Demography and distribution of the North Island robin (*Petroica longipes*) in a fragmented agricultural landscape of New Zealand

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North Island robin (*Petroica longipes*)

Abstract

Habitat loss and fragmentation are recognised worldwide as contributing to declines and extinctions of species. However, the biological factors underlying the effects of fragmentation are still often poorly understood, possibly due to the diversity of scales and approaches taken by researchers. I propose in this thesis an integrative approach that can be applied to any taxa and landscape, using a metapopulation of North Island robins (*Petroica longipes*) inhabiting forest patches of a fragmented agricultural landscape of New Zealand. In particular, I attempt to integrate the effects of habitat fragmentation on both habitat quality and the dispersal-driven broad scale dynamics of populations. I first analysed the distribution of robins based on presence-absence data, relating presence-absence to local habitat factors as well as size and isolation of forest patches (Chapter 2). Their distribution was found to be primarily limited by the isolation of forest patches, but was also related to some habitat factors. However, habitat fragmentation was not found to affect habitat quality, as the factors found to affect survival and productivity were unrelated to size and isolation, independent from the size or isolation of forest patches (Chapter 3). Based on the radio-tracking of juvenile robins, I applied a choice analysis technique to show that robins need woody vegetation for their natal dispersal and that they are unlikely to cross stretches of pasture greater than 150 m (Chapter 4). Juveniles dispersed a median Euclidean distance of 1129 m with a maximum of 11 km, whereas I predicted from the data that they would have dispersed a median distance of 3 km in continuous forest with a maximum of 20 km (Chapter 5). The consequences of this dispersal limitation and of variations in habitat quality were assessed using a spatially-explicit individual-based metapopulation model that incorporated realistic gap-limited dispersal behaviour of juvenile robins (Chapter 6). Whereas the movement of individuals between patches is commonly assumed to improve the persistence of populations, I found that a weaker gap-crossing ability, and therefore reduced landscape connectivity, increased the metapopulation size at equilibrium. This study highlights the complex effects of habitat loss and fragmentation on the distribution of species, but also the limits of excessive model simplification.

Table of contents

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1- Introduction

Understanding the distribution of species is a central goal in both applied and fundamental ecology, and knowledge of the factors involved is essential for reversing declines of species worldwide. Habitat loss and fragmentation induced by human activities have been recognized to be among the major causes of this decline, and there is a large body of research on distributions of species in fragmented landscapes. Habitat fragmentation has been shown to be detrimental to species at two main spatial scales. At a local scale, it leads to an increase in the ratio between the perimeter of patches and their area, resulting in an increased edge area, relatively to the core area of patches. At the edges, changes in microclimate generally occur (Saunders *et al.* 1991), nest predation and brood parasitism levels can increase (Andren & Angelstam 1988; Robinson *et al.* 1995a; Chalfoun *et al.* 2002; Stephens *et al.* 2004), and food availability can decrease (Burke & Nol 1998; Zanette *et al.* 2000; Luck 2003), lowering the habitat quality and ultimately leading to a lower survival and/or reproduction success. At a broader scale, habitat fragmentation can limit the movement of individuals in the landscape. This can result in greater variations of subpopulation densities, thus greater risk of extinction from demographic and environmental stochasticity, reduction in the rescue effect from the immigration of individuals from neighbouring subpopulations, reduction in colonisation rate, and/or in increased inbreeding depression (Brown & Kodric-Brown 1977; Pulliam 1988; Caughley 1994; Sih *et al.* 2000; Keller & Waller 2002; Reed 2004).

Effects at these two scales have traditionally been tackled by different approaches. The local scale habitat quality issues have been studied for the longest time, generally by field biologists using a shotgun approach in which a large number of variables are considered in order to understand empirically the relationship between individuals and their immediate environment. On the other hand, the colonisation/extinction dynamics of subpopulations interconnected by the movement of individuals has been more recently addressed by modellers who developed their approach based on metapopulation theory historically initiated by MacArthur and Wilson's (1967) theory of island biogeography and by Levin's (1969) theory of metapopulation dynamics. Because of the difference in methodology and focus adopted in these two areas of research, the two approaches were generally treated exclusively, resulting in two separate paradigms which Armstrong (2005) called the habitat paradigm and the metapopulation paradigm. The two approaches are complementary, however, with local habitat factors and isolation of subpopulations likely to play joint roles in the dynamics of fragmented populations. A systematic integration of these approaches is likely to provide better recommendations for the management of species in fragmented landscapes. However, both approaches have suffered from methodological problems that can potentially be resolved using more intensive data collection combined with modern analytical techniques.

Habitat quality has often been assessed using indirect clues like population density, whereas it has been shown that density can be a poor indicator of the actual habitat quality (Van Horne 1983). The same problem applies to presence-absence data. For example, individuals can be recorded present in low-quality habitat because of conspecific attraction (Reed & Dobson 1993), because landscape configuration constrains the movement of individuals, because individuals can no longer make optimal habitat selection decisions due to a rapid change in their environment (Remeš 2000) or because transient individuals are recorded, e.g., when dispersing. Conversely, no individuals could potentially be recorded in high-quality habitat because of low detection probability, because density is currently low due to demographic or environmental stochasticity, or because the habitat is unreachable by dispersers. The only way to avoid these confounding factors is to measure habitat quality in terms of survival and reproduction rates achieved in different habitats (Breininger *et al.* 1995; Armstrong 2005) although even this measure may be confounded by differences in the genetic quality of individuals.

On the other hand, metapopulation (sensu Hanski 1998) and other spatially-explicit models rely on data on movements of individuals between subpopulations or the dispersing behaviour of individuals, and these data are generally scarce, incomplete or biased (Van Noordwijk 1995; Koenig *et al.* 1996; Lima & Zollner 1996; Ims & Yoccoz 1997). Dispersal is a highly complex process, often interacting with the configuration and/or composition of landscapes (Ricketts 2001; Bender & Fahrig 2005). Despite its importance for metapopulation dynamics (Ims & Yoccoz 1997; Hanski 2001), dispersal has been overly simplified in most models, reduced to an exponential function that assumes that movements are random and by assuming, for example, a homogenous habitat between subpopulations (e.g. Adler & Nuernberger 1994; Hanski 1994b; Frank & Wissel 2002; Castellón & Sieving 2006). The complexity of dispersal behaviour can, however, be represented more accurately using recent techniques coupled with geographic information systems like least-cost path modelling (Bunn *et al.* 2000).

Simple metapopulation models like those from classical metapopulation theory (Hanski 1994b) are elegant in their formulation, quick to compute, simple to parameterize (a single snapshot of patches occupancy can be sufficient) and their generality makes them widely applicable. Although they have been found to adequately predict the dynamics of some metapopulations (Hanski *et al.* 1996; Thomas *et al.* 2001; Moilanen & Cabeza 2002; Drechsler *et al.* 2003), their use is restricted to large networks of patches in very fragmented landscapes (Hanski 2004). Furthermore, in addition to the limitations previously described, they generally assume a steady state of the systems and ignore local habitat and dynamics (but see Thomas & Hanski 2004 and Moilanen & Hanski 1998). Pattern-oriented modelling from which the classical metapopulation model is a part of (Wiegand *et al.* 2003) relies on an indirect approach that can lead to erroneous conclusions if some factors are confounded (Armstrong 2005). Increasing the complexity of models, especially the treatment of individual movements, can improve the accuracy of the predictions and provide more reliable recommendations for wildlife management, despite the resulting need for greater computing power.

