New Zealand Journal of Ecology (2021) 45(2): 3443 © 2021 New Zealand Ecological Society.

NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

Individual specialists within a generalist niche: variable diet of stoats and implications for conservation

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Abstract: Conservation programmes aiming to suppress or remove invasive small mammal populations that threaten endemic fauna assume that eliminating an individual predator has the same effect as eliminating a conspecific in terms of decreasing risk to the prey species. However, marked between-individual variation in prey take could, at times, lead to uneven predation pressure. Such variation in the diets of introduced predators has long been hypothesised in New Zealand, suggesting that some observed rates of predation are not typical of the prey population as a whole. We used stable isotope analysis to estimate the isotopic dietary niches of stoats *Mustela erminea* (n = 51) caught in three New Zealand National Parks. We modelled $\delta^{13}C$ and $\delta^{15}N$ ratios from five tissue types to estimate the isotopic niche for each individual stoat, and for each population. The isotopic niche used by the population of stoats in Nelson Lakes National Park was substantially larger (5.3 ‰^{2}) than for those at either Mt Aspiring National Park (3.1 ‰^{2}) or Fiordland National Park (2.8 ‰^{2}). Despite this, a measure of individual specialisation (proportional niche use) in stoats at Nelson Lakes National Park (0.4 ± 0.3) was similar to the other two sites. Collectively these data suggest a comparable degree of individual specialisation even within a more generalist population niche. This variability in the range of prey items taken by small carnivores, between populations and individuals of the same species, has consequences for how we design and monitor small mammal control programmes; for example, the threatened species outcomes observed in one area or time period may not be applicable to another.

Keywords: diet, invasive species, Mustela, niche, SIBER, specialisation, stable isotope analysis, stoats

Introduction

Threats posed by alien invasive species are a leading cause of global biodiversity decline (Gurevitch & Padilla 2004; Clavero & García-Berthou 2005; Ducatez & Shine 2017). In island archipelagos such as New Zealand, introduced mammals prey heavily on endemic fauna that have evolved without natural responses to mammalian predators (Blackburn et al. 2004; Towns et al. 2006). Control of invasive species, particularly small mammalian predators, is now a mainstay of island conservation, in which extensive trapping, shooting, and toxin operations are used to reduce predator numbers for the benefit of native fauna (Russell et al. 2016).

Current management of small invasive mammals typically assumes that interactions between introduced predators and their environment vary little among individuals of the same species (Lustig et al. 2019). This implies that any reduction in predator numbers would be equally effective in the protection of prey species, regardless of which individual predators are removed (Moseby et al. 2015). 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). However, individual diets can vary greatly, even within the same species in the same location, an effect called niche partitioning (Sargeant 2007; Araújo et al. 2011; Dickman & Newsome 2015).

This between-individual variation in the diet of introduced predators has long been discussed in New Zealand in terms of its implications for the effective protection of native fauna. This is supported by the observation that the very high predation rates on threatened species recorded in some studies could not be representative of long-term patterns, or the focal native population or species would be extinct (Taborsky 1988; Powlesland 1989; Dowding & Murphy 1993; Reardon et al. 2012; Hope 2014; Moseby et al. 2015). Instead, it is postulated that elevated predation rates must be due either to temporary increases in predator densities, or to temporary increases in the rate of consumption of the study subject. For example, the early 1990s saw drastic declines in populations of New Zealand dotterel (*Charadrius obscurus*) on Stewart Island,

DOI: https://dx.doi.org/10.20417/nzjecol.45.29

due to predation by cats (*Felis catus*; Dowding & Murphy 1993). However, studies of cats on Stewart Island show that they typically avoid the wet, open area above the subalpine scrub layer where dotterels nest (Harper 2004), and more recent nest monitoring has not detected any predation by cats (Hope 2014). It is hypothesised that most predation could be due to a relatively small number of cats adopting a learned behaviour of preying on these ground-nesting birds (Dowding & Murphy 1993; Ray 2013). Similarly, Reardon et al. (2012) describe episodic predation of grand skinks (*Oligosoma grande*) by a single stoat in the open grasslands at Macraes Flat, resulting in nearly half the remaining study population being lost over a period of five days. The sporadic nature of such attacks makes collection of meaningful data difficult, but data available on attractiveness of food lures show not all individuals are attracted to best-practice baits (Robbins et al. 2007; Brown et al. 2015).

