Small mammal dynamics in New Zealand beech forests

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Summary

The conflicting outcomes from previous studies provides the motivation for this more comprehensive field study assessing the effects of stoat control on mouse dynamics. Here we clarify the discrepancy between research suggesting that mesopredator release of rodents will occur in New Zealand forest systems and field studies that have presented limited but conflicting support for increases in mouse abundance following predator control. We used an experimental design to test for differences between areas with and without stoat control after accounting for known effects of resources, density and competition on mouse dynamics in NZ beech forests. We found no evidence to suggest mice will become more abundant after predator removal.

Introduction

Worldwide, but particularly on islands, introduced mammalian predators can have significant impacts on native species (Towns, Atkinson, and Daugherty [2006](#ref-towns2006)). New Zealand’s (NZ) remaining native forests commonly contain four introduced mammalian predators; stoats (*Mustela erminea*; Veale ([2015](#ref-veale2015a))), brushtail possums (*Trichosurus vulpecula Kerr*; Clout and Gaze ([1984](#ref-clout1984))), ship rats (*Rattus rattus*; Innes ([2005](#ref-innes2005)) referred to as rats), and house mice (*Mus mus musculus*; Allen and Lee ([2006](#ref-allen2006))). In NZ forests, stoats are the top predator following their deliberate introduction in the late nineteenth century (King [2017](#ref-king2017)). Stoat control is now commonly undertaken to protect native birds that are vulnerable to predation (White and King [2006](#ref-white2006)), in particular, hole-nesting species like mohua (*Mohoua ochrocephala* ODonnell and Phillipson ([1996](#ref-odonnellPredictingIncidenceMohua1996))). However, the primary food source for stoats in NZ forests are rats and mice (White and King [2006](#ref-white2006)) and consequently there is a concern that reducing stoat populations to protect native birds may allow rodent populations to increase (e.g Rayner et al. ([2007](#ref-rayner2007))). An increase in the number of rats and mice could offset the benefits of stoat control because rodents are known to consume the eggs and chicks of native birds (Allen and Lee [2006](#ref-allen2006)), directly compete with native species for food resources such as flowers and seeds (McQueen and Lawrence [2008](#ref-mcqueen2008)) and predate on invertebrates (Ruscoe et al. [2012](#ref-ruscoe2012)). In this paper we address the question: "does stoat control lead to increased abundance of rodents, particularly mice, in NZ beech forests? Studies elsewhere in the world have shown that removing or reducing the abundance of a top predator often leads to an increase in the numbers of predators at lower trophic levels (termed mesopredator release), which in turn, can lead to unintended and often negative outcomes for native species (for a review see Prugh et al. ([2009](#ref-prugh2009)) and for examples see Rayner et al. ([2007](#ref-rayner2007)); Robles and Desharnais ([2002](#ref-robles2002))). While mesopredator release has been widely documented elsewhere, it is unclear if stoat control in NZ forests will cause rodent populations to increase. Rodent populations in NZ forests are known to respond strongly to variation in food supply (Choquenot and Ruscoe [2000](#ref-choquenot2000); Ruscoe, Goldsmith, and Choquenot [2001](#ref-ruscoe2001); Blackwell, Potter, and Minot [2001](#ref-blackwell2001); Blackwell et al. [2003](#ref-blackwell2003); Ruscoe et al. [2005](#ref-ruscoe2005); Tompkins and Veltman [2006](#ref-tompkins2006); Tompkins, Byrom, and Pech [2013](#ref-tompkins2013); Holland et al. [2015](#ref-holland2015); Latham et al. [2017](#ref-latham2017)), primarily seed availability (Figure 1).

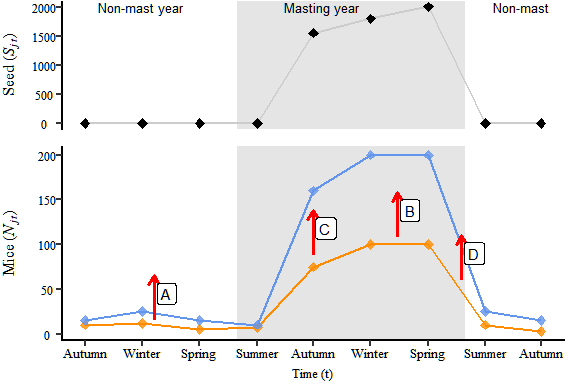


Figure 1: *Expected changes in mouse populations over time in New Zealand forests (bottom panel) in response to changes in seed availability (top panel) during mast and non-mast years.In the bottom panel, the proposed differences between areas with (blue) and without (yellow) stoat control. The arrows labelled A-D point to the four predicted outcomes of stoat removal that we have tested in this paper. A) during non-mast years when little seed is available, B) at the peak of mouse abundance (during winter and spring in mast years), C) during increased seed availability in areas with and without stoat control; D) when mouse populations are declining from peak abundance, areas without stoat control should decrease slower than areas without stoat control.*

This is particularly pronounced in beech forests where, between years, beech seed production is highly variable with little seed produced in most years (Figure 1: non-mast years) and occasional years of high seed production (Figure 1: mast years). Mouse populations are low in non-mast years, due to low food availability (( Choquenot and Ruscoe [2000](#ref-choquenot2000); King [1983](#ref-king1983)). In mast years, when seed becomes abundant, mouse populations can increase quickly following a predictable seasonal cycle. Seed begins to fall and accumulate on the forest floor in late summer (February) allowing mouse populations to increase, with mouse populations typically remaining high through winter (August) and into the following spring (November). Beech seed that is not consumed by mice and other seed predators germinates in spring to early summer, meaning this food resource disappears and mouse populations begin to decline in the subsequent seasons. If the following year is a non-mast year with little seed available, mouse populations fall to low levels. It is unclear whether stoat populations can increase quick enough to exert sufficiently strong predation pressure to alter these food-driven population eruptions. Previous studies have investigated the likely response of mouse populations to stoat control by modelling the outcome of interactions between stoats, mice and seed availability. Blackwell, Potter, and Minot ([2001](#ref-blackwell2001)) made four predictions regarding the likely effects of stoat predation on mouse dynamics (see Figure 1) with a subsequent field study concluding that stoat predation should have minimal effects on the population dynamics of mice. The authors identified three different phases in the eruption cycle where stoats could have an effect (Figure 1) and the subsequent field study (Blackwell et al. [2003](#ref-blackwell2003)) indicated that stoat control has little detectable effect on mouse populations during the peak (**Prediction B**), decline (**Prediction C**) and low (**Prediction A**) phases of the beech eruption cycle. Subsequent modelling work reached similar conclusions (Tompkins and Veltman [2006](#ref-tompkins2006); Tompkins, Byrom, and Pech [2013](#ref-tompkins2013)) but identified that the response of mice to stoat control should depend on interactions with rats. Specifically, (Tompkins, Byrom, and Pech [2013](#ref-tompkins2013)) concluded that, where rats were present, stoat control alone should allow rats to increase, which would have a suppressive effect on mouse populations through either predation or competition. In contrast, when both stoats and rats were controlled, mouse populations could increase to higher levels than in the absence of control (see *Figure 1*). Our aim was to test the predictions outlined in both Blackwell et al. ([2003](#ref-blackwell2003)) and Tompkins and Veltman ([2006](#ref-tompkins2006)) using data from a large-scale field study. Specifically, we measured the abundance of mice and rats on trapping grids over six years in beech forest in two adjacent valleys, one with intensive stoat trapping and one without. In each valley we also manipulated rat densities by including trapping grids where rats were removed and compared these to grids without rat removal. This allowed us to examine if predicted responses of mouse populations to stoat control (see **Prediction A-D**) was influenced by interactions with rats (**Prediction E**).

