

# Estimating the Viability of a Reintroduced New Zealand Robin Population as a Function of Predator Control

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## Abstract

Wildlife managers often have a good understanding of the threats faced by populations, but they need to know the intensity of management required for populations to survive. Managers therefore need quantitative projections for populations under different management regimes rather than just qualitative comparisons. However, quantitative projections are subject to tremendous uncertainty, particularly for small populations monitored for short time spans. We assess the level of predator control needed for a reintroduced population of North Island robins (*Petroica longipes*) to grow, accounting for uncertainty associated with parameter estimation, model structure, and demographic stochasticity. The robin population grew when exotic rats were reduced to low levels (<10% of footprint tunnels tracked in 24 hr) by regular maintenance of poison bait stations. However, the population declined after baiting was stopped 3 years after the reintroduction (March 2002), and it had fallen to 4 pairs by September 2004. We created a simulation model incorporating relationships between vital rates (survival and fecundity) of the robin population and rat tracking rate estimated from 5 years of data. We ran the model 10,000 times at each rat tracking rate, with vital rates sampled from distributions (defined by estimates and standard errors) at the start of each run. Output from a deterministic model suggested that  $\lambda$  (finite rate of increase) would be >1 if rat tracking were <20%, and up to 1.2 with rat tracking at 1%. However, 95% confidence intervals for  $\lambda$  extended <1 at any tracking rate. With demographic stochasticity added, there was >20% probability of further decline in 5 years even when the expected  $\lambda$  was 1.2. With all forms of uncertainty included, 41% of simulations projected a further decline over 5 years if the rat tracking rate were 10%. This proportion was reduced to 30% if initial population size was increased to 20 pairs. Our analysis therefore showed it was most likely that the robin population would grow if intensive rat control were reinstated, particularly if the population was supplemented, but there was substantial risk the population would continue to decline under such management. (JOURNAL OF WILDLIFE MANAGEMENT 70(4):1020–1027; 2006)

## Key words

mainland islands, New Zealand, North Island robin, *Petroica longipes*, population viability, predator control, reintroduction, tracking tunnels, uncertainty.

Population viability analysis (PVA) involves constructing models that are used to assess survival prospects of populations (Reed et al. 2002). The initial focus of PVA was to estimate the long-term probability of extinction in small populations, taking into account genetic, demographic, and environmental stochasticity (Shaffer 1981, Soulé 1987). This focus has shifted (Beissinger 2002) due to the fact that many populations are faced with short-term driven extinction rather than long-term stochastic extinction (Caughley 1994) and that the predictions of PVAs are subject to great uncertainty, particularly when long time frames are considered (Fieberg and Ellner 2000, Ellner et al. 2002). This uncertainty can be acknowledged by keeping PVA projections to short time frames and by using PVA to compare management strategies rather than to estimate absolute probabilities of extinction (Beissinger and Westphal 1998, Brook et al. 2002, Reed et al. 2002, McCarthy et al. 2003). However, restricting the role of PVA to qualitative comparisons is often unsatisfactory for managers. Managers may already know how they can reduce threats to populations, but they need to know the intensity of management required for the populations to persist.

The best approach for dealing with uncertainty is not just to acknowledge it but to confront it, and this involves 2 processes. First, PVA must be preceded by a sound analysis of the data, allowing plausible models to be developed for the factors driving

vital rates and allowing uncertainty in model selection and parameter estimates to be quantified (White 2000a, White et al. 2002). Second, PVA should produce a distribution of projections for any management scenario, and these distributions should account for uncertainty in model structure and parameter estimates in addition to the uncertainty associated with stochasticity (White 2000a, Taylor et al. 2002, Wade 2002).

Population projections can be summarized in terms of probability of extinction or quasi-extinction, persistence time, or population growth rate (Burgman et al. 1993). All can be difficult to interpret, as extinction probability and persistence time both depend on the initial population size, extinction probability depends on the time frame, and growth rate depends on population density. For reintroduced populations the finite rate of increase,  $\lambda$ , provides a good measure of initial viability, as populations are usually reintroduced at low density and expected to grow if conditions are suitable. Reintroduction sites are often actively managed to redress the factors responsible for the extirpation of the species, so the key question is whether the population will grow (i.e.,  $\lambda > 1$ ) under any management regime.

In New Zealand, reintroduction or recovery of many native species depends on management of exotic mammalian predators (Clout 2001). Many reserves on the main islands now have predator control programs, and these reserves are often termed *mainland islands* (Saunders and Norton 2001). The term reflects

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the idea that it may be possible for managed mainland areas to have dense native populations similar to those found on mammal-free offshore islands. Unlike islands, however, unfenced mainland areas are subject to continual reinvasion of predators, so predators can only be controlled rather than eradicated. There is already abundant evidence that predator control can improve survival and/or reproduction of New Zealand bird species in mainland reserves (James and Clout 1996, Innes et al. 1999, Powlesland et al. 1999, Dilks et al. 2003, Moorhouse et al. 2003). The relevant question is not whether predator control is an appropriate management strategy, but what level of control is needed to allow populations to grow. This question can be addressed through an adaptive management (Walters 1986) approach (i.e., by monitoring the population under different levels of control and using the data to predict the subsequent control needed).

