}$ at Mt Aspiring NP and 0.157 c $100TN^{-1}$ at Fiordland NP; no rats were caught at Nelson Lakes NP during the study period. Stoats caught per 100CTN was higher at Nelson Lakes (0.079) compared to Mt Aspiring (0.029) or Fiordland (0.031).

Thirty-five stoat carcasses were in a condition suitable for stomach content analysis (had stomachs intact). Every suitable stoat stomach from Fiordland NP contained mammal hair or tissue, as did 90% of stoats from Mt Aspiring NP (Table 3). In contrast, just 50% of stomachs from Nelson Lakes NP contained mammal hair or tissue, instead containing greater proportions of bird, insects, and skink remains. Nelson Lakes NP was the only site to have any lizard remains in stoat stomachs; four of eleven stomachs sampled (36.6%) contained remains of skinks, including one stomach containing 19 skink feet and two small, entire skinks. Plant items were found in stoat stomachs, including wood, tussock and the flower head of a grass inflorescence.

We collected and analysed 233 prey items for use as inputs for mixing models (see Appendix S1 for species and sample sizes). Five mice and 17 passerines were caught at Nelson Lakes NP in the winter field trip; winter efforts to locate skinks, wētā, grasshoppers and beetles were unsuccessful. K-nearest neighbour simulations could not accurately discriminate between summer and winter isotopic signatures in either mice or passerines at Nelson Lakes NP. We therefore pooled all mice and passerine samples at this site and assumed all differences in isotopic signatures in stoat tissues from different periods were due to differences in stoat diet rather than seasonal differences in isotopic signatures of prey.

Ethanol had no statistically significant effect on either $\delta^{13}C$ (−0.81 to 0.94‰; $P = 0.84$) or $\delta^{15}N$ −0.17 to 1.40‰; $P = 0.37$) values of skinks experimentally tested .No correction was therefore deemed necessary for skink samples from stoat stomachs that had been stored in ethanol.

All consumers' isotopic values ($\delta^{13}C$ & $\delta^{15}N$ in stoat collagen, claw and liver) fell within the prey polygon in the isospace, i.e. the space defined by the measured prey values corrected by the appropriate stoat TEF (Fig 4). This indicates no major prey items were missed in sampling, nor did we detect significant errors in selection of TEF values.

Mixing model results

Mixing model estimates of long-term stoat diet using bone collagen indicate that mammals contributed the largest proportion to diet at all sites. Mean proportions (± SD) ranged from 0.47 ± 0.22 at Nelson Lakes NP to 0.90 ± 0.05 at Fiordland NP (Fig. 5). Mammals also made the largest contribution to diet in both the medium term (claw 0.65 ± 0.09) and short term (liver 0.96 ± 0.04) at Fiordland NP (Fig 5).

Estimates at Nelson Lakes NP were far less certain with wider posterior distributions and larger SDs. The width of a probability distribution depicts the range of estimates returned over many iterations of the model. Mammals at Nelson Lakes NP made up 0.19 (± 0.11) of stoat diet estimated from claws and 0.28 ± 0.14 from liver (Fig. 5). The range of prey items regularly consumed was instead broader at Nelson Lakes NP. Claw estimates indicate insects (0.18 ± 0.09), passerines (0.26 ± 0.18) and, notably, skinks (0.33 ± 0.15) all made a substantial contribution to stoat diet at Nelson Lakes. In contrast, claw models at Mt Aspiring and Fiordland NP suggest stoat diet at

