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Combining prior and post-release data while accounting for dispersal to improve predictions for reintroduction populations

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Abstract

Attempts to reintroduce species to managed areas may be compromised by dispersal into the surrounding landscape. Therefore, decisions regarding the selection and ongoing management of reintroduction areas require predicting dispersal as well as the survival and reproduction rates of the species to be reintroduced. Dispersal can potentially be measured directly by tracking animals, but this is often impractical. However, dispersal can also be inferred from re-sighting surveys done within reintroduction areas if such data are available from multiple areas with varying connectivity to the surrounding landscape, allowing apparent survival and recruitment to be modelled as a function of connectivity metrics. Here, we show how data from 10 previous reintroductions of a New Zealand passerine, the toutouwai (*Petroica longipes*), were used to predict population dynamics at a predator-controlled reintroduction area with high connectivity, and predictions then updated using post-release data. Bayesian hierarchical modelling of the previous data produced prior distributions for productivity, adult survival and apparent juvenile survival rates that accounted for random variation among areas as well as rat density and connectivity. The modelling of apparent juvenile survival as a function of connectivity allowed it to be partitioned into estimates of survival and fidelity. Bayesian updating based on post-release data produced posterior distributions for parameters that were consistent with the priors but much more precise. The prior data also allowed the recruitment rate estimated in the new area to be partitioned into separate estimates for productivity, juvenile survival and juvenile fidelity. Consequently, it was possible to not only estimate population growth under current management, but also predict the consequences of reducing the scale or intensity of predator control, facilitating adaptive management. The updated model could then be used to predict population growth as a function of the connectivity and predator control regime at proposed reintroduction areas while accounting for random variation among areas.

Introduction

Reintroduction biology aims to improve predictive capacity so that reintroductions and other conservation translocations can effectively recover species and restore ecosystems (Ewen *et al.*, 2012; Gaywood *et al.*, 2023). The poor success rate of early reintroduction programmes (Campbell & Wilcox, 1980; Lyles & May, 1987; Dodd & Seigel, 1991) led to numerous calls for increased monitoring to improve predictions (IUCN, 1987; Scott & Carpenter, 1987; Kleiman, 1989). With minimal monitoring, it was still possible to analyse apparent success rates in relation to variables recorded (Griffith *et al.*, 1989; Copley, 1995), and these analyses emphasized the need to consider key factors such as habitat requirements. Such analyses remain useful in situations where numerous reintroductions are being attempted with poor understanding of the conditions needed for success (Cochran-Biederman *et al.*, 2015; Bellis *et al.*, 2019; Choquette *et al.*, 2022), but give little capacity to predict the fates of reintroduced populations.

Improved post-release monitoring has allowed vital rates (survival, reproduction and dispersal) to be estimated, resulting in the development of models to predict the dynamics of many reintroduced populations (Armstrong & Reynolds, 2012; Converse & Armstrong, 2016; Hunter-Ayad *et al.*, 2020). These models allow quantitative predictions about population growth and persistence, the key parameters considered in decision-making (Ewen *et al.*, 2023), and have progressively improved to make good use of the available data and account for uncertainties (Parlato *et al.*, 2021; Ransom *et al.*, 2023). These predictions are most easily applied to decisions about existing populations, such as those concerning supplementary feeding (Armstrong, Castro, & Griffiths, 2007), predator control (Armstrong *et al.*, 2006; Robinson *et al.*, 2020) and genetic augmentation (Campbell-Palmer *et al.*, 2020; Miller *et al.*, 2020).

Predictions for proposed reintroductions are more challenging because data do not yet exist for the reintroduced population. Consequently, predictions used in decision-making exercises for proposed reintroductions are predominantly based on expert judgement (Converse, Moore, & Armstrong, 2013; Ewen *et al.*, 2023). Where it is reasonable to assume that conditions at a proposed reintroduction area are similar to those previously monitored, population models can be constructed based on parameter estimates from those other areas (e.g., Howells & Edwards-Jones, 1997; South, Rushton, & Macdonald, 2000; Bach *et al.*, 2010). However, this is rarely the case, so the key challenge for reintroductions is predicting population parameters based on conditions in a new area compared to other areas where the species has been observed. This means not only estimating the effects of measurable characteristics such as climate, food availability and predator densities, but also accounting for unmeasured variation among areas (Holland *et al.*, 2009).

One key parameter to predict is the degree of dispersal from the managed area (Ewen *et al.*, 2023). Successful reintroduction usually depends on the habitat being restored for the species through management such as predator control. As such, dispersal-related loss of individuals from the managed area can compromise the success of reintroduction programmes (Le Gouar, Mihoub, & Sarrazin, 2011; Richardson *et al.*, 2015; Berger-Tal, Blumstein, & Swaisgood, 2019; Bilby & Moseby, 2023). Dispersal often occurs immediately after release when animals are stressed, but it can also occur in established populations, especially in species with juvenile dispersal phases.

Predicting dispersal requires characterizing the landscape around the proposed reintroduction area in relation to the movement behaviour of the species (Le Gouar, Mihoub, & Sarrazin, 2011; Richardson *et al.*, 2015). This can potentially involve constructing individual-based models incorporating movement rules determined by directly tracking the movements of animals using radio telemetry or other devices. This approach has been useful for predicting the movements of large carnivores following reintroduction due to the detailed large-scale movement data that can be collected from these animals (e.g., Wiegand *et al.*, 2004; Kramer-Schadt, Revilla, & Wiegand, 2005; Gusset *et al.*, 2009). However, obtaining such tracking data may be impractical or expensive, especially for small animals moving large distances through dense vegetation.