Managers also need a tangible measure of the level of predator control they are achieving. Footprint tracking tunnels are used throughout New Zealand to monitor rodents and mustelids, and tracking rates (proportion of tunnels tracked over 1–3 nights) are used to assess the effectiveness of control programs targeted at these mammals (Innes et al. 1995). Exotic ship rats (*Rattus rattus*) and mustelids appear to be the key predators of many native bird species (Clout 2001). It would therefore be useful for managers to know how low tracking rates need to be to allow reintroduced or remnant populations to be viable.

We built a simulation model for the reintroduced North Island robin (*Petroica longipes*) population at Paengaroa Mainland Island and used it to assess the probability of growth and persistence at different predator tracking rates. The population was ideal for this purpose, as rat tracking rates had varied dramatically in the 5 years after reintroduction and there were corresponding changes in the vital rates of the robin population (Armstrong et al. 2006). The reserve appeared to have good habitat for robins in terms of vegetation structure, topography, and food availability (Raeburn 2001), and should have been able to support several hundred robins in the absence of mammalian predators. We aimed to 1) estimate the relationship between  $\lambda$  and rat tracking rate; 2) quantify the uncertainty in this relationship; 3) quantify uncertainty due to demographic stochasticity, and therefore assess the degree to which uncertainty could be reduced by increasing the initial population size; and 4) obtain distributions for the number of robins that would be present after 5 years with different rat tracking rates, taking all these forms of uncertainty into account.

## Study Area

Paengaroa Mainland Island (39°39'S, 175°43'E) is a 101-ha forest remnant 8 km southwest of Taihape in the south-central portion of New Zealand's North Island. At the time of the robin reintroduction (Mar 1999), ship rats and brush-tailed possums (*Trichosurus vulpecula*) were controlled using brodifacoum cereal baits placed in 97 permanent bait stations. This baiting was discontinued briefly in 1999, continued until March 2002, then stopped again, resulting in marked changes in rat abundance over the first 5 years after robins were reintroduced to Paengaroa. Further details are given by Armstrong et al. (2006).

## Methods

### Species

The North Island robin is a small (26–32 g), insectivorous, forest passerine in the family Petroicidae. It is often considered a subspecies of the New Zealand robin along with the South Island robin (*P. australis*), but Holdaway et al. (2001) classified these as separate species. North Island robins typically breed from September to February (Armstrong et al. 2000, Powlesland et al. 2000) and breed in monogamous pairs that occupy permanent territories. Extra males are generally not involved in breeding, although females may practice serial polyandry by switching males between reproductive attempts (Armstrong et al. 2000). Extra females are often fertilized, but they receive no other help from males and produce fewer young than paired females (Armstrong et al. 2006). Juveniles become independent about 4 weeks after fledging and are sexually mature by the start of the next breeding season. Robins are highly susceptible to predation by rats (Brown 1997, Powlesland et al. 1999) and probably by other exotic mammals, and they are now absent from most of the North Island. They were reintroduced to Paengaroa Mainland Island in March 1999 when 40 robins were released there (Raeburn 2001).

### Data Collection and Analysis

We did tri-annual surveys of the Paengaroa robin population to obtain survival data, and we monitored females throughout the breeding season to obtain fecundity data. We measured fecundity as the number of independent young produced per female, and we usually color-banded birds when they reached independence (at about 4 weeks of age). We ran tracking tunnels every 4 months to monitor levels of rats and mustelids. However, mustelids rarely tracked tunnels, so we only analyzed rat tracking rates. We modeled functional relationships between the robin population's vital rates and the rat tracking rate (proportion of tunnels tracked). We first nominated a set of candidate models, and we used Akaike's Information Criterion (AIC) to determine which models best explained the data. We then used these models to estimate the survival probability or mean fecundity expected at any tracking rate and the standard errors associated with those estimates (Table 1; see Armstrong et al. [2006] for analyses). These functions distinguish the survival rates of adult males, adult females, and juveniles (from independence to start of the next breeding season), and they distinguish the fecundity rates of paired versus unpaired females.

We also required a model for sex allocation (i.e., the probability of a bird being male or female). The robins recruited into the Paengaroa breeding population from 2000 to 2004 had a female-biased sex ratio (13 F, 7 M). However, this proportion was not significantly different from 0.5 (95% profile likelihood confidence interval ranged from 0.43 to 0.84), and the proportion of females in 221 robin recruits on Tiritiri Matangi Island from 1993 to 2004 (Armstrong and Ewen 2002; D. P. Armstrong et al., Massey University, unpublished data) was extremely close to 0.5 (95% profile likelihood CI ranges from 0.47 to 0.55). As we have no reason to expect a greater proportion of female recruits at Paengaroa, we assumed a probability of 0.5 for a recruit being male or female.

**Table 1.** Models for predicting vital rates of North Island robins as a function of rat tracking rate, Paengaroa Mainland Island, New Zealand.

