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Research Papers

Natal Dispersal in the North Island Robin (*Petroica longipes*): the Importance of Connectivity in Fragmented Habitats

Dispersion natale chez le Miro de Garnot (*Petroica longipes*) : importance de la connectivité dans les habitats fragmentés

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ABSTRACT. Natal dispersal is an important component in bird population dynamics and can influence the persistence of local and metapopulations. We examined natal dispersal in the North Island robin (*Petroica longipes*), a sedentary bird species distributed in a fragmented forest habitat on Tiritiri Matangi Island, New Zealand. Earlier studies have shown that the only dispersal phase in this species takes place when juveniles leave their natal patch, and that juveniles who fail to find suitable habitat do not survive their first winter. These findings suggest that natal dispersal behavior in this species is important for population viability. We found that juveniles were highly affected by the fragmentation of the forest habitat, with patch occupancy being positively correlated with degree of connectivity of the landscape. Most juvenile movements (52.1%) were observed between patches that were separated by less than 20 m. Juvenile North Island robins were found in all forest habitat types, including young and open stands. This suggests that the juveniles are not dependent on old forest stands during their dispersal phase. Based on these findings, we suggest that management of this regionally-threatened species should focus not only on maintaining populations in occupied patches and increasing the habitat quality of these patches, but also on protecting existing forest patches acting as corridors and creating new forest habitat among patches. This would greatly increase the viability of the species' metapopulations by increasing dispersal success between both unoccupied patches and subpopulations. Additionally, increased connectivity between forest patches could also be expected to increase the probability of successful dispersal of other threatened native species, many of which are also sensitive to the high degree of fragmentation of their habitats.

RÉSUMÉ. La dispersion natale est un élément important de la dynamique des populations d'oiseaux et elle peut avoir de l'influence sur la pérennité des populations locales et des métapopulations. Nous avons étudié la dispersion natale chez le Miro de Garnot (*Petroica longipes*), un oiseau sédentaire qui occupe des habitats forestiers fragmentés de l'île de Tiritiri Matangi, en Nouvelle-Zélande. Selon des études antérieures, la seule période de dispersion chez cette espèce survient lorsque les jeunes quittent leur aire natale, et les jeunes qui ne trouvent pas d'habitats appropriés ne survivent pas à leur premier hiver. Ces éléments indiquent que, chez cette espèce, la dispersion natale est importante pour la viabilité des populations. Nous avons trouvé que les jeunes étaient grandement affectés par la fragmentation des habitats forestiers, l'occupation des parcelles étant corrélée positivement avec le niveau de connectivité du paysage. La plupart (52,1 %) des déplacements des jeunes se sont produits entre des parcelles séparées de moins de 20 m. Les jeunes Miros de Garnot ont été observés dans tous les types d'habitats forestiers, dont des peuplements jeunes et ouverts. Ceci suggère que les jeunes ne dépendent pas des forêts matures durant leur dispersion. D'après nos résultats, nous proposons que la gestion de cette espèce menacée à l'échelle régionale se consacre non seulement au maintien des populations dans les parcelles occupées et à l'amélioration de la qualité des habitats de ces parcelles, mais aussi à la protection des parcelles forestières qui font office de corridors et à la création d'un nouvel habitat forestier entre les parcelles. Ceci augmenterait grandement la viabilité des métapopulations de l'espèce, par le biais d'une hausse du succès de dispersion entre les parcelles inoccupées et les sous-populations. De plus, on peut s'attendre à ce qu'une connectivité plus grande entre les parcelles forestières contribue à une meilleure dispersion d'autres espèces indigènes menacées, parmi lesquelles plusieurs sont sensibles à la fragmentation élevée de leur habitat.

Key Words: *natal dispersal; connectivity; habitat quality; intraspecific competition; habitat use; fragmentation; corridors; dispersal order; isolation; Petroica longipes*

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INTRODUCTION

Habitat fragmentation is a major cause of population decline and species extinction (Bender et al. 1998, Hames et al. 2001, Barbosa and Marquet 2002, Smith and Hellmann 2002). Fragmentation affects the spatial distribution of populations and may create a metapopulation structure in which subpopulations occupying remnant patches are linked only through the dispersal of individuals (Opdam 1991, Travis and Dytham 1998, Fleishman et al. 2002). The long-term survival of a metapopulation and its associated subpopulations is dependent on the interpatch dispersal of individuals, which increases genetic diversity in the different subpopulations and allows recolonization after local extinction (Charlesworth and Charlesworth 1987, Hanski 1999). The probability of interpatch dispersal in a fragmented landscape is a function of the behavioral or physical ability of a species to disperse through the habitat between the fragments (Ims 1995) as well as the size and isolation of the patch (Hansson 1991, Hames et al. 2001, Smith and Hellmann 2002). With reduced connectivity between habitat patches, and thus reduced movement of individuals, each subpopulation is at a higher risk of going extinct (Saunders et al. 1991).