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 (King [1983](#ref-king1983)). Ship rats (*Rattus rattus*; Innes ([2005](#ref-innes2005))) and kiore (*Rattus exulans*; Roberts ([1991](#ref-roberts1991))) are also present but at much lower numbers (Jones et al. [2011](#ref-jones2011)). We tested whether reducing stoat populations by predator control influenced mouse population dynamics as haypothesised in Figure 1, and whether the outcomes were affected by interactions between mice and rats. Specifically, we tested the following five predictions (Blackwell, Potter, and Minot ([2001](#ref-blackwell2001)); Blackwell et al. ([2003](#ref-blackwell2003)); Tompkins and Veltman ([2006](#ref-tompkins2006)); and Tompkins, Byrom, and Pech ([2013](#ref-tompkins2013)); Figure 1: **Prediction A to D**). If stoat control affects mouse population dynamics then, relative to sites with stoat control (Figure 1; yellow symbols), mouse populations at sites with stoat control should exhibit (direction of red arrow; *Figure 1*): A) Higher mouse abundance in non-mast years;

* Higher peak mouse abundance in mast years;
* A faster rate of mouse population increase in response to high seed availability in late summer/winter;
* A slower rate of mouse population decline from peak abundance;
* Predictions A-D should hold only when both stoats and rats are controlled.

Data collection

Our study was carried out in two adjacent valleys: the Hollyford Valley (GPS *co-ord*, S E ) which has had intensive stoat control since 1983 to protect a vulnerable population of mohua (ODonnell and Phillipson [1996](#ref-odonnellPredictingIncidenceMohua1996)) and the Eglinton Valley (GPS *co-ord*, S E ) which had no stoat control conducted prior to and during the first part of our study (*pers comms*). To test **Predictions A-E**, we set up four trapping grids, in each valley, with each grid located at least **xx** kms apart. On each grid, we monitored the abundance of rodent species (mice, rats and kiore) using Elliot traps (**permit numbers?**. Each grid comprised traps with each trap located metres apart in a grid covering a total area of *ha* . We estimated the abundance of rodents on each grid using capture-mark-recapture techniques (CR), assuming a closed population during each trip, which typically lasted 5 nights. Traps were set prior to each night and all rodents captured were marked with ear tags so that individuals could be uniquely identified. Mice had a single unique ear-tag, rats were double-ear tagged, and each individual was ear notched with a notch position that identified the night of first capture so we could identify animals that had been captured but had lost ear tags. We sexed and weighed each captured animal. We aimed to trap for five nights on each trip but due to unfavourable weather fewer nights were trapped on some trips. We experimentally reduced rat (kiore and ship rats collectively) densities on two randomly selected grids in each valley by removing and humanely killing all captured rats on those grids **ref ethics?**). On the remaining two grids in each valley, we marked and released rats, as we did for mice on all grids. To measure food availability, we recorded the amount of seed reaching the forest floor by placing four standard circular seed-traps at **random** locations on each grid. Each trap had a radius of metres which over each trip equates to an overall sampled area on each grid of . These seed traps were in place for the duration of the study, with each trap elevated metres above the ground and covered by wire netting to preclude seed predators. The contents of each seed-trap were collected once during each trip () and the contents were sorted to remove unwanted plant matter (e.g. leaf litter). We counted beech seeds, recording only those with a kernel because rodents are known to only consume the kernel of beech seeds. We undertook a total of *20* trips to the two valleys, with each trip spaced 3 months apart from May 1999 to February 2004. The timing of trips during the year corresponded to each of the four seasons (February = Summer, May = Autumn, August = Winter, and November = Spring). We aimed to test our predictions about the effects of stoat control by comparing mouse population dynamics in the two valleys. However, because we lacked replication at the valley-level, we could not be certain that differences in mouse population dynamics between valleys was due only to the presence or absence of stoat control. To overcome this, we undertook stoat control in the Hollyford Valley commencing in May 2002, allowing us to examine mouse dynamics in the presence or absence of stoat control in the same valley in addition to the between-valley comparison. Stoats were removed in the Hollyford Valley using 13 Fenn Traps (are they following the road wendy? On map?). The original treatments applied to the eight grids (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. From **CHECK** onwards, we stopped collecting data from one rat control grid in each valley (Figure 2).

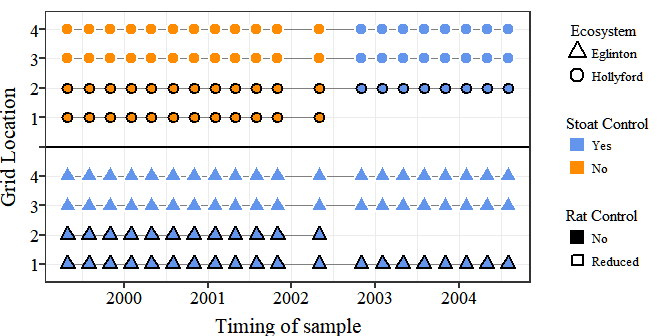


Figure 2: Schematic of the sampling design for this study showing the four grids in each valley labelled on the y-axis. Each symbol represents a trip where mouse abundance, rat abundance and seed availability were measured on each grid. Circles represent grids in the Hollyford Valley and triangles for grids in the Eglinton Valley. Yellow symbols represent the grids with stoat control and blue for grids without stoat control. Black outlined/hollow points represent areas with rat reductions and solid symbols have no rat modifications. From May 2002 onward, stoat control commenced in the Hollyford valley and monitoring ceased on one grid without rat control in each valley.

Statistical modelling

Mouse abundance

We used the capture-recapture (CR) data to estimate the number of mice () on each grid () during each trip (), assuming the numbers of mice on each grid were independent of each other and that the populations on each grid were closed for the duration of each trip. We had data on the number of times each mouse, *i*, was captured on each grid, during each trip (). We used the method described in Royle, Dorazio, and Link ([2007](#ref-royle2007)) to estimate the number of mice from the CR data using data augumentation (Royle [2009](#ref-royle2009), @royle2012). This involved augmenting data for the individual mice captured on each grid during each trip with pseudo-individuals that represented mice that were potentially present on the grid but were not captured during our study. For these pseudo-individuals, the number of captures was set to zero. Each individual mouse, including the pseudo-individuals, was assigned an indicator variable taking the value 1 if the individual was present on the grid and 0 otherwise. For mice that were captured, is known and takes the value 1. For the pseudo-individuals, the value of is unknown and was estimated by modelling it as drawn from a Bernoulli distribution with overall probability of presence on a grid during a trip, :

The probability an individual mouse (including pseudo-individuals) was captured times was drawn from a binomial distribution with probability, , conditional on the number of nights trapping on each grid during each trip .

is the probability an individual was captured during one night of trapping on a grid. This depends on whether the individual was present on the grid or not () and the probability of capture conditional on presence ().

We specified the number of pseudo-individuals () to be the total number of mice captured on each grid during each trip (), which should be sufficient to ensure a non-informative prior (Royle, Converse, and Link [2012](#ref-royle2012a); Ruscoe et al. [2011](#ref-ruscoe2011)). We expected heterogeneity in the capture probabilities between grids and trips, and there is often heterogeneity among individuals in capture probability for small mammals (Krebs et al. [2011](#ref-krebs2011)). We therefore modelled variation in individual capture probability on the logit scale, allowing for heterogeneity by assuming values were drawn from a normal distribution with a different mean for each trip and grid (). and a variance estimated from the data, which reflected unobserved among-individual heterogeneity. The mean capture probabilities for each trip and grid () were modelled hierarchically, treating them as draws from a normal distribution with overall mean and variance estimated from the data.