Estimate <sup>a,b</sup>	Standard error <sup>a,b</sup>	Distribution <sup>c</sup>
$\hat{f}_p = 2.26\{1 - e^{-0.46[p/(1-p)]}\}$	$SE(\hat{f}_p) = \sqrt{0.05\hat{f}_p^2 + \left[0.27\left(\frac{p}{1-p}\right)(2.26 - \hat{f}_p)\right]^2 - 0.09\left(\frac{p}{1-p}\right)(2.26 - \hat{f}_p)\hat{f}_p}$	$\ln(f_p) \sim Normal\left[\ln(\hat{f}_p), \frac{SE(\hat{f}_p)}{\hat{f}_p}\right]$
$\hat{f}_u = 1.03\{1 - e^{-0.46[p/(1-p)]}\}$	$SE(\hat{f}_u) = \sqrt{0.39\hat{f}_u^2 + \left[0.27\left(\frac{p}{1-p}\right)(1.03 - \hat{f}_u)\right]^2 + \left[0.001 - 0.09\left(\frac{p}{1-p}\right)\right](1.03 - \hat{f}_u)\hat{f}_u}$	$\ln(f_u) \sim Normal\left[\ln(\hat{f}_u), \frac{SE(\hat{f}_u)}{\hat{f}_u}\right]$
$\hat{s}_f = 0.64p^{0.24}$	$SE(\hat{s}_f) = \sqrt{0.01\hat{s}_f^2 + 0.027\hat{s}_f^2\ln(p)^2 + 0.011\hat{s}_f^2\ln(p)}$	$\ln\left(\frac{s_f}{1-s_f}\right) \sim Normal\left[\ln\left(\frac{\hat{s}_f}{1-\hat{s}_f}\right), \frac{SE(\hat{s}_f)}{\hat{s}_f(1-\hat{s}_f)}\right]$
$\hat{s}_m = 0.64$	$SE(\hat{s}_m) = 0.065$	$\ln\left(\frac{s_f}{1-s_f}\right) \sim Normal(0.57, 0.28)$
$\hat{s}_j = 0.39$ (A) <sup>d</sup>	$SE(\hat{s}_j) = 0.049$	$\ln\left(\frac{s_j}{1-s_j}\right) \sim Normal(-0.44, 0.21)$
$\hat{s}_j = 0.49p^{0.58}$ (B) <sup>d</sup>	$SE(\hat{s}_j) = \sqrt{0.054\hat{s}_j^2 + 0.211\hat{s}_j^2\ln(p)^2 + 0.117\hat{s}_j^2\ln(p)}$	$\ln\left(\frac{s_j}{1-s_j}\right) \sim Normal\left[\ln\left(\frac{\hat{s}_j}{1-\hat{s}_j}\right), \frac{SE(\hat{s}_j)}{\hat{s}_j(1-\hat{s}_j)}\right]$

<sup>a</sup> See Armstrong et al. (2006) for analyses used to select appropriate models and estimate standard errors.

<sup>b</sup>  $\hat{f}_p$ , mean number of independent young per pair;  $\hat{f}_u$ , mean number of independent young per unpaired female;  $\hat{s}_f$ , probability of an adult female surviving 1 yr;  $\hat{s}_m$ , probability of an adult male surviving 1 yr;  $\hat{s}_j$ , probability of a juvenile surviving from independence until the next breeding season;  $p$ , proportion of tracking tunnels that are not tracked by rats in one night.

<sup>c</sup> Used to incorporate uncertainty in vital rates when performing simulation modeling.

<sup>d</sup> The juvenile survival model is ambiguous as these 2 models (A and B) have similar AIC weights when fitted to the data (Armstrong et al. 2006).

### Population Modeling

We constructed a discrete-time population model (Table 2) that could be applied to any population where 1) animals form breeding pairs, 2) animals are sexually mature adults by the start of the next breeding season after they are born or hatched, 3) survival and fecundity do not change with age once animals reach adulthood, and 4) survival and fecundity are not density dependent. The first 3 conditions clearly apply to North Island robins, and analyses of 12 years of data from the robin population on Tiritiri Matangi Island suggest that survival and fecundity are not age related in adult birds (Armstrong and Ewen 2002, Armstrong et al. 2002; D. P. Armstrong et al., Massey University, unpublished data). We did not incorporate density dependence, as density of the simulated populations always remained low (<1.1 birds/ha, compared to >4 birds/ha on Tiritiri Matangi [Armstrong and Ewen 2002]) over the time frames we considered.

Our model tracked the number of males and females alive at the start of the breeding season. There was no age structure in the model, as we considered all males or females alive at that time to have the same survival probabilities and expected fecundity rates.

We wrote the model as a spreadsheet in Microsoft® Excel (Microsoft Office Professional 2003; Microsoft, Redmond, Washington), where each row represented a different calculation done in a year (Table 2) and each column represented a different year. This spreadsheet approach offers many advantages for modeling wildlife populations, the most important being that the workings of the model are completely transparent and can be explained to managers (White 2000b). We parameterized the model using the functions obtained from analysis of the Paengaroa data (Table 1).

