# Using Bayesian mark-recapture modelling to quantify the strength and duration of post-release effects in reintroduced populations

Doug P. Armstrong[a,*], Christie Le Coeur[b], Joanne M. Thorne[a], Julia Panfylova[a], Tim G. Lovegrove[c], Peter G. H. Frost[d], John G. Ewen[e]

[a] *Wildlife Ecology Group, Massey University, PB 11222, Palmerston North, New Zealand*

[b] *Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Sorbonne Universités, MNHN, CNRS, UPMC, 43 rue Buffon, CP51, 75005, Paris, France*

[c] *Auckland Council, Private Bag 92300, Victoria Street West, Auckland, New Zealand*

[d] *Science Support Service, 87 Ikitara Rd., Whanganui 4500, New Zealand*

[e] *Institute of Zoology, Zoological Society of London, Regent's Park, London, UK*

* Corresponding author at: Wildlife Ecology Group, Massey University, Palmerston North, New Zealand.

*E-mail addresses*: D.P.Armstrong@massey.ac.nz (D.P. Armstrong), christielecoeur@gmail.com (C. Le Coeur), jothorne78@gmail.com (J.M. Thorne), J.Panfylova@gmail.com (J. Panfylova), Tim.Lovegrove@aucklandcouncil.govt.nz (T.G. Lovegrove), pghfrost@xtra.co.nz (P.G.H. Frost), John.Ewen@ioz.ac.uk (J.G. Ewen).

## ABSTRACT

Translocated animals often suffer elevated mortality during some acclimation period after release. Such post-release effects must be accounted for when estimating normal survival rates and therefore predicting population persistence. The standard approach for doing this is to nominate a fixed acclimation period, and either i) exclude survival data over that period, or ii) use model selection criteria to test whether survival differs over that period. We present a more flexible approach where the acclimation period is treated as unknown and is estimated simultaneously with the pre- and post-acclimation survival probabilities. We illustrate this approach using survival data for six reintroduced populations involving three New Zealand forest bird species. Analyses of the complete data sets (22–73 surveys conducted over 4–14 years) indicated that significant post-release effects occurred in at least one sex in five of the six populations, with 30–84% mortality attributable to post-release effects over acclimation periods ranging from 1–9 months. When we applied the approach to just the first year of data for each population, the estimated normal survival rates were consistent with those obtained from the complete data sets, and always at least as accurate as our previous approach of excluding data up to the next breeding season after translocation. The flexible approach therefore appears to be effective for accounting for post-release effects in survival estimation, and is beneficial in quantifying both the strength and duration of those effects so that pre- and post-release management strategies are better informed.

*Keywords:* reintroduction; translocation; survival; mark-recapture; Bayesian; OpenBUGS

## 1. Introduction

The success of reintroduction projects may depend on factors affecting both short-term establishment or long-term persistence of populations (Sarrazin, 2007; Armstrong and Seddon, 2008; IUCN, 2013). Populations can potentially fail to establish despite habitat conditions that would allow long-term persistence if the populations survived the establishment phase. Consequently, it is useful to combine intensive short-term post-release monitoring with long-term monitoring, allowing threats to establishment to be quantified and modelled. These threats include Allee effects and demographic stochasticity, both of which are a function of small initial population sizes (Deredec and Courchamp, 2007). However, the biggest threat may be stresses associated with the translocation process (Maran et al., 2009; Dickens et al., 2010; Jenni et al., 2014) or subsequent acclimation to the reintroduction area (Moorhouse et al., 2009; Hamilton et al., 2010; Jachowski et al., 2011; Mihoub et al., 2011). The short-term increases in mortality or dispersal due to these stresses are called "post-release effects", and can strongly impact the short-term dynamics of reintroduced populations (Armstrong and Reynolds, 2012).

Failure to account for post-release effects may lead to pessimistic biases in population projections, and potentially to poor management decisions (Bar-David et al., 2005; Converse et al. 2013; Panfylova et al., 2016). For example, expensive management interventions might be undertaken in response to short-term declines despite those interventions being unnecessary for long-term growth. Examination of the recent literature suggests that reintroduction biologists generally appreciate the need to account for post-release effects when interpreting data on survival or apparent survival (the product of survival and fidelity). Of the survival studies conducted over time frames long enough to extend beyond the likely acclimation periods, most studies either explicitly accounted for post-release effects or used time-dependent models that could allow *post hoc* inferences about them (Table 1, Appendix A).

It is also important to estimate the impact of post-release effects when evaluating the numbers of individuals that need to be released and when comparing the effectiveness of different release strategies (Tavecchia et al., 2009). Tavecchia et al. (2009) used the term “cost of release” (*CoR*) to describe the proportion of the release group lost due to post-release effects, which is calculated by dividing the survival rate over some post-release period by the rate expected in the absence of post-release effects. Hamilton et al. (2010) used the term “acclimation period” to describe the duration of the post-release period in which survival is depressed, and distinguished between “post-release survival” and “post-acclimation survival”. For simplicity we refer to post-acclimation survival as “normal survival”.

