Contributed Paper

Strategic Rat Control for Restoring Populations of Native Species in Forest Fragments

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Abstract: *Forest fragments have biodiversity value that may be enhanced through management such as control of non-native predators. However, such efforts may be ineffective, and research is needed to ensure that predator control is done strategically. We used Bayesian hierarchical modeling to estimate fragment-specific effects of experimental rat control on a native species targeted for recovery in a New Zealand pastoral landscape. The experiment was a modified BACI (before-after-control-impact) design conducted over 6 years in 19 forest fragments with low-density subpopulations of North Island Robins (Petroica longipes). The aim was to identify individual fragments that not only showed clear benefits of rat control, but also would have a high probability of subpopulation growth even if they were the only fragment managed. We collected data on fecundity, adult and juvenile survival, and juvenile emigration, and modeled the data in an integrated framework to estimate the expected annual growth rate (λ) of each subpopulation with and without rat control. Without emigration, subpopulation growth was estimated as marginal ($\lambda = 0.95$–1.05) or negative ($\lambda = 0.74$–0.90) without rat control, but it was estimated as positive in all fragments ($\lambda = 1.4$–2.1) if rats were controlled. This reflected a 150% average increase in fecundity and 45% average increase in adult female survival. The probability of a juvenile remaining in its natal fragment was 0.37 on average, but varied with fragment connectivity. With juvenile emigration added, 6 fragments were estimated to have a high (>0.8) probability of being self-sustaining ($\lambda > 1$) with rat control. The key factors affecting subpopulation growth rates under rat control were low connectivity and stock fencing because these factors were associated with lower juvenile emigration and higher fecundity, respectively. However, there was also substantial random variation in adult survival among fragments, illustrating the importance of hierarchical modeling for fragmentation studies.*

Keywords: Bayesian hierarchical models, fecundity, predator control, private land, population modeling, survival

Control Estratégico de Ratas para Restaurar Poblaciones de Especies Nativas en Fragmentos de Bosque

Resumen: *Los fragmentos de bosque tienen un valor de biodiversidad que puede mejorarse por medio del manejo, como el control de depredadores no-nativos. Sin embargo, dichos esfuerzos pueden no ser efectivos y se necesita investigar para asegurar que el control se realiza estratégicamente. Usamos modelos jerárquicos bayesianos para estimar los efectos específicos de fragmentos de un control de ratas sobre una especie nativa que se busca recuperar en un paisaje pastoral en Nueva Zelanda. El experimento fue un diseño ADCI (antes-después-control-impacto) modificado conducido a lo largo de 6 años en 19 fragmentos de bosque con sub-poblaciones de baja densidad de petirrojos de North Island (Petroica longipes). El objetivo era identificar fragmentos individuales que no sólo mostraran beneficios claros del control de ratas, sino también que tuvieran una alta probabilidad del crecimiento de sub-poblaciones aunque fuera el único fragmento manejado. Recolectamos datos de fecundidad, supervivencia adulta y juvenil y emigración juvenil, y modelamos los datos en un marco de trabajo integrado para estimar la tasa de crecimiento anual esperado (λ) de cada sub-población con y sin control de ratas. Sin emigración, el crecimiento sub-poblacional se estimó como*

marginal (λ = 0.95-1.05) o negativo (λ = 0.74-0.90) sin control de ratas, pero se estimó como positivo en todos los fragmentos (λ = 1.4-2.1) donde las ratas fueron controladas. Esto refleja un incremento promedio de 150% en la fecundidad y de 45% en la supervivencia de hembras adultas. La probabilidad de que un juvenil permanezca en su fragmento natal fue de 0.37 en promedio, pero varió con la conectividad de los fragmentos. Al añadir la emigración juvenil, se estimó que 6 fragmentos tenían una alta probabilidad (>0.8) de ser autosustentables (λ > 1) con el control de ratas. Los factores clave que afectaron el crecimiento subpoblacional bajo el control de ratas fueron la baja conectividad y el cercado, ya que estos factores se asociaron con una emigración juvenil más baja y una alta fecundidad respectivamente. Sin embargo, también hubo una variación sustancial al azar en la supervivencia de adultos entre los fragmentos, ilustrando la importancia de los modelos jerárquicos para los estudios de fragmentación.

Palabras Clave: Control de depredadores, fecundidad, modelo de poblaciones, modelos bayesianos jerárquicos, suelo privado, supervivencia

Introduction

Habitat fragmentation is a long-recognized conservation problem, especially the fragmentation of forest into small remnants in agricultural landscapes (Harris 1984). Although small remnants are unlikely to conserve large-scale ecosystem processes and population dynamics, they can still be managed to conserve local biodiversity. Such initiatives may be particularly important to community groups and indigenous people, who may highly value the biodiversity on their own land even if species and ecosystems involved are not considered globally threatened. Habitat fragments can present an opportunity for local management, not only because the scale of management may be practical and affordable, but also because the fragmentation may reduce the spread of threats from other areas.

Predator control is a common form of wildlife management on private land and has long been used to protect species valued for intrinsic and utilitarian reasons (Worster 1994; Cote & Sutherland 1997; Smith et al. 2010). It is essential for biodiversity conservation throughout much of the Pacific region due to naivety of native species to non-native mammalian predators (Groombridge 1992; Veitch & Clout 2002). Efforts to restore biodiversity through predator management include large-scale operations run by conservation agencies and smaller scale operations run by community groups or individual land holders such as farmers.