**Deterministic model with no uncertainty.**—We first obtained  $\lambda$  values for different tracking rates assuming parameter estimates (Table 1) were accurate and there was no demographic stochasticity (see Deterministic Model in Table 1). We took  $\lambda$  to be the relative number of females from one year to the next ( $F_t/F_{t-1}$ ), as is conventional when females are the limiting sex (White 2000b). If females are always paired, then  $\lambda$  is given by

$$\lambda = \hat{s}_f + \frac{1}{2}\hat{s}_j\hat{f}_p,$$

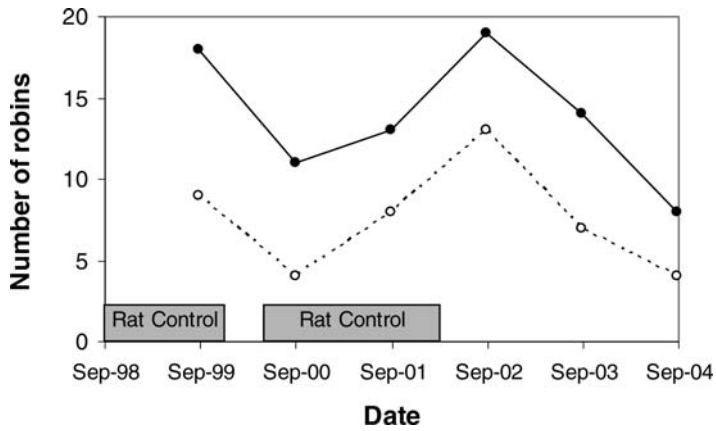
**Table 2.** Deterministic and stochastic models for projecting growth of North Island robin populations, Paengaroa Mainland Island, New Zealand.

Calculation <sup>a</sup>	Deterministic model <sup>b</sup>	Stochastic model <sup>b,c</sup>
No. breeding females	$F = F_1 + F_{2+}$	$F = F_1 + F_{2+}$
No. breeding males	$M = M_1 + M_{2+}$	$M = M_1 + M_{2+}$
No. pairs	$P = \min(M, F)$	$P = \min(M, F)$
No. unpaired females	$U = F - P$	$U = F - P$
No. juveniles produced	$J = f_p P + f_u U$	$J_p \sim \text{Poisson}(f_p P), J_u \sim \text{Poisson}(f_u U)$
No. first-year birds alive next year	$R = s_j J$	$R \sim \text{Binomial}[(J_p + J_u), s_j]$
No. first-year females alive next year	$F_1 = \frac{1}{2}R$	$F_1 \sim \text{Binomial}(R, 0.5)$
No. first-year males alive next year	$M_1 = \frac{1}{2}R$	$M_1 = R - F_0$
No. older females alive next year	$F_{2+} = s_f F_t$	$F_{2+} \sim \text{Binomial}(F_t, s_f)$
No. older males alive next year	$M_{2+} = s_m M_t$	$M_{2+} \sim \text{Binomial}(M_t, s_m)$

<sup>a</sup> Each row of the table corresponds to a row in a spreadsheet model, and the complete set of rows represents 1 yr.

<sup>b</sup> Functions for calculating vital rates are shown in Table 1.

<sup>c</sup> Includes demographic stochasticity in fecundity, survival, and sex allocation, but does not include environmental stochasticity.



**Figure 1.** Changes in the total population of North Island robins (black dots) and number of females (white dots) in the 5 yr after reintroduction to Paengaroa Mainland Island, New Zealand. Points show the numbers of birds known to be alive at the start of each breeding season (Sep). The Department of Conservation controlled rats and possums using brodifacoum cereal baits until Mar 2002, except for Dec 1999 to May 2000.

where  $\hat{s}_f$  is the annual survival of adult females,  $\hat{f}_p$  is the number of independent young per pair, and  $\hat{s}_i$  is survival from independence to adulthood. If females outnumber males at any stage,  $\lambda$  will also depend on  $\hat{s}_m$  (i.e., the annual survival probability of adult males) and  $\hat{f}_u$  (i.e., the number of independent young per unpaired female) and will change over time until the sex ratio stabilizes. We reported the  $\lambda$  values for stable sex ratios.

**Uncertainty in parameter estimates and model structure.**—To account for uncertainty in our estimates of vital rates, we sampled each vital rate from a distribution (Table 1) at the start of each run. We ran the model 10,000 times at each tracking rate to generate a distribution for  $\lambda$  (for discussion of this method, see White 2000a, Taylor et al. 2002, and Wade 2002). We assumed mean fecundity and survival probability to be log-normally distributed and logit-normally distributed, respectively (Table 1). We selected the transformed values using the Excel function NORMINV(probability,mean,standard\_dev), where probability is a uniform random number from 0 to 1 (selected using the function RAND()), and mean and standard\_dev are the estimate and standard error of the transformed value (shown in Table 1). We then back-transformed the values selected to obtain the parameters used in the run.

Our analysis of juvenile survival data (Armstrong et al. 2006) showed that it was ambiguous whether juvenile survival was constant or declined with tracking rate (Table 1). We therefore obtained distributions for  $\lambda$  under both juvenile survival models. In contrast, there was unambiguous support for one adult survival model and one fecundity model (Table 1), and we used these in all simulations.

**Demographic stochasticity.**—We modified the spreadsheet model to incorporate demographic stochasticity in survival, sex allocation, and fecundity (Table 2). We sampled numbers of survivors from the Binomial distribution using the function 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 (White 2000b). We used the same function to determine the number of female

recruits, with probability\_s set to 0.5. We sampled the total number of independent young produced by paired or unpaired females from the Poisson distribution using the Excel formula ROUND(GAMMAINV(probability,alpha,beta)), where alpha is the expected number based on the mean fecundity rate, and beta = 1 (the gamma distribution with  $\beta = 1$  is a continuous analog to the Poisson). We did not attempt to incorporate environmental stochasticity, as it is impossible to estimate accurately from small data sets (White 2000a), and its effects are swamped by demographic stochasticity in small populations (Leigh 1981).

