

Inferential and forward projection modeling to evaluate options for controlling invasive mammals on islands

D. P. ANDERSON,^{1,6} P. MCMURTRIE,² K.-A. EDGE,^{2,3} P. W. J. BAXTER,^{4,5} AND A. E. BYROM¹

¹*Landcare Research, P.O. Box 69040, Lincoln 7640 New Zealand*

²*New Zealand Department of Conservation, P.O. Box 29, Te Anau 9640 New Zealand*

³*Edge-Effect, 48 Bligh Street, Te Anau 9600 New Zealand*

⁴*Centre for Applications in Natural Resource Mathematics, School of Mathematics and Physics, The University of Queensland, St. Lucia, Queensland 4072 Australia*

⁵*Earth, Environmental and Biological Sciences School, Queensland University of Technology, Brisbane, Queensland 4000 Australia*

Abstract. Successful pest-mammal eradications from remote islands have resulted in important biodiversity benefits. Near-shore islands can also serve as refuges for native biota but require ongoing effort to maintain low-pest or pest-free status. Three management options are available in the presence of reinvasion risk: (1) control-to-zero density, in which immigration may occur but reinvasers are removed; (2) sustained population suppression (to relatively low numbers); or (3) no action. Biodiversity benefits can result from options one and two. The management challenge is to make evidence-based decisions on the selection of an appropriate objective and to identify a financially feasible control strategy that has a high probability of success. This requires understanding the pest species population dynamics and how it will respond to a range of potential management strategies, each with an associated financial cost. We developed a two-stage modeling approach that consisted of (1) Bayesian inferential modeling to estimate parameters for a model of pest population dynamics and control, and (2) a forward projection model to simulate a range of plausible management scenarios and quantify the probability of obtaining zero density within four years. We applied the model to an ongoing, six-year trapping program to control stoats (*Mustela erminea*) on Resolution Island, New Zealand. Zero density has not yet been achieved. Results demonstrate that management objectives were impeded by a combination of a highly fecund population, insufficient trap attractiveness, and a substantial proportion of the population that did not enter traps. Immigration is known to occur because the founding population arrived on the island by swimming from the mainland. However, immigration rate during this study was indistinguishable from zero. The forward projection modeling showed that control-to-zero density was feasible but required greater than a two-fold budget increase to intensify the trapping rate relative to population growth. The two-stage modeling provides the foundation for a management program in which broad-scale trials of additional trapping effort or improved trap lures would test model predictions and increase our understanding of system dynamics.

Key words: *Bayesian modeling; control-to-zero density; eradication; forward projection; invasive predator; Mustela erminea; population dynamics; Resolution Island, New Zealand; simulation; stoat.*

INTRODUCTION

Biotic invasions are a serious threat to native biodiversity and ecosystem function (Vitousek et al. 1997, Mack et al. 2000), and invasive predators on islands have resulted in the extinction of many endemic species (King 1985, Savidge 1987). Numerous successful eradications from remote islands (Towns and Broome 2003, Keitt et al. 2011) have provided critical refuges for native biota (Donlan et al. 2003, Keitt and Tershy 2003, Russell et al. 2009a). Near-shore islands have been avoided as potential refuges for native species because of the effort required to maintain their pest-free status (Russell et al. 2009b, Edge et al. 2011). When eradication is not feasible due to high reinvasion risk, three management options remain: (1) control-to-zero density, in

which immigration may occur but reinvasers are subsequently removed; (2) sustained population suppression (to relatively low numbers); or (3) no action. Options one and two have strong potential benefits for native biota (Sinclair et al. 1998, Baxter et al. 2008). The emerging management challenge is to use scientific evidence to inform selection of the appropriate objective and to identify an optimal control strategy. This requires an understanding of and ability to predict how complex invasive-population dynamics will respond to a range of potential management strategies. To provide the means to make evidenced-based decisions for near-shore-management programs, we developed a two-stage modeling approach that consisted of (1) inferential modeling to parameterize an invasive-dynamics and control model, and (2) a forward projection model to simulate management scenarios that allowed for contrasting the predicted probabilities of management success with the associated financial costs.

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⁶E-mail: andersond@landcareresearch.co.nz

To help conservation managers make evidence-based decisions and choose among various strategic options for invasive species management, three fundamental management questions need to be addressed: Where, when, and how to apply control most cost efficiently to obtain the stated objective (i.e., eradication, control-to-zero density, or suppression)? Answers to these questions can be, and often are, provided by a conceptual model formulated by managers that is supported by anecdotal evidence (Sutherland et al. 2004) or ecological theory (Doak and Mills 1994). Anecdotes may lack the information necessary to objectively assess complex relationships (Sutherland et al. 2004, Clark and Gelfand 2006), and while theory incorporates biological complexity, it rarely has the flexibility to integrate system-specific details that are necessary to provide realistic predictions (Driscoll and Lindenmayer 2012).

The movement toward evidence-based environmental management is an ongoing challenge for natural resource managers and applied ecologists (Segan et al. 2011). Ecological science can effectively contribute to invasive-species management by assessing the influence of multiple interacting biological processes (Clark and Gelfand 2006) on the response that is of immediate interest to managers: invasive population size over time as a function of control efforts (Hone 2007:8–9). Processes involved in the management of invasive predators on islands include population growth rate, immigration rate, probability of capturing an animal conditional on it being present, movement behavior, species interactions, and habitat preferences. Management decisions that focus on a single process may be ineffective because system dynamics are the result of a complex web of interacting processes (Kareiva 1990, Hastings 1993, Turchin 2003) that need to be managed in a whole-of-system context (Zavaleta et al. 2001). For example, efforts to stop immigration are critical, but if females are avoiding capture, the population growth rate will likely outpace the capture rate, resulting in a low probability of controlling the population to the desired level.

