

## NEW ZEALAND JOURNAL OF ECOLOGY

## RESEARCH

# Interspecific variation in predation patterns of stoats and weasels in an alpine conservation programme

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Published online: 5 April 2023

**Abstract:** Conservation programmes in New Zealand often suppress populations of a single invasive predator for the benefit of threatened avifauna. However, the establishment of whole guilds of invasive species has created complex competitor and predator-prey relationships, including some well-described trophic cascades. Trap networks designed to target stoats (*Mustela erminea*) are poorly optimised to supress a population of weasels (*M. nivalis*), and may contribute to periodic spikes in weasel numbers due to decreased interspecific competition and aggression. The consequences of stoat removal and possible weasel release have received little attention. In this small-scale pilot study, we used C<sup>13</sup> and N<sup>15</sup> stable isotopes to examine diet and relative trophic position of eight weasels and 20 stoats caught in an alpine ecosystem. We explored three dietary models as a framework with which to examine trophic patterns in feeding behaviour of the two mustelid species and potential impacts on native species. The models suggest that, in this specific scenario, weasels preyed at a higher trophic position than stoats and consumed a greater proportion (per capita) of vulnerable taxa like lizards and passerines. We cautiously highlight the potential for negative outcomes for some native taxa in scenarios in which weasels are released from competition with stoats.

**Keywords:** alpine, intraspecific competition, invasive predators, MixSIAR, *Mustela erminea*, *Mustela nivalis*, stable isotopes

### Introduction

Conservation management on biogeographically isolated islands often relies on suppression of small invasive mammals to prevent extinction of endemic species (Blackburn et al. 2004; Russell et al. 2016). However, the introduction of suites of mammalian predators has created complex competitor and predator-prey relationships and, in some cases, led to well-described trophic cascades (King 1983; O'Donnell et al. 1996; Murphy et al. 1999; White & King 2006; Jones et al. 2011).

Three species of mustelid—ferret (*Mustela furo*), stoat (*M. erminea*), and weasel (*M. nivalis*)—were introduced to New Zealand in attempts to control rabbits (*Oryctolagus cuniculus* cuniculus) (King 2017a). Stoats and weasels quickly established in forest (and likely upper montane) settings and began preying heavily on native species (King 2017b). Today, weasels are considered less common and more patchily distributed in space and time than stoats (King et al. 2018).

While an extensive body of research has assessed the impact of stoats on New Zealand fauna, less is known about weasels in New Zealand (King & Forsyth 2021). An apparent displacement effect between stoats and weasels (King & Moors 1979; Dayan & Simberloff 1994; Foster et al. 2021) exists throughout their native and introduced range, but the mechanisms that drive the degree of overlap in their ecological

niches are not well understood. Haworth (2018) found that both weasels and stoats were able to coexist for periods of time in New Zealand forests, possibly due to high abundance of rodent prey.

To understand predator impacts, several studies have compared weasel and stoat diets in New Zealand. At two forested North Island sites stomach contents showed stoats ate more rats, and weasels more mice (King et al. 1996; Murphy et al. 1998). At these sites, stoats ate a greater proportion of birds while weasels had more lizards in their stomach contents (Murphy & Bradfield 1992). Clapperton et al. (2011) found at Nelson Lakes that stoats had similar amounts of birds and lizards in their guts as weasels. At that site stoats ate more rodents, while weasels ate more invertebrates.

An ever-growing number of conservation programmes aim to suppress populations of stoats for the benefit of native species, including programmes in alpine ecosystems (O'Donnell et al. 2017). Typically, alpine programmes copy a successful formula for the conservation of forest birds and apply it to an alpine setting (Weston et al. 2018). Notably, alpine areas hold lower abundances of rodents (Christie et al. 2017; O'Donnell et al. 2017; Carpenter et al. 2022) important to mustelid diets. While several studies have examined stoat diet in the alpine zone (Cuthbert et al. 2000; Smith et al. 2005; McAulay et al. 2020) no data is published on what weasels prey on in New Zealand alpine settings.