Where mark-recapture data are available from multiple areas, an alternative approach is to measure how apparent survival changes as a function of connectivity to the surrounding landscape, where functional connectivity refers to the degree to which the landscape facilitates or impedes movement of the focal species (Taylor *et al.*, 1993). Apparent survival is the probability that an individual both survives and remains in the monitored area over some interval. Therefore, a correlation with a connectivity metric should reflect the dispersal component, as long as the connectivity metric is not confounded with aspects of habitat quality that have not been accounted for. Through hierarchical modelling, dispersal from proposed reintroduction areas can then be predicted *a priori* based on their connectivity metrics while also accounting for random variation among areas. Similarly, hierarchical modelling of data collected from other areas should allow survival and productivity rates to be predicted as a function of the habitat characteristics of the proposed reintroduction area.

In this paper, we demonstrate how such hierarchical modelling was used to predict the growth of a bird population reintroduced to a managed area surrounded by unmanaged habitat and how the prior model was then updated based on data collected over 3 years following reintroduction. We show that modelling data from previous reintroductions allowed inferences about the effects of management on survival, reproduction and dispersal that were otherwise impossible and allowed all parameters to be estimated with greater precision. We specifically show how the updated model was used to predict how population growth would be affected by potential changes to the scale or intensity of management in the reintroduction area and make similar predictions for potential future reintroduction areas while accounting for random variation. To our knowledge, this is the first example of a prior model being updated following monitoring of a reintroduced population and used to make management decisions.

Materials and methods

Species and reintroduction area

The toutouwai, or North Island robin (*Petroica longipes*), is a small (26–32 g) insectivorous forest passerine endemic to Aotearoa, New Zealand. Toutouwai breed in monogamous pairs from September to February, producing up to three broods of 2–3 juveniles (Higgins, Peter, & Steele, 2001). If populations become female-biased, the few unpaired females may produce eggs and chicks, presumably due to copulation with neighbouring males, but produce far fewer fledglings than paired females (Parlato & Armstrong, 2012). Toutouwai have subtle sexual dimorphism, with older males darker in plumage than first-year males and females, and males tending to be larger in some morphometric measurements. However, males and females are easily distinguished during the breeding season based on behaviour (only males sing, only females incubate eggs and chicks, and males feed females during courtship and incubation). Toutouwai reach sexual maturity in their first breeding season after fledging and are highly territorial and sedentary as adults, with territory sizes ranging from ca. 0.4 to 6 ha depending on population density. Juveniles usually undergo a dispersal phase in the first few months after becoming independent (Richard & Armstrong, 2010), and translocated toutouwai undergo a similar dispersal phase after release (Armstrong *et al*., 2017).

The species is absent from ca. 90% of its original range due to forest clearance and the introduction of exotic mammalian predators, but has been reintroduced to >30 offshore islands and mainland sanctuaries where these predators have been controlled or eradicated (Miskelly & Powlesland, 2013). Analysis of data from 10 mainland reintroductions (Parlato & Armstrong, 2012) showed that both productivity (fledglings per female) and survival of nesting females were negatively correlated with densities of ship rats (black rat, *Rattus rattus*), which are known to be key predators of nests and nesting females (Brown *et al*., 1998). There was no evidence that rat density affected the survival of nonbreeding females, adult males or juveniles. However, apparent juvenile survival was negatively correlated with the sanctuary's connectivity to the surrounding landscape, indicating that population growth was limited by dispersal in some reintroduction areas.

Toutouwai were subsequently reintroduced to Taranaki Mounga (Fig. 1), a mountain with ca. 17 000 ha of continuous native forest within a 34 200-ha national park. The project was the first reintroduction part of the Predator Free 2050 project, which ultimately aims to eradicate rats (*Rattus* spp.), mustelids (*Mustela* spp.) and brush-tailed possums (*Trichosurus vulpecula*) throughout New Zealand to facilitate widespread recovery of native species (www.predatorfree.org). The aim for Taranaki Mounga was to suppress these predators to low levels within a 1000-ha area on the north-eastern slope of the mountain (Fig. 1; 39.243 S, 174.114 E) to recover native populations that could then spread as predator control was expanded. This managed area was 400 ha initially, but was expanded prior to the reintroduction to improve the population's probability of growing. To avoid using toxins, rats and mustelids are killed with a network of 2160 A24 self-setting kill traps (Goodnature Ltd.). A total of 95 toutouwai from Pureora Forest Park were translocated to the management area, with 50 released on 9 April 2017 and 45 released on 11 April 2018. The sex ratio of birds released was estimated to be close to 50:50 based on plumages, measurements and confirmed sexes of birds surviving to the breeding season (see below).

Data collection

For the 10 previous reintroductions, 1–10 years of data were available on survival and productivity (see Parlato & Armstrong, 2012 for a full description of the data collection and analysis). Survival data were obtained by conducting re-sighting surveys of the reintroduction areas at the start and end of each breeding season (most birds were individually colour-banded). The resulting encounter histories generated from the re-sighting surveys were used to estimate apparent juvenile survival, defined as the probability of a fledgling surviving to the next breeding season and remaining in the reintroduction area, and annual adult survival, which was unlikely to include a dispersal component because adults are highly sedentary. The encounter histories excluded the 3–6 months between translocation and the first breeding season, so the survival estimates excluded post-release effects (Armstrong *et al*., 2017). Productivity data were obtained by monitoring breeding pairs and recording the numbers of young fledged.

