

This is a repository copy of *Optimal control of irrupting pest populations in a climate-driven ecosystem*.

White Rose Research Online URL for this paper:  
<http://eprints.whiterose.ac.uk/139309/>

Version: Accepted Version

---

**Article:**

Holland, E Penelope [orcid.org/0000-0002-4334-6234](https://orcid.org/0000-0002-4334-6234), Binny, Rachele N and James, Alex  
Optimal control of irrupting pest populations in a climate-driven ecosystem. PeerJ . ISSN 2376-5992 (In Press)

---

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

# Optimal control of irrupting pest populations in a climate-driven ecosystem

E Penelope Holland <sup>1</sup>, Rachelle N Binny <sup>2</sup>, Alex James <sup>Corresp. 3, 4</sup>

<sup>1</sup> Department of Biology, University of York, York, United Kingdom

<sup>2</sup> Manaaki Whenua Landcare Research, Lincoln, New Zealand

<sup>3</sup> Biomathematics Research Centre, University of Canterbury, Christchurch, New Zealand

<sup>4</sup> Te Pūnaha Matatini, New Zealand

Corresponding Author: Alex James

Email address: alex.james@canterbury.ac.nz

Irruptions of small consumer populations, driven by pulsed resources, can lead to adverse effects including the decline of indigenous species or increased disease spread. Broad-scale pest management to combat such effects benefits from forecasting of irruptions and an assessment of the optimal control conditions for minimising consumer abundance. We use a climate-based consumer-resource model to predict irruptions of a pest species (*Mus musculus*) population in response to masting (episodic synchronous seed production) and extend this model to account for broad-scale pest control of mice using toxic bait. The extended model is used to forecast the magnitude and frequency of pest irruptions under low, moderate and high control levels, and for different timings of control operations. In particular, we assess the optimal control timing required to minimise the frequency with which pests reach 'plague' levels, whilst avoiding excessive toxin use. Model predictions suggest the optimal timing for mouse control in beech forest, with respect to minimising plague time, is mid-September. Of the control regimes considered, a seedfall driven biannual-biennial regime gave the greatest reduction in plague time and plague years for low and moderate control levels. Although inspired by a model validated using house mouse populations in New Zealand forests, our modelling approach is easily adapted for application to other climate-driven systems where broad-scale control is conducted on irrupting pest populations.

# 1 Optimal control of irrupting pest populations in a climate-driven ecosystem

2 Holland EP<sup>1</sup>, Binny RN<sup>2,3</sup> and James A<sup>3,4\*</sup>

3 <sup>1</sup>Department of Biology, University of York, Heslington, York YO10 5DD, UK.

4 <sup>2</sup>Manaaki Whenua – Landcare Research, PO Box 69040, Lincoln 7640, Canterbury, New Zealand.

5 <sup>3</sup>Te Pūnaha Matatini, University of Auckland, Private Bag 92019, Auckland 1011, New Zealand.

6 <sup>4</sup>Biomathematics Research Centre, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand.

7 \*Correspondence author. Email:alex.james@canterbury.ac.nz

8

## 9 **Abstract**

10 Irruptions of small consumer populations, driven by pulsed resources, can lead to adverse effects  
11 including the decline of indigenous species or increased disease spread. Broad-scale pest  
12 management to combat such effects benefits from forecasting of irruptions and an assessment of  
13 the optimal control conditions for minimising consumer abundance. We use a climate-based  
14 consumer-resource model to predict irruptions of a pest species (*Mus musculus*) population in  
15 response to masting (episodic synchronous seed production) and extend this model to account  
16 for broad-scale pest control of mice using toxic bait. The extended model is used to forecast the  
17 magnitude and frequency of pest irruptions under low, moderate and high control levels, and for  
18 different timings of control operations. In particular, we assess the optimal control timing  
19 required to minimise the frequency with which pests reach ‘plague’ levels, whilst avoiding  
20 excessive toxin use. Model predictions suggest the optimal timing for mouse control in beech  
21 forest, with respect to minimising plague time, is mid-September. Of the control regimes  
22 considered, a seedfall driven biannual-biennial regime gave the greatest reduction in plague time  
23 and plague years for low and moderate control levels. Although inspired by a model validated

24 using house mouse populations in New Zealand forests, our modelling approach is easily adapted  
25 for application to other climate-driven systems where broad-scale control is conducted on  
26 irrupting pest populations.

27

28 **Keywords:** broad-scale aerial control, consumer-resource model, invasive species, mast seeding, *Mus*  
29 *musculus*, pulsed resources, rodent management.

30

### 31 **Introduction**

32 Pulses in food resources can drive irruptions of small consumers and trigger cascading responses in  
33 population dynamics across multiple trophic levels (Ostfeld & Keesing, 2000). This can result in the decline  
34 or extinction of indigenous species (Innes *et al.*, 2010) and/or an increase in disease spread (Jones *et al.*,  
35 1998), particularly in ecosystems inhabited by pest species. To avoid or mitigate the impact of pest  
36 populations on the ecological community, it is necessary to forecast irruptions, often using weather-based  
37 forecast models (e.g. Kelly *et al.*, 2013; Magarey & Isard, 2017), and then optimise the timing and intensity  
38 of management operations to reduce pest abundance at critical times of the year (e.g. Singleton *et al.*,  
39 2007).

40 The diverse effects of mast seeding - the synchronous intermittent production of large seed crops (Allen  
41 *et al.*, 2012; Kelly & Sork, 2002) - on ecological communities around the world are illustrated well using  
42 rodent populations in forests. Yellow-necked mice (*Apodemus flavicollis*) have increased winter survival  
43 and rapid population growth following mast seeding in oak (*Quercus robur*) and hornbeam (*Carpinus*  
44 *betulus*) in Białowieża Primeval Forest in Poland, with a corresponding increase and peak in predator  
45 populations such as the pine marten (*Martes martes*) a few months to a year later (Ostfeld & Keesing,

46 2000; Pucek *et al.*, 1993). When rodent prey becomes scarce following an irruption, pine martens  
47 compensate by increasing consumption of alternative resources including birds and berries (Jedrzejewska  
48 & Jedrzejewski, 1998). Forest bird populations are also limited by predation by raptors, e.g. buzzards,  
49 which undergo prey-switching from rodents to birds following a crash in rodent abundance (Jedrzejewska  
50 & Jedrzejewski, 1998). In oak (*Quercus* spp.) forest in the eastern U.S., white-footed mice (*Peromyscus*  
51 *leucopus*) respond similarly to acorn masts, with increased winter survival and breeding success (Jones *et*  
52 *al.*, 1998). However, in this case mice are also predators, playing an important role in suppressing gypsy  
53 moth (*Lymantria dispar*), an invasive and outbreaking species. Defoliation by gypsy moths can delay and  
54 reduce mast production, creating a negative feedback loop for the mast-driven mouse populations with  
55 catastrophic consequences for tree growth and survival as well as reduced mouse abundance (Jones *et*  
56 *al.*, 1998). However, high densities of mice lead to increases in tick (*Ixodes scapularis*) populations, and  
57 the associated spread of Lyme disease in humans (Jones *et al.*, 1998).

58 In South America, rodent outbreaks are associated with emerging viral diseases such as hantavirus (Jaksic  
59 & Lima, 2003). These outbreaks occur after bamboo (*Chusquea* sp. and *Merostachys* sp.) masts, but may  
60 also follow heavy rainfall events (Jaksic & Lima, 2003), emphasizing the need for ecologically sound pest  
61 forecasting models. Introduced bamboo (*Melocanna baccifera*) is a well-used non-timber forest product  
62 in India, but rodent (*Rattus* sp. and *Mus* sp.) migration towards agricultural areas following mast events  
63 can have devastating effects on standing crops and stored grains, as well as increasing the risk of infection  
64 for rodent-borne diseases (Biswas *et al.*, 2016). It has also been suggested that masting by introduced  
65 Asian bamboos into North America, particularly the Pacific Northwest, poses a health risk to humans as a  
66 result of population irruptions and subsequent dispersal of deer mice (*Peromyscus maniculatus*, a  
67 hantavirus carrier) following mast seed depletion (Smith *et al.*, 2015).

68 Broad-scale management of mouse populations to reduce damaging effects is typically attempted  
69 through the application of baits laced with rodenticide toxin, applied either via aerial drops or ground-  
70 based bait stations (Singleton *et al.*, 2010). In Australia, for example, plaguing mouse populations can  
71 exceed densities of 1000 mice per hectare, causing significant damage to cereal crops (Singleton *et al.*,  
72 2001). Sterilised wheat grains coated with zinc phosphide toxin are applied in and around crops, aurally  
73 or using calibrated fertiliser spreaders, and can reduce the mouse population by 40-98% (Mutze & Sinclair,  
74 2004).

