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Influence of food availability, predator density and forest fragmentation on nest survival of New Zealand robins

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ABSTRACT

The decline of avian populations in fragmented landscapes is often attributed to a decrease in nest survival rates for species breeding within these habitats. We tested whether fragment size and connectivity, livestock grazing, predator density or invertebrate biomass were correlated with nest survival rates for an endemic New Zealand species, the North Island robin (*Petroica longipes*). Across three breeding seasons (2002–2005) daily nest survival rate for the 203 robin nests monitored in 15 forest fragments was 0.315 (SE 0.003), with nest survival rates increasing with invertebrate biomass (indexed with pitfall traps) and marginally decreasing with fragment size. Footprint tracking rates for exotic ship rats (*Rattus rattus*), which are likely to be the key nest predator, varied greatly among fragments, but were not a useful predictor of nest survival. We found no relationship between the number of fledglings per successful nesting attempt and invertebrate biomass. We conclude that fragment size and connectivity does not appear to be negatively influencing robin nest survival, potentially because of the already high impact that mammalian nest predators have in this unique system.

1. Introduction

Habitat fragmentation converts areas of continuous habitat into small, isolated remnants. Together with the total loss of habitat, this land transformation is widely inferred as a primary cause of recent biodiversity loss worldwide (Vitousek et al., 1997). For some species, reduction in the size and connectivity of fragments can decrease the overall quality of the remaining habitat (Saunders et al., 1991), as well as increasing local extinction rates by altering the metapopulation dynamics (Hanski and Gaggiotti, 2004). Reduced food availability, increased access by predators, and increased grazing pressure by livestock may affect habitat quality, all of which may reduce survival and reproductive rates of the native species occupying these modified habitats. Concern about the decline of avian populations in fragmented forest systems has led to studies attempting to determine effects of fragmentation on adult survival, fecundity and nest survival (Lampila et al., 2005).

A key finding in many fragmentation studies has been the reduction in nest survival in small forest fragments due to an increased rate of nest predation (Stephens et al., 2003). While increased rates of nest predation are generally attributed to increased density and/or activity of certain nest predators (Gates and Gysel, 1978), there have been few attempts to confirm this assertion via direct data on nest predators (Chalfoun et al., 2002). The few studies conducted show that the response of nest predators to fragmentation depends on the taxon, spatial scale, region and habitat matrix considered (Chalfoun et al., 2002).

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Evidence has emerged that forest fragmentation may also affect avian food availability (Robinson, 1998), with detectable food shortages observed in small habitat fragments (Burke and Nol, 1998; Zanette, 2000; Luck, 2002, 2003). Food availability, like nest predation, is known to be an important factor affecting reproductive success of birds, with higher reproductive output generally associated with years (or areas) with greater food abundance (Newton, 1998; Crawford et al., 2006). Nestling starvation during adverse weather conditions has been associated with decreased invertebrate densities (Högstedt, 1981), as has the number of fledglings per successful nest (Strong et al., 2004). As nest survival is one of the key parameters affecting reproductive output, a reduction in nest survival caused by low food availability, higher nest predation or the synergistic effect of both (Zanette et al., 2003) would obviously be detrimental for species' persistence in fragmented landscapes.

The study of the effects of habitat fragmentation on nest survival is not evenly distributed across geographic regions or habitat types, as the vast majority of the literature focuses on Nearctic and Palearctic passerine migrants from boreal and temperate regions (Stephens et al., 2003; Lampila et al., 2005). The response of nest predators to fragmentation has also been studied mainly in North America (Chalfoun et al., 2002). To understand the potentially different mechanisms driving reduced nest survival in forest fragments, studies should expand across different systems.

No information exists on the effects of forest fragmentation on nest survival in New Zealand, even though extensive fragmentation has taken place over the last 150 years. Exotic mammalian predators have caused many extinctions and severe declines among New Zealand's endemic avifauna (Duncan and Blackburn, 2004), and are believed to be the main cause of ongoing population declines of several species (McLennan et al., 1996; O'Donnell, 1996; Moorhouse et al., 2003). Consequently, conservation management and research focuses heavily on the control or eradication of these exotic predators. However, it is currently unknown whether fragmentation has played a role in these birds' declines, and whether fragmentation interacts with predators or food availability.

We address these gaps in the knowledge of habitat fragmentation by examining nest survival of an endemic New Zealand passerine breeding in a fragmented podocarp–broadleaf forest. Using recently developed methodology to evaluate avian nest survival data (Shaffer, 2004), we assess whether nest survival rates vary with size and connectivity of forest fragments, and whether such variation is attributable to effects of invertebrate biomass, predator activity, and/or grazing pressure. We also assess whether invertebrate biomass affects the number of fledglings produced per successful nesting attempt.

