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

KONSTANS WELLS, *The Environment Institute and School of Biological Sciences, The University of Adelaide, SA 5005, Australia, and Environmental Futures Research Institute, Griffith University, Brisbane, QLD 4111, Australia*

PHILLIP CASSEY, *The Environment Institute and School of Biological Sciences, The University of Adelaide, SA 5005, Australia*

RON G. SINCLAIR, *Natural Resources Management Biosecurity Unit, Biosecurity SA, Adelaide, Australia*

GREG J. MUTZE, *Natural Resources Management Biosecurity Unit, Biosecurity SA, Adelaide, Australia*

DAVID E. PEACOCK, *Natural Resources Management Biosecurity Unit, Biosecurity SA, Adelaide, Australia*

ROBERT C. LACY, *Chicago Zoological Society, Brookfield, Illinois, United States of America*

BRIAN D. COOKE, *Institute for Applied Ecology, University of Canberra, Canberra, ACT 2601, Australia*

ROBERT B. O'HARA, *Biodiversity and Climate Research Centre (BIK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany*

BARRY W. BROOK, *School of Biological Sciences, University of Tasmania, Hobart, TAS 7001, Australia*

DAMIEN A. FORDHAM, *The Environment Institute and School of Biological Sciences, The University of Adelaide, SA 5005, Australia*

ABSTRACT

The effectiveness of invasive species control can be influenced by seasonal fluctuations in reproduction in response to environmental conditions. However, it is difficult to determine how the efficacy of different control efforts is affected by the intricate interplay of demography and environmental conditions from field trials alone. We incorporated an ontogenetic growth model into a hierarchical Bayesian mark-recapture model to estimate age-structured seasonal survival rates for rabbits in Australia, based on a 20 year data set. We integrated this demographic information into an individual-based simulation model, which reproduces seasonal birth-death processes, to test the effectiveness of pest-management schemes that differ in intensity, specificity to age groups, and seasonal timing. Control measures that were simulated to only affect juveniles had a negligible effect on population size, whereas targeting subadults led to considerable population declines when applied after the breeding season. Management schemes that affected rabbits of all age groups caused significant population reductions. However, even repeated control efforts that cause 95% mortality each year only resulted in predictions of local population extirpation after an average of 119 calendar weeks in the absence of immigration. Our simulation study supports the use of pest rabbit control schemes that account for demographic dynamics explicitly, and target those individuals with high reproductive potential. More broadly, we show that local and temporal population extirpation, or recovery, depends largely on the trade-off between control intensity and frequency for species with recurrent population oscillations.

KEY WORDS Bayesian mark-recapture, density dependence, invasive species control, management implementation schemes, *Oryctolagus*, population viability analysis.

The control of undesirable invasive pest species is often costly and time consuming because it can be extremely difficult to significantly reduce or eradicate entire populations (Byers et al. 2002). Population recovery can negate previous efforts, especially for species with high fecundity rates (Boyce et al. 1999). The majority of successful control efforts that led to eradication of vertebrate pest species are documented from islands (Gregory et al. 2014) and have been linked to small population sizes and limited migration (Howald et al. 2007, Harris et al. 2012). However, there is an urgent need to better understand the biological processes and social perceptions that characterise unsuccessful eradication or population reduction efforts in many mainland populations (Parkes 1993, Bomford and O'Brien 1995).