75 In New Zealand, invasive house mouse (*Mus musculus*) populations undergo episodic outbreaks in  
76 response to high seedfall, particularly in the heavy masts of native beech forest (*Nothofagus* species)  
77 (Fitzgerald *et al.*, 1996; King, 1983; Ruscoe, 2001) or rimu (*Dacrydium cupressinum*) (Ruscoe *et al.*, 2004).  
78 Irruptions in beech forest occur predominantly in late summer to autumn (i.e. February-May) (Ruscoe *et*  
79 *al.*, 2003; Wardle, 1984) and are accompanied by an increase in abundance of other seed consumers,  
80 including ship rats (*Rattus rattus*) (Studholme, 2000) and kiore (*R. exulans*) (Ruscoe & Pech, 2010). Small  
81 mammal predators, predominantly invasive stoats (*Mustela erminea*), benefit from the irruptions of prey  
82 and increase after a delay caused by seasonal breeding (King, 1983). These dynamics are harmful to a wide  
83 range of native fauna. For instance, in addition to fallen seed, mouse and rat diets comprise invertebrates  
84 (Fitzgerald *et al.*, 1996; Jones & Toft, 2006; Miller & Miller, 1995; Ruscoe & Murphy, 2005), bird chicks and  
85 eggs (O'Donnell & Phillipson, 1996; Wilson *et al.*, 2006; Wilson *et al.*, 1998), and lizards (Norbury *et al.*,  
86 2014). Stoats also have a flexible diet, and in masting forests will switch from mice as their primary food  
87 source, to predating on birds and invertebrates when mice become scarce (Murphy *et al.*, 2016; Wilson  
88 *et al.*, 1998).

89 Despite the threat posed to native biota, there is currently no broad-scale control targeting mice alone in  
90 mainland New Zealand. This is primarily due to higher prioritisation of control for other small mammal

91 pest targets, e.g. common brushtail possum (*Trichosurus vulpecula*), rats (*Rattus* sp.) and mustelids  
92 (*Mustela* sp.), which are considered to pose a greater risk to native flora and fauna (Innes *et al.*, 2010;  
93 Ruscoe & Pech, 2010). In addition, the lack of cost-effective mouse-specific control tools and public  
94 concern around widespread toxin use, means that the broad-scale management of mice on mainland New  
95 Zealand still presents a major challenge (Ruscoe & Pech, 2010). Ground-based control (e.g. trapping)  
96 targeting mice alone has been undertaken on smaller spatial scales within predator-fenced sanctuaries,  
97 where all other vertebrate pests have been eradicated, and has been shown to confer benefits to  
98 biodiversity (Watts *et al.*, 2017). Broad-scale multi-species control operations involving aerially applied  
99 bait laced within sodium fluoroacetate (1080) toxin are undertaken in New Zealand to control rodents,  
100 possums and stoats (via secondary poisoning when stoats consume poisoned rodents (Murphy *et al.*,  
101 1999)). These operations have been partially successful in reducing mouse abundance but less so than for  
102 other small mammals (Elliott & Kemp, 2016), likely due to lower uptake of the 1080 bait by mice compared  
103 to other targets (Fisher & Airey, 2009; O'Connor *et al.*, 2005). There has been some success with mouse  
104 eradication programmes on New Zealand's offshore islands, predominantly through aerial application of  
105 the second-generation anti-coagulant toxin brodifacoum (Mackay *et al.*, 2007). However, long-term  
106 broad-scale brodifacoum use is avoided on mainland New Zealand due to its persistence in the  
107 environment and risks to non-target species (Eason *et al.*, 2002).

108 Control targeting only a subset of predators in an ecosystem may lead to an increase in abundance of  
109 other smaller predators, an effect termed 'mesopredator release', causing a subsequent decline in  
110 indigenous prey species (Crooks & Soulé, 1999; Ritchie & Johnson, 2009). In New Zealand, mesopredator  
111 release of mouse populations has been observed both on islands (Simberloff, 2002) and on the mainland  
112 (Norbury *et al.*, 2013). It is therefore becoming increasingly important to have the understanding and  
113 technologies in place to effectively forecast and manage irrupting mouse populations over large spatial  
114 scales. In particular, the optimal timing for broad-scale mouse control on mainland New Zealand remains

115 a critical knowledge gap. For eradication of mice on islands, the preferred season for control is winter to  
116 early spring when food is likely to be limiting because this maximizes bait up-take (Broome *et al.*, 2017).  
117 The optimal timing for broad-scale aerial 1080 control targeting irrupting rodents and stoats is between  
118 July and November in a mast year, determined with the aim of minimising rat abundance. However,  
119 operational logistics (e.g. availability of helicopters), weather and legal requirements also place significant  
120 constraints on timing (Elliott & Kemp, 2016). Innes *et al.* (1995) proposed that broad-scale aerial  
121 operations targeting ship rats (*Rattus rattus*) to protect nesting birds should coincide with the onset of  
122 nesting each year. The conceptual model of Wilson *et al.* (1998) for mouse dynamics in beech forest  
123 suggests conducting control in November prior to a mast would have little effect, while the November  
124 after a mast would be too late (see e.g. Fig. 5 in Wilson *et al.* (1998)). However, conducting control in  
125 February at the start of a mast and/or May during heavy seedfall may be optimal.

126 Models for irrupting mouse populations require good predictions of the size and timing of masts.  
127 Temperature and rainfall in the years before the mast event are almost always the primary cue for mast  
128 seeding (Janzen, 1971). Kelly *et al.* (2013) proposed a generic and widely applicable model using the  
129 change in temperature in a set period over the previous two years ( $\Delta T$ ) as the sole predictor. This model  
130 offered much improved predictions over other simple models and has been shown to be applicable to a  
131 wide range of plant species around the world, including oak and many New Zealand species, either as a  
132 cue or a proximate driver of masting (Kelly *et al.*, 2013; Pearse *et al.*, 2014).

133 Holland *et al.* (2015) previously developed a climate-based consumer-resource model for mouse  
134 irruptions in masting forests, parameterised using long-term temperature, hard beech (*Fuscospora*  
135 *truncata*) seedfall and house mouse (*Mus musculus*) abundance data from mixed beech-podocarp-  
136 broadleaved forest in Orongorongo Valley (OV), New Zealand. Seedfall was predicted using the  $\Delta T$  model  
137 (Kelly *et al.*, 2013). In this paper, we extend the Holland *et al.* (2015) model of mouse population dynamics



138 driven by pulses in food resource, to account for broad-scale mouse control. We use the extended model  
139 to forecast population irruptions (timing and size) and the impact of pest control on mouse populations,  
140 to assess if and how we can avoid 'plague' levels of mice while also avoiding excessive poison use.  
141 Predictions of the impacts of tailored vs. untailored vs. no control will be crucial for effective and efficient  
142 broad-scale management of irrupting mouse populations.

## 143 **Methods**

### 144 *Consumer – resource model*

145 The underlying consumer-resource model is the best-fit model developed by Holland *et al.* (2015). Relative  
146 mouse abundance  $M(t)$  is quantified by an index: captures per 100 trap nights ( $C/100TN$ ) (Ruscoe *et al.*,  
147 2001). The rate of change of  $M$  over time  $t$  (years) is given by

$$148 \quad \frac{dM}{dt} = (\alpha g(F) - \mu_1 - \mu_2 M - B(t))M, \quad \text{eqn 1}$$

149 Food availability  $F$  (seeds  $m^{-2}$ ) is predicted by the functional response  $g(F)$  and  $\alpha$  is the demographic  
150 efficiency of mice (i.e. efficiency at converting food into recruitment for the mouse population). The total  
151 mortality rate is  $\mu_1 - \mu_2 M - B(t)$ , where the parameters  $\mu_1$  and  $\mu_2$  are density-independent and density-  
152 dependent mortality rates respectively. They may both be positive or negative depending on non-food  
153 related processes, e.g. predation, social interactions, Allee effects. In this paper, we extend the previously  
154 published model by adding  $B(t)$ , which is a time-dependent, density-independent rate of mortality due  
155 to control by bait application (see below).

156 The original model tested four candidate models for the food availability functional response. The best fit  
157 was a Holling II (Ivlev) function where  $c$  (seeds  $m^{-2}$  mouse $^{-1}$  year $^{-1}$ ) is the maximum per capita feeding rate  
158 and  $e$  ((seeds  $m^{-2}$ ) $^{-1}$ ) is a measure of foraging efficiency:

159  $g(F) = c(1 - \exp(-eF)).$  eqn 2

160 The rate of change of available food over time is modelled by

161  $\frac{dF}{dt} = S(t) - hF - g(F)M,$  eqn 3

162 where the second term,  $hF$ , describes the change in available food that happens throughout the year at  
 163 a constant rate  $h$  ( $\text{year}^{-1}$ ) unrelated to mouse density and the third term,  $g(F)M$ , describes the rate of  
 164 seed consumption by mice. The first term,  $S(t)$ , describes the rate at which food is delivered as a function  
 165 of time, with

166  $S(t) = \begin{cases} \frac{F_y}{0.25} & \text{if } 0 \leq t - \text{floor}(t) < 0.25 \\ 0 & \text{otherwise.} \end{cases}$  eqn 4

167 The floor function rounds  $t$  down to the largest integer smaller than  $t$ . Thus, during the  $y^{\text{th}}$  annual cycle, a  
 168 total amount of seed  $F_y$  is produced, which is delivered at a constant rate over the first quarter of the year  
 169 (nominally February - April). At the start of each year we set  $F(t) = 0$ , i.e. seed is not carried over between  
 170 years. The annual seedfall amount  $F_y$ , was determined by a climate induced seedfall model (see below).  
 171 All parameter values are given in Table 1 and were those determined as best-fit parameter values by  
 172 Holland *et al.* (2015) (Table 2 in Holland *et al.* (2015)). These were chosen by modelling mouse density  
 173 over 25 years using observed annual seedfall data from the OV (starting February 1972) as the annual  
 174 values of seed  $F_y$ . Mouse density at the start of each quarter was extracted from the continuous-time  
 175 model prediction. These predicted values were compared to observed quarterly mouse density data from  
 176 the OV collected over the same time period (quarterly, February 1972 – November 1996) and best-fit  
 177 parameter estimates chosen by minimising the root mean square error. Holland *et al.* (2015) showed that  
 178 with these best-fit parameter values the model predicted all major outbreaks in mouse density occurring

179 in the 25 year observed mouse density (C/100TN) time series, although it tended to slightly under-predict  
 180 the magnitude of outbreaks.