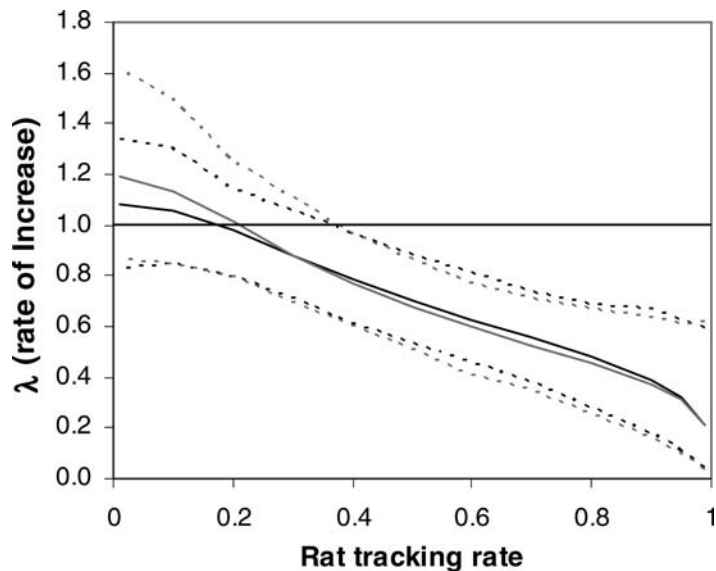
We initially ran the stochastic model using fixed values for vital rates. This allowed us to assess the probability of the population declining when  $\lambda$  was expected to be  $>1$ . Using 10,000 runs for each tracking rate, we estimated the probability of the number of females declining and the probability of the population becoming extinct (0 M or 0 F) over a 5-year time frame. We first ran simulations with an initial population of 4 males and 4 females, the number present at the start of the 2004–2005 breeding season, then did further simulations to assess the degree to which uncertainty could be reduced by increasing population size.

**Incorporating all forms of uncertainty.**—Our final step was to simultaneously incorporate uncertainty due to demographic stochasticity, parameter estimation, and model selection. For these simulations, we incorporated ambiguity in the juvenile survival model by randomly selecting 1 of the 2 models at the start of each run using the RAND() function. The AIC<sub>c</sub> weights for the 2 models were almost identical (Armstrong et al. 2006), hence the probability of either model being selected was 0.5 (this is a form of model averaging and produces similar results to the analytical method given by Buckland et al. 1997). We used these simulations to obtain a distribution for the number of females that would be present after 5 years at any tracking rate, accounting for all forms of uncertainty.

## Results

The Paengaroa robin population consisted of 18 birds (9 pairs) in September 1999, at the start of first breeding season after reintroduction (Fig. 1). The population had decreased to 11 birds by September 2000, but it increased to 19 birds over the next 2 years when rats were at low levels. Rat tracking gradually increased after brodifacoum baiting was stopped in March 2002, reaching 100% in September 2003, and there was a corresponding decline in the robin population. The population consisted of 8 birds (4 pairs) in September 2004.

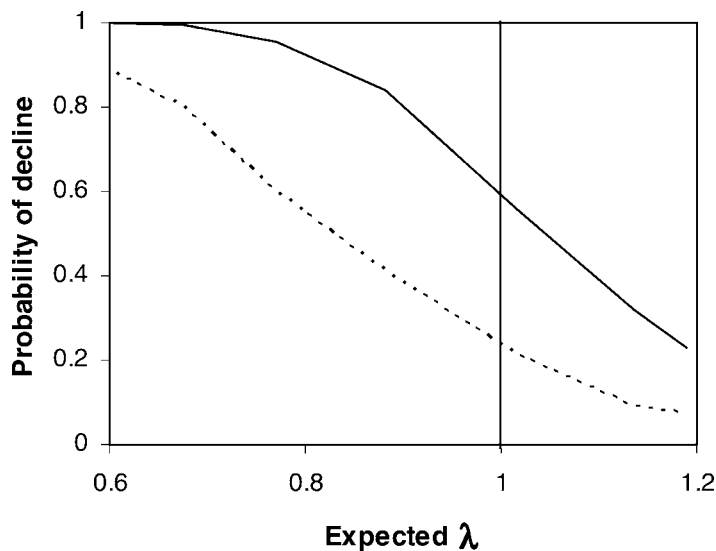
Deterministic calculations of  $\lambda$  suggest the rat tracking rate needs to be less than approximately 20% for the population to increase (i.e., for  $\lambda$  to be  $>1$ ). The ambiguity about the appropriate juvenile survival model (Table 1) makes little difference to this calculation, as  $\hat{\lambda} = 1.0$  when tracking was 18% under model A (where juvenile survival is constant) and when tracking was 21% under model B (where juvenile survival declines as rat tracking increases). However, model B predicted more generous rates of increase when rat tracking was reduced to low levels (Fig. 2). For example, with tracking reduced to 1%, model B predicted  $\lambda$  to be 1.19, corresponding to a 138% increase in population size over 5 years, whereas model A predicted  $\lambda$  to be 1.08, corresponding to a 47% increase over 5 years. The projected



