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# 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

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## ABSTRACT

Invasive mammalian predators pose one of the greatest threats to biodiversity globally, particularly on oceanic islands. However, little is known about the impacts of these invasive predators on bats (Chiroptera), one of the most specious mammal groups, and one of the most widespread groups of mammals threatened on oceanic islands (> 200 spp.). Nearly 50% of the world's threatened bats are island endemics and because they are often the only native mammals on islands, they fulfil important ecological roles such as pollination and seed dispersal. Long-tailed bats (*Chalinolobus tuberculatus*) are critically endangered because of predation by exotic mammals, particularly ship rats (*Rattus rattus*), introduced by humans to the island archipelago of New Zealand. We monitored the survival of bats in three colonies in temperate rainforest in Fiordland over 22 years. Since 2009, we controlled predators during irruption phases and compared survival of bats in previously untreated areas with survival in forest blocks treated using rodenticides deployed in bait stations. Survival was estimated using multi-state mark-recapture models in Program Mark 7.0 with > 15,000 bats tagged. Survival was primarily dependent on year and age of bats, although seedfall intensity of the dominant canopy tree and predator management was also influential. Survival in long-tailed bats was as high as, or higher, than figures for bats generally in years with low predator numbers or predator control. Survival was markedly higher in treatment years when predators were managed (0.82 compared to 0.55). Population modelling indicated managed colonies will increase ($\lambda > 1.05$) whereas unmanaged colonies will decline ($\lambda = 0.89 - 0.98$) under scenarios that reflect increased frequency of beech mast and predator irruptions. Thus, effective predator control is essential for recovering long-tailed bat populations. Warming temperatures indicate that predator irruptions are becoming more frequent, which would require more predator control in the future than at present if declines in bat populations are to be reversed. These results are relevant to the conservation of threatened bats on oceanic islands, given the abundance of exotic mammalian predators, particularly ship rats, on them.

## 1. Introduction

Globally, invasive predator species pose one of the greatest threats to biodiversity (Clavero and Garcia-Berthou, 2005; Donlan and Wilcox, 2008; Leung et al., 2002). In terrestrial systems, introduced predators include mammals, reptiles and invertebrates, all of which have had profound impacts on endemic faunas, particularly on oceanic islands (Atkinson, 1989; Hilton and Cuthbert, 2010). The evidence for extinctions and significant declines in mammals, birds, and reptiles attributable to introduced mammalian predators is unequivocal (e.g., Burbidge and Manly, 2002; Clavero et al., 2009; Jones et al., 2008; Towns et al., 2006). However, little is known about the impacts of these invasive predators on bats (Chiroptera), one of the most specious mammal groups in the world (Fenton and Simmons, 2015). The effects of habitat destruction, degradation and fragmentation and human impacts have tended to be studied more than mammalian predators in bats (Altringham, 2011).

A high proportion of bats are classed as threatened (Hutson et al., 2001). The primary documented causes of decline are generally related to habitat loss and degradation, harvesting and disturbance (Racey and Entwistle, 2003; Voigt and Kingston, 2016). In other cases, the cause of decline is uncertain, given a range of competing threats (e.g., Christmas Island pipistrelle *Pipistrellus murrayi*; Lunney et al., 2011). There are several documented examples of introduced mammalian predators

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preying upon bats, including feral cats (*Felis catus*), stoats (*Mustela erminea*), and rats (*Rattus* spp.) (e.g., Altringham, 2011; Dowling et al., 1994; Hill and Smith, 1984; O'Donnell, 2000a; Scrimgeour et al., 2012) and one example of their impacting on indigenous bat populations (Pryde et al., 2005a). Nevertheless, because few studies have investigated the role of predation, invasive mammals (particularly ship rats *Rattus rattus* because they are so widespread), may pose a significant threat to bats globally, especially on islands. Bats are widely distributed on oceanic islands, on which invasive predators are a common threat (> 200 threatened bat species; Hutson et al., 2001; Mickleburgh et al., 1992). Examination of the IUCN threatened bat list indicates numerous threatened bat species are present in > 50 island archipelagos where ship rats have been introduced (Hutson et al., 2001; Mickleburgh et al., 1992). These same archipelagos have well-documented impacts of rats on both sea and land birds, invertebrates, reptiles and ecosystem functioning (Harper and Bunbury, 2015; Jones et al., 2016; Shiels, 2011). As bats are cryptic and difficult to study, the potential impacts of introduced predators have not been investigated in many species (Hutson et al., 2001). Nevertheless, nearly 50% of the world's threatened bats are island endemics and because they are often the only native mammals on island, fulfil important ecological roles such as pollination and seed dispersal (Jones et al., 2010).

The impacts of introduced predators on indigenous species, including bats, in the island archipelago of New Zealand have been devastating (Innes et al., 2010; Towns and Daugherty, 1994). Invasion by ship rats is blamed for the final extinction of the greater short-tailed bat (*Mystacina robusta*) and predation by rats, stoats, cats and brushtail possums (*Trichosurus vulpecula*) have contributed to significant declines in the two extant species of bat (O'Donnell et al., 2010). Populations of the endangered New Zealand long-tailed bat (*Chalinolobus tuberculatus*) are declining at rates of up to 9% per annum in areas with high predator numbers (Pryde et al., 2006). Over recent decades, New Zealand conservation managers have developed a wide range of tools for controlling introduced predators and monitoring programmes are now demonstrating substantial recovery in a wide range of taxa (Towns and Broome, 2003). These tools include predator trapping, the use of bait stations loaded with rodenticides, and the aerial application of toxins that kill rodents (Edmonds et al., 2017; O'Donnell and Hoare, 2012; O'Donnell et al., 2011; Towns and Broome, 2003; Elliott and Kemp, 2016). Similar techniques are being applied globally to control or eradicate rats on oceanic islands (Harper and Bunbury, 2015).

In this paper, we report on the control of ship rats and stoats using bait stations loaded with rodenticides at a landscape scale (> 1000 ha) to improve survival of long-tailed bats. Careful use of rodenticides can lead to effective control of ship rats, brushtail possums and stoats (Elliott and Kemp, 2016). While the rodenticides target rats directly, stoat control in forests results from secondary poisoning where rats are the primary vector of the toxins (Gillies and Pierce, 1999; Murphy et al., 1999). Pryde et al. (2005a) showed that significant reductions in survival of long-tailed bats coincided with ship rat and stoat population irruptions in the Eglinton Valley, a temperate rainforest in southern New Zealand. Predation appeared to occur in maternity roosts. Although long-tailed bats roost high in trees (Sedgeley and O'Donnell, 1999), both predators commonly live and feed in the forest canopy (Elliott et al., 1996a; Smith et al., 2009). In these forests, predator irruptions follow heavy beech (*Nothofagaceae* spp.) mast seeding in 3–6 year cycles (King, 1983; O'Donnell and Phillipson, 1996). A preliminary population viability analysis using survival data from ten breeding seasons indicated that long-tailed bat populations were declining on average 5% per year (Pryde et al., 2005a). Consequently, the New Zealand Department of Conservation commenced predator control at several key sites as part of its Bat Recovery Programme (O'Donnell, 2010).