Although local initiatives to control non-native predators are desirable, they may also be ineffective, potentially leading to disillusionment. The management may be ineffective at reducing non-native predators due to insufficient intensity or rapid reinvasion. Alternatively, the effects may be insufficient to reverse declines of native species targeted, potentially due to emigration into unmanaged sink habitat. In some cases, the management may actually have negative effects, for example, through release of non-native mesopredators or competitors (Ruscoe et al. 2011) or prey switching by top predators (Wittmer et al. 2013).

Research can play a key role in ensuring that predator control is done strategically (i.e., that management is focused where it will have the greatest benefit). Ideally, this will not simply involve monitoring the native species targeted, but will involve theoretically informed experiments combined with modeling that allows reliable population projections. Fragmented habitats inherently lend themselves to experimentation because individual fragments can be used as replicates. However, effectiveness of predator control may vary among fragments due to differences in both habitat characteristics and landscape context. For example, it may be particularly effective in habitats expected to support high predator densities but ineffective where there is likely to be rapid predator reinvasion or prey emigration. Although such variation can be accounted for to some extent by measuring key habitat and landscape characteristics, there is also great potential for additional variation among fragments. Such variation may reduce one's power to make inferences, especially when sample sizes are small in individual fragments. However, these inferences are facilitated by recent advances in the application of Bayesian hierarchical modeling to ecological data (King et al. 2010; Kéry & Schaub 2012). We examined how experimental predator control combined with Bayesian hierarchical modeling can be used to estimate effects of control on a native species in individual forest fragments and to identify the best fragments for ongoing control.

Methods

Species and Study Site

The native species targeted was the North Island Robin (*Petroica longipes*), a 26- to 32-g insectivorous forest passerine endemic to New Zealand (Higgins & Peter 2002). North Island Robins breed in monogamous pairs on territories, and nesting typically occurs from September to February. Only females sit on nests, and sexes of

pair mates can be distinguished based on behavior. Adults rarely leave their territories once established, but juveniles typically undergo a dispersal phase after independence (Richard & Armstrong 2010*a*). They breed in their first year, and reproductive success is similar for first-year birds and older birds (Dimond & Armstrong 2007).

The species originally occurred throughout forested parts of the North Island, but was extirpated from >90% of its original range due to forest clearance and predation by non-native mammals. The key limiting factor appears to be predation by ship rats (*Rattus rattus*), particularly on nests and nesting females (Brown 1997; Armstrong et al. 2006; Parlato & Armstrong 2012). Although the species is not classified as threatened, many local restoration programs are attempting to recover robin populations through translocation and predator management (Parlato & Armstrong 2012). The small territory sizes (approximately 0.5 ha) and limited movements of robins and their key predator means that populations may be managed on small fragments on private land.

Our study was conducted on 19 forest fragments ranging from 2 to 67 ha on pastoral land near Benneydale in the central North Island (Table 1; 75° 220′E, 38°320′S). Most (16) of the fragments are on Rereahu farms, which are owned by the Ngāti Rereahu hapu (subtribe) indigenous to the area. The fragments all had secondary native broadleaf-podocarp forest with similar species composition, but they differed greatly in understory density due to grazing by sheep and cattle. Most fragments could be considered grazed or ungrazed, but 2 were partially grazed due to stock fences running through them. North Island Robins occurred in all fragments due to natural colonization or translocation, but their densities were low (0.1–0.5/ha) before predator control relative to densities in the absence of mammalian predators (e.g., 5/ha on Tiritiri Matangi Island; Dimond & Armstrong 2007).

Experimental Design

The effects of rat control on robin vital rates were estimated using a modified BACI (before-after-control-impact) design (Table 1). We monitored robins in all fragments over 6 years (September 2005–September 2011) and controlled rats in selected fragments in years 4–6. However, rather than controlling the same fragments over those 3 years, we selected 6–7 fragments each year out of the 13 fragments where rat control was practical, balancing this selection with respect to fragment size, connectivity, grazing, and initial rat and robin densities. This modification of the classic BACI (Morrison 2009) increased the design's robustness to interfragment variation in control effects and random annual variation in robin vital rates. However, the switching of treatments among years meant that we needed to consider the residual effects of rat control the previous year. These could include positive effects of rat densities continuing to be depressed, but could also include negative effects of increases in house mouse (*Mus musculus*) densities due to competitive release.

Rats were controlled over the robin breeding season in the selected fragments through snap trapping and poison baiting at 50-m intervals. In late August, we set standard rat traps baited with peanut butter and repeated this over 10 nights to remove most rats. We then continued control until March using Contrac cereal bait blocks (28 g) that were changed monthly. These contained 0.05 g/kg of the second-generation anticoagulant bromodialone, which is highly toxic to rodents but unlikely to harm invertebrates due to differences in blood clotting biochemistry (Buckle 1994). Traps and bait blocks were deployed inside covers designed to exclude nontarget vertebrates.

Data Collection

Effects of the control on rat and mouse populations were monitored using footprint tracking tunnels (Blackwell et al. 2002). Each tracking tunnel is baited with peanut butter, and an ink pad and cards are placed inside to record whether a rat or mouse passed through the tunnel. The data are used to estimate "tracking rates" (probability of a tunnel being tracked in 24 h), which provide an index of abundance and/or activity for each species. Most fragments had a single set of 16 tunnels at 50 m intervals on a 4×4 grid, but some had 9 (3×3 grid) or 5 (cross) due to space constraints, and the 2 partially fenced fragments had separate grids in the grazed and ungrazed portions. We collected tracking data on 3 occasions each breeding season (October, December, and February) in each of the 6 years.