Between-individual (intraspecific) variation in prey consumed by larger predators has been linked to biological factors (e.g. habitat, body size, or social factors such as matrilineal learning), genetic factors, "personality" (Bolnick et al. 2011), stochastic variation in prey encounter-rates and individual skill acquisition (Tinker et al. 2009). Even in generalist species, significant differences between individuals have been demonstrated where individual specialists act within the generalist niche (Murray & Wolf 2013; Franco-Trecu et al. 2014; Estes et al. 2016; Swan et al. 2017). "Predator profiling" in mammalian carnivores is the identification of a small number of individual predators responsible for a disproportionate impact on a prey population (Swan et al. 2017). Such profiling has been demonstrated in larger top-order predators, such as lynx (*Lynx lynx*; Breitenmoser & Haller 1993), bears (*Ursus* spp; Hopkins et al. 2012), and coyotes (*Canis latrans*; Jaeger et al. 2001). Targeted management of "problem individuals" has, in some instances, led to improved outcomes in human-wildlife or livestock-wildlife conflict scenarios (Swan et al. 2017). Understanding the extent and potential drivers of inter-individual variation and niche partitioning in small, invasive mammalian carnivores, such as stoats and cats, would facilitate efforts to protect endemic prey.

Many of the predator-prey studies rely on labour-intensive direct observation of individuals or their scats, but biochemical tools are expanding our ability to examine diets of whole populations of predators. Stable isotope analysis offers the potential for comparison of an isotopic niche between and within individuals, populations, and communities, using natural biochemical markers (Layman et al. 2015). The technique has been used to study niche width and individual specialisation by predators. Most commonly used within freshwater ecology, the tool has also been applied to study invasive mammals (Shiels et al. 2013; Stewart et al. 2019). This work has mainly been descriptive, aiming to identify the diet or habitat preferences of invasive mammals. To the authors knowledge, no work has yet used stable isotope analysis to test the extent of individual specialisation in the diet of small invasive mammals.

Of New Zealand's introduced predators, stoats may be best suited for the study of between-individual specialisation. A key feature of the pulsed-resource ecosystems within which mustelids have evolved is strong temporal fluctuations in the availability of prey (McDonald et al. 2000; King & Powell 2011). Stoats and weasels (*Mustela nivalis*) have thus evolved a plasticity to exploit a range of temporally available prey and colonise new areas, even those lacking small mammals, their primary prey in their native range (Purdey et al. 2004; King et al. 2010; Murphy et al. 2016). In the wet alpine ecosystems of New Zealand, stoats are thought to act as top-order carnivores due to low abundance of feral cats (*Felis catus*). Flexibility and plasticity of diet and top-order carnivory are common factors in species with high levels of between-individual specialisation (Bolnick et al. 2003). The types and quantities of prey taken by stoats vary between sex and age class (King & Moody 1982c; Purdey et al. 2004; Murphy et al. 2008; Clapperton et al. 2011) and recent evidence suggests matrilineal learning may play a role in foraging behaviours (Little et al. 2017). No research has yet explored diet specialisation by individual stoats, in New Zealand or elsewhere.

In addition to improving our knowledge of small mammal ecology, understanding between-individual diet variation has practical application for the development of conservation management tools. Targeting of problem individuals (or predator profiling), trap design and layout, baiting schedules, and modelling of predator impacts could all be influenced by between-individual variation in the types of prey frequently taken by stoats (Merrick & Koprowski 2017; Banks et al. 2018; Garvey et al. 2020; García-Díaz et al. 2021). We aimed to quantify the extent of variation in the diets of individual stoats within and between populations, and predicted that significant inter-individual specialisation exists within stoats' generalist dietary niche.

Methods

This study was conducted in the alpine zone (above the natural timberline) of three National Parks along the length of the South Island of New Zealand: Nelson Lakes National Parks in the Tasman District, Mt Aspiring National Park in Otago, and Fiordland National Park in Southland. Each site has an existing network of DOC-150 and DOC-200 style (mustelid kill-traps; Peters & Waddington 2004a; Peters & Waddington 2004b) run by the Department of Conservation (DOC) for the protection of alpine fauna. Traps were serviced and rebaited on varying schedules, and trappers provided carcasses from stoats caught. Trapping effort was measured as catch per 100 trap nights (c/100CTN) corrected for sprung traps (Nelson & Clark 1973) over an eight-month period of sample collection. This provides a measure of the relative abundance of stoats and rats (*Rattus* spp.) at each site (Brown et al. 1996). The three sites lie between 750 to 2053 metres above sea level (m a.s.l.), and are a mix of alpine grasslands, sub-alpine scrub, rock, scree, herb, and cushion field vegetation, located above large tracts of beech forest (Nothofagaceae). Full details on trapping regimes, bait types, study sites and collection of stoat tissues are described fully in McAulay et al. (2020).

Selection and preparation of stoat tissue

We selected five stoat tissue types for analysis based on information available on turnover times (the rates of loss and replacement of cells). This informs the period of diet represented by isotopes of those cells. As diets tend to vary across short time periods, using tissues which reflect distinct periods of the diet helps to ascertain the true niche occupied (Bearhop et al. 2004). Liver is a fast-turnover tissue representing average diet in the days before an animal's death, whereas bone collagen has very slow turnover, averaging diet over many months (Dalerum & Angerbjörn 2005). Inert tissues such as fur, whisker, and claw do not turn over and represent the fixed isotopic composition of diet during growth of keratin. Stoat guard hairs in the summer pelage are grown in a 6-week period from October to December (King et al. 2010). Vibrissae (whisker) growth periods are less well defined and a homogenised sample likely represents averaged values over the 6–19 weeks before an animal's death (Purdey et al. 2003). Claw growth in mammals is linear, hence the proximal edge of a stoat claw represents growth in the weeks before an animal's death (Homberger et al. 2009; Ethier et al. 2010). These different tissues provide a range of representative time frames, thus optimising dietary niche estimates (McAulay 2019).