Weasels typically have substantially smaller home ranges and are less likely to encounter a stoat trap (Haworth 2018). Most practitioners set trap trigger weights at 100 g so as not to fill traps with non-target rats (New Zealand Department of Conservation 2021). Almost all female weasels (mean: 70 g, range: 40–100 g) and many males (mean: 112 g, range: 65–210 g) would therefore not trigger standard DOC 200 or 150 series mustelid kill traps (King et al. 2010; Haworth 2018). Unlike stoats, weasels can breed multiple times within one year, and in some studies have shown twice the reproductive potential of stoats during the growth stage of a resource pulse (King & Moors 1979).

These factors likely contribute to the periodic spikes in weasel captures recorded in stoat trapping programmes and combined may help tilt the balance in favour of weasels becoming more locally abundant than stoats in the short-term, with unknown consequences for native biodiversity. In this pilot study, we aimed to compare the likely diets of stoats and weasels killed during an alpine trapping operation using stable isotope analysis. This will help understand possible impacts of weasel predation on threatened species.

## Methods

Weasels and stoats were collected from an alpine conservation kill-trapping programme around the Routeburn Track in Otago/Southland, ranging from 750 to 2052 metres elevation, from November 2016 to May 2017 (Fig. 1). Mustelid species were identified visually in the field and later verified in the lab. The external claw sheath from the dermis of the basal matrix of the nails from both front paws of each individual were removed, cleaned and prepared for stable isotope analysis following the methods described by McAulay et al. (2020).

Stable isotope analysis is a biochemical technique that uses measured differences in the ratios of naturally occurring  $^{13}\text{C}$ :  $^{12}\text{C}$  and  $^{15}\text{N}$ :  $^{14}\text{N}$  isotopes as a biomarker to assess trends in animal diets. These ratios (hereafter  $\delta 13\text{C}$  and  $\delta 15\text{N}$ ) allow us to estimate trophic position of consumers and assess relative quantities of prey that make up their diets. The rate at which stoat and weasel claws grow will dictate the period of diet represented by that keratin. It is likely the claw material sampled represents the diet period between one to ten weeks before the animal's death (McAulay 2019).

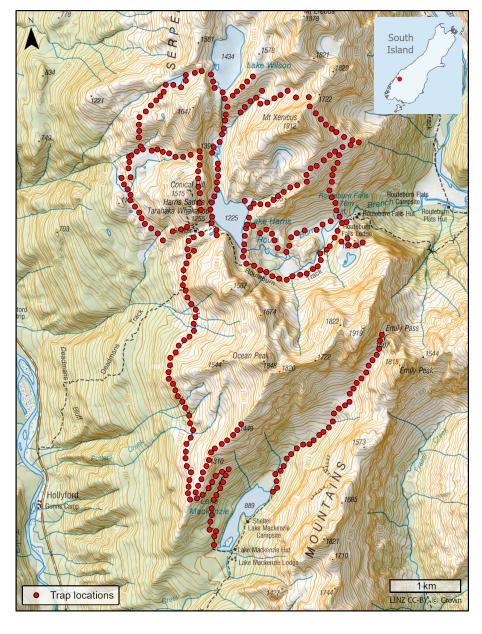


Figure 1. Map showing the network of mustelid kill traps surrounding the Routeburn walking track, along the main divide of southern New Zealand. Each dot shows a kill trap, left permanently in place, rebaited monthly between November 2016 and May 2017. Map projection NZGD 2000 New Zealand Transverse Mercator, LINZ CC-BY, © Crown.

McAulay et al. (2020) published isotopic values from a range of potential prey species of alpine mustelids at this, and other similar, alpine sites. This includes invertebrates, skinks (*Oligosoma* spp.), mice (*Mus musculus*), rats (*Rattus* spp.), brown hare (*Lepus europaeus occidentalis*) and various species of alpine passerine. That work showed no significant difference in the isotopic signature of prey samples between sites, and prey data from all sites were therefore pooled and used as inputs for our stable isotope mixing models, using Bayesian mixing model package MixSIAR (Stock & Semmens 2016) in R version 4.0.2 (R Core Team 2017).