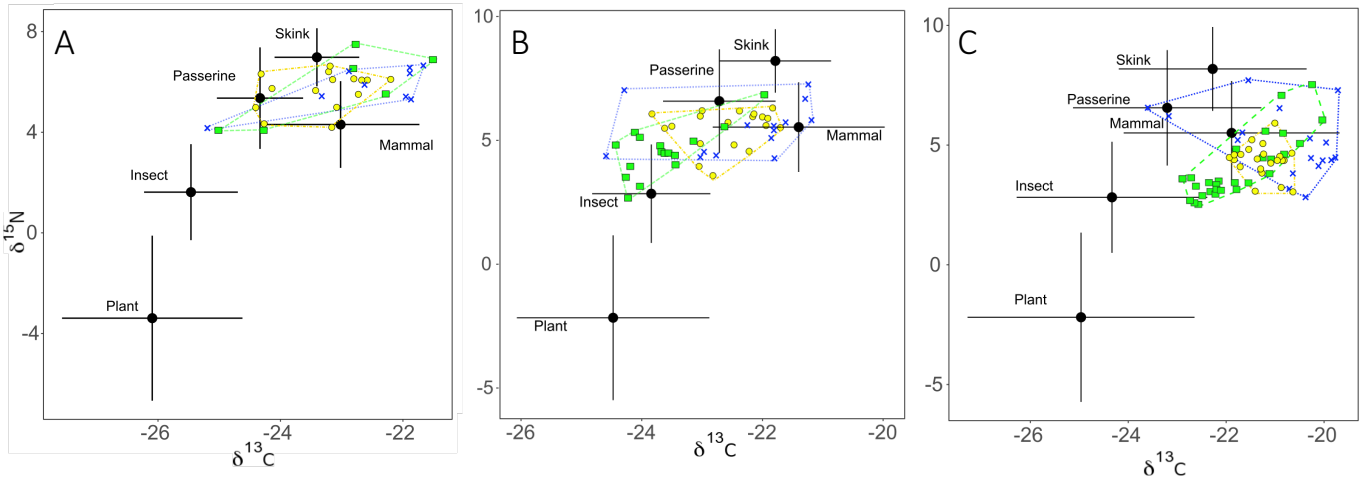

Figure 4. Isospace plots showing $\delta^{13}C$ & $\delta^{15}N$ values of stoats caught in the alpine zone of Nelson Lakes (blue), Mt Aspiring (green), and Fiordland (yellow) National Parks in relation to their prey. Black dots/lines show means/standard deviations for prey values, which have been corrected using tissue specific trophic enrichment factors for the three stoat tissues. (a) liver, representing days before the animal's death; (b) claw, representing weeks before the animal's death; (c) bone collagen, representing months before the animals' death.

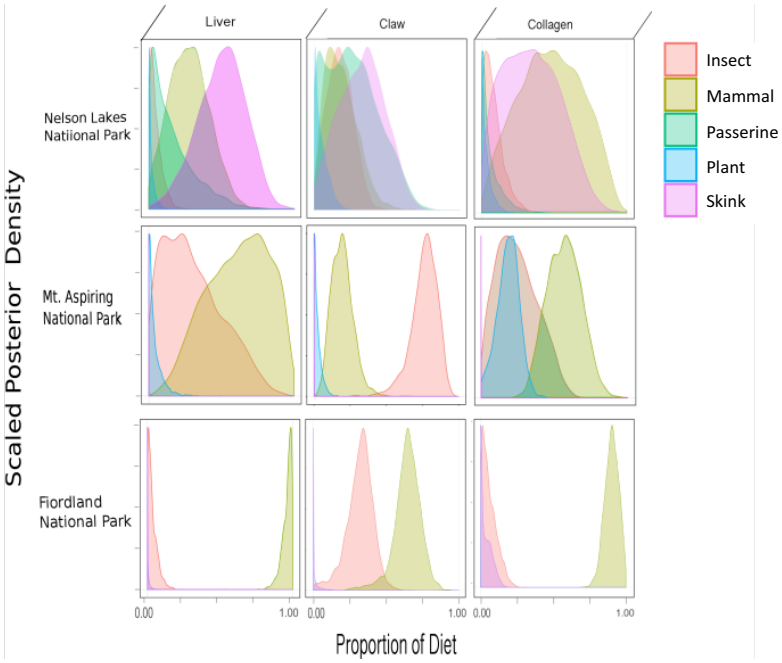

Figure 5. Posterior distributions showing estimated proportional contributions from different prey categories to the diet of stoats in the alpine zone of three National Parks. The width of distributions indicates the range of values returned from the model. Separate models were run for each site, using stomach contents as informative priors.

these sites was much less diverse, with over 95% of the diet consisting of mammals and insects (Mt. Aspiring: mammals 0.20 ± 0.08, insects 0.76 ± 0.09, Fiordland: mammals 0.65 ± 0.09, insects 0.32 ± 0.09; Fig. 5).

The high proportion of skinks eaten at Nelson Lakes NP was consistent across all three tissues and all three time periods, and reflects the high proportion of skinks found in stomach contents at that site. Estimates from collagen models show skinks supplied a large portion (19–57%) of stoats' total metabolic requirements over the long term. Likewise passerines contributed 15% to 26% of the total metabolic requirements of stoats at Nelson Lakes NP, compared to < 2% elsewhere.