We removed a sample of guard hair fur from the nape of each stoat. This area is the first to gain new hairs in the spring moult, and the last to gain new growth in autumn (King & Moody 1982b). Selection of these hairs therefore maximises the chance samples represent the period of growth of the summer pelage (August to December). We cleaned fur by removing visible contaminants and washing three times in 1.5 ml of 2:1 chloroform:methanol solution in an ultrasonic water bath. Fur was then dried and cut into fine segments (< 1 mm) and mixed to homogenise. We removed all posterior vibrissae present on each stoat carcass and cleaned them as above. We discarded the root and a 12 mm section at the whisker base (proximal tip) to exclude the most recently grown tissue (Purdey et al. 2003) and cut the remaining whisker into fine segments (< 1mm) to form a homogenised pool. Excluding the root base ensured we minimised the overlap in time period represented by other tissues (claw and liver) relating to the period directly prior to death. All samples were processed at the IRMS laboratory at Otago University. This process, and the preparation of liver, claw, and collagen are described in (McAulay et al. 2020).

Analysis of niche sizes and specialisation

There are various metrics and indices to measure resource specialisation, each yielding similar, but not identical, values (Bolnick et al. 2002). For this study, we used definitions by Roughgarden (1972), developed by Bolnick et al. (2002). This approach adds the isotopic variation within each individual (the within-individual component, or WIC) and the variation between individuals (between-individual component, or BIC), to provide the total niche width (TNW) of the species. The proportion of the total niche used by each individual is then calculated as WIC/TNW (Bolnick et al. 2002). Although newer, more complex methods (e.g. Ingram et al. 2018) combine multiple data sources in multidimensional space to allow closer examination of niche overlap and community structure, we believe that our approach provides the most intuitive description of specialisation and permits direct comparison to data from other studies (Bolnick et al. 2003).

We quantified isotopic niches using the 40% Standard Ellipse Area (SEA) method (Newsome et al. 2007) in the package SIBER (Stable isotope Bayesian ellipses in R; Jackson et al. 2011) for program R (R Core Team 2017). For comparison, we also calculated the Total Area (TA), the area (in ‰^{2}) delimited by all values in the group. However, as more values are added the TA can only get bigger. Using 40% of isotopic data provides robust estimates of isotopic niche for direct comparison between different sample sizes, and excludes extreme values that could distort the total niche area (Jackson et al. 2011). To reduce potential bias from small sample size, we applied a sample size correction in SIBER, giving SEAc.

We created two sets of ellipses in SIBER. The first set shows the isotopic niche of the population of stoats at each site (the BIC). Using the above method, we inputted all δ13C and δ15N values from all tissues of all stoats at each site to give one ellipse per population of stoats studied (Fig. 1). Next we created individual ellipses to compare isotopic niche size within individuals from the same population (the WIC). We did not create separate ellipses for males and females as previous work showed no difference in isotopic signature between sexes for these same data (McAulay et al. 2020).

To assess differences between ellipses of populations or individuals, we fitted Bayesian multivariate normal distributions to the data, allowing the posterior distributions of covariance matrix for each group (ellipse) to be compared (SEAB). Fitting via the JAGS method, we used two chains of 10 000 iterations, discarding the first 1000 (burn-in). SIBER fits ellipses using an Inverse Wishart prior on the covariance matrix Sigma and a vague normal prior on the group means (Parnell et al. 2013).