Our two-stage analytical process explicitly addressed the inherent system complexity of a program to eradicate invasive stoats (*Mustela erminea*) from Resolution Island, New Zealand, (20,800 ha and 520 m from the New Zealand mainland) by the Department of Conservation. Invasive mustelids are a major predator of endemics worldwide (Bonesi and Palazon 2007, King et al. 2009). Since 2008 a trap network has been deployed in which traps were set and checked three times per year. The population has been greatly reduced, but stoats persist on the island after 6 yr and 24 trapping sessions. The continued presence of stoats could be influenced by a proportion of the population that is very unlikely to enter a trap (Alterio et al. 1999, King et al. 2003, King and Powell 2007). In addition, new immigrants may arrive periodically. The present stoat population was established by natural immigration, and genetic evidence indicates a low rate of immigration from the mainland to the similarly situated Secretary Island, New Zealand (Veale et al. 2013). The narrow channel to the mainland is within stoats'

swimming capabilities (Taylor and Tilley 1984, Elliott et al. 2010, King et al. 2014). Given the high potential for reinvasion, eradication is not likely to be a realistic objective. Consequently, the key management questions are: Is control-to-zero density still feasible? And what is the best cost-efficient control strategy to meet the control-to-zero density objective?

Although successful control-to-zero density would require surveillance and control in perpetuity, it has potential to result in thriving populations of reintroduced native bird species that can tolerate low levels of predation (e.g., Kokako, *Callaeas cinereus*, Innes et al. 1999; and Saddleback, *Philesturnus carunculatus*, Hooson and Jamieson 2003, Prada et al. 2014), and may also buy time until novel control methods are developed and become available. The long-term management objective is to achieve thriving populations of native bird species, and this justifies the current trapping operations. However, the ultimate success of this objective depends on the reduction or removal of stoats from Resolution Island. Our modeling is focused solely on understanding and forecasting the effect of trapping on the stoat population and does not address the potential flow-on effects on native species.

In the first stage, we used Markov chain Monte Carlo and Bayesian logic to make inference on multiple population processes (Clark and Gelfand 2006). Specifically, we asked the following questions: (1) What was the population size at the beginning of each trapping period? (2) What was the population growth rate? (3) What was the immigration rate? (4) What was the spatially explicit probability of capture as estimated from a home-range-size parameter and a trap-capture parameter (sensu Efford 2004)? (5) What was the mean proportion of stoats vulnerable to trapping? (6) And what landscape features influenced stoat habitat selection?

In the second stage, we used forward-projection modeling to simulate different management scenarios with associated management costs to explore system dynamics (Clark 2001). We used the same biological processes and parameter distributions estimated in the explanatory Bayesian model to simulate different hypothetical (but realistic) management scenarios from July 2015 to the end of 2019. Simulation modeling allows additional inference on the system dynamics, and identification of knowledge gaps and potential future experiments to fill those gaps. We used the simulations to address two questions: (1) What was the probability of removing all stoats during the simulated period (i.e., achieving zero density before the end of 2019)? (2) And what was the estimated financial cost in present terms of the management scenarios over the simulated period?

METHODS

Study area

Resolution Island in Fiordland, New Zealand, (45°41.4' S, 166°41.5' E) is 20,800 ha and 520 m from

the New Zealand mainland and reaches 1,069 m in elevation (Fig. 1). Vegetation includes a mix of southern beech (*Lophozonia menziesii* and *Fuscospora cliffortioides*) and podocarp-broadleaf forest dominated by kamahi (*Weinmannia racemosa*) and rimu (*Dacrydium cupressinum*), manuka (*Leptospermum scoparium*) shrublands, tussock grasslands dominated by *Chionochloa acicularis*, and small areas of wetland, coastal scrub and fellfield vegetation. The island is extremely remote and subject to inclement weather events. The climate is cool temperate, with mean annual temperature of $\sim 10^{\circ}\text{C}$ and annual rainfall of $\sim 4,000$ mm spread evenly throughout the year (Baylis et al. 1963). The only introduced mammals on the island are stoats, invasive house mice (*Mus musculus*), and red deer (*Cervus elaphus*).

Trapping data

A network of tracks was created to cover the island, and on each track kill-traps (DOC150; CMI Springs Limited, Auckland, New Zealand) baited with eggs and rabbit meat were spaced at $\sim 100\text{-m}$ intervals (Appendix S1: Fig. S1). The aim was to have no point on the island more than 700 m from a trap, on the assumption that the home range of all stoats present on the island were large enough (King and Murphy 2005) to encounter at least one trap with fresh bait over a maximal period of 14 d. An initial knockdown phase was conducted in which three trap checks occurred over a 20-d period in the austral winter (July–August) of 2008. Subsequently, traps have been checked and re-set every austral summer, spring, and winter (January, November, and July). A total of 2,352 traps were set in each of the 24 sessions up to January 2015. This produced binary capture–no-capture data for each trap, which had associated easting and northing data.