2. Methods

2.1. Species and study site

The North Island robin (*Petroica longipes*) is a small (26–32 g) passerine belonging to the endemic Australo-Papuan Family Petroicidae. The North Island robin and South Island robin (*P. australis*) were formerly considered to be subspecies of "New Zealand robin" but the two subspecies were recently separated based on morphological and molecular differences (Holdaway et al., 2001; Miller and Lambert, 2006). North Island robins are a good model species to test for the effects of habitat fragmentation in New Zealand because: (a) Petroicidae species in Australia have been shown to be area sensitive (Major et al., 1999a, 2001; Zanette, 2000; Cousin, 2004; Watson et al., 2005); (b) they have significantly declined since Polynesian and European colonisation (Oliver, 1955); (c) they are known to be strongly negatively affected by exotic mammalian predators (Powlesland et al., 1999; Armstrong et al., 2006); but (d) they still coexist with mammalian predators in the central North Island unlike many other New Zealand birds that are now restricted to predator-free offshore islands.

North Island robins are socially and genetically monogamous, with pair bonds usually retained throughout the breeding season and subsequent years until the death of the partner (Ardern et al., 1997). Females are multi-brooded and typically incubate clutches of 2–3 eggs for 19 days and brood nestlings for 21 days (Powlesland et al., 2000). Males do not incubate or brood, but bring food to the female and nestlings.

We initially searched for robins in 55 podocarp–broadleaf forest fragments over a 14,000 ha landscape (Fig. 1, 175° 22′E, 38° 32′S) near the township of Benneydale in the central North Island, New Zealand. Agricultural land, used for sheep and cattle grazing, dominated the landscape with large tracts of exotic plantations (*Pinus radiata*) to the south and east. We found robins in 13 forest fragments <150 ha, and selected these for study along with two larger fragments (Table 1). We calculated an index of functional patch connectivity (IFPC; Table 1) for each fragment based on its functional connectivity to other fragments within a 3-km radius of its perimeter. The IFPC for any fragment is given by

$$\sum_i \frac{A_i}{\min \sum_j c_j d_{i,j}}$$

where A_i is the area (ha) of each of i native fragments within the 3-km radius (excluding the focal patch), $d_{i,j}$ is the distance travelled over each of j vegetation types to reach fragment i, and c_j represents the cost perceived by the bird of moving through each vegetation type. We recognised four vegetation types (native forest, pine forest, woody vegetation <2 m high, and pasture), and assumed that the relative costs of moving through these substrates were 1, 2, 3 and 10, respectively based on observations of radio-tracked juvenile robins. The equation assumes that the "least cost path" (Bunn et al., 2000; Adriaensen et al., 2003) is taken, minimizing the distance crossed over pasture, and this path was determined using an iterative routine (Cost Distance tool) from ArcGIS 9.0 (ESRI, Redlands, California, USA). A tool for calculating IFPC and its description are available at: http://www.massey.ac.nz/~yrichard. The 3-km radius corresponds to the median dispersal distance achieved by juvenile robins (Richard, 2007). This index differs from conventional measurements of fragment connectivity that only consider the straight line distance to the nearest forest area of a particular minimum size and ignore the matrix features that impede or facilitate individual movements (Watson et al., 2005).

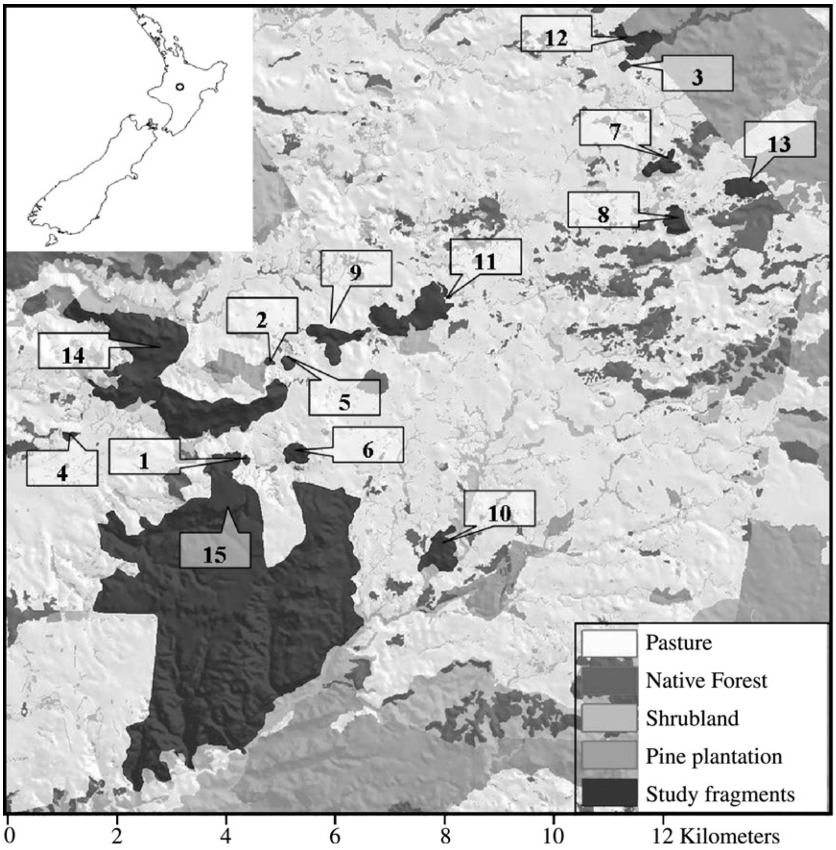

Fig. 1 – Map of study area showing fragments of native forest surrounded by exotic forest and agricultural matrix. The numbers identify the 15 fragments containing robin pairs that we monitored (see Table 1).