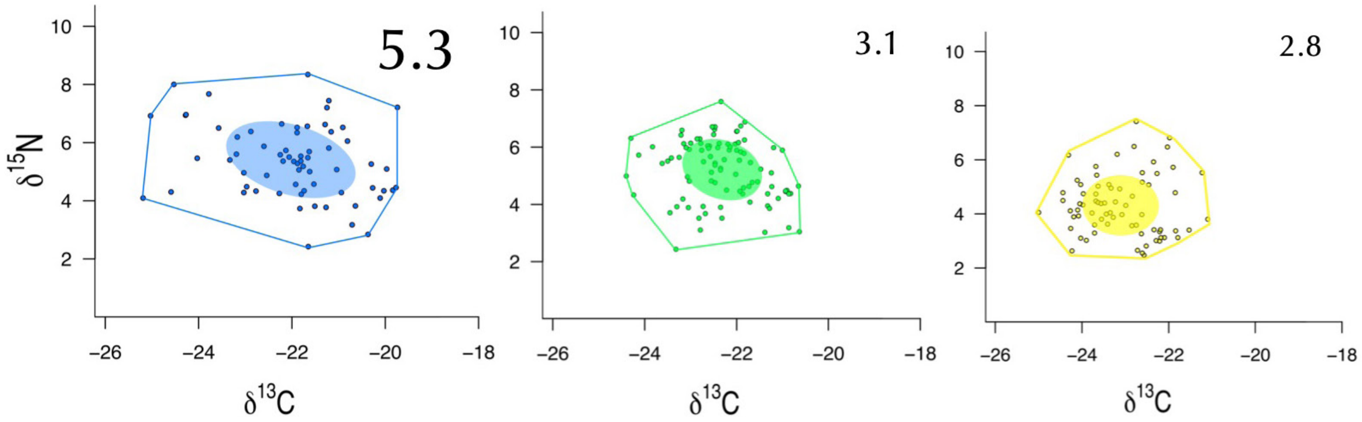

Figure 1. Isotopic dietary niche sizes of three populations of stoats caught in the alpine zone of Nelson Lakes (blue), Mt Aspiring (green) and Fiordland (yellow) National Parks. Each coloured dot represents one tissue sample (claw, collagen, liver, whisker or fur tissue), combined these form the Between Individual Component (BIC) of niche use at the population level for at each site. Solid lines show convex hulls of total area (TA) of each population, coloured ellipses show mean 40% Standard Ellipse Areas corrected for small sample size using package SIBER in R. The niche size for each population (BIC) is also shown in scaled text on each panel. Niche expression δ13C and δ15N values in units per mil (‰). See further niche area metrics in Table 1.

Factors influencing niche expression

We used a linear model to test the effect of site, age, sex and number of tissues used to form ellipses on the expression of individual isotopic niches using, excluding any individuals where the sex or age could not be determined. The timeframes represented by different tissues vary, and not all ellipses included the same tissue types. To test whether the inclusion/exclusion of some tissues affected the size of individual SEAc estimates we conducted another linear model, using presence/absence of each of the four tissue types (excepting fur, which was present in every sample) as a series of two-level factors acting as independent variables, along with site. For both analyses we treated SEAc as the dependent variable in program R (R Core Team 2017) with an alpha of 0.05.

Results

Samples

Fifty-one stoat carcasses suitable for analysis were obtained: 14 from Nelson Lakes NP, 17 from Mt Aspiring NP and 20 from Fiordland NP. These comprised seven adults, 40 juveniles, and four stoats of unknown age. Degradation of carcasses varied from fresh to advanced decay/liquefaction (Gennard 2012), affecting the state of liver tissue and the presence of whiskers and claws in some samples. A total of 51 claw, 50 collagen, 51 fur, 28 liver, and 43 whisker samples were analysed. Rat abundance at Mt Aspiring NP was 0.007 c/100CTN and at Fiordland NP 0.157; no rats were caught at Nelson Lakes NP during the study period. Stoat trap-catch was high at Nelson Lakes (0.079 c/100CTN) compared with Mt Aspiring (0.029) and Fiordland (0.031). Table 1 provides niche metrics for populations at each site, along with sex ratios of stoats caught.

The isotopic niche (BIC) used by stoats at Nelson Lakes NP appears substantially larger (5.3 ‰2) than those at either Mt Aspiring NP (3.1 ‰2) or Fiordland NP (2.8 ‰2) (Table 1; Fig. 1). While these three BIC datapoints are too few to test statistically, the posterior distributions of Bayesian simulations of ellipse areas (SEAB) also suggest a size difference in population niche at Nelson Lakes NP compared to the two other sites (Fig. 2). The size of the niche exploited by a population of stoats was inversely related to rat abundance (c/100CTN) at each site (Fig. 2).

Individual niches and specialisation

The mean WIC of isotopic niche variation followed the same pattern as population niches, with individual stoats at Nelson Lakes NP occupying a larger isotopic niche (mean SEAc 3.00 ‰^{2} ± 2.0 SD, Table 1), but this difference in individual SEAc between sites was not statistically significant (see results of linear models below). The niche-use metric shows that stoats at Nelson Lakes NP did not use a larger proportion of the population total niche (WIC/TNW = 0.4 ± 0.3) compared with stoats at Mt Aspiring and Fiordland NPs (0.4 ± 0.3 and 0.5 ± 0.2, respectively) (Table 1, Fig. 3). For the 46 stoats that met the known age and sex criteria for linear models, there were no statistically significant effects of site, stoat age, stoat sex or number of tissues included on the size of niche occupied (SEAc) (linear model: Site: F2, 42 = 1.63, p = 0.21; Age: F1, 42 = 1.01, p = 0.32; Sex: F1, 42 < 0.01, p = 0.98; Number of tissues: F1, 42 = 0.05, p = 0.68).

Likewise, neither site nor the number of tissues included in each ellipse was a significant predictor of SEAc (linear model: Site F2, 40 = 2.12, p = 0.13; Collagen: F1, 40= 0.08, p = 0.78; Claw: F1, 40 = 0.008, p = 0.92; Liver: F1, 40 < 0.01, p = 0.97; Vibrissae F1, 40 = 0.37, p = 0.54).