We estimated the number of mice on each grid during each trip by summing all the values of .

Prediction A and B

We tested our predictions as follows. To test if *stoat control resulted in more mice in non-mast years when mouse abundance was low* (**Prediction A**), we compared mouse abundance () on grids with and without stoat control during low periods of seed availability using two-way analysis of variance.

To test if stoat control resulted in higher peak mouse abundance (**Prediction B**) we needed to account for the fact that peak abundance on grids would be partly driven by food availability (King [1983](#ref-king1983)). We therefore compared the number of mice per seed () among grids with and without stoat control using the same ANOVA test as **Prediction A**.

Prediction C and D

To test **Prediction C** and **D** we modelled the **rate of increase of mice** () during the relevant seasons (Figure 1) with rate of increase calculated as:

To estimate () and propagate the uncertainty in our abundance estimates we used the complete data likelihood approach described by Schofield and Barker ([2014](#ref-schofield2014)) (for details see Appendix 1.1). To test predictions C and D we compared rates of increase with and without stoat control. To do this, we needed to account for other factors known to affect rates of increase in mouse populations, including seed availability, density dependence, and potential interactions with rats.

Seed availability

We fitted three response models () to assess the relationship between our seed trap data and the (Ruscoe et al. [2005](#ref-ruscoe2005)). We wanted to estimate the relationship between the population growth of mice () and the “intake rate” () however we had to account for the limiting biological factor that seed falls quicker than mice can consume it and therefore does not represent a direct numerical relationship between seedfall and mouse production.

The first two models we fitted to account for this were numerical responses;

1. a simple linear Type I response, where each seed represents a direct linear effect on . Meaning that there is infact a direct linear converson rate between seedfall and mice abundance.
2. the Type II response proposed by Holling ([1959](#ref-holling1959)) which represents a simple logistic curve. We fitted this parameterisation to our field data .

The final response model was a functional response;

1. The data used to fit this model were collected in the Eglinton Valley (Ruscoe et al. [2005](#ref-ruscoe2005)). (**???**) fitted a wide range of functional responses to labratory data harvested from the same valley as rates of increase in mice populations (). They concluded that the IR (type II functional response) proposed by Choquenot and Ruscoe ([2000](#ref-choquenot2000); Ruscoe et al. [2005](#ref-ruscoe2005)).

Each of the functions above () we fitted the rate of increase of mice () estimated from the CR model above to the cumulative beech seedfall data (). We fitted our selection of models to a reduced dataset, where, each data point represents the average seedfall at a given grid () and trip () compared to the rate of population growth over the subsequent period (). We assessed the fit of the three models using r-squared and AIC (Appendix 2). We found that the best fitting functional response was . We used this response to transform the avaliable seed data into a “intake variable”, . accounts for each individual mouses possible intake and transforms this modelled relationship into a formally defined “numerical response”.

Population model

After accounting for the relationship between seedfall and mouse abundance using the *intake rate* () there are still other demographic and enviromental processes that are also known to regulated mouse populations. Population abundance has been identified as a key driver of future mouse abundance in multiple studies under similar conditions (; Choquenot and Ruscoe ([2000](#ref-choquenot2000)); Holland et al. ([2015](#ref-holland2015)); Ruscoe et al. ([2005](#ref-ruscoe2005))). It is still not clear what these density dependent processes are but it is still regarded that they are an important component of mice dynamics in NZ forests (Holland et al. [2015](#ref-holland2015)). In our model we included the estimate of mouse abundance at the previous time step () as a measure of density dependence (). Rats may also influence mouse populations via competition, because rats and mice have overlapping diets (King [2005](#ref-king2005); McQueen and Lawrence [2008](#ref-mcqueen2008)), or possibly through direct predation (Bridgman et al. [2013](#ref-bridgman2013)). We were interested in whether there was a difference between areas with and without rats in relation to the outcome of mice dynamics. To do this we using the minimum number of rats in the season before ().

We identified the most appropriate functional response was:

To test **Prediction C** and **D** respectively (*does stoat control increase the rate at which mouse populations initially increasing/decreasing in response to beech seed intake*) we compared the population model intercept () between grids, with and without stoat control. Where (model intercept) is equivalent to when all other parameters are set to **zero** or **mean**; is the adjusted[[1]](#footnote-1) effect of a intake rate ( ) on ; is the adjusted effect of a single unit change in mouse density at the beginning of the previous season and is the adjusted effect of a single unit change of the minimum number of rats alive ( ) at the beginning of the previous season . If mesopredator release occurs in the increasing seasons; the intercept () for the areas with stoat control will be greater than the uncontrolled areas.

Prediction E

We tested if mesopredator release only occurs when *rat populations are reduced to low densities.* (**Prediction E**) by comparing differences between population model coefficient for rats () grouped into the grids where we reduced rat densities and the others that where not. If rat interactions are sufficiently high to impact mice populations but only when stoats are at low levels would result in differences between these parameter estimates with replicates showing differing population dynamics. We captured rats (ship rats and kiore combined) less often on grids than mice. Rather than a full capture-recapture analysis, we used the number of individual rats captured on each grid during each trip (the minimum number present) as an index of rat abundance. For each trip and grid we estimated seed availability as the number of seeds per , averaged over all seed traps on a grid.

Overall priors

Non-informative prior distributions were selected to allow the data to drive parameter estimation (Gelman and Pardoe [2006](#ref-gelman2006)). The prior distributions of capture histories were assigned binomial distributions and variance terms were assigned broad uniform prior (0-100) as suggested by Gelman and Pardoe ([2006](#ref-gelman2006)). The remaining parameters were assigned normally distributed prior with mean 0 and variance 0.00001. Each model was run for 100 000 iterations with a burn-in of 50 000 iterations, which was sufficient to achieve convergence as judged by visual inspection of the chain histories (Bronder, [n.d.](#ref-bronder)). For a full model description see Appendix 1.

Software

Models were fitted in a Bayesian framework using Markov Chain Monte Carlo (MCMC) methods and implemented in JAGS (Plummer [2011](#ref-plummer2011)), called from R v.4.3.4 using the jagsUI package (Kellner [2018](#ref-kellner2018)).

Results

We captured at total of *2370* individual mice, *219* ship rats, and kiore during a total of *94* trips. The stoat control operation in the Eglinton Valley removed a total of *751* individual stoats (**where did this come from wendy?**) between *May 1999* and *June 2001* (**data missing for rest of study**). During this operation, low numbers of rats were also removed as by-catch in stoat traps but no other independent predator control was conducted in either study Valley (**pers comms?**). Incidental stoat captures during our routine rodent trapping sessions were uncommon (proportion of total captures that were stoats = *0.01*). Lower numbers of stoats were captured in the Eglinton Valley () where the long-term predator control program was undertaken than the Hollyford Valley ().

Seeds

Our study captured two years of high seedfall ( and ). During all other years except the first year (, and ) we observed low seed fall on all grid (Figure 3). As expected, we observed high variability both between and within each trip. For example, in , the difference in seedfall between grids varied from the highest largest estimate of available seed (; Eglinton Valley) and two grids recording zero seedfall for th same period (; Hollyford Valley) on the same trip.