Several reviews and meta-analyses have attempted to find some common patterns among the numerous studies assessing the effects of habitat fragmentation (Opdam 1991; Saunders *et al.* 1991; Andren 1994; Bender *et al.* 1998; Harrison & Bruna 1999; Lahti 2001; Schmiegelow & Mönkkönen 2002; Fahrig 2003; Henle *et al.* 2004; Parker *et al.* 2005; Watling & Donnelly 2006). No generalisation seems to be attainable, mainly due to the diversity of studied landscapes, taxa and life-histories, but the biases and over-simplifications previously described in the majority of studies could also potentially obscure the relationships (Bender & Fahrig 2005).

The goal of this thesis is to develop methods to assess the relative effects of habitat and metapopulation factors on the distribution and dynamics of species, using as a model system a metapopulation of North-Island robins (*Petroica longipes*) in a fragmented landscape in the central North Island of New Zealand. This system is particularly suitable for this study as this forest-dwelling species can still be found at relatively high densities in this area and in forest patches varying in size, isolation and habitat quality. Furthermore, its high territoriality and inquisitiveness, along with the fact that it is non migratory and very responsive to lure territorial calls, makes it easy to monitor and good quality data can be collected about its vital rates (reproduction and survival) and dispersal behaviour. This study has also a conservation interest as robins have greatly declined in range and density since human settlement (Bell 1986) and many reintroduction projects of this species have taken place in New Zealand (Armstrong 1999-2007). An increased knowledge of the factors affecting robins' vital rates and movements would certainly be beneficial to future management strategies of this species. Additionally, our knowledge of robins comes almost exclusively from populations in managed protected areas, whereas only 30% of the New Zealand land area is currently held in the public conservation estate (Norton & Miller 2000). Filling knowledge gaps on species on private land and other less protected areas would certainly help secure the persistence of native fauna in New Zealand.

Recovery of endangered species in New Zealand has so far been largely undertaken following the habitat paradigm. Management under the habitat paradigm focuses on reversing habitat modification associated with species declines, with this modification referring to any biotic or abiotic changes to habitat patches that the species inhabits. The factor that has clearly been responsible for declines of many native species has been the introduction of exotic mammalian predators such as rats (*Rattus* spp.), brush-tailed possums (*Trichosurus vulpecula*), mustelids (*Mustela spp.*) and feral cats (*Felis catus*) (e.g. James & Clout 1996; McLennan *et al.* 1996; Brown 1997; Innes *et al.* 1999; Powlesland *et al.* 2000; Innes *et al.* 2004), most of which arrived since Europeans first landed in New Zealand in 1769 (Atkinson & Cameron 1993). It is therefore not surprising that conservation management has focused on control or eradication of these exotic mammals, and translocation of native species to offshore islands that exotic predators did not reach or to offshore islands or "mainland islands" (Saunders & Norton 2001) where predators have been controlled or eradicated. However, as well as introducing exotic mammals, humans have also removed nearly three quarters of the native forest in New Zealand (Ewers *et al.* 2006), the remaining forest is highly fragmented. Despite the worldwide recognition of the detrimental impact of habitat loss and fragmentation on species viability, there has been little research on this topic in New Zealand. My thesis therefore represents an attempt to partially fill in this gap in local research as well as provide a framework that can be applied to species worldwide.

In chapter 2, I analyse the factors driving the presence and absence of robins in forest patches in my study area, an agricultural landscape of 15,000 ha in the central North Island of New Zealand. By using mixed models, both habitat and metapopulation paradigms can be integrated, and this analysis gives a preliminary indication of the relative roles of habitat quality and patch isolation on the distribution of robins.

As habitat quality can only be reliably measured from vital rates, the chapter 3 presents an analysis of adult robin survival and productivity data obtained from three breeding seasons in 13 forest patches of the study area. The results are used to assess the extent to which the patterns observed in Chapter 1 can by attributed to variation in habitat quality.

In chapter 4, I apply a choice analysis model to post-fledging dispersal data of robins followed daily by radio-tracking. This approach coupled with least-cost path modelling in a geographic information system (GIS) tests whether robins prefer woody vegetation features for dispersing and allows quantification of their sensitivity to gaps in woody vegetation cover.

Chapter 5 describes the dispersal characteristics of juvenile robins in the studied fragmented landscape. From the results of the previous chapter, an estimation of their dispersal distances more accurate than the ones obtained using Euclidean distances can be calculated and used to quantify the restrictive impact of habitat fragmentation on the realised distances of robin natal dispersal. A potential difference in dispersal behaviour between sexes is also estimated, as well as juvenile survival.

In chapter 6, I combine the previous results into a spatially-explicit individual-based metapopulation model, SEXIBAM, in order to assess by simulation the sensitivity of the metapopulation dynamics of robins to both habitat quality and landscape connectivity.

2- Presence/absence of North Island robins driven by patch isolation

Abstract

Although the role of habitat fragmentation has been widely recognized in the decline of species worldwide, its effect on local habitat quality has been considered almost exclusively through presence-absence models. Conversely, metapopulation dynamics where patch size and isolation are the main factors in explaining species distribution are rarely considered in such studies. In this chapter, I compared three approaches to model the distribution of North Island robins in a fragmented agricultural landscape of New Zealand. The first approach only considers local habitat quality, the second approach considers metapopulation factors only (patch size and isolation), and the third approach combines those two types of factors. Robins are preferentially found in mature forests and their occurrence is negatively correlated with isolation from neighbouring patches and from the closest surrounding major forests, which probably act as sources of immigrants. These results suggest that the distribution of North Island robins is best predicted by patch isolation, with a slight increase in prediction power when habitat is also considered. This study highlights the need to incorporate metapopulation dynamics in presence-absence models in fragmented landscapes, as species occurrence can otherwise be a misleading predictor of habitat quality.

Introduction

Identifying the factors driving the distribution of species is at the core of ecology, and is especially important in conservation biology in order to prevent further loss of biodiversity. Habitat fragmentation has been identified to be among the main causes of species decline worldwide (Saunders *et al.* 1991; Vitousek *et al.* 1997). At a local scale, it can lead to habitat deterioration via edge effects, a decrease in food availability, an increase in predators, parasite abundance or disease prevalence (Andren & Angelstam 1988; Yahner 1988; Saunders *et al.* 1991; Paton 1994; Andren 1995; Robinson *et al.* 1995; Burke & Nol 1998; Harrison & Bruna 1999; Doak 2000; Chalfoun *et al.* 2002). At a broader spatial scale, habitat fragmentation can also impede the exchange of individuals between (sub)populations, therefore leading to a diminished rescue effect or to increased inbreeding (Brown & Kodric-Brown 1977; Pulliam 1988; Caughley 1994; Sih *et al.* 2000; Reed 2004). However, few studies have considered the effect of habitat fragmentation at both scales simultaneously when analysing factors limiting species' distribution (Armstrong 2005).

