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Assessing the Effects of Season, Frequency, and Age-specificity of Control Efforts on

Controlling Invasive Rabbits

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28 **ABSTRACT**

29 The effectiveness of invasive species control can be influenced by seasonal fluctuations in

30 reproduction in response to environmental conditions. However, it is difficult to determine

31 how the efficacy of different control efforts is affected by the intricate interplay of

32 demography and environmental conditions from field trials alone. We incorporated an

33 ontogenetic growth model into a hierarchical Bayesian mark-recapture model to estimate age-

34 structured seasonal survival rates for rabbits in Australia, based on a 20 year data set. We

35 integrated this demographic information into an individual-based simulation model, which

36 reproduces seasonal birth-death processes, to test the effectiveness of pest-management

37 schemes that differ in intensity, specificity to age groups, and seasonal timing. Control

38 measures that were simulated to only affect juveniles had a negligible effect on population

39 size, whereas targeting subadults led to considerable population declines when applied after

40 the breeding season. Management schemes that affected rabbits of all age groups caused

41 significant population reductions. However, even repeated control efforts that cause 95%

42 mortality each year only resulted in predictions of local population extirpation after an

43 average of 119 calendar weeks in the absence of immigration. Our simulation study supports

44 the use of pest rabbit control schemes that account for demographic dynamics explicitly, and

45 target those individuals with high reproductive potential. More broadly, we show that local

46 and temporal population extirpation, or recovery, depends largely on the trade-off between

47 control intensity and frequency for species with recurrent population oscillations.

48

49 **KEY WORDS** Bayesian mark-recapture, density dependence, invasive species control,

50 management implementation schemes, *Oryctolagus*, population viability analysis.

51

52   The control of undesirable invasive pest species is often costly and time consuming because it

53   can be extremely difficult to significantly reduce or eradicate entire populations (Byers et al.

54   2002). Population recovery can negate previous efforts, especially for species with high

55   fecundity rates (Boyce et al. 1999). The majority of successful control efforts that led to

56   eradication of vertebrate pest species are documented from islands (Gregory et al. 2014) and

57   have been linked to small population sizes and limited migration (Howald et al. 2007, Harris

58   et al. 2012). However, there is an urgent need to better understand the biological processes

59   and social perceptions that characterise unsuccessful eradication or population reduction

60   efforts in many mainland populations (Parkes 1993, Bomford and O'Brien 1995).

61   Optimizing control efforts to minimize populations of pest species can be particularly

62   challenging when the efficacy of management actions varies over space and time and when

63   density-dependent compensatory responses are strong (Kokko and Lindström 1998). For

64   example, actively removing individuals from a population during the breeding season can

65   trigger relative increases in reproduction and/or survival rates of the remaining individuals

66   due to density-dependent compensatory mechanisms (Xu et al. 2005, Mysterud et al. 2009).

67   Selective removal of individuals from different life stages will cause greater reductions in

68   population size if those with the highest reproductive values are removed (Brooks and

69   Lebreton 2001). Likewise seasonally timed control efforts can help to overcome

70   compensatory regulation (Zipkin et al. 2009). Maximizing the efficacy of control efforts

71   requires targeted and well-planned implementation schemes (Simberloff 2003), but financial

72   constraints usually limit the range of pest management actions that can simultaneously be

73   evaluated in field trials. Simulation studies provide a low-cost alternative tool for exploring

74   the potential efficacy of pest management schemes differing in intensity, timing, and

75   frequency of control efforts. In addition, simulation approaches can provide a cost-effective

76   way to evaluate the potential advantage of new control actions that can then be implemented

77   and tested using field trials (Zurell et al. 2010).

78   In practice, pest managers are often forced to make decisions as to whether to

79   implement control measures over a short time period or to spread their finite resources over a

80   longer period. Quantifying the effects of repeated management actions on population control

81   is particularly important because in practice, control (rather than eradication) efforts are

82   likely to be suspended if population size is perceived to be tolerably low. Therefore, rigorous

83   testing of different management actions with simulations can provide important information

84   on control practices that extend beyond the range of scenarios that are feasible to test in the

85   field. Few simulation studies have investigated directly the importance of the timing of

86   control efforts or other components of pest management schemes (e.g., intensity and

87   frequency of control efforts) on population persistence (Cid et al. 2014).

88   European rabbits (*Oryctolagus cuniculus*) are a severe economic and environmental

89   pest in many temperate and Mediterranean grassland ecosystems (Tablado et al. 2009, Cooke

90   et al. 2013). After they became widely established in Australia in the late 1800s (Williams et

91   al. 1995), early rabbit control actions were widely compromised by conflicting interests of

92   pest control and the commercialization of rabbit products (Cooke et al. 2013). The large-scale

93   economic benefit of rabbit control was only recognised after the deliberate introduction of

94   myxoma virus (MYXV) in 1950 as a control measure, which causes the disease

95   myxomatosis. The more recent release of rabbit haemorrhagic disease virus (RHDV), which

96   causes rabbit haemorrhagic disease (RHD), in 1995/96 led to further widespread population

97   declines (Cooke and Fenner 2002). Both diseases mainly affect juvenile and subadult rabbits,

98   meaning that high proportions of adults in breeding populations are immuno-protected

99   disease-survivors (Robinson et al. 2002, Kerr 2012). Although both diseases continue to

100   affect most Australian rabbit populations, the high initial impact of each disease has declined

101 over time due to adaptive responses, allowing partial recovery of rabbit numbers (Cooke and

102 Fenner 2002).

103   In Australia, numerous field trials to manage invasive rabbits have provided practical

104 guidance for 'best practice' management actions − the application of poison to reduce

105 population levels, followed by deep ploughing (ripping) of warrens to destroy underground