Optimizing control efforts to minimize populations of pest species can be particularly challenging when the efficacy of management actions varies over space and time and when density-dependent compensatory responses are strong (Kokko and Lindström 1998). For example, actively removing individuals from a population during the breeding season can trigger relative increases in reproduction and/or survival rates of the remaining individuals due to density-dependent compensatory mechanisms (Xu et al. 2005, Mysterud et al. 2009). Selective removal of individuals from different life stages will cause greater reductions in population size if those with the highest reproductive values are removed (Brooks and Lebreton 2001). Likewise seasonally timed control efforts can help to overcome compensatory regulation (Zipkin et al. 2009). Maximizing the efficacy of control efforts requires targeted and well-planned implementation schemes (Simberloff 2003), but financial constraints usually limit the range of pest management actions that can simultaneously be evaluated in field trials. Simulation studies provide a low-cost alternative tool for exploring the potential efficacy of pest management schemes differing in intensity, timing, and frequency of control efforts. In addition, simulation approaches can provide a cost-effective way to evaluate the potential advantage of new control actions that can then be implemented and tested using field trials (Zurell et al. 2010).

In practice, pest managers are often forced to make decisions as to whether to implement control measures over a short time period or to spread their finite resources over a longer period. Quantifying the effects of repeated management actions on population control is particularly important because in practice, control (rather than eradication) efforts are likely to be suspended if population size is perceived to be tolerably low. Therefore, rigorous testing of different management actions with simulations can provide important information on control practices that extend beyond the range of scenarios that are feasible to test in the field. Few simulation studies have investigated directly the importance of the timing of control efforts or other components of pest management schemes (e.g., intensity and frequency of control efforts) on population persistence (Cid et al. 2014).

European rabbits (*Oryctolagus cuniculus*) are a severe economic and environmental pest in many temperate and Mediterranean grassland ecosystems (Tablado et al. 2009, Cooke et al. 2013). After they became widely established in Australia in the late 1800s (Williams et al. 1995), early rabbit control actions were widely compromised by conflicting interests of pest control and the commercialization of rabbit products (Cooke et al. 2013). The large-scale economic benefit of rabbit control was only recognised after the deliberate introduction of myxoma virus (MYXV) in 1950 as a control measure, which causes the disease myxomatosis. The more recent release of rabbit haemorrhagic disease virus (RHDV), which causes rabbit haemorrhagic disease (RHD), in 1995/96 led to further widespread population declines (Cooke and Fenner 2002). Both diseases mainly affect juvenile and subadult rabbits, meaning that high proportions of adults in breeding populations are immuno-protected disease-survivors (Robinson et al. 2002, Kerr 2012). Although both diseases continue to affect most Australian rabbit populations, the high initial impact of each disease has declined over time due to adaptive responses, allowing partial recovery of rabbit numbers (Cooke and Fenner 2002).

In Australia, numerous field trials to manage invasive rabbits have provided practical guidance for ‘best practice’ management actions − the application of poison to reduce population levels, followed by deep ploughing (ripping) of warrens to destroy underground burrow systems, and then fumigation of any re-opened warren entrances to kill rabbits that survive the initial actions (Williams and Moore 1995). This approach is most effective during hot and dry weather conditions in mid-late summer for several reasons: 1) poison is more readily accepted after the breeding season when less natural forage is available, rabbit territorial behaviour diminishes and juveniles are old enough to consume baits, 2) rabbit populations have been reduced by the effects of MYXV and RHDV in spring and early summer, 3) warren destruction with machinery is more effective if soils are dry and friable, and, 4) individuals escaping are exposed to heat stress (Williams et al. 1995). This set of control efforts is capable of reducing local rabbit populations with an efficacy of > 98% (Cooke 1981). Warren destruction is a critical component of the process even when population levels are greatly reduced by the initial poisoning treatment because it reduces the survival prospects and the breeding success of remnant populations (Williams et al. 1995).

While rabbit managers in Australia acknowledge the general importance of seasonal timing, intensity of control efforts, and age group on managing rabbits (Fig. 1), simulation studies that couple seasonal population dynamics with different control implementation schemes, provide opportunities to systematically test and compare different management actions. This is an important prerequisite, not only for optimizing the cost-benefit ratio of existing control techniques, but for evaluating the feasibility of new control efforts such as the release of novel biocontrol agents.