Presence-absence data have been commonly used to identify the factors driving species distribution (e.g. Ferrier *et al.* 2002) and for determining suitable habitats for reintroductions or for the selection of habitats to be protected (Van Teeffelen *et al.* 2006). Such data are relatively easy to collect and have been used for a wide range of applications (e.g. Lawton & Woodroffe 1991; Rushton *et al.* 2000; Smart *et al.* 2000). A shortcoming of the use of these data for assessing habitat suitability is the assumption that presence or absence of individuals at a specific location is directly related to habitat quality, and this is likely to be unrealistic in many situations (Van Horne 1983). An individual can be present at a location and not recorded during the sampling process because of low detectability, but it can also be truly absent in good quality habitats due to chance events related to metapopulation dynamics, with good habitat patches not colonised because of their isolation for example. On the other hand, species can be present in low quality habitats, for example in sink populations (Pulliam 1988), with species showing conspecific attraction (Stamps 1988; Smith & Peacock 1990), or when an individual is recorded during its dispersal stage.

Controlling the potential factors leading to a fallacious correlation between habitat quality and presence-absence in species-habitat models is likely to improve the accuracy of the predictions of species occurrence. For example, an increasing number of studies control for low species detectability by explicitly including the detection probability in models and/or by using multiple sampling occasions (MacKenzie & Royle 2005; Wintle *et al.* 2005). Spatial autocorrelation generally occurs from conspecific attraction and can be integrated in presence-absence models (Wintle & Bardos 2006). Recording dispersing individuals can be avoided by sampling during appropriate seasons and by only recording the occurrence of adults, which tend to disperse less than juveniles (Greenwood & Harvey 1982; Paradis *et al.* 1998).

Metapopulation dynamics and dispersal dynamics in general, although likely to mask the true relationships between habitat and species occurrence, have rarely been considered in presence-absence models, and lead to a "habitat" paradigm in which species are believed to be mainly driven by local habitat quality. In contrast, many metapopulation or other spatially-explicit population models follow a "metapopulation" paradigm, focusing solely on the exchange of individuals between (sub)populations and their resulting colonisation/extinction dynamics (Armstrong 2005).

I compared in this study three possible approaches for analysing presence-absence data in a fragmented landscape. The first approach only includes habitat factors and thus follows the "habitat" paradigm whereas the second approach only considers the size of habitat patches and their isolation from putative source populations and from neighbouring patches, thus following the “metapopulation” paradigm. The third approach combines the two paradigms by incorporating both habitat and metapopulation factors.

One problem arising from the inclusion of patch isolation in species-habitat models lies in its definition. Patch isolation indices used in the literature are seldom biologically relevant for most species, as isolation is often measured by the Euclidean distance to the nearest neighbouring patch (e.g. Doebeli 1998; Hanski *et al.* 2000), therefore assuming a random dispersal behaviour and a homogeneous matrix between patches. Patch isolation should be defined relative to species movement behaviour, as the existence of corridors or barriers in the matrix has been showed to greatly enhance or impede individual movements between patches (Potter 1990; Ricketts 2001; Gobeil & Villard 2002; Goodwin & Fahrig 2002; Haynes & Cronin 2006). I used an index of patch connectivity based on least-cost paths between patches, taking into account the permeability of the matrix between patches.

Presence-absence data for this study were collected for the North Island robin (*Petroica longipes*) in the central North Island of New Zealand. This species is an ideal model species for this research as it is locally abundant, although absent in some forest patches (Robertson *et al.* 2007), sedentary, and easy to detect. This species is also interesting from a conservation point of view as its range greatly declined since human settlement (Bell 1986).

The purpose of this study is two-fold. Firstly, the inclusion of patch isolation in the species-habitat models should provide a preliminary clue on the relative importance of metapopulation dynamics and habitat quality on robin distribution, and guidelines for the analysis of presence-absence data can be provided. Secondly, the analysis of robin presence-absence data should improve our knowledge of the factors limiting the distribution of this species in a fragmented landscape and it should ultimately lead to a better management of robins. Surprisingly, despite the high number of species at risk and an intensive deforestation since human settlement 800 years ago (Anderson 1991), very few studies conducted in New Zealand have examined the effect of habitat fragmentation on species distribution and viability.

Methods

Model species

The North Island robin (*Petroica longipes*) is a small (26-32 g) territorial insectivorous passerine endemic to New Zealand (Heather & Robertson 2000), and is one of two closely related species of "New Zealand robins", the other being the South Island robin (*P. australis*). The two taxa were considered to be the same species until recently, but have now been separated based on both morphological and genetic differences (Holdaway *et al.* 2001; Miller & Lambert 2006). Its habitat is typically native podocarp-broadleaf forest, but it can also be found in exotic pine (*Pinus radiata*) plantations. The North Island robin is a non-migratory species, is socially monogamous, shows high site fidelity, and feeds mainly on invertebrates in the leaf litter. Robins are highly territorial and inquisitive; they are strongly attracted by lure territorial calls, giving them a high detectability.

Study area

The study area of 15,000 ha was located in the central North Island of New Zealand, between the township Benneydale (175°22′ E, 38°32′S) and Pureora Forest Park, in a landscape mainly composed by farmland, with some remnants varying in shape, quality and isolation of the continuous podocarp-broadleaf forest that previously covered 96% (Ewers *et al.* 2006) of the North Island before human colonisation 800 years ago (Anderson 1991). The area is surrounded on the eastern and southern part by exotic plantations of *Pinus radiata.*

Data

Data on robin presence-absence were collected between September and May in 2003-04 in 339 sites in 58 patches and again in 2004-05 with an additional 55 sites in 8 more patches. Locations were spread over space in potentially suitable habitats (native or pine forest, scrub with canopy > 2.5 m) which represent most of the woody vegetation in this area. The sites were separated by 150 m to greatly reduce the chance of multiple records of the same individuals. At each site, I recorded the spatial coordinates with a handheld GPS, and visually estimated a set of habitat variables within a 50 m radius. I estimated the height of both the tall canopy (trees > 15 m high) and secondary canopy (trees 2-15 m high). The densities of both tall and small trees were estimated by considering the average distance between nearest neighbours, and the mean diameter-at-breast-height (DBH) of the tall trees. The average height of the understorey (vegetation < 2 m) was also estimated, as well as the density of vines, categorized in four classes. These variables can be related to habitat quality through their relation to forest age, soil composition, and grazing regime, likely to influence the abundance and/or diversity of ground invertebrates (Bromham *et al.* 1999), predator abundance (King *et al.* 1996), nest site availability, or the abundance of perches used by robins to locate their food. Finally, the distance to the closest stream was recorded if one was present within a 75 m radius around the location, as streams and damp gullies are thought to be preferred by robins when establishing their territories (Armstrong *et al.* 2000; Clubb 2003).