Factors affecting stoat diet

Proportions of prey consumed were not significantly related to stoat age, stoat sex or catch elevation for any prey category (mammals, insects or passerines), and no interactions between these factors were significant. Dietary proportions differed between the three sites for all three prey categories (site models, $P \leq 0.001$ in all cases). Full outputs for all nine model configurations are provided in Appendices S2–S4 in Supplementary Materials. Results of AIC model ranking showed models using the categorical 'site' variable better described the proportions of passerines and insects consumed than models using other site-wide variables (i.e. rat or stoat abundance; Table 4). In contrast, models using site-wide rat abundance best described the proportion of mammals consumed (Table 4).

Discussion

The estimates of stoat diet produced by stable isotope mixing models varied across all three study sites and the three periods of diet examined, suggesting that stoat diet in alpine areas can be highly flexible. Models estimated that mammals made the largest contribution to the long-term diet of stoats at all sites, varying from 47% to 92% of the total diet. Estimates from claw samples, reflecting a shorter period over spring/summer, suggest a greater reliance on insects during this period. This finding provides some support for the hypothesis that stoats eat larger proportions of insects, such as wētā, when these are available during periods of warmer temperatures. Higher insect consumption is not evident from short-term liver samples, reflecting a period of days before an animal's death. This might indicate a reliance on insects in early summer, once

Table 4. Results of beta regression models on the diet of individual stoats in the alpine zone of three National Parks. Effect directions are provided for statistically significant continuous variables (P < 0.05). Models are ranked with AIC. ΔAIC shows the difference between each model's score and the lowest ranked (preferred) model.

Dependent variable	Predictor variable	Effect direction	z score	ΔAIC
Proportion mammals in diet	Site	-	4.88	2.91
	Stoat abundance	negative	5.31	64.2
	Rat abundance	**positive**	**4.88**	**0**
Proportion insects in diet	**Site**	**-**	**4.80**	**0**
	Stoat abundance	negative	5.20	60.72
	Rat abundance	negative	5.31	67.2
Proportion passerines in diet	**Site**	**-**	**4.46**	**0**
	Stoat abundance	positive	4.38	20.69
	Rat abundance	-	n/a	117.33

temperatures have warmed sufficiently to enable emergence, but before other summer prey is available. However, lower sample sizes of liver and the fast turnover of liver samples make these patterns susceptible to stochastic variation. Liver results are therefore presented with less confidence that they represent general patterns among the wider stoat population.

Components of diet

Martinoli et al. (2001) showed that fruit made an important contribution to the diet of stoats in the alpine zone of Italy, and we therefore included plant material in this study. Elsewhere in New Zealand stoat diet has contained wood, leaves, and fungi (Murphy et al. 2008; King et al. 2010), and both seeds and tussock grass have been noted in samples from the alpine zone (Smith et al. 2008). However, mixing model results indicate that plant material did not form a significant proportion of the metabolic requirement of stoats in any of the sites or periods in this study. Stoats are generally believed to consume fruit only when 'very hungry' (King et al. 2010). Even at Nelson Lakes NP, the only site without ship rats and with the greatest dietary diversity, plant material made a low (0–2%) overall contribution to the metabolic requirements of alpine stoats. The narrow posterior distributions and low variation in estimated proportions of plant material consumed by individual stoats (Appendix S5 in Supplementary Materials) support the conclusion that plant material does not offer a substantial contribution to the diet of stoats in New Zealand alpine areas.

Models estimate that stoats at all sites ate a high proportion of insects in the mid-term (claw estimates), but, except at Nelson Lakes, stoats ate almost exclusively mammals in the short-term estimate (liver estimates, Fig. 5). Prey selection by predators must combine optimum foraging decisions and local prey availability (Krebs & Davies 2009). It is likely that stoats adjusted their diet as preferred prey types became more available. It is likely that mammals became increasingly abundant during the study period. Beech forests adjacent to the study sites seeded heavily in autumn 2016 causing large increases in ship rat abundance below the timberline (DOC unpubl. data; King & Moller 1997). It is not known how these irruptions affect ship rat density in adjacent alpine areas, and our study lacks data on seasonal shifts in availability of prey such as ship rats. Heavy seeding of *Chionochloa* tussock species can lead to large increases in mouse abundance in alpine grasslands (Wilson & Lee 2010). Tussock masting likely occurred at all study sites in summer 2015/2016 (see methods), but mouse tracking data were available only from the Fiordland NP site, where high mouse tracking was recorded. It is unknown whether mouse abundance at our other study sites was similarly high, or how this might have affected stoat diet. Those seeking to protect threatened species from invasive mammals in the alpine zone should prioritise collection of mammal abundance data.