We used a Bayesian hierarchical mark-recapture model (with an integrated ontogenetic body growth model for age classification) to reconstruct details of birth-death processes over a period of > 15 years for a rabbit population in South Australia affected by both RHDV and MYXV (Mutze et al. 2014). Modelling has shown that the seasonal matching of rabbit recruitment and disease-induced mortality largely determines population growth at the site (Wells et al. 2015). We integrated the mark-recapture results into individual-based stochastic simulation models to explore the efficacy of various pest control implementation schemes, which varied in their timing and duration and targeted age-cohorts.

STUDY AREA

In Australia, rabbits typically reproduce in response to rainfall-driven increases in food supply (native and invasive grass and herb species). Rainfall widely varies in time and space across Australia, causing wide-scale spatial variation in the duration of rabbit reproduction and seasonal peaks in recruitment (Gilbert et al. 1987, Mutze et al. 2002).

Rabbits, and their diseases, have been intensively studied at Turretfield (South Australia, 34°33′S, 138°50′E), where the annual amount of rainfall varies between 215 and 700 mm (SD = 96 mm; based on weather station data 1950–2014 from the Australian Bureau of Meteorology). Rabbits at Turretfield have been live-trapped at least every 4–5 consecutive days at 8–12 week intervals since 1996 in an area of ca. 12 hectares (Peacock and Sinclair 2009, Mutze et al. 2014). The Turretfield study represents the largest long-term capture-mark-recapture monitoring of wild free-living rabbits in the world, providing important insights in population and disease dynamics (Cooke 2014).

METHODS

Hierarchical Mark-recapture Model

We analysed mark-recapture data collected at Turretfield between April 1998 and November 2013. Our analysis included 3,736 individuals with a total of 7,340 capture records of marked individuals over 80 capture sessions. For most captures (98 %), body mass measures were available (to the nearest ± 25 grams using spring balances) and 249 individuals were recovered as carcasses, which makes the time of death of these individuals known. We employed a Bayesian hierarchical mark-recapture model, in which we included an ontogenetic (population-level) growth model to infer individual birth dates from body mass measures (Unnsteinsdottir et al. 2014). We assumed that all weight measures – some obtained as sequences from consecutive captures of the same individuals over known time intervals – represent the population-level ontogenetic growth of rabbits at our field site. Therefore, the birth dates of all individuals can be estimated as a random variable based on body mass information during individual capture histories “(Fig. S1, available online at www.onlinelibrary.wiley.com)”.

We modelled body mass according to the generic West-Brown-Enquist model (West et al. 2001). Estimates of individual birth dates based on the ontogenetic growth function allowed us to estimate the most likely age of individuals (with reduced precision for larger/older rabbits) throughout their capture history and their individual fates. Initial analysis did not reveal any effect of sex on ontogenetic growth or survival, and we therefore did not consider sex as a covariate in our analysis. We used this detailed analytical approach to estimate age-structured survival rates and also provide insights into longevity of individuals that cannot be inferred from the raw data alone. For recovered carcasses, we considered individuals to have died at the time between carcass recovery and previous capture session. We did not infer demographic structure from last capture records (Pradel 2005) because it is biased towards younger ages of individuals (Pradel 2005). Estimates of survival rates were used to inform the simulations (see below), while estimates of longevity were used to interpret the output of the statistical model.

Using a Bayesian state-space capture-recapture modelling approach allowed us to account for various sources of uncertainty in model outputs, including incompleteness of observations, which is difficult to account for in classical maximum likelihood approaches (Brooks et al. 2000, Buckland et al. 2004). Incorporating multiple data streams, such as body mass and recovery data into the state-space framework, reduces uncertainty in estimates of individual fate and survival (Schofield and Barker 2011, King 2012). Accordingly, we constrained birth dates to estimates based on body mass measures and informed the (partially unknown) state-variable of individual presence by known times of deaths. For estimating age-structured survival probabilities, we classified the age of each individual in a capture session in five age categories: ≤ 90 days old (juveniles), 91–120 days (subadults), 121–365 days (young adults < 1 year old), 366–1460 days (adults between 1–4 years old; estimated average longevity), 1460–2920 days (adults between 4–8 years old). The juvenile class included only those animals that survived long enough to enter the trappable population (i.e. ~ 21 days old), so the estimated survival rates do not account for mortality of rabbit kittens inside the warrens.