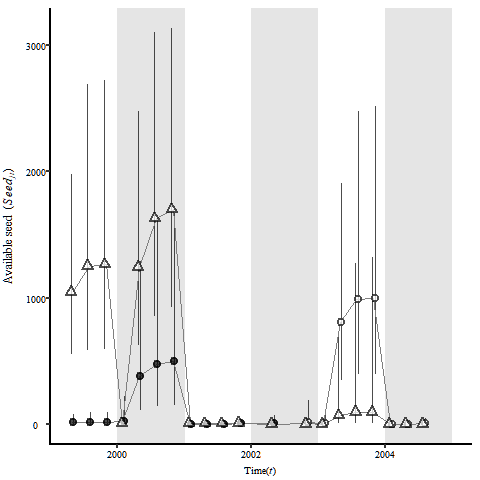


Figure 3: The average avaliable beech seed (; point estimates) collected each season during the study period (Autumn 1999 to Winter 2004). The shape distinguishes the two valleys apart (triangle = Eglinton Valley, circle = Hollyford Valley). Hollow symobols represent cases where stoats are controlled and solid fill in valleys with stoat were uncontrolled.

Mice

We estimated mouse abundance (), where represents each unique grid and for each trip from the overall community dynamics model. We found that mouse abundance was greatest in the Eglinton Valley in grids and trips where seed availability was also high. In any given year mouse abundance was on average greater in the Eglinton Valley (Figure 3.2; triangles) than the Hollyford Valley.

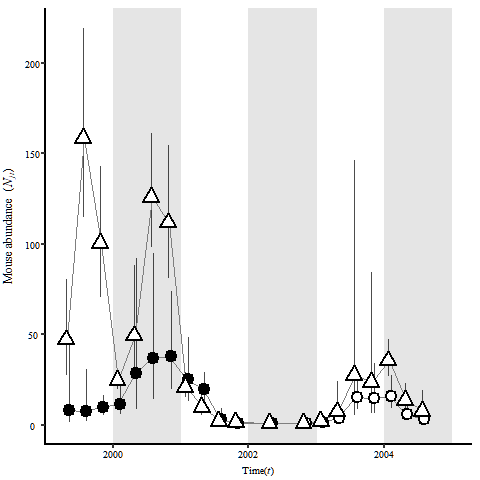


Figure 4: The average avaliable beech seed (; point estimates) collected each season during the study period (Autumn 1999 to Winter 2004). The shape distinguishes the two valleys apart (triangle = Eglinton Valley, circle = Hollyford Valley). Hollow symobols represent cases where stoats are controlled and solid fill in valleys with stoat were uncontrolled.

Rats

Rats and mice displayed a similar response to beech seed (Figure 4 and 5 respectively). However, the overall number of rats captured () remained relatively low in both valleys throughout our six-year study, except for a single trip in Spring 2004 (*n = 25*). The highest rat abundance was recorded where stoat control was undertaken (Hollyford Valley).

## Joining, by = c("trip.no", "date", "valley")

## Warning in data.matrix(rat.dens.df): NAs introduced by coercion  
  
## Warning in data.matrix(rat.dens.df): NAs introduced by coercion

## Warning: Missing column names filled in: 'X1' [1]

## Parsed with column specification:  
## cols(  
## X1 = col\_double(),  
## valley = col\_character(),  
## grid.id = col\_character(),  
## grid = col\_character(),  
## trip.no = col\_double(),  
## recap = col\_double(),  
## n = col\_double()  
## )

## Parsed with column specification:  
## cols(  
## valley = col\_character(),  
## grid.id = col\_character(),  
## grid = col\_character(),  
## trip.no = col\_double(),  
## recap = col\_double(),  
## n = col\_double()  
## )

## [1] "valley" "grid.id" "grid" "trip.no" "recap" "n"

## # A tibble: 2 x 6  
## # Groups: valley, grid.id, grid [1]  
## valley grid.id grid trip.no recap n  
## <chr> <fct> <chr> <int> <dbl> <int>  
## 1 hol MR1 hol MR1 7 4 17  
## 2 hol MR1 hol MR1 18 7 19

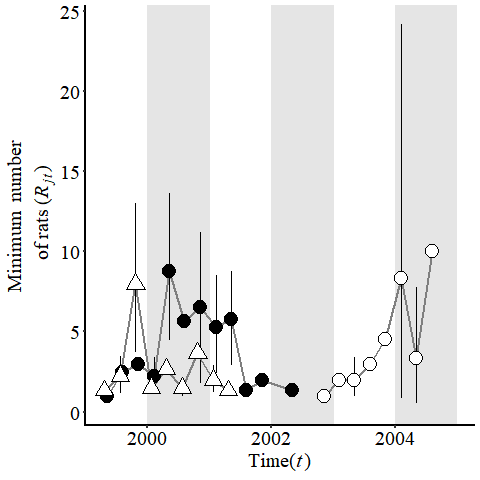


Figure 5: The average avaliable beech seed (; point estimates) collected each season during the study period (Autumn 1999 to Winter 2004). The shape distinguishes the two valleys apart (triangle = Eglinton Valley, circle = Hollyford Valley). Hollow symobols represent cases where stoats are controlled and solid fill in valleys with stoat were uncontrolled.

All other trips with high rat records were in areas with stoat control. In the Hollyford Valley during both mast-years, rats increased irrespective of stoat control. No rats were captured after May 2002 in the Eglinton Valley.

Community dynamics

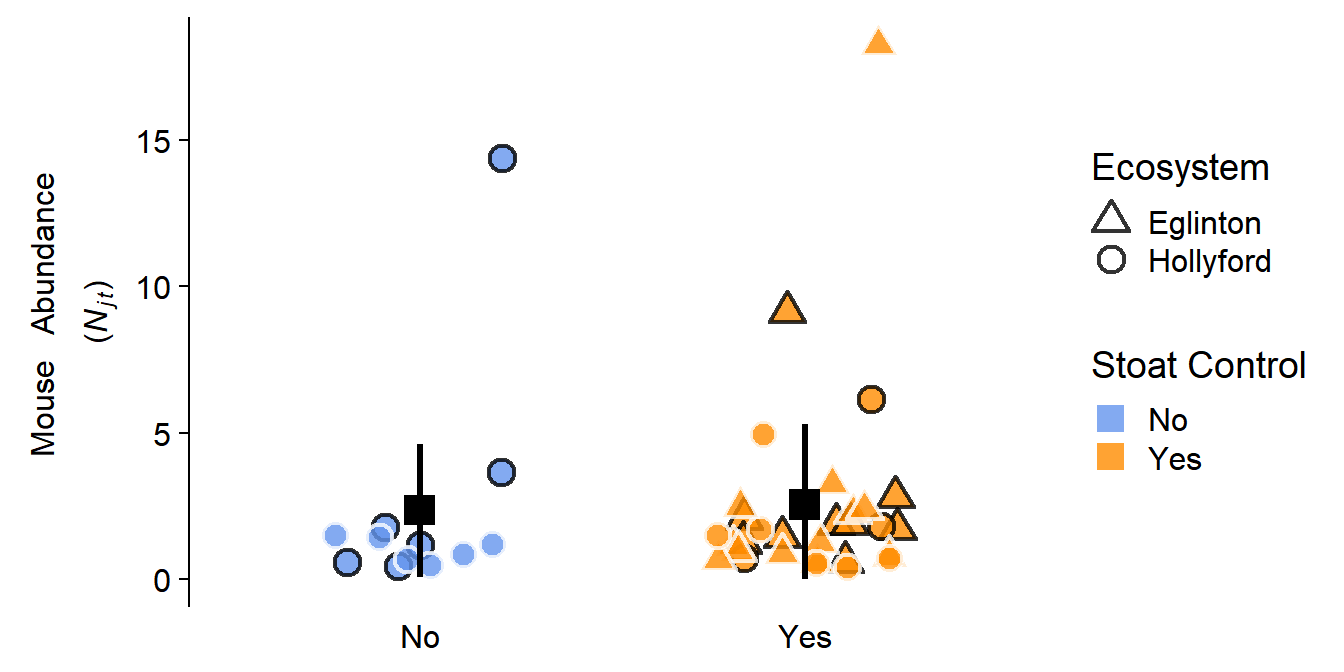
We found that the *intake rate* () always had the greatest impact on . Greater than both mouse density () and rat presence (). We accounted for the confounding effects of community processes such as density and food availability using our Bayesian model and then tested for evidence of mesopredator release of mice during our study. We used the fitted model estimates to assess the differences between the key predictions proposed for areas with and without control after accounting for both the observation error (data collection and population estimates) and process error (population dynamics; Ahrestani, Hebblewhite, and Post ([2013](#ref-ahrestani2013))).

