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The necessity of tailored control of irrupting pest populations driven by pulsed resources

Merlin C. Köhnke[a,b,*], Rachelle N. Binny[c], E. Penelope Holland[d], Alex James[b,e]

[a] *Institute of Environmental Systems Research, School of Mathematics/Computer Science, Osnabrück University, Germany*
[b] *Biomathematics Research Centre, University of Canterbury, Christchurch, New Zealand*
[c] *Manaaki Whenua Landcare Research, Lincoln, New Zealand*
[d] *Department of Biology, University of York, York, United Kingdom*
[e] *Te Pūnaha Matatini, New Zealand*

Abstract

Resource pulses are widespread phenomena in diverse ecosystems. Irruptions of generalist consumers and corresponding generalist predators often follow such resource pulses. This can have severe implications on the ecosystem but also on the spread of diseases or on regional famines. Suitable management strategies are necessary to deal with these systems. In this study, we develop a general model to investigate optimal control for such a system and apply this to a case study from New Zealand. In particular, we consider the dynamics of beech masting (episodic synchronous seed production) leading to rodent outbreaks and subsequent stoat (*Mustela erminea*) irruptions. Here, stoat control happens via secondary poisoning. The results show that the main driver of the optimal control timing (June) is the population density of

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[*] Corresponding author
Email address: `merlin.koehnke@uos.de` (Merlin C. Köhnke)

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the control vector. Intermediate control levels are superior to higher levels if the generalist consumer is necessary as a control vector. Finally, we extend the model to a two-patch metapopulation model, which indicates that, as a consequence of the strong vector dependence, a strategy of alternating control patches yields better results than static control. This highlights that besides control level, also the design impacts the control success. The results presented in this study reveal important insights for proper pest management in the New Zealand case study. However, they also generally indicate the necessity of tailored control in such systems.

Keywords: Pulsed resources, Mast seeding, Invasive species, Conservation biology, Pest management, Rodents, Stoat control

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1. Introduction

Food webs affected by a pulsed resource are widespread and often include irrupting generalist consumer populations accompanied by generalist predator population outbreaks (Ostfeld and Keesing, 2000; Polis et al., 2004). Heavy rainfalls or synchronous intermittent seed production events, commonly referred to as mast seeding are typical examples of pulsed resources (Allen et al., 2012; Kelly and Sork, 2002; Herrera et al., 1998). Due to their short life span, rodent irruptions frequently form an integral part of such systems (Ostfeld and Keesing, 2000). For example, in Japan, *Castanopsis sieboldii* masting is followed by high rat (*Rattus rattus*, *Tokudaia tokunoshimensis*, and *Diplothrix legata*) abundances. Rats, in turn, are preyed on by invasive mongooses (*Herpestes javanicus*) which are threatening endemic vertebrate species (Fukasawa et al., 2013). Singleton et al. (2010) describe bamboo masting (e.g., *Melocanna*) causing rodent irruptions in Asia. As rats damage rice crops, they can be cause for famines in those regions. Furthermore, heavy summer rainfalls in Argentina lead to irruptions of vegetation biomass followed by high corn mouse (*Calomys musculinus*) abundances associated with outbreaks of Argentine hemorrhagic fever virus epidemics (Ostfeld and Keesing, 2000). Additional examples of epidemiological impacts of similar food webs are given by enhanced risk of the spread of rabies in Poland or increased Lyme disease risk in the United States (Jedrzejewska and Jedrzejewski, 2013; Dalgleish and Swihart, 2012). Due to extreme events accompanying climate change, these effects may become even more frequent in the future (Meerburg et al., 2009). Hence, understanding community dynamics affected by pulsed resources is not only crucial for ecosystem management but also epidemiological and even food security issues.

In New Zealand, mast seeding beech (*Nothofagus*) trees form part of about half of local indigenous forests (Wardle et al., 1984; Wiser et al., 2011). Of the 32 terrestrial mammal species in New Zealand, 29 are reducible to biological introductions, and many pose serious risks to indigenous avifauna (King, 2005; Ruscoe et al., 2006). Hence, it is a country in which management of such ecosystems is particularly urgent. Of New Zealand's endemic birds, 41% are already extinct while 77% are threatened and suffering from irruptions of invasive mammals such as possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*), and rats (e.g., *Rattus rattus*) (Innes et al., 2010). Already Riney (1959) suspected a strong connection of mast seeding and threats to native birds. In particular, masting leads to increases of mice, and rats followed by stoat irruptions and high predation pressure on birds — a relationship which is now widely confirmed, e.g., by linking mohua (*Mohoua ochrocephala*) breeding success to stoat irruptions after years with high seed fall (King, 1983; O'Donnell et al., 1996).

Due to the significant threat to indigenous birds, including the national animal of New Zealand, the kiwi (*Apteryx*), the New Zealand Department of Conservation developed a control program named 'Battle for our Birds' (Elliot, 2016). This program mainly consists of pest control using aerial application of biodegradable sodium fluoroacetate (1080) after beech masts (Elliot, 2016). If prefeed is applied, the toxins poison the rats while the toxic rats kill stoats via secondary poisoning (Murphy et al., 1999). In 2014, the operation covered 694,000 ha corresponding to 10% of New Zealand's indigenous forest area, which was highly effective in reducing rat and stoat tracking rates (Elliot, 2016). However, costs of such operations and public concerns regarding environmental side-effects limit the application of 1080 (Green and Rohan, 2012). Hence, it is essential to understand the dynamics to optimize the handling of existing resources and to avert environmental risks.

In this study, we develop a mathematical model describing a food web consisting of a pulsed resource, a generalist consumer, and a generalist preda-

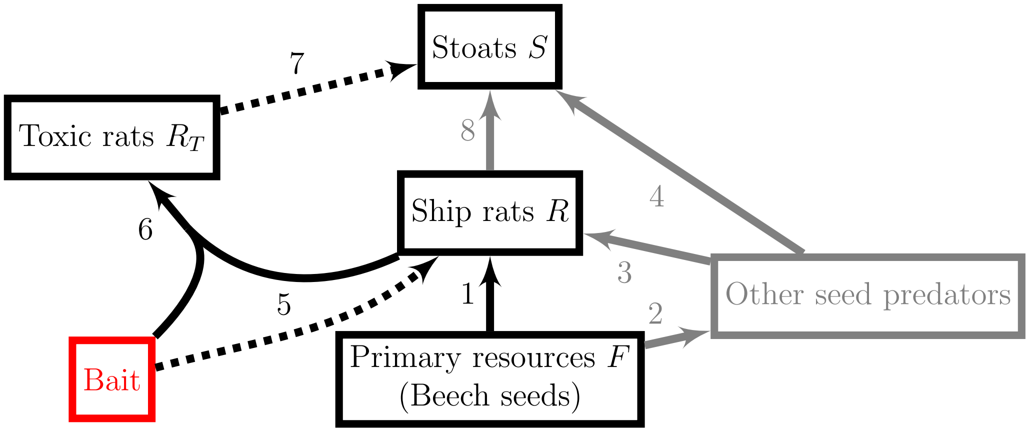

Figure 1: **We consider a food chain with three trophic levels in which top predator control is only possible via the consumer.** The figure shows a conceptual model of the system. Solid lines indicate a positive influence, while dashed lines indicate a negative influence. The red rectangle shows the control mechanism. The gray part of the diagram is modeled implicitly. We use the numbers beside the edges for references in the text.

tor with discrete breeding times and parameterize it as an example with regard to the seed-rat-stoat dynamics from New Zealand. We use the model to improve pest management by optimizing control design, control timing, and control intensity. Control design refers to the control patch size and the control frequency in each of these patches. The results emphasize the necessity of tailored control in such systems.