It is necessary to have some idea of the likely acclimation period when making inferences about post-release effects. In studies that explicitly account for post-release effects (Table 1), the standard approach is to nominate a fixed acclimation period and either i) exclude survival data over that period (e.g., Normande et al., 2015; Ashbrook et al., 2016; Ranke et al., 2017), or ii) use model selection criteria to test whether survival differs from normal survival over that period, and differentiate the two if the difference is significant (e.g., Bertolero and Oro, 2009; Cochran- Biederman et al., 2015; Yu et al., 2015). In contrast, Tuberville et al. (2008) and Panfylova et al. (2016) used a more flexible approach whereby they nominated two alternative acclimation periods and used model averaging to incorporate this source of uncertainty. The extension of this approach is to treat the duration of the acclimation period as unknown, and estimate it from the data at the same time as the survival parameters are estimated.

This flexible approach is likely to be advantageous when the acclimation period is uncertain. If a fixed period is nominated, the estimate of the normal survival rate may be biased if the period is too short (because post-release effects are included) or unnecessarily imprecise if the period is too long (because too much of the data set is excluded). In addition, estimation of acclimation periods will allow management designed to reduce post-release effects to be conducted over appropriate time frames. While it is not possible to estimate the acclimation period in conventional survival models, such as those fitted in Program MARK (White and Burnham, 1999), it is possible with Markov Chain Monte Carlo (MCMC) procedures used in Bayesian modelling software.

We illustrate this approach by applying it to survival data for six reintroductions involving three New Zealand bird species: North Island robin (toutouwai, *Petroica longipes*), North Island saddleback (tīeke, *Philesturnus rufusater*), and hihi (stitchbird, *Notiomystis cincta*). We first used the complete data sets (≥ 4 years) to assess whether the flexible model appeared to give reasonable estimates of normal survival rates, pre-acclimation survival rates, duration of acclimation periods, and costs of release, and whether it fitted the temporal variation in survival shown in the data sets. We then tested whether the model gave comparable estimates of normal survival when fitted to just the first year of data, and compared these to those obtained when either a fixed or no acclimation period was assumed.

## 2. Methods

### *2.1 Species and reintroduction sites*

The three species are all endemic forest passerines that were historically distributed throughout the North Island of New Zealand as well as on some offshore islands, but declined from most of their original ranges after invasion by exotic predatory mammals. North Island robins persisted in some parts of the North Island, whereas North Island saddlebacks and hihi were reduced to a single island population. The three species have similar life histories, as they are territorial and non-migratory, become sexually mature in their first year, and have two or more clutches over a breeding season extending from about September to March. The North Island robin (c. 28 g) and North Island saddleback (c. 90 g male, c. 70 g female) are both monogamous and relatively monomorphic between sexes (Higgins and Peter, 2002). In contrast, the hihi (c. 40 g male, c. 32 g female) has a variable mating system involving frequent extra-pair copulation, and is sexually dimorphic in plumage. Robins are almost exclusively insectivorous, whereas hihi feed extensively on nectar and fruit as well as invertebrates, and saddlebacks, which are largely insectivorous, also feed on nectar and fruit to some extent. All three species have been reintroduced to several sites where mammalian predators have been eradicated or intensively controlled (Miskelly and Powlesland, 2013).

The six reintroductions were to four sites: Tiritiri Matangi (36°36'S, 174°53'E), a 220-ha island 28 km N of Auckland; Mokoia (38°05'S, 176°17'E), a 135-ha island in Lake Rotorua; Bushy Park (39°48’S, 174°56’E), a 87-ha forest block in an isolated mainland reserve 24 km NW of Whanganui; and Wenderholm (36°33’S, 174°43’E), a 60-ha forest block in a mainland reserve 48 km N of Auckland. The first three sites are free of predatory mammals (rats, cats, mustelids) due to the ocean barrier surrounding the islands and an exclusion fence surrounding Bushy Park. These predators are controlled to low densities at Wenderholm through trapping and poisoning (Lovegrove et al., 2002). Pacific rats (kiore, *Rattus exulans*) were present on Tiritiri Matangi at the time of the robin reintroduction, but were eradicated through an aerial poison drop in September 1993. This rat species was not expected to prey on adult robins, but the poison operation caused some robin mortality so needed to be account for in the survival analysis. A similar poison operation needed to be accounted for in the survival analysis for Mokoia saddlebacks.

No dispersal was expected from the first three sites due to their isolation in relation to the dispersal capabilities of the bird species, and none was observed (hihi at Bushy Park were fitted with radio transmitters). Dispersal of robins from Wenderholm was much more likely, hence all habitat within 2 km of the reserve was searched in the initial surveys, and the one male found outside the reserve was included in subsequent monitoring. Consequently, the estimated survival rates probably represent true survival, and we therefore refer to “survival” rather than “apparent survival” for the sake of simplicity.

The reintroductions occurred between 1992 and 2013, with 21-58 birds released per population over one or two releases (Table 2). The birds were translocated from wild source populations at four sites: Tiritiri Matangi, Mokoia, Hauturu, a 3800-ha island 80 km NE of Auckland (36°12'S, 175°04'E), and the Mamaku Plateau (38°2'-38°6'S, 175°57'-176°3'E), a mainland area 15 km NW of Rotorua (Table 2). They were captured using mist nets (saddlebacks, hihi), cage traps at feeders (hihi), or clap traps (robins); colour-banded with individual combinations; and temporarily held in aviaries (saddlebacks, hihi) or individual boxes (robins) at the source site. They were then transported to the release site by some combination of boat, car, and/or helicopter. In five of the six reintroductions, the birds were released < 24 h after arriving at the release site and the time from capture to release was < 4 days. In contrast, most of the saddlebacks reintroduced to Bushy Park were held at the release site for 18-33 days for quarantine. Four saddlebacks were held at Auckland Zoo for six months to be treated for malaria, but these were excluded from the analysis. Further details of these translocations are given by Armstrong (1995), Armstrong and Craig (1995), Armstrong et al. (2002), Lovegrove et al. (2002), Thorne (2007), and Frost (2013).