We did not explicitly partition the effects of RHD and myxomatosis on survival rates in this study, but rather, we assumed that these effects are included in the estimated survival rates. We used a posterior predictive model check (Bayesian p-value) to assess model skill. The metric compares the distribution of randomly drawn data generated from joint posterior estimates to the observed data (Gelman et al. 2005). “Details and model code for the Bayesian state-space capture-recapture model are available online at www.onlinelibrary.wiley.com”.

Simulations of Population Dynamics

We parameterised an individual-based population model using the posterior mode estimates of survival rates from our Bayesian model. This model was previously shown to replicate inter- and intra-annual variation in rabbit abundance, using independent field data and approximate Bayesian computation (Wells et al. 2015). We assumed a mortality rate of 50 % of rabbit nestlings during weaning time because the mark-recapture analysis (outlined above) provided relatively low estimates of per capita-birth rates during the main breeding season (Australian winter). We assumed an average ovulation rate of pregnant rabbits in South Australia of 6 (SD = 1) and an average litter size (embryos carried to term) of 6 (SD = 2) based on data of 2,563 examined females at a nearby field site (Belton, Flinders Range) between 1968 and 1993 (Wells et al., in review). We modelled the demographic dynamics of rabbits at weekly time steps. We assumed an annual peak in recruitment (*RepPeak)* in calendar week 39 and the relative distribution of breeding efforts in all other calendar weeks to follow a Gaussian distribution with one SD (*RepVar* = 4) and a total annual reproductive effort (*RepEff*) of 132 % (Wells et al. 2015). A total annual reproductive effort >100% allows some females to reproduce multiple times in a given year. We simulated a single rabbit population with density dependent reproduction (Rödel et al. 2004) and a maximum carrying capacity of ~1,000 individuals. We did not account for immigration and recolonization events, which can be important if neighbouring rabbit populations are only a few kilometres away from each other (Ramsey et al. 2014). This is because, as a first step, our aim was to better establish the relationship between local seasonal population dynamics and different pest control implementation schemes.

We modelled environmental stochasticity in birth and survival rates, since it can considerably impact population dynamics. Models were built using the VORTEX *10* population viability package (http://www.vortex10.org; version 10.0.7.9), which is a freely available tool for building stochastic, individual age- and sex-structured demographic models (Lacy et al. 2013). VORTEX is widely used in invasion biology and pest management (Prowse et al. 2013) and has been used in wildlife population viability analysis for almost 3 decades, with regular updates, and is readily accessible for practitioners (Lacy 2000, Lindenmayer et al. 2000, Lurgi et al. 2015). All demographic events and state transition dynamics are inherently probabilistic. Furthermore, environmental variation can be simulated using probability distributions and catastrophes. “Details of model specification and implementation in the VORTEX software are available online at www.onlinelibrary.wiley.com”.

Pest Control Scenarios

We simulated different pest control implementation schemes (termed ‘scenarios’), which were modelled as additional mortality on top of the weekly survival rates. Pest control implementation schemes were characterized by the combinations of 4 different parameters which we sampled from discrete values based on expert knowledge:

1. *Control season* ($Seas_{Contr}$): Seasonal timing of pest control efforts simulated as 4 possible values of the (first) calendar week of each year, corresponding to, respectively, the middle and end of summer, and the middle and end of the main reproductive period; $Seas_{Contr} \in$ 3, 13, 35, 45 (‘$\in$’ indicates that a parameter value used in the simulations is element of the given number set);

2. *Control time* (t_{Contr}): Allocation of the total annual control effort over consecutive weeks; $t_{Contr} \in$ 1, 3, 5;

