



## RESEARCH

## Rifleman (*Acanthisitta chloris* sp.) population responses to aerial 1080 (sodium fluoroacetate) predator control in beech forests.

Claire J. Kilner<sup>1\*</sup> , Christine M. Hunter<sup>1</sup> , Ruth E. Cole<sup>1</sup>, Tom E. Allan, Tristan E. Rawlence<sup>1</sup>, Joris S.J. Tinnemans<sup>1</sup>, Mara A.N. Bell<sup>1</sup>, Chris W. Bell<sup>1</sup>, Jason P. Malham<sup>1</sup>, Anja McDonald<sup>1</sup>, Kirsty J. Moran<sup>1</sup> and Graeme P. Elliott<sup>1</sup> 

<sup>1</sup>Department of Conservation, Private Bag 5, Nelson, New Zealand

\* Author for correspondence (Email: [ckilner@doc.govt.nz](mailto:ckilner@doc.govt.nz))

Published online: 12 December 2024

**Abstract:** Aerial 1080 is the primary method of large-scale predator control of ship rats (*Rattus rattus*) and stoats (*Mustela erminea*) in the southern beech (Nothofagaceae) forests of mainland New Zealand. Measuring outcomes for native species of such predator control is essential to ensuring wise use of conservation resources. Rifleman/tītītipounamu (*Acanthisitta chloris* sp.) are a common endemic passerine that are declining, even in large remote forests. We studied annual survivorship and nest success of tītītipounamu in beech forest in the Tararua Ranges, Marlborough Sounds, and South Westland in response to aerial 1080 predator control. We monitored 72 individuals and 337 tītītipounamu nests from untreated and treated sites, which included seven aerial 1080 operations. Our results show strong benefits of aerial 1080 for tītītipounamu from both improved nest success and annual survivorship, with benefits for nest success extending to the second breeding season after an aerial 1080 operation. Nest success ranged from < 58% without treatment to > 77% with treatment. Annual survivorship in non-treatment areas was 19% and 43% and in treatment areas was 62% and 84% for juveniles and adults, respectively. Population modelling indicated that predator control approximately every 3 years is necessary for tītītipounamu population persistence.

**Keywords:** *Acanthisitta chloris chloris*; *Acanthisitta chloris granti*; apparent survival; nest survival; North Island rifleman; population modelling; predator control; South Island rifleman

### Introduction

Conservation management of New Zealand's southern beech (Nothofagaceae) forest ecosystems is complicated by irregular and often massive seed production. These masting events introduce large amounts of energy into the ecosystem and result in exponential increases in invasive predators (King 1983). This process has serious consequences for native bird populations (Murphy & Dowding 1995; White & King 2006), leading to increased nest failure, skewed sex ratios, declines in abundance (Elliott 1996a; O'Donnell 1996; Wilson et al. 1998), and localised extinctions (Gaze 2003; Elliott & Suggate 2007). More than half of New Zealand's remaining indigenous forests contain beech trees and aerial toxin operations are currently the only large-scale multi-predator control tool available. On mainland New Zealand, sodium fluoroacetate (1080) is the main toxin used in such operations (Parliamentary Commissioner for the Environment 2011). While aerial 1080 is the most cost-effective tool for large scale remote areas (Parliamentary Commissioner for the Environment 2011; Brown et al. 2015), these operations are nevertheless expensive, and making informed decisions about allocating resources requires understanding the potential benefits.

Aerial 1080 is an important conservation tool, but

opponents of this toxin are concerned about toxic loading in the environment and poisoning non-target species. Over the last four decades substantial changes have been made to the way that 1080 is applied to reduce negative impacts while maintaining benefits for native species. Examples of these changes include changes in bait type to reduce by-kill, lower sowing rates to reduce toxic loading, improved bait quality, use of smaller baits, pre-feeding with non-toxic bait, and targeted timing of operations to improve efficacy of control of ship rats (*Rattus rattus*; hereafter referred to as rats) and mustelids (*Mustela* sp.; Powlesland et al. 1999; Westbrooke & Powlesland 2005; Eason et al. 2006; Veltman & Westbrooke 2011; Brown et al. 2015). Despite these gains, controversy over the large-scale use of this toxin continues. It is vital, therefore, that conservation managers can be confident that any undesirable consequences of predator control are outweighed by benefits to native taxa and biodiversity. Rifleman/tītītipounamu (*Acanthisitta chloris* sp.) are an example of a species of conservation concern that has suffered negative impacts from 1080 predator control. Prior to 1994 individuals are known to have died from 1080 poisoning (Spurr & Powlesland 1997) but as a species vulnerable to introduced predators (Gaze 1978; Sherley 1985; Higgins et al. 2001; Briskie et al. 2014), tītītipounamu are also expected to benefit from aerial 1080. The net effect of predator control on

tītīpounamu at the population level has not been measured.

Although tītīpounamu are not regarded as threatened (Robertson et al. 2017), they are among the many native forest bird species suffering range reductions toward cooler forests (Walker et al. 2017) and toward the treeline (Elliott et al. 2010; J. Griffiths, Department of Conservation, Nelson, pers. comm.), and local extinctions, even in remote forests (Walker et al. 2017). These changes are likely due to higher levels of predation as rats are more abundant at lower elevations (Christie et al. 2017; Carpenter et al. 2022; Whitau et al. 2022) and in warmer forests (Walker et al. 2019a). Tītīpounamu are tiny passerines (5–8 g) from an ancient endemic avian lineage. Such lineages have suffered more acutely from predation and population declines because they have developed life history traits that increase their vulnerability to introduced mammalian predators (Binny et al. 2021; Fea et al. 2021; Walker et al. 2021). Traits that might increase tītīpounamu susceptibility to or reduce their ability to recover from predation include cavity nesting, long nesting period (44 days) and limited dispersal capability (Elliott 1996b; O'Donnell 1996; Parlato et al. 2015; Walker et al. 2019b, 2021; Fea et al. 2021; Innes et al. 2022).

Outcomes of the few studies investigating tītīpounamu responses to predator control have been mixed. In the Landsborough Valley in South Westland, tītīpounamu increased with aerial 1080 operations every 2–5 years for 20 years alongside ground control methods (O'Donnell & Hoare 2012; O'Donnell 2019). Similarly, a recent meta-analysis found that the sustained suppression or eradication of predators improved tītīpounamu responses (Binny et al. 2021). Further,

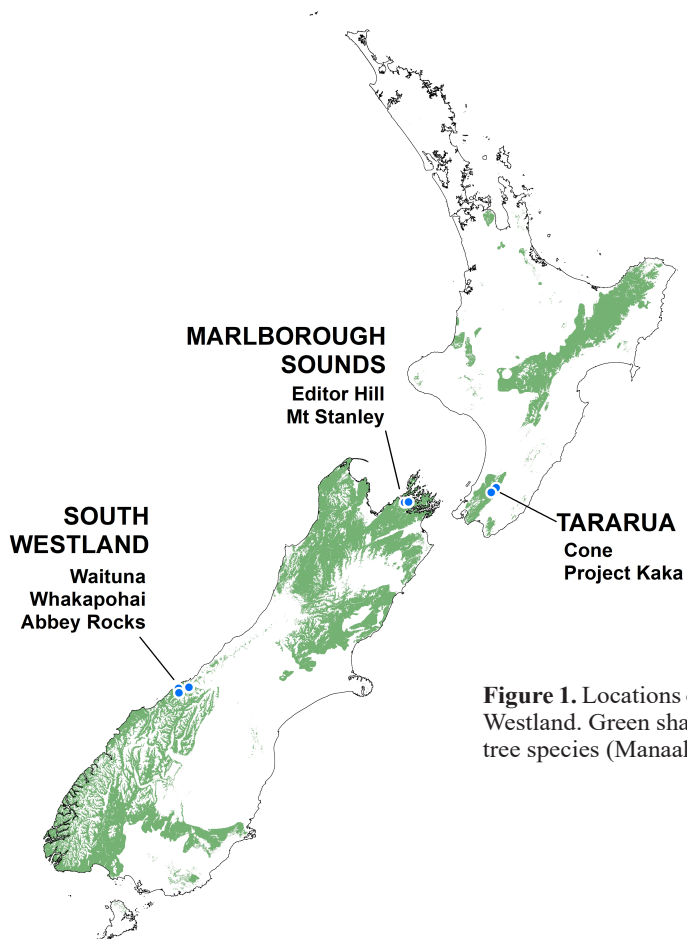
tītīpounamu became extinct in the last 30 years on Rakiura (Harper 2009) but remain on nearby predator-free islands (Leech et al. 2007). Other studies found no effect of predator control for tītīpounamu (Hoare et al. 2013; Van Vianen et al. 2018; Fea et al. 2021). However, many of these studies are based on point counts, which, although valuable for detecting long-term trends, have limited ability to detect short-term change such as response to current management (Armstrong et al. 2006; Buckland 2006). Thus, questions remain regarding the effectiveness of predator control for tītīpounamu.

This study aims to quantify the effect of aerial 1080 operations on tītīpounamu in beech forests by examining productivity and survival of treatment and non-treatment populations. We hypothesised that (1) treatment would increase tītīpounamu nest success and annual survivorship, and (2) that this effect would be stronger when treatment coincided with beech mast events. Previous studies of tītīpounamu have not investigated the effect of predator control on vital rates nor have they been undertaken in beech forests.