106 burrow systems, and then fumigation of any re-opened warren entrances to kill rabbits that

107 survive the initial actions (Williams and Moore 1995). This approach is most effective during

108 hot and dry weather conditions in mid-late summer for several reasons: 1) poison is more

109 readily accepted after the breeding season when less natural forage is available, rabbit

110 territorial behaviour diminishes and juveniles are old enough to consume baits, 2) rabbit

111 populations have been reduced by the effects of MYXV and RHDV in spring and early

112 summer, 3) warren destruction with machinery is more effective if soils are dry and friable,

113 and, 4) individuals escaping are exposed to heat stress (Williams et al. 1995). This set of

114 control efforts is capable of reducing local rabbit populations with an efficacy of $> 98\%$

115 (Cooke 1981). Warren destruction is a critical component of the process even when

116 population levels are greatly reduced by the initial poisoning treatment because it reduces the

117 survival prospects and the breeding success of remnant populations (Williams et al. 1995).

118   While rabbit managers in Australia acknowledge the general importance of seasonal

119 timing, intensity of control efforts, and age group on managing rabbits (Fig. 1), simulation

120 studies that couple seasonal population dynamics with different control implementation

121 schemes, provide opportunities to systematically test and compare different management

122 actions. This is an important prerequisite, not only for optimizing the cost-benefit ratio of

123 existing control techniques, but for evaluating the feasibility of new control efforts such as

124 the release of novel biocontrol agents.

125   We used a Bayesian hierarchical mark-recapture model (with an integrated

126 ontogenetic body growth model for age classification) to reconstruct details of birth-death

127 processes over a period of > 15 years for a rabbit population in South Australia affected by

128 both RHDV and MYXV (Mutze et al. 2014). Modelling has shown that the seasonal

129 matching of rabbit recruitment and disease-induced mortality largely determines population

130 growth at the site (Wells et al. 2015). We integrated the mark-recapture results into

131 individual-based stochastic simulation models to explore the efficacy of various pest control

132 implementation schemes, which varied in their timing and duration and targeted age-cohorts.

133

134 **STUDY AREA**

135 In Australia, rabbits typically reproduce in response to rainfall-driven increases in food

136 supply (native and invasive grass and herb species). Rainfall widely varies in time and space

137 across Australia, causing wide-scale spatial variation in the duration of rabbit reproduction

138 and seasonal peaks in recruitment (Gilbert et al. 1987, Mutze et al. 2002).

139   Rabbits, and their diseases, have been intensively studied at Turretfield (South

140 Australia, 34°33′S, 138°50′E), where the annual amount of rainfall varies between 215 and

141 700 mm (SD = 96 mm; based on weather station data 1950–2014 from the Australian Bureau

142 of Meteorology). Rabbits at Turretfield have been live-trapped at least every 4–5 consecutive

143 days at 8–12 week intervals since 1996 in an area of ca. 12 hectares (Peacock and Sinclair

144 2009, Mutze et al. 2014). The Turretfield study represents the largest long-term capture-

145 mark-recapture monitoring of wild free-living rabbits in the world, providing important

146 insights in population and disease dynamics (Cooke 2014).

147

148 **METHODS**

149 **Hierarchical Mark-recapture Model**

150   We analysed mark-recapture data collected at Turretfield between April 1998 and November

151   2013. Our analysis included 3,736 individuals with a total of 7,340 capture records of marked

152   individuals over 80 capture sessions. For most captures (98 %), body mass measures were

153   available (to the nearest ± 25 grams using spring balances) and 249 individuals were

154   recovered as carcasses, which makes the time of death of these individuals known. We

155   employed a Bayesian hierarchical mark-recapture model, in which we included an

156   ontogenetic (population-level) growth model to infer individual birth dates from body mass

157   measures (Unnsteinsdottir et al. 2014). We assumed that all weight measures – some obtained

158   as sequences from consecutive captures of the same individuals over known time intervals –

159   represent the population-level ontogenetic growth of rabbits at our field site. Therefore, the

160   birth dates of all individuals can be estimated as a random variable based on body mass

161   information during individual capture histories "(Fig. S1, available online at

162   www.onlinelibrary.wiley.com)".

163   We modelled body mass according to the generic West-Brown-Enquist model (West

164   et al. 2001). Estimates of individual birth dates based on the ontogenetic growth function

165   allowed us to estimate the most likely age of individuals (with reduced precision for

166   larger/older rabbits) throughout their capture history and their individual fates. Initial analysis

167   did not reveal any effect of sex on ontogenetic growth or survival, and we therefore did not

168   consider sex as a covariate in our analysis. We used this detailed analytical approach to

169   estimate age-structured survival rates and also provide insights into longevity of individuals

170   that cannot be inferred from the raw data alone. For recovered carcasses, we considered

171   individuals to have died at the time between carcass recovery and previous capture session.

172   We did not infer demographic structure from last capture records (Pradel 2005) because it is

173   biased towards younger ages of individuals (Pradel 2005). Estimates of survival rates were

174 used to inform the simulations (see below), while estimates of longevity were used to

175 interpret the output of the statistical model.

176   Using a Bayesian state-space capture-recapture modelling approach allowed us to

177 account for various sources of uncertainty in model outputs, including incompleteness of

178 observations, which is difficult to account for in classical maximum likelihood approaches

179 (Brooks et al. 2000, Buckland et al. 2004). Incorporating multiple data streams, such as body

180 mass and recovery data into the state-space framework, reduces uncertainty in estimates of

181 individual fate and survival (Schofield and Barker 2011, King 2012). Accordingly, we

182 constrained birth dates to estimates based on body mass measures and informed the (partially

183 unknown) state-variable of individual presence by known times of deaths. For estimating

184 age-structured survival probabilities, we classified the age of each individual in a capture

185 session in five age categories: $\leq$ 90 days old (juveniles), 91–120 days (subadults), 121–365

186 days (young adults < 1 year old), 366–1460 days (adults between 1–4 years old; estimated

187 average longevity), 1460–2920 days (adults between 4–8 years old). The juvenile class

188 included only those animals that survived long enough to enter the trappable population (i.e.