GIS data

We used ArcGIS (ESRI 2008) to assemble a series of rasters with 500-m resolution that characterized the spatial variability of the island landscape and served as covariates in the habitat-selection modeling (see *Methods: Stage 1 modeling*). A 30-m resolution digital-elevation model (DEM) was used to derive the following topographical attributes at a 500-m pixel resolution: elevation, aspect, and slope position. Slope and aspect were derived by rescaling the original DEM to the 500-m resolution and assigning the mean value. Aspect was quantified as a deviation from north and ranged from 0 to π . Slope-position index was a relative measure of the height of the centroid of the 500-m pixel relative to the neighboring 30-m pixels in a 9×9 neighborhood. The index varied from 1 if it was on a summit or ridge (higher than all neighboring pixels) to 0 if it was the lowest in the neighborhood, such as in a valley. Eastings and northings (meters) were also used as

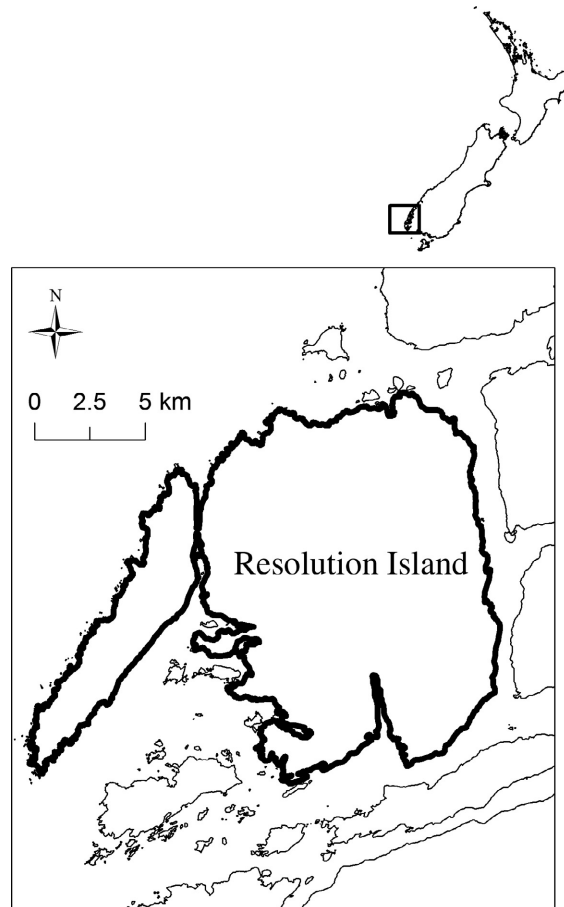


FIG. 1. The map shows the location of Resolution Island (20,800 ha) off the southwest coast of the South Island, New Zealand.

covariates. Percentage cover of vegetation types (e.g., beech, podocarp, coastal, or subalpine) varied little at the 500-m resolution and was not used as a covariate.

Stage 1 modeling: parameter estimation

Conceptual data-generating process.—We used the spatiotemporal trapping data to estimate probabilistically the number of stoats on the island at the onset of each trapping session. The fundamental modeling unit was each individual in the population. For each stoat, we estimated its location as a function of topographic features that influenced habitat preference. In contrast to a binary capture model, we developed a three-state capture model in which each stoat was categorized as being vulnerable and captured, vulnerable but not captured, or not vulnerable. If a stoat was captured, the corresponding trap was identified. After stoats were removed by trapping, the remaining population was allowed to grow to a new population size as a function of population growth and immigration until the traps were reset, at which time the process was repeated.

We made three necessary assumptions in the parameter-estimation stage that were then applied in the simulation modeling. First, each trapping session began with a clean slate of individuals so that stoat identities and locations were independent across trapping sessions. This was necessary because we were not modeling survivorship or mortality of individuals other than by trapping. Second, we assumed an equal sex ratio because it was not possible to determine the sex of trapped animals due to body decomposition. Third, the probabilities of capture and vulnerability were calculated equivalently for males and females.

Quantitative modeling approach.—Following the conceptual data-generating process described previously, we developed a spatially explicit hierarchical model (Fig. 2) and used Markov-chain Monte Carlo to estimate and make inference on the biological and trapping parameters. The observed number of stoats captured at time t (Z_t) depended on the number of stoats present on the island (N_t) and the number available to be trapped. We differentiated the number available from N_t because stoats vary in trapability over time and some stoats can be uncapturable (Alterio et al. 1999, King et al. 2003, King and Powell 2007), at least temporarily. To account for this heterogeneity, we employed a three-state capture model in which each stoat i was either vulnerable and captured (vc), vulnerable and not captured (vmc), or not vulnerable (nv). The probability stoat i at time t being in each of the capture states (s_{it}) was as follows:

$$\Pr(s_{it} = vc) = P_{it} v_t, \tag{1}$$

$$\Pr(s_{it} = vmc) = (1 - P_{it}) v_t, \tag{2}$$

$$\Pr(s_{it} = nv) = (1 - v_t), \tag{3}$$

where P_{it} was the spatially explicit probability of capture, and v_t was the seasonal probability of a stoat being vulnerable to trapping. The capture-state probabilities (Eqs. 1–3) all sum to one. Three v_t parameters were estimated, one for each season (January, July, and November), and followed a high-variance Jeffrey’s prior, Beta(0.5, 0.5). *A priori*, we expected the November and January estimates for v_t to be higher than in July because of the high prevalence of naïve juvenile recruits following birthing in October (King and Powell 2007). The trapping operation began in July 2008, but we expected a high prevalence of vulnerable animals in the initial untrapped population. Consequently, for the purposes of estimating the v_t parameter, we considered the first three sessions to have the January v_t value. The fourth session was in August 2008, and it was assigned the July v_t parameter.

