Merky forests: What can we expect from stoat control in NZ forests

Methods draft

## Summary

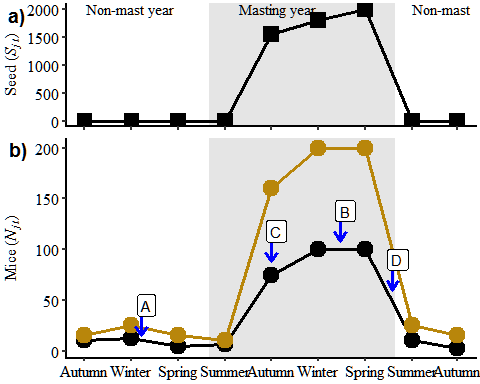
This publication clarifies the discrepancy between; two modelling papers that suggest mesopredator release of rodents is possible in New Zealand forest systems and; several field studies that have presented limited but conflicting support for increases in mouse abundance following predator control. We used an experimental design to test the differences between the two “frames of though” and found that there is no evidence to suggest mice will become more abundant after predator removal.

[*Supporting documents can be found here*](https://davan690.github.io/invasive-species-research/)

## Introduction

Worldwide, but particularly on islands, introduced mammalian predators can have significant impacts on native species (Towns, Atkinson, and Daugherty 2006). Generally, an undesired pattern of predator removal results in the subsequent increase in other invasive predators after the target species has been removed (e.g. mesopredator release; Soule et al. (1988)). New Zealand’s (NZ) remaining native forests commonly contain four introduced mammalian predators; stoats (*Mustela erminea*; (Veale 2015)), brushtail possums (*Trichosurus vulpecula Kerr*; (Clout and Gaze 1984)), ship rats (*Rattus rattus*; (Innes 2005) referred to as rats), and house mice (*Mus mus musculus*; (Allen and Lee 2006)). In these systems, stoats are commonly identified as the top predator since their deliberate introduction to NZ in the late nineteenth century (King 2017). Stoat control is now commonly undertaken to protect native birds that are vulnerable to predation (White and King 2006), for example, hole-nesting species like mohua (*Mohoua ochrocephala* (ODonnell and Phillipson 1996)). However, the primary food source for stoats in NZ forests are smaller introduced mammals (White and King 2006) and a legitimate concern is that by reducing stoat populations to protect native birds this may also allow rodent populations to increase (e.g (Rayner et al. 2007)). This increase of mesopredator abundance (rats and/or mice) would offset the benefits of stoat control as mesopredator abundance increases. On islands, rodent populations are known to consume the eggs and chicks of native birds (Allen and Lee 2006), directly compete for food resources such as the flowers and seeds of native flora (McQueen and Lawrence 2008) and directly predate on invertebrates (Ruscoe et al. 2013) but less is known about mouse predation on native invertibrates (St Clair 2011). Here we address the knowledge gap surrounding the critical question; "Does stoat control lead to increased abundance of rodents, particularly mice, in NZ forests Beech Forests?

Studies elsewhere in the world have shown that removing or reducing the abundance of a top predator often results in mesopredator release, which in turn, can lead to unintended and often negative outcomes for native species (overall review see (Prugh et al. 2009); examples see (Rayner et al. 2007; Robles and Desharnais 2002)). While mesopredator release has been widely documented, it is unclear if stoat control in NZ forests will cause mice populations to increase. Mice populations typically respond strongly to variation in food supply (Latham et al. 2017), primarily seed availability in NZ forests (Figure 1).