## Methods

### Study area

We studied tītīpounamu in three beech forest areas: the Tararua Ranges in the lower North Island, and the Marlborough Sounds and South Westland (Fig. 1) in the South Island. The predominant vegetation in Tararua was silver beech (*Lophozonia menziesii*), red beech (*Fuscospora fusca*), and



**Figure 1.** Locations of study sites in the Tararua Ranges, Marlborough Sounds, and South Westland. Green shading indicates approximate extent of vegetation that contains beech tree species (Manaaki Whenua Landcare Research 2012).

**Table 1.** Specifications of the aerial 1080 operations conducted at the treatment study sites. Toxic operation date, toxic bait size and toxic sow rate are specific to nest study site.

Region	Operation	Operation size (ha)	Toxic operation date	Toxic bait size	Toxic sow rate	Primary target species
Tararua	Project Kaka	22 012	9 Nov 2010	12g	2 kg ha <sup>-1</sup>	Possum
Tararua	Project Kaka	22 224	2 Dec 2013	12g	1 kg ha <sup>-1</sup>	Possum
Marlborough Sounds	Mt Stanley	4300	2 Nov 2013	6g	1 kg ha <sup>-1</sup>	Possum
Marlborough Sounds	Mt Stanley	3939	23 Nov 2014	6g	1 kg ha <sup>-1</sup>	Ship rat/mustelid
South Westland	Abbey Rocks	12 050	3 Jun 2009 <sup>#</sup>	12g	3 kg ha <sup>-1</sup>	Possum
South Westland	Whakapohai	26 269	1 Dec 2010	12 g	2 kg ha <sup>-1</sup>	Possum
South Westland	Abbey Rocks	14 500	27 Oct 2011	6 g	1 kg ha <sup>-1</sup>	Ship rat/mustelid
South Westland	Whakapohai	29 281	23 Nov 2013	12 g and 6 g*	2 kg ha <sup>-1</sup> and 1 kg ha <sup>-1</sup> *	Possum

<sup>#</sup> Although the 2009 Abbey Rocks operation pre-exists our study it affects data collected in 2010.

\* Both specifications were sown at the study site.

kāmahi (*Pterophylla racemosa*). In the Marlborough Sounds, it was silver beech with mountain beech (*F. cliffortioides*), kāmahi, broadleaf (*Griselinia littoralis*), and some red beech. In South Westland, silver beech with Southern rātā (*Metrosideros umbellata*), kāmahi, and montane tōtara (*Podocarpus cunninghamii*) dominated. Accessibility and apparent abundance of tītītipounamu were considerations in choosing sites. The elevation at which we found tītītipounamu declined with latitude. Ninety percent of tītītipounamu nests were found between 660–880 m, 570–780 m, and 430–650 m above sea level in the Tararua Ranges, Marlborough Sounds and South Westland, respectively. Temperature ranges in all regions were similar but rainfall differed. South Westland experienced an annual rainfall of 12 700 mm while Marlborough Sounds received 3 100 mm and Tararua 6000 mm. Each study area included a non-treatment site where no recent predator management had occurred and one (Tararua Ranges and Marlborough Sounds) or two (South Westland) treatment sites where management is believed to have occurred previous to this study. One or two aerial 1080 operations were carried out at each treatment site during the study. All treatments consisted of the aerial application of a non-toxic cereal pre-feed bait followed by a toxic cereal bait between eight and 44 days later (Table 1).

### Monitoring predators

Stoats (*M. erminea*), rats, mice (*Mus musculus*), and brushtail possums (*Trichosurus vulpecula*) were common at all three regions. We expected stoats and rats to be the main predators of tītītipounamu (Sherley 1985; Briskie et al. 2014). Tracking tunnels are the main method used by conservation managers to monitor relative abundance of rodents and mustelids and to measure the effectiveness of aerial 1080 operations (Gillies & Williams 2007; Elliott & Kemp 2016). An extensive tracking tunnel network exists across South Island beech forest. We monitored rat abundance using standard tracking tunnel monitoring protocols and calculated the footprint tracking index (FTI) as the proportion of tunnels that detected rats (Gillies & Williams 2007). We used rat tracking data collected within seven kilometres of our study sites to ensure we had sufficient tracking data whilst still reflecting local conditions. Mustelid survey methodology differed among regions and over time. At Tararua and the Marlborough Sounds prior to 2015 we followed Gillies and Williams’ (2007) three-night surveys.

For reasons outside of this research, in the Marlborough Sounds from 2015 onwards, 14-night surveys were used. At South Westland overnight mustelid surveys were carried out simultaneously with rodent surveys. Mustelid FTI were calculated as the proportion of lines with mustelids present (Gillies & Williams 2007).

### Monitoring tītītipounamu

To aid in nest monitoring we mist-netted and colour-banded tītītipounamu with unique combinations of bands. We determined the sex and age (fledgling or adult) of all birds captured using plumage characteristics (Higgins et al. 2001). Nest survival data was collected between 2010 and 2016. Tītītipounamu nests were found by attracting birds to nesting material (white feathers) with playback calls, then following birds as they returned to nests. As tītītipounamu nest contents were inaccessible, we used observation of adult activity to determine nest age. Once incubation commenced, accessible nest trees were climbed, and trail cameras installed to monitor nest and predator activity. Nests were also monitored by observers to aid in identifying nest transition stages and nest fates. Nests that fledged at least one nestling were considered successful (Dinsmore et al. 2002).

### Modelling nest survival

We used generalized linear models (GLMs) to assess whether aerial 1080 treatment or other explanatory variables affected tītītipounamu nest success. Nest daily survival rate (DSR) was modelled using GLMs with a binomial error distribution (following Rotella et al. 2004), a complementary log-log (cloglog) link function (Bolker 2014), and exposure days as an offset to account for the different observation period lengths (Rotella et al. 2004). For each day a nest was active exposure was equal to one. If a nest failed, exposure was the length of time in days between the last date a nest was observed active and the failure date. Nests that failed at an unknown age were assigned an age equal to the median nest age of their stage. Mean values of continuous explanatory variables were calculated for this final exposure. We refer to this modelling as nest survival or DSR. All modelling in this paper was carried out in R (R Core Team 2021).

To examine collinearity between explanatory variables we used the *vif* function in the R package *car* version 3.0-10 (Fox et al. 2020). The model set was run using the *dredge* function

in the package MuMIn version 1.43.17 (Barton 2020) with rules to limit models to those in the model set. Models were ranked using the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002). We carried out model averaging on models  $\Delta\text{AICc} < 2$  (Burnham & Anderson 2002) using MuMIn to obtain full model-averaged regression coefficients (Barton 2020). Following the approach of Arnold (2010), uninformative models were removed from the model set prior to model averaging and are not reported here.

Nest success (NS) over the 44-day nesting period was calculated by multiplying the appropriate DSR values from day 1 to day 44 (Eqn 1). Bootstrap confidence intervals for nest success were estimated by running 1 000 000 bootstrap simulations using methods similar to those described in Cooch and White (2020).

$$NS = \prod_{i=1}^{44} DSR_i, \text{ where } i = \text{nest day} \quad (1)$$

### Factors affecting nest survival

We evaluated the impacts on nest survival of explanatory variables representing predator management, environmental conditions, and nest characteristics (Table 2). We considered two representations of predator management based on length of effect. First, treatment only affected the breeding season in which the treatment occurred (year of treatment, YO), and second, treatment effects extended into the following breeding season (YO + year after treatment, YA). If an aerial 1080 operation occurred after the start of the breeding season, nests could experience both non-treatment (NT) and YO conditions

within a season, coded as NT for days prior to the operation and YO for days after the operation.

Environmental variables included delta T, site, year, elevation, temperature, and rain. Beech masts may have benefits, i.e. increased invertebrate abundances (Fitzgerald et al. 1996; Alley et al. 2001), and costs, i.e. increased predation, for tītītipounamu. We used delta T model values as a proxy for the likely strength of beech mast in a given year. Delta T, the difference in summer temperatures between two successive years, is a good predictor of the likelihood and magnitude of beech seedfall in the following year (see Kelly et al. 2013; Elliott & Kemp 2016). Two aerial 1080 operations occurred in response to mast events: Mt Stanley 2014 and Abbey Rocks 2011 (Table 1). Year refers to the breeding season over spring and summer, for example, 2010 represents the breeding season of 2010/2011. To account for the latitudinal spread of the study areas we calculated a standardised elevation as the difference in elevation from the nest to the nearest treeline (Table 2). As a small passerine, tītītipounamu are likely to be vulnerable to weather events, especially at the extremes of their range (Sherley 1985). To represent weather conditions we used daily minimum temperature and calculated a rolling cumulative 3-day sum of precipitation using data from the NIWA virtual weather station closest to each site (Table 2; Tait et al. 2006; Tait 2008). Finally, variability in the vulnerability to predation over the lifespan of a nest has been well-documented, including for New Zealand bird species (Elliott 1996b; Armstrong et al. 2002; Grant et al. 2005; van Heezik et al. 2020) so we included a quadratic term for nest age ( $\text{Age} + \text{Age}^2$ ).

**Table 2.** Explanatory variables used in daily nest survival models for tītītipounamu in New Zealand beech forest 2010–2015.

