# Developing population models for guiding reintroductions of extirpated bird species back to the New Zealand mainland

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**Abstract**: Population models are useful tools to guide management as they allow us to project growth and persistence of wildlife populations under different scenarios. Nevertheless, good data are needed to produce reliable models, and this requirement is problematic in some situations. North Island saddlebacks (*Philesturnus rufusater*) were reintroduced to Boundary Stream Mainland Island in September 2004, and this was the first time this species had occurred in an unfenced mainland area since their extirpation in the 19th century. This situation creates a challenging scenario for population modelling, as this species has never been studied in the presence of mainland predators, and management of these predators will be the key factor determining whether the population survives. In this paper we present an approach for developing a "prior model" before a reintroduction takes place. We use data from the reintroduced saddleback population on Mokoia Island to develop a model of how saddleback populations are regulated in the absence of mammalian predators. We use this model to project growth of a reintroduced population when vital rates are reduced by predation and also to project responses of source populations to harvesting of birds for translocation. We then incorporate data from the reintroduced North Island robin (*Petroica longipes*) population at Paengaroa Mainland Island to model the relationship between population parameters and predator tracking rates. The combined model can be used to predict the level of predator control needed to ensure growth of the saddleback population, but the prediction is contingent on guessing the relative vulnerability of robins and saddlebacks to predation. We envision using a Bayesian approach to update such prior models as site-specific data become available after reintroduction.

**Keywords:** adaptive management; mainland islands; population modelling; population viability; predator control; saddleback; sustainable harvesting.

## Introduction

One of the major developments in population modelling over the last 25 years has been the use of population viability analysis (PVA) to guide conservation efforts for threatened species (Beissinger and McCullough, 2002; Reed *et al*., 2002). The initial focus of PVA was to predict minimum population sizes that would be viable over the long term, given inbreeding depression, demographic stochasticity and environmental stochasticity (Shaffer, 1981). In recent years however, there has been greater emphasis on projecting population viability over short time frames under alternative management strategies (Beissinger and Westphal, 1998; McCarthy *et al*., 2003). PVA has therefore become closely integrated with the process of adaptive management, where models are developed, populations are monitored under proscribed management strategies, and then models and management strategies are updated based on data collected (Williams *et al*., 2002).

Reintroductions are frequently used to recover species or restore ecosystems, both in New Zealand (Armstrong and McLean, 1995) and overseas (Griffith *et al*., 1989), and reintroduction programmes can clearly benefit from PVA and adaptive management. Reintroduction can only be successful if the original cause of extirpation has been removed (Kleiman, 1989; Veitch, 1995), hence success is contingent on natural habitat regeneration, active habitat restoration, or ongoing management. In some cases the requirements are relatively straightforward. For example, island reintroductions of saddlebacks, or tieke [*Philesturnus rufusater* for North Island saddleback, *P. carunculatus* for South Island saddleback following Holdaway *et al*. (2001)] have generally been successful as long as

exotic mammalian predators were eradicated (Lovegrove, 1996), suggesting that future reintroductions of saddlebacks to predator-free islands will also be successful. In many other cases, however, it is unclear what is required for a reintroduced population to persist. Consequently, PVA on reintroduced populations has been used to assess whether habitat regeneration has been sufficient to allow population persistence (Armstrong and Ewen, 2002), whether supplementary feeding is needed (Armstrong *et al*., 2002), and what level of predator control is needed (McCallum *et al*., 1995; Southgate and Possingham, 1995 Armstrong *et al*., 2006a). Since reintroduction requires removing animals from other populations, PVA has also been used to assess the number of animals that can be sustainably harvested from source populations (McCarthy, 1994; Saltz, 1998; Dimond, 2001).

One of the most exciting prospects in New Zealand conservation at present is the reintroduction of species gone from the mainland. Many species were extirpated from the mainland (North and South Islands) following invasion of exotic mammalian predators but survived on offshore islands. Examples include the Stephens Island giant weta (*Deinacrida rugosa*), wetapunga (*D. heteracantha*), tuatara (*Sphenodon punctatus* and *S. guntheri*), Duvaucel's gecko (*Hoplodactylus duvaucelii*), Stephens Island frog (*Leiopelma hamiltoni*) and Maud Island frog (*L. pakeka*), hihi (stitchbird, *Notiomysis cincta*), and the North Island and South Island saddlebacks. Hihi and saddlebacks have been reintroduced to Mokoia Island in Lake Rotorua and to the predator-fenced Karori Sanctuary in Wellington (Armstrong, 2005). Now, with the development of "mainland islands" utilising intensive predator control (Saunders and Norton, 2001), there is also the prospect of reintroducing such species to unfenced mainland locations. The first such reintroduction took place in September 2004 when North Island saddlebacks were released in the 800-ha Boundary Stream Mainland Island in Hawke's Bay (Armstrong, 2005).

Reintroducing mainland-extirpated species to unfenced areas is inherently risky given the continual threat of reinvasion by predators, and can potentially threaten island populations if they are overharvested. It is therefore critical that reliable models are developed, both to predict the level of harvesting that island populations can withstand and to predict the level of predator control required for mainland populations to persist. These models can be used to assess whether the cost of mainland reintroductions is sustainable in the long term.

The challenge in the short term is to build a reliable model for a new population in a novel situation. If no prior information is used, then reintroduced populations will probably need to be monitored for at least five years to build a model that can be used to make reasonable predictions (Armstrong *et al*., 2002). Such a time frame is unsatisfactory for risky reintroductions that require rapid re-evaluation of management strategies. Data for other populations can be used to build models prior to reintroduction (Saltz, 1998; South *et al*., 2000), but the projections depend on conditions being similar between sites. The ideal is therefore to adopt a Bayesian approach to PVA whereby a prior model is developed based on data available for other populations, and this model is updated as population-specific data become available (Goodman, 2002).