Bayesian mixing models use isotopic data to produce estimates of the relative contribution of various prey items to the total metabolic requirement of the consumer using informative priors (which use prior diet information to guide the model to the most likely result). For stoats we used informative priors from McAulay et al. (2020) built from stomach contents of the same individual stoats used in this analysis. Relatively less is known of weasel diets in New Zealand, and to the authors knowledge no data are published on weasel diet from alpine areas, in New Zealand or abroad (King & Forsyth 2021). To allow for this, we decided to run the model using three sets of priors.

- (1) using weasel diet from a coastal community in Northland, New Zealand (Strang et al. 2017),
- (2) using stomach contents data of stoats at the Mt Aspiring National Park/Routeburn Track site (McAulay et al. 2020), and
- (3) using uninformative (uniform) priors.

As none of these options will perfectly represent the diet of weasels at our alpine site, presenting a range of data will assist the interpretation of that uncertainty.

We used the claw specific trophic enrichment factor (TEF) of another small-bodied mammalian hyper-carnivore, the arctic fox (*Vulpes lagopus*):  $C^{13}$  2.19 ‰ ± 0.06,  $N^{15}$  3.60 ‰ ± 0.73 (Roth & Hobson 2000). Samples were analysed at IsoTrace lab at Otago University. For full details of study site, prey collection, sample preparation, mass spectrometry calibrations, standards, protocols, and construction of informative priors,

see McAulay et al. (2020). For comparison, we also include in our results mixing model data from 20 stoats previously reported in McAulay et al. (2020).

## Results

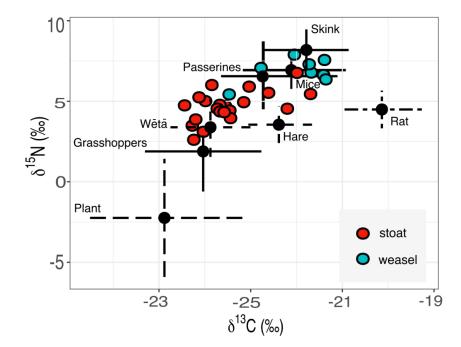
Eight weasels and 20 stoats were returned in a usable state for processing and analysis via mass spectrometer. Both  $\delta^{13}$ C and  $\delta^{15}$ N values for weasels were generally higher than for stoats, indicating a feeding pattern at a higher trophic position (Fig. 2).

All consumers' isotopic values ( $\delta^{13}$ C &  $\delta^{15}$ N values of stoat and weasel claws) fell within the prey polygon in the isospace, i.e. the space defined by the measured prey values (Fig. 2). This suggests no major prey items were missed in sampling, nor did we detect significant errors in selection of TEF values.

The results of Bayesian mixing models suggest invertebrates made up a greater proportion of the overall metabolic requirements of stoats, while weasels preyed more heavily on both mammals and skinks (Table 1). The models returned higher proportions of passerines and skinks in the diet estimates of both stoats and weasels when using uninformative priors compared to informed priors based on stomach contents. This was offset by the modelled proportion of mammals in the diet being higher in models using informative priors (Table 1, Fig. 3). All models suggested stoats were eating a higher proportion of invertebrates (chiefly wētā species) than were weasels.

## Discussion

The ratio of nitrogen isotopes ( $\delta15N$ ) can be used estimate trophic position of consumers, with the  $\delta15N$  of a consumer typically 3–4‰ greater than its diet (Deniro & Epstein 1981; Peterson & Fry 2012). Our modelled diet results suggest these eight weasels were feeding one trophic position higher than stoats at this site.



