

## The role of pine plantations in source-sink dynamics of North Island robins

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**Abstract:** Managed pine plantations now constitute a large portion of mainland New Zealand. Despite many native birds inhabiting these exotic habitats, their value for biodiversity conservation is unclear. Although numerous studies have quantified densities of native bird species in pine plantations, it is unknown whether these individuals constitute self-sustaining populations. Here we address this question for North Island robins (*Petroica longipes*) in a *Pinus radiata* plantation in the central North Island. We compare survival and reproduction data of robins collected in three different compartments of the plantation from 2003–2005 to similar data collected from 20 unmanaged native forest fragments from 2002–2014. We used the data to derive estimates of finite rate of increase ( $\lambda$ ) using a Bayesian hierarchical modelling framework that accounted for site-to-site and temporal variation. The mean reproduction rate was much lower in the pine plantation, with females producing 0.34 (SE 0.15) independent juveniles per year, in comparison to 1.02 (SE 0.21) in fenced native fragments and 0.83 (SE 0.21) in grazed native fragments. These differences are attributable to lower nest survival, as nests in the pines had a 0.09 (SE 0.05) probability of surviving to fledging, compared to 0.33 (SE 0.04) for fenced native fragments and 0.28 (SE 0.06) for grazed native fragments. In contrast, the mean adult female survival probability was 0.64 (SE 0.13) in the pines in comparison to 0.55 (SE 0.04) in the native fragments. The  $\lambda$  estimate for the pine plantation was 0.76 (SE 0.14), meaning  $\lambda$  was unlikely to be  $>1$  as is required for a self-sustaining population. The mean  $\lambda$  was estimated to be 0.89 (SE 0.09) for fenced native fragments and 0.83 (SE 0.09) for unfenced native fragments, but varied among fragments with estimates close to 1 for some fenced fragments. Therefore, the pine plantation probably constituted sink habitat that retained robins due to immigration from the surrounding landscape, whereas at least some of the native fragments could potentially be self-sustaining.

**Keywords:** exotic forest, *Petroica longipes*, population dynamics, predation, reproduction rates, survival

### Introduction

It has long been known that many of New Zealand's indigenous bird species can inhabit exotic plantation forests (Jackson 1971; Colbourne & Kleinpaste 1983; Pawson et al. 2010). Some species appear to reach greater population densities than they do in native forest (Clout & Gaze 1984; Brockie 1992; Duncan et al. 1999). For example, Brockie (1992) reported bird densities of up to 625 pairs of native birds per 100 ha in mature Monterey pine (*Pinus radiata*) plantations in Kaingaroa Forest – the highest bird densities yet recorded in forest habitat on the New Zealand mainland. Duncan et al. (1999) surveyed a population of South Island robins (*Petroica australis*) in a mosaic of regenerating native forest and exotic plantations west of Dunedin and found that the mean number of robins counted per survey station was 5 times greater in stands of mature Douglas fir (*Pseudotsuga menziesii*) than in nearby native forest habitat.

These studies, along with data from King et al. (1996) suggesting that the introduced ship rat (*Rattus rattus*) – a major

predator of many native bird species – is less abundant in mature exotic plantations than in native forest, led Powlesland et al. (2000) to suggest that mature exotic plantations may act as refuges of low predation pressure for some native bird species. Lower rat numbers in these plantations could potentially allow native bird populations to achieve higher growth rates, and thus reach higher population densities, than they do in native forest. If this is the case, exotic plantations could play a valuable role in maintaining bird populations at the landscape and regional scale, not only by increasing connectivity between otherwise isolated areas of native forest habitat, but also by supporting large, viable populations of some native species.

To date, most work on native birds in exotic plantations has consisted of simple assessments of relative or absolute density (Clout & Gaze 1984; Brockie 1992; Duncan et al. 1999). However, population density can be a misleading indicator of habitat quality, as poor-quality habitats can act as sinks that support high densities solely due to immigration from other locations (van Horne 1983). To accurately assess the value of any area for a particular species it is necessary to measure

its survival and reproductive success to determine whether or not the habitat can support a self-sustaining population of that species in the absence of immigration (van Horne 1983; Pulliam 1988). We addressed this question for North Island robins (*Petroica longipes*) in a *Pinus radiata* plantation.

The North Island robin has been extirpated from most of its original range since European settlement due to the combined effects of forest loss and introduced predators, but is still locally common in some areas of the central North Island (Higgins & Peter 2002; Parlato et al. 2015). So, although the species is currently classified as ‘At risk-declining’ (Robertson et al. 2017), it can still be found in sufficient numbers to provide large enough sample sizes for a detailed population study. Furthermore, it is a relatively easy bird to catch and monitor, with much work having already been done to describe its biology and to develop monitoring methods (Powlesland 1997; Armstrong et al. 2000; Powlesland et al. 2000). North Island robins are known to occur commonly in both native and exotic forest (e.g. Gibb 1961; Jackson 1971; Duncan et al. 1999), and appear to be common in mature *P. radiata* plantations in the central North Island. However, it remains unclear whether these plantations are playing a role in maintaining robin populations (Pawson et al. 2010).