Developing a prior model for a reintroduction to the New Zealand mainland requires two types of information. First, we need to know how the population would be regulated in the absence of predation from exotic mammals. We therefore need data on vital rates (survival and reproduction) at different population densities from a location free of mammalian predators. The resulting density-dependent model can be used to predict impacts on the source population, and to project growth of the reintroduced population under intensive predator control. Second, we need to know how vital rates will be affected by predator control. We therefore need data on vital rates from a population where the level of predator control varied over time and was monitored using tracking rates or some other index. This information can then be used to modify the density-dependent model to project population growth under any level of predator control. The difficulty is that most mainland-extirpated species have never been studied in the presence of mainland predators, hence we need to infer relationships between vital rates and predator control using data from other species.

In this paper we show how a prior model was developed for the saddlebacks reintroduced to Boundary Stream Mainland Island in 2004. Initially we present a stochastic simulation model developed from saddleback data collected on Mokoia Island. We use this model to project responses of source populations to different harvest rates, and to project growth of the Boundary Stream population in the absence of predation from exotic mammals. We then assess the extent to which different vital rates (adult survival, juvenile survival, fecundity) could be reduced before the population is driven to extinction. To relate our projections to predator control, we revise the model to incorporate functional relationships between vital rates and predator tracking based on data from the North Island robin (*Petroica longipes*) population at Paengaroa Mainland Island. We use the revised model to project how the Boundary Stream saddleback population might grow at different tracking rates, depending on the relative vulnerability of robins and saddlebacks to predation.

# Methods

## Populations and study sites

North Island saddlebacks were reintroduced to Mokoia Island (38° 05'S; 176°17'E) in Lake Rotorua in April 1992, following the eradication of Norway rats (*Rattus norvegicus*) in 1989–90. The island is 135 ha, and most of it is covered with regenerating broadleaved forest that provides suitable habitat for saddlebacks. At the time of reintroduction the island was free of exotic mammals except for mice (*Mus musculus*) and a small number of horses (*Equus caballus*), neither of which prey on saddlebacks or their nests. The small size of the island meant the population could grow to high density in a short time period, and data collected over the six years after reintroduction showed clear evidence of density dependence in fecundity and juvenile survival (Armstrong *et al*., 2005). This population therefore provides a good model of how saddlebacks are regulated in the absence of predation by exotic mammals.

North Island robins were reintroduced to Paengaroa Mainland Island (39° 39'S, 175° 43'E) near Taihape in March 1999. The reserve consists of 101 ha of broadleaved-podocarp forest on a floodplain and hillside, and is surrounded by farmland. Rats and possums (*Trichosurus vulpecula*) were initially controlled by brodifacoum cereal pellets distributed among 99 permanent bait stations. Baiting was discontinued in December 1999, restarted in May 2000, then discontinued again in March 2002. These management changes were followed by clear changes in rat tracking rates (obtained using footprint tracking tunnels), reflecting changes in the abundance and/or activity of rats in the reserve (Brown *et al*., 1996). There were corresponding changes in robin vital rates, with nest success, fecundity, and survival of adult females all negatively correlated with rat tracking rates (Armstrong *et al*., 2006b). Robins would also be affected by effectiveness of stoat (*Mustela erminea*) control, but too few stoats were tracked at Paengaroa to assess the relationship between stoat tracking and robin vital rates.

As there were no data available on how saddleback vital rates change as a function of predator control, the Paengaroa robin data provided a good surrogate for inferring those relationships for three reasons. First, robins and saddlebacks are both known to be vulnerable to predation by ship rats (*R. rattus*), Norway rats, and stoats (Lovegrove, 1992, 1996; Brown, 1997). Second, robins and saddlebacks are probably vulnerable in similar ways due to shared behavioural traits; e.g. they often forage on the ground, incubation and brooding is done solely by females, and females are reluctant to leave their nests. Third, the Paengaroa robin population was shown to be doomed to extinction in the absence of predator control (Armstrong *et al*., 2006a), and this

would also be the case for any saddleback population reintroduced to the mainland (Lovegrove, 1996).

Saddlebacks were reintroduced to Boundary Stream Mainland Island (39° 06'S, 176° 48'E) on 10 September 2004 when 37 birds from Cuvier Island were released. Boundary Stream Mainland Island is an 800-ha block of broadleaved-podocarp forest 60 km north of Napier. Since 1996 it has had an intensive pest management programme targeting both predators and herbivores. There are possum bait stations throughout the reserve at 150-m intervals (0.44 ha$^{-1}$), and live and kill traps are used to control cats and mustelids.

## Monitoring and data analysis

Resighting surveys of colour-banded birds were conducted to obtain data for estimating survival. The Mokoia saddleback population was surveyed at least four times per year (in September, December, March and June from 1992 to 1997), and the Paengaroa robin population was surveyed three times per year (in September, January and May from 1999 to 2004). Surveys were designed to give even coverage of the island or reserve. All reintroduced birds were individually colour banded, and offspring were colour banded on the nest (Mokoia saddlebacks) or after fledging (Paengaroa robins). Birds were monitored throughout the first five breeding seasons after reintroduction to determine fecundity per female, measured in terms of numbers of fledglings (Mokoia saddlebacks) or independent young (Paengaroa robins). All females were monitored, except for years 4–5 on Mokoia when a sample of 30 females was selected.