Robin fecundity was measured as the number of independent juveniles per female per year, where juveniles are considered to reach independence 4 weeks after leaving the nest. Such data can be recorded accurately for North Island Robins because fledglings make loud begging calls and there are only 2–3 young per brood. We collected these data for 138 females over the 6 years by regularly checking breeding pairs in all fragments.

We attached radio transmitters (Holohil BD-2, 1.05 g) to 83 juveniles at independence to obtain data on their subsequent survival and fidelity to the natal fragment. We checked radio-tagged juveniles at least weekly until they died or could not be located. On each occasion, we recorded whether the animal was alive and whether it remained in its natal fragment. Transmitters had an expected battery life of 6 weeks, but we replaced transmitters of juveniles still being monitored at this stage, so the maximum monitoring period was 89 d.

Survival of adult robins was estimated through triannual surveys (September, January, May) of 249 color-banded individuals from September 2005 to January 2012. Birds were considered to enter this data set when first recorded as banded adults with clearly established

Table 1. Modified BACI (before-after-control-impact) design used to estimate effects of rat control on subpopulations of North Island Robins in forest fragments in the central North Island of New Zealand.

Fragment	Area[a]	CDN[b]	Grazed[c]	Ind[d]	Fem[e]	Rat control[f]					
	(ha)					05/06	06/07	07/08	08/09	09/10	10/11
B86	16	513	0	21	9	0	0	0	1	0	1
Fatty	14	42	1/0	7	4	0	0	0	1	0	0
Flag	8	6702	1	13	4	0	0	0	1	0	0
Iti	9	100	1	4	4	0	0	0	1	0	1
Ted's	6	785	0	11	4	0	0	0	1	0	0
LTutu	2	1029	0	6	3	0	0	0	1	0	1
Tutu	5	1008	0	11	6	0	0	0	1	0	1
Dennis	13	120	0	19	8	0	0	0	0	1	1
Jack's	19	3332	0	18	10	0	0	0	0	1	0
Lucky	6	1872	1	15	8	0	0	0	0	1	0
T74	11	700	1	25	15	0	0	0	0	1	1
Toru	9	1477	1	9	5	0	0	0	0	1	1
Twisted	6	322	0	5	1	0	0	0	0	1	1
Dizzy	56	42	1/0	12	8	0	0	0	0	0	0
Mruhe1	31	313	0	14	7	0	0	0	0	0	0
Mruhe2	67	298	0	12	9	0	0	0	0	0	0
Nui	34	253	0	10	7	0	0	0	0	0	0
Skinny	39	75	0	13	7	0	0	0	0	0	0
T91	18	63	0	24	19	0	0	0	0	0	0

[a]*Area of native forest, usually surrounded by pasture.*
[b]*Cost distance to nearest neighbor, an index of isolation from other forest areas.*
[c]*Whether vegetation was highly modified (1) or not (0) by stock grazing (1/0 means part of fragment affected due to partial fencing).*
[d]*Number of adult color banded robins monitored in each fragment to estimate survival.*
[e]*Number of females monitored in each fragment to estimate fecundity.*
[f]*Whether rats were controlled (1) or not (0) that year through initial snap trapping August and September (start of robin breeding season), then monthly application of poison bait blocks until March.*

territories. These territories were visited in subsequent surveys, and the detections were used to generate a set of encounter histories. Although adult robins rarely shift territories, we also searched throughout the fragments and nearby habitat to detect movements and therefore avoided interpreting movement as mortality.

Modeling

We used the Bayesian updating software WinBUGS 1.4 (Spiegelhalter et al. 2007) to model all data. The Markov chain Monte Carlo (MCMC) iteration in WinBUGS allows multiple random effects (Bayesian hierarchical modeling), so was ideal for our project where individual random variation among fragments needed to be accounted for in addition to other random effects. It also facilitates integrated population modeling (Schaub & Abadi 2011), meaning fecundity, survival, and movement could be modeled simultaneously to generate population projections fully accounting for parameter uncertainty and covariance. All models had uninformative priors, which were taken to be normally distributed ($N[0,10^6]$) for main parameters (regression coefficients) and uniformly distributed priors (U[0,100]) for hyperparameters (standard deviations of random effects). Models were run for at least 10^4 iterations following a burn-in of at least 10^3 iterations to check convergence.

We first fitted separate models to each data set (rat tracking, mouse tracking, robin fecundity, adult robin survival, juvenile robin survival, juvenile robin fidelity) and reduced these models by removing "insignificant" effects. We initially removed fixed effects if the 95% credible interval included zero. However, for marginal effects, we checked that the deviance information criterion (DIC; Spiegelhalter et al. 2002) was lowered by removing the parameter and reinstated it otherwise. Similarly, we removed random effects if the lower portion of the posterior distribution was concentrated near zero (Kéry & Schaub 2012) and checked whether the removal lowered DIC. We then combined the reduced models for robin fecundity, survival, and fidelity to estimate finite rates of increase with and without rat control. Full explanations of the models, the code for fitting them, the data and parameters estimates for the fitted models are provided in Supporting Information.

We modeled rat and mouse tracking rates with a logit link and Bernoulli error distribution, with rat control (current, previous year, or no control) and grazing as fixed effects and fragments, individual tracking tunnels, years, and individual sampling occasions as random effects. Interactions between control effects and random fragment effects were also included. The aims were to assess the degree and duration of the effects of rat control and the variation of these effects among fragments.

We modeled fecundity with a log link function and Poisson error distribution, with fixed effects of rat control and grazing, and random effects among fragments, individual females, and years. We again distinguished between current and residual effects of control and allowed interactions between control effects and random fragment effects.