The probability that stoat i was captured at time t (P_{it}) by any one of J available traps was calculated as

$$P_{it} = 1 - \prod_{j=1}^J \left(1 - g_0 \exp\left(-\frac{Dist_{ij}^2}{2\sigma^2}\right) \right)^{TrapNights_{jt}}, \tag{4}$$

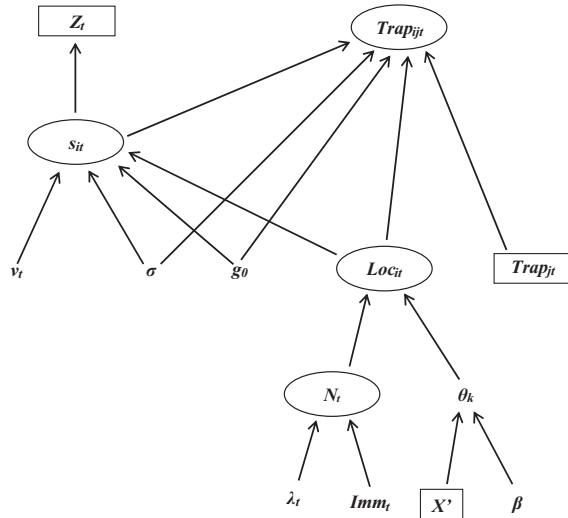


FIG. 2. Directed acyclic graph of the hierarchical model. The spatiotemporal trapping data are summarized in Z_t (number of stoats capture at time t), latent variables are found in ovals, and estimated parameters are not enclosed. Prior distributions were used for all parameters but are not shown here. Abbreviations are s_{it} , capture state of stoat i at time t ; v_t , probability of individual being vulnerable; σ , spatial-decay parameter for a half-normal home-range kernel; g_0 , nightly probability of capture when trap is placed at home range center; $Trap_{ijt}$, latent variable of trap j capturing stoat i at time t ; $Trap_{jt}$, data for trap j at time t ; Loc_{it} , latent location of stoat i at time t ; N_t , population size at time t ; θ_k , multinomial habitat attraction probability for grid-cell k ; λ_t , finite per-capita population growth rate for time t ; Imm_t , immigration rate at time t ; X' , environmental covariates; β , covariate parameters.

where g_0 was a parameter that represents the probability of capturing a stoat in a single night in a trap that was placed at the animal’s home-range center, σ (meters) was the spatial-decay parameter for a half-normal home-range kernel (Efford 2004), $Dist_{ij}$ was the distance between the location of stoat i (Loc_i) and trap j , and $TrapNights_{jt}$ was the number of nights that trap j was available. While traps were potentially available to capture stoats for the entire period between setting and re-checking (up to 185 nights), we set a maximum of 14 trap nights. This is supported by the observation that the vast majority of captured stoats were found to be highly decomposed at the time of rechecking, indicating that they were most likely captured soon after traps were rebaited with fresh material at the previous check. When a trap was sprung but empty or the bait was gone, we halved the number of trap nights (Nelson and Clark 1973, Beauvais and Buskirk 1999). All capture events were assumed to occur on the seventh night, and the available trap nights for these traps was set to seven nights.

The prior distribution for g_0 was also a high-variance Jeffrey’s prior, Beta(0.5, 0.5). We used a normal distribution for σ with mean 255 m and standard deviation 60 (Efford et al. 2009). These were population-level parameters and the posterior distributions were insensitive to the priors.

Traps that captured stoats in a given session were known, but the trap j that captured stoat i at time t was

unobserved and estimated as a latent variable ($Trap_{ijt}$; Fig. 2). To account for stoat–trap competition (Efford 2004), we modeled $Trap_{ijt}$ sequentially for each stoat i with a multinomial process:

$$Trap_{ijt} \sim \text{multinomial}(1, P_{i,(j \in A),t}), \quad (5)$$

where $P_{i,(j \in A),t}$ is an array of probabilities of trapping stoat i for all j traps in the set of available traps A_t (e.g., traps not yet sprung). The $P_{i,(j \in A),t}$ were multinomial probabilities and all summed to 1. The pairwise stoat–trap probabilities (P_{ijt}) were calculated as

$$P_{ijt} = 1 - \left(1 - g_0 \exp\left(-\frac{Dist_{ij}^2}{2\sigma^2}\right) \right)^{TrapNights_{jt}} \quad (6)$$

The quantity $Dist_{ij}$ (Eqs. 4 and 6) was calculated using modeled home-range centers of stoats present on the island (Loc_{it} ; Fig. 2). The latent variable Loc_{it} represented the centroid of one of the 840 raster grid cells with 500-m resolution superimposed on the island (see *Methods: GIS data*). We used the habitat-covariate rasters to generate a habitat-preference model, which then predicted the location of each stoat (Loc_{it}). The locations of all stoats at time t ($Loc_{all,t}$) were distributed as a multinomial,

$$Loc_{all,t} \sim \text{multinomial}(N_t, \theta_k), \quad (7)$$

$$\theta_k = \frac{Habitat_k}{\sum_{k=1}^K Habitat_k}, \quad (8)$$

$$Habitat_k = \mathbf{X}' \beta, \quad (9)$$

where θ_k was a multinomial probability for grid-cell k , and all θ_k summed to one. $Habitat_k$ was a linear prediction from environmental covariates obtained from GIS data (\mathbf{X}'), and β was an array of associated covariate parameters. An intercept parameter was not included in Eq. 9 because the consequent multinomial probability (θ_k) was a relative probability across all grid cells. The β parameters had normal prior distributions with mean 0 and variance 1,000.