2. Model

In the case study, beech (*Nothofagus*) seeds F are the primary resource (see Fig 1), and seed fall and seed decay are the main drivers of their dynamics. Seed fall happens irregularly via beech masting on average every 4–6 years predominantly in autumn (February – May) (Wardle et al., 1984;

Ruscoe et al., 2005). High resource abundances after mast events lead to outbreaks of ship rats (*Rattus rattus*) which prey on seeds (link 1), but also on other seed predators (McQueen and Lawrence, 2008; King et al., 2011; Bridgman et al., 2013). Typically, ship rats breed in spring and summer (September – February), but when resources are highly abundant, as in years with high seed fall, breeding over winter occurs as well (King et al., 2011). Populations of other seed predators with short life spans, e.g., mice, irrupt similarly (link 2). Stoats (*Mustela erminea*), which feed on the seed predators, act as a generalist predator in this system. However, seasonal breeding of stoats is temporally more restrictive, only taking place in early spring (September – October) (O'Connor et al., 2006). The number of offspring produced strongly depends on their habitats' resource abundance ranging from no breeding at all up to 18 kits (King et al., 2003). Hence, a delayed high stoat abundance follows high seed consumer abundance driven by beech masting (O'Donnell et al., 1996). Due to the impact on the native fauna, control focuses on both stoat and ship rat populations. Sodium fluoroacetate (1080) baits are used to control rats and stoats (Elliot, 2016). Here, stoat control happens via secondary poisoning (Murphy et al., 1999). Hence, rats eat baits (link 5) and are converted into toxic rats (link 6). Stoats then get poisoned by feeding on toxic rats (link 7). Note that we include a predation effect of stoats on non-toxic rats in the model only implicitly as rats usually only form a minor part of the stoats' diet. In particular, without poisoning, only $< 10\%$ of the gut content of stoats contained rats (King and Moody, 1982; King, 2005). After 1080 poisoning, this is no longer true, presumably because stoats also feed on the carcasses (Murphy et al., 1999). By modeling it implicitly, we mean that we parameterized a term representing predation on all seed predators (including rats) using observations. Including a weak predation term as a direct link would have been equally possible. However, the other seed predators would still be necessary for agreement with observations. Hence, the model would have been more complicated and also harder to parameterize.

In this section, we introduce the model by successively aggregating the corresponding submodels. We refer to this model as *local* as it does not include dispersal. In Sec. 2.4, we develop a metapopulation model to account for such spatial processes.

Tab. A.1 lists the parameters used in this study with corresponding references. If avaiblable, we have used literature values. Otherwise, we calibrated the particular submodels using parameter estimations based on qualitative and quantitative results of previous studies.

2.1. Pulsed resource

We use the Delta temperature (ΔT) model introduced by Kelly et al. (2013) to describe resource fluctuations. Previous theoretical studies have already exploited this model (Holland and James, 2015; Holland et al., 2018), and applications to different plant species revealed a good correlation between prediction and data (Kelly et al., 2013; Pearse et al., 2014). We use mean annual summer temperatures over the previous two years $\Delta T_y = T_{y-1} - T_{y-2}$ to model resource abundance in year y. For the application of the model, we generated a 500-year random sample temperature time series. As in Holland et al. (2018),

$$T_y \sim \mathcal{N}(14, 1)$$

represents mean summer temperatures between 1972 and 2014 in the Orongorongo Valley in New Zealand. We predict seed fall based on these data and the log-linear model

$$\log_{10} F_y = 0.33 + 0.97\Delta T_y + \epsilon_y \tag{1}$$

parameterized using data from the Orongorongo Valley by Holland and James (2015) with $\epsilon_y \sim \mathcal{N}(0, 1.3)$ to match the correlation between seed fall and temperature as reported by Kelly et al. (2013).

The differential equation

$$\frac{\mathrm{d}F}{\mathrm{d}t} = \sigma(t) - hF - f(F)R \tag{2}$$

models the annual rate of change of food abundance F (seeds m^{-2}). Here, h is the annual degradation rate of seeds, and $\sigma(t)$ describes the resource delivery, i.e., in this case, beech seeding given by

$$\sigma(t) = \begin{cases} \frac{F_y}{0.25} & \text{if } 0 \leq t - \lfloor t \rfloor < 0.25 \\ 0 & \text{otherwise.} \end{cases} \tag{3}$$

$\lfloor t \rfloor$ denotes the floor function giving the largest integer smaller than t. Hence, seeding takes place in the form of a steady influx to the food abundance in the first quarter of the year. The start of the year is defined to be in February as this is the time in which masting typically starts. The term $f(F)R$ represents the consumption of the generalist consumer R with functional response $f(F)$, which we describe in the following section. Fig. 2, row 5 shows a 10-year sample time series with two years with high seed fall to as an illustration of the seed dynamics.

2.2. Generalist consumer

As rodents are prominent examples of generalist consumers (Ostfeld and Keesing, 2000), it is reasonable to model ship rats (*Rattus rattus*) as a representative example of a generalist consumer. The differential equation

$$\frac{\mathrm{d}R}{\mathrm{d}t} = \Phi_R(F, R) = R\left(\rho - \mu_R R + \alpha_1 f(F) + \alpha_2 f(F_{R0}) - B(t)\right), \tag{4a}$$

$$F_{R0} = \frac{\int_{t-1}^{t} F(t')\mathrm{d}t'}{1 + \beta \int_{t-1}^{t} B(t')\mathrm{d}t'}. \tag{4b}$$

models the temporal population dynamics of the ship rat. As ship rats' breeding success declines with density, we consider both, density-independent

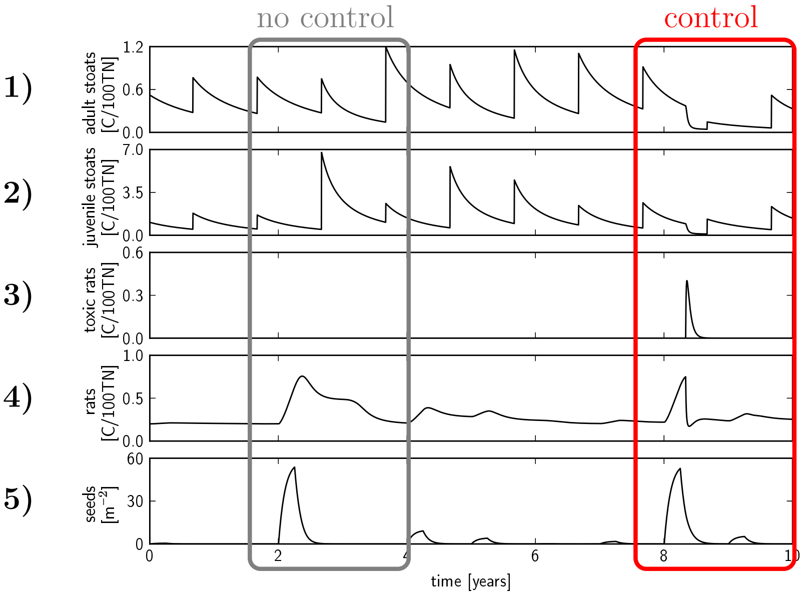

Figure 2: **Phenomenological dynamics follow what is known from data.** A part of a sample run of the local model is shown. Beech masting takes place in year 2 and year 8 of the time series. Bait is applied only in the second mast event (year 8).

ρ and density-dependent μ_R birth/death processes (Efford et al., 2006). Ship rats are seed predators (link 1 in Fig. 1) (King et al., 2011). As there is evidence for predator satiation during years with high seed fall (Kelly and Sork, 2002), we assume the functional response

$$f(F) = c \cdot \left(1 - e^{-\epsilon F}\right) \tag{5}$$

to be of Ivlev type. Note that one can equally justify another saturating functional response such as Holling type II. Some models show structural sensitivity against this choice (see e.g., Fussmann and Blasius (2005); Cordoleani et al. (2011)). However, the results presented in this study do not change qualitatively using Holling type II (results not shown).

A pure predator-prey relationship between rats and seeds would lead to a delayed peak in rat abundance, which would decrease again when seeds degrade. Conversely, data show that rat abundance is high between 15 and 20 months after a year with high seed fall (Elliott and Kemp, 2016; Kemp et al., 2018). This is because the diet of ship rats also depends implicitly on beech seeds (link 2 and 3 in Fig. 1). For instance, they also prey on mice, particularly after beech years with high seed fall (McQueen and Lawrence, 2008; Bridgman et al., 2013). This is taken into account by the term F_{R0} assuming that ship rats also benefit implicitly from seed fall of the last twelve months due to secondary food sources. As an alternative, we could have modeled these secondary as another state variable. However, this state variable would have incorporated a whole set of species that depend (partially) on seeds and are eaten by rats. Thus, parameterization would have been rather difficult. Furthermore, the model would have become even more complicated. Hence, we decided to model it in this indirect way to achieve the observed qualitative behavior. The resulting rat dynamics following a year with high seed fall are evident in Fig. 2, row 4 in the second year of the time series. Rat abundance is particularly high when seed abundance is high as well but stays high for about 15 months before it falls back to the pre-mast level. This is in agreement with what is known from data (Elliott and Kemp, 2016; Kemp et al., 2018).