### *2.2 Monitoring*

The six populations were selected because all had at least monthly survival surveys conducted in the first six months after release, and at least two surveys per year for the first four years (Table 2), making these good data sets for modelling the strength and duration of post-release effects. The number of years of data ranged from 4–14, and the number of surveys ranged from 22–73. The six data sets are available in Appendix B.

Each survey involved one or more observers walking through all forested portions of the island or reserve and recording which individuals were re-sighted (equivalent to being recaptured). We used playback of territorial calls to attract robins but not the other species. The transect lines walked were sufficiently close (< 100 m apart) to give a high probability of detecting any individual. Search effort was consistent among surveys.

In four of the six populations, we only used data from the translocated birds, which ranged from 21–58 individuals (Table 2). However, the high post-release mortality of female hihi (see Results) meant that there were few translocated females left to provide estimates of long-term survival rates. Consequently, the data sets for the two hihi populations also included birds produced at the reintroduction site over the duration of the study. These birds only entered the data set when encountered as late juveniles (March survey, Bushy Park) or adults (September survey, Tiritiri Matangi), avoiding early juveniles which are known to have lower survival (Low and Pärt 2009; Panfylova et al., 2016). The code (see below) included a distinction between translocated and non-translocated individuals so that post-release effects were only applied to the former.

The translocations, banding and monitoring were done under a set of permits issued by the New Zealand Department of Conservation.

### *2.3 Modelling*

We modelled the encounter history for each population separately, using code written in OpenBUGS version 3.2.3 (Lunn et al., 2009; Spiegelhalter et al., 2014) (Appendix B). The code was a modification of the state-space formulation of the Cormack-Jolly-Seber model, in which the survival status of each individual is modelled as a series of missing values after it was last observed (McCarthy, 2007; Schofield et al., 2009; Kéry and Schaub, 2012). Re-sighting probability ($p$) was allowed to vary randomly among surveys (following a logit-normal distribution) but was assumed to be constant among individuals.

As in all survival models with an acclimation period, survival probability was modelled as a step function whereby it changed to a new value at the end of that period. Our model allowed males and females to differ both in their long-term survival probabilities and the strength of the post-release effect, but constrained the acclimation period to be equal for the two sexes. These effects were modelled with a logit link function. The full survival model therefore took the form

$$\log\left(\frac{\phi}{1-\phi}\right) = \begin{cases} \alpha + \beta_r + \beta_s + \beta_{rs} & \text{if } t < T \\ \alpha + \beta_s & \text{otherwise} \end{cases} \tag{1}$$

where $\phi$ is survival probability, $\alpha$ is the intercept, $\beta_r$ is the post-release effect, $\beta_s$ is the sex effect, $\beta_{rs}$ is the interaction between these effects, $t$ is the time since release, and $T$ is the duration of the acclimation period. The code allowed $T$ to occur between encounter occasions, meaning part of the interval between those occasions would have the post-release survival probability and the remainder of the interval would have the normal survival probability.

The results of the full model fitting are shown in Appendix C. If the 95% credible interval (CI) for $\beta_{rs}$ did not include zero, we re-ran the model with separate post-release effects for each sex. We reduced the model by removing $\beta_s$ and/or $\beta_r$ if the 95% CI for these effects included zero. We then used the final model to estimate the remaining parameters, and to simultaneously derive the cost of release, which is given by

$$CoR = 1-(\phi_1/\phi_2)^T \tag{2}$$

where $\phi_1$ is the post-release survival probability and $\phi_2$ is the normal probability of surviving the same time period (Table 3).

For robins, sexes of some individuals were unknown and so were modelled as missing values. This imputation was informed by data on tarsus length and plumage darkness (binary score) which were both known to be sex-related (Armstrong, 2001). For Tiritiri Matangi robins and Mokoia saddlebacks, the model also included a “poison effect” for the intervals immediately after the poison operations on those islands (September-October 1993 and September October 1996 respectively) to account for the additional mortality caused.

Uninformative priors were used for all parameters estimated, and two chains run to assess convergence via standard MCMC diagnostics (Link and Barker, 2010: 70). The priors for the survival and re-sighting parameters were normally distributed with mean 0 and precision 0.01, and the prior for the standard deviation of logit($p$) was uniformly distributed from 0-10. For the flexible model, the prior for $T$ was uniformly distributed between 0 and the duration of the study.

To assess whether the model gave reasonable fit to the temporal variation in survival in the data sets, we compared the output obtained from a model with a random time effect for survival as well as re-sighting probability.

After modelling the complete data sets, we re-ran the models using just the first year of data, comparing output from the flexible model to that obtained when $T$ was fixed. In the latter case $T$ was the time elapsed until the start of the next breeding season after release, as this is the approach we had used previously (e.g., Armstrong et al., 2002), or alternatively set $T$ to zero, meaning there was no acclimation period.