Presence or absence of robins was then recorded by playing a lure territorial call for one minute and scanning the habitat for two additional minutes. This duration seems sufficient to detect robins whose territories encompassed the sampled site, and it was short enough to prevent individuals attracted by the lure tape from moving to habitats where they wouldn't naturally occur (pers. obs.). Despite a high detection probability of robins, in order to prevent sites from being recorded as unoccupied when robins were present but not detected, each site was considered as occupied if the presence of robins was recorded during at least one of the two sampling seasons.

The locations were then input in a geographical information system (GIS) using ArcGIS version 9.0 (ESRI, Redlands, California, USA). The GIS included the vegetation cover map of the study area and additional remote sensing habitat variables obtained from Landcare Research Ltd. The minimum slope was calculated from a 50 m radius buffer around each recorded site because robins are thought to prefer flat areas to establish their territories (Clubb 2003). The distance to the closest stream of the GIS at each site was calculated to complete my on-site measure. The distance to the closest edge, the mean annual solar radiation and the mean temperature during the coldest month (in June, from the Land Environments of New Zealand [LENZ] data; Leathwick *et al.* 2003) were also calculated from the GIS as these factors can potentially affect habitat quality. Patches were defined as discrete vegetation structures of native forest of sufficient size to host at least one pair of robins, and were considered distinct from each other in the GIS if they were separated by a minimum of 75 m of pasture, the approximate minimum width of a robin territory.

In order to incorporate metapopulation dynamics in my models, I assigned an index of size, shape and isolation to each patch. The software Fragstats (McGarigal *et al.* 2002) was used to calculate the size (P_Area) and shape (P_Shape) of each patch. Additionally, I developed a program in Python for ArcGIS to calculate an index of functional patch connectivity (IFPC). This index takes into account the features of the matrix between patches, as it is calculated from the least-cost path between each patch and their surrounding patches, considering the dispersal behaviour of the species, and thus represents a realistic measure of patch isolation. The details of the calculation of the index of functional patch connectivity are presented in Appendix 1.

The forests surrounding the study area contained a relatively high density of robins, and Pureora Forest Park located 10 km to the East is a natural reserve managed by the Department of Conservation where robins benefit from a relatively high productivity and survival because exotic predators such as rats (*Rattus spp.*), mustelids (*Mustela spp.*) and brush-tailed possums (*Trichosurus vulpecula*) are regularly controlled by poison operations. I therefore suspected that these forests could act as source populations and provide immigrants to the study area. The functional distance to the closest major forest, calculated as the cost of the least-cost path between each patch and the closest surrounding major forest (closest distance to continuous forest, CDCF) was then calculated, using a similar approach as in the calculation of the index of functional patch connectivity.

In order to correct for their skewed distributions, density of small trees, understorey height, distance to closest edge and the index of functional patch connectivity were log transformed, and distance to closest stream and cost-distance to closest continuous forest were square-root transformed.

Modelling

In order to assess the importance of patch isolation on occurrence of robins in the study area, three approaches were examined. The first approach only considers the local habitat at each sampling site, the second only "metapopulation" factors (patch size and isolation), and the third combines both local habitat and metapopulation factors.

Generalized linear mixed modelling was used as it performed better with my data than regression trees and artificial neural networks, based on the correct classification rate of presence-absence, the area under the curve of the receiver operating characteristic (ROC) plot and the Cohen's Kappa. Regression trees and artificial neural networks represent alternatives to linear modelling and have been proposed to relax some common statistical assumptions such as normality of data, linear relationship and no correlation between predictors (Manel *et al.* 1999a; Manel *et al.* 1999b; Ozesmi & Ozesmi 1999; Guisan & Zimmermann 2000). Their benefits have, however, received little support in species distribution modelling of some taxa such as birds (e.g. Manel *et al.* 1999b). With generalized linear modelling, the logit of the probability of robin presence at each site is assumed to be a linear function of the predictor variables. The patch was incorporated as a random factor in order to account for the lack of independence between sites within each forest patch, and variation in the logit of occupancy probability was assumed to be normally distributed. The modelling was performed using the software R (R Development Core Team 2006), using the function glmmML (package glmmML) that uses an exact estimation by maximum likelihood.

Table 2.1. Variables considered in the three approaches. CanH: Tall canopy height, SecCanH: Secondary canopy height, TallTreeD: Tall tree density, SmallTreeD: Small tree density, DBH: Diameter of tree trunks at breast height, VineD: Vine density, USH: Understorey height, MinSlope: Minimum slope, MAS: Mean annual solar radiation, Tmin: Mean temperature in June, DistToS: Distance to stream, DistToE: Distance to edge, P_Area: Patch area, P_Shape: Patch shape, CDCF: Cost distance to continuous forest, IFPC: Index of functional patch connectivity

#	Approach	Full model variables
1	Local habitat only	CanH, SecCanH, TallTreeD, SmallTreeD, DBH, VineD, USH, MinSlope, MAS, Tmin, DistToS, DistToE
2	Metapopulation factors	P_Area, CDCF, IFPC
3	Habitat and metapopulation factors	CanH, SecCanH, TallTreeD, SmallTreeD, DBH, VineD, USH, MinSlope, MAS, Tmin, DistToS, DistToE, P_Area, P_Shape, CDCF, IFPC

For each of the three approaches, a full model was first run with all the variables shown in Table 2.1. Variable selection was then performed by backward selection based on Akaike's information criterion (AIC), with lower AIC values indicating a more parsimonious model (Burnham & Anderson 2002). This selection algorithm was chosen as it is considered to perform better than the forward selection in presence of correlated predictors (Harrell 2001). The weight of each predictor in each model was assessed by multiplying the estimate of each predictor by the range of the 90% central quantile values, in order to standardize every variable estimate while removing the extreme values in the calculation.

Model evaluation

To assess the performance of the final models under each approach, a new dataset was first created for each model by leave-one-out cross-validation, where each observation was predicted from the best models calibrated with the remaining observations. The evaluation of the final models was then assessed on the cross-validated datasets using a receiver operating characteristic (ROC) plot. The ROC plot represents the relationship between true-presences and false-presences for a range of threshold values classifying the probability of presence, and the area under the curve (AUC) represents a measure of overall accuracy (Fielding & Bell 1997). I also used the highest Cohen's Kappa (κ) that could be obtained on the whole range of possible cut-off values as an indicator of each model's performance. The Kappa statistic has been proposed to evaluate the predictive success in relation to chance expectation (Cohen 1960; Fielding & Bell 1997; Manel *et al.* 2001), and can be used to classify models agreement as poor ($\kappa < 0.4$), good ($0.4 \leq \kappa < 0.75$), or excellent ($\kappa \geq 0.75$), following Landis and Koch (1977).