We modeled adult survival with a Bayesian version of the Cormack–Jolly–Seber model; survival and resighting probabilities were modeled with logit link functions and Bernoulli error distributions (Schofield et al. 2009). As for fecundity, we assessed current and residual effects of rat control on survival while accounting for effects of grazing, random fragment effects, random temporal variation (4-month intervals rather than years), and interactions between fragment and control effects. The adult survival model also allowed differences among seasons (September–January, January–May, May–September) and differences between sexes from September–May (intervals with nesting). This structure reflected preliminary analysis showing survival was highest from January–May and higher in males from September–May. This preliminary analysis also suggested that the effects of rat control did not vary significantly between sexes and seasons, so these interactions were not included. Resighting was allowed to vary randomly among surveys but was assumed to be similar for the 2 sexes based on previous research (Dimond & Armstrong 2007).

We modeled juvenile survival and fidelity with "nest survival models," which are named as such because of their applicability to nest data but are equally applicable to telemetry data with unsynchronized checks (Rotella et al. 2004). These models produced maximum likelihood estimates of daily survival (or fidelity) probabilities based on the number of days from transmitter attachment until each juvenile was last found alive (or in its natal fragment), and the subsequent number of days until it was found dead (or emigrated) if applicable. Both types of probabilities were modeled with a logit link function. We modeled juvenile survival probability as a step function of time since independence (≤30 d or later based on juvenile mortality patterns estimated by Dimond and Armstrong 2007) with the effect of rat control also considered (current control or other). Our model for daily fidelity probability included a quadratic function of time since independence to allow for expected changes in behavior (an initial increase in probability of emigration, followed by settling). It also included fixed effects of the juvenile's sex (determined from DNA extracted from feathers; Norris-Caneda & Elliot 1998), the natal fragment's area, and natal fragment's connectivity, and a random fragment effect.

We considered 2 alternative indexes of connectivity: the cost distance to nearest neighbor (CDN) and an index of functional patch connectivity (IFPC). The CDN is the minimum cost of reaching another forest fragment (minimum 1.5 ha area) based on the amounts of different vegetation types (pasture, shrubland, or native forest) and lengths of pasture gaps that needed to be crossed. The IFPC is calculated by dividing the area of each fragment within 2 km of the focal fragment by the minimum cost distance required to reach it and summing these (Richard & Armstrong 2010b). The resistance values used to calculate the costs were estimated previously using telemetry data for juvenile robins in the same landscape (Richard & Armstrong 2010a). We log transformed the CDN and IFPC values due to their skewed distribution among the 19 fragments.

We estimated the fragment-specific finite rates of increase (λ) in 2 ways. First, we estimated λ in the absence of immigration and emigration to assess whether each fragment was suitable habitat for robins with and without rat control. These fragment-specific rates of increase are given by

$$\lambda = s_a + 0.5 f s_j, \qquad (1)$$

where s_a is annual survival probability for adult females, s_j is the probability of a juvenile surviving to adulthood, and f is the mean number of juveniles per female per year. This calculation reflects assumptions that fecundity and adult survival do not change with age, that the sex ratio of recruits is 1:1, and females are the limiting sex, all of which are supported by previous research (Dimond & Armstrong 2007; Parlato & Armstrong 2012). We further assumed that subpopulations were not constrained by density-dependent regulation during the study, meaning that λ should be >1 in suitable habitat.

Second, to assess whether subpopulations would be self-sustaining with emigration, we revised the calculation to

$$\lambda = s_a + 0.5 f s_j \gamma, \qquad (2)$$

where γ is the probability of a juvenile remaining in its natal fragment. Our aim was to identify individual fragments that not only showed clear benefits of rat control, but also would have a high probability of subpopulation growth even if they were the only fragments managed.

