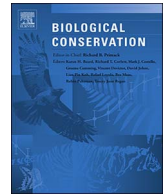




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Using Bayesian mark-recapture modelling to quantify the strength and duration of post-release effects in reintroduced populations



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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 to 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.

1. Introduction

The success of reintroduction projects may depend on factors affecting both short-term establishment and 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 (Dereced 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

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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	

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 Powesland, 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,

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