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

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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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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

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

12 by invasive mongooses (*Herpestes javanicus*) which are threatening endemic
13 vertebrate species (Fukasawa et al., 2013). Singleton et al. (2010) describe
14 bamboo masting (e.g., *Melocanna*) causing rodent irruptions in Asia. As rats
15 damage rice crops, they can be cause for famines in those regions. Further-
16 more, heavy summer rainfalls in Argentina lead to irruptions of vegetation
17 biomass followed by high corn mouse (*Calomys musculus*) abundances as-
18 sociated with outbreaks of Argentine hemorrhagic fever virus epidemics (Os-
19 tfeld and Keesing, 2000). Additional examples of epidemiological impacts of
20 similar food webs are given by enhanced risk of the spread of rabies in Poland
21 or increased Lyme disease risk in the United States (Jedrzejewska and Jedrze-
22 jewski, 2013; Dalglish and Swihart, 2012). Due to extreme events accom-
23 panying climate change, these effects may become even more frequent in the
24 future (Meerburg et al., 2009). Hence, understanding community dynamics
25 affected by pulsed resources is not only crucial for ecosystem management
26 but also epidemiological and even food security issues.

27 In New Zealand, mast seeding beech (*Nothofagus*) trees form part of
28 about half of local indigenous forests (Wardle et al., 1984; Wiser et al., 2011).
29 Of the 32 terrestrial mammal species in New Zealand, 29 are reducible to bi-
30 ological introductions, and many pose serious risks to indigenous avifauna
31 (King, 2005; Ruscoe et al., 2006). Hence, it is a country in which manage-
32 ment of such ecosystems is particularly urgent. Of New Zealand's endemic
33 birds, 41% are already extinct while 77% are threatened and suffering from
34 irruptions of invasive mammals such as possums (*Trichosurus vulpecula*),

35 stoats (*Mustela erminea*), and rats (e.g., *Rattus rattus*) (Innes et al., 2010).
36 Already Riney (1959) suspected a strong connection of mast seeding and
37 threats to native birds. In particular, masting leads to increases of mice, and
38 rats followed by stoat irruptions and high predation pressure on birds — a
39 relationship which is now widely confirmed, e.g., by linking mohua (*Mohoua*
40 *ochrocephala*) breeding success to stoat irruptions after years with high seed
41 fall (King, 1983; O’Donnell et al., 1996).

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

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

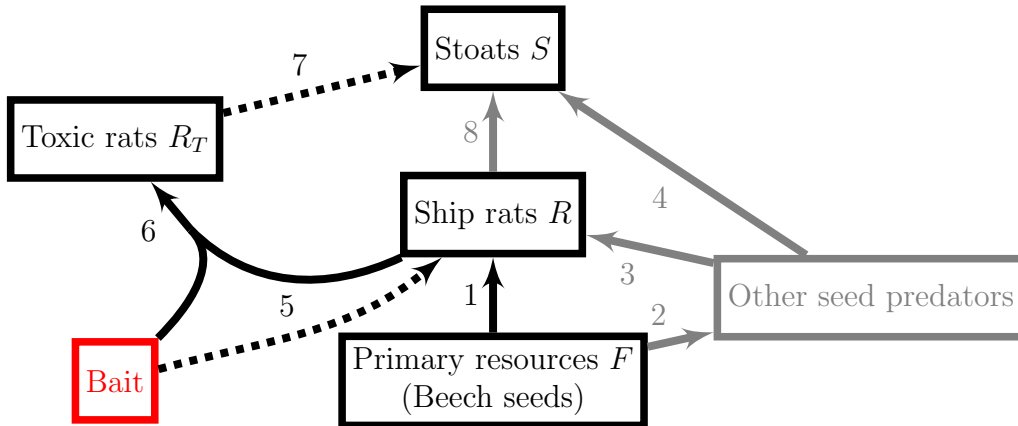


Figure 1: **We consider a food chain with three trophic levels in which top predator control is only possible via the consumer.** The figure shows a conceptual model of the system. Solid lines indicate a positive influence, while dashed lines indicate a negative influence. The red rectangle shows the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

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

64 2. Model

65 In the case study, beech (*Nothofagus*) seeds F are the primary resource
 66 (see Fig 1), and seed fall and seed decay are the main drivers of their dy-
 67 namics. Seed fall happens irregularly via beech masting on average every
 68 4–6 years predominantly in autumn (February – May) (Wardle et al., 1984;