The probability of the observed number of captures was modelled as

$$\Pr(Z_t | N_t, \mathbf{s}) = \left(\frac{N_t!}{N_{vnc}! + N_{nv}!} \right) \prod_{i=1}^{N_t} (\Pr(s_{it})), \quad (10)$$

where N_{vnc} was the number of stoats vulnerable but not captured and N_{nv} the number not vulnerable. The number of stoats vulnerable and captured (N_{vc}) was fixed and therefore not included in the combinatorial term (Eq. 10).

The number of stoats present was distributed as Poisson with a mean predicted from population growth (λ_t) and immigration (Imm_t) parameters,

$$N_t \sim \text{Poisson}(nPredicted_t), \quad (11)$$

$$nPredicted_t = (N_{t-1}^* + Imm_t) \times \lambda_t, \quad (12)$$

$$N_{t-1}^* = N_{t-1} - Z_{t-1}, \quad (13)$$

where λ_t was the finite per-capita population growth rate for the reproductive season (between July and November sessions), and Imm_t was the immigration rate for session t . Density dependence was not modeled because we assumed the controlled population to be well below carrying capacity, and given the presence of mice, competition of a low density population was expected to be minimal (Veale et al. 2015).

Female stoats generally have between eight and 10 kits per reproductive season (McDonald and Harris 2002, King and Murphy 2005). Stoat litters are born early in the austral spring (October; King and Murphy 2005), and juveniles were only available for capture after traps were reset in November. Therefore, the λ_t parameter was set to one (i.e., no population growth) for the intertrapping periods November–January (spring–summer) and January–July (summer–winter). Trapping was assumed to be the primary cause of mortality. Natural mortality was not modeled as it was assumed to be low in comparison due to low intraspecific competition at low population density (Byrom 2002). Population dynamics were rendered stochastic with the Poisson process error (Eq. 11). The λ_t for November followed a high-variance gamma prior distribution (shape = rate = 0.001) and was insensitive to weakly informative priors. We used a uniform prior distribution for all N_t that ranged from the number trapped at time t to 600 individuals.

While evidence exists for juvenile dispersal in the austral summer (King and McMillan 1982), very little is known about seasonal variation in dispersal (King and Powell 2007). Consequently, we estimated separate immigration-rate parameters for the three seasonal intervals leading up to January, July, and November.

We explored models that differed only in the habitat covariates and associated parameters (Eq. 9). We ran univariate models for all habitat covariates and retained those in a final model that had 90% credible intervals that did not overlap zero. For all parameters without standard full-conditional-posterior distributions, conditional posteriors were sampled using a Metropolis algorithm (Clark 2007:175–177). Within-chain serial autocorrelation was assessed to determine the appropriate thinning rate. Convergence on the posterior target distribution was confirmed with a scale reduction factor < 1.2 calculated on four parallel chains (Gelman and Rubin 1992, Gelman et al. 2004). Convergence for all models was achieved following a burn-in of 100,000 iterations. Posterior

summaries were taken from four chains containing 625,000 samples with a thinning rate of 250 (i.e., 2,500 samples in each chain and a total of 10,000). The MCMC algorithm was written in the Python programming language (Python Software Foundation 2013). One week of computation time was required to obtain the posterior distributions.

Stage 2 forward projection: management-scenario simulation

Using the estimated parameters and the same model structure as in stage 1 (Fig. 2), we developed a forward projection simulation model for a range of plausible management scenarios to quantify the probabilities of achieving zero density by November 2019. The biological and trapping processes were rendered stochastic by incorporating the uncertainty in parameter estimates from the stage 1 inferential modeling. A “simulation experiment” refers to forward projection modeling of a unique management scenario. In each simulation experiment, we predicted the population size following each trapping session up to and including the last trapping session in November 2019. Each simulation experiment was repeated 2000 times (iterations) to obtain probabilities of successful control-to-zero density.

The starting population size of each iteration of a simulation experiment was randomly drawn from the last post-trapping-population size estimated from the MCMC data modeling (N_{24}^*), which were stoats that avoided traps set in January (summer) 2015. The population available to be trapped in subsequent trapping sessions (N_t) was predicted by inserting into Eq. 12 the N_{t-1}^* value and random variates from the MCMC posteriors of population-growth parameter (λ_t). As in stage 1 modeling, the value for λ_t was fixed at 1.0 except during the reproductive season. Simulated locations ($Loc_{all,t}$) of stoats were obtained by drawing random multinomial variates using the associated probabilities (θ_k ; Eq. 7). The θ_k probabilities were derived from random draws of the posterior β parameters from the MCMC (Eqs. 7–9). One percent of traps were randomly selected each session and made “sprung empty” (based on field data), which reduced their trap availability by 0.5. The capture state for each stoat (s_{it} ; Fig. 2) was determined by a single multinomial draw with the associated three state probabilities $Pr(s_{it})$, Eqs. 1–3), which were dependent on random variates of the posterior distributions of \mathbf{v} , g_0 , and σ . Captured stoats were removed from the population, which resulted in the updated population size N_t^* .