The denominator of F_{R0} describes the impact of bait application $B(t)$ on secondary food sources, e.g., mice. If no bait is applied, the denominator is one. Conversely, if bait application took place in the last 12 months, secondary food sources are affected. Here, the parameter β represents bait efficacy regarding secondary resources. Bait application can be subject to different control strategies, e.g., annual control or control in years with high seed fall. Then, baits are applied at times t_i^{*b}, where i denotes the ith bait application. Following Holland et al. (2018),

$$B(t) = \begin{cases} B_0 \exp\left(-d(t - t_i^*)\right), & \text{if } t_i^{*b} \leq t < t_{i+1}^{*b} \\ 0, & \text{otherwise} \end{cases} \tag{6}$$

models the dynamics. Hence, bait application happens with an impulse with intensity B_0. Note that the value of B_0 has no actual ecological meaning. However, to compare it with data, it can be converted into killing proportions (see Appendix B). After application, bait decays exponentially with decay rate d. Note that bait is not carried over to the next year. This is a reasonable assumption as, after one year, bait has already decayed to a fraction of $2 \cdot 10^{-22}$ of its original value. Rats are also directly affected by bait applications (link 5 in Fig. 1) which turn rats R into toxic rats R_T (link 6 in Fig. 1). The differential equation

$$\frac{\mathrm{d}R_T}{\mathrm{d}t} = RB(t) - (d_i + \iota S)R_T \tag{7}$$

describes the temporal dynamics of the toxic rat population. The term $RB(t)$

is the conversion term converting susceptible ship rats into toxic rats depending on encounters between rats and bait, which is assumed to be proportional to the product of the densities. The second term describes rat mortality due to poison and subsequent natural degradation of toxin in the carcasses as well as feeding of the generalist predator on toxic rats. Year 8 in the time series of Fig. 2 visualizes the effect of bait application on the rat population. The bait application converts a large proportion of rats into toxic rats, which decay quickly. Conversely to the first year with high seed fall in the time series (year 2), rats are at average (non-mast year) densities following the control application.

2.3. Generalist predator

We consider stoats (*Mustela erminea*) as generalist predators and distinguish between juvenile S_y (subscript for young) and adult stoats S_o (subscript for old). The only difference between age classes we take into account is the density-independent mortality as young stoats have significantly higher mortality rates (King et al., 1996). The set of equations

$$\begin{aligned} \frac{\mathrm{d}S_y}{\mathrm{d}t} &= \Phi_{S_y}(F, R_T, S_y, S_o) = S_y \left(-\mu_{S_y} - \mu_{S2}(S_y + S_o) - \kappa R_T\right) \\ &\quad + ((S_y + S_o)g(F_{S0}) - S_y) \sum_{i=0}^{\infty} \delta\left(t - t_i^{*r}\right), \end{aligned} \tag{8a}$$

$$\begin{aligned} \frac{\mathrm{d}S_o}{\mathrm{d}t} &= \Phi_{S_o}(F, R_T, S_y, S_o) = S_o \left(-\mu_{S_o} - \mu_{S2}(S_y + S_o) - \kappa R_T\right) \\ &\quad + S_y \sum_{i=0}^{\infty} \delta\left(t - t_i^{*r}\right), \end{aligned} \tag{8b}$$

$$F_{S0} = C + \gamma \int_{t-1}^{t} F(t')\mathrm{d}t' \tag{8c}$$

describes the dynamics of the stoat. Stoat populations show density-dependent mortality due to competition (O'Connor et al., 2006). Hence, the two first terms are similar to the rat dynamics and describe density-independent and density-dependent death processes, respectively. The third term $\kappa R_T S$ depicts stoat mortality due to secondary poisoning by toxic rats (link 7 in Fig. 1). The last term represents the rather complicated breeding biology of stoats (see, e.g., King and Moody (1982)). Depending on the resource richness of the environment, stoats may not breed at all or give birth to up to 18 kits (link 4 in Fig. 1) (King et al., 2003). This is taken into account by the term F_{S0} with saturating functional response (Ivlev type) (Jones et al., 2011).

$$g(F) = c_s \cdot \left(1 - e^{-\epsilon_s F}\right). \tag{9}$$

However, as not all of the stoats' diet depends on seed fall-related organisms, the constant C leads to a small number of offspring also in non-mast years. The sum of delta functions represents discrete annual breeding events with time t_i^{*r} representing the ith reproduction event as kits are born mainly between September and October (O'Connor et al., 2006). Note that juvenile and adult stoats give birth. Female stoats become sexually mature when they are still in the nest (3–5 weeks old) while males' sexual maturity starts in August of the next year (Mcdonald and Harris, 2002; Norbury, 2000). Furthermore, note that breeding success is assumed to be independent of bait application, although stoats also prey on mice. This is due to the high flexibility of their diet also including various seed predators which are not affected by the bait application, e.g., passerine and weta (*Anostostomatidae* and *Rhaphidophoridae*) (Murphy et al., 2016; Smith et al., 2005; Wyman et al., 2011).

In the case of no control, the year with high seed fall is followed by a high density of juvenile stoats due to the high amount of offspring. These turn into adult stoats in the following year. Conversely, in the case of the controlled year with high seed fall, the toxic rats yield a high rate of secondary poisoning for both juvenile and adult stoats. Thus, lower stoat densities at the reproduction event yield a smaller number of offspring.

2.4. Metapopulation model

Due to the costs of aerial 1080 application and due to public concerns, bait application only takes place locally, i.e., aerial bait application all over the country is not feasible. To investigate the impact of reinvasion of adjacent habitats, we develop a metapopulation model. In particular, we consider two connected patches with separate dynamics. The seed fall dynamics and the dynamics of toxic rats are equal in both patches. Susceptible rats R can migrate between patches 1 and 2 with a dispersal rate D_R yielding

$$\frac{\mathrm{d}R_1}{\mathrm{d}t} = \Phi_R(F_1, R_1) - D_R\left(R_1 - R_2\right). \tag{10}$$

The dispersal rate is independent of the habitat as simple diffusive behavior is a good approximation for the short time behavior of other rodents (Abramson et al., 2006). This is consistent with the approximately uniform distribution found for ship rats (Innes, 1990). Furthermore, ship rats only show low territorial behavior (Dowding and Murphy, 1994). Note that the equation for patch 2 is similar to replacing subscripts 1 with 2 and vice-versa.

One crucial difference between stoats and rats is that dispersal rates differ significantly between juvenile and adult stoats mainly due to the strong competitive exclusion (Erlinge, 1977). In particular, immigration predominantly happens via young stoats (King and McMillan, 1982). This is consistent with the observation of a dispersal season between November and May following the birth of juvenile stoats (Elliott et al., 2010). To take this complexity into account, the dispersal processes between patches 1 and 2 in the model differ between juvenile and adult stoats

$$\frac{\mathrm{d}S_{y_1}}{\mathrm{d}t} = \Phi_{S_y}\left(F_1, R_{T_1}, S_{y_1}, S_{o_1}\right) - p(S_{o_1})S_{y_1} + p(S_{o_2})S_{y_2}, \tag{11a}$$

$$\frac{\mathrm{d}S_{o_1}}{\mathrm{d}t} = \Phi_{S_o}\left(F_1, R_{T_1}, S_{y_1}, S_{o_1}\right) - D_{S_o}\left(S_{o_1} - S_{o_2}\right). \tag{11b}$$

As adult stoats have already settled in a territory with a certain home range, we assume a constant dispersal rate for simplicity. Conversely, juvenile stoats disperse in order to find a suitable territory. Hence, their dispersal depends on the density of settled (adult) stoats in the patch

$$p(S_o) = \frac{D_{S_y}}{1 + e^{-\psi S_o}}. \tag{12}$$

The choice of this function is arbitrary to a certain extent. However, it is a simple approximation of the primary driver of stoat dispersal. It is sigmoidal, depending on adult stoat density. Note that numerical simulations revealed that results obtained in this study are robust against the exact choice of this function. With high local adult stoat abundance, the likelihood of finding a spare territory in this patch is low, and thus the dispersal rate of young stoats increases. The equations describing the dynamics of patch 2 are similar, replacing subscripts 1 with 2 and vice-versa.

Fig. 3 shows a part of a sample run of the system including seed-, rat-, stoat-, and bait dynamics for the metapopulation model. Dispersal of rats is negligibly small in this case, while the reinvasion of stoats has a definite effect on the dynamics.