## 3. Results

In most populations, survival was clearly reduced for some period after release in one or both sexes (Table 3). The exception was the Mokoia saddleback population. In the other robin and saddleback populations, the estimated *CoR* ranged from 0.30 to 0.38, meaning about 30–38% of the release group was lost due to post-release effects, and the results were consistent for males and females. In contrast, the *CoR* was extremely high (0.80–0.84) among females in both hihi populations, but males had a significantly lower *CoR* (0.50 on Tiritiri Matangi) or no detectable post-release effect (Bushy Park).

The estimated acclimation period (*T*) ranged from 0.07–0.77 years (1–9 months) in the populations where the posterior distributions for *T* had clear upper and lower bounds (Table 3, Fig. 1). In Bushy Park hihi, the high female mortality in the first 6 months, combined with no post-release effect in males, meant there were too few surviving females (4) to constrain the upper portion of the posterior distribution. Nevertheless, the acclimation period was clearly much longer for Bushy Park hihi (≥ 6 months) than Tiritiri Matangi hihi (1 month) despite the similarly high *CoR*.

The mean re-sighting probabilities (with SE) were 0.86 (0.02) for Tiritiri Matangi robins, 0.83 (0.05) for Wenderholm robins, 0.52 (0.03) for Mokoia saddlebacks, 0.85 (0.03) for Bushy Park saddlebacks, 0.90 (0.02) for Tiritiri Matangi hihi, and 0.65 (0.03) for Bushy Park hihi.

The MCMC chains showed good convergence for all populations, both for the full model and reduced models. However, the numbers of samples required varied greatly depending on the complexity of the data sets, hence the burn-ins ranged from 1,000–50,000 samples and the subsequent chain lengths from 30,000–100,000 samples (Appendix C). The resulting posterior distributions for the survival and re-sighting parameters were all smoothly concave. The posterior distributions for $T$ had varying degrees of polymodality (Fig. 1), which reflected the temporal distribution of our surveys. However, the posterior distributions for the derived parameter $CoR$ were smoothly concave, and there were no apparent correlations between $T$ and $CoR$ in any population.

The temporal patterns in survival produced by the random effects model indicate that the estimated step functions fitted the observed post-release changes in survival reasonably well (Fig. 2). Although there was probably additional temporal variation, the time-specific estimates are within the range of sampling error when we consider the uncertainty in these estimates as well as the uncertainty in pre- and post-acclimation survival probabilities.

When applied to just the first year of data for each population, the flexible model produced posterior distributions for survival parameters that were consistent with those obtained from the complete (≥ 4 year) data set. Although the normal survival rate tended to be underestimated to some extent, the 95% credible interval always included the estimate from the complete data set (Fig. 3). This was also the case when fixed acclimation periods were used, but the flexible model always performed at least slightly better in terms of the distributions produced. The flexible model also allowed a reasonable, albeit imprecise, estimate of the normal female survival on Tiritiri Matangi based on just one year of data, whereas no estimate was possible with the fixed acclimation period that had previously been assumed. The model with no acclimation period produced extremely biased survival estimates for all populations with significant post-release effects (Fig. 3).

## 4. Discussion

Our results suggest that the flexible approach presented here provides a promising method for quantifying post-release effects when modelling survival of reintroduced populations. The model fitting appeared to work well based on standard diagnostics, fitted the temporal patterns in the data reasonably well, and produced meaningful results. The modelling revealed significant post-release effects in five of the six datasets, indicated that cost of release (*CoR*) ranged from about 30–84% depending on the population and sex, and indicated that post-release acclimation periods (*T*) ranged from about 1–9 months. Interestingly, high *CoR* was not correlated with longer acclimation periods in these populations. This is particularly evident in the hihi populations reintroduced to Tiritiri Matangi and Bushy Park, which differed widely in the duration of the acclimation period despite the estimated *CoR* for females being similarly high at both sites. This may reflect different mechanisms, as competition with bellbirds (*Anthornis melanura*) is likely to have been an issue on Tiritiri Matangi, and predation by falcons (*Falco novaeseelandiae*) is likely to have been an issue at Bushy Park. Such variation in the strength, duration and sex-specificity of post-release effects can potentially be attributed to release methods, habitat (including site management such as predator control), seasonal effects and weather conditions (Tavecchia et al., 2009; McCarthy et al., 2012; Hardouin et al., 2014). As such, the parameter estimates provide qualitative information that can be used to develop hypotheses about the mechanisms underlying the effects as well as quantitative information essential for ongoing management of the populations.

The flexible approach worked well for producing reliable survival estimates from just one year of data, which is an important finding given that survival over the first year is a standard metric reported for reintroduced populations (Sutherland et al., 2010). In comparison, the standard method of nominating a fixed acclimation period *a priori* performed slightly less well, and ignoring the acclimation period generally produced extremely biased estimates. The performance of models using a fixed acclimation period will depend of course on how accurate the nominated period is. The results show that our previous approach, whereby the acclimation period was assumed to extend to the next breeding season, worked reasonably well. However, there will often be considerable uncertainty about the duration of the acclimation period, and in these cases the flexible approach will be clearly advantageous. We suspect that the main reason that previous researchers have not estimated the acclimation period (Table 1, Appendix A) is that it is difficult to do this with conventional survival models.