Table 1 – Characteristics of forest fragments used to assess effects of fragmentation on nest survival of North Island robins, and the number of females monitored in each breeding season

Fragment[a]	Size (ha)	IFPC[b]	Grazed[c]	Females monitored[d]		
				2002/03	2003/04	2004/05
1	1.6	7768	X	1	1	1
2	2.0	1346		0	0	1 (1)
3	2.9	5460	X	1 (1)	0	0
4	3.7	910	X	1 (1)	0	0
5	4.9	655		2	2	2
6	14.0	1817		1	2 (2)	1
7	14.4	1896	X	2 (2)	2	3
8	17.3	1651		0	1	1 (1)
9	33.7	1606		1	2	3
10	46.8	2664	X	2 (1)	3 (1)	2
11	71.9	835		2 (2)	1	1
12	72.1	3864		4 (1)	5 (3)	4 (2)
13	147.1	2368		3 (1)	4 (2)	4 (1)
14	316.2	5246		5 (3)	6 (1)	6 (1)
15	1625.7	78970		5 (2)	7 (4)	5

a Locations shown in Fig. 1.
b IFPC: An index of functional patch connectivity.
c Unfenced fragments that were grazed and trampled by domestic livestock.
d Figures in parenthesis show how many females died (or otherwise disappeared) before the start of the next breeding season.

We monitored 72 different robin pairs over three breeding seasons (2002/2003–2004/2005), with 30–36 pairs monitored each year (Table 1). Individual pairs had up to three successful broods or five failed nests in a single breeding season (Boulton, 2006). Over 90% of robins were individually colour-banded, so we could account for variation among individual birds when analysing differences between forest fragments (see below). We monitored all breeding pairs in the 13 smaller fragments each year, and selected a minimum of five pairs in the two larger fragments (with the constraint that these pairs had to be >200 m from the forest edge to avoid the edge habitat that constituted only a small portion of these large fragments).

To determine each colour-banded pairs nesting status we followed pairs for at least 30 min each week from late August to late February. This intensive search effort allowed us to estimate approximate laying dates for each nest. We determined the status of nests (incubation, brooding or failure) by observing parental feeding behaviour near nest sites, as most nests were too high (>10 m) to observe the contents without considerable disturbance. During incubation, males feed females away from the nest but fly directly to nests when feeding nestlings. We checked each nest close to the day of fledgling (1–4 days) to determine nest outcome, and for successful nests, counted the number of young (1–3) fledged.

2.2. *Invertebrate biomass*

Powlesland (1981) reported that New Zealand robins spend 90% of their foraging time on or within 2 m of the ground. They search predominately for ground invertebrates in leaf litter either visually or by flushing prey using foot-trembling and wing and tail-flicking motions. Consequently, we indexed food availability using continuous-kill pitfall traps, a common method for sampling surface-active invertebrates (Southwood, 1994). We indexed each robin pair's food availability using a set of six pitfall traps (in 3 × 2 grid at 10 m spacing) placed in the centre of their territory. Pitfall sites were created using sleeves of PVC pipe (75 × 150 mm) inserted into the ground until the lip was flush with the forest floor. A plastic cup (75 × 85 mm) filled two-thirds with ethylene glycol was placed within each sleeve. An aluminium cover (30 × 30 cm), approximately 2 cm above the grounds surface, covered each trap to prevent rainfall, leaves and twigs from falling into the trap. We emptied pitfalls every six-weeks, resulting in 12 six-week sampling periods over three years and 398 samples (2388 pitfalls) from 72 different robin territories. All invertebrates collected were considered to be robin food except for the larger (>2 cm) carabid beetles as robins generally ignored these individuals (Powlesland, 1981, R. Boulton pers. obs.). Samples were dried at 60 °C for 36 h, and dry weight used as the index of food availability (BIOMASS = invertebrate dry weight collected per territory over six-weeks).