Prediction A

*Stoat control does not increase mouse populations at times of low abundance.*

We compared the abundance of mice during trips when both mouse abundance and food availability were low and found no observable or significant differences in the estimates between areas with and without stoat control (f-stat = *?*, CI = *?*, p-value = *?*) during any of the trips during our study. We did find that the variability in mouse abundance between the valley systems was different during these low mouse abundance phases (f-stat = *?*, CI = *?*, p-value = *?*).

We compared the abundance of mice during trips when both mouse abundance was low and food availability were low. We grouped the replicates between control areas (stoats present/absent), valleys( Eglinton and Hollyford Valleys) and rat conditions (rats reduced/not) and tested the differences between each group (Table 1). We did not find any significant difference between areas with and without stoat control (f-stat = *?*, CI = *?*, p-value = *?*). We found that the variation in mouse abundance was similar between our valley systems during these low mouse abundance times (f-stat = *?*, CI = *?*, p-value = *?*). For **Prediction A** we did not need to account for varying seed input because seed fall was biological equivalent to zero for all grids and trips during low abundance seasons (Choquenot and Ruscoe [2000](#ref-choquenot2000)).



For **Prediction A** we did not need to account for varying seed input because seed fall was biological equivalent to zero for all grids and trips during low abundance seasons (Choquenot and Ruscoe [2000](#ref-choquenot2000)).

Prediction B

*Stoat control does not result in higher peak abundance of mice*

Our simple ANOVA model ([see here for analysis](file:///C:\GIT\beech-publication-wr\_book\www.ssnhub.com\beech-forest-publication\)) accounted for the differences in sample size between the areas with and without stoat control and un-equal variances within groups and found no significant difference between the stoat controlled and uncontrolled areas (**What is best here and I can repeat for all?**).

During the years of peak abundance in our study we did observe lower mouse abundance in the Hollyford Valley compared to the Eglinton Valley (f-stat = *?*, CI = *?*, p-value = *?*). Although this is not below the *0.05* threshold. It should be noted that when the rat removal treatment was removed the p-value did drop below *0.05* (f-stat = *?*, CI = *?*, p-value = *?*).

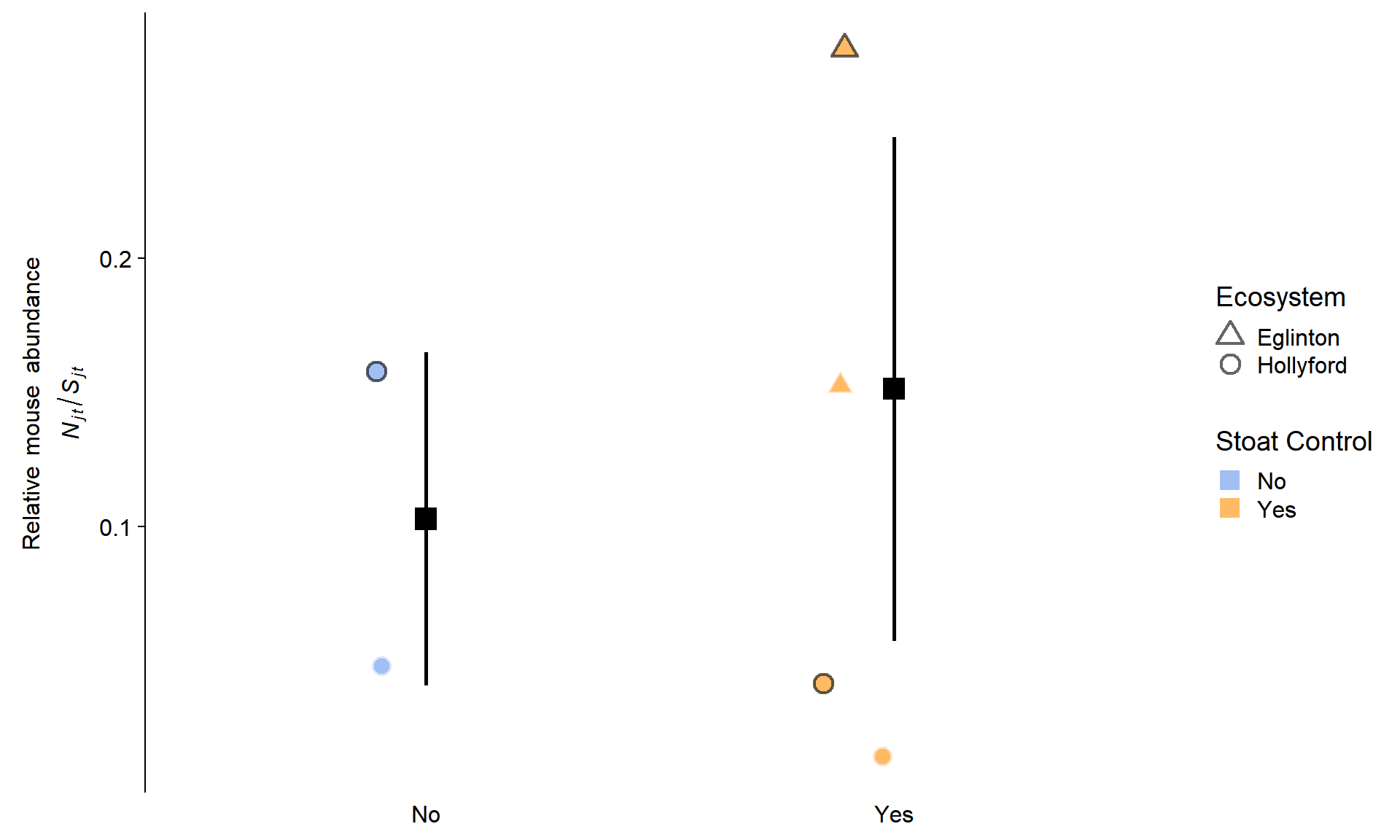


Figure 7: Difference between areas with and without stoat control at peak mouse abundance. The shape distinguishes the two valleys (triangle = Eglinton Valley, circle = Hollyford Valley). The yellow symbols represent cases where stoats are present and absent at points with black symbols and the solid symbols represent cases where rats are present and removed at points with hollow symbols.