Natal dispersal is one of the primary factors moving individuals between subpopulations within a metapopulation. This is the process by which juveniles move away from their natal areas in search of a space in which they can reproduce (Miller et al. 1997, Kennedy and Ward 2003). This dispersal process may be initiated by intraspecific competition (Lambin et al. 2001) and may have evolved as a way to avoid inbreeding (Perrin and Goudet 2001). The success of natal dispersers can have a large impact on subpopulations as well as on the growth and persistence of the metapopulation as a whole (Withey and Marzluff 2005).

Conspecific interaction is one of the major factors driving natal dispersal (Matthysen 2005) because of its influence on the initiation, length, and success of the dispersal phase. Because the occupants of an area will defend it against intruders, every interaction between a dispersing animal and the holder of a territory may prolong the dispersal phase (Armstrong 1995, Lambin et al. 2001). In a habitat patch with a high density of conspecifics and a high frequency of aggressive intraspecific interactions, a higher proportion of dispersing juveniles will be forced to continue searching for a territory, compared with juveniles that encounter a patch with a lower density of conspecifics (Sutherland et al. 2002). The stress from conspecific interactions for the natal dispersers may be further increased by reduced habitat availability and longer dispersal distances because of habitat fragmentation. This accumulative effect should be most severe when the species in focus is a poor disperser and the habitat is highly fragmented.

Much of New Zealand has been deforested, and many of the remaining lowland forests are fragmented and isolated (Myers 1923, McGlone et al. 2005). Despite intensive conservation work and management involving native New Zealand birds (McLennan and Potter 1992, Innes et al. 2004), many species exist in a metapopulation structure because of habitat fragmentation. The North Island robin (*Petroica longipes*) is one of these species. A forest bird endemic to New Zealand's North Island, this species declined dramatically during the 1900s because of habitat loss and the introduction of exotic mammalian predators such as rats, stoats, and cats. The robin is a sedentary and highly territorial species in which adult birds are reported to have poor dispersal abilities and to move over only short distances (Higgins and Peter 2003). Juvenile North Island robins have generally been reported to move only short distances as well, but some studies found movement over several kilometers (Oppel and Beaven 2004). However, there is little detailed data on natal dispersal behavior and habitat use in fragmented areas. It is known that juveniles that do not find an area to occupy during their first winter do not survive (Armstrong et al. 2000, Berggren et al. 2004). Consequently, natal dispersal in the robin is a crucial stage in the life of the individual and for the dynamics of the population.

We studied natal dispersal in a population of North Island robins living in the fragmented forest of Tiritiri Matangi Island, east of the Whangaparoa peninsula in the North Island of New Zealand. In our study we examined the effects of landscape and intraspecific factors on juvenile dispersal behavior to address the following questions.

1. Does habitat use vary between dispersing juveniles and adult robins? We expect that juveniles have the same habitat preferences in vegetation age and vegetation cover as adults do. This is because the basic habitat requirements should be the same for juveniles and adults with respect to predator avoidance,

e.g., predator attacks from above the canopy (Baker-Gabb 1981), and food availability, e. g., insect diversity and abundance related to the higher dead wood load in older forest fragments (Warburton et al. 1992).

2. How do patch quality, patch size, and local and landscape connectivity correlate with juvenile presence in a forest patch? We expect that an increase in a patch's quality, i.e., forest age, size, and connectivity, will increase the number of juveniles found in a patch as a result of this species' preference for old forest (Armstrong and Ewen 2002). Patch size and connectivity have been shown to increase the number of immigrants because of the increased likelihood of individuals finding and reaching the patch (Hansson 1991, Saunders et al. 1991) and larger areas for occupation within the patch (Saunders et al. 1991, Armstrong et al. 2000).

3. Does the density of conspecifics in an area influence the distribution of the dispersing juveniles? We expect that the juveniles that disperse late in the season and are faced with higher bird densities in patches will move to less preferred habitats. This is because the study population has a limited number of patches in which to to establish a territory (Armstrong et al. 2000, Berggren et al. 2004), and those patches fill up as the season progresses. Because North Island robins prefer old forest (Armstrong and Ewen 2002), juveniles should first move to patches with old forest that are well connected to minimize the dispersal cost (Johnson and Gaines 1990). As these patches become full and territorial encounters with established birds increase, juveniles should be forced out of occupied areas and move to a new patch (Lambin et al. 2001, Berggren et al. 2004).