2.3. *Predator density/activity*

Ship rats (*Rattus rattus*) are known to be the main nest predator of North Island robins in podocarp–broadleaf forests (Brown, 1997), so we used footprint tracking tunnels to index rat density (Innes et al., 1995; Gillies and Williams, 2001). The proportion of tunnels tracked in 24 h has been shown to be a good index of rat density in podocarp–broadleaf forest (Brown et al., 1996), and may reflect changes in foraging activity. We used the standard inter-tunnel spacing of 50 m, but positioned tunnels in grids rather than transects due to space constraints in small fragments. We positioned 16 tunnels in fragments 5–15, nine tunnels in fragments 3–4, and five tunnels in fragments 1–2 (one central tunnel). We distributed tunnels throughout fragments 1–13, and in fragments 14–15 we placed the grids in the areas where robins were sampled (Fig. 1 and Table 1). All tracking tunnels were baited with a pea-sized portion of peanut butter and left over a single night every 4–6 weeks (rat tracking rate = tunnels tracked in 24 h/tunnels available). We baited the tracking tunnels 16 times during the study, resulting in 192 tracking grids sampled.

2.4. *Statistical analyses*

2.4.1. *Nest survival*

We modelled daily nest survival rates using the generalised linear modelling approach developed by Shaffer (2004). We fitted logistic exposure models specifying a binomial error distribution and a logit-link function using PROC NLMIXED (Version 9.1 SAS Institute, 1999). We initially included female identity as a random effect to assess whether the apparent effects of any predictor variable were due to confounding effects of the same female being associated multiple times with similar values of a predictor variable. However, we could not fit two fixed effects to the data and obtain model convergence. We therefore modelled each variable potentially affecting nest survival individually, with and without the female included as a random effect, to check that the important effects identified were not due to confounding effects of individual variation among females. We then compared a more complex set of candidate models excluding the random effect.

2.4.2. *Explanatory variables*

We investigated the effects of two landscape variables and three habitat variables on robin daily nest survival rates. The two landscape variables were: (1) individual fragment size ha (SIZE) and (2) index of functional patch connectivity (IFPC). The three habitat variables were: (3) invertebrate biomass g (BIOMASS), (4) rat tracking rate (RTR) and (5) grazing intensity (GRAZED = fragment visited by domestic livestock). Due to variation in invertebrate biomass and rat tracking rates between sampling years and months, each nesting attempt was assigned a measure of invertebrate biomass and rat tracking rate that best corresponded to the time of the nesting attempt. There was no autocorrelation between the landscape and habitat variables (Boulton, 2006). Values for SIZE, IFPC and BIOMASS were log-transformed because of their skewed distributions.

2.4.3. *Candidate models*

Armstrong et al. (2002) demonstrated the importance of nest age and time of year in robin nest survival models. Therefore, before modelling nest survival and the above explanatory variables we first considered time-specific effects of nest age and date on nest survival rates. We found no evidence that daily nest survival varied in a linear or quadratic trend across the breeding season, but nest age (0–40 days old) had a significant effect on daily survival probability and the strength of this effect varied among the three sampling years. We included nest age, year and their interaction in all candidate models {YR*AGE}. We examined whether any of the landscape or habitat variables influenced robin nest survival using an information theoretic approach (Burnham and Anderson, 2002) and constructed candidate models consisting of each variable by itself and then each landscape variable in combination with each habitat variable. This approach kept the number of candidate models to a manageable number, and allowed us to assess whether any apparent effects of landscape variables could be accounted for by the measured habitat variables. In addition to these models, we constructed a global model that included all effects considered in other models.

We compared models based on Akaike's information criterion corrected for small sample size bias ($\mathrm{AIC_c}$) (Burnham and Anderson, 2002), and used the effective sample size (n = total number of days a nest is known to survive + the number of intervals that end in failure, Rotella et al., 2004) when making this correction. After selecting the best model, we derived estimates for daily survival rate and overall nest survival based on the parameter estimates produced by this model. We examined the best model graphically, plotting nest survival as a function of the important predictor variables using values spanning our sample range while holding other predictor variables at their mean values. The delta method (Seber, 1982) was used to obtain approximate standard errors and confidence intervals for these derived estimates. We defined nest survival as the probability of a nest surviving from clutch completion to fledging, hence we estimated the probability of a nest surviving for 40 days, the approximate time from the end of laying to fledging in North Island robins.

2.4.4. *Fledgling number*

We assessed the effect of invertebrate biomass on the number of fledglings produced per successful nest using generalised linear mixed modelling with the SAS GLIMMIX macro (Littell et al., 1996). We treated the number of fledglings (minus one) as a Poisson variable with a log-link function, and included individual female identity as a random effect.

3. Results

3.1. *Estimates of nest survival*

We monitored the fate of 203 North Island robin nests across three breeding seasons, resulting in an effective sample size of 2784. The daily nest survival probability was estimated to be 0.971 (SE 0.003) from the constant model, resulting in a 31.5% (25.1–38.1%) chance of surviving the 40-day period from incubation to fledging. Estimating nest survival rates from the constant-survival model when there are significant effects of predictor variables will result in some degree of bias (Shaffer and Thompson, 2007). However, we present this result for comparison with other studies and present accurate survival rates below using the best model estimates.