69 Ruscoe et al., 2005). High resource abundances after mast events lead to
70 outbreaks of ship rats (*Rattus rattus*) which prey on seeds (link 1), but also
71 on other seed predators (McQueen and Lawrence, 2008; King et al., 2011;
72 Bridgman et al., 2013). Typically, ship rats breed in spring and summer
73 (September – February), but when resources are highly abundant, as in years
74 with high seed fall, breeding over winter occurs as well (King et al., 2011).
75 Populations of other seed predators with short life spans, e.g., mice, irrupt
76 similarly (link 2). Stoats (*Mustela erminea*), which feed on the seed preda-
77 tors, act as a generalist predator in this system. However, seasonal breeding
78 of stoats is temporally more restrictive, only taking place in early spring
79 (September – October) (O’Connor et al., 2006). The number of offspring
80 produced strongly depends on their habitats’ resource abundance ranging
81 from no breeding at all up to 18 kits (King et al., 2003). Hence, a delayed
82 high stoat abundance follows high seed consumer abundance driven by beech
83 masting (O’Donnell et al., 1996). Due to the impact on the native fauna,
84 control focuses on both stoat and ship rat populations. Sodium fluoroacetate
85 (1080) baits are used to control rats and stoats (Elliot, 2016). Here, stoat
86 control happens via secondary poisoning (Murphy et al., 1999). Hence, rats
87 eat baits (link 5) and are converted into toxic rats (link 6). Stoats then get
88 poisoned by feeding on toxic rats (link 7). Note that we include a predation
89 effect of stoats on non-toxic rats in the model only implicitly as rats usually
90 only form a minor part of the stoats’ diet. In particular, without poisoning,
91 only $< 10\%$ of the gut content of stoats contained rats (King and Moody,

92 1982; King, 2005). After 1080 poisoning, this is no longer true, presumably
93 because stoats also feed on the carcasses (Murphy et al., 1999). By modeling
94 it implicitly, we mean that we parameterized a term representing predation
95 on all seed predators (including rats) using observations. Including a weak
96 predation term as a direct link would have been equally possible. However,
97 the other seed predators would still be necessary for agreement with observa-
98 tions. Hence, the model would have been more complicated and also harder
99 to parameterize.

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

104 Tab. A.1 lists the parameters used in this study with corresponding refer-
105 ences. If available, we have used literature values. Otherwise, we calibrated
106 the particular submodels using parameter estimations based on qualitative
107 and quantitative results of previous studies.

108 2.1. Pulsed resource

109 We use the Delta temperature (ΔT) model introduced by Kelly et al.
110 (2013) to describe resource fluctuations. Previous theoretical studies have
111 already exploited this model (Holland and James, 2015; Holland et al., 2018),
112 and applications to different plant species revealed a good correlation between
113 prediction and data (Kelly et al., 2013; Pearse et al., 2014). We use mean

114 annual summer temperatures over the previous two years $\Delta T_y = T_{y-1} - T_{y-2}$
115 to model resource abundance in year y . For the application of the model, we
116 generated a 500-year random sample temperature time series. As in Holland
117 et al. (2018),

$$118 \quad T_y \sim \mathcal{N}(14, 1)$$

119

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

$$123 \quad \log_{10} F_y = 0.33 + 0.97\Delta T_y + \epsilon_y \quad (1)$$

124 parameterized using data from the Orongorongoro Valley by Holland and James
125 (2015) with $\epsilon_y \sim \mathcal{N}(0, 1.3)$ to match the correlation between seed fall and
126 temperature as reported by Kelly et al. (2013).

127 The differential equation

$$128 \quad \frac{dF}{dt} = \sigma(t) - hF - f(F)R$$

129

130 models the annual rate of change of food abundance F (seeds m^{-2}). Here,
131 h is the annual degradation rate of seeds, and $\sigma(t)$ describes the resource

132 delivery, i.e., in this case, beech seeding given by

$$133 \quad \sigma(t) = \begin{cases} \frac{F_y}{0.25} & \text{if } 0 \leq t - \lfloor t \rfloor < 0.25 \\ 0 & \text{otherwise.} \end{cases} \quad (3)$$

134

135 $\lfloor t \rfloor$ denotes the floor function giving the largest integer smaller than t . Hence,
 136 seeding takes place in the form of a steady influx to the food abundance in the
 137 first quarter of the year. The start of the year is defined to be in February as
 138 this is the time in which masting typically starts. The term $f(F)R$ represents
 139 the consumption of the generalist consumer R with functional response $f(F)$,
 140 which we describe in the following section. Fig. 2, row 5 shows a 10-year
 141 sample time series with two years with high seed fall to as an illustration of
 142 the seed dynamics.