The approach we have presented is an extension of that used by Tuberville et al. (2008) and Panfylova et al. (2016), both of whom used model averaging in Program MARK to incorporate uncertainty about the acclimation period. Our more flexible approach is a form of Bayesian model averaging (Barker and Link, 2015) in that we specify a metamodel with an infinite number of acclimation periods ranging from 0 to the length of the study, and the MCMC iterations perform model averaging over that state space. People preferring to use Program MARK could approximate the same approach by averaging over many of discrete models with different acclimation periods. However, the Bayesian updating framework allows a more natural approach, and has other advantages such as facilitating the modelling of missing values and the use of informative priors.

Our approach is still relatively simple in that the post-release effect on survival is approximated by a simple step function, the acclimation period is assumed to be the same for the two sexes, and survival is assumed to be constant among individuals of the same sex. In reality, the decline in post-release effects may be gradual, and individual variation is expected in both their strength and the duration. Ignoring such complexity may lead to bias in parameter estimates and population projections (Vaupel et al., 1979; Robert et al., 2003; Acker et al., 2014). In particular, if there is reason to believe that survival increases with age, it is important to avoid confounding post-release and age effects given that the ages of the translocated animals increase with time since release. Future research could explore the use of more complex models, including using more complex functions for post-release effects and incorporating random individual. However, fitting such models would require large data sets in terms of numbers of individuals and frequency of surveys; the former is rare for reintroduced populations. Even with high-quality data sets and high re-sighting probabilities, the degree of uncertainty in the temporal patterns in the data (Fig. 2) is sufficiently high that we probably would not have found support for models with more realistic levels of complexity. The appropriateness of alternative modelling approaches for different scenarios could potentially be explored through simulation studies.

The relatively simple approach we have presented provides the essential information needed for managing reintroduced populations without the need to assume the duration of the acclimation period. First, it allows unbiased estimates of normal survival probability that can be used to predict future population trajectories, informing long-term management needs (Converse et al., 2013). Second, it quantifies the *CoR*, which is essential for deciding what numbers to release in future translocations, conducting any genetic management based on the founder group size (Weiser et al., 2012), and for adaptive management designed to reduce post-release effects (Canessa et al., 2016). Finally, it allows quantification of the acclimation period, meaning post-release management designed to reduce post-release effects can be conducted over appropriate time frames and monitoring programs designed accordingly.

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## Appendix A. Literature search

## Appendix B. OpenBUGS code and data

## Appendix C. Results of full model fitting

Supplementary data associated with this article can be found, in the online version, at…

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**Table 1**

Summary of approaches used to account for post-release effects in recent analyses of survival rates in reintroduced populations. The figures show numbers of studies using each approach among 79 articles found by searching the Web of Science for the terms ((translocat* OR reintroduc*) AND survival AND population AND monitoring) for the period 2007-2017 (see details and the reference list in Appendix A).

| Approach | Modelled | Described | Total | Explanation |
|---|---:|---:|---:|---|
| Exclude hypothesised acclimation period | 8 | 1 | 9 | Excluded data collected during hypothesised acclimation period or did a separate analysis of those data |
| Test for hypothesised acclimation period(s) | 15 | 3 | 18 | Used formal model selection or other criteria to test for hypothesised acclimation period(s), and distinguish from normal survival if found significant |
| Time-dependence | 23 | 3 | 26 | Modelled or described changes in survival over time (most commonly by year), potentially allowing *post hoc* inferences about acclimation periods |
| Not considered | 4 | 6 | 10 | No apparent consideration of post-release effects |
| Acclimation period only | 8 | 8 | 16 | Survival rates were only estimated shortly after the release, so there was no attempt to estimate the normal survival rate for the population |
| Total | 58 | 21 | 79 | |

**Table 2**

Summary of post-release monitoring data for the six reintroduced bird populations used in this study.

| Species | Reintro. site | Source site | Release | Date | No. released | | | | No. surveys | | | Years of data |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Female | Male | Unk. | Total | 1st mo. | 1st year | Total | |
| Robin | Tiritiri Matangi | Mamaku Plateau | 1st | Apr 1992 | 7 | 25 | 12 | 44 | 2 | 16 | 51 | 14 |
| | | | 2nd | Jun 1993 | 7 | 3 | 4 | 14 | 1 | 8 | 34 | 13 |
| Robin | Wenderholm | Tiritiri Matangi | 1st | Mar 1999 | 9 | 11 | 1 | 21 | 2 | 9 | 22 | 7 |
| Saddleback | Mokoia | Tiritiri Matangi | 1st | Apr 1992 | 16 | 20 | 0 | 36 | 1 | 14 | 73 | 6 |
| Saddleback | Bushy Park | Mokoia | 1st | Jun 2006 | 12 | 22 | 0 | 34 | 3 | 15 | 57 | 4 |
| | | | 2nd | Dec 2006 | 2 | 2 | 0 | 4[a] | NA | NA | NA | NA |
| Hihi | Tiritiri Matangi | Hauturu | 1st | Sep 1995 | 19 | 21 | 0 | 40[b] | 2 | 20 | 40 | 10 |
| | | | 2nd | Aug 1996 | 9 | 4 | 0 | 13[b] | 2 | 5 | 21 | 9 |
| Hihi | Bushy Park | Tiritiri Matangi | 1st | Mar 2013 | 21 | 23 | 0 | 44[b] | 1 | 16 | 30 | 4 |

[a] These birds were excluded from the analysis, as their release was delayed due to being diagnosed with malaria.