METHODS

Study site

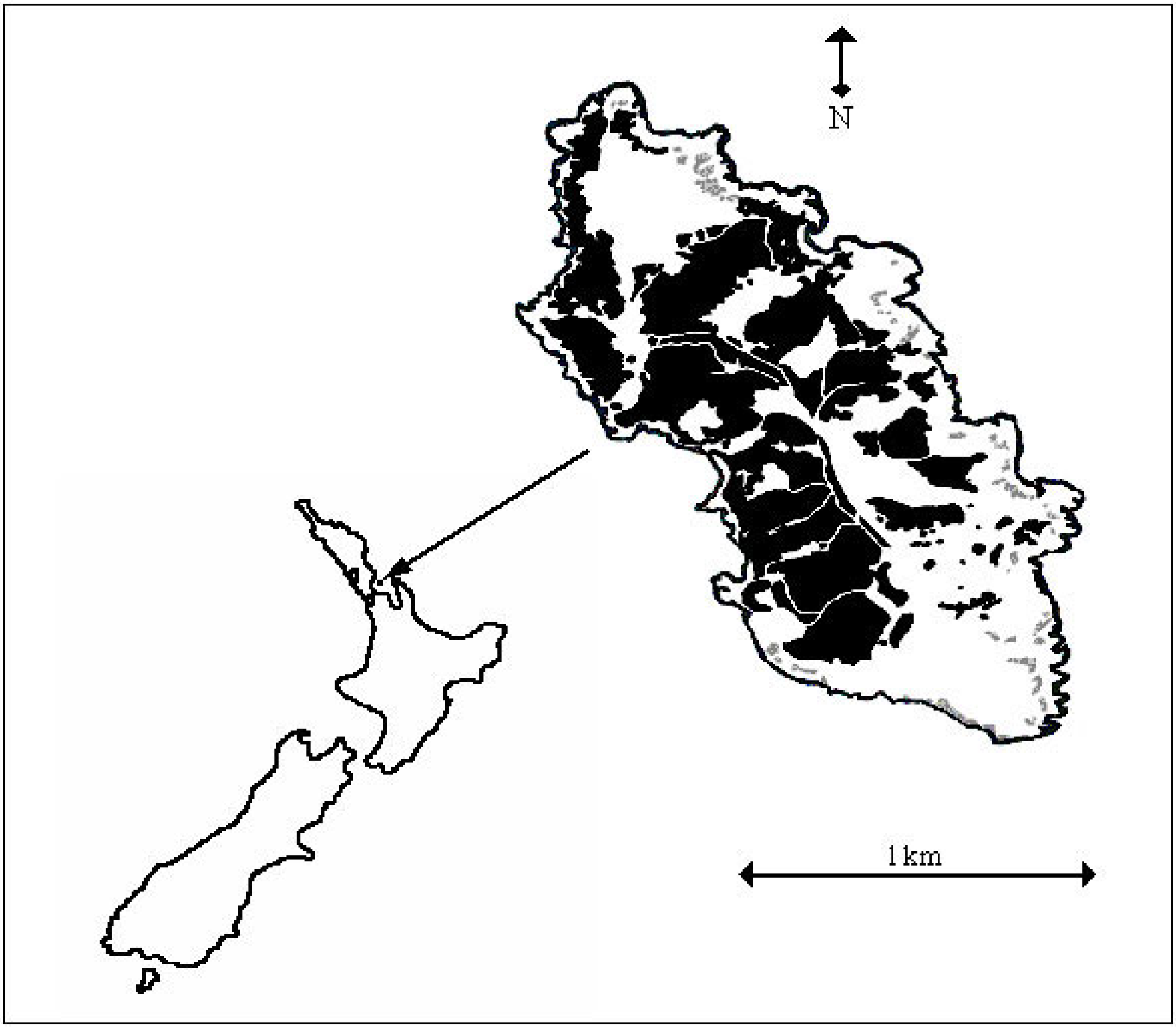
Tiritiri Matangi Island (36°36'S, 174°53'E) is a 220-ha nature reserve located 3.5 km offshore and 28 km north of Auckland, New Zealand. The island was originally covered by broadleaf forest that was largely cleared for farming by Maori and European settlers. In 1970, when farming stopped, only 13 ha of forest remained in fragmented, isolated patches (Armstrong et al. 2002). Extensive replanting of native forest was undertaken between 1983 and 2002, and today forest patches of varying sizes (0.018–9.2 ha) cover 60% of the island's area (Fig.1). Thus, the age of current forest patches on the island varies from recently planted (2–23 yr) to the old remnant stands spared by the early farmers. Although some forest patches are linked via habitat corridors or stepping-stone habitats, many are still surrounded by a matrix of grasslands that may contain solitary trees, most commonly the cabbage tree (*Cordyline australis*), and areas of flax (*Phormium tenax*).

Study species

The North Island robin is a small (26–32 g), endemic, sedentary forest bird found on New Zealand's North Island. It was once distributed across the entire North Island, but its range has decreased dramatically in the last decades (Fleming 1950, Higgins and Peter 2003). Today the species is patchily distributed in the center of the North Island and on a few offshore islands (Higgins and Peter 2003). The conservation status of the New Zealand robin is "regionally threatened," and it is currently not listed in any IUCN threat category. This classification is based on the assumption that the North Island robin is a subspecies, and does not take into account morphological and distributional data that suggest that the North Island and South Island robins (*Petroica australis*) are two separate species (Holdaway et al. 2001).

Earlier studies have shown that robins prefer old forest to regenerating forest, indicating that territories in older forest areas are of higher quality than areas with younger forest (Armstrong and Ewen 2002). Because robins usually remain in the same territory until they die, individuals of this species tend to be highly sedentary once they have settled after the juvenile dispersal phase (Armstrong et al. 2000). The breeding season begins in September and ends in January; pairs can lay up to three clutches per season. Eggs are incubated for 17–20 d, and juveniles fledge at about 17 d of age. Parental food provisioning decreases approximately 30 d after fledging, and at this time juvenile robins begin leaving their parents' territory to find their own breeding territory (Berggren 2006).