181 During a control year, bait is applied as an impulse function at a specific time point  $t_i^*$ , such that  $t - t_i^*$   
 182 describes the time since the  $i^{\text{th}}$  bait application. After application, bait degrades according to a simple  
 183 decay function  $B_0 \exp(-d(t - t_i^*))$ , where  $d$  is the decay rate. The constant  $B_0$  governs peak bait  
 184 availability, i.e. at the time of application ( $t - t_i^* = 0$ ). Therefore, bait availability  $b_i(t)$  from the  $i^{\text{th}}$   
 185 application is described by a piecewise function

$$186 \quad b_i(t) = \begin{cases} B_0 \exp(-d(t - t_i^*)), & \text{if } t_i^* \leq t < t_{i+1}^* \\ 0, & \text{otherwise,} \end{cases} \quad \text{eqn 5}$$

187 and overall bait availability  $B(t)$  at time  $t$  is given by

$$188 \quad B(t) = \sum_{i=1}^{n-1} b_i(t), \quad \text{eqn 6}$$

189 for  $n$  bait applications. In the absence of mice, bait is considered to be inactive after one month, so we  
 190 choose  $d = 50$  (meaning that  $b_i(t)$  has decayed to  $< 2\%$  of its original size one month after the  $i^{\text{th}}$   
 191 application, and  $< 0.02\%$  of its original size after two months. It is presumed that, compared to this decay  
 192 rate, the effect of mouse predation on bait levels is negligible. Note that the actual value of  $B_0$  is defined  
 193 later in terms of the kill success rate.

#### 194 *Climate-induced seedfall model*

195 A 1000 year normally distributed temperature time series  $T_1, T_2, \dots, T_{1000}$ , was generated where

$$196 \quad T_y \sim N(14, 1). \quad \text{eqn 6}$$

197 This represents historical mean summer temperatures (daily average for the three month period  
198 January to March) in the Orongorongo Valley (hereafter OV), 1972-2014. Randomly generating time-  
199 series for the OV in this way was shown to be a valid approach by Holland and James (2015). From this, a  
200 time series was calculated using the  $\Delta T$  model of Kelly *et al.* (2013), where

$$201 \quad \Delta T_y = T_y - T_{y-1}. \quad \text{eqn 7}$$

202 Annual seedfall predictions were made using the following linear relationship fitted to observed OV  
203 beech seedfall data (1972-1996) by Holland *et al.* (2015):

$$204 \quad \log_{10} F_y = 0.33 + 0.97 \Delta T_y + \epsilon_y. \quad \text{eqn 8}$$

205 The noise term was chosen to have distribution  $\epsilon_y \sim N(0, 1.3)$  to give a correlation between change in  
206 temperature and seedfall of  $r^2 \approx 0.54$  corresponding to the findings of Kelly *et al.* (2013). These seedfall  
207 time series were used as annual inputs of  $F_y$  to the mouse model above. Mouse density (C/100TN) was  
208 simulated for each of the control scenarios above, with  $M(0) = 1.0$ .

### 209 *Plague definitions*

210 We define the mouse density plague level,  $M_p = 2.02$ , to be the maximum mouse density in a median  
211 seedfall year if the initial mouse density is one, i.e.  $M(0) = 1$ , (see Figure 1). Using this definition, if the  
212 mouse density was 1 at the start of the year ( $M(0) = 1$ ) 50% of years would be defined as *plague years*  
213 i.e. the mouse density ‘just’ reached plague level at some point during the year. In a longer time series  
214 where no control measures are applied (Figure 2) and the density is continuous across years, i.e. mouse  
215 density at the start of the year is the density at the end of the previous year, the plague level definition is  
216 not changed and the proportion of years that are plague years is much higher, 85%. Specific thresholds  
217 for what constitutes a mouse ‘plague’ or eruption in New Zealand have not been formally defined in the  
218 literature; it is difficult to measure exact population densities, and it is not known exactly at what

219 threshold level mice may have an impact on native biodiversity. We therefore use the term ‘plague’, to  
220 mean greater than average population abundance for an extended period of time, i.e. demonstrably not  
221 an undetectable population and therefore likely to have some impact, and a convenient reference point  
222 with which to compare scenarios. In the 25 year time-series of observed mouse abundance from the OV,  
223 when mouse abundance was above 2.02 the population tended to be undergoing one of seven larger  
224 eruptions. In addition, mouse abundance was above the 2.02 level in 80% of years, suggesting that our  
225 definition for plague level and estimate of proportion of plague years are reasonable in this context. We  
226 also define *plague time*, the proportion of time during which the mouse density is above the plague level.  
227 For example, in Figure 1 the plague time for the mast year trajectory is 0.89. In the long term time series  
228 of Figure 2 the plague time is 0.71. Finally we define the *plague size*, the highest mouse density during the  
229 plague period. In the Figure 1 example, the plague size for the mast trajectory is 6.93. In the long term  
230 series (Figure 2), the expected plague size, given that a plague occurs, is 5.7. Higher values of  $M_p$  could be  
231 used with the same plague definitions given here, with qualitatively similar results.

### 232 *Control definitions*

233 The strength of the control impulse is governed by the parameter  $B_0$ , which is the value of  $B(t)$  at the  
234 time of bait application  $t = t_i^*$  (eqns 5-6). The absolute value of the control impulse is of little practical  
235 use in modelling terms, though operationally it relates to control effort and a parameter value could be  
236 calibrated for a given operation. A more appropriate measure of control size is the *control success*,  
237 typically assessed in terms of percentage kill, defined here as the relative decrease in the mouse density  
238 one month after the control impulse. The control success will change depending on the current mast level  
239 and mouse density but percentage kill is still a useful and widely used measure (Elliott & Kemp, 2016;  
240 Innes *et al.*, 1995). In the example of Figure 1 (black dotted line), where  $B_0 = 150$  and control is applied  
241 at the start of the mast season, control success is 88%. Even with this relatively high level of control

242 (consistent with historic broad-scale aerial poison operations for rodents (Innes *et al.*, 1995)), the mouse  
243 density at the end of the year remains high as the population recovers, and the mouse density rises above  
244 the plague level during September. However, both the plague time (0.31) and the plague size (2.18) are  
245 much lower than in the uncontrolled mast year. Crucially, for the success of native species that rely on  
246 beech mast for food, the seedfall level is much higher in the controlled scenario compared to the  
247 uncontrolled.

#### 248 *Scenarios*

249 To obtain precise estimates for expected plague time, plague size and proportion of plague years under  
250 different control scenarios, we ran the extended model (eqns 1-6) for a 1000 year long simulation with  
251  $M(0) = 1$ , using a seedfall time series generated with eqns 8-9 from a temperature time series generated  
252 using eqn 7. In this longer simulation, the initial mouse density is not reset to 1 each year but continues  
253 with the value at the end of the previous year. Seedfall is reset to zero at the beginning of each year to  
254 reflect the inedibility of the previous year's seed. Note that all the control scenarios used the same  
255 underlying seedfall series.

#### 256 *Optimal control timing*

257 Initially, we assume that control can only be applied once each year and we examine three levels of  
258 control: low, medium and high,  $B_0 = 50, 100, 150$ , respectively. For each level of control, we used the  
259 1000 year weather/seedfall time series, applying control at a range of times throughout the year. We  
260 calculated the proportion of plague years, proportion of time above plague level (i.e. *plague time*), and  
261 average plague size for each control application time.