Models were fitted to the survival data using the live recaptures option in Program MARK (White and Burnham, 1999). Separate models were fitted to adult and juvenile survival, with Mokoia saddlebacks considered to become adults nine months after fledging and Paengaroa robins considered to become adults at the start of the first breeding season after fledging. In all cases, we developed a set of candidate models and selected among them based on Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). For Mokoia saddlebacks, the factors considered in survival models included population density, sex (adults only), fledging date (juveniles only), season and year. For Paengaroa robins, the factors considered in survival models included rat tracking rate, sex (adults only), season and year.

Models were fitted to the fecundity data using PROC MIXED in SAS for Mokoia saddlebacks (with individual female as a random effect) and PROC NLIN in SAS for Paengaroa robins. As for the survival analysis, we selected among candidate models based on AIC. For Mokoia saddlebacks, the factors considered in fecundity models included population density, territory quality (territories occupied in first year after

**Table 1.** Stochastic spreadsheet models for projecting growth of North Island saddleback populations under harvesting or predation. Each row of the table corresponds to a row in a spreadsheet model, and the complete set of rows represents one year. The numeric parameters in Model A determine how the population is regulated in the absence of mammalian predators, and these were estimated using data from the saddleback population on Mokoia Island. The parameter $A$ indicates the available area in hectares. The parameters $p_f$, $p_a$ and $p_j$ were added to simulate reduction of vital rates through predation, and were initially set to 1. The parameter $h$ was added to simulate an annual harvest of females, with harvesting taking place at the start of the breeding season. The additional numeric parameters introduced in Model B determine how vital rates decline with predator tracking rate, and these were estimated using data from the North Island robin population at Paengaroa Mainland Island. The parameter $p_t$ indicates the proportion of tracking tunnels that are not tracked over 24 h, and the parameter $v$ indicates the relative vulnerability of saddlebacks and robins. The models include demographic stochasticity in fecundity, survival and sex allocation, but do not include environmental stochasticity.

| Step | Model A (harvest and predation rate) | Model B (predator tracking rate) |
|---|---|---|
| i. Mean fledged per 1$^{st}$-year female | $f_{1,t} = \text{Max}\left[(1.89 - 1.72 d_t), 0\right] p_f$ | $f_{1,t} = \text{Max}\left[(1.89 - 1.72 d_t), 0\right] \left[1 - e^{\frac{-1}{2.18v}\left(\frac{p_t}{1-p_t}\right)}\right]$ |
| ii. Mean fledged per older female | $f_{2+,t} = \text{Max}\left[(4.34 - 1.72 d_t), 0\right] p_f$ | $f_{2+,t} = \text{Max}\left[(4.34 - 1.72 d_t), 0\right] \left[1 - e^{\frac{-1}{2.18v}\left(\frac{p_t}{1-p_t}\right)}\right]$ |
| iii. No. juveniles | $J_t \sim \text{Poisson}\left(N_{1,t} f_{1,t} + N_{2+,t} f_{2+,t}\right)$ | $J_t \sim \text{Poisson}\left(N_{1,t} f_{1,t} + N_{2+,t} f_{2+,t}\right)$ |
| iv. Pr. adult survives 12 months | $s_{a,t} = 0.89 p_a$ | $s_{a,t} = 0.89 p_t^{0.24v}$ |
| v. Log odds juvenile survives 1 month | $\beta_t = 4.07 - 3.24 d_t$ | $\beta_t = 4.07 - 3.24 d_t$ |
| vi. Pr. juvenile survives 12 months | $s_{j,t} = \left(\frac{e^{\beta_t}}{1 + e^{\beta_t}}\right)^9 0.97 p_j$ | $s_{j,t} = \left(\frac{e^{\beta_t}}{1 + e^{\beta_t}}\right)^9 0.97 p_t^{0.58v}$ |
| vii No. 1$^{st}$-year females next year | $N_{1,pre} \sim \text{Binomial}\left(J_t, 0.5 s_{j,t}\right)$ | $N_{1,t+1} \sim \text{Binomial}\left(J_t, 0.5 s_{j,t}\right)$ |
| viii. No. older females next year | $N_{2+,pre} \sim \text{Binomial}\left[(N_{1,t} + N_{2+,t}), s_{a,t}\right]$ | $N_{2+,t+1} \sim \text{Binomial}\left[(N_{1,t} + N_{2+,t}), s_{a,t}\right]$ |
| ix. No. 1$^{st}$-year females post-harvest | $N_{1,t+1} = \text{Max}\left[\left(N_{1,pre} - h\frac{N_{1,pre}}{N_{1,pre} + N_{2+,pre}}\right), 0\right]$ | |
| x. No. older females post-harvest | $N_{2+,t+1} = \text{Max}\left[\left(N_{2+,pre} - h\frac{N_{2+,pre}}{N_{1,pre} + N_{2+,pre}}\right), 0\right]$ | |
| xi. Population density (females ha$^{-1}$) | $d_{t+1} = \frac{N_{1,t+1} + N_{2+,t+1}}{A}$ | $d_{t+1} = \frac{N_{1,t+1} + N_{2+,t+1}}{A}$ |

reintroduction, second year after reintroduction, or later), age, year, and region of the island. For Paengaroa robins, we considered three different models for the relationship between rat tracking rate and fecundity. See Armstrong *et al.* (2005) and Armstrong *et al.* (2006b) for further details of the monitoring, analysis, and models considered.