Fig. 1. Map of Tiritiri Matangi Island (36°36’S, 174°53’E), New Zealand.



The map shows; □ open matrix (grass and low to medium high vegetation), ■ censused forest habitats (96.5% of the forest on the island), and ▨ non-censused forest habitat (3.5% of the forest on the island).

The main predators of the North Island robin are the native owl (*Ninox novaeseelandie*) from the interior of the forest and the Australasian harrier (*Circus approximans*) from the surrounding matrix (Baker-Gabb 1981, Brown et al. 1998). Whereas owls hunt within the forest patch, harriers prey upon robins when they are visible through the canopy or when individuals cross the matrix between fragments; harriers have been seen circling close to canopy openings to localize robin song transmitted from recorders (A. Wittern and Å Berggren, *personal observation*). Hence, forest patches with little canopy cover may suffer increased predation risk. Also, for the robin as an open-cup nester, a more closed canopy would probably increase the likelihood that chicks would survive heavy rains and storms. The latter is supported by findings of dead chicks in exposed nests after heavy rain and cold weather (A. Witttern and Å. Berggren, *personal observation*).

Study population

During this study in the summer of 2003–2004, the size of the population of North Island robins on Tiritiri Matangi Island was 87 adults, with 74 of these in pairs. One hundred and ten juveniles were produced during the breeding season, and, with the ongoing banding scheme, 98% of the birds in the population were individually color-banded. Of the 110 robin fledglings produced during the breeding season, 34 juveniles were alive and observed dispersing before the end of the study in February 2004 and were incorporated into the analyses. Of these fledglings, two were foster-fed by unrelated males, a behavior previously observed in this species (Armstrong et al 2000, Berggren 2006). Because foster-fed juveniles also go through the natal dispersal phase, these individuals were included in the analyses.

During the breeding season, the territorial boundaries, nesting sites, and breeding success of all the pairs in the population were recorded. The chicks were individually color-banded in the nest when they were between 9 and 15 d old. If a chick was not banded at this stage, it was later captured and banded while still in the parents' territory. The capture was made using a hand net or a manually triggered spring trap after the juvenile was called in by a robin male song from a tape recorder and presented with mealworms, *Tenebrio molitor* (Armstrong 1995).

Dispersal surveys

Data on when juveniles became independent were collected by regularly visiting their natal territories at intervals of 1–5 d (see also below) around the time when they were estimated to start their dispersal, i.e., 30 d after fledging. When an exact dispersal date marking the day the juvenile left the parents' territory was unknown, this date was estimated by using the median date between the day it was last seen in its natal territory and the date it was first seen outside this territory. To examine if the dispersal process was different depending on when during the season juveniles dispersed, juveniles were categorized as being "early" or "late" depending on whether they left their natal territory before or after 14 December, which was the median dispersal date in the study.

To survey for birds outside their natal territories, researchers walked at a slow pace in a weaving pattern across the length and breadth of 51 forest fragments 0.018–9.2 ha in size (mean 1.5 ha ± 0.3) with stops at census points. Care was taken to spend an equal amount of time in each area to minimize the risk of that some areas might be more heavily surveyed than others. Census points had an in-between distance of 50 m. As an aid, we played a tape recording of a male robin's song for 60 s, which attracted any robins in the vicinity. After the tape was played, we waited for 60 s and recorded any incoming birds. This survey technique has been very successful in previous studies, with a detection rate of greater than 90% (Armstrong and Ewen 2002). In the surveys we excluded 3.5% of the forested areas on the island because they were situated on steep cliffs facing the sea and were logistically difficult to work in (see Fig. 1).

All forest patches were visited at least every 5th day. Every robin observed during surveys was identified by its band combination, and its location was determined using a Geographic Positioning System (GPS). If the density of the forest canopy prevented the GPS from accurately determining a position, the bird's location was marked on an aerial photograph (scale 1:3760). All positions were transferred to digital maps using the GIS software Ozi-Explorer (2000). The maps were created from aerial photographs of the island and revegetation maps from the island's revegetation project. These maps were controlled by ground-truthing to update data on vegetation and forest patch borders. On the resulting digitized maps, all North Island robin territory boundaries and all positions of individual birds were entered.

Collection of habitat data

To gather data on the habitats available for the dispersing juveniles, a detailed map of the island's forest patches was produced. A set of transects were created in the forested areas with a 50-m distance between the lines. Depending on the size of the patch, one to nine transect lines crossed each fragment. At every 25 m along the lines, starting from the forest edge, a mapping site with a circle of 0.03 ha (a radius of 10 m) was drawn. Within this circle we classified the vegetation into one of four types: (1) closed stands of old forest, (2) open stands of old forest, (3) closed stands of young forest, and (4) open stands of young forest. The forest was classified as "old" if it consisted of old remnant stands spared by the early farmers, and "young" if it had been planted during the islands' revegetation program. Data for the age of the forest were collected from historical vegetation maps and maps from the revegetation program. A stand was classified as "closed" if it had a canopy covering 50% or more of the area, and as "open" if canopy cover was less than 50%. One person (A. Wittern) did all the classification of the vegetation.