Results

Effects of Management on Rats and Mice

The rat control greatly reduced rat tracking rates in 12 of the 13 fragments where it was conducted (90% reduction on average) but had no effect in one fragment (Fig. 1a). There was a clear residual effect on rat tracking rates, which were 37% lower on average the year after control than before control. Other factors included in the rat tracking model (Supporting Information) all had significant effects. Rat tracking rates were generally much lower in grazed than ungrazed fragments in the absence
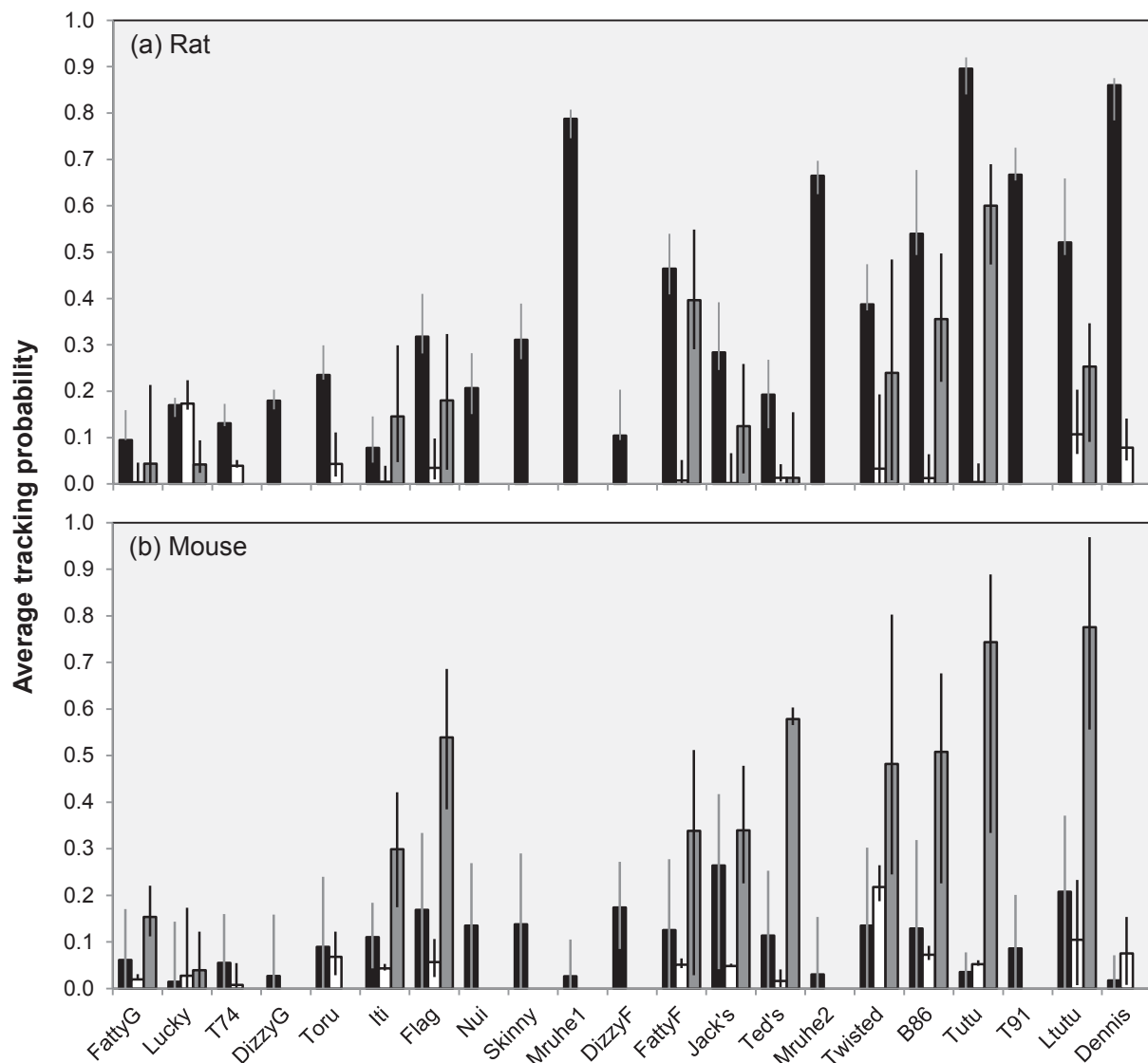
Figure 1. Mean tracking probabilities (SE) for (a) rats and (b) mice in the 19 forest fragments when there is no rat control (black); rat control is currently in effect (white); or rat control was conducted the previous year (gray). Absence of a white bar means there was no control in that fragment, and absence of a gray bar means no data were collected after control was stopped. Fragments are ordered according to understory density, from least dense (grazed fragment FattyG–Flag) to most dense (ungrazed fragment Nui–Dennis). Fatty and Dizzy fragments were partially fenced (F) and partially grazed by stock (G), so these portions are shown separately. The model generating these estimates included rat control and grazing as fixed effects, and fragments, individual tracking tunnels, years, and individual sampling occasions as random effects.

of control (Fig. 1a). However, there was also random variation among fragments, both in the absence of control and in the impact of the control (i.e., interactions between random fragment effects and control effects) and among individual tracking tunnels, years, and sampling occasions.

Mouse tracking increased in some fragments during rat control and decreased in others (no significant change overall) (Fig. 1b). This variation was related to rat tracking rates; mouse tracking tended to increase if rat tracking had been high before control. Grazing was

not a useful predictor of mouse tracking rates, but there was substantial random variation among fragments, individual tracking tunnels, years, and sampling occasions. The main effect of rat control on mice was a huge increase the following year; this occurred on all fragments except the one where rat control was ineffective (Fig. 1b).

Because the fragment with ineffective rat control (Lucky) was a clear outlier (Fig. 1a), it was considered to be uncontrolled when estimating the effects of rat reduction on robin survival and fecundity.
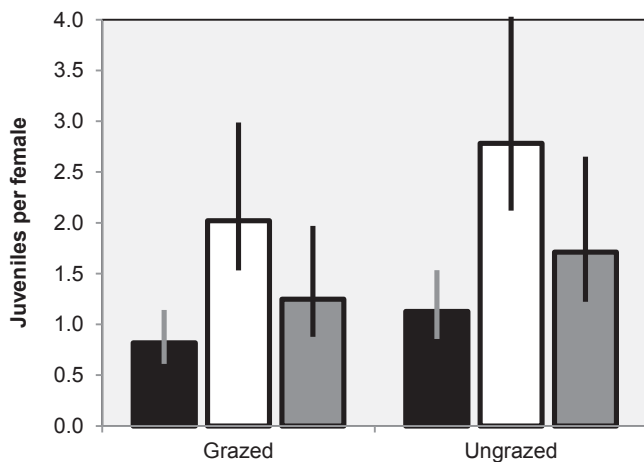
Figure 2. Mean annual fecundity (SE) of North Island Robins in grazed and ungrazed fragments, without rat control (black); when rat control is currently in effect (white); and when rat control was conducted the previous year (gray). The model generating these estimates included random variation among individual females as well as fixed effects of rat control and grazing. Random fragment effects were insignificant so were removed from the model.