Discussion

These results in part support our hypothesis that stoats act as individual specialists within a generalist population niche, but in certain settings only. Despite the population of stoats at Nelson Lakes NP appearing to have a far broader isotopic niche than populations at the other two sites, individual stoats in Nelson Lakes NP did not have a more generalist niche, according to isotopic niche width analysis. The isotopic niche exploited by the stoat population at Nelson Lakes NP (the between-individual component) was 2.2–2.5 ‰^{2} greater than those of the other sites. While the mean isotopic niche of individual stoats (the

Table 1. Sample sizes and isotopic niche metrics (± standard deviations) for stoats caught in the alpine zone of Nelson Lakes, Mt Aspiring and Fiordland National Parks (NP). Mean individual niche size (WIC) was calculated using SEAc values from 40% individual standard ellipses, using program SIBER (Jackson et al. 2011). Population niche size (BIC) represents the niche size of the total population at each site, using the same method. Niche use is calculated as the proportion of the total niche width used by each individual, or WIC/TNW where TNW=BIC+WIC. TA measures the total area of isospace contained by a maximum convex polygon around all datapoints in the set. SEA measures the area contained in a ellipse around 40% of all datapoints in the set, which is less sensitive to extreme values and allows for differing sample sizes.

	Nelson Lakes NP	**Mt Aspiring NP**	**Fiordland NP**
Number of stoats (Female/Male/Unknown)	14 (7/7/0)	17 (7/9/1)	20 (7/11/2)
Sample size per tissue (claw-collagen-fur-whisker-liver)	14-14-13-12-7	16-17-17-14-5	19-19-20-17-14
Mean individual niche size (‰^{2}) (*mean SEA*)	2.1 (± 1.6)	1.5 (± 1.0)	1.8 (± 0.7)
Mean individual niche size, corrected (‰^{2}) (*mean SEAc = mean WIC*)	3.0 (± 2.0)	2.2 (± 1.5)	1.4 (± 0.9)
Population niche size (‰^{2}) (*BIC*)	5.3	3.1	2.8
Mean proportion of individual niche use (*WIC/TNW*)	0.4 (± 0.3)	0.4 (± 0.3)	0.5 (± 0.2)

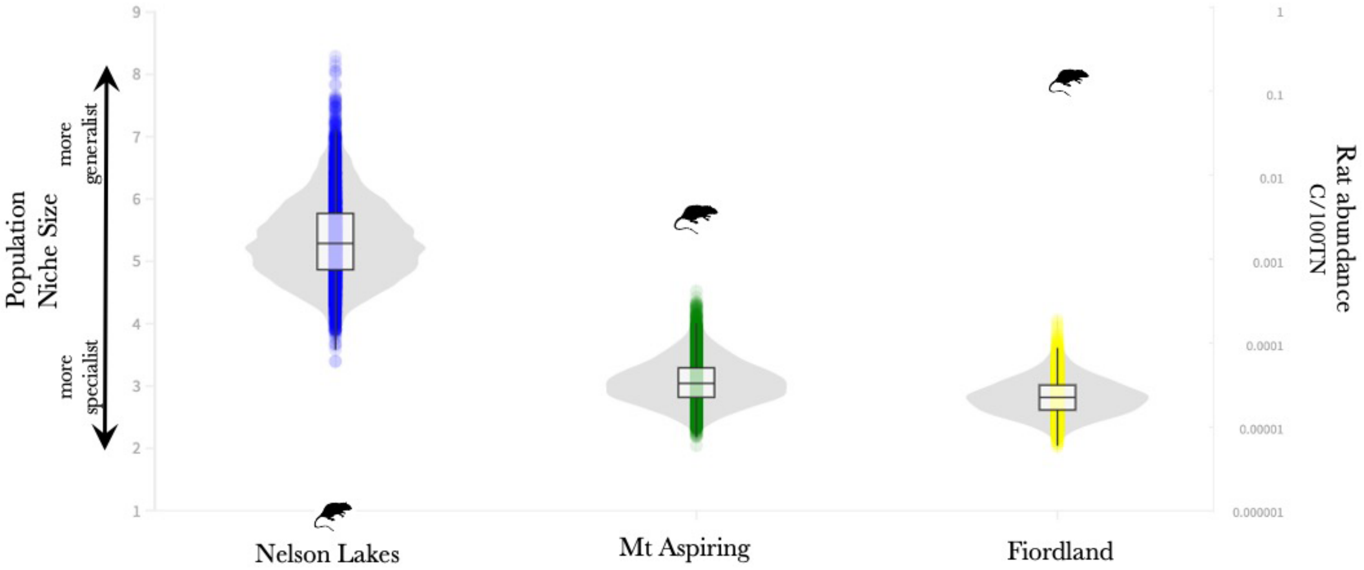

Figure 2. The size of the isotopic niches of three populations of stoats in comparison to the abundance of ship rats at each site. Violin plots show the data distribution of Bayesian Standard Ellipse Areas (SEAB) of the range of values returned from the model (coloured points), boxplots show median (centre line), upper and lower quartile values (box) and 95% intervals (whiskers). Ship rat abundance, indicated by the black rat symbols, is measured in catch per 100 trap nights corrected for sprung traps (c/100CTN), shown on a Log scale.