There have been relatively few studies of the population dynamics and survivorship of bats (Lentini et al., 2015) considering > 1300 species have been identified (Fenton and Simmons, 2015), and few of these have been long-term studies, largely due to logistic challenges in undertaking mark-recapture studies in bats (O'Shea et al., 2004). Nevertheless, knowledge of the factors that influence survival is crucial to understanding drivers of population dynamics of bats, especially as a high proportion of species is threatened. The aims of this paper are to (1) model factors influencing long-term survival of long-tailed bats; (2) examine whether predator control has resulted in biologically significant increases in survival of long-tailed bats; and (3) make predictions about future responses to management using population modelling. Predictive modelling is particularly important because the frequency and spatial extent of rat population irruptions are predicted to increase with climate change (Christie, 2014). The frequency of beech mast and predator irruptions are increasing over the last c.40 years in New Zealand from an average of once every five years in the 1980s (Elliott, 1996) to every 2 in 5 years over the last ten years (Appendix 1).

## 2. Methods

### 2.1. Study area

The study was conducted in the Eglinton Valley, eastern Fiordland in the South Island, New Zealand (44°58′S, 168°01′E) (Fig. 1). The 50-km long valley is glaciated with steep sides and a 0.5–1.5 km wide flat floor. The valley is dominated by temperate beech dominant rainforest (red beech *Fuscopora fusca*, silver beech (*Lophozonia menziessii*), mountain beech *Fuscospora cliffortioides*), which covers gentle glacial terraces and outwash fans on the lower hill-slopes and then rises steeply to the timberline at c. 1200 m above sea level. Mean annual rainfall in the central valley (Knobs Flat) is 2300 mm, but increases markedly in a gradient to > 5000 mm at the head of the valley.

### 2.2. Mark-recapture sessions

Long-tailed bat-capture-recapture sessions were conducted annually during the breeding season over 22 summers (1993–2015). Free-ranging bats were captured in free standing 4.2-m$^2$ harp traps (Faunatech Austbat, Victoria, Australia) during the austral summer (October–March 1993–1998; December–February 1999 – 2015). A subsample of bats caught was fitted with 0.7-g transmitters (BD2A, Holohil Systems, Carp, Ontario, Canada) to identify roost sites and catch all bats present in the roost at the time. Three to five bats carried transmitters at any one time. Transmitters were attached between the scapulae using a latex-based contact adhesive (F2®, Ados Chemical Co., Auckland, New Zealand) after the fur had been partly trimmed. Bats were followed daily for as long as transmitters remained attached or functional, a mean of 11.9 ± 6.4 (*SD*) days (O'Donnell and Sedgeley, 1999).

Roosts were located during the day by radio tracking using hand-held receivers and receivers mounted on vehicles. Bats were caught at a subset of accessible roosts as they emerged at dusk using 2.0-m$^2$ or 4.2-m$^2$ harp traps suspended in front of roost cavities. Roosting cavities were identified either by watching bats flying into or out of the roost tree from the ground at dawn or by climbing the tree (using single rope climbing techniques) and identifying the occupied cavity using a radio receiver at close range.

Each bat was banded on the forearm with an individually numbered 2.9 mm narrow flanged bat band (The Mammal Society and Porzana Ltd., East Sussex, UK). Age, sex, and reproductive status of all bats were recorded. Reproductive (parous) females were defined as animals with large, bare nipples. These females were either pregnant (determined by palpation of the abdomen), lactating, or post-lactating (reproductive females). Nipples remained conspicuous after females gave birth once. Females without visible nipples or with nipples with hair grown over them were classed as non-reproductive (nulliparous). Young of the year (termed juveniles) were identified by their unfused phalangeal

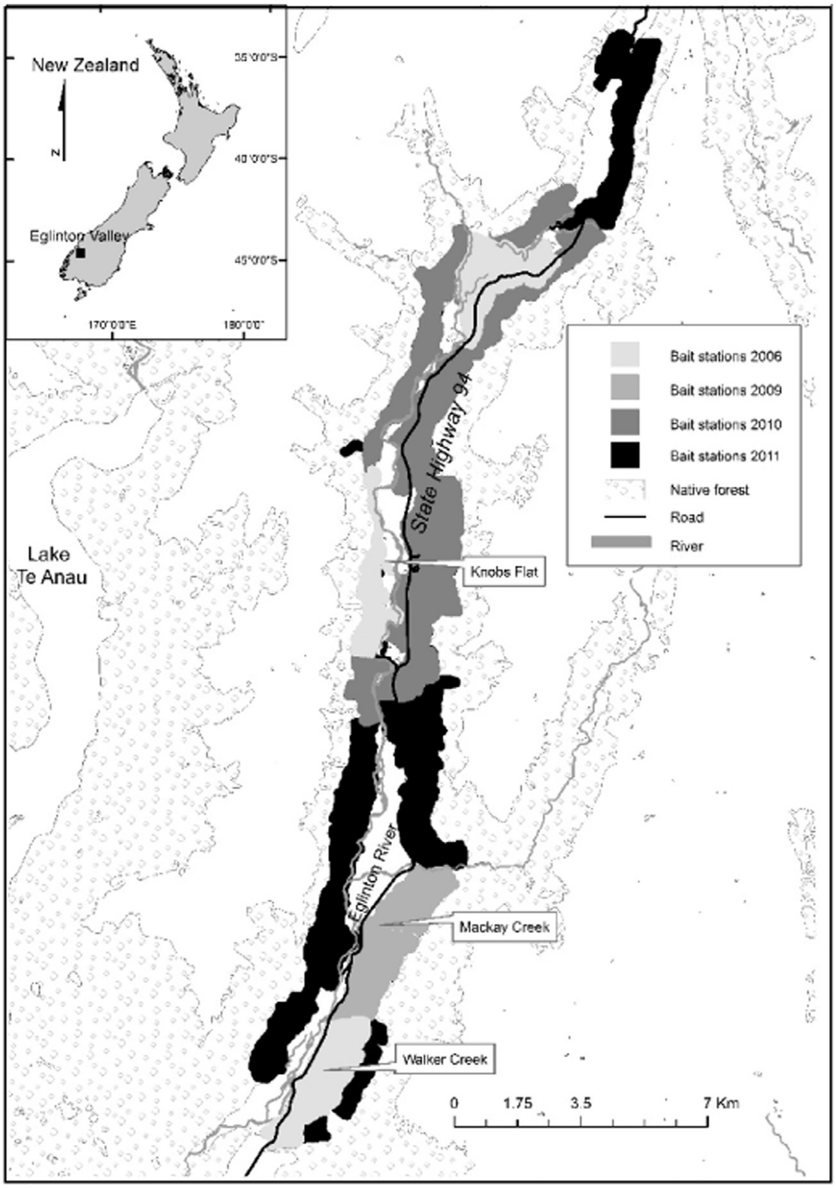

**Fig. 1.** Location of long-tailed bat colony roosting areas where rat control was implemented in the Eglinton Valley, 2006 – 2012.

epiphyses following Racey (1974).

### 2.3. Monitoring beech seedfall

Red, silver and mountain beech seedfall was monitored over the duration of the study. The amount of beech seedfall in a year is a clear indicator of predator levels and predation risk over the subsequent year, so is an early indicator of the need for predator control operations (King, 1983; O'Donnell and Phillipson, 1996). Beech seedfall typically occurs in autumn (from February to March) through to early spring, with the majority of seed falling in March–May (Wardle, 1984). Seedfall was monitored from March to May each year using the standardised New Zealand protocols (sensu Wardle, 1984). Seeds were collected in standard funnels (plastic 0.28-m-diameter funnels, Gyro Plastics, Lower Hutt) placed along three random line transects (8 funnels/transect, 1.25 m off the ground, 50 m apart, > 50 m away from a forest edge or 20 m away from a canopy gap). Seeds that fell into funnels collected in stockings fitted over the narrow ends of the funnels. Funnels were opened on 1 March and closed on 31 May each year. At the end of the collecting period, all seeds were counted and the number of seeds/m$^2$ was calculated. We defined masting events as full (with medium-high seedfall of > 500 seeds/m$^2$), and low (with < 500 seeds/m$^2$).