**Population modelling**

We simulated population dynamics using a stochastic discrete-time female-only matrix model written as a spreadsheet in Microsoft Excel [see White (2000a) for an introduction to modelling population dynamics using spreadsheets]. There were two versions of the model (Table 1). The first was based solely on functions

derived from Mokoia saddlebacks, and was used to assess levels of harvesting and predation that a saddleback population could withstand. The second also incorporated relationships between vital rates and rat tracking rates derived from the Paengaroa robin population, and was used to relate saddleback population growth to the levels of predator control achieved.

Based on the Mokoia saddleback fecundity data, the expected number of fledglings per female in the absence of mammalian predation is given by $1.89 + 2.45a_f - 1.72d_t$, where $a_f = 0$ for first-year females, $a_f = 1$ for older females, and $d_t$ is current population density measured as number of females per hectare at the start of the breeding season. Our simulation model calculated the expected fecundity separately for the two female age-classes (Steps i and ii, Table 1). The best model for explaining the Mokoia data also included male age, and made a distinction between territories occupied in the first year after reintroduction and those occupied later (Armstrong *et al.*, 2005). For this analysis, however, we chose a female-only approach because it produced results that were indistinguishable from those of a more complicated two-sex model. A female-only model implicitly assumes that there are always sufficient males for all females to be paired, and this assumption was supported by the Mokoia data given that the sex ratio of first-year birds was approximately 50:50 and adult survival was similar for males and females. We did not attempt to include a difference in quality of early-occupied and later-occupied territories here, as this distinction is not easily extrapolated to other sites.

The expected number of fledglings produced over a breeding season was calculated by multiplying the number of females in each age class by their expected fecundity rate, then adding the two products. The actual number was sampled from a Poisson distribution to simulate demographic stochasticity in reproduction (Step iii, Table 1). This sampling used the Excel formula ROUND(GAMMAINV(probability, alpha, beta)), where "probability" is a uniform random number from 0 to 1 obtained using the function RAND(), "alpha" is the expected number of fledglings, and "beta" = 1 (the Gamma distribution with beta = 1 is a continuous analog to the Poisson).

Based on Mokoia saddleback survival data, survival of adult saddlebacks is expected to be constant over time and between sexes, whereas juvenile survival is expected to decline with density. In the absence of mammalian predation, the annual adult survival probability is 0.89 (Step iv, Table 1), and the log odds of monthly juvenile survival probability is given by $4.07 - 3.24d_t$ (Step v, Table 1). The probability of a bird surviving its first year after fledging was obtained by logit transforming the monthly log odds, raising to

the power of 9 to extrapolate to 9 months, then multiplying by 0.97, which is the probability of it surviving the 3 months after it becomes an adult (Step vi, Table 1). The actual number of adult and juvenile females that survived to the next breeding season were sampled from the Binomial distribution to simulate demographic stochasticity in survival and sex allocation (Steps vii and viii, Table 1). This sampling used the Excel formula CRITBINOM(trials, probability_s, alpha), where "trials" is the maximum number, "probability_s" is the survival probability, and "alpha" is a uniform random number from 0 to 1. For juveniles, the survival probability was multiplied by 0.5 to give a 50% probability of a surviving juvenile being female.

There was no environmental stochasticity in the model, as our analyses of the Mokoia saddleback data indicated no significant year-to-year variation in vital rates [i.e. observed year-to-year variation was accounted for by sampling variation rather than process variation; White (2000b)].

In the first version of the model (Model A, Table 1), we added four parameters to simulate harvesting and predation. To simulate harvesting, we added a parameter $h$ that determines the number of birds removed in a year. For simplicity, the harvest occurs after the numbers of birds surviving to the next breeding season is calculated (Steps ix and x, Table 1). The model therefore assumed that harvesting occurred near the start of the breeding season (as was the case for the translocation from Cuvier to Boundary Stream), but it could be modified to allow for a harvest at any time of year. The proportional age make-up of the females harvested was assumed to match the proportions of first-year and older females in the population (Steps ix and x, Table 1). To simulate predation, we added parameters that proportionally reduced mean fecundity ($p_f$, see Steps I and ii in Table 1), adult survival probability ($p_a$, see Step iv in Table 1) and juvenile survival probability ($p_j$, see Step vi in Table 1). In all cases, the parameter specifies the proportion of the predator-free rate (i.e. 1 = no predation, 0 = total predation). The proportional predation rates did not change with density, meaning a Type I functional response (Holling, 1959) was assumed for all vital rates.

In the second version of the model (Model B, Table 1), we modified the fecundity and survival functions to incorporate declines associated with increased predator tracking. Based on Paengaroa robin fecundity data, the mean fecundity in proportion to the predator-free rate is given by

$$1 - e^{\frac{-1}{2.18}\left(\frac{p_t}{1-p_t}\right)}$$

where $p_t$ is the proportion of tracking tunnels that are

not tracked over 24 h. This quantity is therefore multiplied by the predator-free fecundity rate to obtain the mean fecundity expected at a given predator tracking rate (Steps I and ii, Table 1). Based on Paengaroa robin survival data, predator-free survival probabilities for adult females and juveniles were multiplied by $p_t^{0.24}$ and $p_t^{0.58}$ respectively to obtain survival probabilities at a given tracking rate (Steps iv and vi, Table 1). We added another parameter, $v$, to each of these equations to account for differences in vulnerability between a reintroduced saddleback population and the Paengaroa robin population (Steps i, ii, iv, and vi in Table 1). Values of $v > 1$ indicate greater vulnerability to mammalian predators than Paengaroa robins, and $v < 1$ indicates lower vulnerability. For simplicity, we assumed that all three parameters determining the strengths of the relationships between vital rates and tracking rates would be multiplied by the same value of $v$.