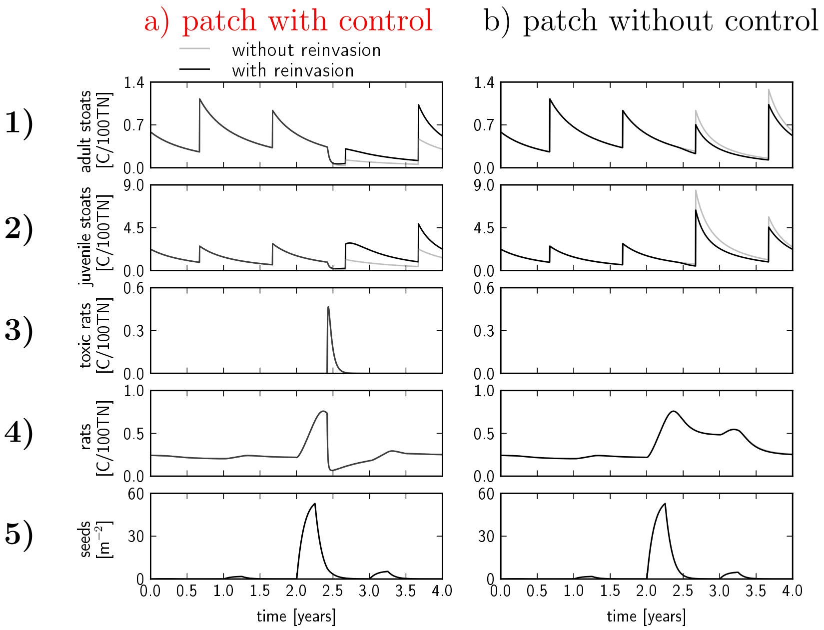

Figure 3: **Reinvasion from adjacent patches can significantly alter control success.** The figure shows a part of a sample run of the local model. The dispersal rate of the rats is $D_R = 10^{-2}$. Note that this is too small to lead to a visible effect on such a time scale for rat dispersal while the significantly higher stoat dispersal already is having a noticeable impact given by the difference between the gray and the black line (see Sec. 3.2 for more details on this).

2.5. Plague metric

This study aims to find patterns for efficient, tailored predator control. This is necessary if the predator is a pest, e.g., due to crop damage, its role as a disease vector, or a threat for other species. It is essential to define the plague metrics corresponding to the problem to obtain consistent results. For instance, the endangered bird kaka (*Nestor meridionalis*) is particularly vulnerable to nest predation in its breeding season, which is taking place mainly before beech masts (Wilson et al., 1998; Moorhouse et al., 2003). Hence only specific years matter. Conversely, some problems do not only depend on the predator but also on the consumer, e.g., *Mohoua ochrocephala* is preyed on by both rats and stoats (Innes et al., 2010). In this study, we consider the impact of stoats on kiwi (*Apteryx*) populations as an example. As a metric, we have chosen mean stoat densities between November and March as kiwi chicks are particularly vulnerable to stoat predation in this time (Robertson et al., 2016). We define control success as the inverse of the mean stoat density between March and November.

3. Results

3.1. Local dynamics

We have compared three different control strategies in the local case, i.e., annual bait application, quadrennial (every fourth year) bait application, and bait application only in years with high seed fall. Here, we define such a year as a year in which seed fall is in the first quartile of the highest annual seed fall. Hence, this also happens once in four year on average.

The optimal control timing is between June and July (see Fig 4). This corresponds to the time of the maximum density of the rats. This is because a higher rat density leads to higher toxic rat densities and thus to higher poison probabilities.

The optimal control level is at about $B_0 = 100$. So far, the control level

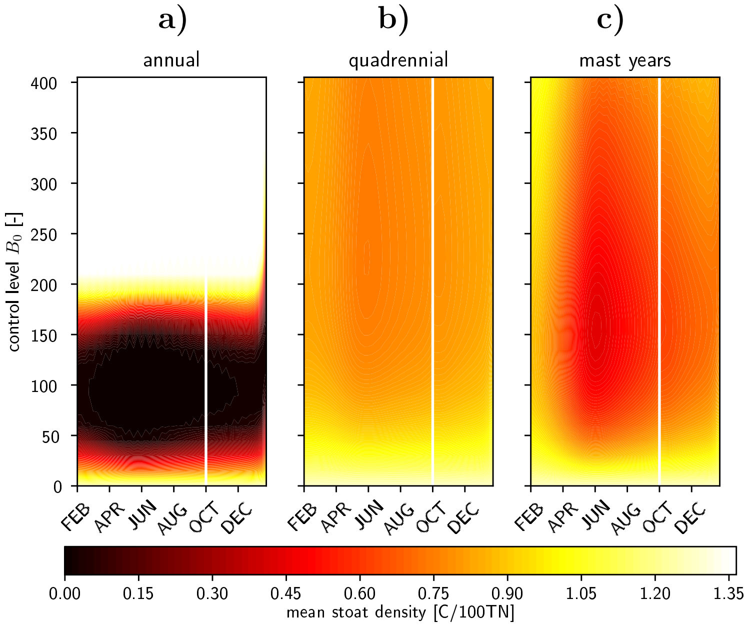

Figure 4: **Control application only in years with high seed fall needs more effective control and strongly depends on the timing.** The figure shows the dependence of the control success on the timing and the intensity of the control for three different control strategies. The mean stoat density in the relevant time of the year represents control success (see Sec. 2.5). The white lines denote the breeding time of stoats.

has no practical meaning. However, one can convert it into a killing proportion of about 95% (see Appendix B). Given this optimal control level, the impact of the control timing is small. Conversely, the impact of control intensity at a fixed time of the year is high. In particular, high levels of control, i.e., $B_0 > 200$, yield the same results as in case of no control. This upper limit beyond which higher control levels are detrimental exists because the rat population may locally go extinct, and there is no other efficient way to control the stoat population. However, the value of the upper limit depends on the control setting. For instance, a lower control frequency gives the rat population more time for recovery. One exception is control application at the end of the year, i.e., January by the definition used in this study. Given a high control intensity, a minimum stoat density is apparent for this timing. However, this is an artifact resulting from the discrete start of seed fall at the beginning of the year. Bait application directly before this time has a minor influence as the rat population is very low and will immediately recover due to the high resource abundance.

Applying control every fourth year corresponds to a less efficient control strategy. Higher control levels are necessary for optimal control success. However, very high control intensities do not impair control success as in the case of annual control. Furthermore, an optimal control timing in June is visible. Note that the asymmetry in the temporal dependence for bait application in years with high seed fall is due to the seed fall at the beginning of the year. Applying high levels of control at this time, the rats cannot recover the rest of the year as the food has already degraded. This can lead to extinction of the rats and, therefore, to extinction of the control vector of the stoats. However, note that the extent of the asymmetry is an artifact resulting from the discrete seed fall start.

Fig. 4 c) shows the dependence of the control success on the timing and the control intensity if control takes place only in years with high seed fall. In general, the control yields higher stoat densities with these control strategies compared to the case of annual control. However, it is more effective than applying control quadrennially, although the number of control application is identical in the long term. The optimal timing for control is in June. This is the same as in the case of annual and quadrennial control applications. However, the control timing has a higher and more complex impact in this case. While the effect of control slightly earlier or slightly later than the optimal timing is the same in the case of annual and quadrennial control, it is asymmetric in the case of control in years with high seed fall. Furthermore, higher control levels are possible and also necessary to obtain optimal control success.