143 2.2. Generalist consumer

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

$$147 \quad \frac{dR}{dt} = \Phi_R(F, R) = R(\rho - \mu_R R + \alpha_1 f(F) + \alpha_2 f(F_{R0}) - B(t)), \quad (4a)$$

$$148 \quad F_{R0} = \frac{\int_{t-1}^t F(t') dt'}{1 + \beta \int_{t-1}^t B(t') dt'}. \quad (4b)$$

149

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

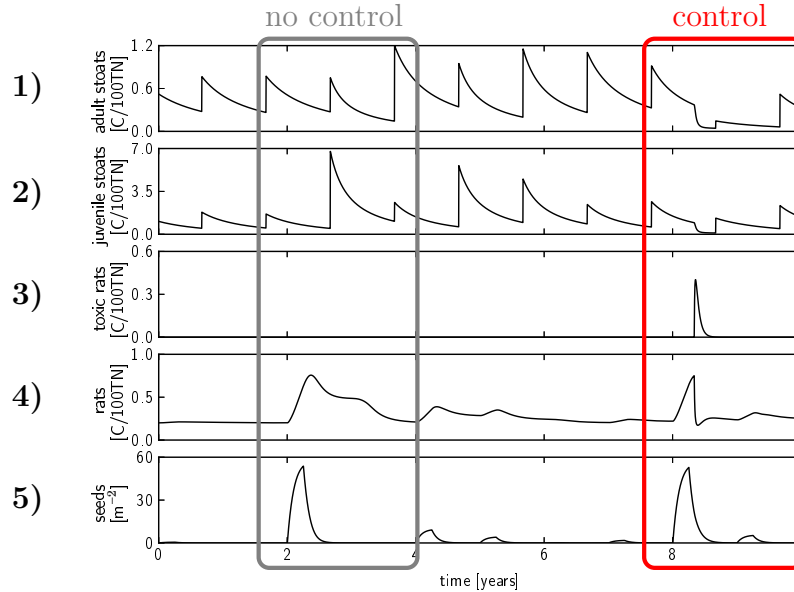


Figure 2: **Phenomenological dynamics follow what is known from data.** A part of a sample run of the local model is shown. Beech masting takes place in year 2 and year 8 of the time series. Bait is applied only in the second mast event (year 8).

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

$$156 \quad f(F) = c \cdot (1 - e^{-\epsilon F}) \quad (5)$$

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

161 change qualitatively using Holling type II (results not shown).

162 A pure predator-prey relationship between rats and seeds would lead to
163 a delayed peak in rat abundance, which would decrease again when seeds
164 degrade. Conversely, data show that rat abundance is high between 15 and
165 20 months after a year with high seed fall (Elliott and Kemp, 2016; Kemp
166 et al., 2018). This is because the diet of ship rats also depends implicitly on
167 beech seeds (link 2 and 3 in Fig. 1). For instance, they also prey on mice,
168 particularly after beech years with high seed fall (McQueen and Lawrence,
169 2008; Bridgman et al., 2013). This is taken into account by the term F_{R0} as-
170 suming that ship rats also benefit implicitly from seed fall of the last twelve
171 months due to secondary food sources. As an alternative, we could have
172 modeled these secondary as another state variable. However, this state vari-
173 able would have incorporated a whole set of species that depend (partially)
174 on seeds and are eaten by rats. Thus, parameterization would have been
175 rather difficult. Furthermore, the model would have become even more com-
176 plicated. Hence, we decided to model it in this indirect way to achieve the
177 observed qualitative behavior. The resulting rat dynamics following a year
178 with high seed fall are evident in Fig. 2, row 4 in the second year of the time
179 series. Rat abundance is particularly high when seed abundance is high as
180 well but stays high for about 15 months before it falls back to the pre-mast
181 level. This is in agreement with what is known from data (Elliott and Kemp,
182 2016; Kemp et al., 2018).

183 The denominator of F_{R0} describes the impact of bait application $B(t)$ on

184 secondary food sources, e.g., mice. If no bait is applied, the denominator
 185 is one. Conversely, if bait application took place in the last 12 months,
 186 secondary food sources are affected. Here, the parameter β represents bait
 187 efficacy regarding secondary resources. Bait application can be subject to
 188 different control strategies, e.g., annual control or control in years with high
 189 seed fall. Then, baits are applied at times t_i^{*b} , where i denotes the i th bait
 190 application. Following Holland et al. (2018),

$$191 \quad B(t) = \begin{cases} B_0 \exp(-d(t - t_i^*)), & \text{if } t_i^{*b} \leq t < t_{i+1}^{*b} \\ 0, & \text{otherwise} \end{cases} \quad (6)$$

192

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

$$202 \quad \frac{dR_T}{dt} = RB(t) - (d_i + \iota S)R_T \quad (7)$$

203

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

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

215 *2.3. Generalist predator*

216 We consider stoats (*Mustela erminea*) as generalist predators and distin-
217 guish between juvenile S_y (subscript for young) and adult stoats S_o (subscript
218 for old). The only difference between age classes we take into account is the
219 density-independent mortality as young stoats have significantly higher mor-