## Results

The Mokoia saddleback population was projected to stop growing when it reached approximately 120 females, and then to fluctuate between approximately 105 and 135 females. Population age structure was projected to consist of 10 first-year females and 110 older females on average. We therefore used these values as the initial population when projecting effects of harvesting.

An initial population of this size on a 135-ha island was predicted to be able to sustain an annual harvest of 33 females with negligible (<1%) chance of extinction over 10 years (Fig. 1). Model populations harvested at this level could potentially survive for longer periods of time, but with a high probability of extinction due to demographic stochasticity (e.g. 70% chance of extinction over 50 years). Harvesting above this level inevitably drove populations to extinction. Harvesting below this level resulted in modest reductions in equilibrium population size, with the equilibrium population size depending on the harvesting rate (Fig. 1). Such harvesting was predicted to be sustainable over long time frames, with populations quickly declining to a new equilibrium then remaining near that level (Fig. 2a). Greater harvests were predicted to be sustainable if the population was not harvested every year. For example, biennial harvests of 60 females were predicted to be sustainable, with the population recovering over the 2 years between harvests (Fig. 2b).

When the area available to the population was increased to 800 ha, to simulate a reintroduction to Boundary Stream Mainland Island, the population was projected to increase to approximately 715 females in
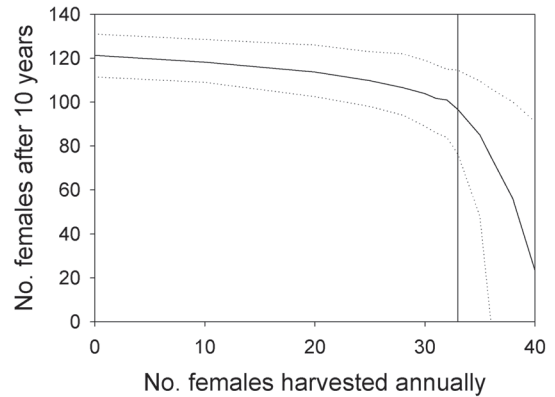


**Figure 1**. Projected sizes of the Mokoia Island saddleback population after 10 years under different harvest rates. The initial population had 10 first-year females and 110 older females, which are the average numbers the population was projected to have with no harvesting. Harvesting is assumed to take place near the start of the breeding season, and the population sizes shown are pre-harvest levels. Projections were made using a simulation model that incorporates density dependence in juvenile survival and fecundity, and demographic stochasticity in survival, fecundity and sex allocation (Table 1, Model A). Harvest rates were manipulated by changing parameter $h$. The solid line shows mean population sizes from 1000 runs, and broken lines show 95% confidence intervals. The vertical line shows the maximum sustainable harvest.

the absence of predation (Fig. 3). We used an initial population of 20 females (10 first-year, 10 older), as this founder group size is typical of many bird reintroductions in New Zealand (i.e. 40 birds with relatively equal sex ratio). If nest predation was incorporated with no predation on adults or fledged juveniles, most populations were projected to grow even if fecundity was reduced by up to 90% (Fig. 4a). Juvenile survival could also be reduced up to almost 90% (Fig. 4b) if predation had no effect on other vital rates, and adult survival could be reduced up to 65% (Fig. 4c). If all three vital rates were reduced by the same proportion, they could be reduced by up to 33% without populations declining (Fig. 5). All populations grew at lower predation rates, but the projected population size after 10 years was inversely correlated with predation rate (Figs. 4–5). Predation rate limited the sizes that populations ultimately reached as well as the number of years taken to reach those sizes (Fig. 3).

When relationships between vital rates and predator tracking were incorporated, using proportional reductions estimated from Paengaroa robins (Table 1, Model B), reintroduced saddleback populations were
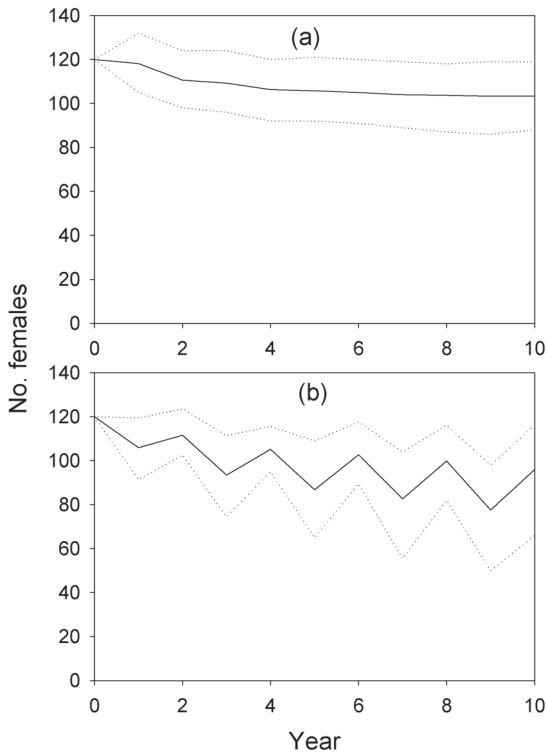
**Figure 2.** Projected trajectory of the Mokoia saddleback population over time with (a) an annual harvest of 30 females, and (b) a biennial harvest of 60 females. Otherwise as for Figure 1.
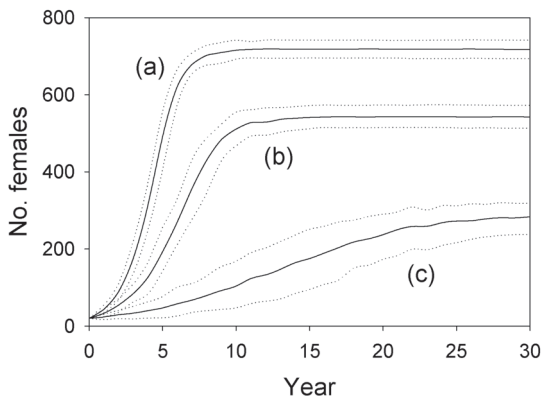