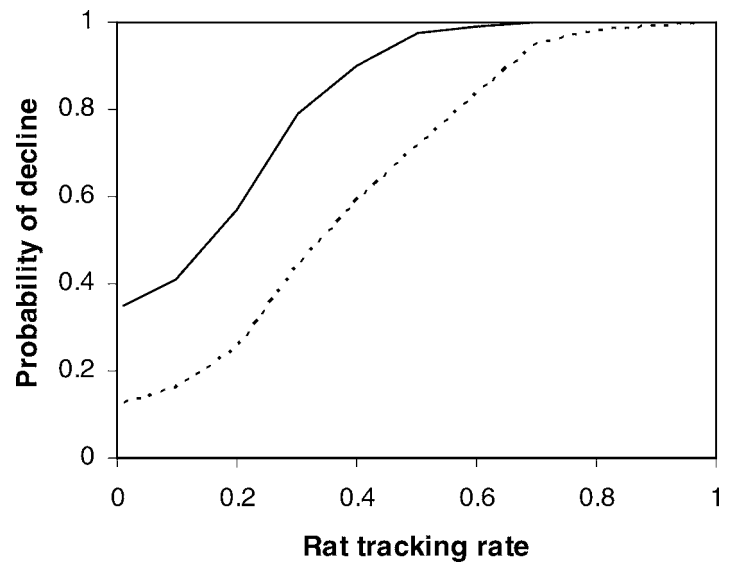
**Figure 2.** Expected rates of increase ( $\lambda$ ) of the North Island robin population, based on functional relationships between the population's vital rates and the rat tracking rate, Paengaroa Mainland Island, New Zealand. Solid lines show  $\lambda$  values calculated using the estimated values of the vital rates (Table 1), and broken lines show 95% CI for  $\lambda$  from 10,000 runs of a deterministic simulation model (Table 2) where each parameter is selected from a distribution (Table 1) at the start of each run. The black (model A) and gray (model B) lines are from simulations using different juvenile survival models.

growth was not much lower with rat tracking at 10%, with  $\hat{\lambda} = 1.06$  under model A and 1.14 under model B.

When we accounted for uncertainty in parameter estimates, it was unclear whether the population was likely to increase at any tracking rate. With rat tracking held to 1%, the 95% confidence interval for  $\lambda$  ranged from 0.84 to 1.35 under model A and from 0.87 to 1.63 under model B (Fig. 2). However, the confidence



**Figure 3.** Effect of demographic stochasticity on viability of the North Island robin population with an initial population of 4 pairs, Paengaroa Mainland Island, New Zealand. Lines show the probabilities of the number of females declining (solid line) or the population becoming extinct (broken line) over 5 yr based on 10,000 runs of a stochastic simulation model. Expected  $\lambda$  values were calculated using the deterministic model (Fig. 2). If  $\lambda$  is expected to be  $>1$ , declines are due to demographic stochasticity.



**Figure 4.** Probability of the North Island robin population declining over 5 yr starting with 4 pairs, accounting for all sources of uncertainty (parameter estimates, juvenile survival model, demographic stochasticity), Paengaroa Mainland Island, New Zealand. We obtained distributions for the numbers of robins after 5 yr using a stochastic simulation model (Table 2), with the juvenile survival model randomly selected at the start of run and the value of each parameter selected from a distribution (Table 1). The probability shown is the proportion of runs in which the number of females declined (solid line) or the population became extinct (broken line).

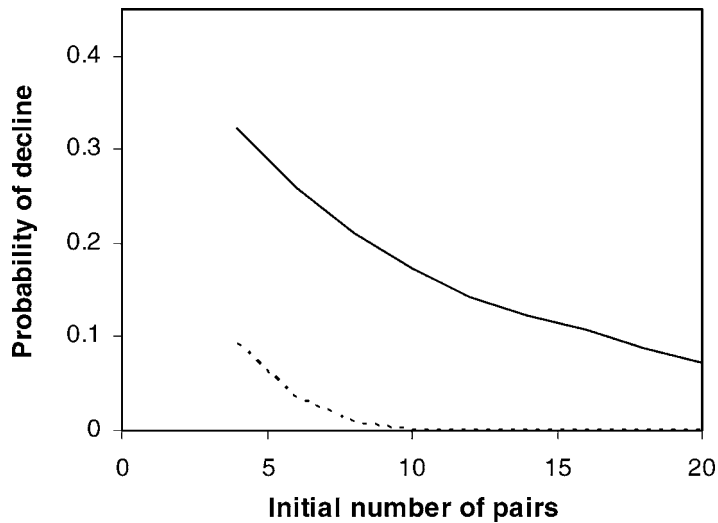
limits for  $\lambda$  were completely below 1 once tracking increased above 40%, suggesting that the robin population was guaranteed to decline under those conditions.