We used the presence and absence of individuals of the species as the dependent variable to examine habitat use, a common procedure in short-term studies of landscape ecology (Opdam 1991). To gather presence and absence data from the different areas, both juveniles and adults were recorded along the transect lines. At every mapping site we recorded if a juvenile was seen or not. Adult robin presence was measured as the presence or absence of an adult territory at the mapping site.

Forest patch characteristics and connectivity

To investigate how the pattern of juvenile presence in a patch related to variables on the landscape and local scale, the following characteristics of the 51 censused forest patches were examined by extracting data from historical vegetation records and digitized maps: (1) mean forest age in the patch, (2) forest patch size, and (3) the distance between forest patches. The distance between forest patches was used to examine the effect of connectivity between forest fragments on two scales: (1) the local scale, or the distance from one patch to its nearest neighboring forest patch, and (2) the landscape scale, the mean distance from one patch to the five closest forest patches. The forest patches were then divided into five different categories showing different degrees of landscape connectivity: 1–20 m, 21–40 m, 41–60 m, 61–80 m, and > 80 m. Within each category, the juveniles observed were calculated as the percentage of the total number of juveniles observed in all patches. The counts were not individual based, i.e., a juvenile was counted as a new observation if it reached a new patch; however, a juvenile was counted only once in each patch. The availability of patches within each category was calculated as the percentage of the total number of patches examined. From this, the number of juveniles in each connectivity class that were expected to be observed if their distribution was random was calculated by dividing the number of observations by the proportion of patch availability.

Analyses

Habitat preference was analyzed with a chi-square goodness-of-fit test comparing the observed number of juveniles and adults with the number expected; the numbers expected were estimated by multiplying the proportion of the habitat type with the total number of observations of juveniles and adults at the respective sites. Only juveniles that left their natal patch were used in analyses. To determine which landscape variables were associated with the likelihood of a dispersing juvenile occurring in a given patch, we used ordinal logistic regression (McCollagh 1980). This statistical technique is useful when dealing with response data that do not conform to normal, Poisson, or binominal distributions (Thomson et al. 1998). The model consisted of four independent landscape variables: (1) mean forest age in the patch, (2) patch size, (3) local connectivity, and (4) landscape connectivity. The number of observed juveniles in the patch was used as the dependent ordinal variable. We used a backward elimination procedure of independent variables, progressively removing nonsignificant variables (partial P to remove = 0.10). Ordinal logistic regression consistently showed a good fit of the data, i.e., lack of fit with a P close to 1. Sample sizes varied among tests because some data could not be obtained for all areas. All analyses were carried out using JMP computer software (SAS 1999).

RESULTS

Patch connectivity and forest age

Of the four landscape variables tested, three had an impact on the number of juveniles that visited the patch: landscape connectivity, patch size, and mean forest age (Table 1, Fig 2A). A patch was more frequently visited during natal dispersal if it was more connected to other patches in the landscape. Also, the number of juveniles visiting the patch was positively correlated with the mean forest age of the patch and with patch size (Fig. 2A). Local connectivity was not significantly correlated to numbers of juveniles in the patch. When we examined the distribution of juveniles during their dispersal more closely, we found that 25 of the 48 counted juveniles (52.1%) were observed in patches with an isolation of less than 20 m, whereas only nine counts (18.8 %) were made in patches belonging to the three lowest connectivity classes with distances of 41–60, 61–80, and > 80 m, resulting in a very dissimilar distribution of observed and expected presences (chi-square test, $\chi^2 = 72.9$, $n = 48$, $P < 0.01$; Fig. 2B).

Dispersal time and behavior

We found significant differences in the habitat type of forest patches in which early-dispersing juveniles were observed when compared to forest patches in which late-dispersing juveniles were seen. Patches occupied by juveniles dispersing early in the season, i.e., before 14 December, showed a higher degree of local connectivity [median and 95% CI early 3.0 m (3.0–3.0) , late 9.0 m (3.0–10.0), Mann Whitney *U* test; $Z = 2.9$, $n_{\text{patches early}} = 36$, $n_{\text{patches late}} = 6$, $P = 0.004$], and landscape connectivity (early 21.4 m ± 3.1, late 44.5 m ± 7.7, Mann Whitney *U* test; $Z = 2.1$, $n_{\text{patches early}} = 36$, $n_{\text{patches late}} = 6$, $P = 0.038$). Early dispersers tended to be found in bigger forest patches (5.0 ha ± 0.5) than were later dispersers (2.7 ha ± 1.3; Mann Whitney *U* test: $Z = 1.9$, $n_{\text{patches early}} = 36$, $n_{\text{patches late}} = 6$, $P = 0.053$). Also, the patches in which early-dispersing juveniles were found showed a higher total number of dispersing juveniles over the study period (early 4.3 ± 0.6, late 1.6 ± 1.4, Mann Whitney *U* test; $Z = 2.1$, $\mathrm{n}_{\text{patches early}} = 27$, $\mathrm{n}_{\text{patches late}} = 5$, $P = 0.033$). Forest patches in which early- and late-dispersing juveniles were observed did not differ in terms of age or the number of adult territories within them (Mann Whitney *U* test, all $P > 0.15$).