**Figure 2.** Isospace plot showing weasel (*Mustela nivalis*; blue dots) and stoat (*Mustela erminea*; red dots) isotope values in relation to possible prey types. Consumer values are corrected to the isospace by a trophic enrichment factor taken from the arctic fox (*Vulpes lagopus*):  $C^{13}$  2.19 ‰  $\pm$  0.06,  $N^{15}$  3.60 ‰  $\pm$  0.73 (Roth & Hobson 2000).

**Table 1.** Mean proportion of prey categories (± standard deviations) estimated in the diets of stoats and weasels, using stable isotope mixing model MixSIAR. Models were run using uninformative priors, priors based on stomach contents in McAulay et al. (2020), and, for weasels, using stomach contents from Strang et al. (2017). For comparison, stoat data is also presented, taken from McAulay et al. (2020).

Consumer	Prior	Invertebrate	Mammal	Passerines	Plant	Skink
Stoats	McAulay et al.	$0.54 \pm 0.19$	$0.30 \pm 0.14$	$0 \pm 0.03$	$0.07 \pm 0.08$	$0.08 \pm 0.15$
Weasels	McAulay et al. Strang et al. Uninformative	$\begin{array}{c} 0.17 \pm 0.13 \\ 0.20 \pm 0.11 \\ 0.13 \pm 0.09 \end{array}$	$\begin{array}{c} 0.62 \pm 0.26 \\ 0.36 \pm 0.19 \\ 0.12 \pm 0.11 \end{array}$	$0 \pm 0.08 \\ 0.10 \pm 0.18 \\ 0.28 \pm 0.24$	$\begin{array}{c} 0.03 \pm 0.03 \\ 0.00 \pm 0.00 \\ 0.04 \pm 0.03 \end{array}$	$0.19 \pm 0.22 \\ 0.33 \pm 0.16 \\ 0.43 \pm 0.18$

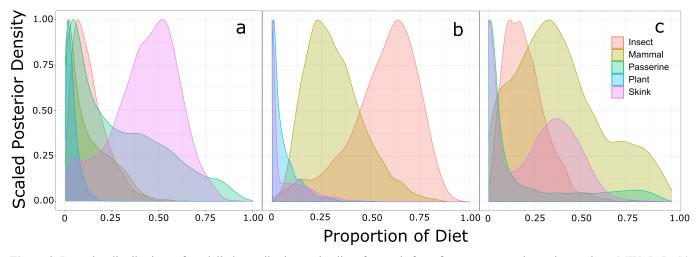


Figure 3. Posterior distributions of modelled contribution to the diet of weasels from five prey categories, using package MIXSIAR. (a) shows results from uninformative priors, (b) using stoat stomach contents priors from McAulay et al. (2020), and (c) using priors from weasel stomach contents from coastal habitat in Northland, New Zealand from Strang et al. (2017).

Notably, the three models of weasel diet estimate a greater proportion of skinks (mean 19%, 33%, and 43%) and passerines (mean 0.1%, 10%, and 28%) consumed by weasels compared to stoats (0.08% skink and 0.1 % passerine). These modelled results align with other results showing weasels regularly preyed on lizards in forested settings (Murphy et al. 1998; Clapperton et al. 2011; Strang et al. 2017; King & Forsyth 2021). Our data suggest that this is also the case in this alpine habitat, and that skinks represent a consistent and metabolically important food source for weasels, making up a substantial proportion of their dietary needs (Fig. 3). However, the variation between our estimates indicates a moderate amount of uncertainty in results and specific diet estimates should be treated with some caution. We do not present these data as exact estimates of weasel diet. Rather they are an indication of weasel diet relative to stoats in this area, highlighting potential consequences for native prey species in programmes in which weasels may be released from competitive pressure.

The limited overlap in dietary niche observed aligns with studies from weasels'native range showing weasels exploited a smaller dietary niche than stoats, concentrated on smaller prey (McDonald et al. 2000a). In the United Kingdom this focussed on voles, while our results suggest weasels preyed heavily on lizards, and possibly small birds and/or mice (McDonald et al. 2000b). However, our results are not reflective of studies comparing weasel and stoat diets in forested New Zealand environments, where a full range of rodent prey are present (Murphy et al. 1998; Haworth 2018).