### 2.4. Monitoring predator levels

Indices of relative abundance of rats were derived from footprint tracking tunnel lines using a standardised protocol (Gillies and Williams, 2002; King et al., 1994). Each tracking tunnel line consisted of 10 tunnels spaced 50 m apart, with 10 randomly spaced lines > 1 km apart in non-treatment areas. Monitoring sessions occurred quarterly (in February, May, August and November) but we used data from August and November (pre-long-tailed bat breeding seasons) in our models (Appendix 1). Rat monitoring was conducted over one night using tunnels baited with peanut butter. Each tracking card was checked for the presence or absence of rat footprints and data summarised as mean percentage of cards tracked/session. Seedfall was strongly correlated with relative abundance of rat tracks in unmanaged sites ($R^2 = 0.95$; Fig. 2). We used seedfall as a surrogate of predator abundance. Rat numbers always increased following full beech masts in non-treatment areas, but following commencement of predator control, rat footprint indices were depressed dramatically. Therefore, in years when management occurred, rat indices did not correlate with seedfall

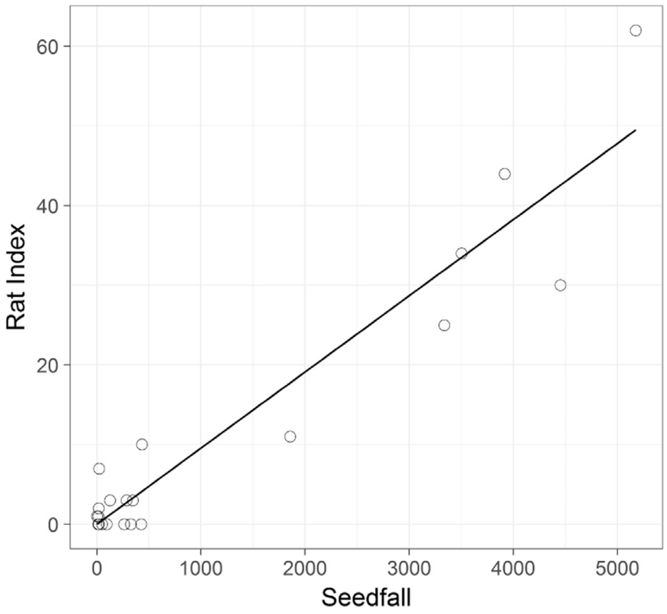

**Fig. 2.** Relationship between beech mast (seeds/m$^2$) and relative abundance of ship rats (*Rattus rattus*) (% Footprint Tracking Rate) in unmanaged areas of the Eglinton Valley, New Zealand, 1993 – 2015. The line represents the results of a linear model on rats against beech mast. Adjusted $R^2$ was 0.90 with a significant linear trend (9.56 ± 1 se 0.71) for relative abundance of rats per 1000 seeds/m$^2$.

but were used to indicate if management was successful (Appendix 1).

### 2.5. Predator control

Rat control was initiated within the roosting ranges of three long-tailed bat colonies, starting with control over a small proportion of the colony roosting ranges of Walker Creek and Knobs Flat colonies (2006; 650 ha) expanding to the entire roosting ranges of all three colonies and covering 3350 ha in 2009 (Fig. 1). Poisoning operations were implemented at times when rodent numbers were increasing following a mast with the aim of achieving complete knockdown in rat numbers. The toxin was removed from bait stations once rat numbers had declined below a threshold foot print tracking rate of 5%.

Control was implemented by filling Philproof Mini® bait stations set out on a 100 × 100 m grid. In 2006/07, 1080 (sodium fluoroacetate) impregnated grain baits were used in the first two fills of the bait stations, then replaced by two different first generation anti-coagulant toxins (Racumin sachets and Diphacinone paste) later in the season in case rodents had become bait shy (Table 1). Pindone cereal baits (another first-generation anti-coagulant toxin) were used in 2009/10 and 2011/12 (Table 1) following observations of New Zealand robins (*Petroica australis*) eating Racumin paste (Pryde et al., 2013).

### 2.6. Survival analysis

We measured the response of long-tailed bats to predator abundance and predator management by estimating annual apparent survival using mark-recapture field data analysed using Program MARK in R (Laake, 2013; R Core Team, 2016; O'Donnell, 2009; White and Burnham, 1999). Survival pre-rat control (no management) was monitored annually in three long-tailed bat colonies (Walker Creek 1994–2005, Mackay Creek 1996–2008, Knobs Flat 2005; Fig. 1) with monitoring continuing post-treatment to February 2015. Our broad aim was to sample each colony up to ten times per breeding season to maximise discovery of all individuals alive each year (O'Donnell, 2000b). We sampled 838 roosts during the study (mean number of catches/colony/yr: Walker colony = 8.4, Knobs colony = 5.5, Mackay colony = 5.7). Data from within each summer catching period were pooled so that each identified bat was either present or absent that year. Capture histories (presence or absence of bats in annual data sets across the entire study) were constructed for up to 22 capture occasions (where year = capture occasion; 1994–2015).

We used a multi-state model (Brownie et al., 1993; Hestbeck et al., 1991), which allows animals to move between age and reproductive states with transition probabilities. These models are an extension of the Cormack-Jolly-Seber (CJS) (Cormack, 1964; Jolly, 1965; Seber, 1965) live recapture model extended to multiple areas or states. We calculated apparent survival ($s$), capture probability ($p$) and the probability of moving from one state to another ($\psi$). Apparent survival is the probability of a bat surviving from one year to the next and remaining in the study population. The capture probability is the probability of catching a bat that is available for capture in the study population (Cooch and White, 2001). We only present survival data for females because recapture probabilities for males were low and the variance in any survival estimates high (author's unpubl. data). The transition states were defined for females as juveniles (J), non-reproductive (N) and reproductive adults (A). A juvenile was only allowed to remain a juvenile for 1 year and then it either changed to a non-reproductive or a reproductive adult. Once a bat transitioned to an adult it was not allowed to go back to non-reproductive. The main model assumptions are: 1) within group homogeneous capture probabilities; 2) within group homogeneous survival probabilities; 3) marks are not lost or missed; and 4) all samples are instantaneous and each release is made immediately after the sample. To satisfy the assumptions we analysed each colony separately because of different management regimes happening in each roosting area.