We estimated survival and reproduction rates (juveniles produced per female) of North Island robins in a mature *P. radiata* plantation to assess whether these populations were self-sustaining, and compared those rates to data from adjacent native forest fragments to assess source-sink dynamics between these habitat types. We also collected data on nest survival rates

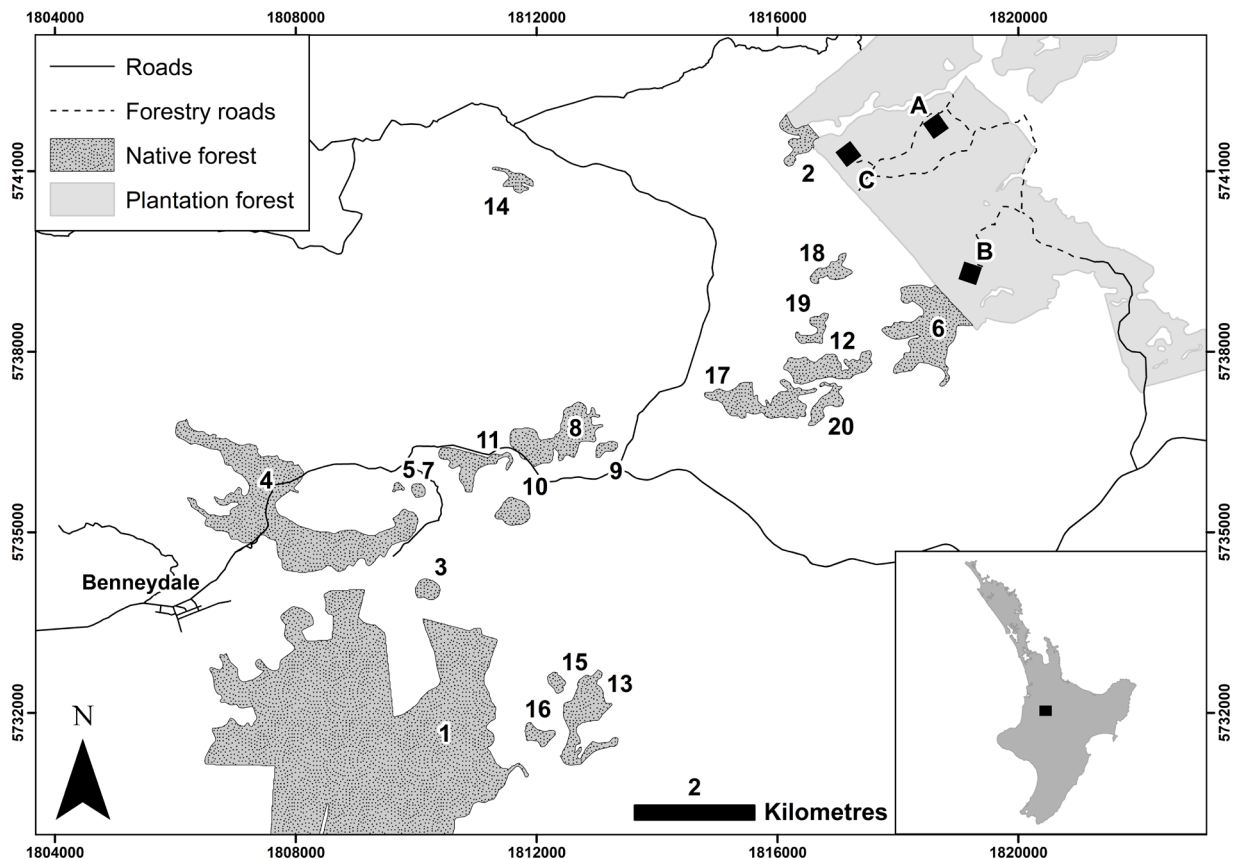
in both habitats to see if these data explained any differences in reproduction rates, and collected rat tracking data (Innes et al. 1995) to assess whether they explained any differences in robin or nest survival. If robin population growth was positive in the pine plantation, emigration of dispersing juveniles to adjacent native fragments could contribute to the stability and persistence of the small semi-isolated populations in those fragments. Conversely, if robin population growth was negative in the pine plantation, it could potentially threaten the stability of native forest fragment populations by acting as a sink for dispersing juveniles, and potentially even an ecological trap (Schlaepfer et al. 2002) if the plantation was particularly attractive to juveniles.