3. *Control efficacy* (Eff_{Contr}): Efficacy of control efforts, given as the mortality rates of individuals on top of their natural mortality rates in a population during control efforts;

$Eff_{Contr} \in 0.3, 0.6, 0.9, 0.95$. For model implementation, mortality based on Eff_{Contr} was assumed as the total effect over the duration of t_{Contr};

4. *Control age group* (Age_{Contr}): Classification of the different age groups affected by control efforts with Age_{Contr} *(juv)* individuals < 13 weeks old, Age_{Contr} *(subad)* individuals < 26 weeks old (including juveniles), and Age_{Contr} *(all)* all individuals.

These pest-control regimes resulted in 144 different scenarios (i.e. all combinations of the four parameters listed above), and we ran 100 samples (stochastic replicates) for each scenario. We also ran a baseline model under a no control scenario consisting of 100 samples with no pest control effects ('untreated population'). We initiated all simulations with 800 juvenile rabbits with an equal proportion of male and females (replicating the number of juveniles in relatively large local population) and used a 25-year burn-in period with no pest control efforts to attain a stable age structure (Wells et al. 2015). We then ran each simulation for a total period of 10 years. We deemed a simulation period of 10 years sufficient to investigate the effects of different control schemes, since management efforts are typically constraint to periods of <10 years.

We also included disease-free simulations. To do this we repeated all simulations with the survival rate of subadults set to those of juveniles, and all else being equal. We did this to test whether the low survival rates of subadults, from our statistical analysis (likely due to the detrimental effect of recurrent RHD outbreaks) (Mutze et al. 2014), affects the efficacy of different pest control regimes.

Statistical Analysis

The primary outputs from the simulation model were 10-year time series of weekly population sizes. This was converted to a binary measure of whether a population was extirpated (local population pool is zero after some time of treatment) or not. For all samples in which populations experienced extirpation, we calculated the average time to extirpation. Further, we calculated the minimum population size during the 10 years of treatment for persistent model runs (McCarthy and Thompson 2001).

We used boosted regression tree (BRT) analyses via the *gbm.step()* routine in the R package *dismo* (Elith et al. 2008) to estimate the relative importance of different pest control parameters for explaining variation in population extirpation (binomial error structure, learning rate l = 0.001, tree complexity of tc = 3) time to extirpation (Gaussian error structure, l = 0.001, tc = 3) and minimum population size (Poisson error structure, l = 0.001, tc = 3). We treated the pest control parameters as categorical model variables.

For testing the sensitivity of the baseline model to variation in selected input parameters, we sampled 1,000 different values for mortality rates of the different age classes (samples ranged between ± 10% of apparent survival rates), maximum litter size (sample range between 5 and 8) and overall yearly reproductive effort (sample range between 100 and 200 %) with a Latin hypercube design (Stein 1981). We then tested which parameters were most influential on changes in mean population size and variation in population size (averaged over the 10-year output period) using BRT analyses.

RESULTS

Rabbit Demography

Analysis of the mark-recapture data showed survival rates of rabbits at Turretfield (a population affected by myxomatosis and RHD) were particularly low for subadults (68 % of individuals surviving the 30-day time window of 90–120 days of age, corresponding to a weekly survival rate of 0.92, CI: 0.92–0.95) compared to those of juveniles (83 % of individuals surviving the 21–90 day period after emergence from the warren, corresponding to a weekly survival rate of 0.98, CI: 0.97–0.99) and older individuals. There was considerable variation in survival rates over years for all age classes.