3.2. Metapopulation dynamics

The results of the metapopulation model are restricted to the case of control in years with high seed fall as this is the more feasible strategy due to the lower costs and less social concerns (Green and Rohan, 2012). Note that the dispersal rate of young and old stoats are defined in terms of the rat dispersal rate (see Tab. A.1). Hence, the relation between the dispersal abilities does not change, but the absolute values do. Changing the absolute values may correspond to different species. However, note that here, it corresponds to varying patch size as dispersal only happens between the two patches. The optimal control timing is June, as in the local results (not shown here). Fig. 5 visualizes the effect of the dispersal rate and the control intensity, assuming that the bait application takes place in June. For plot a), control has always been applied in the same patch, while the control patch

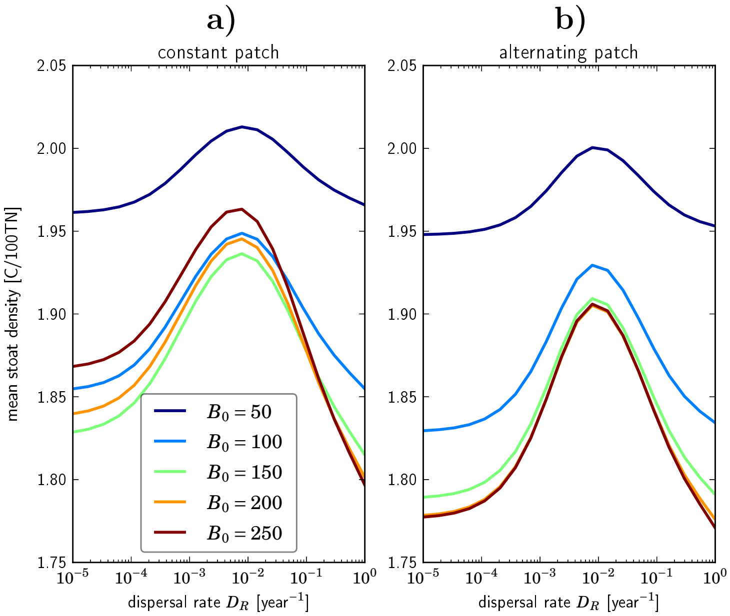

Figure 5: **Alternating the control patch yields higher control success while a suboptimal patch size exists independent of the control strategy.** The figure shows the influence of the rat dispersal rate and control level on the mean stoat density $(S_y + S_o)$ in *Apteryx* chick vulnerability time. In plot a), control is applied in the same patch each bait application. Conversely, control application takes place in an alternating manner in plot b), i.e., the control patch switches after each application. Note that the abscissa is log-scaled.

switched with every bait application for plot b). In both control strategies, one achieves the optimal control outcome with high dispersal abilities because reinvasion increases the potential control vector density. However, in the case of alternating control patches, the corresponding optimal control level is higher than in the case of a constant control patch. Furthermore, the maximum effect of the control is higher in the case of alternating control patches, even if the same level of control is applied.

A clear suboptimal dispersal rate at $D_R \approx 10^{-2}$ year^{-1} exists. In that case, the mean stoat density, i.e., the inverse of the control success, has a maximum independent of the control level. De- or increasing the dispersal rate sufficiently yields significantly higher control success. In both cases, the effect of a change in the dispersal rate is the highest close to the suboptimal point and gets lower further away. Furthermore, the figure depicts the influence of the control level. At low and intermediate control levels, i.e., $B_0 \leq 100$, a change in control level has a high impact. Increasing the control level, the rate of change of the control efficacy with varying control levels tends to zero or is even reversed in the case of a constant control patch.

The suboptimal value for the dispersal rate for which the control is least effective results from a trade-off of the dispersal influence. At low dispersal rates, both rat and stoat dispersal is low. Lower stoat densities in the patch produce less offspring. Furthermore, after the breeding event, stoats reinvade at a lower rate, which means that the stoat population stays low for a longer time while the stoat population in the other patch suffers from higher density-dependent mortality. Conversely, at high dispersal rates, stoat reinvasion is very fast. However, in this regime, invasion rates of rats are important as well. Due to the fast reinvasion, a higher number of potential vectors to control the stoat population is abundant. Furthermore, the extremely high stoat reinvasion rate leads to a higher density in the control patch already shortly after control application. This, in turn, leads to a larger number of stoats, which one can potentially control via secondary poisoning. However, both effects are saturating for very high or low dispersal rates respectively because very low dispersal rates tend to zero, and higher dispersal rates have no impact anymore if densities are already equal in both patches. At intermediate dispersal rates, the dispersal rate of rats is too low for increasing the vector density efficiently directly after bait application while stoat dispersal rates are already high enough to decrease the impact of density-dependent death processes in the uncontrolled patch. However, in the long run, reinvasion still has an effect decreasing natural density-dependent mortality in the patch, which is not controlled and leading to higher stoat densities in the controlled patch (see Fig. 3 for a sample time series showing this relationship).

4. Discussion

4.1. Control timing

Independent of the control strategy or the setting, i.e., local or metapopulation dynamics, the optimal control timing is in June. This also holds for other species which are mainly preyed on by stoats. An example is given by the kaka, which we have also modeled using the same approach (not shown here). Previous studies about rodents have suggested mid-September as optimal control timing (Elliot, 2016; Holland et al., 2018). This demonstrates the importance of tailored control, i.e., control depending on the target. If the rodents act as a control vector, the most effective control corresponds to the highest vector densities. In mid-September, the rat population has already decreased due to intraspecific competition which is why mid-September would be too late for optimal control. Conversely, if rodents are not only control vectors, but control targets themselves, this does no longer hold. However, note that especially in the case of annual bait application but to a certain extent also for bait application in years with high seed fall, controlling in mid-September would still reduce the mean stoat density significantly (although not optimally) if the control level is high enough. In this case, the high control level partly compensates for the lower rat densities because a higher proportion of rats turns into toxic rats. However, applying the control too early is also ineffective as the rat population mainly grows in the first quarter of the year when masting takes place.

Due to public concerns, the annual control application is not feasible. If we neglected public concerns, applying bait annually at a lower level might still yield better results than applying baits in mast years at higher control levels. However, the reduced control level reduces bait material but not (significantly) the costs of the aerial operations. Hence, the results presented here underline the importance of the right timing in years with high seed fall. This calls for better mast identification (e.g., model predictions as in Kelly et al. (2013)) and faster decision-making processes. This becomes even important as the effect of timing is higher if one applies control in years with high seed fall. This is due to the higher control level, which is necessary in this case, which increases the influence of bait application time. However, in practice, data on seed abundance determining years with high seed fall are often usable not earlier than July, and afterward, a political decision-making process is still necessary (Elliot, 2016).

4.2. Control intensity

The results presented in this study reveal one major problem of secondary poisoning, which is the dependence on the vector. Independent of the control strategy, an upper limit of the control intensity exists beyond which higher control levels are detrimental due to the dependence on the control vector. Note that we did not include the effect of 1080 on mice as a secondary (seed predator) food source, which may weaken this effect as the control does not solely depend on the rats. The qualitative results do not depend on this, and even the quantitative results are robust against this distinction if mice were similarly prone to the bait as rats. However, note that 1080 is not as effective for controlling mice.

This critical control density becomes higher with lower control frequency and higher reinvasion of rats through adjacent patches. However, especially if control patches are large and reinvasion is limited, it is essential to note that a high control intensity can be less efficient management in the long run. Before reaching this critical level, the effect of an increase in the control intensity saturates. From a management perspective, this is positive because it means that we can apply significantly lower control levels without losing much of the control success. But this can act as a buffer reducing the risk of killing the vector. The optimal control intensity we found was $B_0 \approx 150$ in the case of control in years with high seed fall without reinvasion and $B_0 \approx 250$ in the case of alternating patch control. However, $B_0 \approx 150$ is nearly as effective as the optimal intensity in the alternating patch control case. This is consistent with data. A reduction in the bait sowing rate, from 11 kg/ha to 4 kg/ha for possum control, for instance, did not significantly alter the killing proportion (Warburton and Cullen, 1995).

This optimal value corresponds to a killing proportion of about 95%. The current management goal of the Department of Conservation in New Zealand is to reduce rat tracking rates to 5% in years with high seed fall via 1080 application (Elliot, 2016). As rat tracking rates in years with high beech seed fall can approximately be between 80% and 100% (Elliot, 2016; Kemp et al., 2018), the goal is in good agreement with the optimal intensity.

4.3. Control strategy

For the local dynamics, the results clearly show that annual control is much more effective than applying control only in years with high seed fall.

However, depending on the specific case, this may not be feasible due to different environmental trade-offs, economic restrictions, and public concerns. Considering dispersal from adjacent patches using the metapopulation model indicates that the strategy of alternating control patches yields better results than static control. This may be counter-intuitive at first glance as focusing on one patch may provide a refuge area for endangered species, which might make sense in some cases. However, considering the mean of the pest population (stoats) over the two patches, the alternating strategy has two advantages. First, the pest population in a patch has more time to recover, and higher pest densities yield higher poisoning probabilities and hence a higher efficacy in that patch. And second, the vector population (rats) has a longer time to recover between bait applications. Hence, a higher potential vector density exists in the patch. This is also the reason why the optimal control level is higher in the case of the alternating strategy. For a given control level, the alternating patch strategy yields better results. However, the optimal control strategy, in this case, clearly also depends on the conservation objective. For some endangered species, refuge areas may be still better suited. This probably depends on the dispersal abilities of this species. Species with high dispersal abilities, e.g., birds capable of flying, may make less use of the refuge areas than species with small home ranges. Further research relating pest management to conservation outcomes for a range of threatened species, and the effects of dispersal on these outcomes, is needed.