## Methods

### Study sites and sampling design

The study sites were a mixture of exotic *P. radiata* and native forest fragments distributed over a landscape of about 10 km by 10 km (Fig. 1, Table 1). This landscape extended from the town of Benneydale to the western boundary of Pureora Forest Park (75° 220' E, 38° 320' S).

From 2003–2005 we collected data from three different compartments of mature *P. radiata* within Horokino Forest, a 1200 ha plantation west of Pureora Forest Park (Table 1). The three sites selected were at least 2 km apart to give a representative sample of the robin population in the plantation. They all had mature pines planted from 1973 to 1984, and were subsequently harvested in 2007 and 2008.



**Figure 1.** Landscape used to compare survival and reproduction rates of North Island robins in a pine plantation to those in native forest fragments. A–C show the three compartments of mature *Pinus radiata* in Horokino Forest where we collected robin data, and 1–20 show the native fragments sampled (see Table 1 for further details). The matrix is mostly pasture. The numbers on the border show New Zealand Transverse Mercator 2000 coordinates.

**Table 1.** Sampling regime for comparing survival and reproduction rates of North Island robins in three compartments of a pine plantation (A–C) to those in 20 native forest fragments.

Label	Name	Type	Area <sup>1</sup> (ha)	Grazed <sup>2</sup>	Reintroduced <sup>3</sup>	Banded adults male	Banded adults female	Females <sup>4</sup> monitored	Tracking tunnels
1	Mangapehi	native	1605	N	N	15	8	11	16
2	T38	native	47	N	N	13	12	9	16
3	Dennis	native	13	N	N	8	5	7	16
4	Herekawe	native	297	N	N	17	13	11	16
5	Little Tutu	native	2	N	N	5	4	3	5
6	T91	native	18	N	N	21	7	24	16
7	Tutu	native	5	N	N	7	5	4	16
8	Mangaruhe2	native	67	N	N	8	8	13	16
9	Teds	native	6	N	Y	6	5	2	9
10	Jacks	native	19	N	Y	9	10	7	16
11	Mangaruhe1	native	31	N	N	9	7	7	16
12	Skinny	native	39	N	Y	7	6	7	16
13	Te Hape Nui	native	33	N	N	8	5	9	16
14	Flag	native	8	Y	Y	7	6	4	9
15	Te Hape Iti	native	9	Y	Y	3	2	3	16
16	Te Hape Toru	native	9	Y	Y	6	3	3	9
17	Dizzy <sup>5</sup>	native	56	Y	Y	5	6	7	9
18	T74	native	11	Y	N	6	6	8	16
19	Lucky	native	6	Y	Y	8	7	8	9
20	Fatty <sup>5</sup>	native	14	Y	Y	7	5	3	5
A	Longden Rd	pine	NA	N	N	10	7	7	16
B	Moloney Rd	pine	NA	N	N	11	5	6	16
C	Stub Rd	pine	NA	N	N	10	3	6	16

<sup>1</sup>The native forest fragments were discrete areas with clear boundaries whereas the three pine sites were different compartments in a continuous 1200 ha forest.

<sup>2</sup>Whether fenced to exclude livestock.

<sup>3</sup>Whether robins were reintroduced to the site or were already present at the start of the study.

<sup>4</sup>Number of females whose reproduction was monitored over at least one breeding season.

<sup>5</sup>Fragments that were partially grazed due to placement of stock fences; the total fragment area is shown but other data apply specifically to the grazed portions because few robins used the fenced portions.

From 2002–2014 we collected data from 24 different native forest fragments in pastoral land to the west of Horokino Forest, but for this analysis excluded fragments where only one breeding female was monitored (Table 1). The 20 fragments used included 11 fragments where robins already occurred, and nine fragments where we re-established the species by translocating birds from pine plantations before they were felled (Armstrong et al. 2013). Although all fragments were dominated by tawa (*Beilschmiedia tawa*), they varied greatly in the composition of the understorey and subcanopy, particularly through impacts of livestock grazing (Richard & Armstrong 2010a). Sampling a large number of fragments over many years (Table 1) allowed us to make a comparison between the pine plantation and native forest fragments that was robust to this vegetation variation. These fragments were normally unmanaged except for low-intensity possum (*Trichosurus vulpecula*) control which had no apparent effect on rat densities. Although some of the fragments have been subjected to experimental rat control (Armstrong et al. 2014), the years affected by rat control are excluded from this analysis. For survival, this meant excluding data for 12 months from September in years where rat control occurred (from September to May). For reproduction, we excluded data from both the year of control and the following year, as our previous analysis had shown a small residual effect of rat control due to reduced rat densities at the start of the next breeding season (Armstrong et al. 2014).