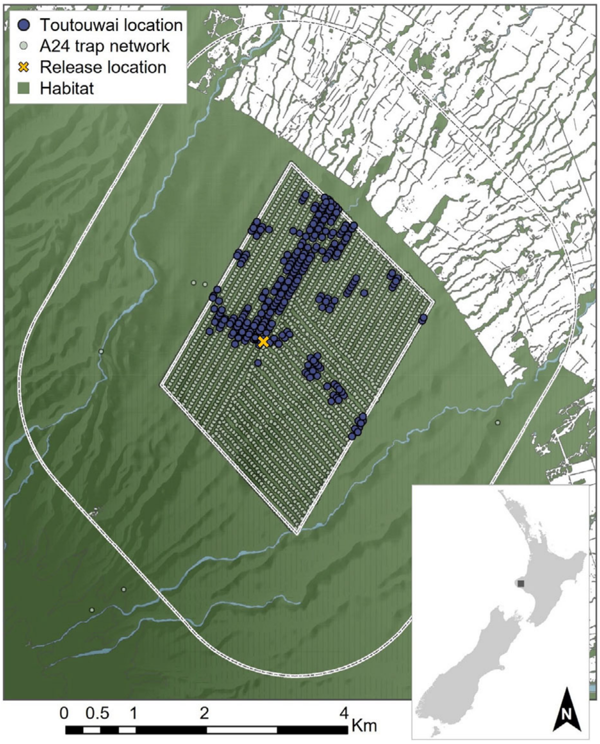


Figure 1 The 1000-ha predator management area on Taranaki Mounga, Aotearoa (New Zealand) in relation to the wider landscape shows the toutouwai (North Island robin) release site, locations of toutouwai sighted over the subsequent 3 years and the network of A24 kill traps used to control rats. The original 400-ha area is the NE portion, which can be identified by the orientation of the trap lines. The amount of accessible habitat within 2 km of the current managed area (i.e., between the perimeter of the managed area and the curved line shown) was divided by the amount of habitat in the managed area to calculate its habitat ratio, a connectivity metric correlated with apparent juvenile survival.

Data were also available on rat tracking, a standard index of rat density obtained by baiting tunnels with peanut butter and using ink pads and paper to record the proportion visited by rats (Innes *et al*., 1995). Connectivity was measured based on each area's habitat ratio, defined as the amount of accessible habitat within 2 km of the perimeter divided by the amount of habitat in the managed reintroduction area (Parlato & Armstrong, 2012); see Fig. 1 for example. Based on previous cost-distance modelling of telemetry data, accessible habitat was defined as forest that could be reached without crossing >120 m of pasture or water (Richard & Armstrong, 2010).

Similar data were collected at Taranaki Mounga, except that insufficient resources were available to monitor toutouwai pairs throughout the breeding season and band the young. Surveys of the 1000-ha area were conducted at the start (September) and end (February) of each breeding season up to September 2020, giving nine encounter occasions, including the two releases. The encounter histories of the original 95 translocated birds were used to estimate the survival of adult males and females while accounting for post-release effects (see below). Any unbanded birds encountered during September surveys could be counted accurately due to their territorial nature and low density. Consequently, the counts of unbanded males and females in September could be used to estimate recruitment when modelled in conjunction with the encounter histories (there are no other toutouwai populations in the region, so the unbanded birds could not have immigrated from elsewhere).

Modelling

Before the toutouwai reintroduction to Taranaki Mounga, we created a prior model based on Parlato & Armstrong's (2012) hierarchical modelling of the 10 previous reintroductions (Fig. 2). This was used to derive prior predictions that led to the proposed reintroduction being approved. We subsequently created an integrated population model for Taranaki Mounga toutouwai based on the first 3 years' data after reintroduction. We initially used uninformative priors for this model to obtain parameter estimates based on Taranaki data only. We then combined the two models so that informative priors were derived based on the previous data from other reintroductions, then updated based on the new data from Taranaki (Fig. 2). The details of the models are shown in the code and data provided (Appendix S1, S2, S3, S4), but the key features are explained below.

The prior model used the log-linear functions for survival and productivity selected in Parlato & Armstrong's (2012) analysis, except that one term was removed from the juvenile survival function following further research (Drummond *et al*., 2019). There is no density dependence in these functions, as all populations were at low density when sampled. The expected number of young fledged by a female in area i over a breeding season j is given by

$$\log\left(u_{i,j,\text{pair}}\right) = \alpha\text{f} + \beta\text{f}1 \times \log\left(1-rt_{i,j}\right) + \beta\text{f}2 \times (1-\text{pair}) + \gamma\text{f}_i \tag{1}$$

where αf is the intercept, βf1 is the effect of rats, $rt_{i,j}$ is the rat tracking rate that breeding season (probability of a tunnel