220 tality rates (King et al., 1996). The set of equations

$$\begin{aligned}
 \frac{dS_y}{dt} = \Phi_{S_y}(F, R_T, S_y, S_o) = & S_y (-\mu_{S_y} - \mu_{S_2}(S_y + S_o) - \kappa R_T) \\
 & + ((S_y + S_o)g(F_{S_0}) - S_y) \sum_{i=0}^{\infty} \delta(t - t_i^{*r}),
 \end{aligned}
 \tag{8a}$$

$$\begin{aligned}
 \frac{dS_o}{dt} = \Phi_{S_o}(F, R_T, S_y, S_o) = & S_o (-\mu_{S_o} - \mu_{S_2}(S_y + S_o) - \kappa R_T) \\
 & + S_y \sum_{i=0}^{\infty} \delta(t - t_i^{*r}),
 \end{aligned}
 \tag{8b}$$

$$F_{S_0} = C + \gamma \int_{t-1}^t F(t') dt'
 \tag{8c}$$

225 describes the dynamics of the stoat. Stoat populations show density-dependent
 226 mortality due to competition (O'Connor et al., 2006). Hence, the two first
 227 terms are similar to the rat dynamics and describe density-independent and
 228 density-dependent death processes, respectively. The third term $\kappa R_T S$ de-
 229 picts stoat mortality due to secondary poisoning by toxic rats (link 7 in
 230 Fig. 1). The last term represents the rather complicated breeding biology
 231 of stoats (see, e.g., King and Moody (1982)). Depending on the resource
 232 richness of the environment, stoats may not breed at all or give birth to up
 233 to 18 kits (link 4 in Fig. 1) (King et al., 2003). This is taken into account by
 234 the term F_{S_0} with saturating functional response (Ivlev type) (Jones et al.,
 235 2011).

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

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

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

257 *2.4. Metapopulation model*

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

$$265 \quad \frac{dR_1}{dt} = \Phi_R(F_1, R_1) - D_R (R_1 - R_2). \quad (10)$$

266

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

273 One crucial difference between stoats and rats is that dispersal rates differ
274 significantly between juvenile and adult stoats mainly due to the strong com-
275 petitive exclusion (Erlinge, 1977). In particular, immigration predominantly
276 happens via young stoats (King and McMillan, 1982). This is consistent with
277 the observation of a dispersal season between November and May following
278 the birth of juvenile stoats (Elliott et al., 2010). To take this complexity into

279 account, the dispersal processes between patches 1 and 2 in the model differ
 280 between juvenile and adult stoats

$$281 \quad \frac{dS_{y1}}{dt} = \Phi_{S_y}(F_1, R_{T1}, S_{y1}, S_{o1}) - p(S_{o1})S_{y1} + p(S_{o2})S_{y2}, \quad (11a)$$

$$282 \quad \frac{dS_{o1}}{dt} = \Phi_{S_o}(F_1, R_{T1}, S_{y1}, S_{o1}) - D_{S_o}(S_{o1} - S_{o2}). \quad (11b)$$

283

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

$$288 \quad p(S_o) = \frac{D_{S_y}}{1 + e^{-\psi S_o}}. \quad (12)$$

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

297 Fig. 3 shows a part of a sample run of the system including seed-, rat-,
 298 stoat-, and bait dynamics for the metapopulation model. Dispersal of rats

299 is negligibly small in this case, while the reinvasion of stoats has a definite
 effect on the dynamics.

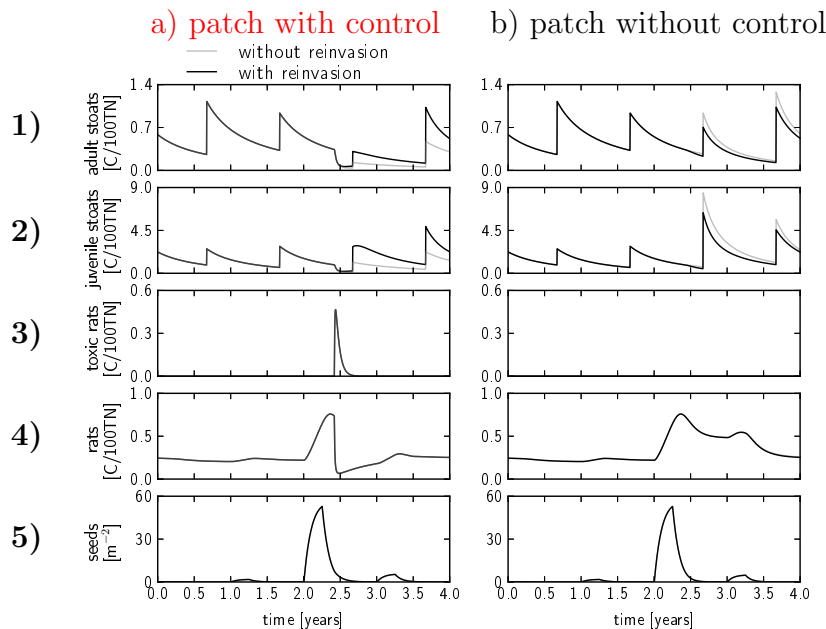


Figure 3: **Reinvasion from adjacent patches can significantly alter control success.** The figure shows a part of a sample run of the local model. The dispersal rate of the rats is $D_R = 10^{-2}$. Note that this is too small to lead to a visible effect on such a time scale for rat dispersal while the 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).