Explanatory variable name	Type of variable	Levels	Description
YO	Factor	YO, NT	YO = year of aerial 1080, i.e. aerial 1080 occurred before or while the nest was active. NT = No aerial 1080 occurred.
YO + YA	Factor	YO, YA, NT	YO and NT as above YA = Year after aerial 1080, i.e. aerial 1080 occurred the season before a nest was active.
Rat*	Continuous		Daily rat tracking rate (0–100%) at nest elevation as projected by GAM.
Mustelid*	Continuous		Daily mustelid tracking rate (0–100%) as projected by GAM.
Delta T	Continuous		Delta T model values of predicted beech mast strength based on climatic conditions. Proxy for beech seedfall.
Site	Factor	7 sites	The seven study sites (Fig. 1).
Year	Factor	2010, ..., 2015**	Year was only included as an interaction term with (1) site, as an alternate explanation for treatment; and (2) delta T.
Elevation	Continuous		Elevation of nest measured in vertical metres below treeline <sup>#</sup> .
Temperature <sup>+</sup>	Continuous		Daily minimum temperature.
Rain <sup>+</sup>	Continuous		Rolling cumulative 3-day sum of precipitation.
Nest age	Integer		Quadratic function of nest age: $\text{Age} + \text{Age}^2$ , where age of nest was 0–44 days.

\* Only used in the South Westland predator tracking rates analysis.

\*\* Year represents season e.g. 2010 was breeding season 2010/11. Specific years varied by site, Tararua and South Westland four seasons 2010–2013 (except Waituna, South Westland three seasons, 2011–2013), Marlborough Sounds six seasons 2010–2015.

<sup>#</sup> Estimated treeline: Tararua = 1140m, Marlborough Sounds = 1300m, South Westland = 1040m.

<sup>+</sup> NIWA data from Agent numbers 29772, 29784, 21481, 27000, 14807, 14904, 14905 (Tait et al. 2006; Tait 2008).

Our candidate model set included all single variable models, most two-way additive models (with a few rules applied), and the interaction terms: delta T \* YO (we predicted that treatment would have a greater effect in most years than non-most years), and site \* year (as an alternative explanation for predator impact). We limited our models by only including YA in combination with YO, not including year as an independent variable as it was strongly associated with treatment and delta T, and finally the interaction site \* year could not occur in models with treatment or delta T.

### Effects of predator tracking rates on nest survival

We used data from the South Westland sites to investigate whether rat and/or mustelid tracking indices provided a better explanation of tītītipounamu nesting survival than predator control. Variability in rat and mustelid survey methods among study locations, and the mismatch in location, elevation, and/or survey timing between tracking tunnel and nest sites precluded the use of rat or mustelid FTIs in the main nest survival analysis. We modelled predator tracking rates using generalized additive models (GAM) which enabled us to predict tracking rates between tracking tunnel surveys and to account for the effect of elevation on the rat tracking index. We created separate GAM models for rats and mustelids using the mgcv package (Wood 2019) with a binomial error distribution, a cloglog link function and a cubic regression spline smoother. We added rat and mustelid GAM tracking rates to the variables used in the main nest survival model set. To avoid collinearity the rat and mustelid variables were not included in the same models as YO, YO + YA, delta T, or site \* year.

### Potential by-kill during aerial 1080 operations

We were interested in evaluating tītītipounamu survival during aerial 1080 operations, however we could not measure by-kill directly nor assess individual survival before and after 1080 operations from our data. Instead we used nest survival as a proxy for individual survival, which assumes that a nest would fail if one or both parents died, a finding supported by previous studies (Sherley 1985). We compared nest survival in treated areas in the week immediately following an aerial 1080 operation to nest survival over the remainder of the season. The model set included models from the main nest survival analysis with  $\Delta AICc < 2$ , with the treatment variables replaced with a binary variable coding whether or not it was within the week after a 1080 operation.

### Annual survivorship analysis

We used tītītipounamu banding and resight data collected during nest survival field work over four seasons (2010 to 2013) to estimate the effect of aerial 1080 treatment on apparent annual survival using Cormack-Jolly-Seber (CJS; Lebreton et al. 1992) models. CJS models cannot distinguish between death and emigration, but for clarity we hereafter refer to this as annual survivorship. Goodness-of-fit (GOF) for the overall dataset and groups was assessed using R2ucare version 1.0.0 (Gimenez et al. 2018) in R. We present results from South Westland only, as less effort was spent resighting individuals in the other two study regions and GOF testing showed that data was too sparse for analysis.

We evaluated a suite of 96 models using the explanatory variables: treatment, age class, sex, and year for survival probabilities; and age class, sex, and year for capture probabilities. Two aerial 1080 operations occurred in this

data set in December 2010 and October 2011. We coded survival probability from 2010 to 2011 and 2011 to 2012 in the corresponding sites as treatment. Birds first captured as adults could not be aged, thus we represented age class as juveniles (fledging to one year), and adults (one year and older). The survival probabilities model set included the null model, all single factor, two-factor additive, and three-factor additive models, and two interaction terms, age \* year and age \* treatment. The exception was that year and treatment could not occur in the same model. For capture probabilities, the null model, all single factor models, and two additive models, age + sex, and age + year, were considered. Modelling and model averaging were carried out using RMark version 2.2.7 (Laake 2013). We followed the approach described above for DSR to rank and select competitive models.

### Population modelling

To evaluate population level responses of tītītipounamu to aerial 1080 treatment we integrated annual survivorship and nest success estimates for different treatment and non-treatment conditions into a population model. We constructed a two-stage pre-breeding female-only matrix population model, where stage one is one year old (juveniles) and stage two is ages two and older (adults) (Caswell 2001). We used our estimates of annual survivorship, nest survival and data from the literature for other parameters (Table 3) to construct annual projection matrices for three treatment conditions: year of treatment, year after treatment, and non-treatment.

$$\mathbf{A}_i = \begin{bmatrix} b_j * ns_i * f * s_{j,i} & b_a * ns_i * f * s_{j,i} \\ s_{a,i} & s_{a,i} \end{bmatrix} \quad (2)$$

where  $b_j$  is probability of breeding for juveniles,  $b_a$  is probability of breeding for adults,  $ns_i$  is nest success for treatment  $i$ ,  $f$  is number of female fledglings per successful nest,  $s_{j,i}$  is juvenile survival under treatment  $i$ , and  $s_{a,i}$  is adult survival under treatment  $i$ . We chose to model one brood per year as double broods were not observed in our study.

Tītītipounamu experience a sequence of conditions following aerial 1080 operations, good conditions for survival and nesting in the year of treatment, moderate conditions in the year after treatment, and poor conditions in the intervening non-treatment years. We constructed periodic and stochastic population models to evaluate tītītipounamu population responses to different frequencies of treatment. The periodic model varied the frequency of treatment from annual treatment, to once every 10 years. We calculated the periodic population growth rate from the appropriate sequence of  $\mathbf{A}_i$  as in Caswell (2001). To parameterise the matrices we calculated predicted annual survivorship and nest survival for given environmental and treatment conditions by drawing beta values for the corresponding model-averaged model from a multivariate normal distribution using the estimates and variance covariance matrices. We drew values from a random normal distribution for our standardised elevation (mean 537, standard deviation 120) and a uniform distribution for site. Probability of breeding and the number of female fledglings per nest were drawn independently from beta and gamma distributions, respectively (Table 3). As our annual survivorship models did not include YA treatment, we assumed for the purposes of population modelling that YA values for adult and juvenile survival were the means of the respective YO and NT values for a given draw. We used Monte Carlo simulations to generate confidence intervals, using 160 000 iterations.

Although predator control through aerial 1080 operations

**Table 3.** Source of parameters used in population modelling. NT = non-treatment, YO = year of treatment, YA = Year after treatment.

Parameter	Estimate	Model or Reference
Nest success <sup>#</sup>	0.48–0.58 (NT) 0.78–0.81 (YO) 0.64–0.70 (YA)	Model average equation from nest survival analysis.
Juvenile survival	0.19 (NT) 0.62 (YO)	Model average equation from annual survivorship analysis.
Adult survival	0.43 (NT) 0.84 (YO)	Model average equation from annual survivorship analysis.
Juvenile female probability of breeding	0.75	Sherley 1985, 1993
Adult female probability of breeding	0.925	Sherley 1985, 1993
Number of broods	1	South Westland data
Number of fledglings	3.2	South Westland data, Higgins et al. 2001, Withers et al. 2019.

<sup>#</sup> For brevity, the range of nest success across sites is listed here (value depends on site, see Fig. 3). The simulation drew daily survival rates based on variables in the model-averaged model to calculate nest success.

can be imposed at regular intervals, in beech forests such operations have most commonly been used to prevent rodents and mustelids reaching plague densities following beech masts. Cycles of treatment and non-treatment years are therefore irregular. We investigated the influence of variation in the frequency of occurrence of treatment (year of and year after) and non-treatment years using a stochastic model. We varied the expected frequency of treatment years from annual to once every 10 years, as in the periodic model. To construct the stochastic model we created an environmental sequence of YO, YA, and NT years of length 11 000. Demographic parameters and the projection matrices were derived as in the periodic model. We estimated the stochastic population growth rate as the average growth rate of the population over 10 000 time steps, discarding the first 1000 time steps to allow convergence to the stationary distribution and thus remove any transient effects (Caswell 2001). We calculated Monte Carlo confidence intervals in the same manner as for the periodic model; the process was repeated 40 000 times for each treatment sequence. We obtained mean population projections for the periodic and stochastic models using the model-averaged estimates of nest success (excluding site variation) and annual survivorship with all other parameters held at mean values (Table 3). All calculations were performed in R.

We calculated elasticities of population growth rate to the demographic parameters for the YO and NT matrices to evaluate the potential effects of changes in the demographic parameters on the average annual population growth. Elasticities are the proportional change in population growth rate resulting from a proportional change in a parameter (Caswell 2001).