189 ~ 21 days old), so the estimated survival rates do not account for mortality of rabbit kittens

190 inside the warrens.

191   We did not explicitly partition the effects of RHD and myxomatosis on survival rates

192 in this study, but rather, we assumed that these effects are included in the estimated survival

193 rates. We used a posterior predictive model check (Bayesian p-value) to assess model skill.

194 The metric compares the distribution of randomly drawn data generated from joint posterior

195 estimates to the observed data (Gelman et al. 2005). "Details and model code for the

196 Bayesian state-space capture-recapture model are available online at

197 www.onlinelibrary.wiley.com".

198

Simulations of Population Dynamics

199

200 We parameterised an individual-based population model using the posterior mode estimates

201 of survival rates from our Bayesian model. This model was previously shown to replicate

202 inter- and intra-annual variation in rabbit abundance, using independent field data and

203 approximate Bayesian computation (Wells et al. 2015). We assumed a mortality rate of 50 %

204 of rabbit nestlings during weaning time because the mark-recapture analysis (outlined above)

205 provided relatively low estimates of per capita-birth rates during the main breeding season

206 (Australian winter). We assumed an average ovulation rate of pregnant rabbits in South

207 Australia of 6 (SD = 1) and an average litter size (embryos carried to term) of 6 (SD = 2)

208 based on data of 2,563 examined females at a nearby field site (Belton, Flinders Range)

209 between 1968 and 1993 (Wells et al., in review). We modelled the demographic dynamics of

210 rabbits at weekly time steps. We assumed an annual peak in recruitment (*RepPeak)* in

211 calendar week 39 and the relative distribution of breeding efforts in all other calendar weeks

212 to follow a Gaussian distribution with one SD (*RepVar* = 4) and a total annual reproductive

213 effort (*RepEff*) of 132 % (Wells et al. 2015). A total annual reproductive effort >100%

214 allows some females to reproduce multiple times in a given year. We simulated a single

215 rabbit population with density dependent reproduction (Rödel et al. 2004) and a maximum

216 carrying capacity of ~1,000 individuals. We did not account for immigration and

217 recolonization events, which can be important if neighbouring rabbit populations are only a

218 few kilometres away from each other (Ramsey et al. 2014). This is because, as a first step,

219 our aim was to better establish the relationship between local seasonal population dynamics

220 and different pest control implementation schemes.

221 We modelled environmental stochasticity in birth and survival rates, since it can

222 considerably impact population dynamics. Models were built using the VORTEX *10*

223 population viability package (http://www.vortex10.org; version 10.0.7.9), which is a freely

224   available tool for building stochastic, individual age- and sex-structured demographic models

225   (Lacy et al. 2013). VORTEX is widely used in invasion biology and pest management

226   (Prowse et al. 2013) and has been used in wildlife population viability analysis for almost 3

227   decades, with regular updates, and is readily accessible for practitioners (Lacy 2000,

228   Lindenmayer et al. 2000, Lurgi et al. 2015). All demographic events and state transition

229   dynamics are inherently probabilistic. Furthermore, environmental variation can be simulated

230   using probability distributions and catastrophes. "Details of model specification and

231   implementation in the VORTEX software are available online at

232   www.onlinelibrary.wiley.com".

233

234   **Pest Control Scenarios**

235   We simulated different pest control implementation schemes (termed 'scenarios'), which

236   were modelled as additional mortality on top of the weekly survival rates. Pest control

237   implementation schemes were characterized by the combinations of 4 different parameters

238   which we sampled from discrete values based on expert knowledge:

239   1. *Control season* ($Seas_{Contr}$): Seasonal timing of pest control efforts simulated as 4 possible

240   values of the (first) calendar week of each year, corresponding to, respectively, the middle

241   and end of summer, and the middle and end of the main reproductive period; $Seas_{Contr} \in 3$,

242   13, 35, 45 ('$\in$' indicates that a parameter value used in the simulations is element of the

243   given number set);

244   2. *Control time* (t_{Contr}): Allocation of the total annual control effort over consecutive weeks;

245      $t_{Contr} \in 1, 3, 5$;

246   3. *Control efficacy* (Eff_{Contr}): Efficacy of control efforts, given as the mortality rates of

247   individuals on top of their natural mortality rates in a population during control efforts;

248    $Eff_{Contr} \in$ 0.3, 0.6, 0.9, 0.95. For model implementation, mortality based on Eff_{Contr} was

249   assumed as the total effect over the duration of t_{Contr};

250   4. *Control age group* (Age_{Contr}): Classification of the different age groups affected by control

251   efforts with Age_{Contr} *(juv)* individuals < 13 weeks old, Age_{Contr} *(subad)* individuals < 26 weeks

252   old (including juveniles), and Age_{Contr} *(all)* all individuals.

253   These pest-control regimes resulted in 144 different scenarios (i.e. all combinations of

254   the four parameters listed above), and we ran 100 samples (stochastic replicates) for each

255   scenario. We also ran a baseline model under a no control scenario consisting of 100 samples

256   with no pest control effects ('untreated population'). We initiated all simulations with 800

257   juvenile rabbits with an equal proportion of male and females (replicating the number of

258   juveniles in relatively large local population) and used a 25-year burn-in period with no pest

259   control efforts to attain a stable age structure (Wells et al. 2015). We then ran each simulation

260   for a total period of 10 years. We deemed a simulation period of 10 years sufficient to

261   investigate the effects of different control schemes, since management efforts are typically

262   constraint to periods of <10 years.