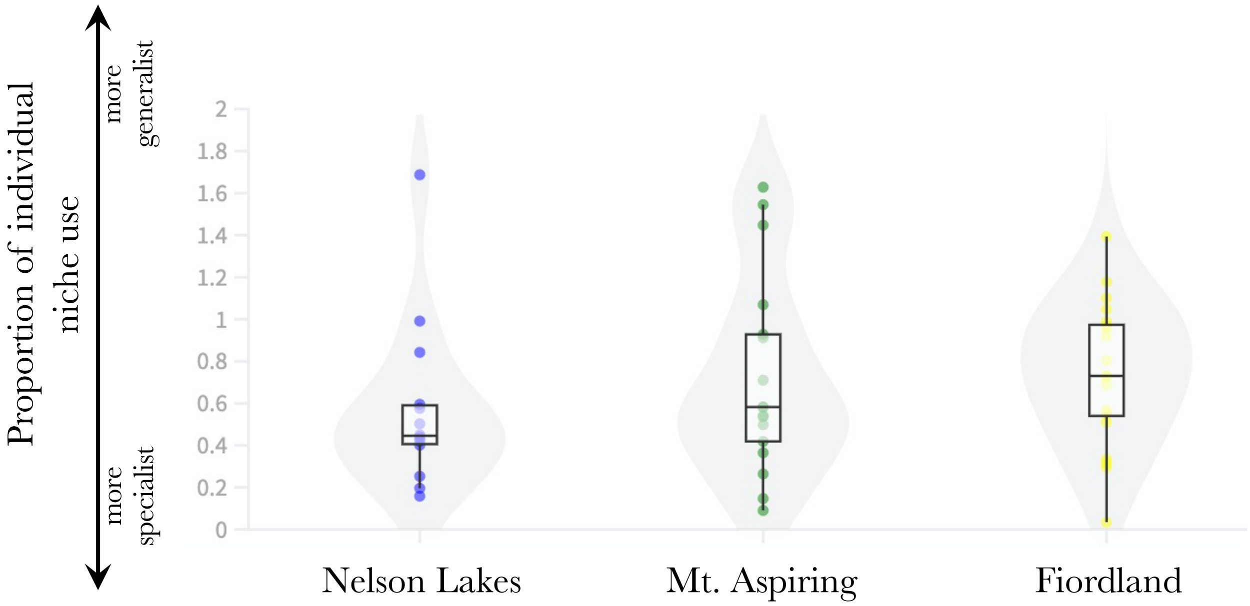

Figure 3. Individual specialisation/niche use metric of individual stoats caught in the alpine zone of Nelson Lakes, Mt Aspiring and Fiordland National Parks. Individual niche use is calculated as the size of an individual stoat's niche (WIC) as a proportion of the true niche width (TNW), at each site. Coloured points show individual niche use values for stoats, grey shading shows data distributions of these points, boxplots show median (dark line), upper and lower quartile values (box) and 95% intervals (whiskers). Data falling outside this range are plotted as outliers (dots).

within individual component) was also larger at Nelson Lakes NP, the proportion of the population-niche used by most stoats was no larger at Nelson Lakes than at other sites.

Why do the population niche sizes vary?

The ecological niche use by a predator can be driven by a variety of factors including resource availability (such as the abundance of prey) (Frentiu 2004) and variable predator density (affecting between-species or within-species competition). Examining resource availability as a possible driver of niche width in the present study is constrained by limited data on prey abundance at our study sites. However, the inverse relationship that we identified between ship rat abundance and population niche size at each site supports previous evidence of the importance of rats to stoat diet (Murphy & Bradfield 1992; Murphy et al. 1998; Murphy et al. 2008; Jones et al. 2011). McAulay et al. (2020) found that the abundance of both ship rats and stoats was a significant factors explaining the proportions of prey consumed by stoats at our study sites; ship rat abundance was positively correlated with the proportion of small mammals in stoat diets. We found that isotopic niches for populations of stoats were smaller at sites with higher rat abundance, signifying a smaller range of prey being at risk of regular predation by stoats at these sites. These results are consistent with practitioner knowledge of stoat management in alpine areas. The increase in stoat abundance following rat population explosions (Murphy et al. 1998; Blackwell et al. 2001) means that alpine birds like takahē (*Porphyrio hochstetteri*) are at greater risk of being preyed upon by stoats during the decline phase of a rodent plague, when stoat numbers remain high (Andrew Digby, DOC, unpubl. data).