Juvenile vs. adult habitat use

The transect surveys in the 51 forest patches produced habitat data from 281 sites. Of the sites with known forest age, 70 (32.3%) were old forests or old, remnant stands and 147 (67.7%) were young, i.e., planted forests. Of the sites with old forest, 58 (82.9%) had closed canopies, and 12 (17.1%) had open canopies. The sites with young forest showed a very similar distribution of canopy cover, with 115 (78.2%) of the sites having closed canopies and 32 (21.8%) having open canopies. Canopy cover was not correlated with age of the forest (chi-square test, $\chi^2 = 0.38$, $n = 217$, $P > 0.54$).

The territories of adult robins were not randomly distributed within the island's forest habitats. As seen in Fig. 3, old forests were used more than expected, and young forest areas were avoided (likelihood ratio test, $\chi^2 = 40.9$, $n = 217$, $P < 0.001$). Adult robins also tended to have their territories in areas with more canopy cover within the patches (likelihood ratio test, $\chi^2 = 3.48$, $n = 281$, $P = 0.06$). In contrast to this, juveniles did not show differences in their habitat use (likelihood ratio test, forest age, $\chi^2 = 1.5$, $n = 217$, $P = 0.28$, canopy cover, $\chi^2 = 0.001$, $n = 281$, $P = 0.98$).

DISCUSSION

Connectivity and patch characteristics

Our results suggest that habitat isolation affects patterns of natal dispersal in the North Island robin (Table 1). More than 50% of the juveniles were observed in patches with a mean patch distance of less than 20 m, and only 10.4% of the juveniles were found in patches that were isolated by more than 60 m (Fig. 2B). The probability of juveniles visiting a patch was also affected by patch size, and the number of juveniles visiting the patch increased with increasing patch size (Table 1, Fig. 2A). This suggests that the dispersal of North Island robin juveniles may be highly affected by fragmentation. Our results support earlier suggestions by O'Donnell (1991) and Higgins and Peter (2003) that robins are reluctant to cross open areas between habitat patches.

Adult North Island robins showed a preference for establishing breeding territories in old forest and also preferred areas with more canopy cover (Fig. 3). This supports previous observations that adult

Fig. 2. Correlations between the three environmental predictors influencing natal dispersal of the North Island robin: A) patch size, B) age class, and C) patch isolation.