5. Conclusions

In this study, we have developed a model describing the dynamics of a food chain consisting of a generalist consumer (e.g., ship rats) and a generalist predator (e.g., stoats) affected by a pulsed resource. We have applied it to a case in New Zealand to show how such a model can support pest management strategies. In particular, it indicates the importance of the control vector for a proper management strategy.

The maximum in the population density of the control vector determines the optimal timing, which is June for rats. This implies that given that various predators (e.g., stoats and possums) feed on the same vector, the optimal control timing stays constant. High control intensities can be counterproductive if they yield extinction of this vector. Hence, intermediate control levels are more effective in the long run. This can lead to huge cost savings. For instance, the reduction of 1080 bait usage for possum control has saved 8.9 million dollars per year without reducing the control success (Morgan et al., 1997). However, one can influence this dependence by the control strategy, e.g., alternating control patches allow for longer recovery periods of the control vector species. This also depends on the patch size. Especially intermediate patch sizes in which reinvasion of the generalist predator may be fast while reinvasion of the generalist consumer is still negligibly small can have a negative impact on the control success. From a management perspective, this intermediate dispersal regime can be prevented by either applying very large or very small control patches or by changing dispersal abilities in another way, e.g., by separation of patches using (leaky) fences. The patch sizes (represented by the proxy of the rats' dispersal rate) yielding high control success found in this study depend not only on the bait application but also on indirect effects after the reinvasion, such as higher density-dependent mortality in the case of low stoat reinvasion rates. Hence, considering spatial dependencies like this makes the combinations of different control mechanisms such as chemical (bait) and biological (density-dependent) mechanisms necessary. Furthermore, this indicates that the spatial design of bait application may play an important role in the pest management.

Note that only the stoat density gives the control success metrics underlying the results of this study. This means that low mean stoat densities in a critical time interval correspond to high control success independent of the ship rat population. The critical time interval for other species may differ. We have also exploited the model presented in this study regarding plague metrics for the conservation of other New Zealand birds such as *Nestor meriodionalis* (New Zealand kaka) or *Mohoua ochrocephala* (mohua). The results, however, are not shown here for the sake of brevity. We have defined the plague metrics for the kaka by its breeding season, which is taking place mainly between October and March before years with high seed fall (Wilson et al., 1998; Moorhouse et al., 2003). As the kaka is also mainly vulnerable against stoat predation, the optimal control timing is the same as it is primarily affected by the maximum in the rat density. However, some native species like, for example, the mohua are also under threat from predation by rats. The results for the mohua (not shown here) reveal the optimal control timing is shifted closer to the reproduction event of the stoats in October (i.e., to middle September) due to the main influence of rats in February. Due to indirect effects such as mesopredator release (Soulé et al., 1988), the optimal control derived in this study can in fact be suboptimal regarding other target species (see e.g., Courchamp et al. (1999) for an example of a similar problem with invasive meso- and invasive superpredator). Hence, before applying the control measure as suggested in this study on a large scale, it should be tested locally, including a monitoring program following the control operation as it is suggested in the review on biological invasions by Courchamp et al. (2003).

One shortcoming of this study is that we developed and parameterized the model using stoat and rat tracking rates. Tracking rates are known to be a saturating activity measure (Gillies and Williams, 2013) whereas the per-capity activity tends to decrease with density (Davidson and Morris, 2001). Especially stoat trappability does not only change with abundance but also with factors such as food availability (Alterio et al., 1999). Note that extensive numerical simulations have shown that the strong influence of the control success on the vector population density is robust against parameter variations. Furthermore, we have tested our model against structural sensitivity of functional responses (predation and dispersal) and found no dependence. However, further studies are necessary for better estimates for rat and stoat population densities to obtain more accurate quantitative results.

The results presented here refer to the pest management of stoats threatening the local *Apteryx* populations. However, pulsed resources lead to irrupting pest populations in many ecosystems worldwide with diverse negative impacts (see Sec. 1). The modeling approach presented here is readily applicable to other species in New Zealand or even to completely different case studies to investigate suitable strategies, e.g., seed-rat-mongoose dynamics in Japan (Fukasawa et al., 2013) or seed-rodent-raccoon-dog dynamics in Poland (Jedrzejewska and Jedrzejewski, 2013). The results for the New Zealand case study indicate the great importance of tailored control strategies in such systems.

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References

Abramson, G., Giuggioli, L., Kenkre, V., Dragoo, J., Parmenter, R., Parmenter, C., and Yates, T. (2006). Diffusion and home range parameters for rodents: *Peromyscus maniculatus* in New Mexico. *Ecological Complexity*, 3(1):64–70.

Allen, R. B., Mason, N. W., Richardson, S. J., and Platt, K. H. (2012). Synchronicity, periodicity and bimodality in inter-annual tree seed production along an elevation gradient. *Oikos*, 121(3):367–376.

Alterio, N., Moller, H., and Brown, K. (1999). Trappability and densities of stoats (mustela erminea) and ship rats (rattus rattus) in a south island nothofagus forest, new zealand. *New Zealand Journal of Ecology*, pages 95–100.

Bridgman, L. J., Innes, J., Gillies, C., Fitzgerald, N., Miller, S., and King, C. M. (2013). Do ship rats display predatory behaviour towards house mice? *Animal Behaviour*, 86(2):257–268.

Clapperton, B. K. et al. (2006). *A review of the current knowledge of rodent behaviour in relation to control devices*, volume 263. Science & Technical Pub., Department of Conservation.

Cordoleani, F., Nerini, D., Gauduchon, M., Morozov, A., and Poggiale, J.-C. (2011). Structural sensitivity of biological models revisited. *Journal of theoretical biology*, 283(1):82–91.

Courchamp, F., Chapuis, J.-L., and Pascal, M. (2003). Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, 78(3):347–383.

Courchamp, F., Langlais, M., and Sugihara, G. (1999). Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology*, 68(2):282–292.

Dalgleish, H. J. and Swihart, R. K. (2012). American chestnut past and future: implications of restoration for resource pulses and consumer populations of eastern U.S. forests. *Restoration Ecology*, 20(4):490–497.

Davidson, D. and Morris, D. (2001). Density-dependent foraging effort of deer mice (peromyscus maniculatus). *Functional Ecology*, 15(5):575–583.

Dowding, J. E. and Murphy, E. C. (1994). Ecology of ship rats (*Rattus rattus*) in a kauri (*Agathis australis*) forest in Northland, New Zealand. *New Zealand Journal of Ecology*, pages 19–27.

Efford, M., Fitzgerald, B., Karl, B., and Berben, P. (2006). Population dynamics of the ship rat *Rattus rattus* L. in the Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology*, 33(4):273–297.

Elliot, G. (2016). The science behind the Department of Conservations predator control response. *Department of Conservation.*

Elliott, G. and Kemp, J. (2016). Large-scale pest control in New Zealand beech forests. *Ecological Management & Restoration*, 17(3):200–209.

Elliott, G., Willans, M., Edmonds, H., and Crouchley, D. (2010). Stoat invasion, eradication and re-invasion of islands in Fiordland. *New Zealand Journal of Zoology*, 37(1):1–12.

Erlinge, S. (1977). Spacing strategy in stoat *Mustela erminea*. *Oikos*, pages 32–42.

Fukasawa, K., Miyashita, T., Hashimoto, T., Tatara, M., and Abe, S. (2013). Differential population responses of native and alien rodents to an invasive predator, habitat alteration and plant masting. *Proceedings of the Royal Society B: Biological Sciences*, 280(1773):20132075.

Fussmann, G. F. and Blasius, B. (2005). Community response to enrichment is highly sensitive to model structure. *Biology letters*, 1(1):9–12.

Gillies, C. and Williams, D. (2013). *DOC tracking tunnel guide: Using tracking tunnels to monitor rodents and mustelids*. Department of Conservation, Science & Capability Group, Hamilton, New Zealand, v2.5.2 edition.

Green, W. and Rohan, M. (2012). Opposition to aerial 1080 poisoning for control of invasive mammals in New Zealand: risk perceptions and agency responses. *Journal of the Royal Society of New Zealand*, 42(3):185–213.