300

301 2.5. Plague metric

302 This study aims to find patterns for efficient, tailored predator control.
 303 This is necessary if the predator is a pest, e.g., due to crop damage, its role
 304 as a disease vector, or a threat for other species. It is essential to define the
 305 plague metrics corresponding to the problem to obtain consistent results.
 306 For instance, the endangered bird kaka (*Nestor meridionalis*) is particularly

307 vulnerable to nest predation in its breeding season, which is taking place
308 mainly before beech masts (Wilson et al., 1998; Moorhouse et al., 2003).
309 Hence only specific years matter. Conversely, some problems do not only
310 depend on the predator but also on the consumer, e.g., *Mohoua ochrocephala*
311 is preyed on by both rats and stoats (Innes et al., 2010). In this study, we
312 consider the impact of stoats on kiwi (*Apteryx*) populations as an example.
313 As a metric, we have chosen mean stoat densities between November and
314 March as kiwi chicks are particularly vulnerable to stoat predation in this
315 time (Robertson et al., 2016). We define control success as the inverse of the
316 mean stoat density between March and November.

317 **3. Results**

318 *3.1. Local dynamics*

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

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

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

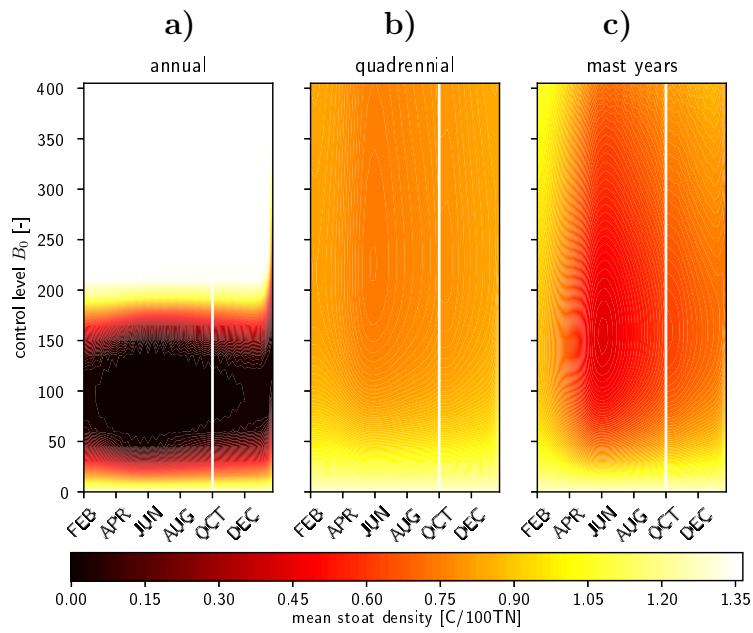


Figure 4: **Control application only in years with high seed fall needs more effective control and strongly depends on the timing.** The figure shows the dependence of the control success on the timing and the intensity of the control for three different control strategies. The mean stoat density in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

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

345 Applying control every fourth year corresponds to a less efficient control
346 strategy. Higher control levels are necessary for optimal control success.
347 However, very high control intensities do not impair control success as in
348 the case of annual control. Furthermore, an optimal control timing in June
349 is visible. Note that the asymmetry in the temporal dependence for bait
350 application in years with high seed fall is due to the seed fall at the beginning
351 of the year. Applying high levels of control at this time, the rats cannot

352 recover the rest of the year as the food has already degraded. This can lead
353 to extinction of the rats and, therefore, to extinction of the control vector
354 of the stoats. However, note that the extent of the asymmetry is an artifact
355 resulting from the discrete seed fall start.

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

369 *3.2. Metapopulation dynamics*

370 The results of the metapopulation model are restricted to the case of
371 control in years with high seed fall as this is the more feasible strategy due
372 to the lower costs and less social concerns (Green and Rohan, 2012). Note
373 that the dispersal rate of young and old stoats are defined in terms of the

374 rat dispersal rate (see Tab. A.1). Hence, the relation between the dispersal
 375 abilities does not change, but the absolute values do. Changing the abso-
 376 lute values may correspond to different species. However, note that here,
 377 it corresponds to varying patch size as dispersal only happens between the
 378 two patches. The optimal control timing is June, as in the local results (not
 379 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),