#### 262 *Tailored control*

263 We now consider how other control options with similar costs could offer greater benefit if tailored. An  
264 alternative to annual control could be a biannual-biennial regime, i.e. control is applied twice a year every  
265 two years. In some cases this may be more cost effective as resources only need to be acquired every  
266 other year; it may also be socially advantageous if the application of poison is somewhat controversial  
267 and its use needs to be limited. As operational costs may be considerable (particularly labour and  
268 transport/flight-time), and the amount of bait applied contributes relatively little to the overall cost of  
269 each control dose, we do not consider control via very frequent smaller doses here. We used the 1000  
270 year seedfall simulation to compare three biannual-biennial regimes with no control and the annual  
271 control regime described above:

- 272 1. Regular biennial control: Control occurs every second year and is executed in early September  
273 and a month later in early October, i.e. straddling the optimal control period (see *Results*).
- 274 2. Seedfall determined control: Control occurs in years when seedfall is above the median (i.e. with  
275 the same long term average frequency as regular biennial control), in early September and early  
276 October.
- 277 3. Climate determined control: Control occurs in years when the seedfall temperature driver  $\Delta T$  is  
278 above the median (i.e. with the same long term average frequency as regular biennial control but  
279 with more opportunity for error in true/false seedfall prediction), in early September and early  
280 October.

281 Regime two could be used if the seedfall could be measured early enough to plan a control application  
282 that year. In cases where this was too late to muster a control application then regime three may be of  
283 use.

284

285 **Results**

286 When mice are not controlled, 85% of years are plague years, the mouse density is above the plague level  
287 for 71% of the time and the average plague size is 5.71 (see Figure 2 for a 20 year time series example).

### 288 *Optimal control timing*

289 As the control time is changed across the year the plague time varies (Figure 3, top). The different control  
290 levels (low, medium and high) have a much stronger effect on the plague time than the control timing.  
291 For example, under the low control regime, where the control success rate is between 50 and 60%, the  
292 optimal control timing to reduce plague time is spring (mid-September) before the mast season starts  
293 when plague time is 0.36. Conversely the lowest reduction is seen in autumn (late April) at the end of the  
294 mast season which reduces the plague time to 0.42. The optimal control time at medium and high control  
295 levels is also around mid-September. Medium control, which has an 80-85% success rate, reduces the  
296 plague time to 0.20, while high control has a 92-94% success rate and reduces the plague time to 0.045.

297 In contrast, the expected plague size (Figure 3, bottom) appears to be strongly affected by control timing,  
298 in particular for low and medium control levels. The optimal timing to reduce plague time gives the least  
299 reduction in expected plague size. Initially this seems counter-intuitive but less so after recalling the  
300 definition of expected plague size (the maximum mouse density *given* that there is a plague). On  
301 examination of the time series (Figure 4) for control during the mast season (March - left column) and  
302 after (September - right column) we see that the small reduction in plague time between the control  
303 timings comes from the years where the plague threshold is only just exceeded. For low control effort  
304 both timings have relatively little impact on the maximum mouse density reached for large plagues, but  
305 in post mast control (September) the timing is appropriate to reduce mouse density to below the plague  
306 threshold for smaller plagues. This means that, for low level control post mast season small plagues are  
307 often avoided but if control is during the mast the small plagues still occur. Larger plagues still occur and  
308 reach similar maximum densities as in the absence of control for both timings. When calculating an



309 expected plague size over the entire time-series, smaller plagues will reduce the average. Therefore, while  
310 the larger expected plague size for low control may seem counter-intuitive, the reduction in small plagues  
311 driving this is actually a desirable outcome. Using an alternative metric of plague severity, for example the  
312 expected density over the entire time-series, loses this subtlety and gives results similar to the plague  
313 time metric.

#### 314 *Tailored control*

315 Seedfall- and climate-determined biennial-biannual control regimes are more effective in reducing  
316 proportion of plague years and time above plague levels than a regular biennial-biannual control regime  
317 (Table 2). For both the low and medium control levels a seedfall driven biennial-biannual control regime  
318 is more effective than annual control (Table 2). If the control trigger is based on climatic variables rather  
319 than actual seedfall, the biennial-biannual regime is slightly less effective than annual control, though the  
320 differences in plague time between these methods is relatively small.

#### 321 **Discussion**

322 Management to mitigate the adverse effects of irrupting small consumers should be optimised to ensure  
323 that the limited resources available to managers are implemented to have the greatest impact and to  
324 meet control objectives. In this work, we offer insights into the dynamics of an irrupting rodent population  
325 undergoing broad-scale aerial control in an ecosystem with pulsed resources. It is clear from our results  
326 that the timing and frequency of control can affect the time spent above the plague threshold. While we  
327 have focused on mouse irruptions in beech forest, insights from this work have clear ramifications for  
328 dynamics of predators, prey and disease spread in other systems with climate-driven pulsed resources  
329 and outbreaking consumers worldwide.

330 There is currently no broad-scale control of mice alone in mainland New Zealand, due, in part, to the  
331 higher prioritisation of other vertebrate pest targets. In addition, achieving a large reduction in mouse  
332 abundance at large spatial scale is difficult with the control tools currently available on the mainland  
333 (Ruscoe & Pech, 2010). As a result, considerably less is known about the optimal control practices when  
334 targeting mice, compared to other small mammals. In a year of high seedfall and in the absence of control,  
335 our model predicts that mouse populations exceed the plague threshold and drive a rapid decline in the  
336 amount of available seed. As seedfall is depleted, mouse density decreases but still remains above the  
337 plague threshold by the end of the mast year. As well as the local impacts of this prolonged high mouse  
338 density, there is a risk that after seedfall depletion mice may disperse out of beech forest into other  
339 adjacent areas or habitats (Choquenot & Ruscoe, 2000; Ostfeld & Keesing, 2000). Dispersal of outbreaking  
340 rodents has been reported globally and contributes to disease spread (Deter *et al.*, 2008; Smith *et al.*,  
341 2015), damage to agriculture (Biswas *et al.*, 2016; Newsome, 1969; Ruscoe, 1996) or declines in  
342 indigenous biota (Smith *et al.*, 2016). However, conducting high level mouse control in mast years can  
343 successfully reduce mouse density to below plague level and to an extent where seed abundance is closer  
344 to that observed in the absence of mice. This should provide more food resource for other indigenous  
345 consumers competing for seedfall, and reduce the risks of dispersal and predation by mice and stoats.

346 Our model quantifies relative mouse abundance as an index of captures per 100 trap nights. Measuring  
347 actual mouse density in the field is difficult and costly, therefore indices such as C/100TN or a rodent  
348 tracking index (i.e. mean percentage of 'run-through' tracking tunnels containing mouse prints per line)  
349 are commonly used (Blackwell *et al.*, 2002; Ruscoe *et al.*, 2001). Quantifying relative abundance in this  
350 way facilitates model parameterisation and validation of model predictions using observation data that is  
351 more readily available to managers. Our model assumes logistic-type density dependence in the mouse  
352 population, which has been shown to be a good description of density-dependent dynamics in small  
353 rodent populations (see e.g. Turchin and Ostfeld (1997)). The best-fit parameters were similar to those

354 used in other models of house mouse population dynamics, for example the model of Choquenot and  
355 Ruscoe (2000) also had a positive density-independent growth term and a negative density-dependent  
356 growth term.

357 The three values chosen for peak bait availability to model low, moderate and high control levels, gave  
358 control success rates (measured as percentage kill) in the ranges 50-60%, 80-85% and 92-94%,  
359 respectively. How these ranges relate to success for real control operations, that aim to suppress as  
360 opposed to eradicate mouse populations, will depend on control objectives. To date, very little has been  
361 published on the density-impact relationships for mouse abundance and biodiversity in New Zealand.  
362 These knowledge deficits currently present a major barrier for managers, both in terms of setting  
363 conservation aims and measuring success of mouse control operations. However, our modelling  
364 framework provides predictions of mouse abundance and kill rates that can be readily applied to real  
365 control operations, as research advances in this area and new thresholds for successful suppression of  
366 mouse populations on mainland New Zealand are set.

367 Our model predicts that the optimal timing for mouse control in beech forest, with respect to minimising  
368 plague time, is mid-September. This timing fits within the recommended range for broad-scale aerial 1080  
369 control targeting rats and stoats (Elliott & Kemp, 2016). Across all the regimes considered here, the  
370 seedfall driven biannual-biennial regime gave the greatest reduction in plague time and plague years for  
371 low and moderate control levels, although the differences between regimes were relatively small.  
372 Managers will need to take additional factors into consideration when selecting an optimal approach, for  
373 instance the benefits of seedfall driven control need to be weighed against the cost and effort associated  
374 with collecting the necessary seedfall data, while temperature data required for the climate driven regime  
375 is readily available.

376 An important advantage of this modelling approach is its simplicity and generality. This work considered  
377 a case study of optimal control for mouse populations in New Zealand hard beech forest, where the aim  
378 is to minimise plague time. Different compositions of masting species in other forests will drive slightly  
379 different seedfall and mouse dynamics. For example, Ruscoe *et al.* (2004) reported a later onset of mouse  
380 population increase due to heavy rimu (*D. cupressium*) masting occurring two to three months later than  
381 in beech forest. Therefore, optimal control conditions will likely differ for other forest compositions.  
382 Nonetheless, our model and approach could be easily adapted for application to other habitats with  
383 climate-driven pulsed resources, for which temperature, resource, and consumer abundance data is  
384 available for parameterisation. Similarly, it would be straightforward to alter our model to account for  
385 additional drivers of population irruptions, such as the effect of rainfall alongside bamboo masts on rodent  
386 outbreaks in South America (Jaksic & Lima, 2003), or to adjust the thresholds for conducting control.