### 2.7. Modelling survival

We used AIC (Akaike Information Criteria) for model selection, choosing the best fitting, most parsimonious models to characterise survival (Burnham and Anderson, 2002). The covariates that were investigated were year as a factor, average minimum winter temperature,

**Table 1**
Summary of toxin applications to control predator irruptions in the Eglinton Valley, New Zealand, 2006 – 2012.

| Treatment no. | ha | Colonies treated (% roosting range) | Timing | Toxin applications | Bait density g/ station |
|---|---|---|---|---|---|
| 1. 2006/07 | 650[P] | Walker (30%), Knobs (40%), Mackay (0%) | June 2006 | Non-toxic bait (rat prefeed) then 0.15% w/w 1080 (sodium fluoroacetate cereal baits | 400 |
| | | | July–May 2007 | Racumin sachets (0.0375% coumatetralyl) | 250–350 |
| | | | December 2006 | 0.15% w/w 1080 cereal baits | 250 |
| | | | April–May 2007 | Diphacinone paste 0.005% | 350 |
| 2. 2009/10 | 1500–3350[a] | Walker (60%), Mackay (50%), Knobs (100%) | Sept 2009–May 2010 | Pindone 0.005% 2 g cereal baits | 500 |
| 3. 2011/12 | 4800 | Walker, Mackay, Knobs (all 100%) | July 2011–March 2012 | Pindone 0.005% 2 g cereal baits | 500 |

P: experimental treatment.
[a] Bait station network gradually expanded over the period; it covered 1500 ha at the beginning of the breeding season, and was gradually expanded throughout the summer.

age and three factors relating to predator control and seed mast: Seed0 — no seed and no pest management, Seed1 — seed mast and no pest management or Seed2 — seed mast and pest management. The model with Seed1 and not Seed2 tests the hypothesis that Seed0 = Seed2; i.e. management keeps survival at the same level as when there is no seed mast. The full model was defined as $s$(age ∗ year), $p$(age + year) and $\psi$(age:year) with a logit link for both $s$ and $p$ and a multinomial logit link for $\psi$. A full interaction term is denoted by "∗" and just the interaction, not the additive terms, is denoted as ":". The effects of the previous year of seed mast when managed (Seed2$_{\text{Year-1}}$) and not managed (Seed1$_{\text{Year-1}}$) were included. The average mean minimum temperature was calculated for the winter months (June, July, August for each survey year) from the National Climate Database of New Zealand (NIWA, Agent numbers 9350, 8811 & 8813). The estimated coefficients are reported on the logit scale.

Survival probabilities were used in the population modelling. However, since one of our aims was to predict differences under increased seed mast events, survival was predicted using the best fitting model of the interaction between management and seed. This is equivalent to taking the average survival over different seed and management combinations.

### 2.8. Population modelling

We used population modelling to predict the impacts of different management decisions in response to high seed mast years in the future. The following Leslie matrix modelled population change of females annually for 4 life stages (juvenile, adult year 1, adult year 2 and adult year > 2).

$$M = \begin{pmatrix} 0 & b_1 & b_2 & 0.5 \\ s_J & 0 & 0 & 0 \\ 0 & s_A & 0 & 0 \\ 0 & 0 & s_A & s_A \end{pmatrix}$$

Where $s_i$ are survival probabilities of juvenile ($i = J$) and adult ($i = A$) Beta distribution with mean and variance based on the capture-recapture models. The birth rates of females $b_j$ are drawn from a Beta distribution ($j = 1$, mean = 0.088 ± 0.02; $j = 2$, mean = 0.068 ± 0.04) and then multiplied by a sex ratio of 0.5. After 2 years, all adult females were assumed to give birth with a 0.5 sex ratio (O'Donnell, 2002).

Survival probabilities in the matrix M depended on seed mast and whether there was management. Simulations ($n = 1000$) were run under these scenarios with full management or no management for each colony. The different seed mast scenarios used in the projections were full mast 1 in 5 years (the historical average; Elliott, 1996), 2 in 5 years (approximate rate over the duration of the present study; Appendix 1), or as frequent as 1 in 2 years (reflecting the increased rate of seed years over the last 10 years and wider trends in New Zealand forests; Richardson et al., 2005). Each year a seed level was assigned with probability equal to the seed mast rate. The average annual growth rate (lambda, λ) of the population in each simulation was calculated as the first Eigen value of the product of M through time raised to the inverse of time. Starting population sizes were based on the total number of adult females being monitored in each colony in 2014/15.

## 3. Results

### 3.1. Survival

Female long-tailed bats had relatively higher recaptures rates than males and were seen often across the duration of the study (Table 2). The oldest female bat in the study was > 23 years (banded as a breeding adult in the first year). The estimated annual apparent survival probabilities varied between 0.46 and 0.96 (mean = 0.78, 95% CI = 0.6, 0.89) for adult females and 0.35 and 0.93 (mean = 0.73, 95% CI = 0.03, 0.98) for juvenile females (Walker colony only). Survival varied over time in all colonies (Fig. 3).

**Table 2**
Summary of captures and recaptures of male and female long-tailed bats from three colonies in the Eglinton Valley, New Zealand, 1993–2015.

| Colony | Sex | N | Recaptured (%) | Number of times individual bats were caught during the study | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | > 5 |
| Walker | M | 502 | 44.22 | 0.56 | 0.23 | 0.11 | 0.05 | 0.02 | 0.03 |
| | F | 482 | 63.69 | 0.36 | 0.19 | 0.12 | 0.08 | 0.06 | 0.20 |
| Knobs | M | 386 | 46.37 | 0.54 | 0.28 | 0.11 | 0.06 | 0.02 | 0 |
| | F | 324 | 64.20 | 0.36 | 0.22 | 0.14 | 0.07 | 0.07 | 0.14 |
| Mackay | M | 502 | 32.07 | 0.68 | 0.24 | 0.05 | 0.02 | 0.01 | 0.01 |
| | F | 537 | 65.00 | 0.35 | 0.21 | 0.13 | 0.10 | 0.06 | 0.15 |

Survival was best explained by annual variation (Table 3). Age had a significant impact only in the Walker colony (based on AIC, Table 3) where juvenile survival was lower than adult (Age = − 0.52, ± 1 se = 0.16). There was little support for average minimum winter temperature affecting survival (Table 3). For investigating the impacts of predator control the best fitting predation/management model shows the differences in average survival for managed and unmanaged years using AIC to test whether management (Seed2) boosted survival to low predation years when no management action was necessary (Seed0) (Tables 3 and 4). Overall, survival was lower in seed years without predator management for all colonies (adult females mean = 0.55, 95% CI = 0.34, 0.91; juvenile females mean = 0.55, 95% CI = 0.22, 0.86) compared to years with no seed or years with seed and predator management (adult females mean = 0.82, 95% CI = 0.48, 0.99; juvenile females mean = 0.76, 95% CI = 0.35, 0.99; Fig. 3). Using the best fitting model that included management, not managing seed masts had a negative impact on survival at the Walker Colony (Seed1 = − 1.06, ± 1 se = 0.16; Table 4).

Annual survival at Mackay colony could not be explained by just age, management, or seed (Table 3). However, considering the best fitting management model, unmanaged seed masts had lower survival than when there was no seed or the seed was managed (Seed1 = − 1.04, ± 1 se = 0.18). The year following a seed mast saw a positive response in survival compared with no seed the previous year regardless of management (Table 4). Knobs Flat colony had constant annual survival except for 2007, the only year where predators were not managed in a seed year (Seed1 = − 1.23, ± 1 se = 0.27; Table 4).

### 3.2. Population modelling

Population modelling indicated that average annual growth rate of the three populations in each population projection was positive when predator management occurred (λ = 1.05 – 1.09; Table 5) and population growth was predicted to be rapid in the two scenarios when more frequent predator irruptions occurred, but management was in place (Fig. 4). In comparison, λ was < 1 in seven of the nine scenarios with no management (Table 5) and in most situations populations were predicted to decline slowly (Fig. 4). In the two scenarios with positive lambda that had no management, the lower 95% quantiles were negative, indicating uncertainty about the estimates of lambda. Population decline was predicted to be most dramatic in the Knobs colony, which has been monitored for a shorter duration and during a period when seed mast was more frequent.