Effects of Rat Reduction on Robin Fecundity and Survival

Robin fecundity increased 150% on average when rat control was conducted and 50% the year following rat control relative to precontrol levels (Fig. 2). Fecundity was also affected by grazing; it was 30% lower on average in grazed fragments than ungrazed fragments. There was significant random variation in fecundity among individual females and years. However, there was no apparent random variation among fragments, either in baseline fecundity or the effects of control. Despite fecundity and rat tracking rates both being correlated with grazing (Figs. 1 & 2), post hoc analysis showed that the precontrol rat tracking rate in a fragment was not a useful predictor of fecundity. Post hoc analysis also showed there was no apparent interaction between the control and grazing effects, meaning the effects of rat reduction on fecundity appeared to be consistent for grazed and ungrazed fragments.

Adult survival also increased under rat control, the average annual survival probability rising from 0.58 to 0.84 in females and from 0.64 to 0.87 in males. However, adult survival the year after rat control was similar to precontrol levels. Adult survival varied significantly among fragments in the absence of rat control (Fig. 3), but neither grazing nor rat tracking rates were useful predictors of this variation. There was even greater variation among fragments in degree to which adult survival increased during rat control (Fig. 3). This variation was also unrelated to grazing. However, post hoc analysis showed this varia-

tion was correlated with precontrol rat tracking rates; the increase in adult survival from rat control tended to be highest in fragments with high rat tracking rates before control. The variation in survival increase was nevertheless treated as a random effect when estimating fragment-specific finite rates of increase, partly because the effect of precontrol rat tracking rate was marginally significant and partly because the effect was only considered post hoc. The average resighting probability was estimated to be 0.92, with a standard deviation of 0.04 among surveys.

There was no indication that rat control improved juvenile survival. There were 9 deaths among the 83 juveniles monitored, including 4 in fragments with rat control. Eight of the deaths occurred within 30 d of independence and the other at 64–70 d. The estimated survival probability for the first 30 d was 0.87 (95% credible interval 0.78–0.94). When calculating the probability of juveniles surviving to adulthood (s_j), we assumed that this probability applied to the first 30 d and that the fragment-specific adult male survival probability applied to the next 7 months (time from independence to adulthood is 8 months on average).

Emigration of Juvenile Robins

Under the quadratic function in the fitted fidelity model (Supporting Information), the daily probability of emigrating peaked at 18 d after independence and then declined and became negligible after 40 d. It was therefore reasonable to estimate the cumulative probability of a juvenile remaining in each fragment based on the telemetry data. This probability averaged 0.37 but varied among fragments. Fidelity was correlated with the natal fragment's CDN, and we also retained random variation among fragments in the fidelity model, although this variation was ambiguous (Fig. 4). The IFPC was a slightly less effective predictor of fidelity that CDN (ΔDIC = 0.4), and there was no indication that fidelity probability was affected by the natal fragment's area or differed between males and females.

Finite Rates of Increase

Ignoring immigration and emigration, finite rates of increase (λ) were estimated to be close to 1 or <1 without rat control and to rise to 1.4–2.1 with rat control (Fig. 5a). When juvenile emigration was included, most point estimates for λ were still >1 (Fig. 5b), but there was greater uncertainty. The probability that subpopulations would be self-sustaining ($\lambda > 1$ with juvenile emigration) was >0.8 for 6 of the 12 fragments with effective rat control. Five of these 6 fragments were selected for ongoing control (Fig. 5b); the sixth fragment (Jack's) was ineligible for further use of rodenticides due to the organic status of the surrounding farm. Due to the estimated effect of grazing on fecundity, 5 of the 6 fragments with high (>0.8)
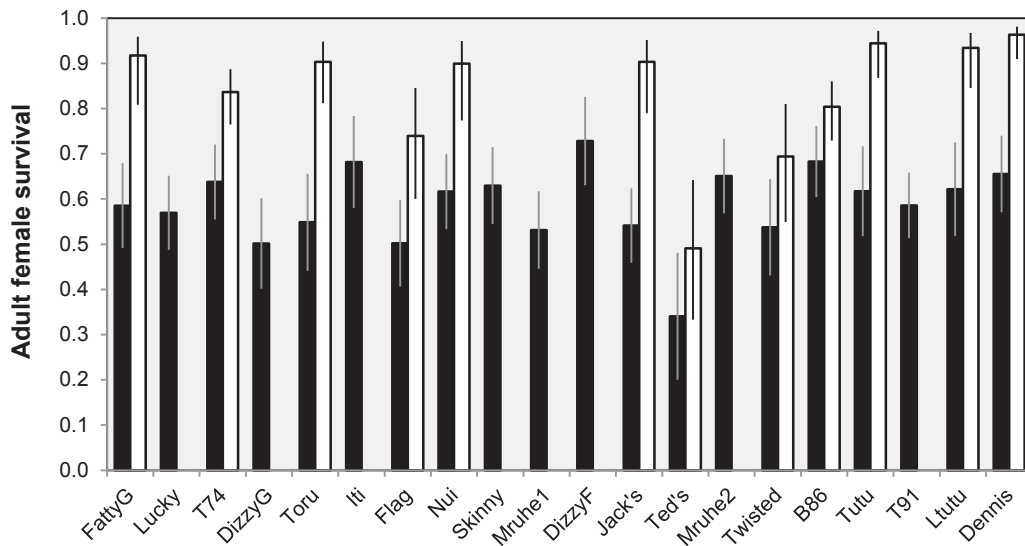
Figure 3. Annual survival probabilities (SE) of adult female North Island Robins in 19 forest fragments, without rat control (black) and when rat control is currently in effect (white). Fragments are ordered on the x-axis as in Fig. 1. The model generating these estimates included rat control (current vs. other), season (September–January, January–May, May–September), and sex as fixed effects, and allowed random variation among fragments, both in baseline survival and in the effects of control. The sex effect only applied from January to May (intervals with nesting). Grazing and residual control effects (rat control previous year) were insignificant so were removed from the model.
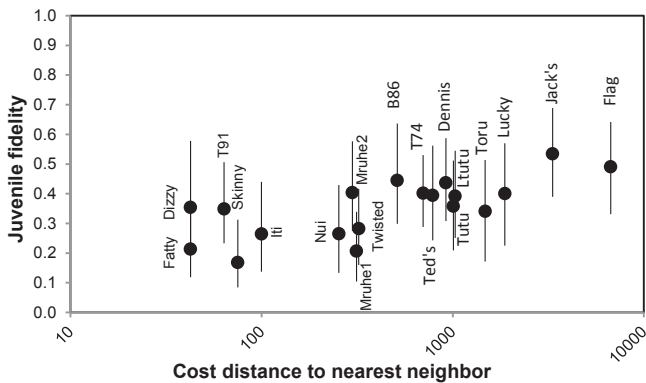
Figure 4. Juvenile fidelity probabilities for North Island Robins (SE) for each of the 19 forest fragments. These are probabilities of juveniles remaining in their natal fragments if they survive to the next breeding season, and are based on daily fidelity probabilities modeled as a logit-quadratic function of time since independence. This model also included the natal fragment's cost distance to nearest neighbor (CDN) as a fixed effect and a random fragment random effect. The CDN is an index of the minimum cost incurred in reaching another forest area, and reflects resistance values assigned to different vegetation types based on previous research (Richard & Armstrong 2010a).