We were able to infer individual birth dates and ages with reasonable confidence. The credible intervals (95%) of estimated birth dates were < 100 days for 64% of individuals (2,406 out of 3,736). However, estimates of longevity were less precise, with only 463 out of 3,736 estimates (12 %) having credible intervals ≤ 100 days uncertainty. Because of this uncertainty, longevity was deemed to be unrealistically high, at 7–8 years for 31 % of individuals. The overall demographic structure of the rabbit population was characterised by as much as 60 % of recorded individuals dying before one year of age (Fig. 2). Capture probabilities varied over seasons and time periods between 0.07 (CI: 0.07–0.08) and 0.37 (CI: 0.35–0.38) being highest in spring (Sept–Nov) and increasing towards the end of the study period.

The simulation model predicted population size fluctuations (without control actions) to oscillate between ~ 350 and 650 individuals (Fig. 3), which corresponds to the observed numbers in the field at Turretfield when accounting for non-trappable juveniles. Sensitivity analysis showed that fluctuations in population size (based on observed differences from a baseline model without control efforts) were most sensitive to changes in survival rates of juveniles and subadults (i.e. the age classes with lowest survival rates): 56 % and 29 % BRT relative importance weights, respectively. Replacing the low survival rates of subadults with those of juveniles in ‘disease-free’ simulations resulted in population oscillations between ~ 570–800 individuals (Fig. 3).

Efficacy of different Control Scenarios

Only control scenarios that affected all age groups (Age_{Contr} *(all)*) and with control efficacies (Eff_{Contr}) of ≥ 60 % resulted in significant rabbit population reduction or extirpation (Fig. 4).

Age specificity had the strongest influence on population extirpation, followed by control efficacy, with BRT relative importance weights of 66 % and 33 %, respectively (Fig. 5). For those populations that experienced extirpation, control efficacy (Eff_{Contr}) had the greatest impact (90 % relative importance) on time to extirpation. Notably, even the highest simulated control efficacies of 95 % led to extirpation in only 88 % of simulations, occurring after an average of 119 ± 23 (i.e., ± SD) weeks (Fig. 6).

Removing both juveniles and subadults in control scenarios (Age_{Contr} *(subad)*) induced considerable reductions in minimum population sizes but did not cause extirpation (Fig. 4). These control scenarios reduced populations most effectively when applied outside the breeding season (end of the year or early in the year with $Seas_{Contr} \in 3, 45$). However, the seasonal timing of control scenarios had less impact on population reductions (6 % relative importance) than control efficacy (93 % relative importance) (Fig. 5).

In our ‘disease -free’ simulations (equal survival rates for juveniles and subadults), rabbit extirpation was also restricted to those control scenarios that affected all age groups (Age_{Contr} *(all)*). However, higher control efficacies (Eff_{Contr}) of ≥ 90 % were needed to cause extirpation. Overall, reductions in rabbit populations followed similar patterns in the two sets of simulations, demonstrating the additive nature of control efforts on top of possible disease effects.

DISCUSSION

Deciding on the optimum manner to control invasive and unwanted species is often challenging for pest managers. This is partly because of a lack of empirical and experimental support for alternative control actions (Cacho et al. 2006, Hauser and McCarthy 2009). Management success can be influenced by multiple factors, including control intensity, timing, and method, all of which work in synergy with the demographic dynamics of the targeted species (Abrams 2009). Therefore, a strong understanding of the interplay of demographic processes, environmental stochasticity, and pest control implementation schemes is critical for guiding ongoing and future pest control actions.