Herrera, C. M., Jordano, P., Guitián, J., and Traveset, A. (1998). Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *The American Naturalist*, 152(4):576–594.

Holland, E. P., Binny, R. N., and James, A. (2018). Optimal control of irrupting pest populations in a climate-driven ecosystem. *PeerJ*, 6:e6146.

Holland, E. P. and James, A. (2015). Assessing the efficacy of population-level models of mast seeding. *Theoretical ecology*, 8(1):121–132.

Hone, J., Duncan, R. P., and Forsyth, D. M. (2010). Estimates of maximum annual population growth rates (r_m) of mammals and their application in wildlife management. *Journal of Applied Ecology*, 47(3):507–514.

Innes, J. (1990). Ship rat-the handbook of New Zealand mammals. King, CM (ed), pg 206-225.

Innes, J., Kelly, D., Overton, J. M., and Gillies, C. (2010). Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology*, 34(1):86.

Jedrzejewska, B. and Jedrzejewski, W. (2013). *Predation in vertebrate com-*

munities: the Bialowieza Primeval Forest as a case study, volume 135. Springer Science & Business Media.

Jones, C., Pech, R., Forrester, G., King, C. M., and Murphy, E. C. (2011). Functional responses of an invasive top predator *Mustela erminea* to invasive meso-predators *Rattus rattus* and *Mus musculus*, in New Zealand forests. *Wildlife Research*, 38(2):131–140.

Kelly, D., Geldenhuis, A., James, A., Penelope Holland, E., Plank, M. J., Brockie, R. E., Cowan, P. E., Harper, G. A., Lee, W. G., Maitland, M. J., et al. (2013). Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters*, 16(1):90–98.

Kelly, D. and Sork, V. L. (2002). Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology, and Systematics*, 33(1):427–447.

Kemp, J. R., Mosen, C. C., Elliott, G. P., and Hunter, C. M. (2018). Effects of the aerial application of 1080 to control pest mammals on kea reproductive success. *New Zealand Journal of Ecology*, 42(2):158–168.

King, C. (1983). The relationships between beech (*Nothofagus sp.*) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *The Journal of Animal Ecology*, pages 141–166.

King, C., Flux, M., Innes, J., and Fitzgerald, B. (1996). Population biology of small mammals in Pureora Forest Park: 1. Carnivores (*Mustela erminea,* *M. furo, M. nivalis*, and *Felis catus*). *New Zealand Journal of Ecology*, pages 241–251.

King, C. and McMillan, C. (1982). Population structure and dispersal of peak-year cohorts of stoats (*Mustela erminea*) in two New Zealand forests, with special reference to control. *New Zealand Journal of Ecology*, 5:59–66.

King, C. and Moody, J. (1982). The biology of the stoat (*Mustela erminea*) in the national parks of New Zealand IV. reproduction. *New Zealand Journal of Zoology*, 9(1):103–118.

King, C. M. (2005). *The handbook of New Zealand mammals.* Oxford University Press.

King, C. M., Innes, J. G., Gleeson, D., Fitzgerald, N., Winstanley, T., OBrien, B., Bridgman, L., and Cox, N. (2011). Reinvasion by ship rats (*Rattus rattus*) of forest fragments after eradication. *Biological Invasions*, 13(10):2391.

King, C. M. and Moller, H. (1997). Distribution and response of rats *Rattus rattus, R. exulans* to seedfall in New Zealand beech forests. *Pacific Conservation Biology*, 3(2):143–155.

King, C. M., White, P. C., Purdey, D. C., and Lawrence, B. (2003). Matching productivity to resource availability in a small predator, the stoat (*Mustela erminea*). *Canadian Journal of Zoology*, 81(4):662–669.

Mcdonald, R. A. and Harris, S. (2002). Population biology of stoats mustela erminea and weasels mustela nivalis on game estates in great britain. *Journal of Applied Ecology*, 39(5):793–805.

McQueen, S. and Lawrence, B. (2008). Diet of ship rats following a mast event in beech (*Nothofagus spp.*) forest. *New Zealand Journal of Ecology*, pages 214–218.

Meenken, D. and Booth, L. (1997). The risk to dogs of poisoning from sodium monofluoroacetate (1080) residues in possum (*Trichosurus vulpecula*). *New Zealand Journal of Agricultural Research*, 40(4):573–576.

Meerburg, B. G., Singleton, G. R., and Kijlstra, A. (2009). Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology*, 35(3):221–270.

Moorhouse, R., Greene, T., Dilks, P., Powlesland, R., Moran, L., Taylor, G., Jones, A., Knegtmans, J., Wills, D., Pryde, M., et al. (2003). Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: reversing the decline of a threatened New Zealand parrot. *Biological Conservation*, 110(1):33–44.

Morgan, D., Thomas, M., Meenken, D., and Nelson, P. (1997). Less 1080 bait usage in aerial operations to control possums. In *Proceedings of the New Zealand Plant Protection Conference*, volume 50, pages 391–396.

Murphy, E., Robbins, L., Young, J., and Dowding, J. (1999). Secondary poisoning of stoats after an aerial 1080 poison operation in Pureora Forest, New Zealand. *New Zealand Journal of Ecology*, pages 175–182.

Murphy, E. C. and Dowding, J. E. (1995). Ecology of the stoat in *Nothofagus* forest: home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology*, pages 97–109.

Murphy, E. C., Gillies, C., Maddigan, F., McMurtrie, P., Edge, K.-A., Rohan, M., and Clapperton, B. K. (2016). Flexibility of diet of stoats on Fiordland islands, New Zealand. *New Zealand Journal of Ecology*, 40(1):114–120.

Norbury, G. (2000). The potential for biological control of stoats (mustela erminea). *New Zealand Journal of Zoology*, 27(3):145–163.

O'Connor, C., Turner, J., Scobie, S., and Duckworth, J. (2006). *Stoat reproductive biology*. Science & Technical Publishing, Department of Conservation.

O'Donnell, C. F., Dilks, P. J., and Elliott, G. P. (1996). Control of a stoat (*Mustela erminea*) population irruption to enhance mohua (yellowhead)(*Mohoua ochrocephala*) breeding success in New Zealand. *New Zealand Journal of Zoology*, 23(3):279–286.

Ostfeld, R. S. and Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15(6):232–237.

Pearse, I. S., Koenig, W. D., and Knops, J. M. (2014). Cues versus proximate drivers: testing the mechanism behind masting behavior. *Oikos*, 123(2):179–184.

Polis, G. A., Power, M. E., and Huxel, G. R. (2004). *Food webs at the landscape level*. University of Chicago Press.

Riney, T. (1959). Lake Monk expedition: An ecological survey in Southern Fiordland. *New Zealand Department of Science and Industry Research Bulletin*, 135:1–75.

Robertson, H., Craig, E., Gardiner, C., and Graham, P. (2016). Short pulse of 1080 improves the survival of brown kiwi chicks in an area subjected to long-term stoat trapping. *New Zealand Journal of Zoology*, 43(4):351–362.

Ruscoe, W., Norbury, G., and Choquenot, D. (2006). Trophic interactions among native and introduced animal species. In *Biological Invasions in New Zealand*, pages 247–263. Springer.

Ruscoe, W. A., Elkinton, J. S., Choquenot, D., and Allen, R. B. (2005). Predation of beech seed by mice: effects of numerical and functional responses. *Journal of Animal Ecology*, 74(6):1005–1019.

Singleton, G. R., Belmain, S., Brown, P. R., Aplin, K., and Htwe, N. M. (2010). Impacts of rodent outbreaks on food security in Asia. *Wildlife Research*, 37(5):355–359.

Smith, D., Jamieson, I., and Peach, R. (2005). Importance of ground weta (*Hemiandrus spp.*) in stoat (*Mustela erminea*) diet in small montane valleys and alpine grasslands. *New Zealand Journal of Ecology*, pages 207–214.

Soulé, M. E., Bolger, D. T., Alberts, A. C., Wrights, J., Sorice, M., and Hill, S. (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, 2(1):75–92.

Warburton, B. and Cullen, R. (1995). Cost-effectiveness of different possum control methods.

Wardle, J. et al. (1984). *The New Zealand beeches: ecology, utilisation and management.* New Zealand Forest Service.

Wilson, P., Karl, B., Toft, R., Beggs, J., and Taylor, R. (1998). The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological conservation*, 83(2):175–185.