387 Interactions between mice and their competitors or predators are captured implicitly in the model via the  
388 density-independent and density-dependent growth rates. However, making these interactions explicit  
389 by including rate of change of equations for other interacting species in the system, could offer additional  
390 insights, e.g. into cascading responses across different trophic levels. For instance, an equation for stoat  
391 density could be included in the model to consider the effectiveness of targeting mice as vectors for  
392 secondary poisoning of stoats. In addition, this work could be extended to relate the mouse densities  
393 expected under different control regimes to outcomes for indigenous biota, as this will be another key  
394 factor for determining the optimal approach and assessing whether conservation objectives are being  
395 met.

396 In this work, we have attempted to maintain approximately equal costs across each control scenario by  
397 comparing regimes with similar long-term frequency (e.g. annual vs. biennial-biannual). We assume that  
398 low, moderate and high effort poisoning will likely have similar overall costs since the operational costs

399 (e.g. aerial transport and/or application, labour costs) are relatively large and constant compared to  
400 equipment costs (e.g. traps, bait). However, a cost-benefit analysis of higher and lower frequency control  
401 regimes could also be undertaken.

402 Our results assume the same distribution of summer temperatures over a 1000 year time-series; however  
403 the effects of climate change could be investigated by relaxing this assumption. If consumer-resource  
404 dynamics are altered due to climate change, our model could be useful for guiding how management  
405 timing and intensity should be modified to still be effective in reducing the mouse population. For  
406 example, our model would be compatible with a recently developed framework, based on the Kelly *et al.*  
407 (2013) model, that uses climate projections to assess whether climate change might affect the frequency  
408 or spatial extent of beech forest masts (Barron *et al.*, 2016).

409

## 410 **Conclusions**

411 With large-scale predator control campaigns causing pest control to ramp up across New Zealand's  
412 mainland (Russell *et al.*, 2015), there are opportunities to answer increasingly complex questions around  
413 the impacts of broad-scale invasive pest management for ecosystems, and to determine optimal control  
414 practices. We have attempted to fill an important knowledge gap concerning broad-scale control of  
415 irrupting mouse populations in masting beech forest, however a deeper understanding of climate-driven  
416 consumer-resource dynamics and control outcomes will benefit managers globally. In a rapidly changing  
417 world, having the modelling tools in place to make good predictions about the behaviour of such  
418 systems, puts us in a stronger position to anticipate and mitigate the potential adverse effects of  
419 change.

420

421 **Authors' Contributions**

422 EH and AJ conceived the ideas and developed the model. EH, AJ and RB interpreted the results and  
423 drafted the manuscript. All authors contributed critically to the drafts and gave final approval for  
424 publication.

425

426 **Data Accessibility**

427 Data used to parameterise the model (temperature, seedfall, and trap catch of mice) are the same as for  
428 Holland *et al.* (2015) and are publicly available from the Landcare Research Manaaki Whenua DataStore  
429 database at the URL [https://datastore.landcareresearch.co.nz/dataset/climate-driven-consumer-](https://datastore.landcareresearch.co.nz/dataset/climate-driven-consumer-resource-models-data)  
430 [resource-models-data](https://datastore.landcareresearch.co.nz/dataset/climate-driven-consumer-resource-models-data) or at the DOI <http://dx.doi.org/10.7931/J2W66HPB>.

431

432 **Acknowledgements**

433 The authors thank John Innes for helpful discussions, and Andrea Byrom and Roger Pech for useful  
434 comments on manuscript drafts.

435 Figure Captions

436 **Figure 1:** Example one year (Feb-Feb) time series of mouse density (C/100TN) (top) and seedfall (seeds m<sup>-2</sup>) (bottom, log scale) through time, modelled using three different seedfall levels: high (a mast year, the 75<sup>th</sup> percentile of the seedfall distribution, black solid line); median (50<sup>th</sup> percentile of the seedfall distribution, blue dashed line); low (25<sup>th</sup> percentile of the seedfall distribution, green dot-dashed line). The mouse plague level is defined such that, for an initial mouse density of 1, if the seedfall is at or below the median level, there is no plague (grey horizontal line, top only). Note that the start of the year coincides with the start of the seedfall season. When high level control takes place at the start of the seedfall season (February 1) in a mast year (black dotted line, top and bottom), the mouse density is much reduced compared to no control in a mast year (c.f. black solid line, top) and seed remains available until the end of the year (c.f. black solid line, bottom). With control, the seedfall is closer to the seedfall in the absence of mice (red dashed line, bottom only).

447

448 **Figure 2:** A 20 year example time series for mouse density (top) and seedfall (bottom, log scale) in the absence of control. The dashed lines show the defined plague level for the mouse population and the seedfall mast level. The plague threshold is exceeded in 85% of years and for 71% of the total time.

451

452 **Figure 3:** The effect of timing of annual control on plague time (top) and plague size (bottom), for low (red), medium (blue dashed) and high (green dot-dashed) control levels, and compared to no control (black dashed). If control has a low success rate then optimal control timing is mid-September. However, if control is more effective then there is little difference in plague time if control is applied at different

456 times throughout the year. Plague size is more strongly affected by control timing, particularly for low and  
457 medium control levels.

458

459 **Figure 4:** Time series of mouse density (C/100TN) for each of the three control levels (low, medium and  
460 high) applied annually (red lines), compared against mouse density with no control (black lines). The black  
461 dashed line shows the mouse density plague level. The left column shows control applied in autumn  
462 (March), the right column control applied in early spring (September). Low control stops plagues in only  
463 the years with the lowest plague size. Contrastingly, high control reduces mouse density to below the  
464 plague threshold in almost all years but in the highest plague years mouse populations still persist.

465

466



467 **References**

468

- 469 Allen, R. B., Mason, N. W. H., Richardson, S. J., & Platt, K. H. (2012). Synchronicity, periodicity and  
470 bimodality in inter-annual tree seed production along an elevation gradient. *Oikos*, *121*(3), 367-  
471 376. doi:10.1111/j.1600-0706.2011.19306.x
- 472 Barron, M. C., Pech, R. P., Christie, J. E., Tait, A., Byrom, A., & Elliot, G. (2016). *Climate change impacts*  
473 *and implications: an integrated assessment in the alpine case study*. Synthesis report: RA2 Alpine  
474 Case Study. The beech forests of New Zealand. Climate Change Impacts and Implications for  
475 New Zealand to 2100. MBIE contract C01X1225. 19 p.
- 476 Biswas, S., Kumar, S., & Mittal, V. (2016). A note on rodent migration following gregarious bamboo  
477 flowering in north eastern hill region with particular reference to Mizoram (India) and its  
478 consequences. *Journal of Common Diseases*, *48*(3), 1-12.
- 479 Blackwell, G. L., Potter, M. A., & McLennan, J. A. (2002). Rodent density indices from tracking tunnels,  
480 snap-traps and Fenn traps: do they tell the same story? *New Zealand Journal of Ecology*, *26*(1),  
481 43-51.
- 482 Broome, K., Golding, C., Brown, K., Horn, S., Corson, P., & Bell, P. (2017). Mouse eradication using aerial  
483 baiting: Current agreed best practice used in New Zealand (Version 1.0). New Zealand  
484 Department of Conservation. Wellington, New Zealand.
- 485 Choquenot, D., & Ruscoe, W. A. (2000). Mouse population eruptions in New Zealand forests: the role of  
486 population density and seedfall. *Journal of Animal Ecology*, *69*, 1058-1070.
- 487 Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented  
488 system. *Nature*, *400*, 563. doi:10.1038/23028
- 489 Deter, J., Chaval, Y., Galan, M., Gauffre, B., Morand, S., Henttonen, H., Laakkonen, J., Voutilainen, L.,  
490 Charbonnel, N., & Cosson, J.-F. (2008). Kinship, dispersal and hantavirus transmission in bank  
491 and common voles. *Archives of Virology*, *153*(3), 435-444.
- 492 Eason, C. T., Murphy, E. C., Wright, G. R. G., & Spurr, E. B. (2002). Assessment of risks of brodifacoum to  
493 non-target birds and mammals in New Zealand. *Ecotoxicology*, *11*, 35-48.
- 494 Elliott, G., & Kemp, J. (2016). Large-scale pest control in New Zealand beech forests. *Ecological*  
495 *Management & Restoration*, *17*(3), 200-209. doi:10.1111/emr.12227
- 496 Fisher, P., & Airey, A. T. (2009). Factors affecting 1080 pellet bait acceptance by house mice (*Mus*  
497 *musculus*). *DOC Research and Development Series 306*. New Zealand Department of  
498 Conservation. Wellington, New Zealand.
- 499 Fitzgerald, B. M., Daniel, M. J., Fitzgerald, A. E., Karl, B. J., Meads, M. J., & Notman, P. R. (1996). Factors  
500 affecting the numbers of house mice (*Mus musculus*) in hard beech (*Nothofagus truncata*)  
501 forest. *Journal of the Royal Society of New Zealand*, *26*(2), 237-249.
- 502 Holland, E. P., & James, A. (2015). Assessing the efficacy of population-level models of mast seeding.  
503 *Theoretical Ecology*, *8*(1), 121-132. doi:10.1007/s12080-014-0238-4
- 504 Holland, E. P., James, A., Ruscoe, W. A., Pech, R. P., & Byrom, A. E. (2015). Climate-based models for  
505 pulsed resources improve predictability of consumer population dynamics: outbreaks of house  
506 mice in forest ecosystems. *PLoS One*, *10*(3), e0119139. doi:10.1371/journal.pone.0119139
- 507 Innes, J., Kelly, D., McC. Overton, J., & Gillies, C. (2010). Predation and other factors currently limiting  
508 New Zealand forest birds. *New Zealand Journal of Ecology*, *34*(1), 86-114.