We were unable to obtain model convergence when we included female identity as a random effect with more than one predictor variable, restricting the analysis to models with single predictor variables. However, the important result is that nest age, invertebrate biomass, and fragment size are still shown to affect daily nest survival when variation among individual females is accounted for (Table 2).

Nest survival rates increased substantially with nest age in 2002–2003, whereas a much smaller increase occurred in the other two years (Fig. 2). Of the models considered, four received substantial support with Δ_i values $\leqslant 2$ (Table 3). Under the best model, the daily survival of robin nests was a function of the interaction between year and nest age plus invertebrate biomass and fragment size.

When invertebrate biomass was added to the model {YR*AGE}, it improved the model considerably, with a decrease of 2.166 $\Delta\mathrm{AIC_c}$ units (Table 3). The estimated effect of invertebrate biomass was positive, meaning nest survival increased with invertebrate biomass (Table 4). The addition of fragment size to the best model also improved the model (a decrease of 0.555 $\Delta\mathrm{AIC_c}$units). The effect was negative, with reduced nest survival in larger forest fragments, but the 95% confidence

Table 2 – Comparative rankings of simple models for daily survival of North Island robin nests with (*) and without female included as a random effect

Model[a]	K[b]	$\mathrm{AIC_c}$[c]	Δ_i[d]	w_i[e]	Model*	K	$\mathrm{AIC_c}$	Δ_i	w_i
AGE	2	599.095	0.000	0.722	AGE	3	600.859	0.000	0.434
SIZE	2	603.823	4.728	0.068	BIOMASS	3	603.150	2.291	0.138
BIOMASS	2	604.030	4.935	0.061	SIZE	3	603.777	2.918	0.101
YR	3	604.727	5.632	0.043	CONSTANT	2	603.976	3.117	0.091
CONSTANT	1	604.743	5.648	0.043	GRAZING	3	604.427	3.568	0.073
GRAZING	2	604.884	5.789	0.040	YR	4	604.676	3.817	0.064
IFPC	2	605.754	6.659	0.015	IFPC	3	604.827	3.968	0.060
RTR	2	606.028	6.933	0.023	RTR	3	605.750	4.891	0.038

Models were fitted using the logistic exposure method with a binomial error term and logit-link function.

[a] Predictor variables taken to affect daily nest survival rate under the model: AGE, number of days since laying; YR, sampling years 2002/03, 2003/04, 2004/05; SIZE and IFPC, see Table 1; GRAZING, fragment visited by domestic livestock; BIOMASS, dry eight (g) of invertebrates collected on the robin pair's territory during 6-week period when clutch laid; RTR, proportion of tracking tunnels visited by rats in 24 h period corresponding to each nesting attempt in a forest fragment.

[b] Number of parameters in model.

[c] Akaike's information criterion corrected for small sample sizes.

[d] Difference in AIC value from that of the best model.

[e] Akaike weights, indicating the relative support for the models.

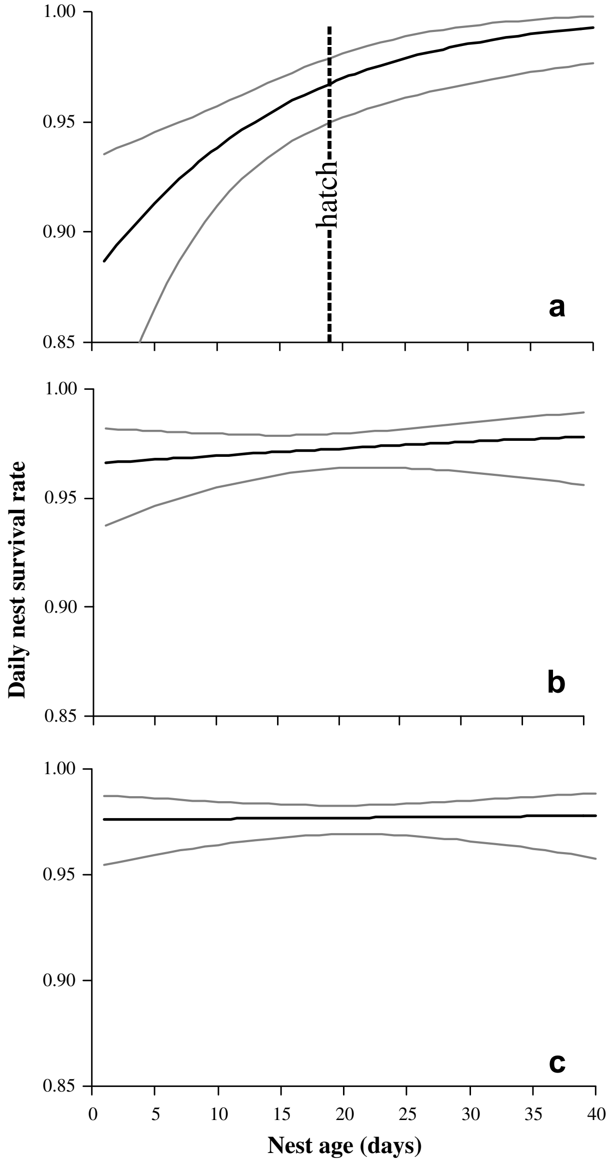

Fig. 2 – Estimated daily nest survival rates for North Island robin during (a) 2002–2003, (b) 2003–2004 and (c) 2004–2005 breeding seasons in the Benneydale region of New Zealand. These estimates are derived from the model {YR*AGE + SIZE + BIOMASS} (Table 2), with $\log_{10}$ fragment size and $\log_{10}$ invertebrate biomass set at the mean values. 95% confidence intervals were obtained using the delta method (Seber, 1982).