263   We also included disease-free simulations. To do this we repeated all simulations with

264   the survival rate of subadults set to those of juveniles, and all else being equal. We did this to

265   test whether the low survival rates of subadults, from our statistical analysis (likely due to the

266   detrimental effect of recurrent RHD outbreaks) (Mutze et al. 2014), affects the efficacy of

267   different pest control regimes.

268

269   **Statistical Analysis**

270   The primary outputs from the simulation model were 10-year time series of weekly

271   population sizes. This was converted to a binary measure of whether a population was

272   extirpated (local population pool is zero after some time of treatment) or not. For all samples

273   in which populations experienced extirpation, we calculated the average time to extirpation.

274   Further, we calculated the minimum population size during the 10 years of treatment for

275   persistent model runs (McCarthy and Thompson 2001).

276   We used boosted regression tree (BRT) analyses via the *gbm.step()* routine in the R

277   package *dismo* (Elith et al. 2008) to estimate the relative importance of different pest control

278   parameters for explaining variation in population extirpation (binomial error structure,

279   learning rate $l = 0.001$, tree complexity of $tc = 3$) time to extirpation (Gaussian error

280   structure, $l = 0.001$, $tc = 3$) and minimum population size (Poisson error structure, $l = 0.001$,

281    $tc = 3$). We treated the pest control parameters as categorical model variables.

282   For testing the sensitivity of the baseline model to variation in selected input

283   parameters, we sampled 1,000 different values for mortality rates of the different age classes

284   (samples ranged between $\pm$ 10% of apparent survival rates), maximum litter size (sample

285   range between 5 and 8) and overall yearly reproductive effort (sample range between 100 and

286   200 %) with a Latin hypercube design (Stein 1981). We then tested which parameters were

287   most influential on changes in mean population size and variation in population size

288   (averaged over the 10-year output period) using BRT analyses.

289

290   **RESULTS**

291   **Rabbit Demography**

292   Analysis of the mark-recapture data showed survival rates of rabbits at Turretfield (a

293   population affected by myxomatosis and RHD) were particularly low for subadults (68 % of

294   individuals surviving the 30-day time window of 90–120 days of age, corresponding to a

295   weekly survival rate of 0.92, CI: 0.92–0.95) compared to those of juveniles (83 % of

296   individuals surviving the 21–90 day period after emergence from the warren, corresponding

297   to a weekly survival rate of 0.98, CI: 0.97–0.99) and older individuals. There was

298   considerable variation in survival rates over years for all age classes.

299   We were able to infer individual birth dates and ages with reasonable confidence. The

300   credible intervals (95%) of estimated birth dates were < 100 days for 64% of individuals

301   (2,406 out of 3,736). However, estimates of longevity were less precise, with only 463 out of

302   3,736 estimates (12 %) having credible intervals ≤ 100 days uncertainty. Because of this

303   uncertainty, longevity was deemed to be unrealistically high, at 7–8 years for 31 % of

304   individuals. The overall demographic structure of the rabbit population was characterised by

305   as much as 60 % of recorded individuals dying before one year of age (Fig. 2). Capture

306   probabilities varied over seasons and time periods between 0.07 (CI: 0.07–0.08) and 0.37 (CI:

307   0.35–0.38) being highest in spring (Sept–Nov) and increasing towards the end of the study

308   period.

309   The simulation model predicted population size fluctuations (without control actions)

310   to oscillate between ~ 350 and 650 individuals (Fig. 3), which corresponds to the observed

311   numbers in the field at Turretfield when accounting for non-trappable juveniles. Sensitivity

312   analysis showed that fluctuations in population size (based on observed differences from a

313   baseline model without control efforts) were most sensitive to changes in survival rates of

314   juveniles and subadults (i.e. the age classes with lowest survival rates): 56 % and 29 % BRT

315   relative importance weights, respectively. Replacing the low survival rates of subadults with

316   those of juveniles in 'disease-free' simulations resulted in population oscillations between ~

317   570–800 individuals (Fig. 3).

318

319   **Efficacy of different Control Scenarios**

320   Only control scenarios that affected all age groups (Age_{Contr} *(all)*) and with control efficacies

321   (Eff_{Contr}) of ≥ 60 % resulted in significant rabbit population reduction or extirpation (Fig. 4).

322 Age specificity had the strongest influence on population extirpation, followed by control

323 efficacy, with BRT relative importance weights of 66 % and 33 %, respectively (Fig. 5). For

324 those populations that experienced extirpation, control efficacy (Eff_{Contr}) had the greatest

325 impact (90 % relative importance) on time to extirpation. Notably, even the highest simulated

326 control efficacies of 95 % led to extirpation in only 88 % of simulations, occurring after an

327 average of 119 ± 23 (i.e., $\pm$ SD) weeks (Fig. 6).

328 Removing both juveniles and subadults in control scenarios (Age_{Contr} *(subad)*) induced

329 considerable reductions in minimum population sizes but did not cause extirpation (Fig. 4).

330 These control scenarios reduced populations most effectively when applied outside the

331 breeding season (end of the year or early in the year with $Seas_{Contr} \in 3, 45$). However, the

332 seasonal timing of control scenarios had less impact on population reductions (6 % relative

333 importance) than control efficacy (93 % relative importance) (Fig. 5).

334 In our 'disease -free' simulations (equal survival rates for juveniles and subadults),

335 rabbit extirpation was also restricted to those control scenarios that affected all age groups

336 (Age_{Contr} *(all)*). However, higher control efficacies (Eff_{Contr}) of ≥ 90 % were needed to cause

337 extirpation. Overall, reductions in rabbit populations followed similar patterns in the two sets

338 of simulations, demonstrating the additive nature of control efforts on top of possible disease

339 effects.