**Figure 3**. Projected trajectories of saddleback populations reintroduced into an 800-ha reserve, where (a) relationships between vital rates and density are similar to those estimated on Mokoia Island, (b) all vital rates are reduced by 15% by setting parameters $p_f$, $p_a$ and $p_j$ (Table 1, Model A) to 0.85, and (c) all vital rates are reduced by 30% by setting parameters $p_f$, $p_a$ and $p_j$ to 0.70. The initial populations included 10 first-year females and 10 older females. Otherwise as for Figure 1.
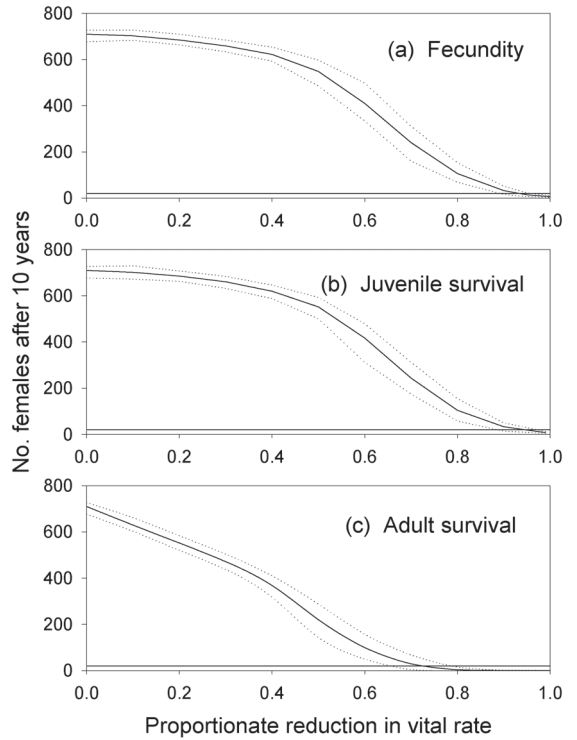


**Figure 4**. Projected sizes of saddleback populations after 10 years in relation to vital rates, when (a) fecundity is reduced through parameter $p_f$, (b) juvenile survival is reduced through parameter $p_a$, and (c) adult survival is reduced through parameter $p_j$. The other two parameters are set to 1 in all cases, meaning the other vital rates follow the relationships estimated on Mokoia Island. The horizontal line shows the initial number of females. Otherwise as for Figure 3.
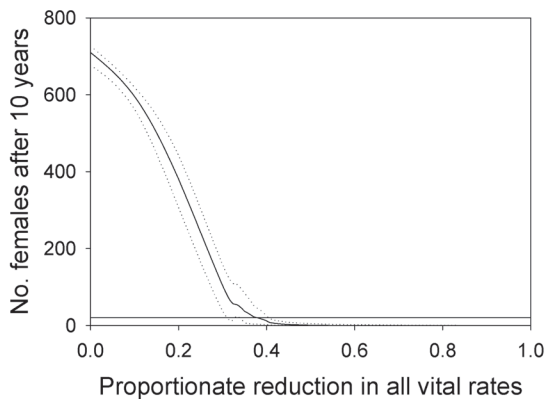


**Figure 5.** Projected sizes of saddleback populations after 10 years in relation to vital rates, when all vital rates are reduced by the same proportion. Otherwise as for Figure 4.
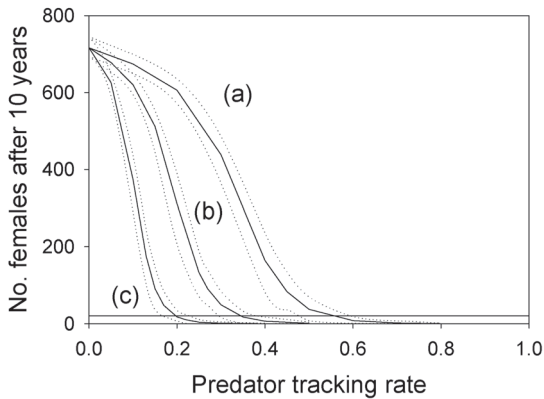
**Figure 6.** Projected sizes of saddleback populations after 10 years in relation to predator tracking rates, when (a) proportional reductions in vital rates are similar to those estimated for Paengaroa robins (Table 1, Model B), (b) parameter $v$ is increased to 2 so that vulnerability to predation is higher than for Paengaroa robins, and (c) parameter $v$ is increased to 4. Otherwise as for Figure 4.

projected to increase if the tracking rate was less than 50% (Fig. 6). If the parameter $v$ was increased from 1 to 2, so that saddlebacks were more vulnerable to predation than Paengaroa robins were, populations were projected to increase if the tracking rate was less than 30%. With $v$ increased to 4, the tracking rate needed to be less than 15% for populations to increase.

# Discussion

The simulation results presented here suggest that island saddleback populations could withstand considerable harvesting without being driven to extinction. The population on the relatively small (135 ha) Mokoia Island was predicted to be able to withstand annual harvests of 30 females, which would equate to a total harvest of 60 birds taking an even sex ratio. This prediction assumes birds are removed near the start of the breeding season, and would equate to slightly larger harvests at other times of year since some mortality would be expected between harvesting and the start of the breeding season. Larger harvests could be sustained if the island were larger with higher carrying capacity.