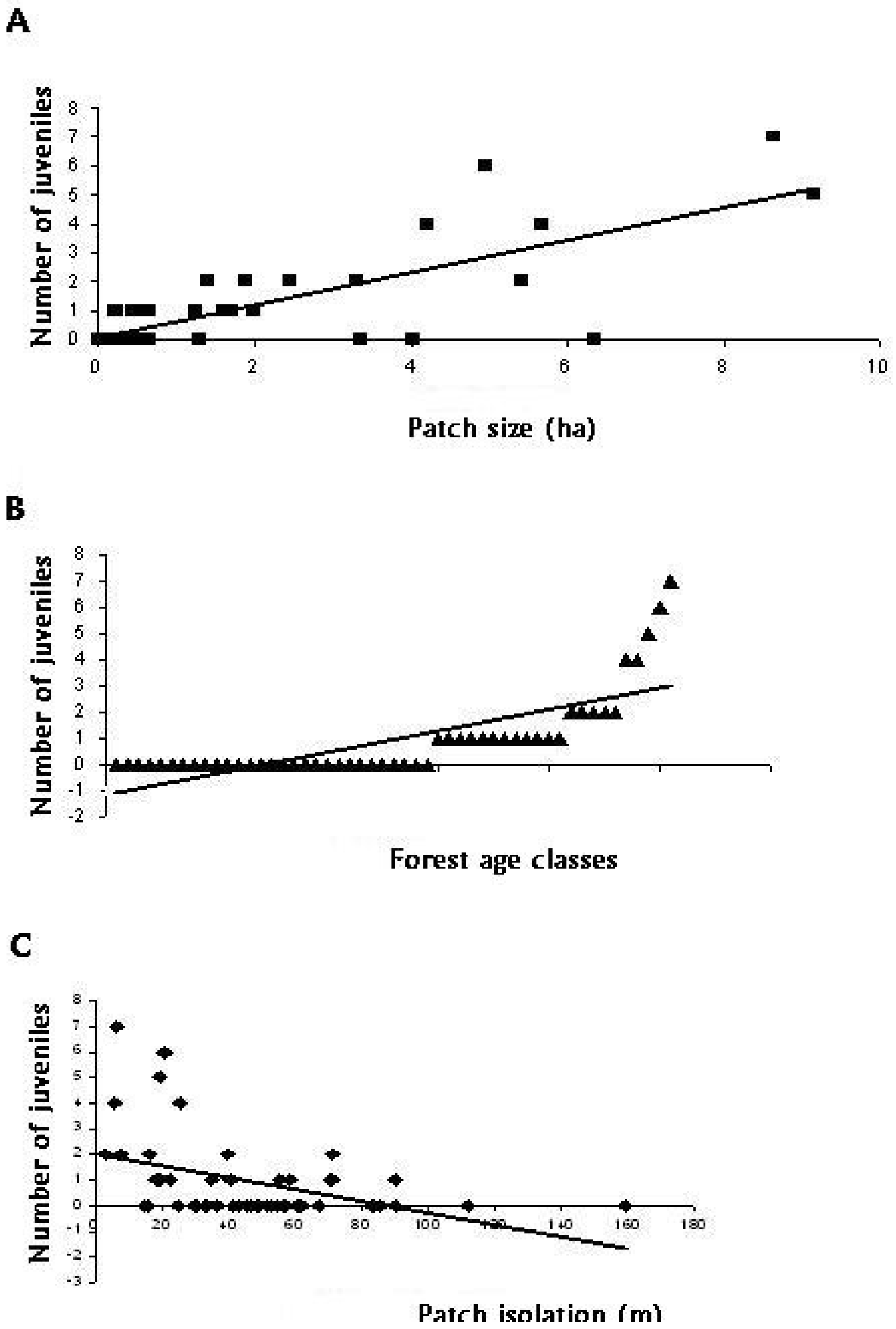
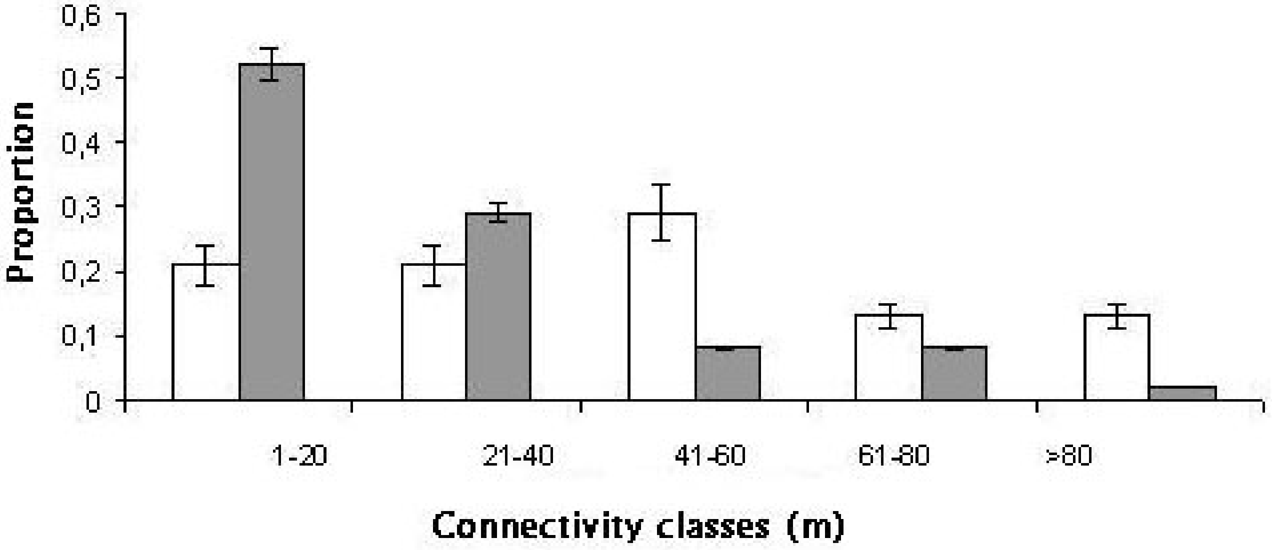


Fig. 3. Observed (dark) vs. expected (white) use of available forest patches by dispersing juvenile North Island robins. Patches are grouped based on their degree of landscape connectivity, i.e., mean distance to the five closest forest patches.



North Island robins are predominantly found in older forests and that forest age is an indicator of habitat quality for this species (O'Donnell 1991, Spurr et al. 1992, Higgins and Peter 2003). Additionally, the assumptions of the importance of canopy cover for reduced adult and chick mortality from predation and bad weather are supported by the observed preference of territory establishment in sites with more canopy cover.

During dispersal, juveniles should settle in habitats that are similar to their predispersal habitat, a process called "habitat training" (Stamps 2001). This is to save energy resources for reproduction that would otherwise be used for learning how to live in a new kind of habitat; thus adult and juvenile North Island robins should be found in similar habitats. However, we found no habitat associations for juvenile birds during the post-fledging dispersal (see also Miller et al. 1997, Anders et al. 1998). One reason for this is that normal measures of habitat quality for robins, i.e., forest age, are less important than areas that provide food and shelter from predators. A preference for old forest was found when examining the habitat preference of juveniles at the landscape scale, i.e., the patches to which the juveniles were moving (Table 1, Fig. 2B). This difference between habitat selection at the landscape scale and selection at the smaller scale within the patches could be explained by juveniles searching for high-quality patches suitable for breeding, but being unable to settle in high-quality areas within these areas because of high rates of aggression from resident adults (Lambin et al. 2001, Berggren et al. 2004, Doligez et al. 2004). As a result, juveniles must search for unoccupied areas in: (1) unoccupied and low-quality patches; (2) edge areas of high-quality patches, which often consist of young forest; (3) areas between existing territories, which can consist of either old or young forest; or (4) an area left temporarily vacant as a result of the death of the territory owner.