Table 3 – Comparison of models for factors affecting daily nest survival rates of North Island robins in forest fragments over three years

Model[a]	K	AIC$_c$	Δ_i	w_i
YR*AGE[b] + SIZE + BIOMASS	8	592.637	0.000	0.247
YR*AGE + BIOMASS	7	593.189	0.552	0.187
YR*AGE + IFPC + BIOMASS	8	593.691	1.055	0.146
YR*AGE + SIZE	7	594.558	1.921	0.094
YR*AGE	6	595.355	2.718	0.063
YR*AGE + GRAZING	7	595.853	3.216	0.049
YR*AGE + IFPC	7	595.993	3.356	0.046
YR*AGE + SIZE + GRAZING	8	596.283	3.646	0.040
YR*AGE + SIZE + RTR	8	596.569	3.932	0.035
YR*AGE + RTR	7	596.823	4.186	0.030
YR*AGE + IFPC + GRAZING	8	596.926	4.289	0.029
YR*AGE + IFPC + RTR	8	597.743	5.106	0.019
Global model[c]	11	598.323	5.686	0.014

a See Table 2 for explanation of variables.
b Includes main effects of year and age as well as the interaction among these variables.
c Includes all variables considered in other models.

Table 4 – Parameter estimates for the best logistic exposure model {YR*AGE + SIZE + BIOMASS} of daily survival rate for 203 North Island robin nests

Parameter[a]	Estimate	SE	95% CI	
			Lower	Upper
Intercept (YR1)	2.215	0.407	1.414	3.016
YR2	1.358	0.475	0.423	2.293
YR3	1.719	0.484	0.766	2.671
AGE	0.074	0.021	0.032	0.116
YR2*AGE	−0.061	0.027	−0.114	−0.008
YR3*AGE	−0.071	0.026	−0.122	−0.019
BIOMASS	0.884	0.444	0.009	1.758
SIZE	−0.184	0.115	−0.409	0.043

a See Table 2 for explanation of variables.

interval overlapped zero (Table 4). Overall nest survival rates derived from the best model using an average $\log_{10}$ invertebrate biomass (0.106 g) and $\log_{10}$ fragment size (1.78 ha) and extrapolated over the 40-day nesting period were 0.193 (SE 0.082) for 2002/2003, 0.328 (SE 0.082) for 2003/2004, and 0.393 (SE 0.083) for 2004/2005.

To evaluate the effect of fragment size and invertebrate biomass on nest survival, we first derived estimates of daily survival probability from the best model across a range of fragment sizes and biomass measurements (in the range recorded within the study). We then obtained the estimated nest survival (probability of surviving 40 days) from the product of the 40 daily nest survival rates (Fig. 3).

3.2. *Fledgling number*

An average of 1.89 nestlings (SE = 0.078) fledged from the 82 successful nests where we could confidently quantify the number of fledglings. The number of fledglings was not significantly related to the invertebrate biomass on the pair's territory during the nesting attempt (log-link intercept = −0.109, SE = 0.110, estimate = −0.368, SE = 0.391, P = 0.353).

4. Discussion

Our results suggest that North Island robins experienced food shortages at least some of the time, given the finding that nest survival correlated positively with invertebrate biomass. With no strong support for a relationship between fragment size and nest survival this reduction in invertebrate biomass