The 170-ha Cuvier Island, where North Island saddlebacks were sourced for Boundary Stream, has been harvested for at least 11 translocations since 1977, with 24–50 saddlebacks taken on each occasion (Lovegrove, 1996; Armstrong, 2005). This harvesting is justified by the assumption that Cuvier has about 1200 saddlebacks (Owen, 1998; Sullivan, 2004). This

number appears to be a guess rather than a formal estimate, and is about four times higher than the maximum densities projected by our models. Nevertheless, our projections suggest that a much smaller population could withstand this rate of harvesting with negligible impact. The much smaller (23 ha) Big Island has been harvested for 12 translocations of South Island saddlebacks since 1970, with 16–30 birds removed on each occasion. Big Island has been assumed to have about 200 saddlebacks, and to be able to withstand harvests of up to 30 birds every second year (Beaven, 1999). The actual size of the population is unknown, but our model would allow biennial harvests of 30 saddlebacks from a population of about 60 if harvesting occurred near the start of the breeding season.

Our projections also suggest that reintroduced saddleback populations could withstand considerable predation without being driven to extinction. If vital rates are similar to the Mokoia estimates in the absence of mammalian predation, productivity could probably be reduced by 90% if there was no predation on adults or juveniles, or all vital rates could be reduced by 30%. Saddleback populations are predicted to be most sensitive to reduction in adult survival, as is often the case for vertebrate populations (Caswell, 2001). Saddleback reproductive and juvenile survival rates are density dependent (Armstrong *et al.*, 2005), allowing these rates to compensate for low-to-moderate levels of predation.

These results suggest that there may be good prospects for saddlebacks surviving in unfenced mainland areas with some predation pressure. At this point, however, we can only guess about the management required to ensure predation is limited to a sustainable level. Since tracking tunnels are typically used to monitor effectiveness of rodent and mustelid control in New Zealand (Innes *et al.*, 1995), it would be extremely useful if managers could project the likely growth of reintroduced populations based on predator tracking data. We have therefore developed a general method for doing this, incorporating relationships between vital rates and predator tracking rates obtained from robins at Paengaroa Mainland Island. Our projections from this model (Fig. 6) incorporated completely hypothetical values for the relative vulnerability ($v$) of robins and saddlebacks to predation as it was impossible to say what values might be realistic. However, it will be possible to estimate $v$ for different species in the future if the necessary data become available, and these estimates would be extremely useful for management of mainland reserves. It would be simplest to obtain a single estimate per species, but it may turn out to be necessary to have a suite of estimates for different vital rates and different predators.

The post-release data for saddlebacks at Boundary Stream Mainland Island are difficult to interpret but suggest extreme vulnerability. Of the 37 saddlebacks released at Boundary Stream on 10 September 2004, only three males were known to be alive by the end of that year. There is often a period of high mortality immediately after reintroduction (e.g. Kurzejeski and Root, 1988; Slough, 1989; Lovegrove, 1992; Wilson *et al*., 1992; Musil *et al*., 1993; Armstrong, 1995), and this mortality should be excluded when estimating future survival rates for population projections (Armstrong *et al*., 2002). However, this is difficult to do if most of the population disappears shortly after reintroduction. A week of bad weather (windy and low temperatures) immediately after the Boundary Stream release may have caused substantial mortality, perhaps due to birds being unfamiliar with their environments and stressed by the translocation procedure (the birds were held in captivity for 30 days for disease screening). Nevertheless, at least nine birds were alive in mid-October and these formed four pairs. The four females then disappeared one-by-one over the next 2 months, and the behaviour of the birds prior to disappearance suggests they were preyed on while nesting. If we use those four females to estimate the survival rate expected in the long term, we would conclude that a female saddleback had <2% chance of surviving a year (i.e. $s_a$ <0.02). The tracking rates after the reintroduction were about 1% (i.e. $p^t = 0.99$) for both rats and stoats. If we put these values into our model for female survival ($s_a = 0.89p_t^{0.24v}$, Table 1), we conclude that $v$ >129 for Boundary Stream saddlebacks relative to Paengaroa robins. If this is an accurate indication of saddleback vulnerability, then saddlebacks will not be able to coexist with extremely low densities of predators despite their potential ability to withstand considerable predation (e.g. fecundity reduced by > 80% or adult survival reduced by >60%, Fig. 4). For example, a single stoat that is undetected by tracking tunnels might be sufficient to exterminate saddlebacks from a reserve the size of Boundary Stream Mainland Island. If this is the case, it will be impossible to conclude that a reintroduced population of saddlebacks is likely to survive unless it can be confirmed that mammalian predators have been totally eradicated.

The failed saddleback reintroduction to Boundary Stream Mainland Island has provided little opportunity to update the prior model we produced, except to tentatively suggest a minimum value for $v$. However, there may be further attempts to reintroduce saddlebacks to unfenced mainland areas, and a second reintroduction to Boundary Stream is currently being planned in conjunction with an intensification of predator control (W. Sullivan, Department of Conservation, Napier, N.Z., pers. comm.). Species such as robins and kaka (*Nestor meridionalis*) will also continue to be reintroduced to unfenced mainland areas, and there have been proposals to reintroduce hihi to such areas. We therefore think there will be considerable opportunity to apply the approach we are advocating to guide management of mainland reintroduction, i.e. develop prior models based on existing data then update those models as data become available after reintroduction. There are at least six issues to address when further developing this approach.