Table 1. Full logistic regression model showing the relationship of the number of juvenile North Island robin visiting a patch during natal dispersal after leaving the natal patch on four landscape variables recorded for each patch. Whole model (df = 4, chi-square =38,36, $p < 0.0001$); CONN is short for connectivity.

Variable	Estimate ± SE	df	Log likelihood ratio χ^2	*p*
CONNlandscape	-0.04 ± 0.02	1	5.06	0.0245
CONNlocal	0.02 ± 0.04	1	0.34	0.5604
AGEpatch	0.97 ± 0.49	1	4.09	0.0431
SIZEpatch	0.66 ± 0.19	1	12.39	0.0004

Juveniles that left their natal area earlier in the season occupied patches that were less isolated and more popular among juveniles, i.e., with more juveniles visiting the patch, than juveniles leaving later. High competition for space between both adults and older juveniles may force later-arriving juveniles to choose patches they would normally avoid. Thus, the distribution of robins on Tiritiri Matangi Island more or less follows the predictions for an ideal despotic distribution (Calsbeek and Sinervo 2002), assuming that juveniles that left their natal habitat later in the season are younger and thus less experienced in competing for habitat than any older birds. This could negatively influence the survival for late dispersers in terms of higher predation risk and less food availability in nonpreferred areas. Although we acknowledge that the sample size of late-dispersing juveniles is low ($n = 6$), we believe that the results are valid and may partly explain the density-dependent juvenile survival suggested by Armstrong et al. (2002, see also Arcese et al. 1992, Stamps 2001).

CONCLUSION

The North Island robin is a highly threatened, forest-living bird species that is sedentary in its territory throughout the year after the initial phase of natal dispersal (Higgins and Peter 2003). Much of New Zealand has been deforested, and many of the remaining lowland forests are fragmented and isolated (Myers 1923, McGlone et al. 2005). Our study indicates that the dispersal of the North Island robin is highly affected by fragmentation and that the species is reluctant to cross gaps (see also Armstrong et al. 2000, Berggren et al. 2004), a factor likely to be more pronounced in sedentary bird species like the North Island robin (Saunders et al. 1991, Andrén 1994, Sieving et al. 2000, Hames et al. 2001). One method suggested for reducing the extinction risk of species with poor dispersal abilities is the preservation or creation of habitat corridors linking the remaining habitat (Meffe and Caroll 1994, Macdonald and Johnson 2001, Berggren et al. 2002, Haddad et al. 2003). Vegetation strips (corridors) or small fragments (stepping stones) between larger habitat areas increase landscape connectivity and, thus, may increase the movement of individuals between the isolated fragments (Ims 1995, Tischendorf and Fahrig 2000). In addition, wide corridors offer additional habitat that can be used for breeding (Merriam 1991). The birds most likely to benefit from corridors are forest-habitat specialists: those species with low mobility in open habitats and of a high conservation status (O’Donnell 1991). New Zealand robins have been listed as one of eight native birds of that class in New Zealand, and one of the species most likely to decline after any form of habitat modification (O’Donnell 1991, Spurr et al. 1992).

The suggested fragmentation sensitivity of the robin in combination with the results from our study indicates that any improvement of the landscape to increase connectivity would benefit the long-term survival of the species. We found dispersing juvenile North Island robins in all forest habitats, including young and open forest areas, i.e., poor breeding habitat. This suggests that juvenile robins make dispersal decisions on a broader habitat scale and are not dependent on the older forest stands during their dispersal phase. Thus, landscape connectivity could be increased for robins during natal dispersal by restoring low-quality forest patches between higher quality patches (Wiegand et al. 2005). Increased connectivity between forest patches would also be expected to increase the successful dispersal of other threatened native species (Vols et al. 2002). The relationship between number of visiting juveniles and patch size may indicate that the benefit of a corridor or stepping stones would increase with increasing size of the element. There may even be a threshold below which the element is not used. To estimate the dispersal behavior of the North Island robin in corridors and stepping stones, more studies are needed.

There is a risk with corridors that they can have detrimental effects for the individuals traveling through them, because they may provide dispersal abilities not only for threatened species but also for noxious agents such as fire, disease, or pests (Simberloff et al. 1992). Because of the high fraction of edge habitat in corridors, they might further provide habitat for edge-inhabiting predators and thus act as a sink for the animals using them. However, the improvement of dispersal in a target species living in a highly fragmented landscape is likely to far outweigh any potential negative effects. Dispersal through corridors or other types of structural links between habitats would give individuals in a population an escape route when conditions deteriorate, which would reduce the risk of inbreeding and extinction of the population (Saunders and Hobbs 1991).

Understanding dispersal in a species like the North Island robin that lives in a highly fragmented habitat is essential for future conservation and management. With such knowledge it is possible to change the management of both the species in focus and the landscape it inhabits so that individuals can recolonize former habitats and, thus, increase their long-term survival. More studies are needed on the effect of re-created habitats on individual dispersal in this species, but the combination of earlier studies and the findings from this study suggest that efforts made to increase the connectivity between habitats used by the North Island robin may be effective in increasing the dispersal and longevity of the populations.

Responses to this article can be read online at:
http://www.ace-eco.org/vol2/iss2/art2/responses/

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