The high prevalence of skink remains in stoat stomachs at Nelson Lakes NP will be of concern to conservation managers, with one individual stoat containing at least seven individual skinks. The results of stable isotope analysis (SIA) from three time periods indicate this predation pattern was consistent throughout the study period, and that skinks form a long-term metabolically important prey source to stoat at that site. In the alpine zone of the Kaikōura ranges, skinks were found in 9–20% of stoat scats, despite high abundance of alternative prey (Cuthbert et al. 2000). Elsewhere lizards have not been reported in the diet of alpine stoats (Smith et al. 2005; Smith et al. 2008), nor do they form a substantial portion of diet in most studies (Murphy et al. 1998; Purdey & King 2004; Murphy et al. 2008; Murphy et al. 2016). In addition to Cuthbert et al. (2000), two exceptions come from sub-alpine systems east of the main divide: lizards remains were found in 9% of stoat scats in the Tasman Valley (Dowding et al. 2015) and 20% in non-alpine grasslands near Mt Cook Village (King & Moody 1982). It appears likely that where lizards are abundant, they will form a substantial portion of stoat diet, perhaps linked to limited availability of alternate prey sources (such as ship rats) at these locations. This variation in diet would provide a mechanism to explain the drastic declines and episodic predation recorded in Reardon et al. (2012).

The proportion of birds in stoat diet was lower than expected at most sites and in most periods, and generally lower than reported by Smith et al. (2005). Passerines contributed less than 2% to stoat diet in most samples, among the lowest proportions recorded anywhere in New Zealand (Smith et al. 2005; King et al. 2010; Dowding et al. 2015; Murphy et al. 2016). The exceptions were the Nelson Lakes NP where over a quarter the metabolic requirements were met by passerines in one estimate. Nelson Lakes NP was the only site in which ship rats were not present during the study period. At a time of high abundance of alternative prey (Hutton's shearwaters *Puffinus huttoni*) in the alpine zone of the Kaikōura Ranges, Cuthbert et al. (2000) found no passerine or passerine egg remains in stoats' stomachs. Our data are consistent with a pattern of higher consumption of passerines at times and sites when alternative prey is scarce.

We note however, that stoats are kill-and-cache predators and engage in surplus killing (Oksanen et al. 1985). In a New Zealand study of stoat food caches, birds were the most commonly cached food items, appearing in nearly twice the proportion of food caches than that of scats (Dowding et al. 2015). Consumption of birds may therefore under-represent total predation on birds. Further, while alpine passerines contributed only a small proportion of the total metabolic requirement of stoats, stoats may still present a substantial risk to their population persistence. Multi-year, multi-site monitoring of alpine passerines (rock wrens *Xenicus gilviventris*) show that these populations are heavily affected by predation by stoats (Weston et al. 2018).

Does rat or stoat abundance explain stoat diet?

Ship rat abundance was positively correlated with mammal consumption by stoats. No data are available on the abundance of other mammalian prey other at our study sites, but changing mouse abundance does not generally lead to changes in stoat diet (King 1983; Murphy & Dowding 1995; White & King 2006). In modelling the functional response of stoats to changing rodent abundance, Jones et al. (2011) found that even at very high mouse abundance, the proportion of stoat stomachs containing mice did not exceed 0.4. Consumption of rats, however, rose consistently with increasing rat abundance, and did not reach an asymptote. Even at (theoretical) maximum kill rates, stoats would be unable to fulfil daily energetic requirements on mice alone (Jones et al. 2011).

No ship rats were detected at Nelson Lakes NP in this study, and stoats at this site consumed greater proportions of non-mammalian prey. These findings are consistent with the hypothesis that in low-or-zero-rat alpine environments in New Zealand, stoats cannot survive on other mammal species alone (e.g. mice) and must consume other taxa. This suggests per capita predation of native fauna by stoats may be lower in periods or places with high ship rat abundance.