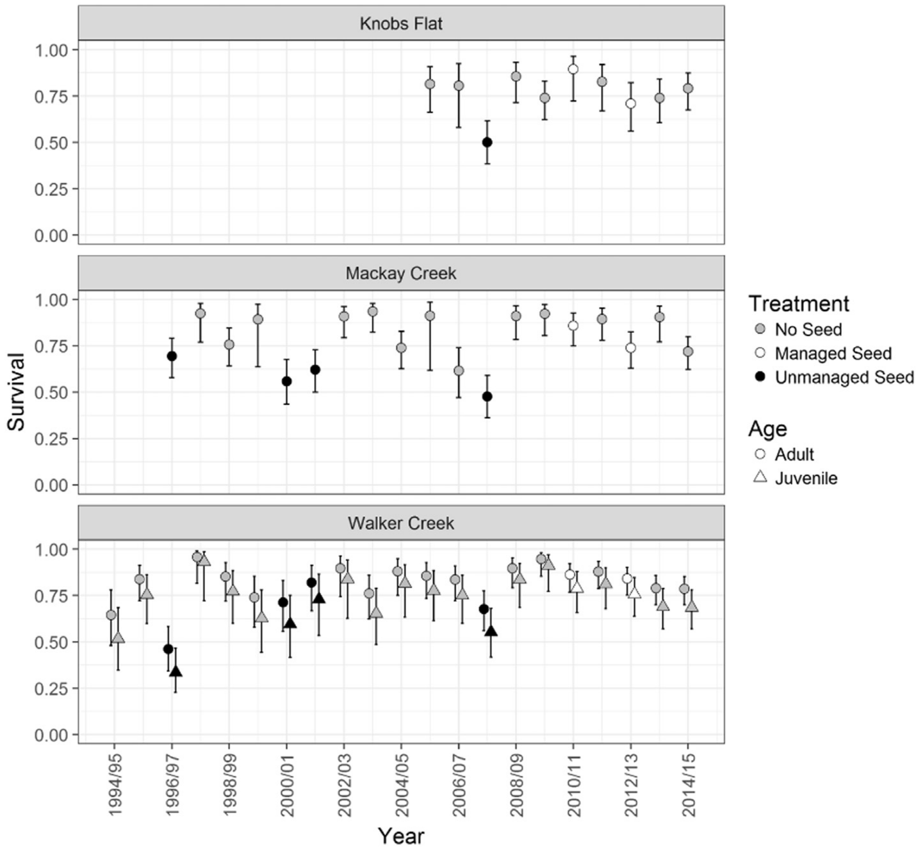

**Fig. 3.** Apparent annual survival of female long-tailed bats from three colonies in the Eglinton Valley, New Zealand, 1994 – 2015. Age was important based on AIC (Akaike Information Criterion; Table 3) only in the Walker colony, thus juvenile survival was similar to adults in the remaining colonies.

**Table 3**
Best models describing apparent survival in long-tailed bats in the Eglinton Valley, New Zealand, 1993–2015. Where k = number of parameters, AIC = Akaike information criterion, ΔAIC = differences in AICs, Seed = high seed years, Seed1 = unmanaged seed, Seed2 = managed seed, Seed1$_{\text{Year-1}}$ = effect of unmanaged seed the year before, Seed2$_{\text{Year-1}}$ = effect of managed seed the year before.

| Model — Walker Colony | k | AIC | ΔAIC |
|---|---|---|---|
| Age + Year | 51 | 6902.79 | 0 |
| Age * Year | 93 | 6906.59 | 3.80 |
| Year | 49 | 6908.06 | 5.27 |
| Age + Seed1 | 31 | 6914.66 | 11.87 |
| Age + Seed1 + Seed2 + Seed1$_{\text{Year-1}}$ + Seed2$_{\text{Year-1}}$ | 34 | 6914.87 | 12.09 |
| Age + Seed1 + Seed2 + Seed1$_{\text{Year-1}}$ | 32 | 6916.30 | 13.24 |

| Model — Mackay Colony | k | AIC | ΔAIC |
|---|---|---|---|
| Year | 49 | 11,492.19 | 0 |
| Age + Year | 51 | 11,495.07 | 2.88 |
| Seed1 + Seed2 + Seed1$_{\text{Year-1}}$ + Seed2$_{\text{Year-1}}$ | 32 | 11,502.31 | 10.13 |
| Seed1 + Temperature | 30 | 11,509.17 | 16.98 |
| Seed1 + Seed2 + Temperature | 31 | 11,509.60 | 17.41 |
| Seed1 | 31 | 11,511.44 | 19.25 |
| Seed1 + Seed2 | 93 | 11,513.17 | 20.98 |

| Model — Knobs Colony | k | AIC | ΔAIC |
|---|---|---|---|
| Seed1 | 18 | 14,529.46 | 0 |
| Seed1 + Temperature | 19 | 14,531.26 | 1.81 |
| Seed1 + Seed2 | 19 | 14,531.46 | 2.00 |
| Age + Seed1 | 20 | 14,533.14 | 3.69 |
| Seed1 + Seed2 + Temperature | 20 | 14,533.22 | 3.76 |
| Seed1 + Seed2 + Seed1$_{\text{Year-1}}$ + Seed2$_{\text{Year-1}}$ | 21 | 14,533.96 | 4.50 |

**Table 4**
The estimated coefficients ± 1 se on the logistic scale from the best fitting management model. These results use the outputs from the models shown in Table 3. Seed0 = no seed and no pest management, Seed1 = unmanaged seed, Seed2 = managed seed, Seed1$_{\text{Year-1}}$ = effect of unmanaged seed the year before, Seed2$_{\text{Year-1}}$ = effect of managed seed the year before. Colonies = Knobs, Mackay, and Walker.

| | Knobs | Mackay | Walker |
|---|---|---|---|
| Intercept (Seed0/Adult) | 1.32 ± 0.10 | 1.38 ± 0.11 | 1.67 ± 0.10 |
| Seed1 | − 1.23 ± 0.27 | − 1.04 ± 0.18 | − 1.06 ± 0.16 |
| Seed2 | | 0.02 ± 0.25 | |
| Seed1$_{\text{(Year-1)}}$ | | 1.08 ± 0.35 | |
| Seed2$_{\text{(Year-1)}}$ | | 0.65 ± 0.32 | |
| Age (juvenile) | | | − 0.52 ± 0.16 |
| Age (non-breeder) | | | − 0.05 ± 0.18 |

## 4. Discussion

### 4.1. *Comparison with survivorship in other bat species*

We have determined previously that survival in male and juvenile long-tailed bats was significantly lower than adult females, and that survival also varied with colony and over-winter temperatures (Pryde et al., 2005a). Lower survival in first-year bats is typical of other species (Lentini et al., 2015). However, survival of males is sometimes higher than females (Monadjem et al., 2015) or male and female survival can be almost equal (Sendor and Simon, 2003).

The most common factors influencing survival and population dynamics in bats include the effects of time, age and sex class (e.g., Pryde et al., 2005a; Schorcht et al., 2009; Lentini et al., 2015; Grieneisen et al., 2015; Monadjem et al., 2015). Time and age were also important influences in the present study. Time can mask a range of life history attributes and disentangling the effect of time from other, subtler, or hard-to-quantify variables that interact with time, can be challenging.