At the end of each iteration, (i.e., following the last simulated trapping session in November 2019), control-to-zero density was deemed successful if the population had been reduced to zero during the simulation period. The probabilities of control-to-zero density were calculated as the number of successes divided by the 2,000 iterations.

We simulated seven different management scenarios. The first was to maintain the current trapping regime. The second was to remove the July trapping sessions,

which tend to have low trapping rates. This would become necessary if funding was drastically reduced. The third was to add a fourth trapping session in autumn (March) of each year. The fourth was to add 164 traps at 200-m intervals along transects in large gaps between trap lines (gap traps). The fifth was to add gap traps and an autumn trapping session. The sixth was to make a US\$300,000 investment in research that produces an improved lure (or trap design). The seventh was to add an autumn trapping session and invest in new lures. For scenarios that added an autumn session (3, 5, 7), the vulnerability probability (v_t) for autumn was calculated as the mean of random variates drawn from the summer (January) and winter (July) posteriors.

For all scenarios, we estimated the start-up and annual running financial costs over the simulated period and expressed this as a net-present value (NPV), which weights the costs close to the present more than in the future (Gren et al. 2014, Norbury et al. 2014). An 8.0% discount rate is the New Zealand Treasury standard for public-sector cost analyses. Due to potential sensitivity of resulting management recommendations to the discount rate (Gren et al. 2014), we calculated the NPV using three different discount rates: 5.0%, 8.0%, 10%. Results are presented in US\$.

RESULTS

A total of 644 stoats were captured in 24 trapping sessions between July 2008 and January 2015 (Table 1). The first three sessions occurred over a three-week period,

TABLE 1. Data shown are approximate dates of baiting and the number of stoats captured in each of the 24 trap sessions.

Session	Date of baiting	Stoats captured
1	17 July 2008	231
2	21 July 2008	27
3	24 July 2008	32
4	11 August 2008	8
5	12 November 2008	79
6	18 January 2009	40
7	18 July 2009	2
8	8 November 2009	34
9	18 January 2010	15
10	18 July 2010	0
11	18 November 2010	2
12	21 January 2011	2
13	6 July 2011	1
14	4 November 2011	26
15	28 January 2012	16
16	20 July 2012	2
17	16 November 2012	27
18	25 January 2013	12
19	12 July 2013	3
20	7 November 2013	31
21	31 January 2014	13
22	25 July 2014	0
23	15 November 2014	33
24	29 January 2015	8

Note: It took several days to check and reset all the traps on the island, therefore dates are approximate because not all traps were baited on the same day.

TABLE 2. The median, mean, and 90% credible intervals for the posterior distributions of model parameters that were estimated in the stage 1 Bayesian modeling.

Parameters	5th percentile	Median	95th percentile	Mean
Eastings	-0.0371	0.0225	0.084	0.0226
Northings	-0.001	0.0493	0.106	0.0484
N_1	398.0	448.0	508.0	449.701
N_2	112.0	145.0	190.0	147.169
N_3	70.0	92.0	122.0	93.198
N_4	27.0	43.0	65.0	44.380
N_5	129.0	143.0	161.0	143.730
N_6	52.0	61.0	73.0	61.306
N_7	9.0	15.0	24.0	15.928
N_8	49.0	56.0	65.0	56.633
N_9	17.0	20.0	25.0	20.281
N_{10}	1.0	2.0	4.0	2.246
N_{11}	5.0	7.0	12.0	7.642
N_{12}	5.0	7.0	12.0	7.686
N_{13}	6.0	10.0	16.0	10.528
N_{14}	41.0	48.0	56.0	48.076
N_{15}	18.41	27.0	34.0	27.194
N_{16}	9.0	12.0	19.0	12.852
N_{17}	46.0	48.0	57.0	48.763
N_{18}	18.0	24.0	31.0	24.119
N_{19}	9.0	14.0	21.0	14.861
N_{20}	46.0	53.0	62.0	53.242
N_{21}	18.0	23.0	30.0	23.082
N_{22}	6.0	11.0	17.0	10.884
N_{23}	43.0	50.0	58.0	50.265
N_{24}	10.0	15.0	22.0	15.057
Population growth, λ_t	2.960	4.340	7.368	4.616
g_0	0.009	0.015	0.027	0.016
Home range, σ	295.347	355.708	417.772	355.296
Vulnerable January, v_{jan}	0.802	0.756	0.710	0.756
Vulnerable July, v_{jul}	0.452	0.335	0.239	0.338
Vulnerable November, v_{nov}	0.804	0.753	0.698	0.752

Note: N_t is the estimated number of stoats present on the island prior to each trapping session.

and of 290 stoats captured during that initial period, 224 were females and 66 were males.

Stage 1 results: parameter estimation

Using MCMC, we explored various habitat models embedded within the larger hierarchical model (Fig. 2). Early analyses showed that the posterior distribution of Imm_t tended toward zero when the high variance gamma priors were used. Further, the posterior Imm_t was highly sensitive to different prior distributions. This suggested that while immigration may occur (Veale et al. 2013), it was at very low rates and was indistinguishable from the stochasticity in the model. All subsequent modeling did not estimate immigration parameters.

Univariate analysis of the environmental covariates (*Methods: GIS data*) showed that only the posterior distributions for eastings and northings had 90% credible intervals that did not overlap zero. Therefore, we included these two variables in a single model and found that both were distinctly positive, but the lower 90% credible interval for both slightly overlapped zero (Table 2). Both variables were retained in the final model, which indicated a weak tendency for stoats to be located to the north and east of the island.