**Figure 1:** Each arrow and label represents a prediction we tested (Prediction B to D). Each prediction represents a collection of previous studies that have suggested how mouse populations may respond to seed availability in the presence or absence of stoats. A) during the years when no seed is avaliable (non-mast years; Panel A); B) at the peak of mouse abundance (winter or spring); C) the season when mice populations are responding rapidly to increasing seed abundance (summer to winter in mast years; Panel B); D) when mouse abundance declines (spring to summer; Panel B). The top panel represents the average seed avaliability cycle in New Zealand Native Beech Forests between non-mast (no shading) and mast years (shaded grey). The bottom panel represents the expected response of mouse abundance () to the variation in seed availability ($Seed\_{j,t}) above where solid yellow symbols represent locations where stoats are un-controlled

This is particularly prominent in New Zealand beech forests (Figure 1), which collectively contribute to over of all remaining native forest (Wardle 1991). Between years, beech seed production is highly variable with little seed produced in most years (Figure 1: non-mast years) and occasional years of substantial seed production (Figure 1: mast years). Mouse populations remain low in non-mast years, primarily due to low food availability (Figure 1b; **Prediction A** = label “A”; Choquenot and Ruscoe (2000), King (1983)). In mast years, when seed becomes abundant, mouse populations can increase rapidly but show predictable fluctuations in response to seasonal changes in beech seed availability (Figure 1b: **Prediction B to D** = label “B-D”; ). Seed begins to fall in late summer and begins to accumulate on the forest floor, allowing mouse populations to increase from late summer onward, with mouse populations typically remaining high through winter and into the following spring. Beech seed that is not consumed by mice and other seed predators, then germinates in spring to early summer, meaning this food resource disappears and mouse populations begin to decline. If the following year is a non-mast year and little further seed becomes available, mouse populations fall to low levels. It is unclear whether stoats could exert sufficiently strong predation pressure to alter these food-driven population eruptions.

Previous research has investigated this in two ways, papers have modelled the likely outcome of interactions between stoats, mice and seed availability. Blackwell, Potter, and Minot (2001) simulated this relationship and predicted that impacts of stoat predation on mice populations would have limited effects on the population dynamics of mice but would vary during different seasons of the mast cycle (Figure 1). In a subsequent study, Blackwell and colleagues tested their predictions in the field and found evidence that in general, stoats may be able to slow, but not prevent rodent eruptions (Blackwell et al. 2003). They also observed varying support to suggest that the control of stoats could modify rodent population at the peak (**Prediction B**), decline (**Prediction C**) or low (**Prediction A**) seasons. However, the limited geographical scale of the study, low statistical power and replication between different forest types makes it difficult to compare the effect of different treatment types during the four different seasons. The effects of stoat control on mice and rats are therefore still unclear in NZ beech forests (Blackwell et al. 2003). More recently, the population dynamics of interacting invasive mammals in NZ forests have also incorporated the interactions between mice, rats, possums and stoats (Blackwell, Potter, and Minot 2001; Blackwell et al. 2003; Tompkins and Veltman 2006; Tompkins, Byrom, and Pech 2013). Tompkins and colleagues simulated different removal scenarios and found:

1. stoat removal through trapping caused rats but not mice to increase in the subsequent year;
2. removal of both rats and mice lead to lower numbers of stoats in the following years;
3. mice numbers only increased during model simulations if rats or both rats and stoats were removed.

The community models (Tompkins and Veltman 2006; Tompkins, Byrom, and Pech 2013) suggested two additional relationships between mice and rats as well as stoats and rodents(**Prediction E**). Both these relationships were not observed in field studies (Blackwell, Potter, and Minot 2001; Blackwell et al. 2003) but laboratory experiments do indicte that mice and rats avoid interactions (Bridgman et al. 2013). To experimentally test this a gradient of rat densities could create an observable difference to the population dynamics of mice and rats in the wild.

Our aim was to test the predictions outlined in both Blackwell et al. (2003) and Tompkins and Veltman (2006) using data from a large-scale field study. Specifically, we measured the abundance of mice and rats over six years in beech forest in two adjacent valleys, one with stoat trapping and one without. In each valley we also manipulated rat densities by including treatment areas where rats were trapped to compare these to areas without rat trapping. This allowed us to examine the response of mouse populations to stoat removal, and to determine if those responses were influenced by interactions with rats. The response of mice populations to predator removal needs to be clarified as NZ embarks on a predator-free mainland (Russell et al. 2015).