probability of being self-sustaining were ungrazed, whereas 5 of the other 6 fragments were grazed. The one grazed fragment where ongoing control was being conducted (T74) has now been fenced to allow regeneration.

Discussion

Our results showed that management substantially reduced ship rats in 12 of the 13 forest fragments and that this translated into improved fecundity and survival of North Island Robins, the species targeted for recovery. Mouse irruptions occurred after rat control, presumably due to competitive release (Caut et al. 2007; Ruscoe et al. 2011; Goldwater et al. 2012) before rat populations recovered. However, this did not translate into negative effects on robins; their fecundity was significantly higher the year after rat control compared with precontrol levels, and adult survival was similar to precontrol levels.

In the absence of rat control, λ was estimated to be close to 1 (0.95–1.05) in about half of the 19 fragments studied. It was lower (0.74–0.90) in the other fragments, suggesting these fragments may be unable to support robin subpopulations without immigration. In principle, λ estimates close to 1 could reflect density-dependent regulation (Turchin 1999). However, this possibility can be rejected due to the extremely low robin densities compared with sites free of non-native predators and
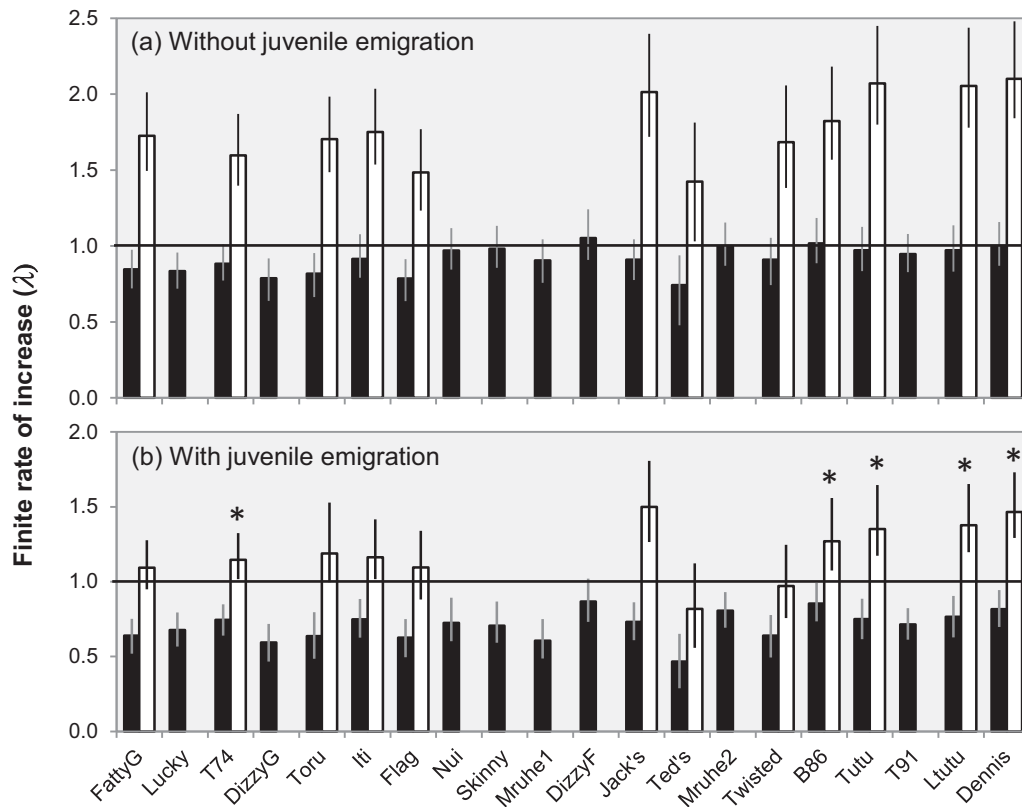
Figure 5. Fragment-specific finite rates of increase (SE) in North Island robin subpopulations with rat control (white) or without rat control (black) based on the parameter estimates in Figs. 2–4 and the estimated juvenile survival probability (see text). The two panels show rates of increase expected (a) if all juveniles remained in their natal fragments and (b) with juvenile fidelity estimates from Fig. 4 and no immigration. Fragments are ordered on the x-axis as in Fig. 1. Asterisks show the 5 fragments selected for ongoing rat control based on these results. The Jacks fragment was not selected because it is part of a block where rodenticides cannot be used.