[b] Because of the small number of females that survived the acclimation period, the analysis for these populations also included birds produced at the reintroduction site (259 Tiri, 49 Bushy Park); to avoid age-related bias, these birds were considered to enter the population as late juveniles (March, Bushy Park) or adults (September, Tiritiri Matangi) to be comparable with the translocated birds.

**Table 3**

Estimated post-release effects for each of the six reintroduced populations based on modelling of the complete data sets. The estimated parameters are $\alpha$, the logit of the normal annual survival probability, $\beta_r$, the reduction in logit survival probability during the acclimation period, and $T$, the duration of the acclimation period (see Equation 3). These are used to derive the survival rates that occurred during ($\phi_1$) and after ($\phi_2$) the acclimation period, and the cost of release (*CoR*) which is given by $1-(\phi_1/\phi_2)^T$. Sex effects and post-release effects were removed if the 95% confidence interval included zero (Appendix C). Standard errors are shown in parentheses.

| Species | Reintro. site | Sex | T (years) | $\alpha$ | $\beta_r$ | $\phi_1$ (annual) | $\phi_2$ (annual) | *CoR* |
|---|---|---|---|---|---|---|---|---|
| Robin | Tiritiri Matangi | F/M | 0.27 (0.07) | 1.36 (0.18) | -3.09 (1.46) | 0.21 (0.13) | 0.79 (0.03) | 0.30 (0.09) |
| Robin | Wenderholm | F/M | 0.37 (0.69) | 1.30 (0.33) | -2.43 (0.97) | 0.28 (0.16) | 0.78 (0.05) | 0.38 (0.14) |
| Saddleback | Mokoia | F/M | NA | 1.86 (0.26) | NA | NA | 0.86 (0.03) | NA |
| Saddleback | Bushy Park | F/M | 0.77 (0.22) | 1.18 (0.33) | -1.54 (0.51) | 0.42 (0.10) | 0.76 (0.06) | 0.36 (0.12) |
| Hihi | Tiritiri Matangi | F | 0.07 (0.003) | 0.63 (0.15) | -23.6 (4.60) | 6.7E-8 (5.7E-7) | 0.65 (0.03) | 0.80 (0.07) |
|  |  | M |  | 0.68 (0.10) | -10.59 (2.82) | 7.0E-4 (1.2E-3) | 0.68 (0.03) | 0.50 (0.10) |
| Hihi | Bushy Park | F | 1.29 (0.86) | -0.10 (0.38) | -2.14 (0.76) | 0.11 (0.06) | 0.48 (0.09) | 0.84 (0.14) |
|  |  | M | NA | 0.38 (0.25) | NA | NA | 0.59 (0.06) | NA |

**Fig. 1.** Posterior distributions for the duration of the acclimation period (years) in the five reintroduced populations where post-release effects were detected.

**Fig. 2.** Fit of estimated post-release effects to temporal patterns of survival in six reintroduced populations. Dots show changes in survival probability (on an annual time frame) based on a model where time is treated as a random effect, with vertical bars showing 95% credible intervals. Dashed lines show the fitted step functions, where survival probability changes after an acclimation period that is estimated from the data (the uncertainty around those functions is omitted to avoid clutter). There were two translocations of robins and hihi to Tiritiri Matangi Island, so separate step functions are shown for these translocations. Females (black) and males (grey) are shown separately for the two hihi populations due to significant sex differences in post-release effects, whereas data for the other populations show males and females combined. The intervals immediately after the poison drops on Tiritiri Matangi and Mokoia are excluded from the graph to avoid clutter (see Methods).

**Fig. 3.** Comparison of three approaches for estimating survival rates of reintroduced populations based on short-term data. The black bars show the normal annual female survival probability estimated based on the complete data set for each population (Table 1, Table 2). The remaining bars show estimates based on the first year of data using three different approaches: 1) estimating the duration of the acclimation period (dark grey); 2) assuming the acclimation period extends to the next breeding season after release (light grey); or 3) assuming there is no acclimation period (white). The second approach was not applicable to the Tiritiri Matangi hihi population because birds were reintroduced at the start of a breeding season, meaning the acclimation period was assumed to last a full year under that approach. Error bars show 95% credible intervals.