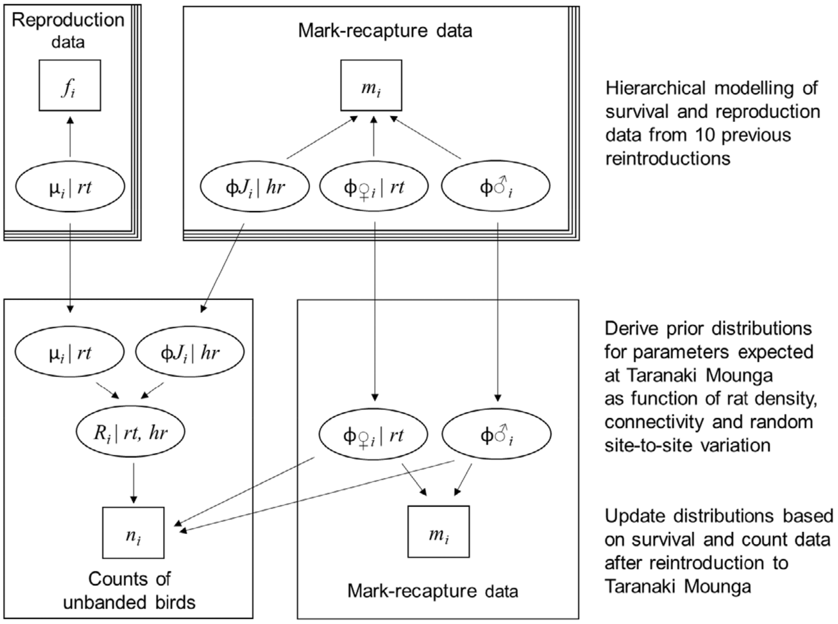


Figure 2 A simplified graph of the model is used to predict population parameters for a proposed toutouwai reintroduction to a predator-managed area (Taranaki Mounga), then update those parameters after the reintroduction took place. Data are shown in rectangles (f = numbers of young fledged by monitored females, m = encounter histories of banded birds, n = counts of unbanded birds) and parameters in ellipses (μ = mean fledglings per female per year, φJ = apparent juvenile survival probability, $\varphi_♀$ = annual survival of adult females, $\varphi♂$ = annual survival of adult males, R = recruits per female), with i indicating the specific reintroduction area. The parameters shown are derived from the main and hyper-parameters in the model (equations 1–3 in text) and are contingent on indices of rat density (rt) in the managed area and proportion of accessible habitat outside that area (hr) as well as area-specific random effects. The inclusion of data from previous reintroductions made it possible to partition the recruitment rate at Taranaki Mounga into productivity (fledglings per female) and apparent juvenile survival, and in turn partition apparent juvenile survival into juvenile survival and fidelity, therefore making it possible to predict how vital rates would respond to changes in the scale or intensity of predator control.

being tracked in 24 h), $\beta f2$ is the effect of the female being unpaired (pair = 1 if paired, 0 otherwise), and γf_i is the random area effect. Sex-specific adult survival probabilities at area i over an interval j are given by

$$\log\left(\emptyset A_{i,j,\text{sex}}\right) = \alpha sA + \beta s1 \times \log\left(1 - rt_{i,j}\right) \times (1-\text{sex}) \times bs_{i,j} + \gamma sA_i \tag{2}$$

where αsA is the intercept, $\beta s1$ is the effect of rats on breeding females (sex = 1 if male, 0 otherwise; $bs_{i,j} = 1$ if interval in breeding season, 0 otherwise), and γsA_i is the random area effect. Survival of adult females is therefore affected by rat density during the breeding season only and is otherwise equal to male survival, which is unaffected by rats. The apparent juvenile survival probability at area i s is given by

$$\log(\emptyset J_i) = \alpha sJ + \beta s3 \times hr_i + \gamma sJ_i \tag{3}$$

where αsJ is the intercept, $\beta s3$ is the effect of connectivity, hr_i is the area's habitat ratio (see above), and γsJ_i is the random area effect. The juvenile survival expected in the absence of dispersal ($\emptyset J0_i$) is obtained by setting hr_i to zero, meaning complete isolation from the surrounding landscape. The estimated juvenile fidelity, the probability of remaining in the reintroduction area, is therefore given by $\emptyset J_i / \emptyset J0_i$. We specified prior distributions for the parameters that potentially constrained them to plausible ranges, but in most cases, these priors did not constrain the posterior distributions, so they can be considered uninformative. The exceptions were priors for the intercept and random effect for apparent juvenile survival, which were weakly informative (Banner, Irvine, & Rodhouse, 2020).

To obtain pre-release predictions for Taranaki Mounga, we fitted this prior model to data on survival, productivity, habitat ratios, and rat tracking for the 10 previous reintroductions and derived survival and productivity rates for the new reintroduction area based on its habitat ratio and pre-release rat tracking data (Appendix S1 and S4). Following Parlato & Armstrong (2012), we used raw data for productivity, but for survival probabilities, we used estimates and standard errors for each interval rather than raw encounter histories. However, sampling error was incorporated by sampling the survival probabilities from state spaces defined by the estimates and standard errors. We used raw data on the number of tracking tunnels set and tracked, so we also accounted for sampling error in the rat tracking rates. When deriving survival and productivity rates for Taranaki Mounga, random variation among areas was incorporated by sampling the random effects from distributions with standard deviations estimated from the previous reintroductions, and estimation error for all parameters was incorporated through the MCMC (Markov chain Monte-Carlo) fitting used.

The estimated vital rates were used to predict the Taranaki Mounga population's finite rate of increase, which was calculated as

$$\lambda_i = \emptyset F_i + \frac{1}{2} \times \emptyset J_i \times u_i \tag{4}$$

where $\emptyset F_i$ is the annual adult female survival probability calculated from both the breeding and non-breeding rates, the sex ratio of recruits was assumed to be 50:50, and all females were assumed to be paired. The vital rates were also incorporated into a stochastic population model (Appendix S1) used to project population sizes over the first 3 years (Fig. 3). Those projections required predicting the numbers of translocated birds that would establish (survive the 3–6 months to the first breeding season and remain in the reintroduction area). The population model therefore incorporated an additional function that predicted the numbers of males and females establishing based on data from previous toutouwai reintroductions (Parlato & Armstrong, 2013).

We modelled adult survival at Taranaki Mounga by fitting a state-space formulation of a live-recaptures model (Schofield, Barker, & MacKenzie, 2009) to the encounter histories of the 95 translocated toutouwai, which were all colour-banded (Appendix S2 and S4). Under this formulation, the survival status of each individual is modelled as a missing value for each survey after it was last detected, so the number of individuals alive can be estimated by

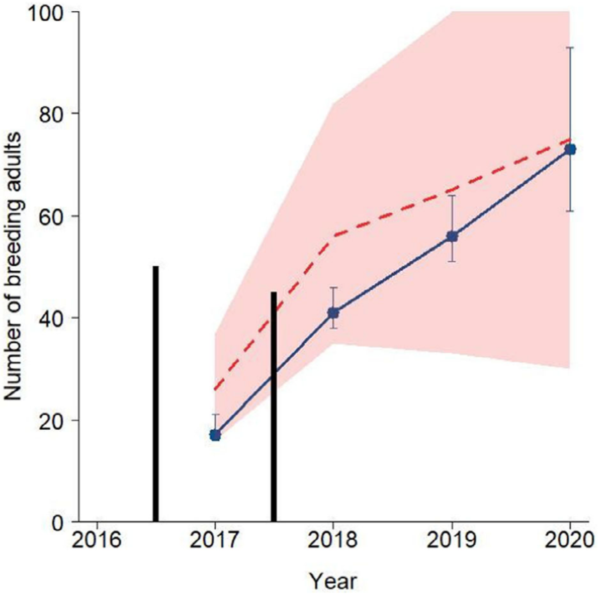


Figure 3 Estimated growth of the toutouwai population in the predator-management area on Taranaki Mounga in comparison to prior projections made by modelling data from previous reintroductions. Columns show numbers of toutouwai released in April 2017 and April 2018, and points and error bars show estimates and 95% credible intervals for the numbers of toutouwai at the start of the first four breeding seasons (September). The shaded area shows the 95% prediction limits from prior projections, with the median shown by the dotted line. Those projections were based on predicted post-release establishment from April to September and the subsequent survival and productivity rates expected based on the area's rat density and level of connectivity to the surrounding landscape.