An increasing body of literature highlights the bias induced by a spatial autocorrelation of data that results in an overestimation of habitat variables (Legendre & Fortin 1989; Legendre 1993; Keitt *et al.* 2002; Betts *et al.* 2006). The presence of spatial autocorrelation in the models was assessed from the semivariograms of the residuals of each model, using the package GeoR in R (Ribeiro Jr & Diggle 2001; available at http://www.r-project.org). Semivariograms are plots of the semivariance against lag distance. The semivariance is the sum of squared differences between all points that are separated by distance t. If the compared points are increasingly different as t increases, the semivariance increases, and conversely, the semivariance decreases with the similarity of the compared points. The significance of spatial autocorrelation from the semivariograms was assessed visually by calculating an envelope obtained by Monte-Carlo simulation. For each simulation, the data values are randomly allocated to the spatial locations, and the envelope therefore represents the variation in the semi-variance of the residuals expected solely by chance in absence of spatial autocorrelation (Ribeiro Jr & Diggle 2001).

Results

Robins were recorded as present during at least one of the two sampling seasons in 139 (35%) out of 394 sampled sites, and in 28 (42%) out of 66 forest patches (Figure 2.1). They were recorded in 74 (19%) of the 339 sampled sites in 2003-04 and in 125 (32%) of the 394 sites in 2004-05. Among the 339 sites used in both seasons, 41 of them were occupied in 2004-05 but not in 2003-04, and 14 were occupied in 2003-04 but not in 2004-05.

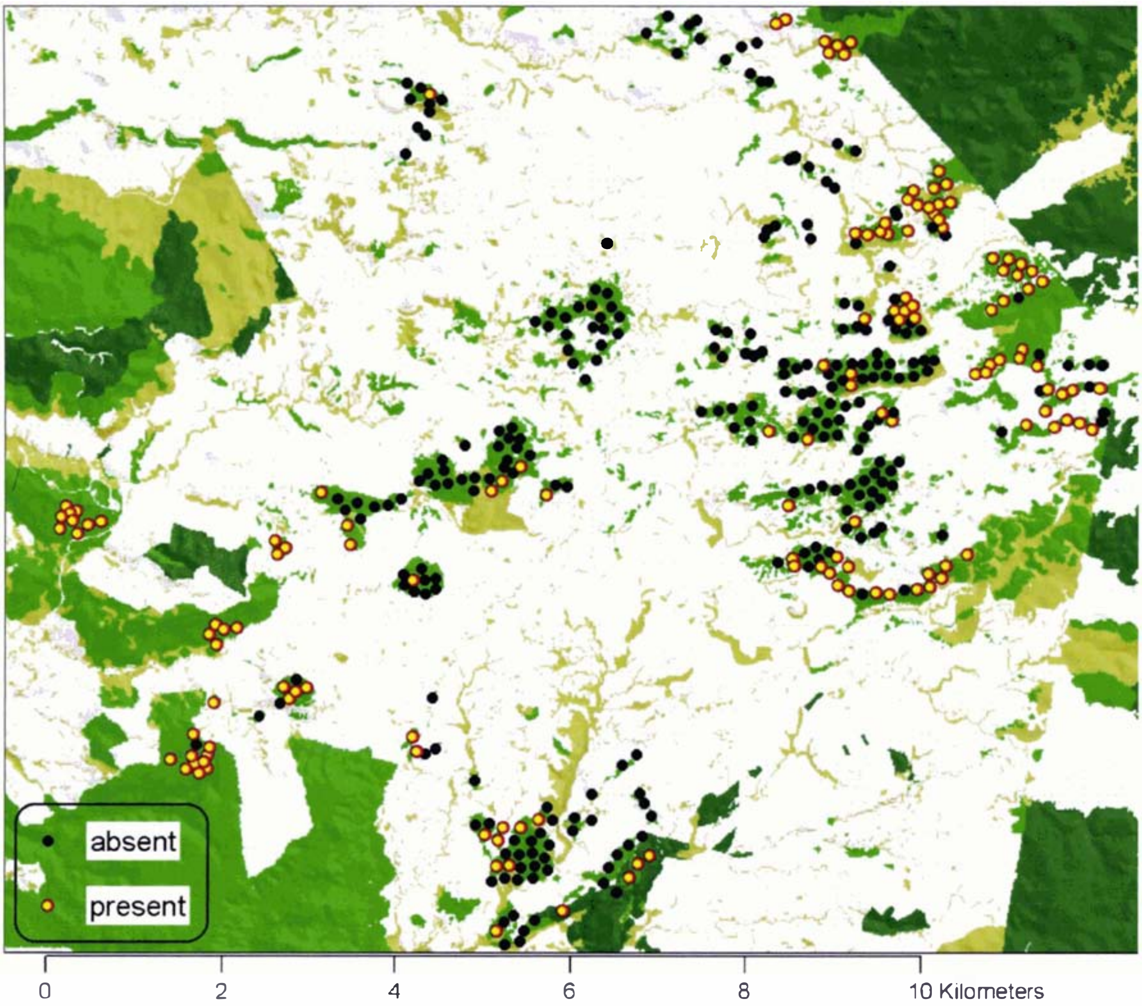


Figure 2.1: Site occupancy of North Island robins. Sites where at least one robin has been detected during the two sampling seasons are represented in yellow.

Models selected under the three approaches

Unsurprisingly, the selected variables from the final models under the three approaches were different (Table 2.2). However, the approach considering both habitat and metapopulation factors surpasses the two other models in term of AIC (Table 2.3). Its area under the ROC curve is also much higher, indicating better overall accuracy. Having an AUC above 0.8, this model is qualified as excellent according to Hosmer and Lemeshow (2000). However, the model under the approach that only considers patch size and isolation (metapopulation factors) performs slightly better in term of correct classification rate and Cohen's Kappa, despite of having a higher AIC and a lower AUC. The approach ignoring factors affecting metapopulation dynamics (patch size and isolation) performed poorly, as indicated by its high AIC as well as its low values of AUC, correct classification rate and Kappa.

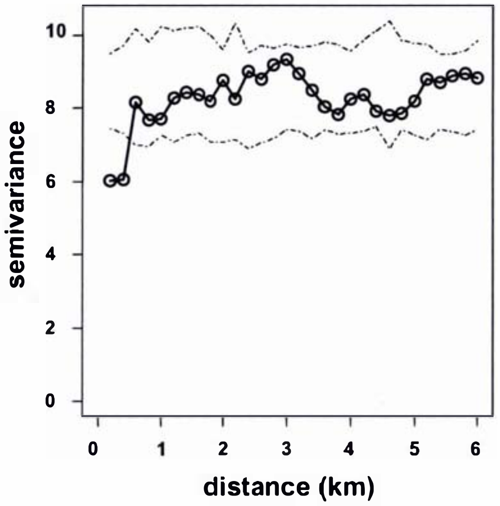
The semivariograms of the residuals of the best model under each approach revealed some degree of negative spatial autocorrelation for lag distances of less than 500 m for the first and second approach (Figure 2.2), indicating that sampled sites separated by less than 500 m were similar in terms of robin presence-absence. However, the residuals of the model considering both habitat and metapopulation factors (approach 3) did not show any significant spatial autocorrelation, indicating that the variables included in the model absorbed it.