## Data collection

The data set included 330 individually colour-banded adult robins, with 46 of these birds holding territories in the pine plantation (15 females, 31 males), and 288 birds holding territories in one of the 20 native forest fragments (122 females, 166 males; Table 1). Four birds occur in both data sets due to being translocated from pine to native forests in May–June 2005. We captured most birds using clap traps baited with mealworms, and the remaining birds using mistnets. Survival estimates were entirely based on data from these banded birds, whereas the reproduction and nest survival estimates included data from unbanded individuals (Table 1).

We conducted survival surveys at 4-month intervals in the native forest fragments from September 2002 to September 2014, and at 2-month intervals in the pine plantation from September 2003 to May 2005. The greater frequency of surveys in the pine plantation was designed to compensate for the shorter duration of the study, i.e. increasing the number of surveys from 6 to 11 allowed greater precision in survival estimates. Surveys involved visiting the territory of each banded bird and recording whether or not they were detected. The robins often approached the observer, as they had learned to associate people with provision of mealworms. However, if no bird was detected immediately we played a tape recording of male territorial song for one minute, then waited for 3 minutes. If only the male of a pair was detected, we gave him one or more mealworms, which typically results in the male calling

in the female during courtship or incubation periods. If the female did not respond but was likely to be on the nest, we re-checked the pair later and recorded the female as detected if subsequently seen.

We intensively monitored the selected pairs (Table 1) each breeding season from 2002/03 to 2004/05 in the pine plantation and from 2002/03 to 2010/11 in the native forest fragments to determine their reproduction rates (number of independent juveniles produced) and obtain data on nest survival. This monitoring involved checking each pair at least weekly from September to March, and providing them mealworms both to find nests and subsequently monitor the fates of nests (Powlesland 1997). The loud begging of older chicks and fledglings make it fairly easy to determine whether broods have successfully fledged and count the number of fledged young. We considered fledglings to have reached independence 4 weeks after fledging as it is the minimum time they stay with their parents before dispersing (Armstrong et al. 2000; Powlesland et al. 2000).

We also collected rat tracking data in each of the three compartments of the pine plantation and each of the 20 native forest fragments in the years that breeding data were collected. The tracking tunnels were spaced 50 m apart, with a set of 16 tunnels (4 x 4 grid) used if there was sufficient space, and 5–9 tunnels otherwise (Table 1). We collected tracking data 3–6 times per year, with sampling done on the same nights for the pine and native sites in the years the pine plantation was sampled. On each occasion all tunnels were left out for one night with peanut butter at both ends of the tunnel.

## Analysis

We used the Bayesian updating software OpenBUGS 3.2.3 (Spiegelhalter et al. 2014) to analyse the data. The Markov Chain Monte Carlo (MCMC) procedures in OpenBUGS allow multiple random effects (Bayesian hierarchical modelling), making it possible to simultaneously account for random variation among sites, times, and individual birds. It also facilitated the integration of survival and reproduction data to derive finite rates of increase (see below). 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 hyper-parameters (standard deviations of random effects). Models were run for 30 000 iterations following a burn-in of 1000 iterations to check convergence. The code is provided in Appendices S1–3 and the data are provided in Appendices S4–6 (see supplementary material for appendices).

We modelled adult survival using a state-space formulation of the Cormack-Jolly-Seber model (Kéry & Schaub 2012), with survival and re-sighting probabilities modelled with logit link functions and Bernoulli error distributions (Appendix S1). The model included fixed effects of forest type (pine versus native), sex, and season (Sep–Jan, Jan–May, May–Sep) on survival, with an interaction between the effects of forest type and sex. The sex effect was assumed to only apply to intervals with nesting (Sep–May). The model also included random site and year effects on survival, and allowed re-sighting probability to vary randomly among surveys.

We modelled reproduction (number of independent juveniles per pair per year) using a hierarchical generalised linear model with a log link function and Poisson error distribution. The model included fixed effects of forest type and grazing, with the latter included due to previous research showing a negative effect on grazing on reproduction rates

in native fragments (Armstrong et al. 2014). It included random effects of site, year, and individual female, with the latter effect included to account for repeated measures from the same females over successive years. The same fixed and random effects were used in our analysis of nest survival, which inferred daily survival rates based on the dates each nest was found, was last found active (the approximate fledging date for successful nests), and last checked. The approach used is similar to that developed in MARK and SAS (Rotella et al. 2004), but coded in OpenBUGS to allow the multiple random effects. The estimated daily survival rates were then converted to probability of surviving 40 days, which is the typical interval from egg laying to fledging (Powlesland et al. 2000).