Prediction C

*Stoat control did not increase mouse populations as food becomes available.*

We tested the differences in the rate of increase of mouse populations between the four seasons, two valleys and stoat control areas (excluding the rat treatment) during seasons when mouse population were increasing (August; Autumn - Winter). We found was no significant differences between mice populations () during the increasing seasons of mouse dynamics. All 95% credible intervals for the differences between these trips included zero (Figure 10).

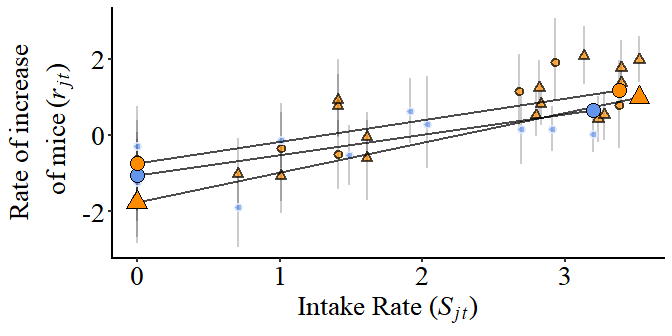


Figure 8: Visual representation of the effect of stoat control on the rate of increase of mouse populations during the increasing seedfall (Autumn to Winter; **Prediction C**). The different shapes distinguish the two valley systems (triangles = Eglinton Valley; circles = Hollyford Valley) and all solid symbols represent cases where rats are present and removed at points with hollow symbols.

Prediction D

*Stoat control did not hasten the decline from peak abundance.*

This prediction specifically focused on the Spring and Summer seasons, when rodent populations are crashing (Figure 3.1 vs. Figure 3.2). Overall density had a weak negative effect on mice dynamics under all conditions (Figure 3.2) but was greatest during the declining seasons of mice dynamics. After accounting for seed and density in the population model there was a faster rate of decline in the Hollyford Valley (dashed lines) compared to the Eglinton Valley but this was not statistically significant.

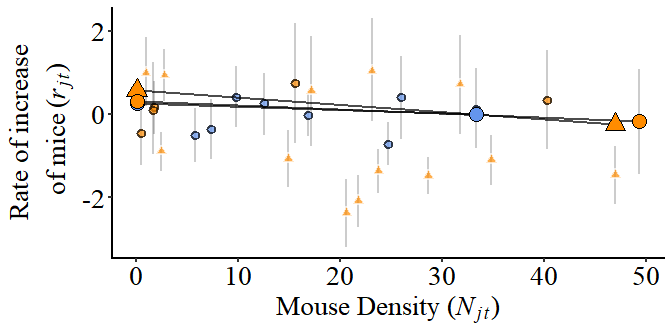


Figure 9: Visual representation of the effect of stoat control during decreasing mouse abundance (Spring to Summer; *Prediction D*). The different shapes distinguish the two valley systems (triangles = Eglinton Valley; circles = Hollyford Valley) and all solid symbols represent cases where rats are present and removed at points with hollow symbols.

Prediction E

*Does the presence of rats impact the population dynamics of mice at each of the seasons tested in Predictions A-D.*

We found that rat numbers had the smallest overall effect on mice dynamics ($\mu(\beta\_3 | All \space Seasons)= 0.007$) and was the most variable parameter in our community model (). We recorded the highest number of rats in February and May, at the same times of high mouse abundance (Figure 3.3).

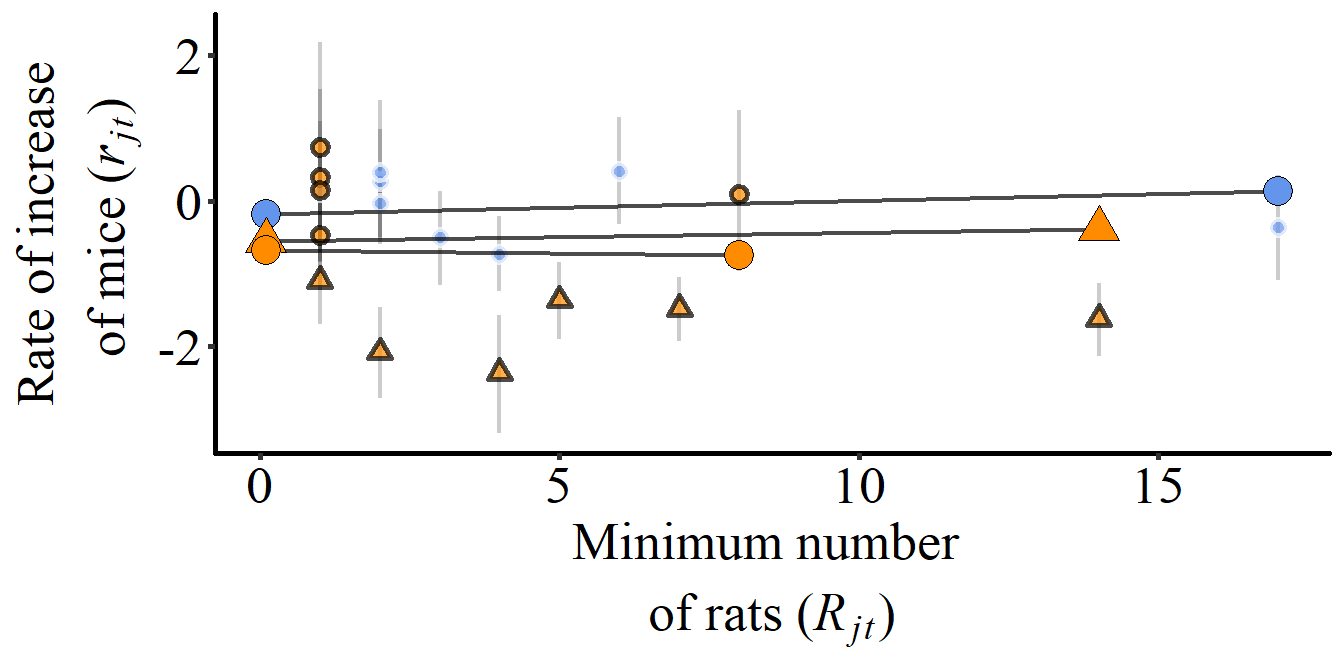


Figure 10: Differences in estimates between rats during each season of mice dynamics.

The relationship between rats and mice was examined by comparing the estimated differences between treatments (Figure 8; lines represent mean relationships in the three treatment groups). We also statistically testing the difference between each different treatment and found no differences across all parameters (Figure 9).

We did not have enough data to estimate a statistical interaction between rats and mice (non-linear relationship) or other more complex non-linear models for rat dynamics.