summing the marginal totals for this variable. The survival function was the same as equation 2, but in this case the encounter histories included the post-release acclimation period, so we included an additional term ($\beta pre_{i,j}$) to account for post-release effects. The sexes of birds were unknown if they did not survive to the breeding season and did not clearly have male plumage, so these missing values were modelled based on tarsus and wing lengths. The sex-specific detection probabilities for each survey were given by

$$\operatorname{logit}\left(p_{i,j}\right) = \alpha p + \beta \mathrm{sex}p \times \mathrm{sex}_i + \gamma tp_j \tag{5}$$

where αp is the intercept, $\beta \mathrm{sex}p$ is the effect of the individual's sex on its probability of being detected, and γtp_j is a random effect accounting for variation among surveys. We considered the numbers of unbanded males and females found in September surveys to be sampled from binomial distributions with the same detection probabilities as banded birds, allowing us to estimate the number of unbanded birds present. These were then added to the estimated numbers of banded birds to derive the total number of individuals present each September (Fig. 3).

Estimating the numbers of unbanded birds present also allowed recruitment to be estimated, as the number of recruits of each sex is given by the number of unbanded birds of that sex minus the number of survivors from the last breeding season, which were considered to be binomial samples from the numbers present last year (with sex-specific adult survival probabilities estimated from the banded birds). The sex allocation of recruits was also considered to be a binomial process, with the probability of a recruit being male estimated from the data. The total number of recruits (NO_y) was considered to be a Poisson sample from the expected number, which in the Taranaki-only model was given by

$$\overline{\mathrm{N0}}_y = R \times \mathrm{NF}_{y-1} \tag{6}$$

where R is the recruitment rate and NF_{y-1} is the number of females at the start of the previous breeding season. In the model with informative priors, this function was replaced with

$$\overline{\mathrm{N0}}_y = \emptyset J_i * \left(f_{i,\mathrm{paired}} \times \min\left(\mathrm{NF}_{y-1}, \mathrm{NM}_{y-1}\right) + f_{i,\mathrm{unp}} \times \max\left(0, \mathrm{NF}_{y-1} - \mathrm{NM}_{y-1}\right)\right) \tag{7}$$

where NM_{y-1} is the number of males the previous season, and $f_{i,\mathrm{paired}}$ and $f_{i,\mathrm{unp}}$ are the expected productivity rates for paired and unpaired females, respectively (see equation 1). The inclusion of the prior model therefore allowed the estimated recruitment to be partitioned into productivity and apparent juvenile survival, and also allowed the potential effects of sex ratio to be accounted for, assuming that a female-biased sex ratio would result in all males pairing with females and the extra females being unpaired.

We used the updated model (Appendix S3) to predict the effects of potential changes in rat tracking rate and habitat ratio on survival and productivity and the resulting effect on λ. We first assessed the potential effects of increasing or relaxing the intensity of rat control on Taranaki Mounga, both for the current 1000-ha area and an alternative scenario where rat control was restricted to the original 400-ha area. We then made predictions for potential future reintroduction areas within continuous forest while accounting for random variation. We assumed these future managed areas would be square in shape and have at least 2 km of continuous forest on all sides, giving a habitat ratio of

$$hr = \frac{4(2L + \pi)}{L^2} \tag{8}$$

where L is the length of each side in km.