## Results

### Rat and mustelid tracking

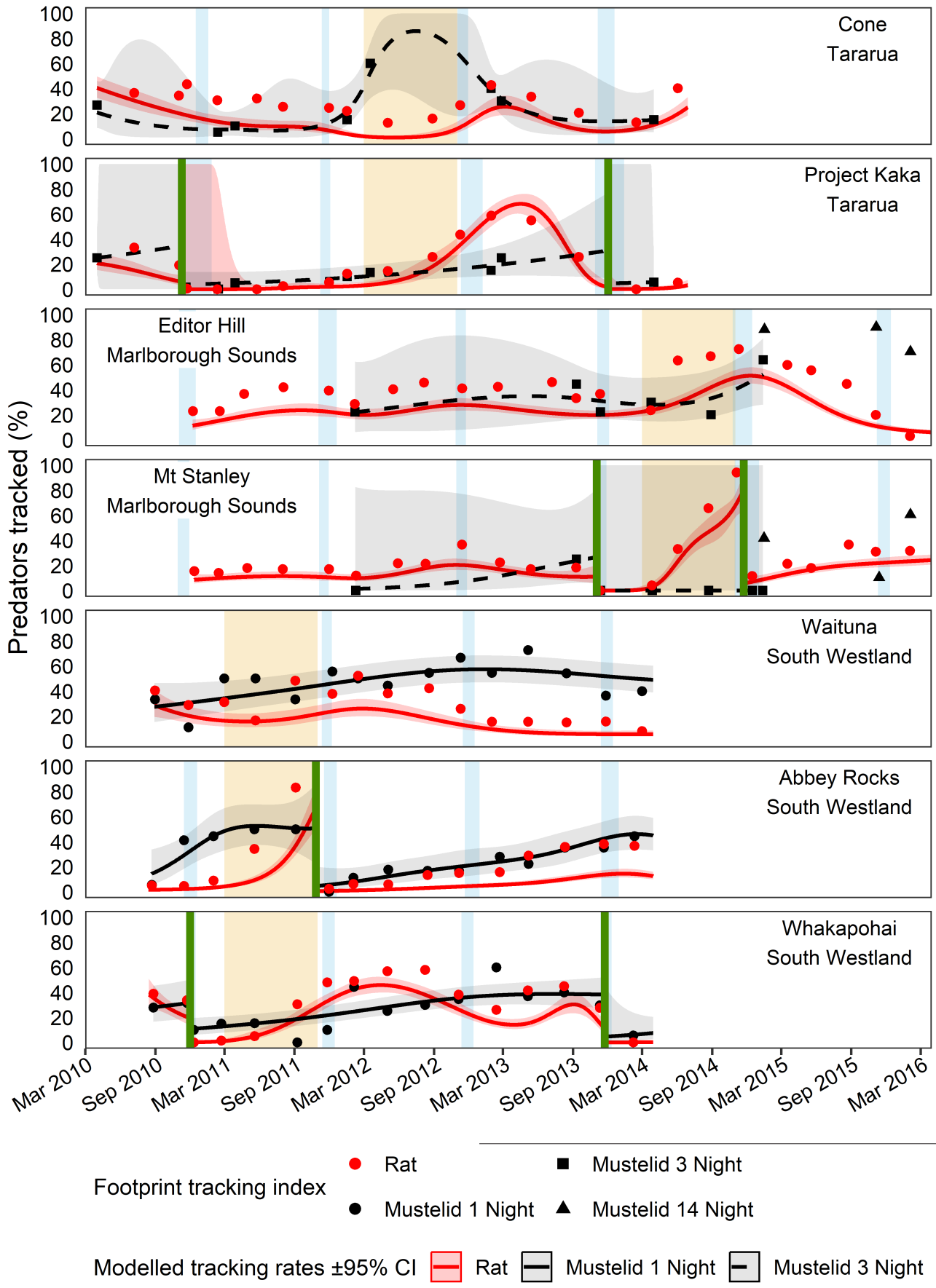
The aerial 1080 operations occurring during this study all reduced rat and mustelid indices to very low (mostly undetectable) levels, except the 2014 Mt Stanley operation, which reduced rat FTI from 94% to only 12% (Fig. 2). Managers aim to reduce rat FTI to below 5% (Elliott & Kemp 2016), so would not consider this operation successful. Small sample sizes, differing background rat and mustelid abundances,

different timing and frequency of aerial 1080 treatments, and different timing of beech mast events limit our ability to generalise. However, rats appeared to recover slowly following control in the absence of beech masting (for example, Project Kaka 2010, Abbey Rocks 2011), but can clearly recover quickly when mast events occur within a year of a 1080 treatment (for example, Mt Stanley 2013). The rat tracking GAM projected lower tracking at higher elevations. As the mean elevation of tracking tunnels was lower than most nests, the GAM rat tracking rates used in the South Westland tracking rate analysis were lower than the FTI.

### Nest survival

In total, 337 nests were monitored across the seven sites (Table 4), giving a daily nest survival sample size of 7607 days (Rotella et al. 2004). The earliest confirmed incubation was 9 October, and the last date any nest was monitored was 3 February. Most nests were monitored between 29 October (10th percentile) and 18 December (90th percentile). The first fledglings were seen in mid-November in both Tararua and Marlborough Sounds and in the last week of November in South Westland. Ninety-seven nests were known to have failed. Cause of failure was determined for 35 nests: predators were identified from camera data as the cause of failure at 27 nests (rat = 17, stoat = 10), and natural causes were confirmed by examining nest contents for eight nests. The cause of failure of the remaining 62 failed nests could not be determined.

We found strong evidence for effect of treatment on DSR, higher DSR in the breeding season of an aerial 1080 operation (YO) and of a quadratic effect of nest age (Table 5). YO was the only covariate with a 95% CI that did not include 0. DSR generally decreased with nest age, this effect was minimal in treatment years when DSR was high, but more pronounced under non-treatment conditions (Appendix S1). There was weaker evidence for the effect of YA, site and elevation. The model selection process had difficulty distinguishing among models with site, elevation or neither covariate, and more data is needed to clarify the importance of these variables. There was no evidence for an effect of any of the other covariates on DSR. Estimated nest success over the 44-day nesting period clearly improved with aerial 1080 management. Nest success was highest in the year of treatment, greater than 77%, and



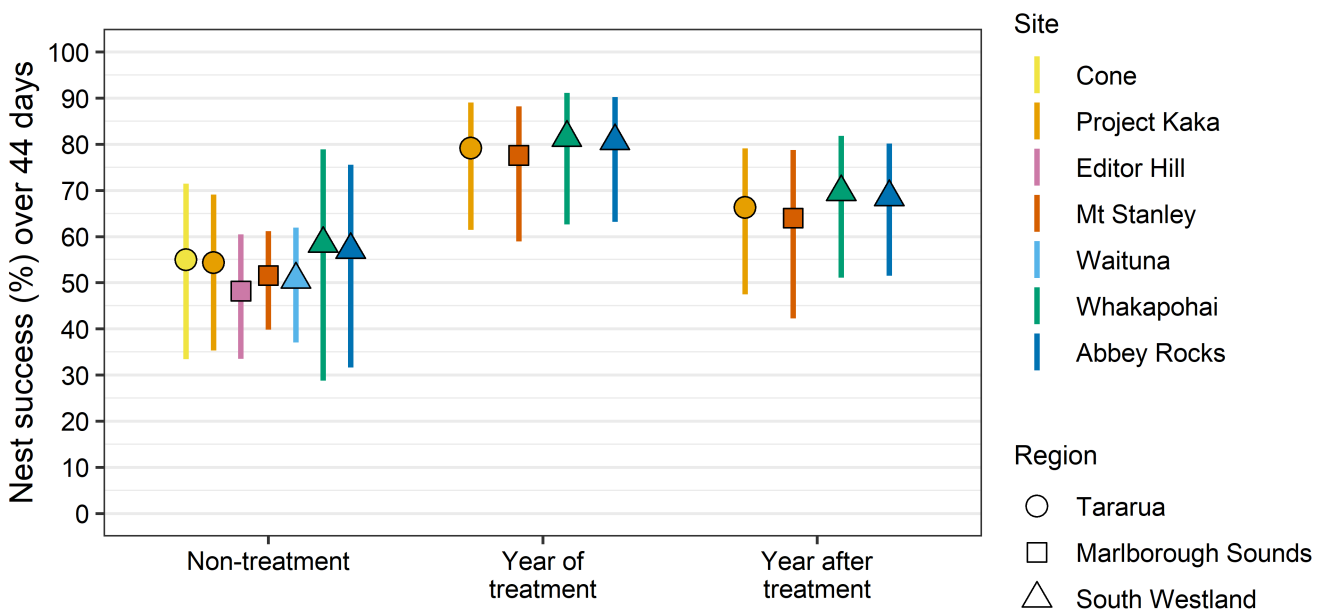
**Figure 2.** Rat and mustelid FTI (points) and GAM modelled tracking rates (lines with  $\pm 95\%$  CI ribbon). GAM rat tracking rates plotted at each site’s median nest elevation. There was insufficient data to model 14-night mustelid surveys. Green line = 1080 operation, yellow shading = mast year, blue shading = nest monitoring season.

**Table 4.** Nest monitoring sample size by treatment and site. Total number of exposure days and the number of nests, in brackets. (Forty-three nests contributed days to both non-treatment and treatment groups and appear in the table twice.)