Conclusion

One

*Mouse populations* ***were not*** *affected by stoat control during any of the four seasonal seasons of New Zealand beech forests.*

Two

*Outcomes from predictions A-D did* ***not change*** *when rat populations were manually reduced to lower densities.*

Discussion

Overall our study found no evidence of mesopredator release in the mouse populations we monitored. We used a Bayesian Hierarchical Model (BHM) to test our five predictions by experimentally manipulating ecosystem scale predator control to compare differences between areas with or without stoat control and a rat removal treatment on half our replicates. Our model replicated the mouse dynamics in our data and produced similar results to other NZ mammals community models (Choquenot and Ruscoe ([2000](#ref-choquenot2000)); Ruscoe, Goldsmith, and Choquenot ([2001](#ref-ruscoe2001)); Ruscoe et al. ([2005](#ref-ruscoe2005)); Tompkins and Veltman ([2006](#ref-tompkins2006)); Tompkins, Byrom, and Pech ([2013](#ref-tompkins2013)); Holland et al. ([2015](#ref-holland2015)); summarised in Figure 1). High food availability resulting in high mouse abundance is commonly observed in a range of NZ forest types (Innes et al., [n.d.](#ref-innes); Sweetapple, [n.d.](#ref-sweetapple); Ruscoe et al. [2011](#ref-ruscoe2011), [2012](#ref-ruscoe2012)). Modelling has incorporated these parameter estimates to represent invasive species dynamics in NZ forests (Tompkins and Veltman [2006](#ref-tompkins2006); Tompkins, Byrom, and Pech [2013](#ref-tompkins2013); Holland et al. [2015](#ref-holland2015)) A naive investigation of our summarised data (Figure 3.1, 3.2, and 3.3) might have falsely lead to similarly low powered conclusions, that rats may have an effect on mice dynamics as well as many generally accepted relationships. By using a BHM framework we were able to test the theoretical relationships proposed using experimental data.

Seed avaliablilty

When we fit our community model to the replicated CR data we found that beech seed and the subsequent *intake rate* had the greatest impact on mice populations in all seasons. We found that was strongest on grid and trips when beech seed was increasing. After comparing a selection of functional responses to our data (Appendix 1.3) we found the best type II response and converted our estimated per to the “*intake rate*” . We found that the effect of mouse density () and rats () was lower than the “*intake rate*” (). We observed that the effects of density were greatest during the declining seasons. These differences in effect sizes are similar to other studies.

Mouse density

The effect of mouse density and rats on was much lower and were also similar to other published results (Choquenot and Ruscoe [2000](#ref-choquenot2000)). We and many other studies observed high heterogeneity in abundance estimates. This type of data can be difficult to model correctly in many frequentest frameworks. To account for this heterogeneity in the biological data we used experimental manipulation and bayesian modelling framework to account for the confounding effects of food availability, mouse density, and rats to simultaneously assess the overall effect of stoat control on mice dynamics. Importantly, our model captured both the observational and process variability within NZ beech forests. We also conclude that the underlying heterogeneity in small mammal populations was sufficiently large to make estimating true response of mice to rats difficult in biological experiments (Figures 4-9).

Rat presence

Our results suggest that it is unlikely that rats have strong impacts on the rate of increase of mice in our large scale study system. Contrary to this, previous laboratory experiments suggested that interactions between mice and rats were negatively related to predation or competition effects and limited evidence of competition release has been observed in mixed podocarp-tawa forests in NZ. We found that rats had the smallest impact on mice dynamics (Figure 8). In part, this is due to the high variability in the number of rats and kiore between grids and sampling trips in our study (**??**), which is often the case in non-laboratory studies. Instead of rats/kiore being present but at low numbers in all grids (low effect size and low uncertainty), there were only a few grids that had comparability high numbers. This result suggests that refugee areas may exist and can support larger rodents in beech forests that current averages suggest. Overall, it is likely that beech forests do not have enough resources to support larger spatially uniform populations of rats.

Bayesian modelling

The application of BHM’s in ecology has been increasing over the past decade (King [2012](#ref-king2012)). BHM modelling can provide challenges when selecting models and assessing model fit (Auger-Méthé et al. [2016](#ref-auger-methe2016)). To account for this, we used the general associations above as well as AIC and r-squared. We then used these parameters to fit the proposed theoretical population model. We investigated the patterns in our model to insure we adequately encapsulated the patterns in the data with our model to assess the effects of our parametrisation above. Large-scale ecological experiments are very informative but often need to be interpreted with caution due to often unique problems. We address these below and add additional direction to address these uncertainties in the results we found.

Our population model representation is relatively simplistic compared to some of the previous models that incorporated more interacting species and subsequently complex interactions. Our experimental design was just a big taking advantage of the situation to built a simple population model from CR data. A benefit to a simple BHM model is the ability to use bayes theorem to re-assess additional data in context of the proposed predictions. In the context of the data we have used in this experiment and uninformative priors. We choose to focus on high quality data collection methods and the key dynamics already identified with invasive species dynamics in NZ beech forests. There are however several key aspects that may be confounding our results, to the observational and population model choices.

Stoat control

An alternative explanation for the lack of any observed effects of stoat control on mouse abundance was that the removal of animals was potentially limited by the effectiveness of a particular stoat control program, management or experimental design.

If trapping did not remove a sufficient number of individual stoats to reduce predation pressure we will not observe the theoretical responses proposed by Tompkins, Byrom, and Pech ([2013](#ref-tompkins2013)) and others.

High individual heterogeneity in the capture rates of stoats at both high and low mouse densities makes reductions to zero individuals virtually impossible targets. This was the case in our study where by-catch of stoats in controlled areas was observed. As an indication of removal, times more stoats were removed from the stoat control program (Hollyford Valley 2001-2004) than caught in by-catch in areas already being controlled prior to the experiment. Our before/after treatment tested this and verified that we did not find differences within the grid when experimental treatments were changed. We may also be missing the impact of by-catch of other pests in stoat traps. We believe that any effect this may have on mice dynamics would be limited due to the limited impacts of rat removal in our data. Biologically, the differences in home range size of rodent species (10’s ha; (Bramley [2014](#ref-bramley2014); Innes and Skipworth [1983](#ref-innes1983); Pryde, Dilks, and Fraser [2005](#ref-pryde2005))) relative to the home range of stoats and the scale of trap line (100’s ha; (Miller, Elliot, and Alterio [2001](#ref-miller2001); Murphy and Dowding [1995](#ref-murphy1995))) which suggests that population level impacts from these removals is unlikely due to the limited number of animals removed and the re-invasion biology of rodents (Bramley [2014](#ref-bramley2014)).

**<- is this too critical given ?… ->**

(Blackwell, Potter, and Minot [2001](#ref-blackwell2001); Blackwell et al. [2003](#ref-blackwell2003)): 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.

Repleccate and extend on larger scale. **<- is this too critical given ?… ->**

Resource pulse systems

During our study we found stoat control had minimal impact on mice populations compared to beech seed. Beech forests have previously defined as *resource pulse systems* (Wardle, [n.d.](#ref-wardle)). Strong resource pulses cause strong effects throughout an ecosystem (Yang et al. [2008](#ref-yang2008)). The process behind for this phenomenon is that even in the absence of control, stoats cannot attain high enough densities to limit mouse populations under conditions of high food availability (King [1983](#ref-king1983)). Furthermore, the intrinsic differences in the reproductive and growth rates (life history traits) of each species reduces the ability of stoats to regulate mouse populations at the beginning of a masting event(King and Powell [2011](#ref-king2011)). By taking the proposed processes that effect mice dynamics and applying a hierarchical model framework allows us to test and estimate effect sizes that further reduce uncertainty in the outcomes of predator control in NZ beech forests.

The effects of climate change and other human lead impacts will have lasting impacts on on future rodent dynamics (Holland et al. [2015](#ref-holland2015)). Population models of climate change indicate a shift to prolonged but lower overall mast events where it may be possible to observe mesopredator release of mice with the removal of predators (Tompkins, Byrom, and Pech [2013](#ref-tompkins2013)). Mice populations monitored in more complex forest ecosystems suggest complex interactions between top-down and bottom-up effects (Ruscoe et al. [2011](#ref-ruscoe2011), [2012](#ref-ruscoe2012)). These studies suggest that rodent populations would increase in other NZ forest ecosystems after the removal of stoats (Ruscoe et al. [2011](#ref-ruscoe2011)) or other invasive predators (Rayner et al. [2007](#ref-rayner2007)).