- 509 Innes, J., Warburton, B., Williams, D., Speed, H., & Bradfield, P. (1995). Large-scale poisoning of ship rats  
510 (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *New Zealand Journal of*  
511 *Ecology*, 19(1), 5-17.
- 512 Jaksic, F. M., & Lima, M. (2003). Myths and facts on ratadas: Bamboo blooms, rainfall peaks and rodent  
513 outbreaks in South America. *Austral Ecology*, 28, 237-251.
- 514 Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics*, 2, 465-492.
- 515 Jedrzejewska, B., & Jedrzejewski, W. (1998). Predation in Vertebrate Communities. The Bialowieza  
516 Primeval Forest as a Case Study. *Ecological Studies*, 135, 230-231. Springer-Verlag Berlin  
517 Heidelberg.
- 518 Jones, C., & Toft, R. (2006). Impacts of mice and hedgehogs on native forest invertebrates: a pilot study.  
519 *DOC Research and Development Series 245*. New Zealand Department of Conservation.  
520 Wellington, New Zealand.
- 521 Jones, C. G., Ostfeld, R. S., Richard, M. P., Schaubert, E. M., & Wolff, J. O. (1998). Chain reactions linking  
522 acorns to gypsy moth outbreaks and Lyme disease risk. *Science*, 279(5353), 1023-1026.
- 523 Kelly, D., Geldenhuys, A., James, A., Penelope Holland, E., Plank, M. J., Brockie, R. E., Cowan, P. E.,  
524 Harper, G. A., Lee, W. G., Maitland, M. J., Mark, A. F., Mills, J. A., Wilson, P. R., & Byrom, A. E.  
525 (2013). Of mast and mean: differential-temperature cue makes mast seeding insensitive to  
526 climate change. *Ecol Lett*, 16(1), 90-98. doi:10.1111/ele.12020
- 527 Kelly, D., & Sork, V. L. (2002). Mast Seeding in Perennial Plants: Why, How, Where? *Annual Review of*  
528 *Ecology and Systematics*, 33(1), 427-447. doi:10.1146/annurev.ecolsys.33.020602.095433
- 529 King, C. M. (1983). The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice  
530 (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in  
531 three New Zealand forests. *Journal of Animal Ecology*, 52(1), 141-166.
- 532 Mackay, J. W. B., Russell, J. C., & Murphy, E. C. (2007). Eradicating house mice from islands: successes,  
533 failures and the way forward. Paper presented at the *Managing vertebrate invasive species:*  
534 *proceedings of an international symposium*, Fort Collins, USDA/APHIS/WS, National Wildlife  
535 Research Centre.
- 536 Magarey, R. D., & Isard, S. A. (2017). A troubleshooting guide for mechanistic plant pest forecast models.  
537 *Journal of Integrated Pest Management*, 8(1).
- 538 Miller, C. J., & Miller, T. K. (1995). Population dynamics and diet of rodents on Rangitoto Island, New  
539 Zealand, including the effect of a 1080 poison operation. *New Zealand Journal of Ecology*, 19,  
540 19-27.
- 541 Murphy, E., Gillies, C., Maddigana, F., McMurtrie, P., Edge, K.-A., Rohan, M., & Clapperton, K. (2016).  
542 Flexibility of diet of stoats on Fiordland islands, New Zealand. *New Zealand Journal of Ecology*,  
543 40(1). doi:10.20417/nzjecol.40.13
- 544 Murphy, E. C., Robbins, L., Young, J. B., & Dowding, J. E. (1999). Secondary poisoning of stoats after an  
545 aerial 1080 poison operation in Pureora Forest, New Zealand. *New Zealand Journal of Ecology*,  
546 23(2), 175-182.
- 547 Mutze, G., & Sinclair, R. (2004). Efficacy of zinc phosphide, strychnine and chlorpyrifos as rodenticides  
548 for the control of house mice in South Australian cereal crops. *Wildlife Research*, 31, 249-257.
- 549 Newsome, A. E. (1969). A population study of house-mice temporarily inhabiting a South Australian  
550 wheatfield. *Journal of Animal Ecology*, 38, 341-359.
- 551 Norbury, G., Byrom, A., Pech, R., Smith, J., Clarke, D., Anderson, D., & Forrester, G. (2013). Invasive  
552 mammals and habitat modification interact to generate unforeseen outcomes for indigenous  
553 fauna. *Ecological Applications*, 23(7), 1707-1721.

- 554 Norbury, G., van den Munckhof, M., Neitzel, S., Hutcheon, A., Reardon, J., & Ludwig, K. (2014). Impacts  
555 of invasive house mice on post-release survival of translocated lizards. *New Zealand Journal of*  
556 *Ecology*, 38(2), 322-327.
- 557 O'Connor, C. E., Morriss, G., & Murphy, E. C. (2005). Toxic bait avoidance by mice. Paper presented at  
558 the *Proceedings of the 13th Australasian Vertebrate Pest Conference*, Wellington, New Zealand.
- 559 O'Donnell, C. F. J., & Phillipson, S. M. (1996). Predicting the incidence of mohua predation from the  
560 seedfall, mouse, and predator fluctuations in beech forests. *New Zealand Journal of Zoology*, 23,  
561 287-293.
- 562 Ostfeld, R. S., & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in  
563 terrestrial ecosystems. *TREE*, 15(6), 232-237.
- 564 Pearse, I. S., Koenig, W. D., & Knops, J. M. H. (2014). Cues versus proximate drivers: testing the  
565 mechanism behind masting behaviour. *Oikos*, 123, 179-184.
- 566 Pucek, Z., Jedzrejewski, W., Jedzrejewski, B., & Pucek, M. (1993). Rodent population dynamics in a  
567 primeval deciduous forest (Biolowieza National Park) in relation to weather, seed crop and  
568 predation. *Acta Theriologica*, 38(2), 199-232.
- 569 Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity  
570 conservation. *Ecology Letters*, 12, 982-998.
- 571 Ruscoe, W. A. (1996). Spatial variability in population levels of *Rattus sordidus* in north Queensland cane  
572 growing districts: ecological and gene flow hypotheses (PhD Thesis). Queensland University of  
573 Technology, Brisbane, Australia.
- 574 Ruscoe, W. A. (2001). Advances in New Zealand mammalogy 1990-2000: House mouse. *Journal of the*  
575 *Royal Society of New Zealand*, 31(1), 127-134.
- 576 Ruscoe, W. A., Choquenot, D., Heyward, R., Yockney, I., Young, N., & Drew, K. (2003) Seed production,  
577 predators and house mouse population eruptions in New Zealand beech forests. *ACIAR*  
578 *Monograph No. 96. Rats, mice and people: rodent biology and management* (pp. 334-337).
- 579 Ruscoe, W. A., Goldsmith, R., & Choquenot, D. (2001). A comparison of population estimates and  
580 abundance indices for house mice inhabiting beech forests in New Zealand. *Wildlife Research*,  
581 28, 173-178.
- 582 Ruscoe, W. A., & Murphy, E. C. (2005). House Mouse. In: C. M. King (Ed.), *The handbook of New Zealand*  
583 *mammals* (pp. 203-221). Melbourne, Australia: Oxford University Press.
- 584 Ruscoe, W. A., & Pech, R. P. (2010). Rodent outbreaks in New Zealand. In: G. Singleton, S. Belmain, P.  
585 Brown, & B. Hardy (Eds.), *Rodent outbreaks: ecology and impacts* (pp. 239-251). Manila,  
586 Philippines, International Rice Research Institute.
- 587 Ruscoe, W. A., Wilson, D., McElrea, L., McElrea, G., & Richardson, S. J. (2004). A house mouse (*Mus*  
588 *musculus*) population eruption in response to rimu (*Dacrydium cupressinum*) seedfall in  
589 southern New Zealand. *New Zealand Journal of Ecology*, 28(2), 259-265.
- 590 Russell, J. C., Innes, J. G., Brown, P. H., & Byrom, A. E. (2015). Predator-free New Zealand: conservation  
591 country. *Bioscience*, 65(5), 520-525.
- 592 Simberloff, D. (2002) Today Tiritiri Matangi, tomorrow the world!: are we aiming too low in invasives  
593 control? *Turning the tide: the eradication of invasive species*. (pp. 4-12). IUCN, Gland,  
594 Switzerland and Cambridge, UK. IUCN SSC Invasive Species Specialist Group.
- 595 Singleton, G., Belmain, S., Brown, P., & Hardy, B. (2010). *Rodent outbreaks: ecology and impacts* (G.  
596 Singleton, S. Belmain, P. Brown, & B. Hardy Eds.): International Rice Research Institute.
- 597 Singleton, G., Krebs, C. J., Davis, S., Chambers, L., & Brown, P. (2001). Reproductive changes in  
598 fluctuating house mouse populations in southeastern Australia. *Proceedings of the Royal Society*  
599 *of London. Series B: Biological Sciences*, 268(1477), 1741-1748. doi:10.1098/rspb.2001.1638