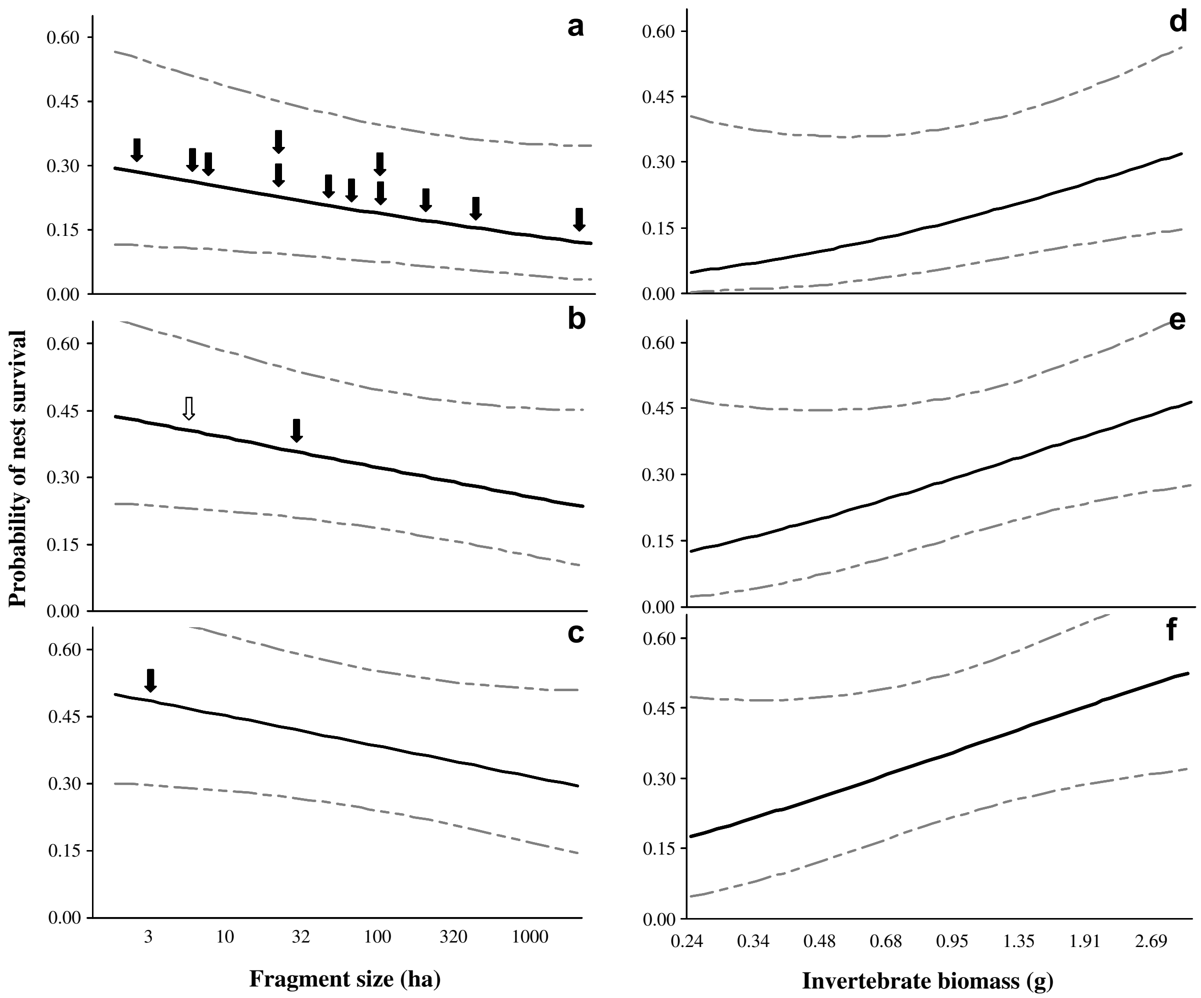

Fig. 3 – Effect of fragment size (a–c) and invertebrate biomass (d–f) on the overall survival of robin nests during 2002–2003 (a & d), 2003–2004 (b & e) and 2004–2005 (c & f). Estimates were calculated from the model {YR*AGE + SIZE + BIOMASS} using the mean $\log_{10}$ biomass in the fragment size functions and the mean $\log_{10}$ fragment size for the biomass functions, and are plotted on a log-scale. 95% confidence intervals were obtained using the delta method (Seber, 1982). Black arrows in graph (a) indicate actual fragment sizes in the study during 2002–2003, additional black arrows in the following two years represent new fragments, while the white arrow indicates a fragment where robins were no longer breeding after the first season.

appears to vary at the territory scale. Without similar nest survival studies in fragmented landscapes of New Zealand, we cannot say whether other New Zealand species show similar responses to habitat fragmentation or that North Island robins show the same response in other landscapes. A similar study on a closely related species, the Eastern yellow robin (*Eopsaltria australis*) of Australia found reduced food abundance in small fragments but no decrease in nest survival (Zanette et al., 2000; Zanette and Jenkins, 2000), concluding that area-sensitivity in this species was caused by nest predation at a large fragmented landscape scale. Although we found a negative relationship between fragment size and nest survival this result was not strongly supported. Similarly, other studies within Australia have tended to find no clear relationship between fragment size and nest survival (Taylor and Ford, 1998; Matthews et al., 1999; Walters et al., 1999; Brooker and Brooker, 2001; Cooper et al., 2002), although two studies found higher nest survival in large compared to small fragments (Major et al., 1999b) and an unfragmented compared to a fragmented landscape (Luck, 2003). These studies and the results presented here demonstrate the complexity of drawing broad conclusions across different species and ecological systems.