## Materials and methods

We carried out our study in beech forests in the South Island of New Zealand where stoats are the main predator and mice are the most abundant rodent species. Ship rats (*Rattus rattus*; (Innes 2005)) and kiore (*Rattus exulans*; (Roberts 1991)) are also present but at much lower numbers (Jones et al. 2011). We tested whether reducing stoat populations by predator control influenced mouse population dynamics, and whether the outcome was affected by interactions between mice and rats. To do this we needed to account for the observation error associated with the data collection methods and the process error (seasonally predictable fluctuations in mouse abundance). We then tested five predictions regarding how stoat control might impact mouse populations ((Blackwell, Potter, and Minot 2001); (Blackwell et al. 2003); (Tompkins and Veltman 2006); and (Tompkins, Byrom, and Pech 2013); Figure 1: **Prediction A to D**):

1. stoat control could result in a lower peak abundance of mice;
2. stoat control could increase mouse populations in non-mast years when food availability is low. In addition, the model of Tompkins and Veltman (2006) makes a further prediction;
3. stoat control could increase the rate at which mouse populations initially increase in response to high seed availability in late summer;
4. stoat control could hasten the rate at which mouse populations decline from peak abundance;
5. mouse populations might be affected by stoat control (i.e. we observe the outcomes in **Predictions A to D**) but only when rat populations are reduced to low densities.

We modelled the data collection methods and the associated observation error as well as major factors known to influence mouse population dynamics over time (seasonally and annually).

## Data

Since 1983, the Hollyford Valley (GPS *co-ord*, $44^{\circ} \space S, \space 168^{\circ} 1 \space E$) has had intensive stoat control undertaken to protect a vulnerable population of mohua (ODonnell and Phillipson 1996). In contrast, the Eglinton Valley ( GPS *co-ord*: $44^{\circ} 2 \space S, \space 168^{\circ} 5 \space E$ ) had no stoat control conducted prior to and during the first part of our experiment (*pers comms*). To test **Predictions A-D**, we set up four independent grids, in each valley. On each grid, the abundance of rodent species (mice, rats and kiore) were monitored using Elliot traps. Each grid comprised of traps with each trap located metres apart in a grid covering a total area of $2.56 \space ha \space (25600 \space m^2)$.

We estimated the abundance of rodents on each grid using capture-mark-recapture (CR). All rodents were captured and marked with ear tags so that individual could be uniquely identified. Individual rodents had single unique ear-tags and rats were double ear tagged. Each individual was also ear notched using notch position to identify the night of first capture and to identify animals that had been captured but lost ear tags. For each rodent captured, we collected data on each individual capture, trip and grid location, as well as tag number and notch position. We aimed to trap for five nights on each trip but due to unfavourable weather restrictions during some trips, the number of trapping nights on those trips were reduced. We carried out a total of trips and trapped for three nights on *2* trips, *4* nights for a total of four nights and three nights on *14* trips.

To experimentally reduce rat (kiore and ship rats collectively) densities on some grids we randomly selected two grids from each valley and we physically reduced rat densities on these grids by removing all captured rats on those grids by humanely killing them. For the remaining two grids in each valley, we marked and released rats, as we did for mice captures.

We sampled the amount of seed reaching the forest floor we placed four standard circular seed-traps **randomly** on each grid. These traps were permanent over the duration of the study and each trap was elevated metres above the ground and covered by wire netting to preclude seed predators. This allowed seed traps to capture any falling seed within the area of the trap for the duration between two consecutive trips. The contents of each seed-trap was collected once during each trip ().