Region	Site	Treatment	Exposure days (number of nests)		
			Non-treatment	Year of treatment	Year after treatment
Tararua	Cone	Non-treatment	542 (27)	-	-
Tararua	Project Kaka	Treatment	435 (20)	229 (13)	121 (7)
Marlborough Sounds	Editor Hill	Non-treatment	1415 (68)	-	-
Marlborough Sounds	Mt Stanley	Treatment	548 (30)	516 (32)	570 (32)
South Westland	Waituna	Non-treatment	688 (27)	-	-
South Westland	Abbey Rocks	Treatment	236 (10)	404 (13)	632 (21)
South Westland	Whakapohai	Treatment	454 (35)	390 (25)	427 (17)

**Table 5.** Top ten competitive GLM models for tītītipounamu daily nest survival weighted by  $\Delta AICc$ ; k = number of parameters in the model, Weight = model weight.

Model	k	AICc	$\Delta AICc$	Weight
YO + YA + Nest age + Elevation	6	854.93	0.00	0.05
YO + YA + Nest age	5	855.03	0.10	0.05
YO + Nest age + Site	10	855.56	0.63	0.04
YO + YA + Nest age + Site	11	857.02	2.09	0.02
YO + Nest age + Elevation	5	857.08	2.15	0.02
YO + YA + Nest age + Delta T + Delta T * YO	7	857.10	2.17	0.02
YO + Nest age + Site + Rain	11	857.10	2.17	0.02
YO + YA + Nest age + Delta T + Elevation + Delta T * YO	8	857.18	2.25	0.02
YO + Site	8	857.39	2.46	0.02
Nest age + Site	9	857.42	2.49	0.02

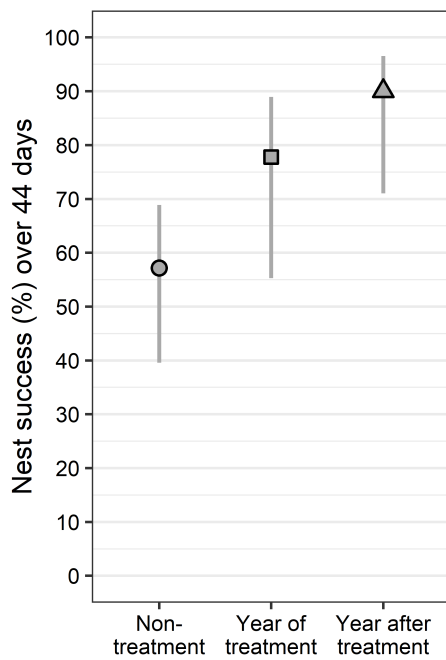


**Figure 3.** Model-averaged tītītipounamu nest success ( $\pm$  95% CI) by treatment condition and site. Elevation set to 550 m below treeline. Regions are indicated by shape for clarity, though not modelled.



**Table 6.** Top seven competitive GLM models for tītītipounamu daily nest survival in South Westland weighted by  $\Delta AICc$ .  $k$  = number of parameters in the model, Weight = model weight.

Model	$k$	AICc	$\Delta AICc$	Weight
YO + YA + Nest age	5	260.57	0.00	0.26
YO + YA + Nest age + Elevation	6	261.52	0.96	0.16
YO + YA + Nest age + Site	7	263.54	2.98	0.06
YO + YA + Nest age + Elevation + Site	8	265.10	4.53	0.03
Nest age + Site	5	265.77	5.21	0.02
Nest age + Mustelid	4	265.79	5.23	0.02
Nest age + Site + Site * Year	13	266.73	6.17	0.01



**Figure 4.** Model-averaged tītītipounamu nest success ( $\pm$  95% CI) by treatment condition in South Westland. Elevation set to 516 m below treeline.

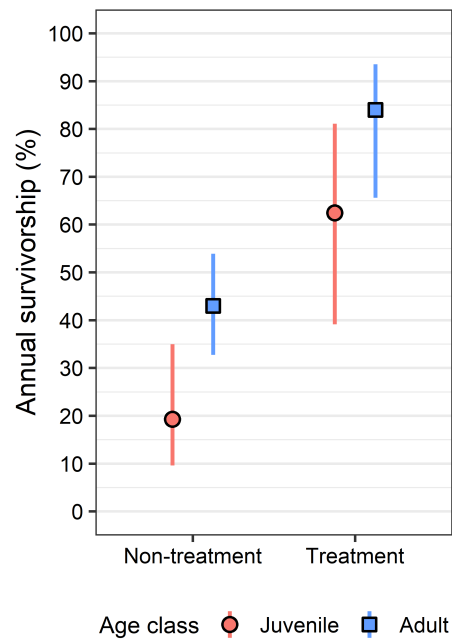
although not as strong, that benefit continued through the year after treatment (64–70%, Fig. 3). In contrast, only 48–58% of nests under non-treatment conditions fledged young (Fig. 3). Nest success declined with elevation, but this effect was weak and had high uncertainty (Appendices S2 and S3). Similarly, differences in nest success among sites were limited, particularly for treatment (YO and YA) conditions (Fig. 3).

**Effects of predator tracking rates on nest survival**

Our predator tracking rate analysis (South Westland data) had a sample size of 3231 days from 124 nests. This included 29 confirmed failures, of these, four nests were predated by stoats and one by a rat. Models with treatment effects better explained nest survival than models with tracking rates (Table 6). Model results mirrored those of the full data set with strong evidence for the YO, YA and nest age, and weak evidence for elevation effects (Table 6, Fig. 4). Of note, the estimated nest survival for YA was very high for this data set, which may be a small sample effect.

**Potential by-kill through aerial 1080 operations**

Eighty-five nests were monitored in the week following



**Figure 5.** Model-averaged tītītipounamu annual survivorship ( $\pm$  95% CI) by treatment condition and age class in South Westland.

an aerial 1080 operation. We found no support for adverse effects on nest survival, or by implication individual survival, immediately after a 1080 operation (weak support and opposite direction of effect). With all other covariates held at mean values, estimated DSR for a nest active in the week post-1080 was 0.991 [0.969, 0.997, 95% CI] compared to 0.989 [0.968, 0.996, 95% CI] for other nests.

**Annual survivorship**

A total of 177 tītītipounamu were banded in South Westland, of which 72 were seen in more than one season (Table 7). There was strong support for differences in annual survivorship among

**Table 7.** Number of tītītipounamu banded in South Westland, number of individuals recaptured in subsequent monitoring seasons in parentheses.

Age class at capture	Female	Male
Juvenile	28 (9)	33 (9)
Adult	49 (24)	67 (30)

treatment and age classes (Table 8). Mean annual survival was higher for both adults 0.84 [0.66, 0.94, 95% CI] and juveniles 0.62 [0.39, 0.81, 95% CI] during treatment years (Fig. 5) but rather bleak in non-treatment years, 0.43 [0.33, 0.54, 95% CI] and 0.19 [0.10, 0.35, 95% CI] for adults and juveniles, respectively. Capture probabilities were moderately high with weak support for an effect of year; 0.80 [0.59, 0.92, 95% CI], 0.75 [0.55, 0.87, 95% CI] and 0.77 [0.44, 0.93, 95% CI] for 2011 to 2013, respectively.

**Population modelling**

Both the periodic and stochastic modelling showed a higher frequency of treatment resulted in higher population growth rates, most notably at short treatment intervals (Fig. 6). As expected, the stochastic model was more conservative.

Our modelling emphasises the importance of frequency of treatments for maintaining populations long-term. Unfortunately, the high parameter uncertainty limits our ability to identify the treatment interval at which *tītītipounamu* populations would be stable.

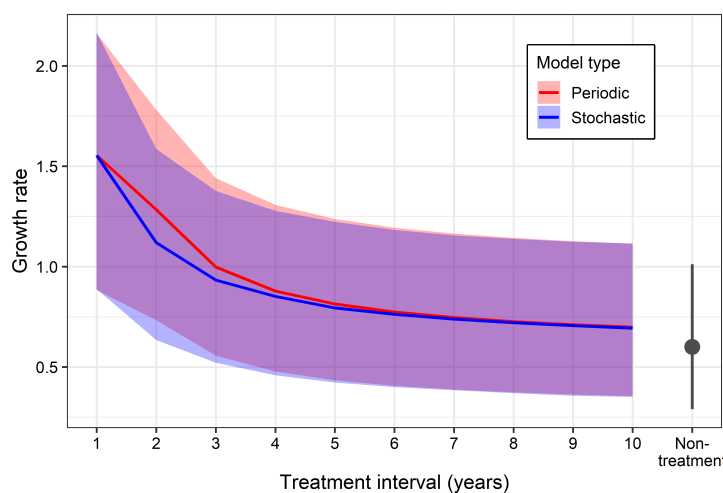
The elasticity analysis revealed that adult survivorship and productivity parameters had similar effects on population growth rate when treated and untreated, but adult survival was much more important under non-treatment conditions (Table 9). We compared the impact of increasing the number of broods from one brood raised per year to 1.5 as in Sherley (1985). Adjusting this parameter did not change the relative importance of parameters but further reduced the difference between adult and juvenile survival under treatment conditions.

**Table 8.** Top seven competitive models of *tītītipounamu* annual survivorship in South Westland ranked by  $\Delta AICc$ . k = number of parameters in the model, Weight = model weight, Phi = survival probability, p = capture probability, Age = age class.

Model	k	AICc	$\Delta AICc$	Weight
Phi (Treatment + Age) p (Constant)	4	352.54	0.00	0.41
Phi (Treatment + Age) p (Year)	6	354.15	1.61	0.18
Phi (Treatment + Age) p (Age + Year)	7	355.19	2.65	0.11
Phi (Treatment) p (Age + Year)	6	355.26	2.72	0.11
Phi (Treatment) p (Age)	4	356.64	4.10	0.05
Phi (Treatment) p (Constant)	3	358.43	5.89	0.02
Phi (Treatment) p (Sex + Age)	5	358.72	6.18	0.02

**Table 9.** Elasticities of population growth rate to mean demographic parameter values for the non-treatment (NT) and treatment (YO) matrices.