To assess whether robin populations were self-sustaining in either the pine plantation or native fragments, we derived a finite rate of increase for each site based on the survival and reproduction models described above. For North Island robin populations, it is reasonable to calculate the finite rate of increase as

$$\lambda = s_a + 0.5fs_j, \quad (1)$$

where  $s_a$  is annual survival probability for adult females,  $f$  is the mean number of juveniles per female per year, and  $s_j$  is the probability of a juvenile surviving to adulthood (Armstrong et al. 2014). Estimation of juvenile survival requires radio telemetry due to the dispersal typically undertaken at this life stage. We did not collect such data in the pine plantation. However, tracking of 83 juveniles in the native fragments from 2006 to 2012 indicated that they had a 0.87 (SE 0.04) probability of surviving the first 30 days after independence, and that their subsequent survival rate was indistinguishable from that of adults (Armstrong et al. 2014). To calculate  $s_j$  at any site, we assumed that this survival probability applied to the first 30 days after independence, which we took to run from mid-January (the average date of independence) to mid-February. The survival probability was then multiplied by the site-specific probability of an adult surviving from February to September to get the probability of surviving from independence until adulthood.

To compare rat tracking rates among sites, we fitted the tracking data to a hierarchical generalised linear model with a logit link and Bernoulli error distribution. This model included forest type and grazing as fixed effects, and sites, individual tracking tunnels, year, and individual sampling occasions as random effects.

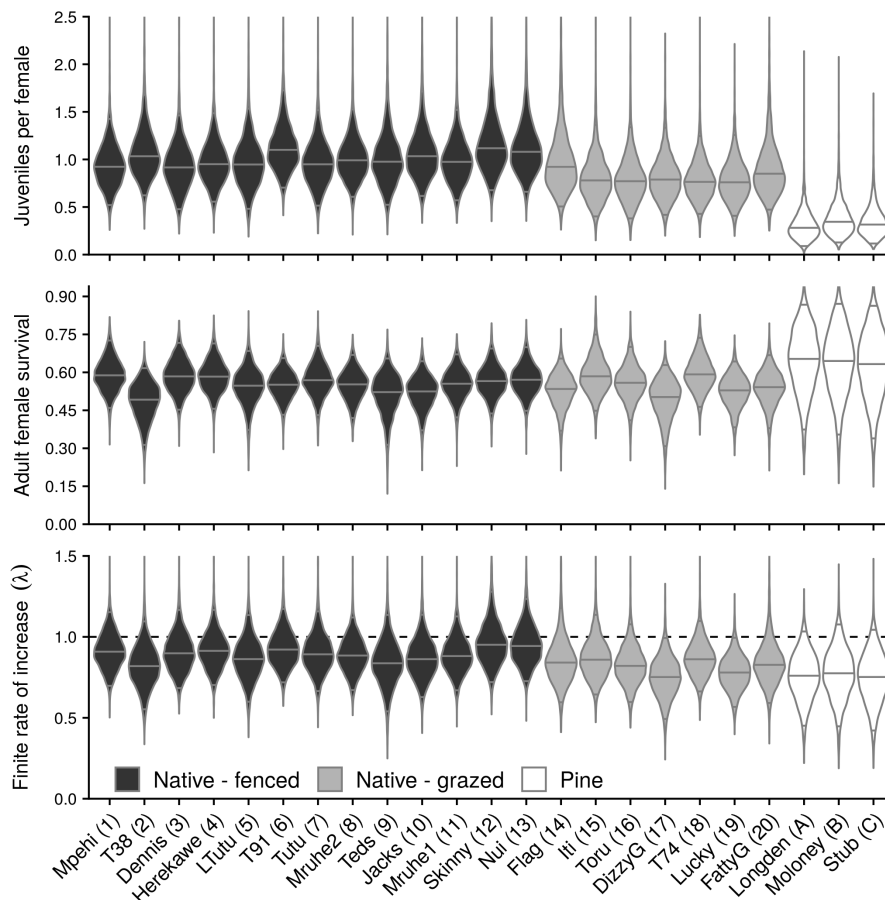
## Results

The notable difference between the forest types was that robin reproduction rates were significantly lower in the pine plantation, as indicated by the 95% credible interval for the effect of forest type on the mean reproduction rate (Table 2). Breeding pairs in the pine plantation produced 0.34 (SE 0.15) independent juveniles per year on average, in comparison to 1.02 (SE 0.21) for fenced native fragments and 0.80 (SE 0.21) for grazed native fragments (Fig. 2). There was random variation among sites, as well as among individual females and years (Table 2). However, the estimated reproduction rates in the three compartments of the pine plantation were well below those for any of the individual forest fragments based on the hierarchical model, regardless of understorey density, position in the landscape (Fig. 1), and whether or not robins had been reintroduced to the fragment (Table 1). These differences in reproduction rates between the forest types reflect differences