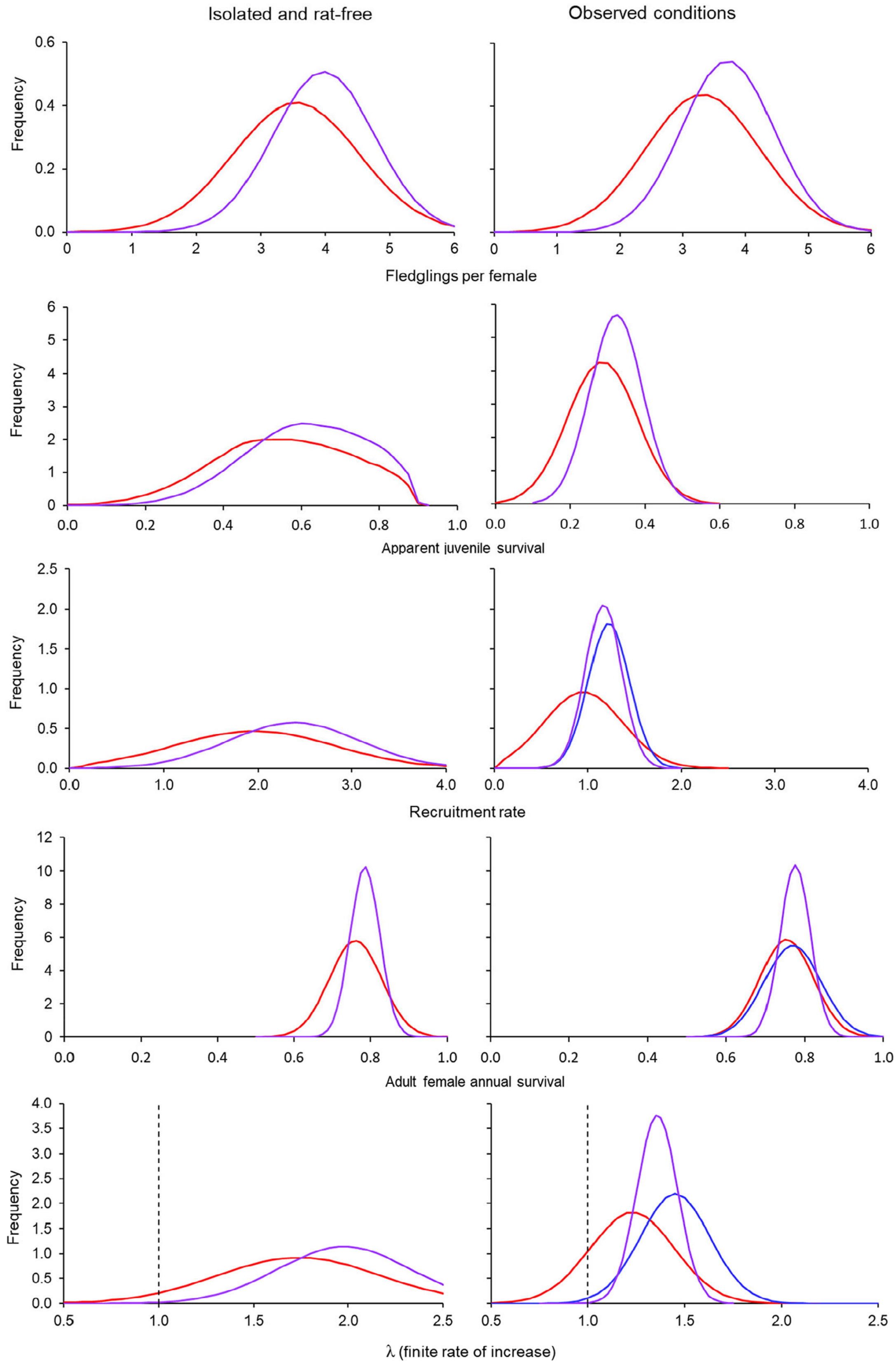
We modelled the data using OpenBUGS 3.2.3, using standard diagnostics to check for convergence of chains and discard burn-in (Link & Barker, 2010). The models (Appendix S1, S2, S3) can be fitted to the data (Appendix S4) using OpenBUGS by following instructions in the user manual (Spiegelhalter *et al.*, 2014), or alternatively can be called through R (Kéry & Schaub, 2012). The estimates reported in the text are means from posterior distributions, with standard errors in parentheses. The full model outputs are provided in Appendix S5, S6, S7.

Results

The habitat ratio of the 1000-ha managed area on Taranaki Mounga is 2.96, which is substantially lower than the habitat ratio of 5.68 for the original 400-ha area due to both its increased area and the greater proximity to farmland (Fig. 1). The rat tracking rate was 0.075 (SE: 0.036) for the breeding season before reintroduction and 0.087 (SE: 0.022) for the subsequent three breeding seasons. There was no indication that the rat tracking rate varied among breeding seasons, but it did vary among individual sampling occasions, so this was included as a random effect in the model.

Based on the prior model, it was predicted that rats would have little impact at the observed tracking rates but that connectivity would have a substantial effect. Paired females were predicted to fledge an average of 3.32 (0.92) young per year, in comparison to 3.55 (0.98) expected with no rats, and annual adult female survival was predicted to be 0.75 (0.07), in comparison to 0.76 (0.07) expected with no rats (Fig. 4). Juveniles

Figure 4 Prior distributions for Taranaki Mounga toutouwai population parameters based on data from previous reintroductions (red); distributions from new data collected in the first 3 years after reintroduction to Taranaki Mounga (blue); and posterior distributions based on all data combined (purple). The prior data allowed the estimated recruitment rate to be partitioned into productivity (fledglings per female) and apparent juvenile survival and allowed the effects of rat predation and dispersal to be inferred (left-hand *vs.* right-hand panels). It is assumed here that all breeding females are paired and that 50% of recruits are female.


Isolated and rat-free
Observed conditions
Frequency
Fledglings per female
0.0
0.2
0.4
0.6
0
1
2
3
4
5
6
Apparent juvenile survival
0
1
2
3
4
5
6
0.0
0.2
0.4
0.6
0.8
1.0
Recruitment rate
0.0
0.5
1.0
1.5
2.0
2.5
3.0
4.0
Adult female annual survival
0
2
4
6
8
10
12
λ (finite rate of increase)
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0

were predicted to have a 0.29 (0.09) probability of surviving to the next breeding season and remaining in the managed area, compared to a 0.55 (0.18) probability if the habitat ratio was set to zero, meaning 45% of potential recruits were predicted to disperse (Fig. 4). The resulting λ estimate was 1.23 (0.22), compared to the 1.74 (0.43) expected if the managed area were isolated and rat-free, but this still gave a 0.96 probability that λ would be >1, meaning a toutouwai population was expected to persist.

The survival and recruitment rates estimated from the Taranaki toutouwai after reintroduction were slightly higher than those from the prior model; hence, the posterior distributions from the updated model had higher means as well as greater precision (Fig. 4). Posterior estimates of 0.79 (0.04) adult female survival probability and 1.17 (0.19) recruits per female resulted in an updated λ estimate of 1.42 (0.16), with this distribution now completely >1 (Fig. 4). The estimated population size after 3 years almost exactly matched the mean prediction from the prior model, with the initial number of birds established being slightly lower than predicted but the subsequent population growth being slightly higher (Fig. 3).

Based on the partitioning of recruitment components made possible by the prior information, the updated model estimated 3.72 (0.73) fledglings per paired female and a 0.32 (0.07) probability of juveniles surviving and remaining in the managed area. The latter probability was predicted to drop to 0.19 (0.08) if management were restricted to the original 400-ha area. Based on the effects of rats on productivity and adult female survival, it was predicted that rat tracking rates in the 1000-ha managed area could increase up to 0.37 before the probability that $\lambda > 1$ drops below 95% (Fig. 5). With the original 400-ha area, the probability that $\lambda > 1$ was less than 95% even with no rats, but the median λ remained >1 until the rat tracking rate was over 0.36 (Fig. 5). Consequently, the managers are retaining rat control over a 1000-ha area but are shifting it northward to be adjacent to the farmland (Fig. 1), slightly reducing the habitat ratio.