**Table 5**
Predicted intrinsic rates of increase (λ) estimated from matrix modelling of three long-tailed bat colonies in the Eglinton Valley, New Zealand under no predator control scenarios and full management scenarios at different frequencies (1 in 5 years, 2 in 5 years and one in two years).

| Location | Management | Average λ | | | 95% Quantile | | |
|---|---|---|---|---|---|---|---|
| | | 1 in 5 | 2 in 5 | 1 in 2 | 1 in 5 | 2 in 5 | 1 in 2 |
| Walker Creek | Full | 1.08 | 1.08 | 1.08 | 1.08, 1.08 | 1.08, 1.08 | 1.08, 1.08 |
| | No | 1.03 | 0.98 | 0.96 | 0.99, 1.07 | 0.93, 1.03 | 0.91, 1.01 |
| Mackay Creek | Full | 1.08 | 1.09 | 1.09 | 1.07, 1.10 | 1.07, 1.10 | 1.07, 1.10 |
| | No | 1.03 | 0.99 | 0.96 | 0.99, 1.06 | 0.93, 1.03 | 0.91, 1.02 |
| Knobs Flat | Full | 1.05 | 1.05 | 1.05 | 1.04, 1.06 | 1.04, 1.06 | 1.04. 1.06 |
| | No | 0.98 | 0.91 | 0.89 | 0.89, 1.05 | 0.82, 1.02 | 0.79, 0.99 |

Variation in survival over time (most often expressed as year) may include the combined influences of a variety of factors that cannot be parameterised easily in population models, such as environmental stressors, influence of disease, inherited traits, food availability, spacing behaviour, social structure and their interactions. For example, Amengual et al. (2007) and Hayman and Peel (2016) attempt to discern the additive effects of disease cycles and variable hunting pressure respectively on annual survival of bats.

Annual apparent survival of adult female long-tailed bats, in years when introduced predator numbers were low, was similar to or higher than estimates from many other bats. For example, in a review of survival in 44 bat species, annual survival rates estimated from studies of adult female bats conducted in summer averaged 0.774 (95% CI = 0.617, 0.890; Lentini et al., 2015). In contrast, annual survival estimates in predator-irruption years, were markedly lower (frequently < 0.6) when compared to many bat species, and demonstrated

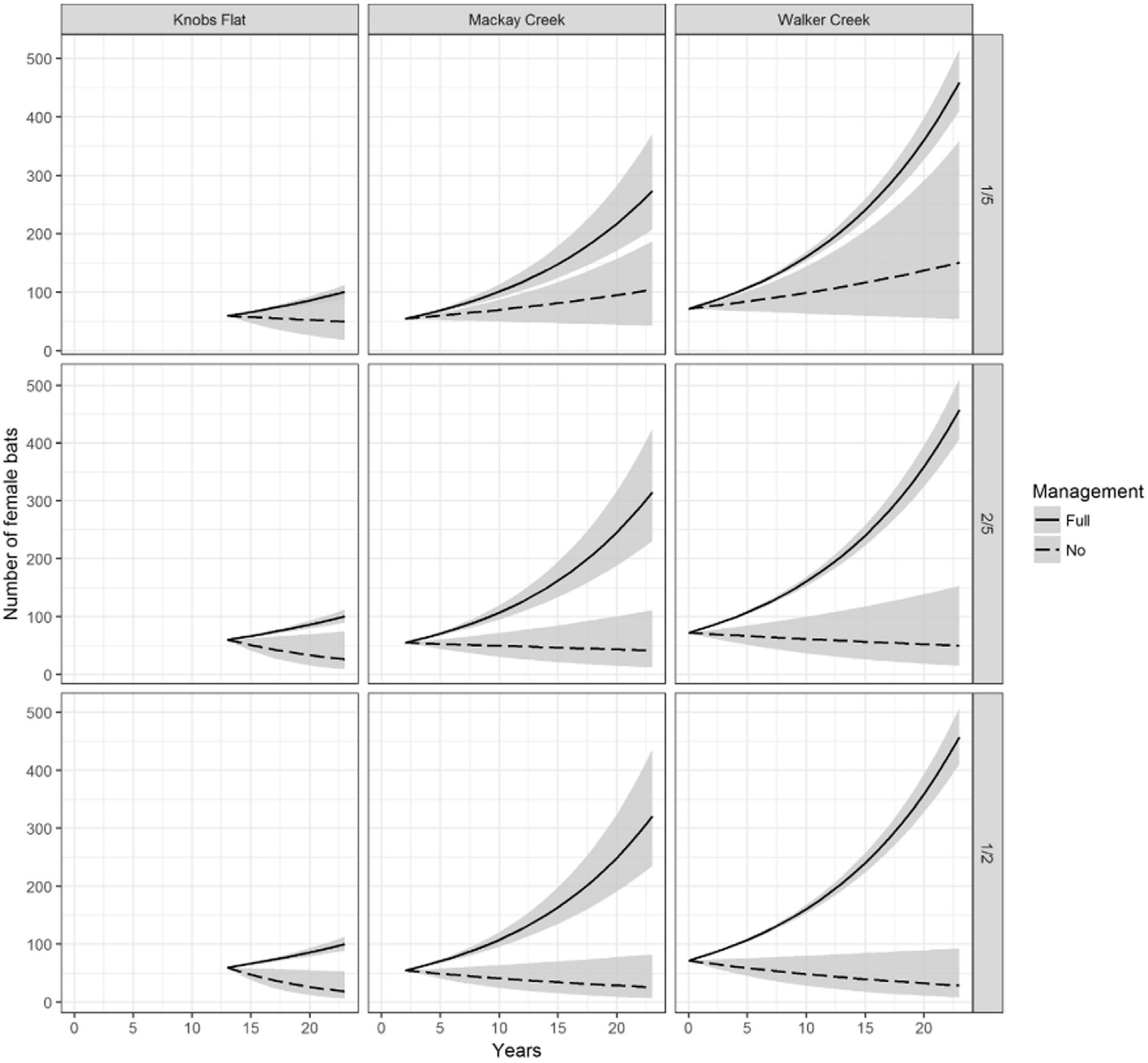

**Fig. 4.** Predicted female long-tailed bat population trajectories resulting from matrix modelling in three colonies in the Eglinton Valley, New Zealand with no predator management (dashed lines) or predator management (solid lines). Scenarios displayed are seed years 1 in 5 years, 2 in 5 years and 1 in 2 years. Errors are 95% quantiles. Starting population sizes were 72, 55, and 60 for Walker, Mackay, and Knobs respectively.

marked difference in survival from year to year. In contrast to long-tailed bats, variability of over-winter survival in bats is usually low but significant (e.g. *Pipistrellus pipistrellus*; Sendor and Simon, 2003). Survival estimates in the literature are variable, however, in many older studies, factors that influence survival were not modelled, and in some cases survival and capture probabilities were confounded (see review by O'Shea et al., 2004).

Overwinter temperatures are likely to effect survival bats that hibernate, either potentially increasing survival during milder winters or reducing it in harsher ones. However, effects of these temperatures on bats appear equivocal (Schorcht et al., 2009). Our models in the present study, with a longer time-series, did not support an effect of overwinter temperature on survival, as was evident in our shorter, ten-year study of long-tailed bats (Pryde et al., 2005a). In our previous study, there was evidence for an effect of high over-winter temperatures reducing survival although this effect was not compelling. We suggested that lower survival in warm winters may reflect more frequent waking from torpor in situations when food availability was inadequate to restore fat reserves.