Figure 1

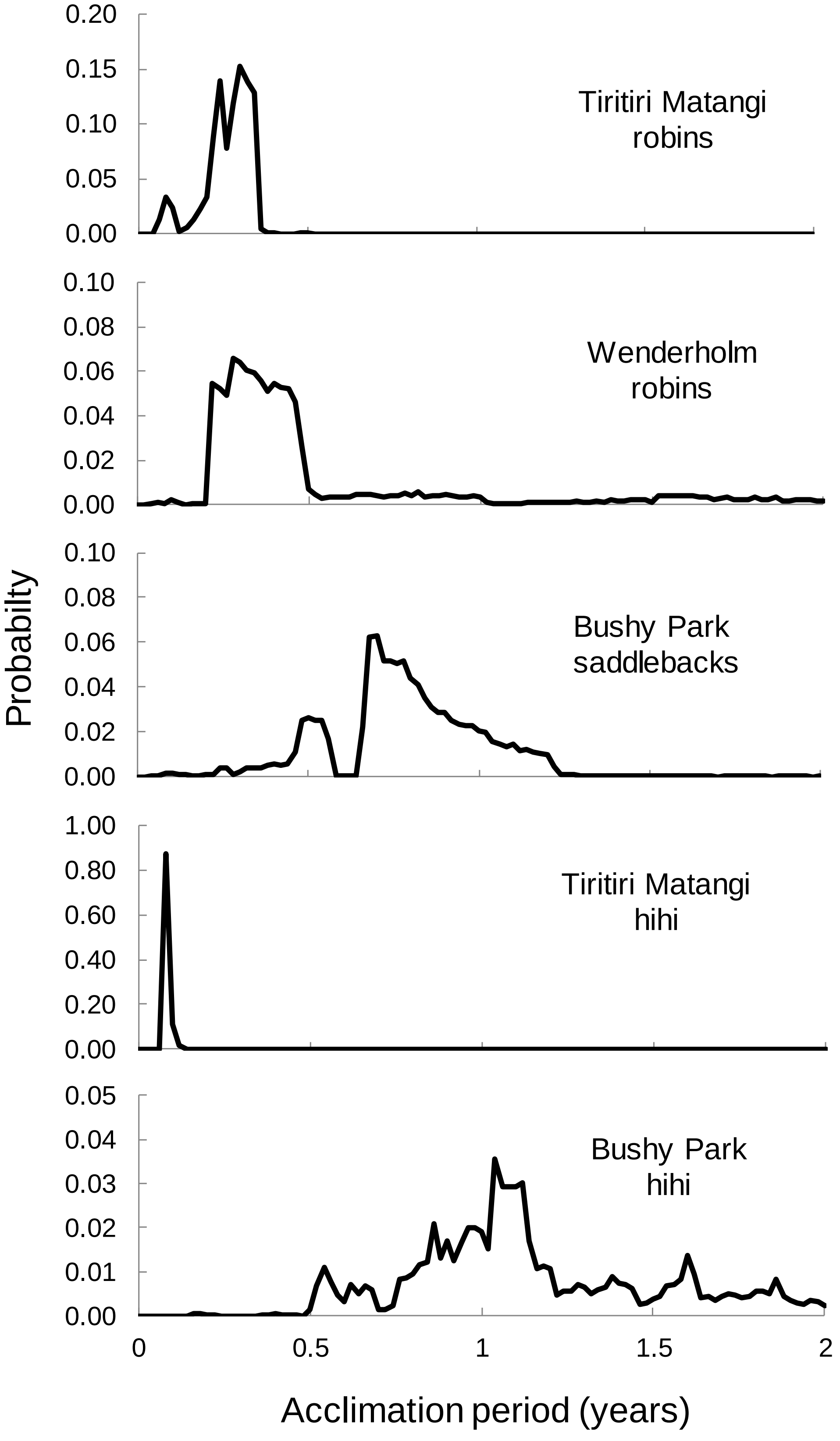

0.20
0.15
0.10
0.05
0.00
Tiritiri Matangi robins
0.10
0.08
0.06
0.04
0.02
0.00
Wenderholm robins
0.10
0.08
0.06
0.04
0.02
0.00
Bushy Park saddlebacks
1.00
0.80
0.60
0.40
0.20
0.00
Tiritiri Matangi hihi
0.05
0.04
0.03
0.02
0.01
0.00
Bushy Park hihi
Probabilty
0
0.5
1
1.5
2
Acclimation period (years)