Estimation of the posterior distributions of the number of stoats present at the beginning of each session (N_t)

showed a mean of 449 stoats (90% CI 398–508; Table 2) prior to the onset of winter trapping in July 2008. This translates to approximately 2.2 stoats/km². The population was subsequently suppressed to very low levels between the winters of 2010 and 2011 (Fig. 3). However, the population rebounded in spring 2011.

The posterior mean for λ_t was 4.62 (90% CI 2.96–7.37; Table 2), which represents the mean population growth rate just prior to the November trapping session. Female stoats are reported to produce between eight and 10 kits per litter (King and Murphy 2005), and the estimated mean falls within this range with 9.2 kits/female. Despite the annual November increase in the population from reproduction, not all stoats were available to be trapped. The mean proportion of vulnerable animals in November was 0.753 (v_t ; Table 2). The proportion vulnerable in January ($v_t = 0.756$) was similar to November, but July was much lower ($v_t = 0.338$). The posterior mean of g_0 was 0.016 (CI 0.009–0.027), and the mean σ was 355.29 (CI 295.35–417.77).

Stage 2 results: management-scenario simulation

A simulation of the current trapping regime showed that there was 0.210 probability of achieving zero density on the island before the end of 2019. If the trapping

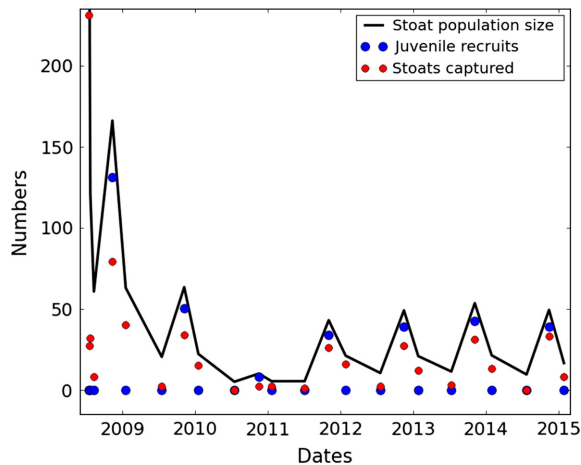


FIG. 3. Plot shows mean estimated population size (black line), number of recruits (blue dots), and the number of stoats removed (red dots) in each of the 24 sessions.

program ceased, the stoat population rebounded to its starting population size (≈ 448) within three reproductive seasons. If the winter (July) trap check and resetting was discontinued, the probability of successful control-to-zero was only 0.050. In the third scenario, the trapping effort was increased by the addition of annual trap session in autumn (March), which increased the probabilities of control-to-zero density to 0.710. The fourth scenario, in which 164 additional traps were placed in the gaps between trapping lines (thereby reducing the maximum distance between trap lines), resulted in a 0.285 probability of successful control-to-zero density. In the fifth scenario, an autumn trapping session was added and the 164 traps were deployed in gap areas, and this resulted in a 0.810 probability of success. In scenario six, a research investment produced an improved lure with a mean g_0 of 0.03, and this resulted in a probability of success of 0.647. Lastly, combining the addition of an autumn session with improving the lure increased the probability of success to 0.966.

We calculated the NPV for the seven management scenarios. While removing the July session reduced the NPV by 33%, the probability of successfully reaching zero density before the end of 2019 was very low (scenario 2; Fig. 4). The addition of the autumn session (scenario 3) resulted in the largest increase in the probability of success for the investment: a 238% increase in the probability of success for a 33% increase in budget. The addition of gap traps greatly increased the NPV from current levels, but the associated increase in the probability of management success was minor (scenario 4; Fig. 4). Combining an added autumn session with either gap traps or improved lure resulted in high probabilities of success (0.81 and 0.97, respectively), but required a two- to three-fold increase in the NPV (Fig. 4). The anticipated NPV over the simulation period was most sensitive to increases in upfront costs, such as adding gap traps and

new research investment (scenarios 4–7). Lastly, the NPV was sensitive to the discount rate only when ongoing annual costs were high, such as when the autumn session or gap traps were added.

DISCUSSION

Obtaining the required probabilities of control-to-zero density under different scenarios required a two-stage modeling approach to estimate parameters and simulate system dynamics. The use of MCMC permitted flexibility to simultaneously model multiple biological and observation processes (Gelfand and Smith 1990) that are supported by theory (Driscoll and Lindenmayer 2012) and previous studies. Important insight was gained from inference on model parameters by our Bayesian model, but the management questions could only be addressed through subsequent forward projection modeling. The simulations showed what effort and financial investment was required to achieve the management objective and allowed for exploration of hypothetical scenarios, such as adding traps or sessions, or improving the lure. While this model was developed for Resolution Island, the approach could be easily adapted to many invasive-species management systems that employ trap-removal methods.

From the stage 1 inferential modeling, it was apparent that the immigration rate was too low to be differentiated from the Poisson process in the population model (Eq. 11). Results showed that the population process was sufficiently explained by *in situ* reproduction. We conclude that immigration rates were indistinguishable from zero. Estimates of very low rates may be possible with genetic techniques (Veale et al. 2012, 2013).

The finding of weakly positive parameters for northings and eastings was likely due to an unmeasured environmental factor and unlikely related to the settling location of new immigrants. The lack of a clearly significant habitat covariate suggests that stoats can easily colonize all of Resolution Island and that all habitats are generally suitable.