Demographic stochasticity also created a lot of uncertainty with an initial population of just 4 pairs. As noted above, if we treated parameter estimates as known, using model B for juvenile survival, and set tracking to 10%, then  $\lambda$  was expected to be 1.14, giving 8 females after 5 years. With demographic stochasticity, however, the actual number of females ranged from 0 to 17, and there was 32% probability that the number of females declined from the original 4 (Fig. 3). When we incorporated uncertainty in parameter estimates and the juvenile survival model in addition to demographic stochasticity, the 95% confidence interval for the number of females after 5 years ranged from 0 to 24, and there was a 41% probability that the number of females would decline (Fig. 4).

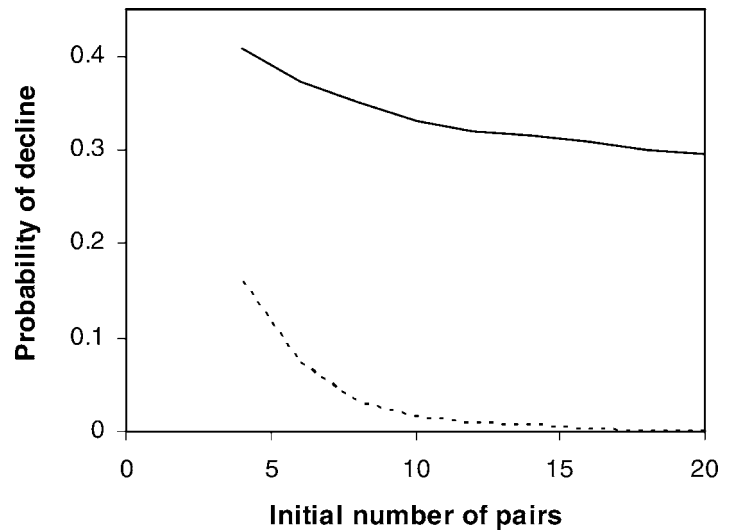
The uncertainty due to demographic stochasticity can be reduced somewhat by increasing the initial population size. If we set the tracking rate at 10% and treated population parameters as known, then an initial population of 20 pairs had a 7% probability of declining over 5 years, as compared to 32% for an initial population of 4 (Fig. 5). However, the effect of initial population size was less pronounced when all forms of uncertainty were incorporated. With an initial population of 20 pairs, there was a 30% probability that the number of females would decline after 5 years, as compared to a 41% probability of decline with an initial population of 4 pairs (Fig. 6).

## Discussion

Our analysis suggests that the rat tracking rate at Paengaroa Mainland Island needs to be  $<20\%$  for the reintroduced North



**Figure 5.** Effect of the initial number of pairs on the probability of the North Island robin population declining due to demographic stochasticity, assuming estimates of vital rates (Table 1) are accurate, Paengaroa Mainland Island, New Zealand. Rat tracking rate is set at 10%. Otherwise as for Fig. 3.



**Figure 6.** Effect of the initial number of pairs on probability of the North Island robin population declining, accounting for all sources of uncertainty, Paengaroa Mainland Island, New Zealand. Rat tracking rate is set at 10%. Otherwise as for Fig. 4.

Island robin population to grow (i.e., for  $\lambda$  to be  $>1$ ). When poison bait stations were maintained consistently, from 2000 to 2002, rat tracking rates at Paengaroa ranged from 0 to 9%. The effectiveness of control may vary from year to year because of natural fluctuations in rodent densities (Innes et al. 1995). However, our results suggest that it is quite feasible to maintain rats at levels sufficiently low to allow the robin population to grow. If rat tracking were maintained at about 10%, our analysis suggested the robin population would be most likely to grow at approximately 10% per year. If this were the case, the growth rate would ultimately decline toward 1 through density dependence as the population increased. Analysis of the reintroduced population on Tiritiri Matangi (Armstrong and Ewen 2002, Armstrong et al. 2002) suggested that robin populations were regulated by density dependence in juvenile survival in the absence of mammalian predators, and were likely to maintain relatively stable densities.

There was considerable uncertainty about our projections, however, as expected from data collected over 5 years for a small population. Because of uncertainty in parameter estimates, it was unclear whether the population was expected to grow at any tracking rate, and because of demographic stochasticity it was unclear whether the population would survive even if positive growth was expected. The problem of demographic stochasticity became even more acute following the deaths of 2 of the 4 remaining females during the 2004–2005 breeding season.

It is important to note that our uncertainty would be much greater if we had not collected data on vital rates. We could have calculated  $\lambda$  just from changes in the number of females each year (Fig. 1), giving values of 0.44, 2.00, 1.63, 0.54, and 0.57 for the 5 years. A predictive model could be obtained by regressing  $\ln(\lambda)$  against  $\ln(p)$  (using average tracking rate for each year). The resulting function would be  $\hat{\lambda} = 1.44p^{0.88}$ , suggesting the population will grow if the tracking rate ( $1 - p$ ) were  $<34\%$ . However, the confidence intervals would be so huge that the prediction would be meaningless. For example, with a 34% tracking rate the confidence interval for  $\hat{\lambda}$  would range from 0.20

to 4.94, in comparison to the confidence interval of 0.67 to 1.06 that we generated using data on vital rates (Fig. 2). Although it would save monitoring effort just to track population trends, many years of monitoring (e.g., 30+) are needed before reasonable predictions can be made using this approach (Elkinton 2000, Fieberg and Ellner 2000). If management decisions need to be made over shorter time frames, it is imperative that data on vital rates are collected.