### 4.2. Impacts of predators on long-tailed bats

Our results show that survival in years with high predator numbers and no management was lower than in managed seed years or low predator years. In the absence of predators, long-tailed bat survival levels were high, and managing predators brought survival back up to their normal survival levels. Although this is an observational study, the results were replicated across the three study colonies. Our results are also consistent with our knowledge of this population and others we have studied in the short term previously (Pryde et al., 2005a, 2006). For example, a fourth long-tailed bat colony in the study area was virtually extirpated following rat plagues of 1999/2000 and 2000/2001 (Monks and O'Donnell, 2017). In addition, predation by both stoats and rats also has significant impacts on forest birds that nest in similar tree cavities to bats in our Eglinton Valley study area (> 50% nest predation rates in untreated years: kaka, *Nestor meridionalis* Dilks et al., 2003; yellow-crowned parakeet, *Cyanorampus auriceps* Elliott et al., 1996b; mohua, *Mohoua ochrocephala* O'Donnell et al., 1996). Such cyclic population irruptions of rodents following pulses of super food abundance, like that provided by beech mast in New Zealand, are not unusual globally (e.g. Cornulier et al., 2013; Henden et al., 2009).

The effects of predator control were unlikely to be absolute, as suggested by our modelling. Rat control operations also control brushtail possums but not feral cats, which are known to prey upon long-tailed bats (Daniel and Williams, 1981, 1984). In addition, while stoats are usually controlled effectively through secondary poisoning, in this case we are uncertain about what proportion of stoats was controlled. The relationship between footprint tracking tunnel indices and numbers of rats are well understood (Innes et al., 1995) and we are confident rat indices declined markedly following control in 2010/11 and 2012/13. However, there is no known similar relationship with stoat footprint indices. There were no stoats recorded on tracking lines in February 2011 but 7.1% on lines around the Walker Creek bat colony in February 2013.

We are also uncertain about when predation occurs at long-tailed bat roosts and the relative impacts of ship rats compared with stoats. Numerically rat numbers are higher than stoats in the study area (> 6.5/ha compared to c. 1/ha for stoats, O'Donnell et al., 1996; Smith et al., 2009). We suspect that predation of bats is highly variable in terms of numbers and age classes affected. Infrared video footage has confirmed that rats and stoats enter bat roosts, but unfortunately, these and other anecdotal observations has given no evidence as to actual numbers of bats effected during any one predator visit (Lloyd, 2005; O'Donnell, 2000a; S. Wills, pers. comm.). However, on one occasion, a feral cat was known to kill over 100 short-tailed bats (*Mystacina tuberculata*) at a roost in beech forest in the North Island of New Zealand (Scrimgeour et al., 2012). Ship rats in the Eglinton Valley primarily hunt at night (Pryde et al., 2005b; Smith et al., 2009), whereas stoats are both diurnal and nocturnal predators (Murphy and Dowding, 1995). Long-tailed bats can be solitary or communal, be torpid or active in their roosts at any time of the year, and groups vary greatly in size each night because of their fission-fusion social structure (O'Donnell and Sedgeley, 1999; O'Donnell, 2000b, 2005). Thus, the impact of predation each breeding season will vary not only with the frequency of predation attempts but also with the numbers of bats present in roosts, and whether lactating females are out of the roost foraging when a predator visits. When stoats climb trees in search of prey in the study area, they appear to focus on noise of fledgling birds being fed (Dilks et al., 2003; Elliott et al., 1996a), whereas rats appear to hunt systematically or randomly and mainly den in the canopy in cavities in the same beech trees occupied by bats (Pryde et al., 2005b; Smith et al., 2009). In addition, the length and magnitude of rat irruptions depends on the rat densities at the beginning of their spring growth period, over winter temperatures and when primary seed sources begin to germinate and thus are no longer available to them (J. Kemp, pers. comm.).

### 4.3. Response to predator management

Our models indicated that survival of female long-tailed bats varied with time, and population growth rate ($\lambda$) was < 1.00 in most situations following beech mast years without predator control. Although models that included terms for predator control (management) showed an increase in survival, it was unclear the extent to which control was beneficial, largely because control effort varied with year as the bait station network was gradually expanded over time. Small scale use of bait stations in 2006/07 had no discernable benefit for the Walker and Knobs colonies, with apparent survival between c. 0.5 and 0.65, similar to years when no predator control occurred. This is because in small bait station areas immigration is considerable, and rat numbers recover in an area within three weeks of any initial knock down in numbers (Smith et al., 2009; E. Oyston, pers. comm.). Rat control is targeted for the end of winter to reduce numbers before their exponential growth phase in spring. In 2006/07, however, rat numbers had recovered by November (Smith et al., 2009), at a time when female long-tailed bats had formed colonies and were preparing to give birth (O'Donnell, 2002).

In contrast, long-tailed bat population growth rate was positive in the three study-colonies ($\lambda = 1.05 - 1.09$), with rat control using bait stations once the management area was sufficiently large (> 3000 ha; 2009/10, 2011/12). Extensive use of bait stations in rat irruption years appears to have contributed to stabilising the long-tailed bat colonies, and may be sufficient to cause overall increase and recovery of the colonies, as predicted by our matrix model projections (albeit acknowledging the broad 95% quantiles on the estimates). We are uncertain if male long-tailed bats, similarly benefit from predator control. Recapture probabilities for males were low and any estimates of survival had large variances. Males largely occupy solitary roosts in the same areas as colonial maternity roosts (O'Donnell and Sedgeley, 1999).

Predictions from our population growth models reflected what was happening in the recovering bat colonies. For example, the minimum number adult female bats alive in Walker colony has increased from a low of 25 following unmanaged predator irruptions in 1996/97 to 68 in 2011/12 following the initiation of widespread predator control (Monks and O'Donnell, 2017) and > 80 in 2014/15 (author's unpubl. data). Predicting whether recovery is sufficient in the future will depend on how often beech trees mast and then predator numbers irrupt. Frequency of beech mast and rat irruptions has been increasing in New Zealand (Richardson et al., 2005), with historic masting frequencies (1 irruption in 5 years; Elliott, 1996; King, 1983) increasing to 2 in 5 years. The current rate of beech masting sees $\lambda$ for long-tailed bat populations estimated at $0.91 - 0.98$ without predator management, lowering to as low as 0.89 if masting increases to a pessimistic rate of one in every two years. This is now plausible based on global climate change scenarios (Jones and Rebelo, 2013). Effects of climate change on rodent cycles may be variable. For example, with warming in arctic habitats, the amplitude and regularity of vole and lemming cycles have diminished (Elmhagen et al., 2011; Ims et al., 2008), resulting in reduced viability of some arctic fox (*Vulpes lagopus*) populations (Henden et al., 2009). In contrast, if the pattern of increased beech masting continues in New Zealand, however, not only would rat irruptions occur more frequently, but we predict the top-order invasive predators, stoats, would likely maintain higher population levels. In addition, Christie (2014) predicted that rats would spread to higher altitudes in New Zealand, potentially creating refuges for reinvasion into areas with predator control.

Managing rat irruptions using the current bait station network demonstrates that predator control can be effective at restoring long-tailed bat numbers. However, the Eglinton Valley supports at least eight long-tailed bat colonies (O'Donnell et al., 2016), and one large short-tailed bat colony, which collectively range over c. 15,000 ha (Christie and O'Donnell, 2015). These populations represent one of the few viable sites for these threatened species remaining in the South Island of New Zealand (O'Donnell et al., 2010), with the nearest small population of long-tailed bats being c. 50 km distant and the nearest short-tailed bat population on Whenua Hou-Codfish Island c. 200 km distant. It would be both expensive, and impractical over the steep mountainous terrain of the whole valley, to expand the bait station network to protect the whole bat population present in the valley. The current bait station network (4800 ha) mainly covers the relatively flat forest floor. In addition, the cost of the bait station network, estimated at c. $NZ 35/ha is expensive compared to c. $NZ 15–20 for the aerial application of the toxin sodium fluoroacetate (compound 1080) (E. Oyston, pers. comm.), These costs do not account for the large initial costs of setting up a bait station network, nor ongoing maintenance costs for the stations. Aerial application of toxins is commonly used to control predators and restore populations of forest birds in New Zealand (O'Donnell and Hoare, 2012) and is likely to be more cost effective for protecting long-tailed bats at a landscape scale.