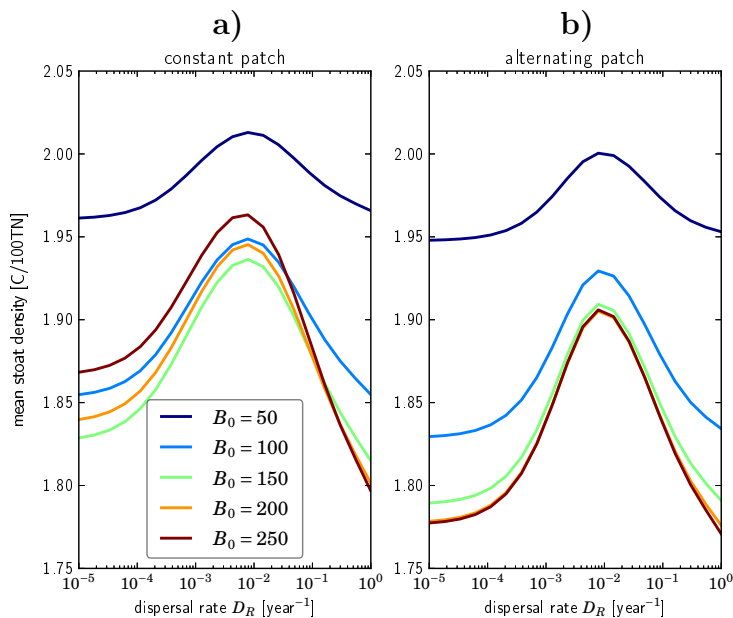


Figure 5: **Alternating the control patch yields higher control success while a suboptimal patch size exists independent of the control strategy.** The figure shows the influence of the rat dispersal rate and control level on the mean stoat density ($S_y + S_o$) in *Apteryx* chick vulnerability time. 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.

380

381 control has always been applied in the same patch, while the control patch

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

389 A clear suboptimal dispersal rate at $D_R \approx 10^{-2} \text{ year}^{-1}$ exists. In that
390 case, the mean stoat density, i.e., the inverse of the control success, has a
391 maximum independent of the control level. De- or increasing the dispersal
392 rate sufficiently yields significantly higher control success. In both cases, the
393 effect of a change in the dispersal rate is the highest close to the subopti-
394 mal point and gets lower further away. Furthermore, the figure depicts the
395 influence of the control level. At low and intermediate control levels, i.e.,
396 $B_0 \leq 100$, a change in control level has a high impact. Increasing the control
397 level, the rate of change of the control efficacy with varying control levels
398 tends to zero or is even reversed in the case of a constant control patch.

399 The suboptimal value for the dispersal rate for which the control is least
400 effective results from a trade-off of the dispersal influence. At low dispersal
401 rates, both rat and stoat dispersal is low. Lower stoat densities in the patch
402 produce less offspring. Furthermore, after the breeding event, stoats invade
403 at a lower rate, which means that the stoat population stays low for a longer
404 time while the stoat population in the other patch suffers from higher density-

405 dependent mortality. Conversely, at high dispersal rates, stoat reinvasion is
406 very fast. However, in this regime, invasion rates of rats are important as
407 well. Due to the fast reinvasion, a higher number of potential vectors to
408 control the stoat population is abundant. Furthermore, the extremely high
409 stoat reinvasion rate leads to a higher density in the control patch already
410 shortly after control application. This, in turn, leads to a larger number of
411 stoats, which one can potentially control via secondary poisoning. However,
412 both effects are saturating for very high or low dispersal rates respectively
413 because very low dispersal rates tend to zero, and higher dispersal rates have
414 no impact anymore if densities are already equal in both patches. At inter-
415 mediate dispersal rates, the dispersal rate of rats is too low for increasing the
416 vector density efficiently directly after bait application while stoat dispersal
417 rates are already high enough to decrease the impact of density-dependent
418 death processes in the uncontrolled patch. However, in the long run, rein-
419 vasion still has an effect decreasing natural density-dependent mortality in
420 the patch, which is not controlled and leading to higher stoat densities in the
421 controlled patch (see Fig. 3 for a sample time series showing this relation-
422 ship).

423 **4. Discussion**

424 *4.1. Control timing*

425 Independent of the control strategy or the setting, i.e., local or metapop-
426 ulation dynamics, the optimal control timing is in June. This also holds for

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

445 Due to public concerns, the annual control application is not feasible. If
446 we neglected public concerns, applying bait annually at a lower level might
447 still yield better results than applying baits in mast years at higher control
448 levels. However, the reduced control level reduces bait material but not
449 (significantly) the costs of the aerial operations. Hence, the results presented

450 here underline the importance of the right timing in years with high seed
451 fall. This calls for better mast identification (e.g., model predictions as in
452 Kelly et al. (2013)) and faster decision-making processes. This becomes even
453 important as the effect of timing is higher if one applies control in years with
454 high seed fall. This is due to the higher control level, which is necessary in
455 this case, which increases the influence of bait application time. However, in
456 practice, data on seed abundance determining years with high seed fall are
457 often usable not earlier than July, and afterward, a political decision-making
458 process is still necessary (Elliot, 2016).