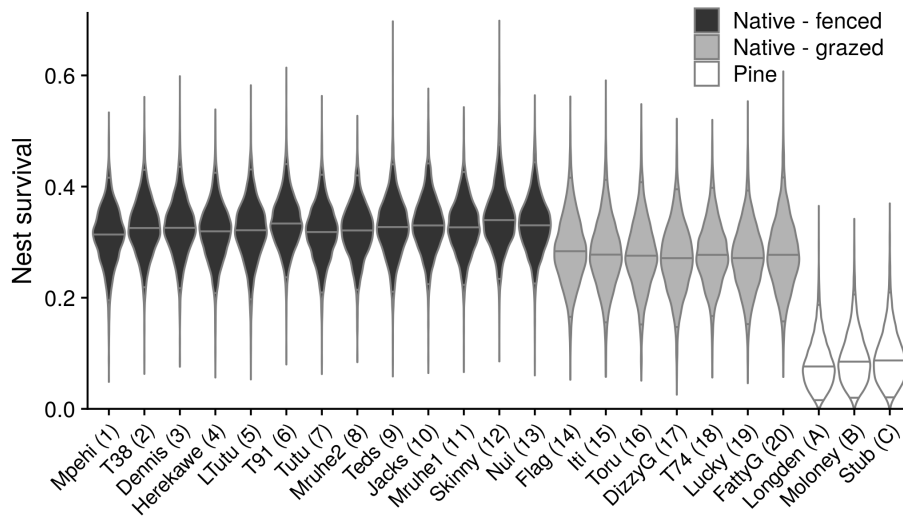
**Table 2.** Parameter estimates (with standard errors and 95% credible intervals) for adult annual survival probabilities and reproduction rates (number of independent young per female per year) of North Island robins in a pine plantation and native forest fragments.

Parameter <sup>1</sup>	Explanation	Mean	SE	2.5%	97.5%
a.phi	Survival intercept (logit of mean female survival probability in native fragments May–Sep)	1.737	0.183	1.371	2.104
b.sj.phi	Effect of season (Sep–Jan) on logit survival	-0.694	0.216	-1.110	-0.260
b.jm.phi	Effect of season (Jan–May) on logit survival	0.267	0.279	-0.262	0.833
b.pine.phi	Effect of forest type (pines) on logit survival	0.367	0.514	-0.568	1.466
b.sex.sm.phi	Effect of sex (male) on survival over breeding season (Sep–May)	0.823	0.193	0.442	1.197
b.pine.sex.phi	Interaction between effects of forest type and sex on survival	-0.874	0.682	-2.238	0.440
s.site.phi	Random variation (standard deviation) in survival among sites	0.200	0.119	0.014	0.463
s.year.phi	Random variation in survival among years	0.246	0.152	0.015	0.603
a.p	Logit of mean re-sighting probability	2.149	0.164	1.846	2.494
s.t.p	Random variation in re-sighting probability among encounter occasions	0.741	0.171	0.447	1.116
a.f	Reproduction intercept (log of mean reproduction rate in fenced native forest fragments)	-0.004	0.202	-0.409	0.379
b.pine.f	Effect of forest type (pine) on mean reproduction rate	-1.166	0.423	-2.041	-0.375
b.gr.f	Effect of livestock grazing on mean reproduction rate	-0.214	0.220	-0.637	0.231
s.site.f	Random variation in reproduction rate among sites	0.188	0.126	0.013	0.478
s.year.f	Random variation in reproduction rate among years	0.425	0.180	0.172	0.868
s.fem	Random variation in reproduction rate among individual females	0.435	0.133	0.129	0.689

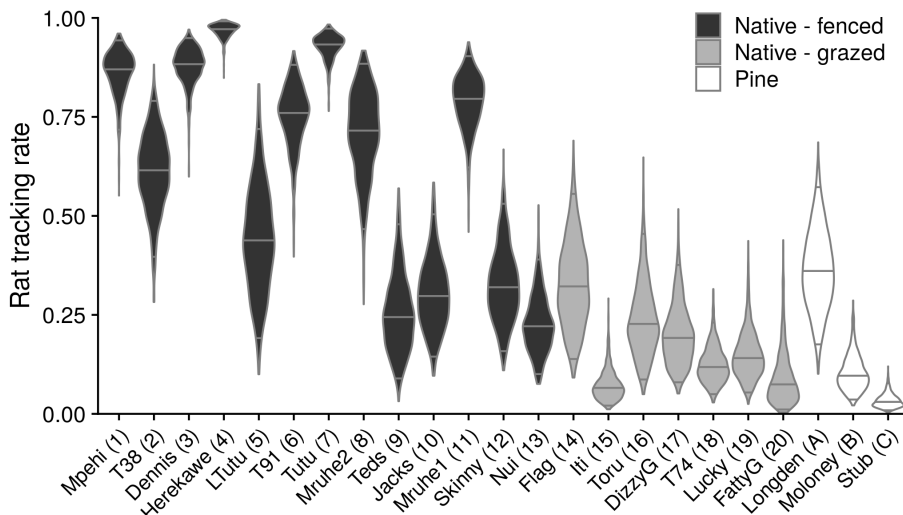
<sup>1</sup>Code used to estimate these parameters is provided in Appendix S1.