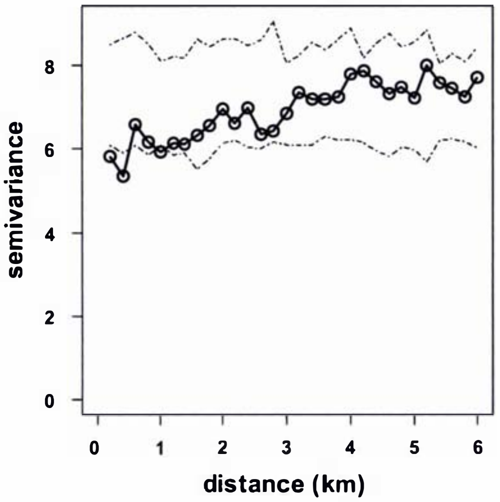
Table 2.2. Best models under each of the three approaches. The factors included in the three final models are shown, along with their estimates (change in logit of occupancy probability with a one unit increase in the value of the factor), their standard errors and their weights (change in logit of occupancy probability as factor changes over the range of its 90% central quantile values). See Table 2.1 for explanation of the factors.

Approach	Indep. Var.	Estimate	S.E.	Weight
Local habitat only	Tmin	-1.48521	0.96558	1.485
	USH	0.70745	0.27589	1.418
	SmallTreeD	-0.99261	0.43376	1.383
	MinSlope	-0.45581	0.2896	1.367
	TallTreeD	-0.08257	0.05527	0.826
Metapopulation factors only	CDCF	-0.015	0.004	3.342
	P_Area	1.213	0.378	2.784
Habitat and metapopulation factors	CDCF	-0.012	0.004	2.600
	IFPC	1.652	0.567	2.323
	USH	0.751	0.244	1.506
	DBH	0.035	0.016	1.234

Table 2.3. Comparison of the performance of the best models under each of the three approaches. AIC: Akaike's Information Criterion, AUC: Area under the ROC curve, CCR: Correct classification rate, Kappa: Cohen's Kappa statistic.

Approach	AIC	AUC	Sensitivity	Specificity	CCR	Kappa
Local habitat only	391.2	0.685	0.230	0.945	0.693	0.207
Metapopulation factors only	375.5	0.765	0.597	0.929	0.812	0.561
Habitat and metapopulation factors	366.1	0.831	0.734	0.808	0.782	0.531


(1) Local habitat factors only


(2) Metapopulation factors only

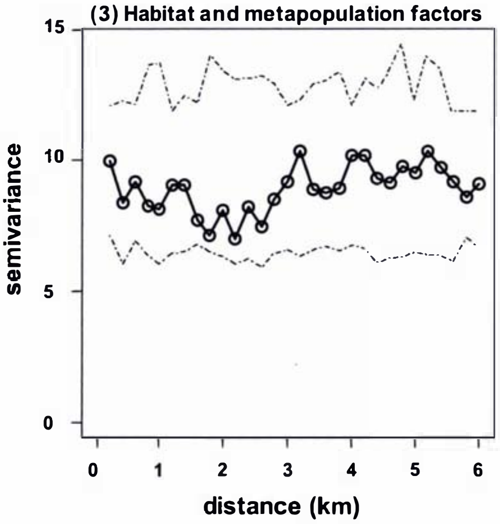

(3) Habitat and metapopulation factors

Figure 2.2. Semivariogram of the residuals of the best models under the three modelling approaches. The dashed lines represent the envelope obtained from 100 Monte Carlo simulations. Any point outside this envelope represents a significant spatial autocorrelation at α=0.01.

Further considerations of the best model

The best model, which combines both habitat and metapopulation factors, indicates that robins are preferentially found at sites with large trees and tall understorey, and in well connected patches close to a continuous forest. Furthermore, by examining the last steps of the backward selection process based on AIC, five models are within two units of AIC from the best model that considers both habitat and metapopulation factors (Table 2.4). This indicates that four other variables are potential candidates to explain the occurrence of robins (Burnham & Anderson 2002). They are: patch area, patch shape, distance to the closest stream and distance to the closest patch edge. The examination of the associated coefficients revealed that the chance of a robin being present at a site increased with patch area ($\beta_{P\_Area} = 0.450$, s.e. = 0.352), decreased with the degree of elongation of the patch ($\beta_{P\_Shape} = -0.548$, s.e. = 0.420), decreased with the distance to the closest stream ($\beta_{DistToS} = -0.047$, s.e. = 0.037), and increased with the distance to the closest edge ($\beta_{DistToE} = 0.563$, s.e. = 0.550).

Table 2.4. The five best presence models under the approach combining both habitat and metapopulation factors.

Model	**AIC**
DBH + USH + CDCF + IFPC (final model)	366.05
DBH + USH + CDCF + IFPC + P_Area	366.24
DBH + USH + CDCF + IFPC + P_Area + P_Shape	366.69
DBH + USH + CDCF + IFPC + P_Area + P_Shape + DistToS	367.05
DBH + USH + CDCF + IFPC + P_Area + P_Shape + DistToS + DistToE	367.98

Discussion

These results clearly show that the consideration of metapopulation dynamics, by incorporating patch size and isolation, greatly improved the accuracy of the models of robin presence-absence in the fragmented landscape. The approach considering only patch size and isolation performed well, as indicated by the correct classification rate, the Cohen's Kappa statistic and the AUC. Nevertheless, I believe that the approach considering both habitat and metapopulation factors performed the best, as the AUC is generally preferred over the correct classification rate and the Kappa statistic as these indices have been shown to be sensitive to species incidence (Fielding & Bell 1997; Lehmann *et al.* 2002; Berg *et al.* 2004), which was 35% in this study. Furthermore, the approach considering both types of factors led to a model for which residuals were not spatially autocorrelated, whereas the spatial dependence might introduce a bias in the analyses ignoring either habitat or metapopulation factors. The failure of considering both types of factors simultaneously would therefore lead a modeller to wish to consider more complicated models such as Bayesian ones (e.g. Wintle & Bardos 2006), which are more complicated to construct and might present problems of convergence.

Although patch size has received some support from the second approach, patch isolation was the best predictor of robin occurrence in the studied landscape. This emphasises the limitation of species-habitat analyses based only on the relationship between presence-absence data and local habitat variables. Demographic and environmental stochasticity can drive local populations to extinction and their isolation can potentially impede the immigration of new individuals, thus increasing the chance of good habitat being unoccupied. This result is expected based on metapopulation theory (Hanski & Gaggiotti 2004) but is curiously overlooked in most studies looking at species occurrence (e.g. Cowley *et al.* 2000; Fleishman *et al.* 2003; Whittingham *et al.* 2007). If species occurrence was assumed to be directly related to habitat quality, the poor performance of the distribution models could be attributed to the consideration of wrong predictors of habitat quality. Additionally, some factors would be found to be important in explaining robin distribution such as the mean minimum temperature, the tree density or the minimum slope (Table 2.2), whereas these relations are likely to be spurious as these factors were not selected in the models considering the isolation of patches. For instance, the fact that the mean minimum temperature was selected in the model not considering patch isolation can be explained by the topography of the study area similar to a geographical basin, with the central part being lower, and thus warmer, than the border area where more robins are present due to the short distance to continuous forests.