459 *4.2. Control intensity*

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

470 This critical control density becomes higher with lower control frequency
471 and higher reinvasion of rats through adjacent patches. However, especially

472 if control patches are large and reinvasion is limited, it is essential to note
473 that a high control intensity can be less efficient management in the long
474 run. Before reaching this critical level, the effect of an increase in the control
475 intensity saturates. From a management perspective, this is positive because
476 it means that we can apply significantly lower control levels without losing
477 much of the control success. But this can act as a buffer reducing the risk
478 of killing the vector. The optimal control intensity we found was $B_0 \approx 150$
479 in the case of control in years with high seed fall without reinvasion and
480 $B_0 \approx 250$ in the case of alternating patch control. However, $B_0 \approx 150$ is
481 nearly as effective as the optimal intensity in the alternating patch control
482 case. This is consistent with data. A reduction in the bait sowing rate, from
483 11 kg/ha to 4 kg/ha for possum control, for instance, did not significantly
484 alter the killing proportion (Warburton and Cullen, 1995).

485 This optimal value corresponds to a killing proportion of about 95%. The
486 current management goal of the Department of Conservation in New Zealand
487 is to reduce rat tracking rates to 5% in years with high seed fall via 1080
488 application (Elliot, 2016). As rat tracking rates in years with high beech seed
489 fall can approximately be between 80% and 100% (Elliot, 2016; Kemp et al.,
490 2018), the goal is in good agreement with the optimal intensity.

491 *4.3. Control strategy*

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

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

516 **5. Conclusions**

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

523 The maximum in the population density of the control vector determines
524 the optimal timing, which is June for rats. This implies that given that vari-
525 ous predators (e.g., stoats and possums) feed on the same vector, the optimal
526 control timing stays constant. High control intensities can be counterproduc-
527 tive if they yield extinction of this vector. Hence, intermediate control levels
528 are more effective in the long run. This can lead to huge cost savings. For
529 instance, the reduction of 1080 bait usage for possum control has saved 8.9
530 million dollars per year without reducing the control success (Morgan et al.,
531 1997). However, one can influence this dependence by the control strat-
532 egy, e.g., alternating control patches allow for longer recovery periods of the
533 control vector species. This also depends on the patch size. Especially inter-
534 mediate patch sizes in which reinvasion of the generalist predator may be fast
535 while reinvasion of the generalist consumer is still negligibly small can have a
536 negative impact on the control success. From a management perspective, this
537 intermediate dispersal regime can be prevented by either applying very large
538 or very small control patches or by changing dispersal abilities in another way,

539 e.g., by separation of patches using (leaky) fences. The patch sizes (repre-
540 sented by the proxy of the rats' dispersal rate) yielding high control success
541 found in this study depend not only on the bait application but also on indi-
542 rect effects after the reinvasion, such as higher density-dependent mortality
543 in the case of low stoat reinvasion rates. Hence, considering spatial depen-
544 dencies like this makes the combinations of different control mechanisms such
545 as chemical (bait) and biological (density-dependent) mechanisms necessary.
546 Furthermore, this indicates that the spatial design of bait application may
547 play an important role in the pest management.

548 Note that only the stoat density gives the control success metrics under-
549 lying the results of this study. This means that low mean stoat densities
550 in a critical time interval correspond to high control success independent
551 of the ship rat population. The critical time interval for other species may
552 differ. We have also exploited the model presented in this study regarding
553 plague metrics for the conservation of other New Zealand birds such as *Nestor*
554 *meridionalis* (New Zealand kaka) or *Mohoua ochrocephala* (mohua). The
555 results, however, are not shown here for the sake of brevity. We have defined
556 the plague metrics for the kaka by its breeding season, which is taking place
557 mainly between October and March before years with high seed fall (Wilson
558 et al., 1998; Moorhouse et al., 2003). As the kaka is also mainly vulnerable
559 against stoat predation, the optimal control timing is the same as it is pri-
560 marily affected by the maximum in the rat density. However, some native
561 species like, for example, the mohua are also under threat from predation by

562 rats. The results for the mohua (not shown here) reveal the optimal control
563 timing is shifted closer to the reproduction event of the stoats in October
564 (i.e., to middle September) due to the main influence of rats in February.
565 Due to indirect effects such as mesopredator release (Soulé et al., 1988), the
566 optimal control derived in this study can in fact be suboptimal regarding
567 other target species (see e.g., Courchamp et al. (1999) for an example of
568 a similar problem with invasive meso- and invasive superpredator). Hence,
569 before applying the control measure as suggested in this study on a large
570 scale, it should be tested locally, including a monitoring program following
571 the control operation as it is suggested in the review on biological invasions
572 by Courchamp et al. (2003).

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

585 The results presented here refer to the pest management of stoats threat-
586 ening the local *Apteryx* populations. However, pulsed resources lead to ir-
587 rupting pest populations in many ecosystems worldwide with diverse negative
588 impacts (see Sec. 1). The modeling approach presented here is readily ap-
589 plicable to other species in New Zealand or even to completely different case
590 studies to investigate suitable strategies, e.g., seed-rat-mongoose dynamics in
591 Japan (Fukasawa et al., 2013) or seed-rodent-raccoon-dog dynamics in Poland
592 (Jedrzejewska and Jedrzejewski, 2013). The results for the New Zealand case
593 study indicate the great importance of tailored control strategies in such sys-
594 tems.