340

341 **DISCUSSION**

342 Deciding on the optimum manner to control invasive and unwanted species is often

343 challenging for pest managers. This is partly because of a lack of empirical and experimental

344 support for alternative control actions (Cacho et al. 2006, Hauser and McCarthy 2009).

345 Management success can be influenced by multiple factors, including control intensity,

346 timing, and method, all of which work in synergy with the demographic dynamics of the

347   targeted species (Abrams 2009). Therefore, a strong understanding of the interplay of

348   demographic processes, environmental stochasticity, and pest control implementation

349   schemes is critical for guiding ongoing and future pest control actions.

350   In Australia, European rabbits have been actively managed for more than a century

351   and, although control measures are highly cost effective when properly applied in agricultural

352   landscapes (Williams et al. 1995), rabbits continue to damage agricultural production and

353   have detrimental effects on native biodiversity (Cooke et al. 2013). Our model simulations

354   revealed that overall control efficacy is the key factor for reducing the abundance of rabbits

355   (at least at local scales), but only if control efforts target the age cohort of rabbits with high

356   reproductive values (adults). Moreover, our simulations indicate that even highly effective

357   control efforts (i.e., removing 95 % of individuals) require repeated control actions over

358   multiple years for local populations to eventually experience extirpation. Why then have field

359   studies demonstrated long-term suppression of Australian rabbit populations by intensive,

360   short-term application of conventional control methods in arid rangelands (Mutze 1991) and

361   high-rainfall agricultural landscapes (McPhee and Butler 2010)? The key to understanding

362   this apparent contradiction may be that our model simulated immediate population reductions

363   without incorporating subsequent changes in vital rates under novel conditions, such as

364   increased exposure to predation and heat stress following warren destruction. This particular

365   case of novel conditions after warren destruction can limit the recovery of suppressed

366   populations without further control actions (Mutze 1991). Our results support the view that

367   poisoning alone can provide only short-term suppression of rabbit populations and previous

368   recommendations that poisoning should be used in conjunction with warren destruction

369   unless warrens are inaccessible or rabbits are living in surface habitats that cannot be

370   removed. We therefore argue that using general insights from simulation models is a useful

371   first step towards informing the planning of on-ground management actions. However,

372   follow-up field trials will always be needed to account for variability in site-based conditions

373   and model uncertainty. This information can be used to further improve model predictions

374   following an adaptive management type approach (Chee and Wintle 2010).

375   To parameterize our simulation study as accurately as possible, we refined a previous

376   mark-recapture analysis (Fordham et al. 2012) by directly accounting for the age of

377   individuals throughout their capture history and by using a state-space approach to

378   incorporate the uncertainty in birth dates and lifetimes of all individuals. This new analysis

379   showed that survival probabilities of subadults are much lower than those of juveniles

380   (captured after emergence from the burrow). We expect that the low relative survival rates of

381   subadults to be due to a disproportionate effect of RHD on subadults; juveniles have lower

382   mortality rates from RHD (Robinson et al. 2002) and most adults are immune due to having

383   survived infection at a younger age (Mutze et al. 2014). The advantage of the state-space

384   approach is that it accounts for missing data on the fates and ages of individuals by using a

385   likelihood approach to account for the probability that individuals survive beyond last capture

386   dates. We were unable to estimate the ages of older rabbits with a high level of confidence

387   due to moderate field-based capture rates. More precise lifetime estimates would require

388   continuously tracking the fate of individuals using more intense capture efforts (which is not

389   feasible, considering that field efforts at our study site are already very high; see Methods) or

390   individual logger devices; such information would better inform the birth-death processes in

391   our mark-recapture analysis (King 2012).

392   Baseline simulations (i.e. no control actions) parameterised firstly with subadult

393   survival equal to the empirically based low survival rate and secondly, a higher survival rate

394   (equal to that of juveniles) to replicate a 'disease-free' population, led to recurrent

395   oscillations, albeit with different population sizes (Fig. 3). Population size in the former

396   scenario was much lower than in the latter scenario. This suggests that RHDV − which

397 causes RHD predominantly in subadults after protection from maternal antibodies has

398 vanished − reduces rabbit populations effectively. This finding is in strong agreement with

399 observations that natural rabbit populations affected by MYXV and RHDV maintain lower

400 densities than before the release of these viruses as biocontrol agents (Bowen and Read 1998,

401 Mutze et al. 1998).

402   We show that any further increases in subadult mortality, through additional control

403 actions (poisoned baiting, warren ripping, etc.) or new biocontrol agents, are likely to lead to

404 considerable reductions in population sizes. Therefore, assessing the feasibility of future

405 potential pest-management actions for controlling species with high fecundity rates, such as

406 rabbits, needs to account for the recruitment process by targeting life stages with the highest

407 reproductive value. Furthermore, we show that, increasing the virulence of established

408 biocontrol agents for rabbits will not necessarily cause a negative long-term effect on the

409 population growth rate if mostly juveniles die from disease. In this situation, high virulence

410 can cause high severity (relatively high number of severe cases), yet have little effect on

411 population growth due to compensatory regulation. This finding is supported by field

412 experiments, which revealed increased survival of rabbits after suppressing reproduction

413 (Williams et al. 2007). Pathogen strains and biocontrol agents (with the same virulence) that

414 cause older rabbits to die are more likely to depress long-term population growth.

415   The results from our simulation modelling also suggest that the dynamics of host-

416 pathogen interactions need to be considered when evaluating the efficacy of novel biocontrol

417 agents. If certain pathogens are only active in certain seasonal time windows, the interaction

418 between timing of pathogen susceptibility and target age cohort can potentially be as

419 important as virulence in determining the long-term effect of biocontrol agents on host

420 populations. Seasonal matching of host demography and virus activity, for instance, can

421   largely impact disease severity from RHDV and other immunizing diseases (Wells et al.