When the updated model was used to predict λ at potential future reintroduction areas, those estimates became slightly lower due to Taranaki having above-average survival and recruitment and less precise due to the absence of site-specific data (Fig. 6). Consequently, the 95% credible interval for λ includes 1 even for large areas with intensive rat control. However, the λ estimates suggest that a managed area within continuous forest would generally need to be >400 ha with a 0.05 rat-tracking rate and >600 ha with a 0.25 rat tracking rate.

Discussion

Reintroductions are inherently uncertain because data are not available *a priori* for the species at the proposed reintroduction area, and this uncertainty is a major challenge for decision makers (Ewen *et al.*, 2023). Reintroduction biology seeks to reduce this uncertainty; hence, there continue to be frequent calls for increased monitoring (e.g., Sutherland

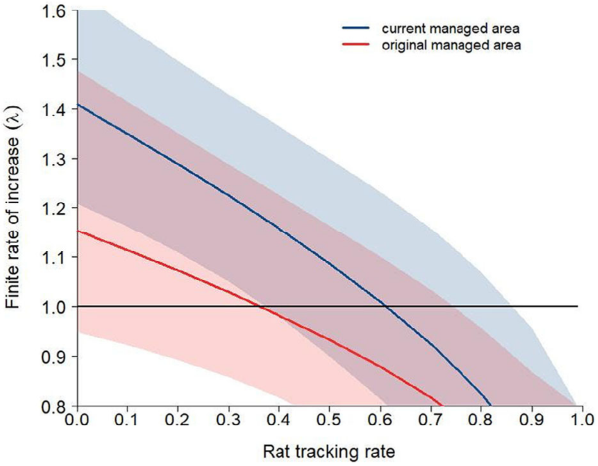


Figure 5 Predicted impacts of changing the scale or intensity of rat control on the finite rate of increase (λ) of the Taranaki Mounga toutouwai population based on the updated model. The blue line and shaded area show the estimates and 95% credible intervals for λ if rat control is maintained over the current 1000-ha management area. The red line and shaded area show predictions if rat control were restricted to the original 400-ha area, which was in the NE portion of the current area. Predictions assume that toutouwai dispersing beyond the managed area are lost from the population. $\lambda < 1$ would result in the population declining to extinction.

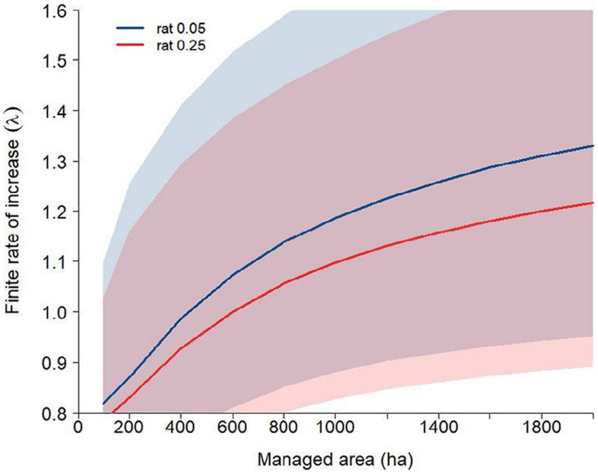


Figure 6 Predicted finite rate of increase (λ) of a toutouwai population at a hypothetical area within continuous forest as a function of the scale and intensity of rat control. It is assumed that the managed area is square in shape and that toutouwai dispersing beyond the managed area are lost from the population. The blue line and shading show estimates of 95% credible intervals for λ under a rat tracking rate requiring intensive management (0.05), whereas the red line and shading show predictions under a rate (0.25) requiring moderate management. $\lambda < 1$ would result in the population declining to extinction. These predictions incorporate random variation in vital rates among areas, so are less precise than predictions specific to Taranaki Mounga.

et al., 2010; Berger-Tal, Blumstein, & Swaisgood, 2019; Bubac *et al.*, 2019; Dalrymple & Bellis, 2023). However, monitoring is expensive, so there is often a tension between investing in the monitoring needed for the current programmes and the monitoring that will inform future reintroductions. Most importantly, it needs to be clear that the monitoring will improve the predictions needed for decision-making. The approach we have presented here provides a means for generating quantitative predictions to inform both ongoing management of populations and future reintroduction proposals.

For the toutouwai reintroduction to Taranaki Mounga, the key uncertainties were the impact of dispersal on population establishment and persistence and the effectiveness of rat control. This was because most successful toutouwai reintroductions have been to isolated islands and predator-fenced areas, where connectivity is low and ship rats are usually absent (Parlato & Armstrong, 2012, 2013; Miskelly & Powlesland, 2013). In contrast, most reintroductions to areas like Taranaki Mounga, i.e. connected to the wider landscape, have declined towards extinction because survival and productivity could not offset losses to dispersal (Parlato & Armstrong, 2012; Miskelly & Powlesland, 2013). Controlling rats in such areas is challenging due to continual reinvasion (Ross *et al.*, 2020).