- 600 Singleton, G. R., Tann, C. R., & Krebs, C. J. (2007). Landscape ecology of house mouse outbreaks in south-  
601 eastern Australia. *Journal of Applied Ecology*, *44*, 644-652.
- 602 Smith, H., Dickman, C., & Banks, P. (2016). Nest predation by commensal rodents in urban bushland  
603 remnants. *PLoS One*, *11*(6), e0156180.
- 604 Smith, M. C., Gomulkiewicz, R., & Mack, R. N. (2015). Potential role of masting by introduced bamboos  
605 in deer mice (*Peromyscus maniculatus*) population irruptions holds public health consequences.  
606 *PLoS One*, *10*(6).
- 607 Studholme, B. (2000). Ship rat (*Rattus rattus*) irruptions in South Island beech (*Nothofagus*) forest.  
608 *Conservation Advisory Science Notes: 318*. New Zealand Department of Conservation.  
609 Wellington, New Zealand.
- 610 Turchin, P., & Ostfeld, R. S. (1997). Effects of density and season on the population rate of change in the  
611 meadow vole. *Oikos*, *78*(2), 355-361.
- 612 Wardle, J. A. (1984). The New Zealand beeches: ecology, utilization and management. New Zealand  
613 Forest Service. Wellington, New Zealand.
- 614 Watts, C., Innes, J., Wilson, D., Fitzgerald, N., Bartlam, S., Thornburrow, D., & Smale, M. (2017). Impacts  
615 of mice alone on biodiversity: final report of a Waikato field trial. Landcare Research contract  
616 report LC2747.
- 617 Wilson, D. J., McElrea, G. J., McElrea, L. M., Heyward, R. O., Peach, R. M. E., & Thompson, C. (2006).  
618 Potential conservation impacts of high-altitude small mammals: a field study and literature  
619 review. *DOC Research and Development Series 248*. New Zealand Department of Conservation.  
620 Wellington, New Zealand.
- 621 Wilson, P. R., Karl, B. J., Toft, R. J., Beggs, J. R., & Taylor, R. H. (1998). The role of introduced predators  
622 and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand.  
623 *Biological Conservation*, *83*(2), 175-185.  
624

**Table 1** (on next page)

Parameters and variables

1 **Table 1.** Parameters and variables

Parameters	Symbol	Value	Units
Demographic efficiency	$\alpha$	1	mice (seeds m <sup>-2</sup> ) <sup>-1</sup>
Density independent birth	$\mu_1$	-1.23	year <sup>-1</sup>
Density dependent mortality	$\mu_2$	0.76	mouse <sup>-1</sup> year <sup>-1</sup>
Maximum per capita feeding rate	$c$	6.74	seeds m <sup>-2</sup> mouse <sup>-1</sup> year <sup>-1</sup>
Foraging efficiency	$e$	1.08	(seeds m <sup>-2</sup> ) <sup>-1</sup>
Seedfall decay	$h$	9.48	year <sup>-1</sup>
Bait decay	$d$	50	year <sup>-1</sup>
Control level	$B_0$	50, 100, 150	--
<b>Variables</b>			
Mouse density	$M(t)$	--	mice (measured as an index = captures per 100 trap nights (C/100TN))
Available resource density	F(t)	--	seeds m <sup>-2</sup>
Resource delivery rate	S(t)	--	seeds m <sup>-2</sup> year <sup>-1</sup>
Mortality rate due to control	B(t)	--	year <sup>-1</sup>

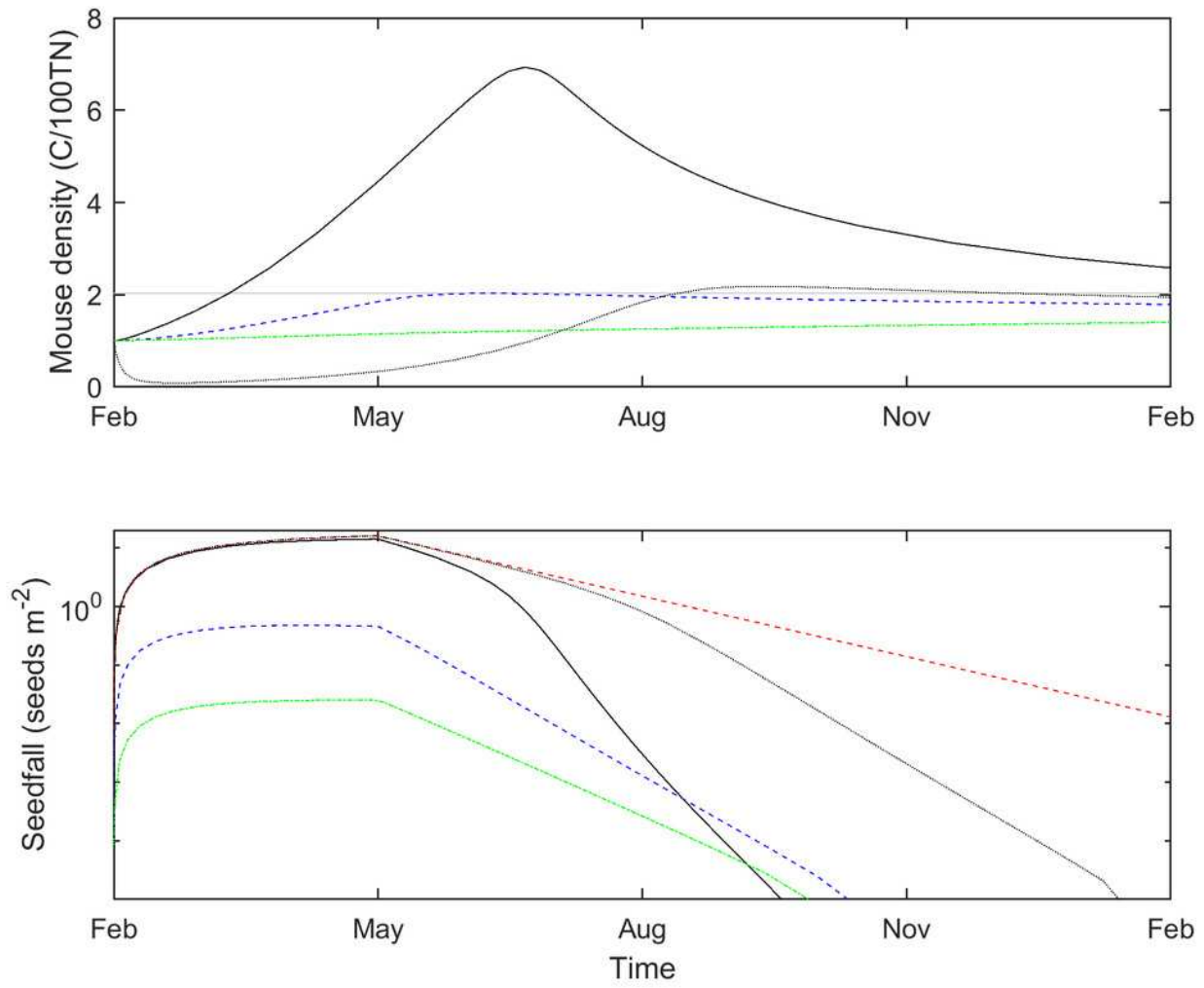
2

3

# Figure 1

Example one year (Feb-Feb) time series of mouse density and seedfall

Example one year (Feb-Feb) time series of mouse density (C/100TN) (top) and seedfall (seeds m<sup>-2</sup>) (bottom, log scale) through time, modelled using three different seedfall levels: high (a mast year, the 75<sup>th</sup> percentile of the seedfall distribution, black solid line); median (50<sup>th</sup> percentile of the seedfall distribution, blue dashed line); low (25<sup>th</sup> percentile of the seedfall distribution, green dot-dashed line). The mouse plague level is defined such that, for an initial mouse density of 1, if the seedfall is at or below the median level, there is no plague (grey horizontal line, top only). Note that the start of the year coincides with the start of the seedfall season. When high level control takes place at the start of the seedfall season (February 1) in a mast year (black dotted line, top and bottom), the mouse density is much reduced compared to no control in a mast year (c.f. black solid line, top) and seed remains available until the end of the year (c.f. black solid line, bottom). With control, the seedfall is closer to the seedfall in the absence of mice (red dashed line, bottom only).