Challanges

Population level responses such as abundance and rate of increase are often measured using indices (e.g. MNA). This can lead to difficulty in estimating population level parameters such as density. We aimed to avoid this bias as we estimated mice abundance using capture-recapture (CR) data and an integrated population model to correctly account for uncertainty in abundance estimation when fitting the population model of mice dynamics. However due to limited population numbers and data, only indices could be used to represent rat interactions. Independent research in beech forests has shown a high correlation between indices of rats in this valley and CR data. Nevertheless, increasing the quality of the rat/kiore data would most likely reduce uncertainty on the estimates of these parameter estimates. By calculating the maximum increase from the fitted population model we were able to compare the maximum population growth rate to other studies (; Hone, Duncan, and Forsyth ([2010](#ref-hone2010))), however, analogous models are not directly comparable because they do not include a resource component (e.g. beech seed production) or use indices (e.g. ). Field studies are also difficult to directly compare because may studies incorporate structurally different ecosystems (e.g Ruscoe et al. ([2011](#ref-ruscoe2011))), species indices instead of true abundance estimation using CR models or did not report effect sizes. Although this limitations exist our comparisons to general trends were all comparable to our model estimates and our estimates are all biologically viable.

Management implications

Our model has subtle but important differences compared previous research when in comes to management application. We have incorporated a reproducible workflow(British Ecological Society [2018](#ref-britishecologicalsociety2018)) for the future development of model testing for different and new datasets (Wickham [2014](#ref-wickham2014)). In doing this we have incorporated leading reproducible science techniques to help address any aspects of our study may need for further support. Often studies of such large scale can address key population-level questions however these studies struggle to find replication because of the scale at which they are conducted (Oksanen [2001](#ref-oksanen2001)). Many issues that many confront a PFNZ2050 will be reduced by using simple but well fitted BHMs for predicting and allocation management resources.

Predator-free NZ

Our integrated population modelling approach and the large, high-quality CR data used to parametrise the model allowed us to predict and report the biologically relevant effect sizes. We used this to address the direct question of stoat control in NZ Beech Forests. Future studies can now test and assess the beech forest ecosystem compared to the data they collect. By using the unified modelling framework presented in this paper (Appendix 3; [Davidson ([2019](#ref-davidson2019))), reproducible research practises and “tidy-data” (Wickham [2014](#ref-wickham2014)). Many of the processes we have verified were previously hypothesized using indices of mice abundance (Blackwell, Potter, and Minot [2001](#ref-blackwell2001); Blackwell et al. [2003](#ref-blackwell2003)), laboratory experiments (Bridgman et al. [2013](#ref-bridgman2013)), novel systems such as remote islands (Mulder et al. [2009](#ref-mulder2009)) and small patches of mainland forest (Blackwell, Potter, and Minot [2001](#ref-blackwell2001); Blackwell et al. [2003](#ref-blackwell2003)). We have integrated these results into a framework that can now test these results in other systems that are hypothesized to be different. It will be important for future work to continue monitoring this system for anomalies and unexpected patterns such as increases in other invasive predators, particularly rats.

Prerequisites

This is a *sample* book written in **Markdown**. The whole book structure is written in bookdown using RStudio and GIT.

My notes

1. You can use anything that Pandoc’s Markdown supports, e.g., a math equation .
   1. but you need to install pandoc?
2. The **bookdown** package can be installed from CRAN or Github:
3. Remember each Rmd file contains one and only one chapter,
   1. a chapter is defined by the first-level heading #.
4. To compile this example into PDF, you need XeLaTeX.
   1. You are recommended to install TinyTeX (which includes XeLaTeX): <https://yihui.name/tinytex/>.

References

Status

All other data and resources to render project from raw data (copied from my private GIT repository) can be found on [dropbox](https://www.dropbox.com/home/phd-drafts-anthony) and online [here](https://www.ssnhub.com/beech-forest-dynamics/) and are currently at a draft quality as I build my phd thesis.

|  |  |  |
| --- | --- | --- |
| GIThub Document | Overview | Status |
| *Pre-registration* | not needed | NA |
| [Current draft] | As I am developing this approach to reproducible research this draft will look better and better. | Online [here](https://www.ssnhub.com/beech-forest-dynamics/) |
| Online [link here](https://github.com/davan690/beech-fororest-dynamics/) | Dropbox is currently the backup for this as I get better at build gitbooks using RStudio and bookdown. This is currently only accessible if you have the private link that I will have sent through email. | Dropbox [link here](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/drafts/Davidson_2019_BeechForest.html) |
| [Abstract] | Always last..ish a overview is online [here](https://www.ssnhub.com/beech-forest-dynamics/) | [*additional resources for collaborators here*](https://www.dropbox.com/home/phd-drafts-anthony) |
| [Style sheet] | A way of recording semantic choices for this research project. | Dropbox [Link here](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/Styles_manual_sheet.md/) |
| [Introduction](#intro) | Currently within the draft manuscript | Dropbox [Link here](https://www.dropbox.com/sh/5h4mp67p7u6t1lj/AAAQVKS4qnvu2oQLu53JQUofa?dl=0); Online [link here](https://www.ssnhub.com/beech-forest-dynamics/intro.html) |
| [Methods](#method) | manuscript methods can be found here and other extensions below | Online [link here](https://www.ssnhub.com/beech-forest-dynamics/method.html) |
|  | This report takes the raw CR data and generates simple average plots of beech seed, mice and rat abundances | [Model wrangling](https://www.ssnhub.com/Beech-forest-publication/) |
|  | To estimate the differences between Prediction A and B | [Simple ANOVAs](https://www.ssnhub.com/simple/) |
|  | To estimate the differences between Prediction C, D, and E | [Model outputs](https://www.ssnhub.com/outputs/) |
|  | Simulation model | Full simulation document [here](https://www.ssnhub.com/simulation/) |
| [Results](#results) | The figures can be found here | Online [link here](https://www.ssnhub.com/beech-forest-dynamics/results.html) |
| [Discussion](#discussion) |  | Online [link here](https://www.ssnhub.com/beech-forest-dynamics/discussion.html) |
| Bayesian methods |  | [Dropbox](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/A1_full_bayesian_model.pdf) |
| Figures |  | [Dropbox](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/figs) |
| Functional response |  | [Dropbox](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/Davidson_2019_BeechForest_Appendix.pdf) |
| Mapping | coming online soon | [Dropbox](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/figs) |
| [References](#references) |  | [Dropbox](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/figs) |
| [Appendix] |  | [Dropbox](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/figs) |
| Extra resources |  | [Dropbox](https://www.dropbox.com/home/phd-drafts-anthony/beech-forest-dynamics/figs) |
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 {%- assign gh-project = "davan690/beech-forest-dynamics" -%}  
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 <img src="https://img.shields.io/github/stars/{{- gh-user -}}/{{- gh-project -}}.svg?style=social&label=Stars" alt="Github" title="Github Stars">  
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My notes

Follow up on these comments:

#We did this by selecting only non-mast years over the duration of our study.   
#---------------  
# You have a before-after design (ANCOVA?)  
# how did your analysis account for this.   
# And what about rats?

seed estimation

# This needs a clearer explanation to step the reader through what you did.

And posts so far to help with development below:

{% for post in site.tags[“beech”] %} {{ post.title }} ({{ post.date | date\_to\_string }}) {{ post.description }} {% endfor %}

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