This prediction is supported by experimental evidence in the alpine zone showing that predation of wētā by stoats declined following the increased availability of mammalian prey (Smith et al. 2010). While rat abundance was inversely correlated with proportion of insects consumed, models using site alone performed better than those using rat abundance to predict consumption of insects and passerines. This indicates that other factors likely play an important part in governing stoat diet at these sites.

Increased density of conspecific predators are linked with expansions of dietary niches of generalist carnivores, and greater individual specialisation in diet (Svanbäck & Bolnick 2007; Araújo et al. 2011). Internationally, increased density of mustelids can cause increased intraspecific competition for localised prey (Biggins et al. 2004; Yamaguchi & Macdonald 2003). In our study, stoat trap catch was important, but not as important as rat trap catch, in predicting the diet of stoats. Difficulties in estimating abundance of stoats in alpine areas complicates interpretation of such results (see Smith & Weston 2017).

These results show abundance of key prey sources and, to a lesser extent, intraspecific competition, were important factors in the diet of alpine stoats. Site differences likely encompass a complex interaction of these components acting in concert with other factors not recorded in this study (for example: abundance of other prey types, climatic effects, micro habitat). Further study, with more complete data on prey and predator abundances, might enable teasing apart the relative influence of these two factors and form a clearer picture of how changes in predator densities affect the per capita consumption of prey.

Other factors affecting stoat diet

There was no evidence in this study that male and female stoats consume prey types at different proportions, in contrast to past studies (King & Moody 1982). However, differences in prey consumption between sexes in past studies are only statistically significant between proportions of mammalian prey, largely mice and ship rats (King & Moody 1982; Murphy et al. 2008). Because we 'lumped' all mammalian prey into a single prey category, such variation would not have been detectable with SIA. There is no evidence that either male or female stoats consume greater proportions of native fauna, and thus present a greater threat to threatened species in the alpine zone.

The diet of individual stoats did not vary with trap elevation in this study, providing no evidence elevation acts as a proxy for ship rat availability driving variation in stoat diet. An underlying assumption of this study was that all stoats caught in the alpine zone are permanently resident there, even those caught at or near the forest edge. Some adult stoats live consistently in the alpine zone during summer months, but it is not known whether they remain in the alpine zone over winter (Smith et al. 2007). Further work is needed to understand stoat dispersal and immigration patterns. The utilisation of forensic techniques such as SIA may prove useful in resolving these questions, e.g. stable isotope 'labelling' of catchments or ecosystems with isotope biomarkers could track the movements and provenance of pest animals. These techniques have been successfully applied to seed and animal movements (e.g. Carlo et al. 2009).

Limitations

Given the large geographic spread of sampling sites and uncontrolled environmental variables, our sample size of 55 individuals is small and limits the interpretation of these data. Isospace plots show that all stoat tissues were within the range of standard deviations of prey $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 3), providing an indication that there were no major errors in the Trophic Enrichment Factors (TEF) taken from surrogate species (Fry 2006; Stock & Semmens 2016). However, TEF values are species and tissue-specific, and the use of surrogate values for stoats in our study has introduced an unknown amount of uncertainty into these results. Until stoat-specific TEFs can be calculated with empirical feeding trials, all results presented here must be treated with caution. The negative shift in $\delta^{13}C$ in claw isospace plots relative to collagen and liver at all sites may result from error in the claw $\delta^{13}C$ TEF value. The TEF for stoat claw modelled by program SIDER (used to estimate TEF for collagen, but not for claw in this study) would provide claw values closer to those of collagen and liver in the isospace (SIDER claw TEF: $\delta^{13}C$ 1.57, $\delta^{15}N$ 3.66, arctic fox claw TEF: $\delta^{13}C$ 2.19, $\delta^{15}N$ 3.64) and would result in mixing model outputs more similar to those from other tissues. Despite this consideration, we had no *a priori* reason to choose this SIDER modelled TEF value for claw and any errors could reasonably be attributed to erroneous collagen and liver TEFs instead. Although small (a potential difference of 0.62 ‰), any such an error may have influenced mixing model outputs, particularly in how the model separates insects and mammals along the $\delta^{13}C$ axis (Fig. 3). Several other factors can also influence the expression of $\delta^{13}C$ and $\delta^{15}N$ isotopes, including age, sex, dietary lipid content and environmental stress (Bearhop et al. 2015; Gorokhova 2017; Karlson et al. 2018). While no effect of age or sex on dietary estimates was detected, wider variation in our data could have masked small effects.