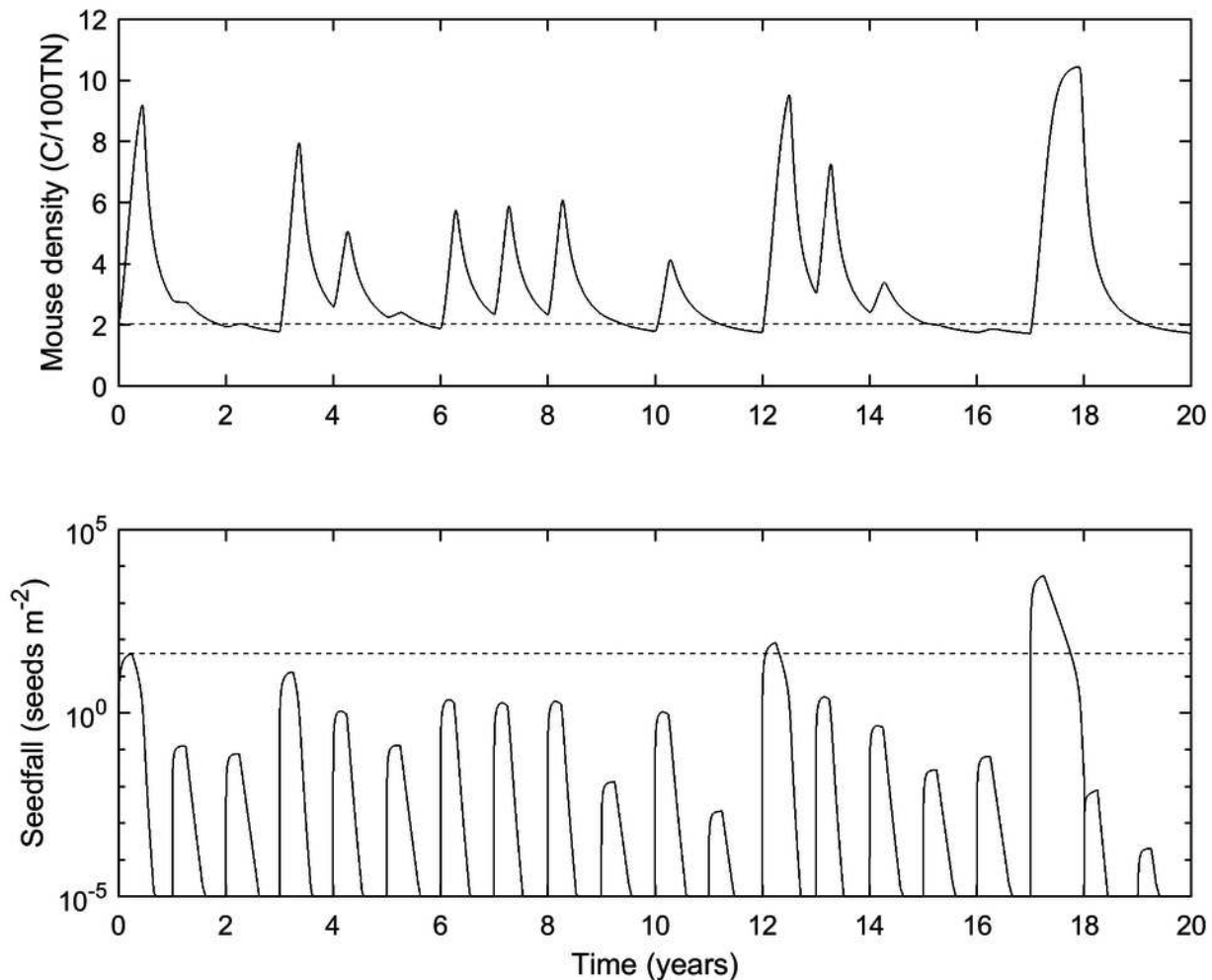




## Figure 2

A 20 year example time series for mouse density and seedfall in the absence of control

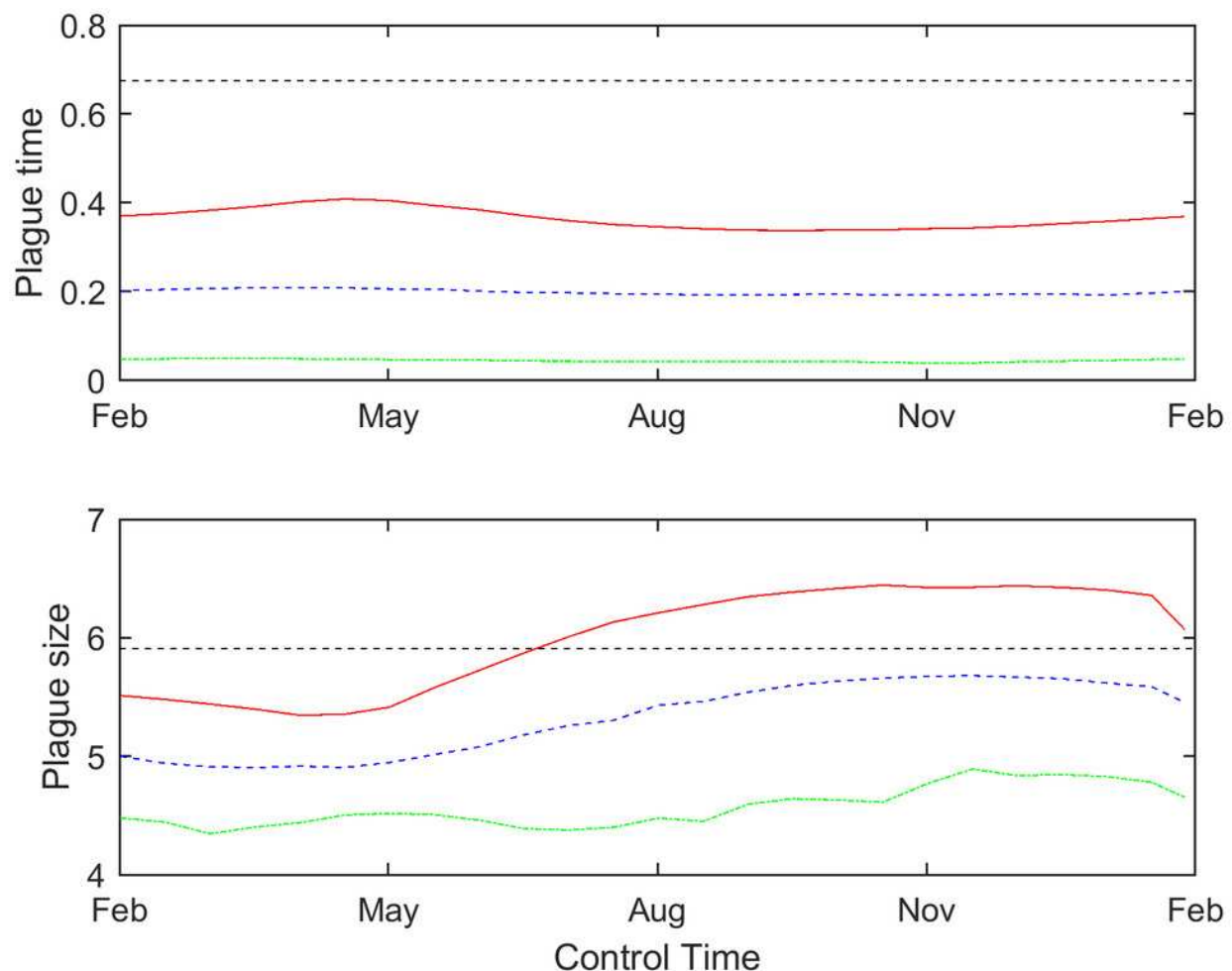
A 20 year example time series for mouse density (top) and seedfall (bottom, log scale) in the absence of control. The dashed lines show the defined plague level for the mouse population and the seedfall mast level. The plague threshold is exceeded in 85% of years and for 71% of the total time.



## Figure 3

The effect of timing of annual control on plague time and plague size

The effect of timing of annual control on plague time (top) and plague size (bottom), for low (red), medium (blue dashed) and high (green dot-dashed) control levels, and compared to no control (black dashed). If control has a low success rate then optimal control timing is mid-September. However, if control is more effective then there is little difference in plague time if control is applied at different times throughout the year. Plague size is more strongly affected by control timing, particularly for low and medium control levels.



## Figure 4

Time series of mouse density for each of the three control levels applied annually, compared against mouse density with no control

Time series of mouse density (C/100TN) for each of the three control levels (low, medium and high) applied annually (red lines), compared against mouse density with no control (black lines). The black dashed line shows the mouse density plague level. The left column shows control applied in autumn (March), the right column control applied in early spring (September). Low control stops plagues in only the years with the lowest plague size. Contrastingly, high control reduces mouse density to below the plague threshold in almost all years but in the highest plague years mouse populations still persist.