Other research also suggests that prey consumption in the alpine zone is linked to resource abundance. In a 12-day food-addition experiment in Fiordland National Park, stoats functionally responded to the extra resources by switching to the newly available food source (frozen rabbit *Oryctolagus cuniculus*) and reducing their intake of hares (*Lepus copenus europaeus*) and wētā (flightless members of the Orthoptera order) (Smith et al. 2010). This experimental evidence shows short-term constriction of niche use as a more optimal resource becomes available. No rats were detected during the study period of that experiment. In the beech forest at Rotoiti, when mice were abundant and rat abundance had been reduced, mouse consumption appeared to provide a buffer preventing a diet switch to birds and invertebrates (Clapperton et al. 2011).

Although no data are available on the abundance of house mice (*Mus musculus*) at our study sites, moderate to high mouse numbers are not believed to elicit a change in the per capita consumption of prey by stoats (King 1983). Similarly, increased mouse tracking rates in mixed podocarp forest were not related to the diet of stoats, but increased rat tracking aligned with greater rat consumption and lower consumption of other prey types by stoats (Murphy et al. 2008). These patterns could be due to marginal bioenergetic benefits of hunting house mice, compared with other small mammals (Raymond et al. 1990; White & King 2006). Intraspecific competition can significantly affect the sizes of dietary niches exploited by predators (Bolnick et al. 2011) and lead to increased individual specialisation within the niche (Holbrook & Schmitt 1992). The size of isotopic population niches were proportional to the stoat trap-catch at each of our study sites. However, the cryptic biology and large widths of stoat home ranges complicate measures of stoat abundance in alpine areas (Smith & Weston 2017; Rawlence 2018). Density of stoat traps and geographic layout at our study sites varied greatly, further complicating the use of stoat trap catch as a measure of stoat abundance. Hence, effects of intraspecific competition should be interpreted with some caution. McAulay et al. (2020) showed that rat abundance and site-level variation are more meaningful than stoat abundance in explaining diet of alpine stoats, but that intraspecific competition is a factor in the proportions of prey consumed. The differences in niche size between sites in this study are likely an interaction of multiple factors combined. The relatively few rats and relatively many stoats at Nelson Lakes NP aligned with a large population niche and high level of individual specialisation in the diet of stoats. Conversely at Fiordland NP, with high rat abundance and fewer stoats than at other sites, the dietary niche was small and concentrated on the energetically rewarding mammalian prey (McAulay et al. 2020).

These findings have implications for conservation managers attempting to predict periods when stoats consume a greater proportion of threatened alpine species. Our data suggest that the range of species regularly preyed on by stoats varies spatially, and is correlated with the abundance of a preferred mammal prey (ship rats), although our study had too few replicates to test this correlation formally. In the New Zealand alpine zone managers should expect that non-mammal fauna (including many threatened species) will form a greater proportion of stoat diet in periods or regions of low ship rat abundance. This relationship demonstrates the importance of considering both numerical and functional factors when assessing risks posed by invasive species.

Why do individuals not consume a wider range of prey?

Our data suggest that, despite the wide ecological niche exploited by stoats at Nelson Lakes NP, the proportions of this niche used by individual stoats were no larger than elsewhere; stoats at that site acted as individual specialists within a generalist niche. Individuals that specialise on one prey strategy likely form more effective search images and can optimise their foraging success, giving them an advantage over generalist individuals (Bolnick et al. 2003). Such foraging trade-offs, targeting a limited number of prey types with greater success, may be driven by a number of factors including limited prey recognition, learned behaviour, forager physiology, social status, or microhabitat selection (reviewed in Bolnick et al. 2011). Adult hunting preferences in ferrets (*Mustela purorious*) are linked to olfactory imprinting stimuli introduced during early life (pre and post-natal) when neural synapse contacts are still being formed (Apfelbach 1986).

Stoat kits learn to hunt in family groups before becoming independent of their mother (King et al. 2010). Little et al. (2017) showed video evidence of four stoats visiting the nest of an alpine passerine, entering and exiting repeatedly. Little et al. (2017) propose this was a party of young stoats learning to hunt and suggested that such social learning can lead to uneven predation pressure unrelated to stoat density at a larger scale. Our data support this hypothesis, and may help explain the unsustainably high levels of predation observed in that species, and others (Taborsky 1988; Powlesland 1989; Dowding & Murphy 1993; Reardon et al. 2012; Hope 2014; Moseby et al. 2015; Weston et al. 2018). If predation rates observed reflect behaviour of individual specialists rather than the population as a whole, this could explain why the native prey species of interest has not become extinct in areas where very high predation rates have been observed.

Individual specialisation could also explain the very large responses in conservation outcomes in some cases – for example the removal of a limited number of stoats from breeding sites of the alpine passerine rock wren (*Xenicus gilviventris*) led to large increases in nesting success (Weston et al. 2018). We hypothesise that, as in medium-bodied carnivores (Swan et al. 2017), predator profiling targeting specialised stoats could reduce predator-prey interactions of conservation concern with greater impact than a non-targeted approach.