422   2015).

423   We emphasize that our study provides insights that are relevant at a local (but not

424   necessarily regional) scale and for short time periods. Furthermore, our simulations are likely

425   to be sensitive to spatial variation in birth and death rates. Future research should focus on

426   determining whether survival and recruitment rates change following control actions such as

427   warren destruction, the potential recolonization of extirpated patches (Fordham et al. 2013,

428   Ramsey et al. 2014), the economic cost of different management options, and the role of

429   socio-economic factors that may impair the local implementation of control actions (Stenseth

430   et al. 2003).

431

432   **MANAGEMENT IMPLICATIONS**

433   Our simulations provide a theoretical basis to support recommended 'best practice' for rabbit

434   control, which was originally established from field observations of rabbit management

435   operations. We show that 1) control efforts will be optimized if subadult rabbits are targeted

436   after the breeding season (i.e., individuals with the highest reproductive potential); and 2)

437   repeated control efforts must cause 95% mortality of all individuals for more than two

438   consecutive years to result in extirpation. More generally, we show that simulation studies

439   provide a useful platform for understanding how complex interactions between demography,

440   seasonality and pest management schemes are likely to affect rabbit control in Australia.

441

445

446 **LITERATURE CITED**

447 Abrams, P. A. 2009. When does greater mortality increase population size? The long history

448   and diverse mechanisms underlying the hydra effect. Ecology Letters 12:462-474.

449 Bowen, Z., and J. Read. 1998. Population and demographic patterns of rabbits (*Oryctolagus*

450   *cuniculus*) at Roxby Downs in arid South Australia and the influence of rabbit

451   haemorrhagic disease. Wildlife Research 25:655-662.

452 Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation

453   and harvesting. Oikos 87:419-426.

454 Brooks, E. N., and J.-D. Lebreton. 2001. Optimizing removals to control a metapopulation:

455   application to the yellow legged herring gull (*Larus cachinnans*). Ecological

456   Modelling 136:269-284.

457 Brooks, S. P., E. A. Catchpole, and B. J. T. Morgan. 2000. Bayesian animal survival

458   estimation. Statistical Science 15:357-376.

459 Buckland, S. T., K. B. Newman, L. Thomas, and N. B. Koesters. 2004. State-space models

460   for the dynamics of wild animal populations. Ecological Modelling 171:157-175.

461 Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E.

462   Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002.

463   Directing research to reduce the impacts of nonindigenous species. Conservation

464   Biology 16:630-640.

465 Cacho, O. J., D. Spring, P. Pheloung, and S. Hester. 2006. Evaluating the feasibility of

466   eradicating an invasion. Biological Invasions 8:903-917.

467 Chee, Y. E., and B. A. Wintle. 2010. Linking modelling, monitoring and management: an

468   integrated approach to controlling overabundant wildlife. Journal of Applied Ecology

469   47:1169-1178.

470 Cid, B., F. M. Hilker, and E. Liz. 2014. Harvest timing and its population dynamic

471   consequences in a discrete single-species model. Mathematical Biosciences 248:78-

472   87.

473 Cooke, B. 1981. Rabbit Control and the conservation of native Mallee vegetation on

474   roadsides in South Australia. Wildlife Research 8:627-636.

475 Cooke, B., P. Chudleigh, S. Simpson, and G. Saunders. 2013. The economic benefits of the

476   biological control of rabbits in Australia, 1950–2011. Australian Economic History

477   Review 53:91-107.

478 Cooke, B. D. 2014. Australia's war against rabbits. The story of rabbit haemorrhagic disease.

479   CSIRO Publishing, Collingwood, Australia.

480 Cooke, B. D., and F. Fenner. 2002. Rabbit haemorrhagic disease and the biological control of

481   wild rabbits, *Oryctolagus cuniculus*, in Australia and New Zealand. Wildlife Research

482   29:689-706.

483 Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees.

484   Journal of Animal Ecology 77:802-813.

485 Fordham, D. A., H. R. Akçakaya, B. W. Brook, A. Rodriguez, P. C. Alves, E. Civantos, M.

486   Trivino, M. J. Watts, and M. B. Araujo. 2013. Adapted conservation measures are

487   required to save the Iberian lynx in a changing climate. Nature Climate Change 3:899-

488   903.

489 Fordham, D. A., R. G. Sinclair, D. E. Peacock, G. J. Mutze, J. Kovaliski, P. Cassey, L.

490   Capucci, and B. W. Brook. 2012. European rabbit survival and recruitment are linked

491   to epidemiological and environmental conditions in their exotic range. Austral

492   Ecology 37:945-957.

493 Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2005. Bayesian data analysis. 2nd

494   edition. Chapman & Hall/CRC, Boca Raton, FL, USA.

495   Gilbert, N., K. Myers, B. D. Cooke, J. D. Dunsmore, P. J. Fullagar, J. A. Gibb, D. R. King, I.

496   Parer, S. H. Wheeler, and D. H. Wood. 1987. Comparative dynamics of Australasian

497   rabbit populations. Australian Wildlife Research 14:491-503.

498   Gregory, S. D., W. Henderson, E. Smee, and P. Cassey. 2014. Eradications of vertebrate

499   pests in Australia: A review and guidelines for future best practice. Invasive Animals

500   Cooperative Research Centre.

501   Harris, D. B., S. D. Gregory, L. S. Bull, and F. Courchamp. 2012. Island prioritization for

502   invasive rodent eradications with an emphasis on reinvasion risk. Biological Invasions

503   14:1251-1263.

504   Hauser, C. E., and M. A. McCarthy. 2009. Streamlining 'search and destroy': cost-effective

505   surveillance for invasive species management. Ecology Letters 12:683-692.