**Figure 2.** Posterior probability distributions for reproduction rates (independent juveniles produced per female per year), annual adult female survival probabilities, and finite rates of increase for North Island robins in native forest fragments (black and grey bars) and three compartments of a pine plantation (white bars). The native fragments are ordered based on a score of understorey density (Richard & Armstrong 2010a), with the highest-density fragments shown on the left and fragments grazed by livestock shown in grey. The distributions were produced by Bayesian hierarchical models that include forest type, grazing (reproduction only), and sex (survival only) as fixed effects, and sites, years and individual females (reproduction only) as random effects. Horizontal lines show medians and 2.5% and 97.5% quantiles.



**Figure 3.** Probabilities of nests surviving 40 days (approximate time from egg laying to fledging) in native forest fragments (black and grey bars) and three compartments of a pine plantation (white bars). These estimates are derived from daily survival rates estimated using a Bayesian hierarchical model that included forest type and grazing as fixed effects, and sites, years, and individual females as random effects. Other conventions as for Figure 2.



**Figure 4.** Rat tracking rates (probability of a tracking tunnel being visited by one or more rats over one night) in native forest fragments (black and grey bars) and three compartments of a pine plantation (white bars). The estimates are based on a Bayesian hierarchical model that included forest type and grazing as fixed effects, and sites, tunnels, and years, and sampling occasions as random effects. Other conventions as for Figure 2.

in nest survival; the probability of an average nest surviving from egg laying to fledging was 0.09 (SE 0.05) for the pine plantation, 0.33 (SE 0.04) for fenced native fragments, and 0.28 (SE 0.06) for grazed native fragments (Fig. 3).

In contrast to the reproduction and nest survival results, mean annual survival probability for adult females was 0.64 (SE 0.13) in the pine plantation in comparison to 0.55 (SE 0.04) in the native fragments (Fig. 2), although this difference was not significant – i.e. the credible interval for the effect of forest type overlapped zero (Table 2). Female survival was significantly lower from September to January than other seasons, male survival was significantly higher than female survival during breeding intervals, and there was clearly residual random variation among sites and years. Re-sighting probability was 0.85 on average, and varied among surveys (Table 2).

Based on these survival and reproduction rates, the mean finite rate of increase ( $\lambda$ ) was estimated to be 0.76 (SE 0.14) for the pine plantation, in comparison to 0.89 (SE 0.09) for fenced native fragments and 0.82 (SE 0.09) for unfenced native fragments (Fig. 2). The posterior distributions for  $\lambda$  were mostly  $<1$  in all three compartments of the pine plantation (Fig. 2), meaning the plantation was unlikely to have a self-sustaining robin population. The point estimates for  $\lambda$  in native fragments were also all  $<1$ . However, the posterior distributions suggest that there is a reasonable probability that at least some of the fenced native fragments could be self-sustaining.

The mean rat tracking rate was much lower in the pine plantation (0.11) and grazed native fragments (0.14) than in the fenced native fragments (0.66), and there was also a large amount of additional site-to-site variation (Fig. 4). There was

also extensive random variation among tunnels, years, and sampling occasions. There was a weak positive correlation between rat tracking and reproduction rates ( $r^2=0.19$ ) due to the pine plantation having both low rat tracking rates and low reproduction rates. There was no correlation between rat tracking and adult female survival rates ( $r^2=0.01$ ).

## Discussion

Our results show that the population of North Island robins in mature *P. radiata* forest adjacent to Pureora was unlikely to be self-sustaining, and that its low finite rate of increase was due to poor nest survival. Therefore, the idea that pine plantations could act as refuges for robins due to low rat density is not supported in this landscape. Instead, the robin population in this pine plantation has probably acted as a sink, relying on immigration of juvenile robins from the surrounding landscape. However, pine plantations are unlikely to act as ecological traps for robins, as dispersing juvenile robins have been shown to prefer mature native forests even though they also readily disperse into mature pines (Richard & Armstrong 2010b).