### *4.4. Implications for conservation of bats on oceanic islands*

Bait stations loaded with toxins have been used as a tool to either eradicate or control rodents, including Pacific rats (*Rattus exulans*), Norway rats (*R. norvegicus*), but particularly ship rats, on hundreds of oceanic islands since the 1980s (Courchamp et al., 2003; Jones et al., 2016; Taylor and Thomas, 1989; Towns and Broome, 2003). While bait stations have frequently been used in attempts to control ship rats and recover populations of threatened bird, lizard and small ground-dwelling mammal species on oceanic islands (e.g. Igual et al., 2006; Robertson et al., 1994; Vanderwerf and Smith, 2002), rats have not been widely reported as a significant predator of bats (Mickleburgh et al., 2002; Racey and Entwistle, 2003; Voigt and Kingston, 2016). The only reports of bat species extinctions related to a rat invasion come from Taukihepa/Big South Cape Island in the New Zealand archipelago, when greater short-tailed bats (*Mystacina robusta*) disappeared, along with several bird species after ship rats were introduced in 1962 (Daniel, 1990) and Lord Howe Island, where the endemic long-eared bat (*Nyctophilus howensis*) disappeared (Hutson et al., 2001). This lack of acknowledgment of the impacts of rats and other invasive predators likely reflects a paucity of population studies of bats on islands generally and difficulties in studying these cryptic species. Nevertheless, ship rats appear to be a potential threat to bats on islands where they have been introduced, particularly tropical islands where ship rat densities are far higher than on many temperate islands (Harper and Bunbury, 2015). The population models we have constructed indicate that rat predation may contribute to insidious long-term decline in bat populations, especially if rat numbers fluctuate over time in relation to variable food availability, as is the case in New Zealand.

Introduced rats are present on 80% of archipelagos worldwide (Atkinson, 1985). They overlap with the range of threatened bats on numerous island archipelagos across the Indian, Pacific and Atlantic oceans and given the well documented impacts of rats on all other classes of animal biodiversity on most of these islands, it seems unlikely that bats would be immune to this threat. Fifteen percent of bat species are listed as threatened by the IUCN (Voight and Kingston, 2016), and a disproportionately high number are island endemics (nearly 50%) and because they are often the only native mammals on island-, fulfil important ecological roles such as pollination and seed dispersal (Jones et al., 2010). The global action plan for the conservation of echolocating microchiropteran bats (Hutson et al., 2001) records > 200 threatened or at risk species occurring on at least 51 island archipelagos which are also islands where ship rats have been introduced (IUCN Invasive Species Specialist Group Database http://issg.org/). In addition, many species of the family Pteropodidae are recorded largely or entirely from islands and 13 of the 29 Critically Endangered bats are found only on islands (Mickleburgh et al., 2002). Although these estimates of the number of threatened species on islands with invasive rats are out of date, the potential impacts of rats are widespread (IUCN, 2016). If our population models reflect typical behaviour of ship rats, resulting in a slow stepwise decline over timescales of > 100 years (Pryde et al., 2005a), predation by ship rats alone could explain the recent extinction of species such as the Christmas Island pipistrelle (notwithstanding other potential explanations; Lunney et al., 2011). We recommend that conservation managers responsible for the management and recovery of threatened bats on islands consider the potential role of ship rats in the decline of threatened bat species.

## 5. Conclusions

Our study suggests that survival of long-tailed bats was negatively impacted in years following high beech seedfall and irruptions of introduced mammalian predators. In contrast, survival appeared to be significantly higher in years following control using toxins in bait stations. Population projections suggest that effective predator control is essential for recovering critically endangered New Zealand long-tailed bat populations. Warming temperatures indicate that predator irruptions are becoming more frequent, thus requiring more numerous predator control responses in the future than at present if declines in bat populations are to be reversed. However, given that long-tailed bats, and many other indigenous forest species affected by predation are wide ranging, bait station networks will be an expensive option for implementation at a landscape scale. We suggest that future research should focus on developing more cost-effective predator control methods that can be applied at a landscape scale. Effective management of predator irruptions is essential for improving the long-term survival of threatened native species in New Zealand forests. We also suggest that this case study of the impacts of ship rats on long-tailed bats indicates a threatening process that may impact on island bats generally and offers potential management solutions for alleviating such threats.

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## Appendix 1

Summary of beech seedfall, rat footprint tracking indices (% tunnels tracking rats), and rat-control schedules for three long-tailed bat colonies at Knobs Flat, Eglinton Valley, New Zealand, 1993–2015. No footprint tracking tunnel results were recorded in August pre-1999. Treatment history: survival data available for NT = No treatment, Treated = Rat control (Rats: low = 0–4%, medium = 4–10%, high ≥ 10%).[a]

| Year | Seed/m$^2$ | Rat index (August) (%) | Rat index (November) (%) | Seed estimate | Colony predator control history | | |
|---|---|---|---|---|---|---|---|
| | | | | | Walker | Mackay | Knobs Flat |
| 1993/94 | 261 | | 0 | Low | | | |
| 1994/95 | 94 | | 0 | Low | NT | | |
| 1995/96 | 4453 | | 30 | High | NT | NT | |
| 1996/97 | 346 | | 3 | Low | NT | NT | |
| 1997/98 | 426 | | 0 | Low | NT | NT | |
| 1998/99 | 19 | | 0 | Low | NT | NT | |
| 1999/00 | 3504 | 26 | 34 | High | NT | NT | |
| 2000/01 | 5175 | 61 | 62 | High | NT | NT | |
| 2001/02 | 50 | 0 | 0 | Low | NT | NT | |
| 2002/03 | 13 | 0 | 0 | Low | NT | NT | |
| 2003/04 | 326 | 0 | 0 | Low | NT | NT | |
| 2004/05 | 126 | 6 | 0 | Low | NT | NT | |
| 2005/06 | 22 | 8 | 7 | Low | NT | NT | NT |
| 2006/07 | 3916 | 34 | 44 | High | P | NT | P |
| 2007/08 | 17 | 0 | 2 | Low | NT | NT | NT |
| 2008/09 | 285 | 3 | 3 | Low | NT | NT | NT |
| 2009/10 | 1856 | 2 | 11 | High | Treated | Treated | Treated |
| 2010/11 | 1 | 1 | 1 | Low | NT | NT | NT |
| 2011/12 | 4272 | 9 | 4 | High | Treated | Treated | Treated |
| 2012/13 | 15 | 2 | 1 | Low | NT | NT | NT |
| 2013/14 | 432 | 4 | 9 | Low | NT | NT | NT |
| 2014/15 | 3336 | 28 | 25 | High[a] | Treated | Treated | Treated |

P = experimental partial treatment of small area of roosting range (see Table 1).

[a] Management in 2014/15 changed to using aerial application of 1080 toxins and survival post management will form part of a separate study, therefore outcomes of this operation are not included in the present paper.

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