Parameter	Elasticity	
	Non-treatment	Treatment
Adult survival	0.723	0.565
Juvenile survival	0.227	0.411
Nest success	0.227	0.411
Number of fledglings	0.227	0.411
Probability of breeding adult	0.171	0.244
Probability of breeding juvenile	0.056	0.167



**Figure 6.** Periodic and stochastic *tītītipounamu* population growth rates (lines with  $\pm$  95% CI ribbon) for annual aerial 1080 treatment to a treatment interval of 10 years. Overlapping values are purple. Population growth rate without treatment plotted as a grey point for contrast.

## Discussion

Our findings provide strong evidence that aerial 1080 predator control improves both nest success and annual survivorship in tītītipounamu. The strength of these results supports the argument that predation by introduced mammals is the primary limiting factor for New Zealand avifauna (Innes et al. 2010). Our results generally align with previous studies that have measured tītītipounamu nesting success. Briskie et al. (2014) estimated nest success of 15.8% ( $n = 12$ ) for natural nests without predator control, far lower than our estimate of 48–58% nest success. At a site with natural nests and predator control, Schlesselmann et al. (2023) found nest success of 62% [41, 78, 95% CI;  $n = 55$ ]. This is lower than our estimate of > 77% but they did not have a non-treatment site so the strength of any treatment effect at their site cannot be assessed. Other studies of annual survivorship also support our results. Leech et al. (2007) found annual survivorship rates of a translocated population on a predator-free island almost identical to our survivorship with aerial 1080. At a non-treatment remnant forest site, Sherley (1985) found slightly higher annual survivorship rates (23% juveniles, 57% adults) than our non-treatment results (19%, 43% respectively), but recent estimates for this population (Khawaja et al. 2023; 18%, 49%) almost matched ours. Like other studies (Sherley 1985; Leech et al. 2007; Withers et al. 2019; Khawaja et al. 2023), we found lower survival rates for juveniles than adults. Our results add tītītipounamu to the growing list of species for which aerial 1080 predator control operations benefit nesting success and/or annual survivorship: wren/tuke (*Xenicus gilviventris*; Rawlence 2019), North and South Island robins/toutouwai (*Petroica* sp.; Powlesland et al. 1999; Bell et al. 2021), South Island fernbirds/mātātā (*Poodytes punctatus punctatus*; Kilner et al. 2022), fantail/pīwakawaka (*Rhipidura fuliginosa*; Robertson 2019), kea (*Nestor notabilis*; Kemp et al. 2018, 2023), North Island brown kiwi/kiwi-nui chicks (*Apteryx mantelli*; Robertson 2019) and western weka (*Gallirallus australis australis*; Tinnemans et al. 2018).

The second season benefit of predator control on nest success is weaker and more variable than the treatment year effect. This is logical and likely a response to predator numbers increasing through reinvasion and/or population growth. Suppression of rodents and mustelids for more than one year following aerial 1080 predator control has been observed previously (Elliott & Kemp 2016; Robertson 2019), as has sustained benefits for other native New Zealand birds (Powlesland et al. 1999; Rawlence 2019; Robertson 2019). These benefits might be improved through actions that reduce reinvasion or regrowth of predator populations such as larger treatment areas, lower edge to area ratios in treatment areas, fewer exclusion zones and better predator control (Griffiths & Barron 2016).

Elevation and delta T, two factors we expected to influence nest success had no detectable effect. This contradicted our expectation that elevation would affect tītītipounamu nest survival through its relationship with temperature, forest productivity and predator abundances (Christie et al. 2017; Whaitau et al. 2022). Unfortunately, in our study tītītipounamu were abundant enough to study only in a narrow and relatively high elevation band which limited elevational variation in our data set and therefore our ability to detect any relationship if it existed. Our study also did not support predator control providing greater benefits in mast years even though predator numbers are knocked back from higher levels under these conditions (O'Donnell & Phillipson 1996; Elliott & Suggate

2007; Elliott & Kemp 2016). Our failure to detect an effect of masting on the relationship between treatment and nest survival may be due to a number of reasons: (1) masts do not improve insect availability in a way that benefits tītītipounamu; (2) the impacts of masts on predators or food resources are weaker near the treeline where we studied tītītipounamu; (3) the mast events that occurred during our study were relatively weak (according to the delta T predictions and field observations) or highly variable; or (4) we had insufficient data to evaluate this relationship. Schlesselmann et al. (2023) investigated the impact of elevation and food availability on tītītipounamu productivity and did not find a strong relationship, however this research occurred in North Island non-beech forest. More data is needed to clarify the effects of both elevation and masting in beech forest.

Our best estimates of vital rates for tītītipounamu and population modelling shows aerial 1080 predator control at approximately three year intervals is necessary to maintain stable or increasing tītītipounamu populations. This is in line with results from studies modelling population growth of other New Zealand native species in relation to predator control scenarios, specifically aerial 1080 (Robertson 2019), or aerial 1080 in combination with ground-based control methods (Basse et al. 2003; O'Donnell et al. 2017). This modelling assumes frequent treatment continues to be effective. Our stochastic population model was slightly more pessimistic than the periodic model. This is an inherent property of these models resulting from strings of years of low productivity (in this context non-treatment years) occurring by chance in the stochastic model. Climate change is an additional source of stochasticity and is expected to increase the frequency of mast events (Richardson et al. 2005) and heighten predator levels (Tompkins et al. 2013), which is likely to increase the frequency of low productivity years for tītītipounamu. It is of interest that adult survival had such a high elasticity under non-treatment conditions (Table 9). Generally adult survival would be far more important than components of productivity for long-lived species while contributions of survival and productivity would be more balanced for short-lived species like tītītipounamu (Caswell 2001; Stahl & Oli 2006). The very poor outcomes for productivity make survival extremely important under non-treatment conditions. That is, birds need to survive and attempt reproducing over several years to have any chance of offspring surviving.

Effective predator control for tītītipounamu at lower elevations and/or in warmer forests is needed to future-proof tītītipounamu populations. Tītītipounamu are restricted to a narrower and higher elevation range than they previously inhabited. If their range further constricts they will become more vulnerable to stochastic events and local extinctions. Fragmented populations are at increased risk of local extinction as tītītipounamu have limited dispersal ability and will not readily re-invade isolated forests (Withers et al. 2019; Walker et al. 2021). Further, if climate change and increasing temperatures alter rat and stoat distributions (Christie et al. 2017), tītītipounamu at higher elevations will become at greater risk (Walker et al. 2019b). The low abundance of tītītipounamu at lower elevations suggests aerial 1080 regimes at these elevations are currently insufficient. If an effective treatment regime was found, we expect lower elevation tītītipounamu could experience greater benefits than demonstrated here as these lower elevations may provide better resources or conditions for breeding (Schlesselmann et al. 2023).

Only a small portion of tītītipounamu habitat is treated with

aerial 1080 at a frequency necessary to maintain population growth. For example, of the approximately 4 million hectares of forests containing beech species in New Zealand (Wardle 1984) over the six years of this study (2010–2015) 859,000 ha of beech forest were treated with aerial 1080 (J. Kemp, Department of Conservation, Nelson, pers. comm.; Manaaki Whenua Landcare Research 2012). However, only a fraction of that area was treated at a frequency required for tītītipounamu population persistence.

Our study did not determine the relative importance of the predators of tītītipounamu and highlighted some challenges with using tracking tunnels to measure predator impacts on native species. Although we detected rats preying upon tītītipounamu nests more often than stoats, there were many apparently preyed upon nests where we could not identify the predator. We can only conclude that both rats and stoats have an impact on tītītipounamu. We expected that predator abundance indices would be better predictors of nest survival and annual survivorship than the presence or absence of a predator control operation. This was not the case, and we speculate that our indices were imprecise because of variability in time and space, whether particular to the nature of the methods or our study, for example, the limited elevational range of our study nests translated to a limited range of tracking rates. Thus, for our study, the combination of predator abundance is better summarised by the presence or absence of predator control operations than our indices. Nevertheless, this outcome highlights potential issues for researchers using tracking tunnels to quantify predator impacts on specific parameters for native species. Tracking tunnels provide coarse indices of relative abundance and are usually sparsely distributed on the landscape (Blackwell et al. 2002; Gillies & Williams 2007; Smith & Weston 2017). Researchers have had mixed success using tracking tunnel indices to identify predator thresholds at which native species are adversely affected (Armstrong et al. 2006; Boulton et al. 2008; Fea & Hartley 2018; Bell et al. 2021). Going beyond estimating predator impacts and quantifying the population level effects of predator management is a step towards identifying predator thresholds.

Our findings suggest there is reason to be optimistic about the persistence of tītītipounamu populations where appropriate management is maintained. In their favour, species from deep endemic lineages have been found to recover more quickly than introduced species after predator eradication or suppression to 0% FTI (Binny et al. 2021). Tītītipounamu have proved even more resilient than other deep endemics in New Zealand, probably because they are able to maintain higher population densities with fewer resources than larger bodied birds (see Walker et al. 2021). Further, although our findings apply to beech forests, similar benefits of predator control for tītītipounamu would be expected in other ecosystems (Murphy et al. 1999, Harper 2009). Continued population persistence and reversal of range retractions will, however, require considerable management investment.

## Acknowledgments

We are very grateful to everyone who participated in fieldwork for this research, especially Athena Irvine and Lucy Rossiter. Thank you also to the Department of Conservation Operations staff and landowners who supported this research and allowed us access to research sites. We thank Terry Greene and Kerry Weston and two anonymous reviewers for providing

constructive comments on earlier drafts. We especially acknowledge our colleague Tom Allan, who sadly passed away before this manuscript was completed.