The lumping of prey categories (e.g. mammals) in our study results in a lack of resolution to tease apart the relative contribution of rats, mice, and hares. These three groups occupy distinct areas of the isospace (Fig. 2) and lumping provides the average between all, poorly reflecting any biological reality. This limitation is evident in the bimodal distribution of mammal estimates (Fig. 3) and is an indication this lumping of mammal prey likely obscures what is happening in reality.

## Trophic level effects on native species

The overall risk of an individual being preyed upon is a complex mix of both the number of predators present and their functional responses to their environment (Murphy et al. 1998; Joly & Patterson 2003; Zimmermann et al. 2015). Sometimes, as here, this equation involves multiple predator species and their interactions. Overall assessments of the risk to individual prey species are thus incredibly challenging. Higher position in the food chain does not necessarily mean higher impact on species of conservation interest, and it is not clear what would drive weasels' higher trophic status. However, due to the patterns of predation presented here, we cautiously present the potential for a conservation mediated trophic cascade, while acknowledging the behavioural response (feeding) is only part of this complex risk equation. The trapping of stoats could, through removal of interspecific aggression, facilitate short periods of elevated densities of weasels, as has been shown in a forested environment (King et al. 1996). If the results of this pilot study represent a wider trend, the natural differential specialisation of weasels higher in trophic position could then place additional predation pressure on some native taxa. While a higher trophic position does not signify a greater conservation concern for all species, the results of this pilot study demonstrate three possible scenarios of which prey groupings would be most affected.

King & Moors (1979) argue that, while stoats have superiority in interference (aggressions), weasels have superiority in exploitation. They suggest the large heterogeneity of New Zealand habitat allows weasels to avoid stoats and capitalise on their strengths, exploiting small prey, and responding quickly to increases in rodents (differential specialisation).

Weasels appear to benefit from increases in small mammals in their native range (Pounds 1981) and New Zealand forests in years when rodents are abundant (Haworth 2018). In a New Zealand alpine context, lacking voles (Arvicolinae) and with just mice and limited numbers of two rat species, it is not clear whether weasels or stoats would benefit most from elevated mice and/or rat abundance. Differences in habitat heterogeneity between this alpine environment (which includes scrub, tussockland, rock, and fellfields) and lowland northern hemisphere habitats also place limits on useful comparisons between these systems. Weasels also appear less common now than when first introduced (King et al. 2018), with one explanation that they have eaten their way through small native prey that once acted as a surrogate for small mammals of their native range (King & Forsyth 2021). We propose that resource use by both species is highly plastic as environmental factors including competitor dominance, prey availability, and differences in breeding strategy continually tip the fine balance between these two species. Conservation management (stoat trapping) likely also affects this balance, although the net effects on native taxa is yet unclear, and further work is needed.

## **Data limitations**

Trophic Enrichment Factors (TEF) are species and tissue specific correction factors, and errors in TEF can cause errors in modelled results (Peterson & Fry 2012). However, a potentially incorrect TEF would not explain the full amount of variation between these stoats and weasels (greater than + 2 \% for both  $\delta^{13}$ C and  $\delta^{15}$ N). Phylogenetic relatedness is a good predictor of TEF values (Healy et al. 2018), and we would not expect the TEF of these two closely related species to differ to this extent (> 2 %). In an examination of how TEFs vary across the Felidae family, just  $0.8 \% \delta^{15}$ N separated the TEFs for congeneric carnivores Lynx canadensis and Lynx rufus, with  $< 1.4 \% \delta^{15}$ N separating the most extreme values amongst all five species of large felid (Parng et al. 2014). Further, lack of accurate dietary information to form Bayesian priors forced us to use two proxy values which may have introduced further uncertainty to these results.