506   Howald, G., C. J. Donlan, J. P. Galvan, J. C. Russell, J. Parkes, A. Samaniego, Y. Wang, D.

507   Veitch, P. Genovesi, M. Pascal, A. Saunders, and B. Tershy. 2007. Invasive rodent

508   eradication on islands. Conservation Biology 21:1258-1268.

509   Kerr, P. J. 2012. Myxomatosis in Australia and Europe: a model for emerging infectious

510   diseases. Antiviral Research 93:387-415.

511   King, R. 2012. A review of Bayesian state-space modelling of capture-recapture-recovery

512   data. Interface Focus 2:190-204.

513   Kokko, H., and J. Lindström. 1998. Seasonal density dependence, timing of mortality, and

514   sustainable harvesting. Ecological Modelling 110:293-304.

515   Lacy, R. 2000. Structure of the VORTEX simulation model for population viability analysis.

516   Ecological Bulletins 48:191-203.

517   Lacy, R. C., P. S. Miller, P. J. Nyhus, J. P. Pollak, B. E. Raboy, and S. L. Zeigler. 2013.

518   Metamodels for transdisciplinary analysis of wildlife population dynamics. PloS one

519   8:e84211.

520   Lindenmayer, D. B., R. C. Lacy, and M. L. Pope. 2000. Testing a simulation model for

521   population viability analysis. Ecological Applications 10:580-597.

522   Lurgi, M., B. W. Brook, F. Saltré, and D. A. Fordham. 2015. Modelling range dynamics

523   under global change: which framework and why? Methods in Ecology and Evolution

524   6:247-256.

525   McCarthy, M. A., and C. Thompson. 2001. Expected minimum population size as a measure

526   of threat. Animal Conservation 4:351-355.

527   McPhee, S. R., and K. L. Butler. 2010. Long-term impact of coordinated warren ripping

528   programmes on rabbit populations. Wildlife Research 37:68-75.

529   Mutze, G., P. Bird, J. Kovaliski, D. Peacock, S. Jennings, and B. Cooke. 2002. Emerging

530   epidemiological patterns in rabbit haemorrhagic disease, its interaction with

531   myxomatosis, and their effects on rabbit populations in South Australia. Wildlife

532   Research 29:577-590.

533   Mutze, G., B. Cooke, and P. Alexander. 1998. The initial impact of rabbit hemorrhagic

534   disease on European rabbit populations in South Australia. Journal of Wildlife

535   Diseases 34:221-227.

536   Mutze, G. J. 1991. Long-term effects of warren ripping for rabbit control in semi-arid South

537   Australia. The Rangeland Journal 13:96-106.

538   Mutze, G. J., R. G. Sinclair, D. E. Peacock, L. Capucci, and J. Kovaliski. 2014. Is increased

539   juvenile infection the key to recovery of wild rabbit populations from the impact of

540   rabbit haemorrhagic disease? European Journal of Wildlife Research 60:489-499.

541   Mysterud, A., N. G. Yoccoz, and R. Langvatn. 2009. Maturation trends in red deer females

542   over 39 years in harvested populations. Journal of Animal Ecology 78:595-599.

543   Parkes, J. P. 1993. Feral goats: designing solutions for a designer pest. New Zealand Journal

544   of Ecology 17:71-83.

545   Peacock, D. E., and R. G. Sinclair. 2009. Longevity record for a wild European rabbit

546   (*Oryctolagus cuniculus*) from South Australia. Australian Mammalogy 31:65-66.

547   Pradel, R. 2005. Multievent: An extension of multistate capture-recapture models to uncertain

548   states. Biometrics 61:442–447.

549   Prowse, T. A. A., C. N. Johnson, R. C. Lacy, C. J. A. Bradshaw, J. P. Pollak, M. J. Watts, and

550   B. W. Brook. 2013. No need for disease: testing extinction hypotheses for the

551   thylacine using multi-species metamodels. Journal of Animal Ecology 82:355-364.

552   Ramsey, D. S. L., S. R. McPhee, D. M. Forsyth, I. G. Stuart, M. P. Scroggie, M. Lindeman,

553   and J. Matthews. 2014. Recolonisation of rabbit warrens following coordinated

554   ripping programs in Victoria, south-eastern Australia. Wildlife Research 41:46-55.

555   Robinson, A. J., P. T. M. So, W. J. Muller, B. D. Cooke, and L. Capucci. 2002. Statistical

556   models for the effect of age and maternal antibodies on the development of rabbit

557   haemorrhagic disease in Australian wild rabbits. Wildlife Research 29:663-671.

558   Rödel, H. G., A. Bora, J. Kaiser, P. Kaetzke, M. Khaschei, and D. Von Holst. 2004. Density-

559   dependent reproduction in the European rabbit: a consequence of individual response

560   and age-dependent reproductive performance. Oikos 104:529-539.

561   Schofield, M. R., and R. J. Barker. 2011. Full open population capture-recapture models with

562   individual covariates. Journal of Agricultural Biological and Environmental Statistics

563   16:253-268.

564   Simberloff, D. 2003. How much information on population biology is needed to manage

565   introduced species? Conservation Biology 17:83-92.

566   Stein, M. 1981. Large sample properties of simulations using latin hypercube sampling.

567   Technometrics 29:143–151.

568   Stenseth, N., H. Leirs, A. Skonhoft, S. Davis, R. Pech, H. Andreassen, G. Singleton, M.

569   Lima, R. Machang'u, R. Makundi, Z. Zhang, P. Brown, D. Shi, and X. Wan. 2003.

570   Mice, rats, and people: the bio-economics of agricultural rodent pests. Frontiers in

571   Ecology and the Environment 1:367-375.

572   Tablado, Z., E. Revilla, and F. Palomares. 2009. Breeding like rabbits: global patterns of

573   variability and determinants of European wild rabbit reproduction. Ecography 32:310-

574   320.