The high proportion of juvenile stoats in our sample is likely to have had an influence on the isotope results presented here. The earliest stoats caught, in December trap-checks, were likely less than three months old (Grue & King 1984). The young age of these individuals might have led to estimates from claw and collagen models acting as non-independent samples, representing the same dietary periods in the earliest caught juvenile stoats. While the timing of stoat breeding (and thus juvenile cohort dispersal) varies with latitude (Purdey & King 2004), catch date was not a significant predictor of diet in beta regression models. However, the frequency of trap checks (which varied between sites, with up to 4 months between checks) confounds proper examination of catch date and stoat age on diet and dietary estimates. The small sample size and high proportion of juvenile stoats in our sample also increases the likelihood of related individuals in the sample. In peak breeding years female stoats raise very large litters, meaning multiple related juveniles in the sample could increase the influence of genetic or environmental factors (e.g. matrilineal learning) on prey selection.

Enriched δN values have been noted in some studies of nursing or young mammals (Hobson et al. 1997; Hobson et al. 2000). Offspring can appear one trophic position above their true position due to a reliance on protein derived from maternal tissue (Fuller et al. 2006). While examination of age class (juvenile or adult) was limited by a small sample size of adults, the age in days of juvenile stoats had no detectable effects on diet, and all stoat values fell within the prey isospace expected for their trophic position. These results indicate that a nursing effect was unlikely to have affected δN results in this study.

Conclusions

The application of SIA has enabled this first study of alpine stoat diet to incorporate meaningful spatial and temporal variation. The data presented here suggest that stoat diet in alpine areas is highly variable across both time and space. This highlights the need to treat all estimates of stoat diet (and those of stoat density, abundance etc.) as snapshots of a dynamic environment, in which predator and prey abundance might be as meaningful indicators of predation risk as any geographic delineations.

Lack of ship rats at one site coincided with a far greater range of prey being regularly consumed by stoats. If consumption of indigenous prey by stoats depends strongly on ship rat abundance, then conservation managers should be aware that declines in rat abundance could increase the per capita rate at which stoats consume non-mammal fauna (such as passerines and insects). However, many other variables, including density of intraspecific competitors, likely acted in concert to influence the functional response of stoats to their environment. Regular monitoring of abundance of all small mammals should be a priority in alpine conservation programmes, enabling further examination of functional and numerical responses of stoats to their environment.

Acknowledgements

Trappers from Friends of Flora, Friends of Cobb, DOC St Arnaud and The Mammalian Corrections Unit (Te Anau) all willingly put rotten stoat carcases in their packs to make this work happen. We hope that this research can help you in your task. Many volunteers helped in the field and lab including Frazer Maddigan, Joel Zwartz, Graeme Oatley, Nichola Greaves, Marian Milne, Lesley Hadley, Lucie Machin, Janet Musker, Jen Waite, Ciaran Campbell, Emma McCool, Ash Muralidhar and Kat Kruger. Thanks to Robert van Hale and Dianne Clark at the Otago University Isotrace who both freely gave much knowledge, help and support; and to the two reviewers who volunteered helpful feedback to improve this manuscript. This work was supported by a grant from the Miss E. L. Hellaby Indigenous Grasslands Trust.

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Received 9 October 2019; accepted 23 February 2020
Editorial board member: Jamie Wood

Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Samples collected from the alpine zone of Nelson Lakes, Mt Aspiring and Fiordland National Parks.

Appendix S2. Results of beta regressions to examine factors affecting the proportion of mammals in the diet of individual stoats caught in the alpine zone of three National Parks.

Appendix S3. Results of beta regressions to examine factors affecting the proportion of invertebrates in the diet of individual stoats caught in the alpine zone of three National Parks.

Appendix S4. Results of beta regressions to examine factors affecting the proportion of passerines in the diet of individual stoats caught in the alpine zone of three National Parks.

Appendix S5. Posterior distributions showing proportional contributions from different prey categories to the diet of individuals stoats in the alpine zone of Nelson Lakes, Mt. Aspiring and Fiordland National Parks.

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