Wiser, S. K., Hurst, J. M., Wright, E. F., and Allen, R. B. (2011). New Zealand's forest and shrubland communities: a quantitative classification based on a nationally representative plot network. *Applied Vegetation Science*, 14(4):506–523.

Wyman, T. E., Trewick, S. A., Morgan-Richards, M., and Noble, A. D. (2011). Mutualism or opportunism? Tree fuchsia (*Fuchsia excorticata*) and tree weta (*Hemideina*) interactions. *Austral Ecology*, 36(3):261–268.

Appendix A. Parameters

Tab. A.1 shows the variables and parameters used in this study. Note that we sometimes express unit in terms of the state variable for a more straightforward interpretation. If we have taken the parameters from a specific study, the table states the reference. If the parameters are estimated based on the results of particular studies, we have denoted this with *based on reference*. All submodels have been tested and compared with literature with good agreement of the results.

Table A.1: The table shows parameters and variables with values and references used for the numerical simulations of the local model in this study. The units of rat and stoat densities are measured using the index C/100TN (catches per 100 trap nights).

Symbol	Definition	Value	Unit	Reference
$F(t)$	resource abundance	-	seeds m^{-2}	-
$R(t)$	rat density	-	C/100TN	-
$R_T(t)$	toxic rat density	-	C/100TN	-
$S_y(t)$	juvenile stoat density	-	C/100TN	-
$S_o(t)$	adult stoat density	-	C/100TN	-
t	time	-	years	-
t_i^{*r}	stoat reproduction time	$i + 2/3$	years	O'Connor et al. (2006)
$\sigma(t)$	seed fall	-	seeds m^{-2} year^{-1}	-
$B(t)$	bait-induced mortality	-	year^{-1}	-
B_0	control level	-	-	-
d	bait decay	50	year^{-1}	Holland et al. (2018)

h	resource decay	9.48	year^{-1}	Holland et al. (2018)
ρ	density independent birth (rats)	3.6	year^{-1}	Hone et al. (2010)
μ_R	density dependent mortality (rats)	18	rat^{-1} year^{-1}	based on King and Moller (1997)
α_1	demographic efficiency of rats for primary resources (seeds)	0.1	rats seeds^{-1} m^2	based on King and Moller (1997), Holland et al. (2018)
α_2	demographic efficiency of rats for secondary resources (seed predators)	0.1	rats seeds^{-1} m^2	based on King and Moller (1997), Holland et al. (2018)
β	bait efficacy regarding secondary resources	10	-	based on Kemp et al. (2018)
c	maximum per capita feeding rate	67.4	seeds m^{-2} rats^{-1} year^{-1}	based on King and Moller (1997), Holland et al. (2018)

ϵ	foraging efficiency of rats	0.1	seeds^{-1} m^{2}	based on King and Moller (1997), Holland et al. (2018)
d_i	mortality of toxic rats	20	year^{-1}	based on Meenken and Booth (1997)
ι	encounter probability of stoats and toxic rats	1	(stoat year)$^{-1}$	based on Kemp et al. (2018)
μ_{S2}	density dependent mortality of stoats	0.4	stoats^{-1} year^{-1}	based on Kemp et al. (2018)
κ	poison induced mortality	60	year^{-1} toxic rats^{-1}	based on Kemp et al. (2018)
C	seed fall independent resources	0.69	seeds m^{-2}	median of annual food abundance
γ	adjustment factor	800	year^{-1}	based on King et al. (2003)
c_s	maximum per capita stoat reproduction	9	.	based on King et al. (2003)

ϵ_s	foraging efficiency of stoats	0.0018	seeds^{-1} m^2	based on King et al. (2003)
$\mu_{S_y 1}$	density independent mortality of juvenile stoats	0.7	year^{-1}	King et al. (1996)
$\mu_{S_o 1}$	density independent mortality of adult stoats	0.5	year^{-1}	King et al. (1996)
D_R	dispersal rate of rats	-	year^{-1}	
D_{S_o}	dispersal rate of adult stoats	$100D_R$	year^{-1}	based on Murphy and Dowding (1995), Clapperton et al. (2006)
D_{S_y}	maximum dispersal rate of juvenile stoats	$4D_{S_o}$	year^{-1}	based on Murphy and Dowding (1995), King and McMillan (1982)
ψ	territorial competitive exclusion factor	1	stoats^{-1}	based on Erlinge (1977), King and McMillan (1982)

Appendix B. Killing proportion

To compare the control level values B_0 with data, we define a killing proportion. The expression

$$\chi = 1 - \frac{\min_{t\in\Upsilon} R(t)}{R(t = t_b)} \tag{B.1}$$

defines this proportion. Here, $\min_{t\in\Upsilon} R(t)$ refers to the minimum of the rat population in the 12 months after the bait application Υ over the rat population at bait application time t_b in a controlled environment. Controlled environment means that we neglected all other effects on the rat population, e.g., seed fall. We simulated a sample time series of 1000 years calculating χ for 30 different values of B_0 and used semi-logarithmic linear regression, to obtain the following relationship for the killing proportion

$$\chi = 1 - e^{\frac{-B_0}{49.8}}. \tag{B.2}$$

Fig. B.6 visualizes this relationship.

Appendix C. Reinvasion time

A controlled environment without bait application and seed fall and using semi-logarithmic linear regression similar to Sec. 4.2 results in the following dependence

$$D_R = e^{\frac{0.94\text{years}-\tau}{0.28\text{years}}}. \tag{C.1}$$

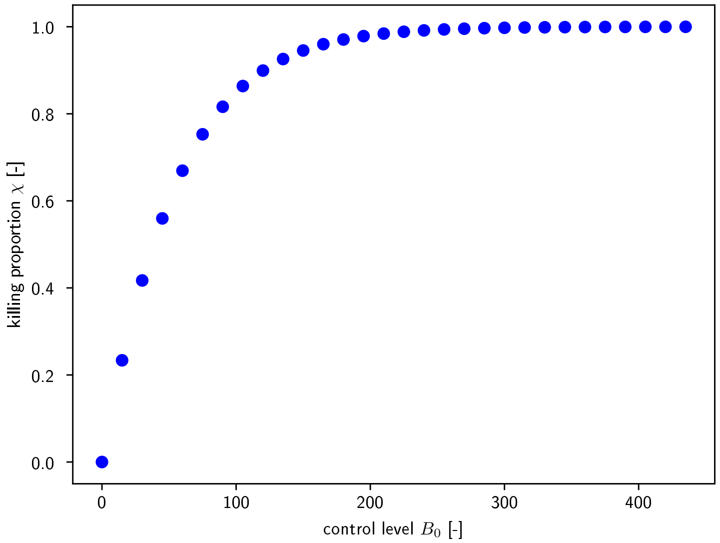

Figure B.6: **The killing proportion saturates exponentially with respect to the control level.** The figure shows the relationship between control level and killing proportion.

for the time τ it takes for the rats from invading into a new habitat until the population reaches 90% of its carrying capacity. Fig. C.7 visualizes this relationship.

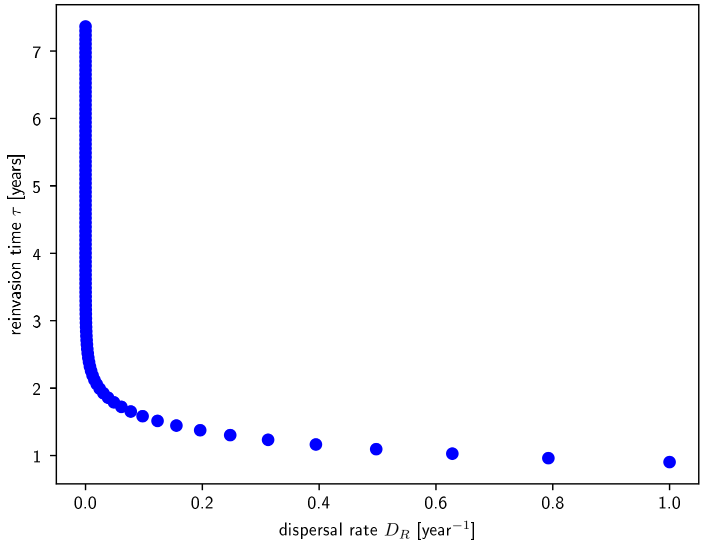

Figure C.7: **Reinvasion times decrease exponentially with increasing dispersal rates.** The figure shows the relationship between reinvasion time and the dispersal rate of rats.