Within their native range, stoats have evolved to exploit short-term population expansions of rodents such as rats (*Rattus* spp.) and lemmings/voles (Arvicolinae) (Korpimäki et al. 1991; Gilg et al. 2006). The ability of stoat populations to expand their dietary niche as individuals specialise on different taxa as this core resource diminishes may be an evolved strategy to prolong survival through the decline phase temporally of available resource pulses typical of stoats native range. Further study of stoat diet in relation to numerical fluctuations in alpine stoat and rodent population abundance following beech (Nothofagaceae) and tussock (*Chionochloa* spp.) masting events would assist in assessing whether stoat niche expansions are linked to fluctuating predator and prey densities.

Limitations and other factors affecting niche widths

Two recent studies found that niche widths can be significantly affected by severe nutritional stress (Gorokhova 2017; Karlson et al. 2018). Karlson et al. (2018) showed SEAc increased by 40–110% in amphipods *Monoporeia affinis* under nutritional stress, and decreased in those fed a high-quality diet. There is no published experimental work examining factors affecting the expression of SEAc in multi-tissue studies or in mammals. Lack of important prey, such as rats, could cause nutritional stress leading to biased estimates of SEAc in this study. It is possible that the 170–189% difference in population SEAc (BIC) between our sites was caused or augmented by nutritional stress. However, given the long turnover period of bone collagen and lack of effects of age or tissue on SEAc estimates, we believe it unlikely that extreme nutritional stress caused the full difference in niche sizes observed in this study. Differences in isotopic signatures in consumers can be caused by changes in diet of their prey; McAulay et al. (2020) showed no difference in isotopic composition of stoat prey items at our sites during the study period.

The use of 40% stable ellipse areas, which do not incorporate extreme values in niche size estimates, gives us confidence that few stoats are not skewing the population niche estimate (BIC) at one site. However, given the small sample size at each site and high number of juveniles in the sample, it is plausible that one large cohort of related juveniles could have biased results at any site. Because in post beech mast years (such as during our study period), stoats may produce litters of up to 13 young (King & Moody 1982a), and given the proposed matrilineal learning pathway in stoats acquiring hunting skills (Little et al. 2017), differences observed might have been augmented by relatedness among individuals and shared learning experiences. In future studies of species with large litters and matrilineal learning, we suggest analysing genetic relatedness as a potential confounding factor.

Implications for landscape style management

Our results suggest that in landscape-level predator control programmes, the widespread assumption that removal of any one individual will be of equal benefit to native wildlife is not always justified. While further research is needed to understand the drivers behind such variation and the temporal plasticity of individual foraging preferences, this information should influence how we manage this invasive species, particularly in an alpine setting. Our findings also demonstrate issues with a bioindicator species monitoring approach. When monitoring threatened species outcomes (e.g. survival or nesting success) in response to stoat control we should not assume that the same benefits accrue to other sensitive species in the area, as has already been shown for forest birds in New Zealand (Hoare et al. 2013).

A high level of individual specialisation in a low rodent environment might affect capture probability of stoats in some settings and could explain the variable response of stoats to trapping operations (Robertson et al. 2016). Individual specialisation could explain the difficulty in eradicating stoats from islands where optimum mammalian prey are absent, such as rat-free Maud or rodent-free Secretary Islands (Crouchley 1994; Edge et al. 2011). A multi-method approach may increase the success of such operations, because capture probability in traps may differ between individual specialists with unique foraging preferences (Linklater et al. 2013; Clapperton et al. 2017; Garvey et al. 2020). Incorporating a selection of trap designs and bait types within stoat control networks could increase the overall probability of capturing stoats. Similarly, alternative trapping lures could achieve greater outcomes for native species by targeting specialists within the niche (Robbins et al. 2007; Clapperton et al. 2017). For example, sonic lures of nestling bird recordings or olfactory lures might target individuals that have learned to specialise on this prey type. Alternately, non-lure-based methods (e.g. predator repellents) could reduce impacts from individual specialists less likely to interact with lethal control tools (Clapperton 2018; Garvey et al. 2020). Further research into the optimum niche of alpine stoats could highlight optimum prey, and hence bait items, central to the preferred niche of stoats.

Acknowledgements

Colin O'Donnell and Kerry Weston provided great impetus, feedback and assistance to get this study off the ground. Many volunteers helped in the field and lab; including Fraser 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 to this study. 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 research happen. We hope that our results can help you in your task. This study was conducted under Otago University Animal Ethics Committee approved protocol number ET27/2016 and was conducted under the Department of Conservation Alpine Research Programme. This work was supported by a grant from the Miss E.L. Hellaby Indigenous Grasslands Trust, and the manuscript was helped by two reviewers who volunteered feedback to improve this work.

Author Contributions

All authors conceptualised and designed the study. JM carried out all data collection and analysis, and wrote the manuscript, to which all authors contributed revisions and refinements. All authors read and approved the final manuscript.

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Received: 5 October 2020; accepted 17 May 2021
Editorial board member: Jason Tylianakis