



Forum

## Avoiding Hasty Conclusions about Effects of Habitat Fragmentation

### Importance d'éviter les conclusions hâtives quant aux effets de la fragmentation de l'habitat

*Doug P. Armstrong*<sup>1</sup>, *Yvan Richard*<sup>1</sup>, *John G. Ewen*<sup>2</sup>, and *Wendy J. Dimond*<sup>3</sup>

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#### INTRODUCTION

Habitat fragmentation can potentially have negative impacts on many species because of both changes in habitat quality associated with edge effects (Saunders et al. 1991) and changes to population dynamics caused by the loss of connectivity (Hanski 1998). The practical implication is that it may be necessary to conserve a species in large continuous areas of habitat, rather than in several small areas (Burkey 1995), or to create corridors or stepping stones between fragments (Hobbs 1992). However, it is important that such management is based on evidence, rather than a priori assumptions about negative effects of fragmentation, and that the data are interpreted carefully. Otherwise, the conservation value of fragmented landscapes may be underestimated, or extensive resources may be invested in management that turns out to be ineffective or even deleterious.

For example, based on observations of 34 dispersing North Island Robin (*Petroica longipes*) juveniles on a small island 220 ha in size offshore of New Zealand, Wittern and Berggren (2007) concluded that dispersal was highly affected by the fragmentation of the forest habitat on the island. Based on this conclusion, they suggested that management of the species should focus on creating new forest habitat among the existing patches and that this would greatly increase the viability of the species' metapopulations by increasing dispersal.

Although we wholeheartedly agree that forest fragmentation and metapopulation dynamics are key issues to consider in the management of North Island Robin, Wittern and Berggren's (2007) recommendations are unwarranted based on their data. We use this case to illustrate three points with general relevance to fragmentation research: the scale and connectivity of the study system need to be appropriate in relation to the dispersal dynamics of the species; dispersal data need to be interpreted carefully to avoid misleading confounds; and evidence of dispersal limitation does not necessarily imply that higher connectivity would be beneficial.

#### CHOOSING AN APPROPRIATE STUDY SYSTEM

Although it is sometimes difficult to know the degree of habitat isolation that is likely to impede a species' dispersal, it is important to take previous observations and research into account. New Zealand Robin (*P. longipes* and *P. australis*) is well known to be reluctant to cross large stretches of pasture. In particular, Flack (1979), who performed intensive anecdotal research on *P. australis* on the South Island, noted that "they are highly intolerant of large treeless areas, and reluctant to cross even 100 m of open ground." Consequently, there is good reason to expect robins to be affected by forest fragmentation on the New Zealand mainland (North and South Islands) given that forest remnants are

<sup>1</sup>Massey University, <sup>2</sup>Zoological Society of London, <sup>3</sup>University of Canberra



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often separated by hundreds of meters of pasture. However, it was extremely unlikely that robin dispersal would be significantly affected by forest fragmentation on Tiritiri Matangi Island at the time of Wittern and Berggren's (2007) study.

Most of Tiritiri Matangi Island was used for livestock grazing until 1971, at which time there were several small remnants of  $\leq 4$  ha separated by up to 120 m of pasture. However, a revegetation program that began in 1983 (Mitchell 1985) resulted in the coverage of most of the island by regenerating native forest by the time North Island Robin was reintroduced to the island in April 1992. Although robin breeding territories are still largely restricted to the original remnants, post-release observations of translocated birds indicate that the birds dispersed readily through the planted vegetation (Armstrong 1995); this was also the case for subsequent juvenile dispersal (Armstrong and Ewen 2002). Armstrong and Ewen (2002) analyzed the settlement locations of juvenile robins from 1995 to 1997 to assess whether the fragmentation of the remnant forest on the island had any effect on population dynamics. To do this, they fitted data on the number of juveniles settling in each fragment each year to the model

$$S \cdot (A_i - \beta R_i) \sum_{j=1}^n f_j e^{-\alpha d_{ij}} / \sum_{i=1}^n \left( (A_i - \beta R_i) \sum_{j=1}^n f_j e^{-\alpha d_{ij}} \right) \quad (1)$$

where  $S$  is the total number of juveniles that survive to the next breeding season,  $A_i$  is the area of the focal fragment,  $R_i$  is the number of surviving residents in the focal fragment,  $f_j$  is the number of juveniles produced in each fragment that has suitable habitat for robins,  $d_{ij}$  is the distance between the focal fragment and each of the other fragments, and  $\alpha$  and  $\beta$  are parameters to be estimated. The term

$$\sum_{j=1}^n f_j e^{-\alpha d_{ij}} \quad (2)$$

models the effect of fragment isolation by weighting possible settlers as a function of their distance from

the focal patch; parameter  $\alpha$  gives the strength of this effect. The model fit the data well, and comparisons with simpler candidate models showed that there was no evidence of any isolation effect (see Table 5 in Armstrong and Ewen [2002]). In contrast, the effect of parameter  $\beta$  was highly significant;  $\beta$  was estimated to be 0.17, meaning that each resident robin makes approximately 0.17 ha unavailable for other robins.