In Australia, European rabbits have been actively managed for more than a century and, although control measures are highly cost effective when properly applied in agricultural landscapes (Williams et al. 1995), rabbits continue to damage agricultural production and have detrimental effects on native biodiversity (Cooke et al. 2013). Our model simulations revealed that overall control efficacy is the key factor for reducing the abundance of rabbits (at least at local scales), but only if control efforts target the age cohort of rabbits with high reproductive values (adults). Moreover, our simulations indicate that even highly effective control efforts (i.e., removing 95 % of individuals) require repeated control actions over multiple years for local populations to eventually experience extirpation. Why then have field studies demonstrated long-term suppression of Australian rabbit populations by intensive, short-term application of conventional control methods in arid rangelands (Mutze 1991) and high-rainfall agricultural landscapes (McPhee and Butler 2010)? The key to understanding this apparent contradiction may be that our model simulated immediate population reductions without incorporating subsequent changes in vital rates under novel conditions, such as increased exposure to predation and heat stress following warren destruction. This particular case of novel conditions after warren destruction can limit the recovery of suppressed populations without further control actions (Mutze 1991). Our results support the view that poisoning alone can provide only short-term suppression of rabbit populations and previous recommendations that poisoning should be used in conjunction with warren destruction unless warrens are inaccessible or rabbits are living in surface habitats that cannot be removed. We therefore argue that using general insights from simulation models is a useful first step towards informing the planning of on-ground management actions. However, follow-up field trials will always be needed to account for variability in site-based conditions and model uncertainty. This information can be used to further improve model predictions following an adaptive management type approach (Chee and Wintle 2010).

To parameterize our simulation study as accurately as possible, we refined a previous mark-recapture analysis (Fordham et al. 2012) by directly accounting for the age of individuals throughout their capture history and by using a state-space approach to incorporate the uncertainty in birth dates and lifetimes of all individuals. This new analysis showed that survival probabilities of subadults are much lower than those of juveniles (captured after emergence from the burrow). We expect that the low relative survival rates of subadults to be due to a disproportionate effect of RHD on subadults; juveniles have lower mortality rates from RHD (Robinson et al. 2002) and most adults are immune due to having survived infection at a younger age (Mutze et al. 2014). The advantage of the state-space approach is that it accounts for missing data on the fates and ages of individuals by using a likelihood approach to account for the probability that individuals survive beyond last capture dates. We were unable to estimate the ages of older rabbits with a high level of confidence due to moderate field-based capture rates. More precise lifetime estimates would require continuously tracking the fate of individuals using more intense capture efforts (which is not feasible, considering that field efforts at our study site are already very high; see Methods) or individual logger devices; such information would better inform the birth-death processes in our mark-recapture analysis (King 2012).

Baseline simulations (i.e. no control actions) parameterised firstly with subadult survival equal to the empirically based low survival rate and secondly, a higher survival rate (equal to that of juveniles) to replicate a ‘disease-free’ population, led to recurrent oscillations, albeit with different population sizes (Fig. 3). Population size in the former scenario was much lower than in the latter scenario. This suggests that RHDV − which causes RHD predominantly in subadults after protection from maternal antibodies has vanished − reduces rabbit populations effectively. This finding is in strong agreement with observations that natural rabbit populations affected by MYXV and RHDV maintain lower densities than before the release of these viruses as biocontrol agents (Bowen and Read 1998, Mutze et al. 1998).

We show that any further increases in subadult mortality, through additional control actions (poisoned baiting, warren ripping, etc.) or new biocontrol agents, are likely to lead to considerable reductions in population sizes. Therefore, assessing the feasibility of future potential pest-management actions for controlling species with high fecundity rates, such as rabbits, needs to account for the recruitment process by targeting life stages with the highest reproductive value. Furthermore, we show that, increasing the virulence of established biocontrol agents for rabbits will not necessarily cause a negative long-term effect on the population growth rate if mostly juveniles die from disease. In this situation, high virulence can cause high severity (relatively high number of severe cases), yet have little effect on population growth due to compensatory regulation. This finding is supported by field experiments, which revealed increased survival of rabbits after suppressing reproduction (Williams et al. 2007). Pathogen strains and biocontrol agents (with the same virulence) that cause older rabbits to die are more likely to depress long-term population growth.

The results from our simulation modelling also suggest that the dynamics of host-pathogen interactions need to be considered when evaluating the efficacy of novel biocontrol agents. If certain pathogens are only active in certain seasonal time windows, the interaction between timing of pathogen susceptibility and target age cohort can potentially be as important as virulence in determining the long-term effect of biocontrol agents on host populations. Seasonal matching of host demography and virus activity, for instance, can largely impact disease severity from RHDV and other immunizing diseases (Wells et al. 2015).