due to the strong increase in λ when rats were controlled. We instead conclude that the fragments with λ close to 1 are marginal habitat in the absence of rat control. A system of small subpopulations in marginal habitat will be highly vulnerable to extinction (Lande et al. 2003), so it is likely that occupancy depends on immigration from larger forest areas nearby. This conclusion is supported by previous research showing that connectivity, both to nearby continuous forest and other fragments, was the main predictor of fragment occupancy by robins (Richard & Armstrong 2010b). The system therefore appears to be a classic mainland-island system (Harrison et al. 1988), although immigration from the "mainland" may be enhanced by management such as the predator control operations conducted in nearby Pureora Forest Park (5 km to E) by the New Zealand Department of Conservation. The consequence is that occupancy of the fragment system is likely to be sensitive to reduction of connectivity to continuous forest, and such reduction has occurred recently with the felling of pine plantations between the farm landscape and Pureora.

Rat control may therefore be essential for maintaining robins in the fragments and is clearly essential for increasing densities toward natural levels. The high λ estimates (1.4–2.1) under rat control suggest that all fragments would provide good-quality habitat if rats were controlled. However, these estimates drop considerably (0.8–1.5) when juvenile emigration is added, meaning it is unclear whether many of the fragments would be self-sustaining.

The fragments with the highest probabilities of being self-sustaining, and therefore selected for ongoing rat control, all had low-to-medium connectivity (Figs. 4 & 5). Although high connectivity is often expected to improve metapopulation viability in unmanaged landscapes (Hanski 1999; Reed 2004), it is problematic when it facilitates emigration from managed to unmanaged areas (Le Gouar et al. 2012). Complete isolation of fragments would also be undesirable due to inbreeding, but we expect the level of movement in our landscape is well above that needed for genetic rescue (Tallmon et al. 2004). The alternative to selecting isolated fragments would be to manage all fragments or a well-connected network. However,

in our scenario the aim was to identify individual fragments that would have a high probability of being self-sustaining under management.

Livestock grazing also affected selection of fragments for ongoing control. The higher mean fecundity in ungrazed fragments meant they supported the only subpopulations with a high probability of being self-sustaining under management. This selection may have been different if λ estimates for robins had been higher overall; grazed fragments may then have had a high probability of being self-sustaining without rat control, meaning management would best be focused on ungrazed fragments. The selection may also have been different under a network approach because increases in λ may be equally valuable in grazed and ungrazed fragments if they are highly connected. It may appear paradoxical that grazing is associated with both low fecundity and low rat tracking rates in the absence of rat control. However, although rat tracking rates are an effective measure of the effectiveness of control, variation in tracking rates among sites with different vegetation types is not expected to reflect variation in rat densities (Blackwell et al. 2002). The positive effect of fencing on robin fecundity is a useful result for fragment restoration because it illustrates that the benefits of fencing may extend beyond vegetation restoration.

The substantial variation in adult survival among fragments is unexplained and was unrelated to grazing or rat tracking rates. This translates into additional variation in λ that also affected the selection of fragments for ongoing control. This additional variation was detected due to the inclusion of random fragment effects in all models, illustrating the relevance of hierarchical modeling to fragmentation studies.

The translation of research results into management decisions always reflects the values and constraints of stakeholders (Burgman 2005). In our scenario, the focus on the strategic value of managing individual fragments reflected the fact that long-term rat control needed to be conducted within the constraints of a commercial farming operation, where investment in biodiversity conservation would be modest. As noted above, a commitment to managing a larger network of fragments could lead to a different decision based on the same results. In addition, there could be a fuller valuation of the costs and benefits of the management. For predator control operations conducted to benefit native species, the benefits must be weighed against the ethical costs and potential nontarget impacts as well as financial costs (Warburton & Norton 2009). Although nontarget impacts are not expected with our control methods, the slow death of rodents from anticoagulants (Eason et al. 2010) is a significant ethical cost. It would therefore be useful for future researchers to assess the costs and benefits of toxin-free rodent control methods in forest fragments. In addition, although the Ngāti Rereahu landowners have supported the control,

application of toxins incurs some negative impact on the mauri, or spiritual integrity, of the ecosystem.

Although clear decision criteria are important, the most essential requirement for strategic predator control is sound information on its effects (Warburton & Norton 2009). Such information is often lacking. For example, in Reddiex and Forsyth's (2006) review of vertebrate pest-control operations in Australia, they reported that most operations had no monitoring of the pest species or biodiversity response, and that it was extremely rare to have replicates or controls. This lack of information is probably most pronounced in small operations conducted in habitat fragments by private landowners. Research to support these initiatives is becoming increasingly important as biodiversity values are incorporated into management plans by farmers and other land owners, and the experimental and modeling methods illustrated in our study should be invaluable for future research.

Acknowledgments

Supporting Information

The full model explanations (Appendices S1–S2), Win-BUGS code for model fitting (Appendices S3–S4), data (Appendices S5–S6), and parameter estimates (Appendices S7–S8) are available on-line. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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