Patch isolation was here defined at two different scales, isolation from neighbouring patches and from the surrounding continuous forest, as I suspected that the major forest near the study area would act as a source of immigrants, or "continent" following MacArthur and Wilson (1967). Patch isolation from putative sources (i.e. from major forest areas) was indeed the best predictor of robin occurrence, indicating that the study area benefits from the immigration of individuals from habitats surrounding it. The nearest forests are mainly exotic plantations of *Pinus radiata* where robins are present in locally high densities. However, a study on robin vital rates in this habitat showed extremely low productivity in robins inhabiting pine forests (McArthur, in prep.). It is therefore more likely that the immigrants in the study area originate from Pureora Forest Park, where populations of predators such as rats, possums and stoats, considered as the main causes of the decline of native species in New Zealand, are regularly controlled by poison and trapping operations. Pureora Forest Park is located only 10 km to the east and is well connected to the study area by the exotic forests, without major gaps between forests. Furthermore, robin juveniles followed by radiotracking have been recorded moving distances up to 20 km (Chapter 5).

These results suggest that North Island robins are preferentially found in mature forests, characterized by a high mean diameter of tree trunks at breast height, and in habitats with tall understorey, suggesting a negative impact of grazing animals such as goats, pigs, rabbits, cows and sheep, all introduced by humans during colonisation. A sparse or inexistent understorey can potentially be associated with a low diversity in insect communities and perhaps a lower food resource for robins (Bromham *et al.* 1999).

Patch area was only a useful predictor in the approach ignoring local habitat quality, but received some support from the approach integrating both habitat and metapopulation factors. It has been used as a predictor in numerous studies looking at habitat fragmentation (e.g. Helzer & Jelinski 1999; Connor *et al.* 2000; Mac Nally & Horrocks 2002; Posillico *et al.* 2004; Castellón & Sieving 2006; Guadagnin & Maltchik 2007; Manu *et al.* 2007), yet its underlying ecological mechanisms need to be clarified if one wants to lessen the impact of habitat loss and fragmentation on biodiversity. Following the metapopulation paradigm, a larger patch is more viable as it is likely to have a lower risk of extinction and receive more immigration from its neighbourhood, whereas following the habitat paradigm, a larger patch is less affected by edge effect and thus benefits from a higher habitat quality.

This study highlights the need to consider the factors related to metapopulation dynamics in species distribution models when analysing data on species occurrence. Ignoring patch size and isolation while considering local habitat variables can lead to spurious relationships between species occurrence and habitat, and requires the implicit assumption that the distribution of species is not affected by individual movements across the landscape. Like the opposite approach of ignoring the effect of habitat fragmentation on habitat quality, this could ultimately lead to erroneous recommendations for the management of species in fragmented landscapes. The relative effects of habitat fragmentation on metapopulation dynamics and habitat quality can only be assessed by measuring meaningful variables of habitat quality. Although I used in this study presence-absence data for this purpose, habitat quality can only truly be assessed by analysing the factors affecting species' vital rates, such as survival and productivity (Van Horne 1983; Armstrong 2005) and this approach is used in the next chapter.

3- Adult survival and productivity in relation to habitat fragmentation

Abstract

Species conservation in New Zealand has mainly focused on the role of introduced predators on species persistence, whereas the effects of habitat fragmentation have been largely overlooked. The latter has often been argued to be detrimental to species through a decrease in habitat quality. Although many studies have analysed species occurrence and distribution to study the effect of habitat fragmentation, the effects of habitat quality can only truly be assessed from the analysis of species vital rates (survival and reproduction). I estimated adult survival and productivity over 3 years for 71 pairs of North Island robins (*Petroica longipes*) in 13 forest patches in a fragmented agricultural landscape in the central North Island of New Zealand. I analysed these vital rates in relation to habitat variables including food availability and predator abundance, and to the size and isolation of patches. Adult survival was positively correlated with the diameter of tree trunks and the presence of streams, and negatively correlated with understorey height in forest patches, but none of these variables were related to patch size or isolation. I did not find any relationship between productivity, as defined by the number of juveniles produced per female per year that reached independence, and any of the considered habitat variables or the size and isolation of forest patches. The hypothesis of a detrimental impact of habitat fragmentation on habitat quality is therefore not supported by this study.

Introduction

New Zealand was the last major land area to be colonised by humans, 800 years ago (Anderson 1991). Maori, the first colonisers, introduced the pacific rat (Kiore, *Rattus exulans*) and 500 years later ago, Europeans settlers introduced among many other animals the ship and Norway rat (*Rattus rattus* and *R. norvegicus*), the house mouse (*Mus musculus*), the possum (*Trichosurus vulpecula*), and three species of mustelids. These species are major predators of New Zealand's naive native fauna, and are considered to be the main cause of its loss (Holdaway 1999). The urgency of the situation has compelled conservation managers to focus on the control and eradication of these pest species, leading to intensive projects that proved to be successful in the rescuing of some critically endangered species like the South Island saddleback (*Philesturnus carunculatus*) which was saved from extinction when the island holding its single population was invaded by ship rats (Merton 1975). However, human colonisation also led to an extensive loss of the native forest due to conversion of land into agricultural areas, with a reduction of indigenous forest cover from 96% to 23% in the North Island (Ewers *et al.* 2006). In most cases, habitat loss has been associated with habitat fragmentation and the remaining forest remnants have been mainly left in steep or wet areas not suitable for farming and perhaps also of lower quality for wildlife. Despite the extensive literature pointing to the role of habitat loss and fragmentation in the worldwide decline of biodiversity (Vitousek *et al.* 1997), virtually no studies have been conducted in New Zealand on this topic (e.g. Ewers & Didham 2006, 2007), and the few existing fragmentation studies mainly looked at microclimate gradients across forest edges (Young & Mitchell 1994; Davies-Colley *et al.* 2000; Denyer *et al.* 2006).

The effect of habitat fragmentation potentially occurs at two scales. At a local scale, the habitat quality of remnant patches might decrease due to edge effects. Physical factors such as light, temperature or humidity vary with distance to edge, and small remnants may have reduced food supply for some species, e.g. reduced abundance of invertebrates for forest birds to feed on (Burke & Nol 1998; Zanette *et al.* 2000). Predation also has been found to be positively related to habitat fragmentation, although the effects vary greatly among studies (Paton 1994; Robinson *et al.* 1995;

Donovan *et al.* 1997; Chalfoun *et al.* 2002; Huhta *et al.* 2004). At a broader scale, habitat fragmentation can negatively affect population dynamics by impeding individual movements between populations thus increasing the chance of local extinction (Hanski & Simberloff 1997).

Differentiating the two types of effect is essential to understand how habitat fragmentation may affect species persistence and to provide adequate management. For this purpose, habitat quality needs to be assessed accurately and this can only be achieved by identifying the predictors of species vital rates which are the only measures truly reflecting habitat quality (Armstrong 2005), and assess their relation to habitat fragmentation. For this purpose, I used the North Island robin (*Petroica longipes*) as model species. It is particularly suitable for this study as it is non migratory, very territorial, inquisitive and relatively abundant although it declined from most of its range (Bell 1986). It is now patchily distributed mainly around the centre of the North Island (Robertson *et al.* 2007), and it can be found in small remnants (Chapter 2).