## Additional information and declarations

**Author contributions:** GE conceptualised the design and provided supervision. CH, GE and CK contributed to methodology. CK wrote the original draft, carried out data curation and visualisation. CK and CH carried out the analysis. CH, CK and GE revised the manuscript. RC, TA, TR and JT oversaw field investigations. JM, MB, CB, AM, KM and CK contributed to field investigations.

**Funding:** This study was funded by the Department of Conservation.

**Data and code availability:** The data and code from this article may be made available by contacting the corresponding author.

**Ethics:** No permits required as the research was carried out by Department of Conservation staff.

**Conflicts of interest:** The authors report no conflicts of interest.

## References

- Alley JC, Berben PH, Dugdale JS, Fitzgerald BM, Knightbridge PI, Meads MJ, Webster RA 2001. Responses of litter-dwelling arthropods and house mice to beech seeding in the Orongorongo Valley, New Zealand. *Journal of the Royal Society of New Zealand* 31(2): 425–452.
- Armstrong DP, Raeburn EH, Powlesland RG, Howard M, Christensen B, Ewen JG 2002. Obtaining meaningful comparisons of nest success: data from New Zealand robin (*Petroica australis*) populations. *New Zealand Journal of Ecology* 26(1): 1–13.
- Armstrong DP, Raeburn EH, Lewis RM, Ravine D 2006. Modeling vital rates of a reintroduced New Zealand robin population as a function of predator control. *The Journal of Wildlife Management* 70(4): 1028–1036.
- Arnold TW 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74(6): 1175–1178.
- Barton K 2020. MuMIn: multi-model inference. Version 1.43.17 <https://cran.r-project.org/web/packages/MuMIn>
- Basse B, Flux I, Innes J 2003. Recovery and maintenance of North Island kokako (*Callaeas cinerea wilsoni*) populations through pulsed pest control. *Biological Conservation* 109: 259–270.
- Bell M, Armstrong D, Tinnemans J, Rawlence T, Bell C, McDonald A, Moran K, Elliott G 2021. The effects of beech masts and 1080 pest control on South Island robins (*Petroica australis*). *New Zealand Journal of Ecology* 45(2): 3452.
- Binny RN, Innes J, Fitzgerald N, Pech R, James A, Price R, Gillies C, Byrom AE 2021. Long-term biodiversity trajectories for pest-managed ecological restorations: eradication vs. suppression. *Ecological Monographs* 91(2): e01439.
- Blackwell GL, Potter MA, McLennan JA 2002. Rodent density indices from tracking tunnels, snap-traps and Fenn traps: do they tell the same story? *New Zealand Journal of Ecology* 26(1): 43–51.

- Bolker B 2014. Odds ratios vs hazard ratios. <https://rpubs.com/bbolker/hazodds> (accessed 1 November 2018).
- Boulton RL, Richard Y, Armstrong DP 2008. Influence of food availability, predator density and forest fragmentation on nest survival of New Zealand robins. *Biological Conservation* 141(2): 580–589.
- Briskie JV, Shorey L, Massaro M 2014. Nest-boxes increase fledging success in the declining rifleman *Acanthisitta chloris*, New Zealand. *Conservation Evidence* 11: 12–15.
- Brown K, Elliott G, Innes J, Kemp J 2015. Ship rat, stoat and possum control on mainland New Zealand: an overview of techniques, successes and challenges. Wellington, Department of Conservation. 36 p.
- Buckland ST 2006. Point-transect surveys for songbirds: robust methodologies. *The Auk* 123(2): 345–357.
- Burnham KP, Anderson DR 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. New York, Springer Science & Business Media, LLC. 488 p.
- Carpenter JK, Monks A, Innes J, Griffiths J 2022. Pushing the limits: ship rat (*Rattus rattus*) population dynamics across an elevational gradient in response to mast seeding and supplementary feeding. *Biological Invasions* 24(10): 3065–3081.
- Caswell H 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sunderland, MA, Sinauer Associates. 722 p.
- Christie JE, Wilson PR, Taylor RH, Elliott G 2017. How elevation affects ship rat (*Rattus rattus*) capture patterns, Mt Misery, New Zealand. *New Zealand Journal of Ecology* 41(1): 113–119.
- Cooch E, White G 2020. Appendix B: the ‘Delta method’. In: Program MARK: a gentle introduction. p. 1–44.
- Dinsmore SJ, White GC, Knopf FL 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83(12): 3476–3488.
- Eason C, Morgan DR, Fisher PM, Hopkins B, Cowan P 2006. Reflections on improvements in the use of vertebrate pesticides in New Zealand: 1996–2006. In: Timm RM, O’Brien JM, editors. Proceedings 22nd Vertebrate Pest Conference. Davis, CA. University of California, Davis. p. 406–412.
- Elliott GP 1996a. Mohua and stoats: A population viability analysis. *New Zealand Journal of Zoology* 23(3): 239–247.
- Elliott GP 1996b. Productivity and mortality of mohua (*Mohoua ochrocephala*). *New Zealand Journal of Zoology* 23(3): 229–237.
- Elliott G, Kemp J 2016. Large-scale pest control in New Zealand beech forests. *Ecological Management & Restoration* 17(3): 200–209.
- Elliott G, Suggate R 2007. Operation Ark: three year progress report. Christchurch, Department of Conservation. 84 p.
- Elliott GP, Wilson PR, Taylor RH, Beggs JR 2010. Declines in common, widespread native birds in a mature temperate forest. *Biological Conservation* 143(9): 2119–2126.
- Fea N, Hartley S 2018. The balancing act of nest survival: survival of a small endemic bird in the face of ship rat predation and other risk factors. *Avian Conservation and Ecology* 13(2): 11.
- Fea N, Linklater W, Hartley S 2021. Responses of New Zealand forest birds to management of introduced mammals. *Conservation Biology* 35(1): 35–49.
- Fitzgerald BM, Daniel MJ, Fitzgerald AE, Karl BJ, Meads MJ, Notman PR 1996. Factors affecting the numbers of house mice (*Mus musculus*) in hard beech (*Nothofagus truncata*) forest. *Journal of the Royal Society of New Zealand* 26(2): 237–249.
- Fox J, Weisberg S, Price B, et al. 2020. car: Companion to applied regression. Version 3.0-10 <https://cran.r-project.org/web/packages/car>.
- Gaze P 2003. The rise and fall of mohua (*Mohoua ochrocephala*) on Mt Stokes. *Notornis* 50(3): 176–177.
- Gaze P 1978. Breeding biology of the North Island rifleman. *Notornis* 25(3): 244.
- Gillies C, Williams D 2007. DOC tracking tunnel guide V2. 5.1. Hamilton, Department of Conservation.
- Gimenez O, Lebreton J-D, Choquet R, Pradel R 2018. R2ucare: An R package to perform goodness-of-fit tests for capture–recapture models. *Methods in Ecology and Evolution* 9(7): 1749–1754.
- Grant TA, Shaffer TL, Madden EM, Pietz PJ 2005. Time-specific variation in passerine nest survival: new insights into old questions. *The Auk* 122(2): 661–672.
- Griffiths JW, Barron MC 2016. Spatiotemporal changes in relative rat (*Rattus rattus*) abundance following large-scale pest control. *New Zealand Journal of Ecology* 40(3): 371–380.
- Harper G 2009. The native forest birds of Stewart Island/Rakiura: patterns of recent declines and extinctions. *Notornis* 56(1): 63–81.
- Higgins PJ, Peter JM, Steele WK eds. 2001. Handbook of Australian, New Zealand and Antarctic birds. Vol 5, Tyrant-flycatchers to chats. Melbourne, Oxford University Press. 1269 p.
- Hoare JM, Monks A, O’Donnell CFJ 2013. Do population indicators work? Investigating correlated responses of bird populations in relation to predator management. *Ecological Indicators* 25: 23–34.
- Innes J, Kelly D, Overton JM, Gillies C 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology* 34(1): 86–114.
- Innes J, Miskelly C, Armstrong D, Fitzgerald N, Parker K, Stone Z 2022. Movements and habitat connectivity of New Zealand forest birds: a review of available data. *New Zealand Journal of Ecology* 46(2): 3481.
- Kelly D, Geldenhuis A, James A, Holland EP, Plank MJ, Brockie RE, Cowan PE, Harper GA, Lee WG, Maitland MJ, Mark AF, Mills JA, Wilson PR, Byrom AE 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters* 16(1): 90–98.
- Kemp J, Mosen C, Elliott G, Hunter C 2018. Effects of the aerial application of 1080 to control pest mammals on kea reproductive success. *New Zealand Journal of Ecology* 42(2): 158–168.
- Kemp JR, Young L, Mosen C, Bolitho L, Orr-Walker T, Yockney I, Elliott G 2023. Irruptive dynamics of invasive carnivores and prey populations, and predator control, affect kea survivorship across the Southern Alps. *New Zealand Journal of Zoology* 50(2): 279–304.
- Khwaja N, Preston S, Hatchwell B, Briskie J 2023. Recruitment, survival and breeding success in a declining rifleman population. *New Zealand Journal of Ecology* 45(1): 3507.
- Kilner C, Kemp J, Elliott G 2022. Short term effects of an aerial 1080 operation on mātātā (South Island fernbird, *Poodytes punctatus punctatus*) in a South Island wetland. *Notornis* 69: 203–210.
- King CM 1983. The relationships between beech (*Nothofagus*

- sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52(1): 141–166.
- Laake JL 2013. RMark: An R interface for analysis of capture-recapture data with MARK. Seattle, NOAA. 25 p.
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62(1): 67–118.
- Leech TJ, Craig E, Beaven B, Mitchell DK, Seddon PJ 2007. Reintroduction of rifleman *Acanthisitta chloris* to Ulva Island, New Zealand: evaluation of techniques and population persistence. *Oryx* 41(3): 369–375.
- Manaaki Whenua Landcare Research 2012. Potential vegetation of New Zealand. <https://iris.scinfo.org.nz/layer/48289-potential-vegetation-of-new-zealand/> (accessed 29 September 2021).
- Murphy E, Robbins L, Young J, Dowding J 1999. Secondary poisoning of stoats after an aerial 1080 poison operation in Pureora Forest, New Zealand. *New Zealand Journal of Ecology* 23: 175–182.
- Murphy EC, Dowding JE 1995. Ecology of the stoat in *Nothofagus* forest: home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology* 19(2): 97–109.
- O'Donnell CFJ 1996. Predators and the decline of New Zealand forest birds: An introduction to the hole-nesting bird and predator programme. *New Zealand Journal of Zoology* 23(3): 213–219.
- O'Donnell CFJ 2019. Benefits of long-term predator control for forest bird populations in the Landsborough Valley, South Westland, over 21 years. Annual progress report. Christchurch, Department of Conservation.
- O'Donnell CFJ, Hoare JM 2012. Quantifying the benefits of long-term integrated pest control for forest bird populations in a New Zealand temperate rainforest. *New Zealand Journal of Ecology* 36(2): 131–140.
- O'Donnell CFJ, Phillipson SM 1996. Predicting the incidence of mohua predation from the seedfall, mouse, and predator fluctuations in beech forests. *New Zealand Journal of Zoology* 23(3): 287–293.
- O'Donnell CFJ, Pryde MA, van Dam-Bates P, Elliott GP 2017. Controlling invasive predators enhances the long-term survival of endangered New Zealand long-tailed bats (*Chalinolobus tuberculatus*): implications for conservation of bats on oceanic islands. *Biological Conservation* 214: 156–167.
- Parlato EH, Armstrong DP, Innes JG 2015. Traits influencing range contraction in New Zealand's endemic forest birds. *Oecologia* 179(2): 319–328.
- Parliamentary Commissioner for the Environment 2011. Evaluating the use of 1080: Predators, poisons and silent forests. Wellington, Parliamentary Commissioner for the Environment. 87 p.
- Powlesland RG, Knegtmans JW, Marshall ISJ 1999. Costs and benefits of aerial 1080 possum control operations using carrot baits to North Island robins (*Petroica australis longipes*), Pureora Forest Park. *New Zealand Journal of Ecology* 23(2): 145–159.
- R Core Team 2021. R: a language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. <https://www.r-project.org>.
- Rawlence T 2019. The efficacy of aerial 1080 poison applied on a landscape scale to control alpine predators and the reproductive response of rock wren (*Xenicus gilviventris*). Unpublished MSc thesis. University of Otago, Dunedin, New Zealand. 128 p.
- Richardson SJ, Allen RB, Whitehead D, Carswell FE, Ruscoe WA, Platt KH 2005. Climate and net carbon availability determine temporal patterns of seed production by *Nothofagus*. *Ecology* 86(4): 972–981.
- Robertson HA 2019. Landscape-scale applications of 1080 pesticide benefit North Island brown kiwi (*Apteryx mantelli*) and New Zealand fantail (*Rhipidura fuliginosa*) in Tongariro Forest, New Zealand. *Notornis* 66: 1–15.
- Robertson HA, Baird K, Dowding JE, Elliott GP, Hitchmough RA, Miskelly CM, McArthur N, O'Donnell CFJ, Sagar PM, Scofield RP, Taylor GA 2017. Conservation status of New Zealand birds, 2016. New Zealand Threat Classification Series 19. Wellington, Department of Conservation. 23 p.
- Rotella JJ, Dinsmore SJ, Shaffer TL 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27(1): 187–205.
- Schlesselmann A-K, Innes J, Fitzgerald N, Monks A, Walker S 2023. Invertebrate food supply and reproductive success of two native forest passerines along an elevational gradient. *New Zealand Journal of Ecology* 47(1): 3514.
- Sherley GH 1985. The breeding system of the South Island rifleman (*Acanthisitta chloris*) at Kowhai Bush, Kaikoura, New Zealand. Unpublished PhD thesis. University of Canterbury, Christchurch, New Zealand.
- Smith DHV, Weston KA 2017. Capturing the cryptic: a comparison of detection methods for stoats (*Mustela erminea*) in alpine habitats. *Wildlife Research* 44(5): 418–426.
- Spurr EB, Powlesland RG 1997. Impacts of aerial application of 1080 on non-target native fauna: review and priorities for research. Science for Conservation No. 62. Wellington, New Zealand, Department of Conservation. 31 p.
- Stahl J, Oli M 2006. Relative importance of avian life-history variables to population growth rate. *Ecological Modelling* 198: 23–39.
- Tait AB 2008. Future projections of growing degree days and frost in New Zealand and some implications for grape growing. *Weather and Climate* 28: 17–36.
- Tait A, Henderson R, Turner R, Zheng X 2006. Thin plate smoothing spline interpolation of daily rainfall for New Zealand using a climatological rainfall surface. *International Journal of Climatology: A Journal of the Royal Meteorological Society* 26(14): 2097–2115.
- Tinnemans J, Elliott G, Rawlence T, McDonald A, Nydegger Bell M, Bell C, Moran K 2018. Costs and benefits of aerial 1080 operations to Western weka (*Gallirallus australis australis*). *New Zealand Journal of Ecology* 43(1): 3353.
- Tompkins DM, Byrom AE, Pech RP 2013. Predicted responses of invasive mammal communities to climate-related changes in mast frequency in forest ecosystems. *Ecological Applications* 23(5): 1075–1085.
- van Heezik Y, Ray S, Jamieson I, Allen O, Schadewinkel R 2020. Impacts of aerial 1080 predator control on nest success and adult survival of South Island robins. *New Zealand Journal of Ecology* 44(2): 3407.
- Van Vianen J, Burge OR, MacFarlane AT, Kelly D 2018. The effects of single aerial 1080 possum-control operations on common forest birds in the South Island, New Zealand.

- New Zealand Journal of Ecology 42(2): 169–178.
- Veltman CJ, Westbrooke IM 2011. Forest bird mortality and baiting practices in New Zealand aerial 1080 operations from 1986 to 2009. *New Zealand Journal of Ecology* 35(1): 21–29.
- Walker S, Monks A, Innes J 2017. Status and change in native forest birds on New Zealand’s mainland, 1969–1979 to 1999–2004. LC2786. Dunedin, Manaaki Whenua Landcare Research. 67 p.
- Walker S, Kemp JR, Elliott GP, Mosen CC, Innes JG 2019a. Spatial patterns and drivers of invasive rodent dynamics in New Zealand forests. *Biological Invasions* 21(5): 1627–1642.
- Walker S, Monks A, Innes J 2019b. Thermal squeeze will exacerbate declines in New Zealand’s endemic forest birds. *Biological Conservation* 237: 166–174.
- Walker S, Monks A, Innes JG 2021. Life history traits explain vulnerability of endemic forest birds and predict recovery after predator suppression. *New Zealand Journal of Ecology* 45(2): 13.
- Wardle J 1984. The New Zealand beeches ecology, utilisation and management. Wellington, New Zealand Forest Service. 447 p.
- Westbrooke IM, Powlesland RG 2005. Comparison of impact between carrot and cereal 1080 baits on tomtits (*Petroica macrocephala*). *New Zealand Journal of Ecology* 29(1): 143–147.
- Whitau K, Kelly D, Galloway T, MacFarlane A, van Vianen J, Rossignaud L, Doherty K 2022. Effects of altitude, seedfall and control operations on rat abundance in South Island *Nothofagus* forests 1998–2016. *New Zealand Journal of Ecology* 47(1): 3502.
- White PCL, King CM 2006. Predation on native birds in New Zealand beech forests: the role of functional relationships between stoats *Mustela erminea* and rodents. *Ibis* 148(4): 765–771.
- Wilson PR, Karl BJ, Toft RJ, Beggs JR, Taylor RH 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological Conservation* 83: 175–185.
- Withers S, Armstrong D, Ward-Smith T, Parsons S, Hauber ME 2019. Improved methods for reducing translocation mortality and obtaining reliable population projections for reintroduction of the New Zealand rifleman *Acanthisitta chloris*. *Bird Conservation International* 29(4): 542–557.
- Wood S 2019. mgcv: Mixed GAM computation vehicle with automatic smoothness estimation. Version 1.8-31 <https://cran.r-project.org/web/packages/mgcv>.

Received: 25 August 2023; accepted: 11 July 2024  
 Editorial board member: Isabel Castro

## Supplementary Materials

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Model-averaged tītītipounamu daily nest survival (DSR, dashed line with 95% CI ribbon) by treatment condition over nest age. Elevation below treeline held at 550 m.

**Appendix S2.** Model-averaged tītītipounamu daily nest survival (DSR, dashed line with 95% CI ribbon) by treatment condition over elevation measured below treeline. Nest age held at 22 days.

**Appendix S3.** Model-averaged tītītipounamu nest success ( $\pm$  95% CI) by treatment condition over a range of elevations measured below treeline at Project Kaka, Tararua Ranges.

The New Zealand Journal of Ecology provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.