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800 **Appendix A. Parameters**

801 Tab. A.1 shows the variables and parameters used in this study. Note
802 that we sometimes express unit in terms of the state variable for a more
803 straightforward interpretation. If we have taken the parameters from a spe-
804 cific study, the table states the reference. If the parameters are estimated
805 based on the results of particular studies, we have denoted this with *based*
806 *on reference*. All submodels have been tested and compared with literature
807 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).

45

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 $\text{m}^{-2} \text{ year}^{-1}$	-
$B(t)$	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	$\text{rat}^{-1} \text{ year}^{-1}$	based on King and Moller (1997)
α_1	demographic efficiency of rats for primary resources (seeds)	0.1	$\text{rats seeds}^{-1} \text{ m}^2$	based on King and Moller (1997), Holland et al. (2018)
α_2	demographic efficiency of rats for secondary resources (seed predators)	0.1	$\text{rats seeds}^{-1} \text{ m}^2$	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	$\text{seeds m}^{-2} \text{ rats}^{-1} \text{ year}^{-1}$	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)
μ_{S_y1}	density independent mortality of juvenile stoats	0.7	year ⁻¹	King et al. (1996)
μ_{S_o1}	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)

808 **Appendix B. Killing proportion**

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

$$811 \quad \chi = 1 - \frac{\min_{t \in \Upsilon} R(t)}{R(t = t_b)} \quad (\text{B.1})$$

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

$$819 \quad \chi = 1 - e^{\frac{-B_0}{49.8}}. \quad (\text{B.2})$$

820 Fig. B.6 visualizes this relationship.

821 **Appendix C. Reinvasion time**

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

$$825 \quad D_R = e^{\frac{0.94 \text{years} - \tau}{0.28 \text{years}}}. \quad (\text{C.1})$$

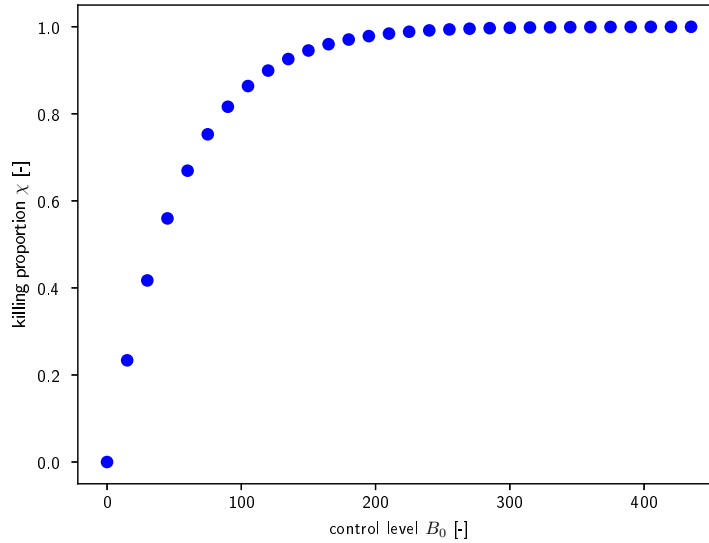


Figure B.6: **The killing proportion saturates exponentially with respect to the control level.** The figure shows the relationship between control level and killing proportion.

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

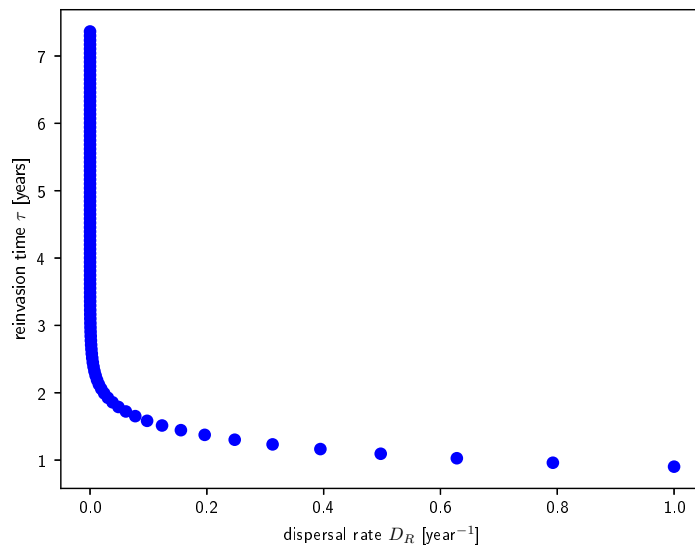


Figure C.7: **Reinvasion times decrease exponentially with increasing dispersal rates.** The figure shows the relationship between reinvasion time and the dispersal rate of rats.