Inferential modeling showed that stoats were difficult to trap and that there was high heterogeneity in trappability. The g_0 parameter was slightly lower, and σ was similar to estimates from other forested environments (Smith et al. 2008, Efford et al. 2009). The relatively low g_0 in this study could have been due to differences in trapping methodologies and the highly persecuted nature of the Resolution Island stoat population. The estimated v_{it} indicated that there was a seasonally variable portion of the population that was untrappable (Alterio et al. 1999, King et al. 2003, King and Powell 2007). Including this parameter was essential for obtaining reasonable estimates of λ_t . In the absence of the v_t parameter, the low capture rates in July followed by high rates in November (post-reproduction) would result in unreasonably high estimates of λ_t (>8.0). In other words, modeling the big increase in capture rates between July and November required either (1) an unrealistically high reproductive

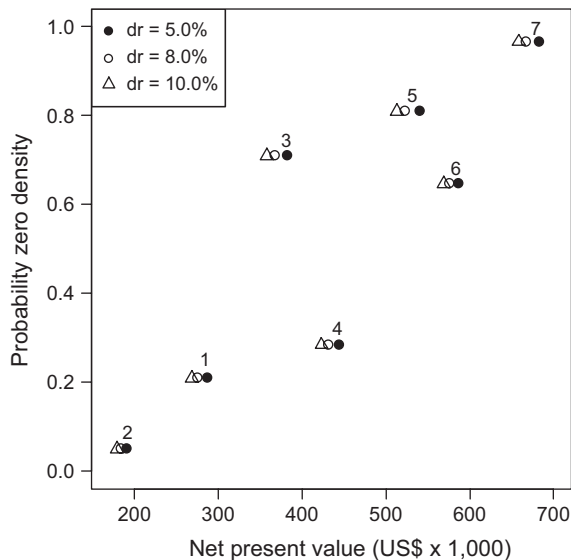


FIG. 4. Plots showing the net present value using three different discount rates (5%, 8%, 10%) for seven management scenarios through 2019 and the associated predicted probabilities of control to zero density. The seven scenarios were (1) current regime, (2) remove July session, (3) add March trapping session, (4) add gap traps, (5) add March session and gap traps, (6) research investment into improved lure, and (7) add March session and improve lure.

rate or (2) a substantial portion of the July population to be untrappable (Alterio et al. 1999, King et al. 2003, King and Powell 2007).

The relatively low v_t in July was likely due to most of the vulnerable stoats (juvenile recruits) being removed in the preceding November and January sessions, leaving mostly invulnerable stoats. Females are known to be difficult to capture during the reproductive period (Alterio et al. 1999), but the implantation of blastocysts and active pregnancy was not expected to begin until late August or September (King and Powell 2007). Therefore, the low July v_t was probably not related to the reproductive status of the population. Further, females were captured at more than a 3:1 ratio in the initial four trapping sessions in July and August 2008, indicating the potential for high trappability in July.

Given the low capture rate in winter (July; Table 1, Fig. 3), a logical cost-saving proposal was to discontinue this session (scenario 2). The resulting poor probability of success for this simulated scenario ($Pr = 0.05$) instead demonstrated the importance of removing as many animals as possible prior to the reproductive season. Stoats are highly fecund (King and Murphy 2005, King and Powell 2007), and our estimated λ_t of 4.6 indicates a high reproductive potential on Resolution Island. This suggests that for every female alive in July, there will be on average 9.2 kits in November. The presence of mice and a low population density on the island create favorable conditions for female growth and reproduction (Veale et al. 2015).

The forward projection modeling showed that it is feasible to achieve a high probability of successful control-to-zero density within four years (end of 2019) but it will require a substantial increase in operational funding above present levels. In the exploration of the seven management scenarios, it was only the combination of the addition of an autumn session with either new gap traps (scenario 5) or research investment to improve the lure (scenario 7) that resulted in a probability of success exceeding 0.80 (Fig. 4). These scenarios would present the best chance for achieving healthy populations of native bird species. However, scenarios 5 and 7 would require an NPV investment of more than double the NPV of the present trapping regime. If scenarios 5 or 7 are financial prohibitive, the addition of the autumn session (scenario 3) would be the most cost-effective alternative. The additional session increased the probability of success by 238%, but only required a 33% increase in budget.

In conclusion, control-to-zero density of this invasive mustelid from Resolution Island is feasible. However, success will require a substantial increase in financial investment to increase the rate at which individuals are removed relative to the population growth rate. The management program, coupled with the present modeling, offers the opportunity to initiate an adaptive management program (Walters 1986, Shea et al. 2002, McCarthy and Possingham 2007), the lessons from which would help increase the efficiency of near-shore control-to-zero density or suppression operations worldwide. Broad-scale trials of adding an additional trapping session, trialing new traps to attract females or to increase general trappability should be attempted. In addition, our model assumptions represent gaps in data and our understanding of the system and could be addressed with specific research projects. Genetic analyses could potentially inform the sex bias in captured animals and annual immigration rates (Veale et al. 2013), and these details could be incorporated into the two-stage modeling to improve predictions. Near-shore pest management presents the additional complication of immigration but has strong potential for important biodiversity benefits. (King 1985, Savidge 1987, Vitousek et al. 1997, Mack et al. 2000).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1415/full>

DATA AVAILABILITY

Data and Python scripts are available at the Landcare Research DataStore: <http://doi.org/10.7931/J2KK98PK>