We emphasize that our study provides insights that are relevant at a local (but not necessarily regional) scale and for short time periods. Furthermore, our simulations are likely to be sensitive to spatial variation in birth and death rates. Future research should focus on determining whether survival and recruitment rates change following control actions such as warren destruction, the potential recolonization of extirpated patches (Fordham et al. 2013, Ramsey et al. 2014), the economic cost of different management options, and the role of socio-economic factors that may impair the local implementation of control actions (Stenseth et al. 2003).

MANAGEMENT IMPLICATIONS

Our simulations provide a theoretical basis to support recommended ‘best practice’ for rabbit control, which was originally established from field observations of rabbit management operations. We show that 1) control efforts will be optimized if subadult rabbits are targeted after the breeding season (i.e., individuals with the highest reproductive potential); and 2) repeated control efforts must cause 95% mortality of all individuals for more than two consecutive years to result in extirpation. More generally, we show that simulation studies provide a useful platform for understanding how complex interactions between demography, seasonality and pest management schemes are likely to affect rabbit control in Australia.

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Associate Editor:

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s website.

FIGURE LEGEND

Figure 1. Illustration of possible constraints and sensitivities of different rabbit control actions on seasonal population dynamics. Control actions differ in their chance to kill adults (*grey rabbits*) and juveniles/subadults (*blue rabbits*). The broken diagonal lines signify rabbits eliminated from the population through active control. Note that shooting is only included for conceptual illustration, but is not deemed to be a reasonable action for large-scale rabbit control in Australia.

Figure 2. Demographic population structure of rabbits at Turretfield (South Australia) shown as a frequency distribution of posterior modes of estimated longevity in days (*d*) or years (*yr*). Numbers at the right of each bar represent the average posterior range of individual birth date (*BD*) and longevity (*LT*) estimates for each age class using credible intervals. Individuals with uncertainty in *BD* > 100 days have been excluded from the plot i.e., those mainly with age estimates of 7-8 years.

Figure 3. Seasonal population fluctuations of rabbits simulated over 10 years. The left panel (*Disease-burdened*) shows simulated population size at weekly intervals based on apparent survival rates from the capture-mark-recapture analyses (see results). The right panel (*Disease-free*) shows simulations with the apparent survival rate of subadults set to those of

juveniles (ϕ_{subadult} = 0.42 rather than 0.03 as in the Disease-burdened scenario), all else being equal. Grey lines represent single simulation outputs after a burn-in period of 25 years, the black lines show the mean over 100 samples. Dashed lines represent year intervals.

Figure 4. Expected minimum population size for all scenarios (mean values are shown as symbols and ± SD as error bars). Panels show the effect of control scenarios on minimum population size for different age groups (*Juv* = management of only juveniles; *Juv & Subad* = management of juveniles and subadults; *All* = management of juveniles, subadults and adults). Within panels, scenarios are sorted by control efficacy in increasing order (i.e., control efficacy = 0.3, 0.6, 0.9, 0.95), separated by dashed lines. Different symbols represent different calendar weeks when control efforts are conducted (■=3, ◇=13, Δ=35, ●=45). Panel *NC* shows minimum population size for all ages under a no control scenario.

Figure 5. Relative importance of parameters in the pest control scenarios on three measures of rabbit population decline (population extirpation, time to extirpation, minimum population size). The parameters are *control age group* (Age_{Contr}), *control efficacy* (Eff_{Contr}), *control time* (t_{Contr}) and *control season* ($Seas_{Contr}$). See methods for further details.

Figure 6. Box-Whisker plot of the average time to extirpation in weeks for pest control scenarios with different control efficacy (% mortality on top of natural mortality rates), affecting all age groups. Extirpation did not occur with control efficacies of ≤ 30 %.