To measure the available food for mice populations we only recorded seeds with a kernel because rodents are known to only consume the kernel of beech seeds. Each trap had a radius of metres which over each trip equates to an overall sampled area on each grid of

We undertook a total of *20* trips spaced *3* months apart from May 1999 to February 2004 ( trips in total), with each trip corresponding to one of four pronounced seasonal differences in mice dynamics (May = Autumn, August = Winter, November = Spring and February = Summer). The treatments applied to each grid (two valleys; one with stoat control, one without, and; four grids in each valley, two with rat control and two without) were maintained from May 1999 to August 2002. We removed rats from two grids (one in each valley) to experimentally test the effects of interactions between mice and rats. Data collection was reduced to three grids in each valley from November 2002 onwards to focus on the before/after treatment (before = no stoat control, after = stoats controlled) in the Hollyford Valley. Our statistical model below incorporates the data collection methods above to compare the five predictions we are interested in.

## References

Allen, Robert B, and W G Lee. 2006. *Biological Invasions in New Zealand*.

Blackwell, G L, M A Potter, J A McLennan, and E O Minot. 2003. “The Role of Predators in Ship Rat and House Mouse Population Eruptions: Drivers or Passangers?” *Oikos* 100 (3): 601–13.

Blackwell, G. L., M. A. Potter, and E. O. Minot. 2001. “Rodent and Predator Population Dynamics in an Eruptive System.” *Ecological Modelling* 142 (3): 227–45. <https://doi.org/10.1016/S0304-3800(01)00327-1>.

Bridgman, L. J., J. Innes, C. Gillies, N. B. Fitzgerald, S. Miller, and C. M. King. 2013. “Do Ship Rats Display Predatory Behaviour Towards House Mice?” *Animal Behaviour* 86 (2): 257–68. <https://doi.org/10.1016/j.anbehav.2013.05.013>.

Choquenot, David, and Wendy A Ruscoe. 2000. “Mouse Population Eruptions in New Zealand Forests: The Role of Population Density and Seedfall.” *Journal of Animal Ecology* 69: 1058–70.

Clout, M. N., and P. D. Gaze. 1984. “Brushtail Possums (Trichosurus Vulpecula Kerr) in a New Zealand Beech (Nothofagus) Forest.” *New Zealand Journal of Ecology*, 147–55.

Innes, John G. 2005. “Ship Rat.” In *The Handbook of New Zealand Mammals*, edited by Carolyn M King, 2nd ed., 187–203. Melbourne: Oxford University Press.

Jones, Christopher, Roger Pech, Guy Forrester, Carolyn M. King, and Elaine C. Murphy. 2011. “Functional Responses of an Invasive Top Predator Mustela Erminea to Invasive Meso-Predators Rattus Rattus and Mus Musculus, in New Zealand Forests.” *Wildlife Research* 38 (2): 131–40. <https://doi.org/10.1071/WR10137>.

King, Carolyn M. 2017. “Pandora’s Box down-Under: Origins and Numbers of Mustelids Transported to New Zealand for Biological Control of Rabbits.” *Biological Invasions* 19 (6): 1811–23. <https://doi.org/10.1007/s10530-017-1392-6>.

King, Carolyn M. 1983. “The Relationships Between Beech (Nothofagus Sp.) Seedfall and Populations of Mice (Mus Musculus), and the Demographic and Dietary Responses of Stoats (Mustela Erminea), in Three New Zealand Forests.” *Journal of Animal Ecology* 52 (1): 141–66.

Latham, A. David M., Bruce Warburton, Andrea E. Byrom, and Roger P. Pech. 2017. “The Ecology and Management of Mammal Invasions in Forests.” *Biological Invasions* 19 (11): 3121–39. <https://doi.org/10.1007/s10530-017-1421-5>.

McQueen, Shirley, and Barry Lawrence. 2008. “Diet of Ship Rats Following a Mast Event in Beech (Nothofagus Spp.) Forest.” *New Zealand Journal of Ecology* 32 (8): 214–18.