We do not therefore present these models as highly precise estimates of exactly what proportion of various prey types are in weasel diets. Instead, the model provides a useful conceptual tool to assess overall trends and possible trophic positioning of two species of introduced predators. When used as such, and accounting for the uncertainty presented here, we believe this modelling approach will provide another tool to help conservationists build our understanding of the trophic level effects of lethal control programmes.

Traditional methods of assessing predator diets, such as stomach contents or scat, show items eaten in the last 4–8 hours before sample collection (Vander Zanden et al. 2015).

The stable isotope data from claw material likely reveals predator hunting behaviours over a period of several weeks (Ethier et al. 2010; McAulay et al. 2020) and thus a substantial increase in temporal integration when compared to past studies. Our models assume uniform prey availability over a non-heterogenous landscape; differing habitat selections (and therefore prey availability) might also explain our data.

#### Implications for management

Based on the data of this pilot study, conservationists should be aware of the potential for both weasels and stoats to be preying on threatened lizards and birds in alpine areas. The eight weasels in this study preyed at a higher trophic position than stoats; future research is required to better understand the relative effects of weasels on prey populations and how these might change with differing management scenarios. For example, will suppression of stoat populations have a positive or negative effect for conservation of threatened lizards? This is particularly important given the complexity of large increases in stoat and rat control associated with Predator Free New Zealand (Peltzer et al. 2019). Stable isotope analysis can help conservationists better understand trophic level effects of predator control, particularly in settings in which a full suite of predators create a complex range of predator-prey and competitor relationships. Controlled feeding experiments to determine TEF values specific to New Zealand pests would be a valuable contribution to the field and increase the accuracy of this tool.

To fulfil New Zealand's aspirations of removing weasels permanently from New Zealand (and/or to increase the probability of effectively supressing weasel population for protection of threatened species) conservationists require traps and trapping grids designed and optimised for the capture of the smaller mustelid species. Traps need to be designed for humane kills of mustelids at trigger weights less than 80 grams; the current suite of traps are unlikely to be effective in this task. Additionally, the layout of trap networks must be optimised according to the generally smaller home range size of weasels. Spatially based trapping simulation models (such as TrapSim; Gormley & Warburton 2017) would help us understand what is required for effective multi-mustelid suppression.

It is important to note that several species are demonstrated or thought to benefit from stoat trapping programmes in alpine areas, albeit largely in the absence of weasels (Hegg 2006; Wilson et al. 2006; Weston et al. 2018). Relatively fecund species such as rock wrens (*Xenicus gilviventris*) can likely tolerate short bouts of high nest predation. K-selected species (which are long lived and slow to reproduce) such as many alpine lizards (e.g. Knox et al. 2019) may be less likely to persist with even occasional increases in predation pressure. Data from long-term, community-wide studies are required to understand potential ecological losers when management may shift this balance between mustelid species. Those species affected by a complex suite of interacting stressors likely require restoration of entire ecosystems (Hare et al. 2019).

## Acknowledgements

Many thanks to the willing trappers at the Mammalian Corrections Unit, Te Anau, who put rotten mustelid carcases in their packs to make this research happen. This manuscript was developed as part of the (excellent) New Zealand Ecological

Society mentorship programme between Jamie McAulay and Mel Galbraith: see society website for details. Phil Seddon and Deb Wilson contributed strongly to the original stoat diet work on which this study is based. Funding for field transport and analysis was provided by the Miss E. L. Hellaby Indigenous Grassland Trust, with support from the Department of Conservation. Thanks to the three reviewers, whose input greatly improved the manuscript.

## **Author Contributions**

Jo Monks and Jamie McAulay contributed to the study design, interpretation of results and writing of the manuscript. Jamie McAulay led sample collection, lab work, data analysis and writing.

## Data and Code availability

The data from this article are openly available; see Appendix S1 in supplementary material. There is no publicly available code associated with this article.

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Received: 31 January 2022; accepted: 24 January 2023 Editorial board member: Cilla Wehi

## Supplementary material

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

### Appendix S1. Stable isotope data.

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