If robins were food limited, we might expect nestling starvation to be higher on those territories with low biomass, resulting in a positive correlation between the number of nestlings fledged and invertebrate biomass (Strong et al., 2004). We did not detect such a relationship in this study. There are three reasons why low invertebrate biomass might result in complete nest failure, thus creating low nest survival rather than reducing the number of young fledged from successful nests. Firstly, due to the small clutch size (mean 2.60) of North Island robins (Powlesland et al., 2000), a reduction due to starvation could result in complete nest failure (Luck, 2002). Secondly, the risk of nest predation may be increased when food availability is low because of increased begging by nestlings (Leech and Leonard, 1997). Thirdly, adults foraging on low biomass territories may need to leave nests unattended more frequently (Zanette et al., 2000), potentially increasing the risk of nest predation (Arcese and Smith, 1988).

Avian nests predators, particularly the large omnivorous members of the Corvidae Family, are more likely than mammalian nest predators to respond positively to habitat fragmentation, increasing in abundance, activity, and species richness (Chalfoun et al., 2002). The absence of these avian predators from the native New Zealand avifauna may account for the lack of a negative relationship between fragment size and nest survival. Although exotic Australian magpies (*Gymnorhina tibicen*) were relatively common within the study region, they tended to keep to the open pastures and were never located >50 m into any forest fragment. They seem unlikely to be important predators of robin nests given that two recent studies in the region found only a small proportion of nests failed due to magpie predation (1/18 lethal events, Boulton and Cassey, 2006; 1/22, Morgan et al., 2006). The other major cause of reduced nest survival in forest fragments outside of New Zealand is brood parasitism (Brittingham and Temple, 1983; Robinson et al., 1995). Although the two cuckoo species of New Zealand (*Eudynamys taitensis* and *Chrysococcyx lucidus*) have the potential to be diurnal nest predators (J. Briskie pers. obs.) they do not parasitise robin nests (Gill, 1983; Briskie, 2003) and were relatively uncommon within this system, all but eliminating this potentially negative impact on nest survival.

Ship rats are major predators of robin nests within New Zealand (Brown, 1997; Brown et al., 1998), yet rat tracking indices were poor predictors of nest survival in this study. Tracking indices have been shown to be well correlated with actual rat population densities in situations with moderate to high rat densities (Blackwell et al., 2002), and Armstrong et al. (2006) found that changes in robin nest survival over five years at a site mirrored changes in rat tracking rates associated with changes in the predator control regime. Most of the fragments recorded 70–100% rat tracking rates, with little variation between months or years. This is substantially higher than in the tawa-podocarp forest in the Blackwell et al. (2002) study, and these results show none of the variation observed in rat tracking indices after initiation of intensive management programs (<10–100% indices, Armstrong et al., 2006). Alternatively, because tracking rates are likely to be susceptible to rodent activity levels research on the effects of habitat fragmentation on rat behaviour needs further consideration. These effects are currently unknown, but the generally variable and adaptive nature of wild ship rats (Innes and Skipworth, 1983; Hooker and Innes, 1995; Innes, 2001) suggests that shifts in behaviour with fragmentation are quite plausible. Such behavioural responses are worth investigating in New Zealand or any other area subject to impacts of exotic mammalian predators.

Robin nest survival increased considerably with nest age during the first breeding season. We would generally expect the opposite pattern for altricial species, as increased parental activity at the nest during the nestling period should increase nest predation (Skutch, 1949). Other studies have also found an increase in nest survival with age (Martin, 1992; Roper and Goldstein, 1997), and Martin et al., 2000 demonstrated that this effect was caused by poor nest-sites incurring rapid predation. Once nest-site effects were taken into account, predation showed a strong proximate increase with parental activity during the nestling stage. Vulnerable robin nest-sites are almost certainly located quickly, as demonstrated by Brown (1997) when ship rats depredated 49% of North Island robin and tomtit (*P. toitoi*) nests within five days of clutch completion. The inability to choose 'safe' nesting sites from mammalian predators probably highlights the robin's naïve evolutionary history in the complete absence of mammalian predators (Holdaway, 1989). The inconsistent predation levels between nest ages imply a complex interaction between nest predator abundance and assemblages between sites and years.

In summary, neither fragment size nor connectivity appeared to influence robin nest survival negatively, potentially because of the already high impact that mammalian nest predators have in this unique New Zealand ecosystem. The critical factor affecting robin nest survival within one of the largest intact podocarp–broadleaf forests remaining in the North Island (78,000 ha) is nest predation. With 60% nest survival with predator control and 25% without predator control (Powlesland et al., 1999; Armstrong et al., 2002). Food availability appeared to be limiting nest survival within our study, but distinguishing between nest failures caused by predation or nestling starvation was not possible. Nestling starvation can lead to predation, with the two sources of mortality operating simultaneously (Högstedt, 1981), while complete brood failures due to starvation would be indistinguishable from predation for inaccessible nests (Luck, 2002). These results highlight the need for food limitation to be considered in habitat restoration projects. Food supplementation experiments could provide valuable information about the processes underlying food limitation within this system, and reveal the potential reproductive output achievable by these birds.

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