ODonnell, C F J, and S M Phillipson. 1996. “Predicting the Incidence of Mohua Predation from the Seedfall, Mouse, and Predator Fluctuations in Beech Forests.” *New Zealand Journal of Zoology* 23 (3): 287–93. <https://doi.org/10.1080/03014223.1996.9518087>.

Prugh, Laura R., Chantal J. Stoner, Clinton W. Epps, William T. Bean, William J. Ripple, Andrea S. Laliberte, and Justin S. Brashares. 2009. “The Rise of the Mesopredator.” *BioScience* 59 (9): 779–91. <https://doi.org/10.1525/bio.2009.59.9.9>.

Rayner, Matt J, Mark E Hauber, Michael J Imber, Rosalie K Stamp, and Mick N Clout. 2007. “Spatial Heterogeneity of Mesopredator Release Within an Oceanic Island System.” *Proceedings of the National Academy of Sciences of the United States of America* 104 (52): 20862–5. <https://doi.org/10.1073/pnas.0707414105>.

Roberts, Mere. 1991. “Origin, Dispersal Routes, and Geographic Distribution of Rattus Exulans, with Special Reference to New Zealand!” *PACIFIC SCIENCE* 45: 8.

Robles, Carlos D, and Robert Desharnais. 2002. “History and Current Development of a Paradigm of Predation in Rocky Intertidal Communities.” *Ecology* 83 (6): 1521–36. [https://doi.org/10.1890/0012-9658(2002)083[1521:HACDOA]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083%5B1521:HACDOA%5D2.0.CO;2).

Ruscoe, Wendy A., Peter J. Sweetapple, Mike Perry, and Richard P. Duncan. 2013. “Effects of Spatially Extensive Control of Invasive Rats on Abundance of Native Invertebrates in Mainland New Zealand Forests: Effects of Invasive Rat Control.” *Conservation Biology* 27 (1): 74–82. <https://doi.org/10.1111/j.1523-1739.2012.01932.x>.

Russell, James C., John G. Innes, Philip H. Brown, and Andrea E. Byrom. 2015. “Predator-Free New Zealand: Conservation Country.” *BioScience* 65 (5): 1–6. <https://doi.org/10.1093/biosci/biv012>.

Soule, Michael E, Douglas T Bolger, Allison C Alberts, John Wright, and Scott Hill. 1988. “Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands.” *Conservation Biology* 2 (1): 75–92.

St Clair, James J. H. 2011. “The Impacts of Invasive Rodents on Island Invertebrates.” *Biological Conservation* 144 (1): 68–81. <https://doi.org/10.1016/j.biocon.2010.10.006>.

Tompkins, Daniel M., Andrea E. Byrom, and Roger P. Pech. 2013. “Predicted Responses of Invasive Mammal Communities to Climate-Related Changes in Mast Frequency in Forest Ecosystems.” *Ecological Applications* 23 (5): 1075–85. <https://doi.org/10.1890/12-0915.1>.

Tompkins, Daniel M, and Clare J Veltman. 2006. “Unexpected Consequences of Vertebrate Pest Control: Predictions from a Four-Species Community Model.” *Ecological Applications* 16 (3): 1050–61.

Towns, David R., Ian A. E. Atkinson, and Charles H. Daugherty. 2006. “Have the Harmful Effects of Introduced Rats on Islands Been Exaggerated?” *Biological Invasions* 8 (4): 863–91. <https://doi.org/10.1007/s10530-005-0421-z>.

Veale, Andrew J. 2015. “The Invasion Ecology and Molecular Ecology of Stoats (Mustela Erminea) on New Zealand’s Islands.” PhD thesis, Waitako University.

Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press.

White, Piran C L, and Carolyn M. King. 2006. “Predation on Native Birds in New Zealand Beech Forests: The Role of Functional Relationships Between Stoats Mustela Erminea and Rodents.” *Ibis* 148 (4): 765–71. <https://doi.org/10.1111/j.1474-919X.2006.00579.x>.