The results of this study may not apply to other pine plantations, as robin demographic rates will depend on a range of factors such as climate, topography, and predator management. The presence of robins throughout large areas of continuous *P. radiata* forest such as on the Kaingaroa Plateau (ca. 250 000 ha) suggest that they are unlikely to be maintained by immigration from native forest in those areas. Even where pine forests are unable to support robins, they could play an important role in maintaining connectivity between areas of native forest as robins are generally unwilling to cross pasture gaps of >110 m (Richard & Armstrong 2010b). Given that it is unclear whether the native fragments in our study were self-sustaining, it is possible that these populations rely on immigration from the managed native forest at Pureora, and that such immigration is facilitated by the pine plantation, which lies between Pureora and the native fragments. Pine plantations have also provided useful source populations for robin reintroductions (e.g. Armstrong et al. 2013).

Our results, like those of King et al. (1996) and Innes et al. (2001, 2010) reveal lower rat tracking indices in pine plantations and grazed native fragments than nearby native forests. However, lower tracking rates did not lead to higher nest survival or reproductive success, particularly in the pine plantation where both were extremely low. Given that ship rats have been shown to respond differently to vegetation structure in this fragmented landscape (Ruffell et al. 2014), it is possible that the absence of a negative correlation between rat tracking indices and reproductive success may be caused by problems in interpreting rat tracking rates across different vegetation types (Blackwell et al. 2002). Although Innes et al. (2010) corroborated that the grid-based tracking tunnel system did provide a promising relationship between approximate rat densities when trapping indices were <30%, ship rat behaviour may differ in grazed fragments as they probably spend less time on the ground. This could partly explain the fact that robins have higher reproductive rates in fenced fragments than grazed fragments despite significantly lower tracking rates in grazed fragments.

The somewhat higher female survival in pines, but much lower reproduction rates, could be explained by a difference in predator composition. Stoats (*Mustela erminea*) are active predators during both the day and night (Alterio & Moller 1997),

appear attuned to nestling activity (Spurr & O'Connor 1999), and have been found to be more abundant in mature exotic plantations than native forest within our study landscape (King et al. 1996). Little and King (2017) highlighted the significant impact stoat nest predation had on rock wrens (*Xenicus gilviventris*), with stoats causing nest failure predominately during the day and at the nestling stage. Such predation was observed twice in the pine plantation during our study. This type of predatory behaviour, coupled with the finding of King et al. (1996) may help explain the differences we observed in female survival and reproduction between the pine plantation and the native forest fragments, highlighting the importance of understanding predator-prey dynamics in modified landscapes. If the low reproductive success in the pine plantation was indeed due to stoat predation, then this problem could be managed by controlling stoats. Given the extensive home ranges of stoats (e.g. Miller et al. 2001), it is possible that the low nest success could have been due to a single stoat.

Although the North Island robins in the pine plantation were almost certainly a sink population in the system studied, this is not expected to be the case for all native species or all locations. Plantations across the world can play an important role in conservation of native biodiversity, particularly in an agricultural landscape (Brockerhoff et al. 2008). In the only other study we know of that compares demographic rates of a New Zealand species in pines and native forest, Seaton et al. (2009) concluded that the productivity of New Zealand falcons (*Falco novaeseelandiae*) in pine plantations was similar to those inhabiting other habitats in New Zealand. While it is well known that a large number of New Zealand's native avifauna inhabit pine plantations (Pawson et al. 2010), it generally remains unknown whether these constitute self-sustaining populations. Our research reiterates van Horne's (1983) point that population density is a misleading indicator of habitat quality, and that pine plantations with apparently abundant bird populations could in some cases be poor-quality sink habitats. Further research into survival and reproductive rates in pine plantations is required to better understand their impact at the population level and to provide forest managers with valid management recommendations. For North Island robins, pine plantations could be strategically managed to facilitate or restrict connectivity between areas of native forest, or could potentially be converted into sustainable populations through management to improve nest survival, particularly stoat control.

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## Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

**Appendix S1.** OpenBUGS code for estimating adult annual survival probabilities, reproduction rates (number of independent young per female per year), and finite rates of increase for North Island robins in a pine plantation and native forest fragments.

**Appendix S2.** OpenBUGS code for estimating nest survival probabilities for North Island robins in a pine plantation and native forest fragments.

**Appendix S3.** OpenBUGS code for estimating rat tracking rates (probability that at least one rat passes through a baited tracking tunnel in 24 h) in a pine plantation and native forest fragments.

**Appendix S4.** Data used to estimate adult annual survival probabilities, reproduction rates (number of independent young per female per year), and finite rates of increase for North Island robins in a pine plantation and native forest fragments.

**Appendix S5.** Data for estimating nest survival probabilities for North Island robins in a pine plantation and native forest fragments.

**Appendix S6.** Data for estimating rat tracking rates (probability that at least one rat passes through a baited tracking tunnel in 24 h) in a pine plantation and native forest fragments.

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