Our projections are sufficiently precise to show that any robin population at Paengaroa Mainland Island would be doomed to extinction without predator control. Our modeling suggests a population would be guaranteed to decline if rat tracking were above 40%, and tracking rates have climbed to well over 40% since poison baiting was discontinued in March 2002. This result has implications for understanding the current distribution of robins and other species that have been partially extirpated from their former ranges following introduction of exotic mammals. Given that robins survive in many locations in the absence of predator control, and they tend to be found in large forest blocks, their absence from other areas could be attributed to metapopulation dynamics (Drechsler et al. 2003) rather than to differences in predator levels or other aspects of habitat quality. Recent research suggests that metapopulation dynamics are largely responsible for explaining local distributions of robins among small, unmanaged forest fragments in the central North Island (Y. Richard and R. L. Boulton, Massey University, unpublished data). However, our data for Paengaroa show that  $\lambda$  will be well below 1 if rats are not controlled, meaning the future absence of robins will be due to driven extinction (*sensu* Caughley 1994) rather than to stochastic extinction and failure to recolonize.

Populations can potentially be driven to extinction in small and isolated fragments because of dispersal into surrounding sink habitat (Basse and McLennan 2003). Such dispersal occurred to some extent at Paengaroa, as one juvenile was found 10 km from the reserve (dispersal is unlikely in adults, which are highly sedentary). Our survival models estimate local survival, and it is

unknown how much of the estimated juvenile mortality was due to emigration. In the absence of emigration, the most optimistic scenario would probably be for juvenile survival probability to equal the annual survival probability of adult males. Under this scenario, the maximum rat tracking rate that would allow positive growth was estimated to be 34% under model 1 (constant juvenile survival) or 28% under model 2 (juvenile survival declines from intercept value as rat tracking rate increases). Given that rat tracking rates at Paengaroa rose to >80% after cessation of control, it seems unlikely that the extirpation of robins from Paengaroa can be attributed to emigration alone. We therefore suspect that aspects of the habitat at Paengaroa reduce vital rates below those occurring at sites where robins are able to survive without predator control. It is possible that this inferior habitat quality was associated with edge effects (e.g., through increased predation rates or greater exposure [Murcia 1995]), but there are no New Zealand data available to assess this possibility.

It is also possible that the low density of the reintroduced population at Paengaroa contributed to low vital rates (i.e., that an Allee effect was operating). Allee effects can occur through several mechanisms (Courchamp et al. 1999), including higher per capita predation rates at low density. Such elevated predation may occur through increased hunting effort by predators, resulting in the classic Type II functional response of predator-prey theory. Sinclair et al. (1998) noted that if predation by exotic predators on native prey had a Type II functional response, then the level of predator control required at low densities would be higher than that required after populations recovered. It could also be argued that reintroductions should involve large numbers of founders to increase initial population density. However, we are skeptical about Type II functional responses occurring in North Island robins or other New Zealand birds threatened by exotic mammals. These bird species make up a tiny portion of the food taken by any predator species, so it is unlikely that predators would significantly change their hunting effort in response to density of these prey. We are also skeptical about other forms of Allee effects operating in North Island robins, given that they are distributed as individuals or pairs, meaning foraging and predator defense are largely unaffected by density and that they have shown themselves to be highly capable of seeking out mates. We therefore think it is unlikely that vital rates of robins would have increased with density, so we did not include such an effect in our simulation model.

Although the Paengaroa robin reintroduction has been unsuccessful at establishing a population, it has met Southgate's (1994) criterion for success in that it has provided information that can be used to improve future management. The methods we

developed can be extrapolated to any population where the species has a similar biology, and they can be used to relate population viability to predator tracking rates. The methods are therefore widely applicable to New Zealand mainland island programs (Saunders and Norton 2001), where the primary management is predator control, predator levels are measured by tracking rates, and key management objectives include maintaining viable populations of native forest birds.

## Management Implications

Our analysis showed that the North Island robin population at Paengaroa will inevitably decline to extinction if exotic predators are not controlled. This case study therefore illustrates the risk involved in reintroducing New Zealand species to mainland areas where ongoing predator control cannot be guaranteed. Such reintroductions may be justifiable on a local scale if there is reason to believe that absences are attributable to chance extinction, and therefore that reintroduction could provide a substitute for natural dispersal to ameliorate the effects of habitat fragmentation (Armstrong and McLean 1995, Lubow 1996). However, where a reintroduction constitutes a range extension, as was the case with Paengaroa, we suggest that policy needs to be in place to ensure the necessary predator control is continued.

Our analysis also showed that a robin population would be most likely to survive at Paengaroa if effective predator control were reinstated, but that its persistence could not be guaranteed under any level of control. It is not our role to decide whether predator control should be reinstated in such circumstances. However, the distributions of outcomes we reported provided the information necessary for the managers responsible to make an informed decision. If predator control is reinstated, translocation could be used to again reintroduce robins to Paengaroa should the remaining females die or to supplement the population to reduce the substantial risk of extinction through demographic stochasticity. The distributions of outcomes obtained under different initial population sizes would then provide managers with the information needed to make that decision. Our results therefore illustrate how quantification of uncertainty can be imperative for informed decisions about management of populations.

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