Figure 2

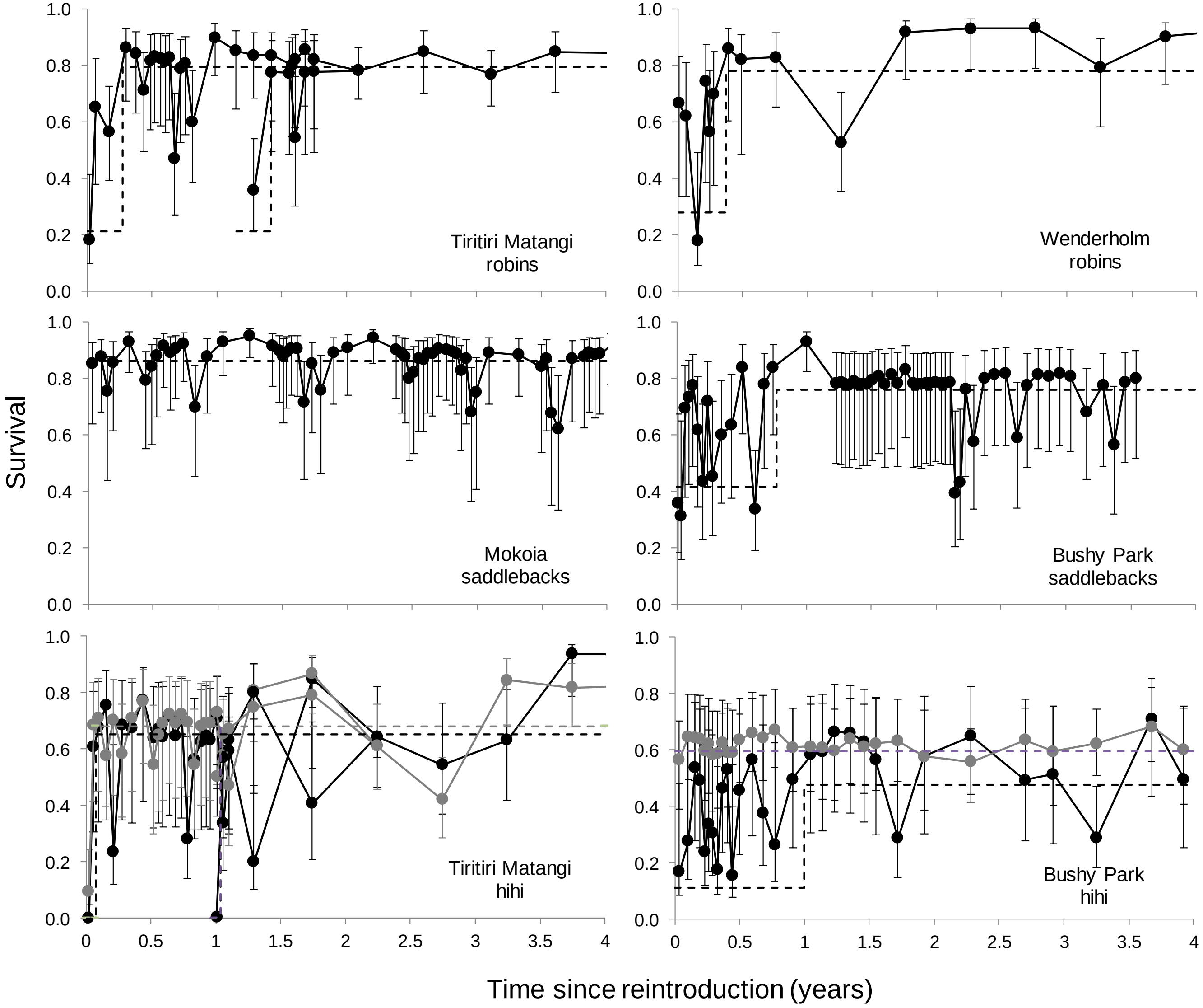
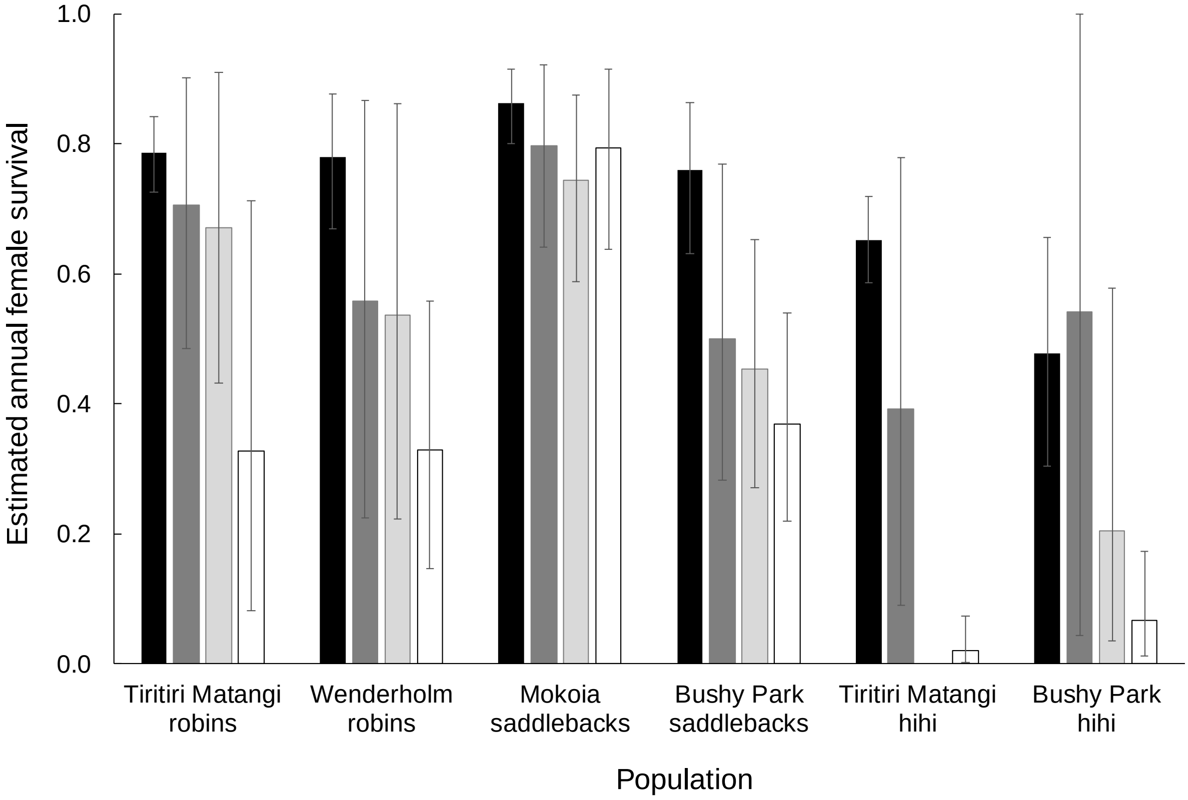

Survival
Time since reintroduction (years)
Tiritiri Matangi robins
Wenderholm robins
Mokoia saddlebacks
Bushy Park saddlebacks
Tiritiri Matangi hihi
Bushy Park hihi
0.0
0.2
0.4
0.6
0.8
1.0
0
0.5
1
1.5
2
2.5
3
3.5
4

Figure 3



1.0
0.8
0.6
0.4
0.2
0.0
Estimated annual female survival
Tiritiri Matangi robins
Wenderholm robins
Mokoia saddlebacks
Bushy Park saddlebacks
Tiritiri Matangi hihi
Bushy Park hihi
Population