Useful monitoring data are surprisingly scarce for New Zealand bird reintroductions, despite ca. 15 reintroductions being conducted annually (Miskelly & Powlesland, 2013). However, because toutouwai can be monitored relatively easily, data were available to build the prior model used to predict population dynamics at proposed reintroduction areas, including areas where dispersal may be problematic (Parlato & Armstrong, 2012, 2013). This model generated quantitative predictions indicating that while juvenile dispersal would reduce population growth, the population would probably still increase under a moderate level of rat control, leading to the decision to reintroduce the species. The model has also been used to make pre-release predictions for five other translocation proposals involving toutouwai. However, Taranaki Mounga is the first area where data were subsequently collected that could be used to update the prior predictions. This updating resulted in predictions that were much more precise than those from either the prior model or the Taranaki data alone. In addition, the prior data allowed the estimated recruitment to be partitioned into productivity, juvenile survival and juvenile fidelity, making it possible to predict the consequences of reducing the scale or intensity of predator control and therefore adapt management as necessary. The updating also improved predictions about the size and scale of predator control needed at potential future reintroduction areas, which will contribute to future translocation proposals. This improved predictive capacity is invaluable to managers, not only because it guides their ongoing decisions about predator control but also because it reassures them that their investment in monitoring will guide decisions about future proposed reintroductions.

Although we found a simple connectivity metric, the habitat ratio, to be useful for predicting apparent juvenile survival and, therefore, dispersal, predicting dispersal from managed areas is a major challenge for reintroduction practitioners (Berger-Tal, Blumstein, & Swaisgood, 2019). Selecting appropriate metrics is not straight forward (Zeller *et al.*, 2018; Keeley, Beier, & Jenness, 2021), and ideally functional connectivity metrics should reflect detailed knowledge of the movement behaviour of the focal species (Le Gouar, Mihoub, & Sarrazin, 2011; Richardson *et al.*, 2015). For toutouwai, we benefited from a previous cost-distance analysis quantifying habitat selection and gap-crossing ability of dispersing juveniles (Richard & Armstrong, 2010). However, it remains possible that alternative metrics may better capture the variation in dispersal among reintroduction areas. Multiple metrics could potentially be considered in a multi-model framework (Burnham & Anderson, 2002), but this approach would increase data requirements, particularly the number of areas needed. In many cases, it will be necessary to obtain connectivity scores through expert elicitation (Beier & Noss, 1998; Martin *et al.*, 2012).

A further challenge is that it may sometimes be necessary to consider the source-sink dynamics (Pulliam, 1988) of the population inside and outside the managed area. The primary objective of the Taranaki Mounga reintroduction was to establish a growing population of toutouwai within a core 1000-ha management area; hence, we focused on estimating λ within this area. However, it is possible that a spreading population could grow even if $\lambda < 1$ within the managed area. Such growth requires survival and recruitment from dispersed individuals to be sufficient to raise the overall $\lambda > 1$, which can only be inferred if dispersed individuals can be monitored. Without this wider monitoring, the minimum requirement for growth is for $\lambda > 1$ with no dispersal. Hence, it is useful to be able to partition vital rates to make such prediction as shown in Fig. 4.

Regardless of the factors likely to affect the fates of reintroductions, the general approach illustrated here is ideal for the adaptive management of reintroduced populations. This approach involves: (1) generating pre-release predictions about population growth through hierarchical modelling of existing data; (2) if the reintroduction proceeds, updating that prior model based on post-release monitoring data to inform ongoing management of the population and (3) using the updated model to generate predictions for evaluating subsequent proposals. Despite this adaptive management cycle being well known in principle (Ewen *et al.*, 2023) and thousands of papers being published in reintroduction biology (Seddon & Armstrong, 2016), we are not aware of any previous papers illustrating this process using a fully data-based approach.

The key limiting factor for this type of analysis is data availability, particularly data on survival and reproduction rates, which are essential for estimating population growth in the absence of long-term data sets (Armstrong & Reynolds, 2012). Although such data had been collected from multiple toutouwai reintroductions, Parlato & Armstrong (2012, 2013) needed to communicate widely to access those data, in many cases deciphering and extracting the data from field notebooks. We then needed to follow a similar process 10 years later with the Taranaki Mounga data before integrating the two data sets. Such processes will become much more difficult when expanded to cover multiple species, which is essential to providing the breadth needed to inform reintroduction programmes. It is therefore not surprising that broad multi-species analyses have focused on trends that can be gleaned from the literature, such as the methodologies and success rates of reintroductions featured in publications (Resende *et al.*, 2020; Morris *et al.*, 2021) and the immediate post-release survival of translocated animals (Thomas *et al.*, 2023). Although these broad analyses provide useful descriptive information, they do not provide the predictions needed to make decisions about translocation proposals or the ongoing management of reintroduced populations. The modelling of demographic data needed to make such predictions is challenging but is progressively becoming more feasible due to online data repositories, improved data management, faster processors and integrated modelling methods (e.g., Parlato *et al.*, 2021; Ransom *et al.*, 2023). As well as reiterating the call for targeted monitoring of reintroductions (Sutherland *et al.*, 2010; Berger-Tal, Blumstein, & Swaisgood, 2019; Bubac *et al.*, 2019; Dalrymple & Bellis, 2023), we encourage practitioners not only to make raw data accessible but also to continue developing the modelling techniques needed to improve predictive capacity and decision-making for multiple species.

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Author contributions

DPA modelled the data both before and after the reintroduction, contributed to fieldwork and data organization, and wrote the first draft; *ZLS* contributed to fieldwork and data organization; *EAP* contributed to the modelling; *GN* played major roles in collective and collating the data; *EK* oversaw the field programme; *SG* and *SZ* participated in the translocation and are kaitiaki for the reintroduced population; *KAP* led the translocation. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data are provided in Appendix S4.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. OpenBUGS code for the prior model for the toutouwai population reintroduced to Taranaki Mounga.

Appendix S2. OpenBUGS code for modelling the toutouwai population reintroduced to Taranaki Mounga based solely on data collected after reintroduction.

Appendix S3. OpenBUGS code for the updated model for the toutouwai population reintroduced to Taranaki Mounga.

Appendix S4. Data for modelling establishment and subsequent vital rates of the toutouwai population reintroduced to Taranaki Mounga.

Appendix S5. Output from prior model.

Appendix S6. Output from the Taranaki-only model.

Appendix S7. Output from the updated model.