First, PVA projections should incorporate uncertainty associated with parameter estimation and model structure rather than just uncertainty due to demographic and/or environmental stochasticity (Wade, 2002). Methods for incorporating such uncertainty have now been developed (White, 2000b; Goodman, 2002; Taylor *et al*., 2002; Wade, 2002), and have recently been used in projections for the Paengaroa robin population at different rat tracking rates (Armstrong *et al*., 2006a). However, these projections assume that conditions will be the same as when data were collected. Our saddleback projections are based on data collected on Mokoia Island from 1992 to 1997, but vital rates will inevitably be different at other sites and possibly at other times (e.g. mice were subsequently eradicated from Mokoia, leading to an apparent increase in the saddleback population). If data exist for different habitat types, it may be possible to explicitly incorporate the effect of habitat when selecting prior estimates for vital rates at a new site. Craig (1994) suggested that saddlebacks had highest reproductive rates in regenerating forest such as that found on Mokoia Island, hence we might *a priori* expect lower reproduction at more mature sites such as Boundary Stream.

Second, when site-specific data become available after reintroduction, we need to decide how to weigh these against data collected from other sites. Bayes theorem (Williams *et al*., 2002: 685–686) allows us to generate a posterior distribution for a parameter by updating a prior distribution using current data, and this same methodology can be used to update model structure. Bayes theorem normally treats data from different sources as being equally reliable. However, following a reintroduction we would usually have more data from other sites, but have greater faith in the accuracy of site-specific data collected after the reintroduction. To sensibly apply Bayes theorem, we would need to flatten the prior distribution to some extent to account for uncertainty associated with site-specific effects.

Third, when extrapolating to other sites, we need to consider the possibility that emigration rates will be different. For example, saddlebacks are normally expected to have zero emigration from islands, but some birds might emigrate from populations reintroduced to managed mainland areas. Such birds

will be lost to the reintroduced population, hence emigration effectively lowers the survival rate of the reintroduced population regardless of the fate of the dispersing birds. Basse and McLennan (2003) modelled this effect using dispersal data for kiwi, and attempted to estimate the minimum size of predator-controlled area needed to support a population. The emigration rate will also depend on the shape of the reserve, the connectivity to other areas of habitat, and the dispersal behaviour of the species. Our model did not account for emigration, hence it was assumed that there would be negligible emigration from the 800-ha Boundary Stream Mainland Island. This assumption may be reasonable given that Boundary Stream has relatively poor connectivity to other forest areas, none of the translocated birds were detected leaving the reserve (10 had transmitters), and there appears to have been little emigration of saddlebacks from the smaller (210 ha) Karori Sanctuary. It is important that this assumption be continuously re-evaluated as saddlebacks are reintroduced into additional mainland reserves. Collection of radio-tracking data for dispersing juveniles should therefore be a priority for species being reintroduced to mainland reserves. Even if emigration is initially low, it may increase over time through density dependence in dispersal and become a key factor regulating populations.

Fourth, when modelling the relationship between vital rates and predators it may be necessary to consider indices for two or more predator types (e.g. tracking rates for rats and stoats). Such indices are likely to be highly correlated if all predators are controlled using the same method. However, if different methods are being used (e.g. brodifacoum targeting rats, poisoned eggs targeting stoats), it will be important to consider the indices separately to know where to best allocate management effort.

Fifth, it may sometimes be important to estimate the by-kill from poison baits. Saddlebacks are known to consume cereal baits (Spurr, 1993), and 40% of the saddlebacks on Mokoia Island are estimated to have died following an aerial drop of brodifacoum cereal pellets in 1996 (Davidson and Armstrong, 2002). By-kill is expected to be much less if poisons are distributed in stations, but there is still some risk from bait scattered on the ground by possums or rats. While poison-based predator control may substantially increase vital rates of some native species, this result may occur from a net gain that includes some by-kill (Powlesland *et al*., 1999). That by-kill can potentially confound relationships between vital rates and predator indices. For example, survival could differ between sites with comparable predator indices if the control is achieved with methods that result in different levels of by-kill.

Finally, we should consider the possibility that predation rates will have a Type II or Type III functional response, where per capita predation rates decrease as prey density increases. Sinclair *et al.* (1998) suggested this was the case for reintroductions of Australian marsupials, and noted that it would have implications for management. In particular, the intensity of predator control needed to sustain reintroduced populations could potentially be reduced when those populations reached high density, and it could be argued that large numbers of animals should be released to minimise per capita predation. However, uncritical acceptance of this notion could result in adoption of unsustainable predator-control programmes in the hope that they could be reduced in the future, or result in large numbers of animals being released to become fodder for predators. We think it is most realistic to assume a Type I functional response, as native species reintroduced to the mainland are likely to be a minor component of predators' diets at any realistic density, meaning foraging effort of predators will be unaffected by changes in prey density. Nevertheless, investigation of functional responses in New Zealand predator-prey systems could be a worthwhile, albeit challenging, research area.

A substantial number of mainland reintroductions have been conducted in recent years (Armstrong, 2005), and many more are in the pipeline, including further attempts to reintroduce mainland-extirpated species to unfenced areas. It is imperative that these programmes do not proceed by trial and error, but instead adopt a true adaptive management approach where explicit models are developed and refined based on experience. Since the data requirements for such modelling are also substantial, it will be inefficient, if not impossible, for model development to occur on a case-by-case basis. An integrated approach to PVA modelling (Maunder, 2004) is therefore needed for mainland reintroductions, and the models presented here are intended to be a first step in that direction. This approach should see a gradual improvement in our ability to project the fates of mainland reintroductions under different management regimes, allowing us to grasp exciting opportunities to restore our biodiversity without unnecessarily sending animals to their deaths.

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