575   Unnsteinsdottir, E. R., P. Hersteinsson, J. P. Jonasson, and B. J. McAdam. 2014. Using

576   Bayesian growth models to reconstruct small-mammal populations during low-

577   trapping periods. Journal of Zoology 292:206-211.

578   Wells, K., B. W. Brook, R. C. Lacy, G. J. Mutze, D. E. Peacock, R. G. Sinclair, N.

579   Schwensow, P. Cassey, R. B. O'Hara, and D. A. Fordham. 2015. Timing and severity

580   of immunizing diseases in rabbits is controlled by seasonal matching of host and

581   pathogen dynamics. Journal of the Royal Society Interface 12:

582   doi:10.1098/rsif.2014.1184.

583   West, G. B., J. H. Brown, and B. J. Enquist. 2001. A general model for ontogenetic growth.

584   Nature 413:628-631.

585   Williams, C., and R. Moore. 1995. Effectiveness and cost-efficiency of control of the wild

586   rabbit, *Oryctolagus cuniculus* (L.), by combinations of poisoning, ripping, fumigation

587   and maintenance fumigation. Wildlife Research 22:253-269.

588   Williams, C. K., C. C. Davey, R. J. Moore, L. A. Hinds, L. E. Silvers, P. J. Kerr, N. French,

589   G. M. Hood, R. P. Pech, and C. J. Krebs. 2007. Population responses to sterility

590   imposed on female European rabbits. Journal of Applied Ecology 44:291-301.

591   Williams, K., I. Parer, B. Coman, J. Burley, and M. Braysher. 1995. Managing vertebrate

592   pests: rabbits. Bureau of Resource Sciences/ CSIRO Division of Wildlife and

593   Ecology.

594   Xu, C., M. S. Boyce, and D. J. Daley. 2005. Harvesting in seasonal environments. Journal of

595   Mathematical Biology 50:663-682.

596   Zipkin, E. F., C. E. Kraft, E. G. Cooch, and P. J. Sullivan. 2009. When can efforts to control

597   nuisance and invasive species backfire? Ecological Applications 19:1585-1595.

598   Zurell, D., U. Berger, J. S. Cabral, F. Jeltsch, C. N. Meynard, T. Münkemüller, N. Nehrbass,

599   J. Pagel, B. Reineking, B. Schröder, and V. Grimm. 2010. The virtual ecologist

600   approach: simulating data and observers. Oikos 119:622–635.

601   *Associate Editor:*

602

603 **SUPPORTING INFORMATION**

604 Additional supporting information may be found in the online version of this article at the

605 publisher's website.

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608

609 **FIGURE LEGEND**

610 **Figure 1**. Illustration of possible constraints and sensitivities of different rabbit control

611 actions on seasonal population dynamics. Control actions differ in their chance to kill adults

612 (*grey rabbits*) and juveniles/subadults (*blue rabbits*). The broken diagonal lines signify

613 rabbits eliminated from the population through active control. Note that shooting is only

614 included for conceptual illustration, but is not deemed to be a reasonable action for large-

615 scale rabbit control in Australia.

616

617 **Figure 2**. Demographic population structure of rabbits at Turretfield (South Australia) shown

618 as a frequency distribution of posterior modes of estimated longevity in days (*d*) or years (*yr*).

619 Numbers at the right of each bar represent the average posterior range of individual birth date

620 (*BD*) and longevity (*LT*) estimates for each age class using credible intervals. Individuals

621 with uncertainty in *BD* > 100 days have been excluded from the plot i.e., those mainly with

622 age estimates of 7-8 years.

623

624 **Figure 3**. Seasonal population fluctuations of rabbits simulated over 10 years. The left panel

625 (*Disease-burdened*) shows simulated population size at weekly intervals based on apparent

626 survival rates from the capture-mark-recapture analyses (see results). The right panel

627 (*Disease-free*) shows simulations with the apparent survival rate of subadults set to those of

628   juveniles ($\phi_{\text{subadult}} = 0.42$ rather than 0.03 as in the Disease-burdened scenario), all else being

629   equal. Grey lines represent single simulation outputs after a burn-in period of 25 years, the

630   black lines show the mean over 100 samples. Dashed lines represent year intervals.

631

632   **Figure 4**. Expected minimum population size for all scenarios (mean values are shown as

633   symbols and ± SD as error bars). Panels show the effect of control scenarios on minimum

634   population size for different age groups (*Juv* = management of only juveniles; *Juv & Subad* =

635   management of juveniles and subadults; *All* = management of juveniles, subadults and

636   adults). Within panels, scenarios are sorted by control efficacy in increasing order (i.e.,

637   control efficacy = 0.3, 0.6, 0.9, 0.95), separated by dashed lines. Different symbols represent

638   different calendar weeks when control efforts are conducted (■=3, ◇=13, Δ=35, ●=45).

639   Panel *NC* shows minimum population size for all ages under a no control scenario.

640

641   **Figure 5.** Relative importance of parameters in the pest control scenarios on three measures

642   of rabbit population decline (population extirpation, time to extirpation, minimum population

643   size). The parameters are *control age group* (*Age$_{Contr}$*), *control efficacy* (*Eff$_{Contr}$*), *control time*

644   (*t$_{Contr}$*) and *control season* (*Seas$_{Contr}$*). See methods for further details.

645

646   **Figure 6.** Box-Whisker plot of the average time to extirpation in weeks for pest control

647   scenarios with different control efficacy (% mortality on top of natural mortality rates),

648   affecting all age groups. Extirpation did not occur with control efficacies of ≤ 30 %.