Armstrong and Ewen (2002) therefore concluded that intraspecific competition plays a strong role in settlement, but that fragmentation poses no barrier to the occupation of available habitat and is irrelevant to the population's dynamics. Hence, models used in the subsequent management of the population have treated it as a homogenous unit (Armstrong and Ewen 2002, Dimond and Armstrong 2007). Fragmentation was even less likely to be relevant by the 2003–2004 breeding season when Wittern and Berggren (2007) conducted their study because remnants were largely connected by continuous vegetation  $> 3$  m in height at that stage, except for mowed strips  $< 10$  m wide used for walking and vehicle tracks. Tiritiri Matangi Island therefore appears to be a highly unsuitable site for studying the effects of fragmentation on the dispersal of North Island Robin.

## AVOIDING MISINTERPRETATION OF DISPERSAL DATA

Taken at face value, Wittern and Berggren's (2007) study appears to contradict previous research on North Island Robin on Tiritiri Matangi Island by showing 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." However, the patterns that Wittern and Berggren (2007) cited as evidence of barriers to patch occupancy are expected to occur in the absence of any such barriers. They observed that juveniles are more likely to be found in larger patches, older patches, and highly connected patches, but this is to be expected given that most of the juveniles were produced in large, older, well-connected fragments located near the centre of the island and that the observations were made during the breeding season shortly after the birds left their natal territory. Such a pattern gives no evidence that there is any barrier to robins settling in patches of suitable habitat.

Wittern and Berggren (2007) also observed that the proportions of juveniles that were observed in lower connectivity classes (21–40, 41–60, 61–80, and > 80 m) were lower than the availability of fragments within these categories, but calculated availability based on the relative numbers of these fragments, rather than the area that they comprised. Given that most of these low-connectivity fragments would have been tiny (see Fig. 1 of Wittern and Berggren [2007]), it is to be expected that only a small fraction of the observations of dispersing juveniles would occur in these fragments. Both patterns were further exacerbated by Wittern and Berggren's (2007) rather liberal interpretation of what constituted a habitat fragment. They searched 51 fragments ranging to as small as 0.018 ha, but only 25 fragments on Tiritiri Matangi Island have ever supported a robin territory, and 0.018 ha is < 1/10 of the area that is required to support a robin based on Armstrong and Ewen's (2002) analysis described above and the maximum densities recorded in any fragment over 16 yr of monitoring. Therefore, a further reason for the absence of robins from isolated fragments is that many of these fragments would have been unsuitable for settlement and so would be visited only briefly.

The available evidence still indicates that fragmentation is irrelevant to the population dynamics of North Island Robin on Tiritiri Matangi Island; this is not surprising given the small size of the island and the high degree of connectivity among forest remnants. The limits to dispersal imposed by less connected systems can now be inferred using extensive data on the dispersal of radio-tracked robins among mainland forest fragments, with least-cost-path modeling suggesting that juveniles cross stretches of pasture of up to 100 m and travel up to 20 km in total distance (Richard 2007).

## PROJECTING EFFECTS OF INCREASED CONNECTIVITY

If Wittern and Berggren's (2007) conclusions are taken at face value, managers would need to create an impractical level of connectivity, i.e., forest fragments separated by no more than 20 m. Such conclusions might actually discourage people from attempting to manage connectivity at a broader scale, resulting in lost opportunities. However, the more worrisome aspect of Wittern and Berggren's (2007) recommendations is that they are based on the assumption that robin metapopulations would

benefit from enhanced connectivity. There is no evidence to support this assumption.

Although metapopulation theory indicates that enhanced connectivity increases the size and persistence of metapopulations under some conditions (see Hanski 1998 and many related publications), there are other conditions in which increased connectivity is detrimental (Hess 1996, Crooks and Suarez 2006, McCallum and Dobson 2006). In particular, increased connectivity can facilitate the movement of threats to a species, e.g., predators and pathogens, and/or facilitate the movement of individuals from source to sink habitat. If researchers are going to recommend the manipulation of connectivity to conserve particular species, we suggest that the recommendations should be based not only on reliable dispersal models, but also on metapopulation models that are realistic for the species and landscape under consideration.

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