I previously studied robin occupancy among forest remnants in a fragmented pastoral landscape, and found that their occurrence was driven mainly by the isolation of forest remnants but was also related to local habitat characteristics with robins being preferentially found in forests with large tree trunks and a tall understorey (Chapter 2).

In this chapter, I report data on two vital rates (adult survival and productivity) of the robins in 13 forest remnants varying in size, isolation and apparent quality. I assess whether these vital rates were correlated with potential variables of habitat quality such as food abundance, predator density and grazing regime, as well as the size and isolation of the forest patches they inhabit.

Methods

Model species

The North Island robin is a small endemic New Zealand passerine of approximately 30 g. Its typical habitat is mature native broadleaf-podocarp or beech forest. Its diet is mainly composed by the invertebrates of the leaf litter. It is socially and genetically monogamous, with pair bonds usually retained throughout the breeding season and subsequent years until the death of the partner. It is very territorial and non migratory, and its detectability is particularly high due to its inquisitiveness and strong response to lure territorial calls.

Study area and pair monitoring

I initially searched a pastoral area of 15,000 ha in the central North Island of New Zealand between the township of Benneydale (175°22′ E, 38°32′S) and Pureora Forest Park for the presence of robin pairs in patches of native broadleaf-podocarp forest by playing a lure territorial call. In 2002, at the beginning of the project, I found robins to be present in 13 patches varying in size and isolation (Figure 3.1; Table 3.1). All the pairs found in the 9 smaller patches were monitored, whereas five pairs were selected from each of 4 largest patches. In the two largest patches (> 300 ha), it was impractical to sample robins throughout the whole area, hence I selected robins from an area of about 5 ha in each these patches. These areas were a minimum of 200 m from the forest edge in order to represent the interior habitat making up the majority of these patches (Norton 2002). All the individuals were caught and banded with unique colour combinations.

In total, 71 distinct robin pairs (133 individuals) were intensively monitored from August to February over three breeding seasons (29 in 2002-03, 36 in 2003-04 and 34 in 2004-05), and survival data were collected from August 2002 to September 2005. The breeding monitoring consisted of checking each pair at least once a week, and recording the breeding stage (non breeding, incubating, with nestlings, or with fledglings) and the number of young present once they fledged. Pairs could usually be located just by walking through the territory, but lure tapes were used occasionally when pairs could not be found easily. Nests were found either by feeding mealworms to the birds (resulting in the male calling the incubating female off the nest or either parent taking the mealworms to the nest) or by observing natural foraging behaviour and movements.

Figure 3.1. Map of the study area showing the 13 studied forest patches (in red). Green indicates other areas of native forest (lighter green) or pine plantations (darker green), whereas grey indicates pasture.

Table 3.1. Characteristics of the 13 studied forest patches. N: number of monitored adults, Area: Area of the forest patches, IFPC: Index of functional patch connectivity, DBH: mean tree diameter at breast height, USH: understorey height, RTR: rat tracking rate (an index of rat density and/or activity); InvBiom. : dry invertebrate biomass, Stream: presence of streams, ResRTR: residuals from the regression between RTR and USH.

#	Patch	N	Area (ha)	IFPC	DBH (cm)	USH (cm)	RTR	InvBiom (g)	Stream	ResRTR
1	12th	2	2	38183	40	0	0.120	1.453	1	-0.125
2	Ballantine 86	3	17	4340	35	39	0.495	2.179	0	-0.066
3	Dennis	6	14	8145	33	57	0.863	1.499	1	0.156
4	Herekawe	31	316	10295	40	54	0.967	1.303	0	0.284
5	Little Tutu	2	2	2501	30	60	0.440	0.850	0	-0.292
6	Mangaaruhe	13	106	2322	36	36	0.787	1.600	1	0.250
7	Mangapehi	23	1625	95456	44	67	0.880	1.570	1	0.092
8	Thompson 37	3	3	13720	20	10	0.300	1.327	0	-0.026
9	Thompson 38	20	72	4170	30	74	0.733	1.525	1	-0.112
10	Thompson 74	6	14	6989	36	12	0.223	1.754	0	-0.119
11	Thompson 91	11	147	56320	34	40	0.803	1.758	0	0.234
12	Te Hape	7	47	3236	29	36	0.397	1.682	1	-0.140
13	Tutu	6	5	2113	45	100	0.920	1.814	1	-0.136

Predictors of vital rates

As an estimate of relative predator density and activity, a rat tracking index was calculated for each patch, based on the proportion of baited tracking tunnels showing rat imprints in each patch. The tunnels were spaced out by 50 m and arranged as grids of 4x4, 3x3, or 2x2 with one in the middle, depending on the size of the patch. They were baited and checked 24 hours later, and this procedure repeated every 6 weeks during the breeding season. The rat tracking index was obtained by calculating the average tracking rate in each patch over the total number of samples. See Boulton (2006) for details on the design.

Food availability has been shown to impact nest success in robins (Boulton 2006) and other bird species (Martin 1987; Simons & Martin 1990; Rodenhouse & Holmes 1992; Williams *et al.* 1993; Evans *et al.* 1997; Sjoberg *et al.* 2000), as well as juvenile and adult survival (Boutin 1990; Oro & Furness 2002). Food availability was estimated at the territory scale by the dry biomass of ground invertebrates sampled by a grid of 2x3 continuous kill pitfall traps in each territory, collected every 6 weeks. The traps within each grid were separated by a distance of 10 m, and the grid was situated relatively to the first recorded nest of each robin pair. See Boulton (2006) for details on the method. The food availability for each individual was calculated as the mean dry biomass of the samples collected over the time period each individual was monitored for.

In a previous analysis in the same study area using robin presence-absence data at random sites within the forest patches, I found that robin presence was positively correlated with the mean diameter at breast height of tree trunks and with the amount of understorey (Chapter 2). I therefore considered the averages of both variables, calculated for each patch over the sampled locations.

Because of a strong correlation between the amount of understorey and the rat tracking index (linear regression: $r = 0.749$), these variables were not included simultaneously in any model to avoid collinearity. However, the residuals of this regression were used to represent some habitat variables not directly measured that could potentially have an impact on robin vital rates.

By observing the habitat choice of translocated adults on Tiritiri Matangi Island and at Boundary Stream, it has been suggested that robins tend to prefer territories where a stream is present (Armstrong *et al.* 2000; Clubb 2003). A binary variable was created at the patch level and considered in the models, where 1 was assigned to patches where the majority of the robin territories included a stretch of stream and 0 otherwise.

The area and connectivity of each patch were also considered, as they were shown to be important variables in explaining the occurrence of robins in the study area (Chapter 2). I used the same functional connectivity index of the forest patches as in Chapter 2. This index includes the area of neighbouring forest patches and their functional connectivity (least-cost distance) to each studied patch. Both patch size and isolation were log-transformed.

Adult survival

Once an adult robin was banded, its subsequent presence or absence was recorded three times of year, in September, January and May, giving 10 encounter occasions from September 2002 to September 2005. Data from several weekly visits were used on each of these occasions, and this approached allowed detection probability to be equal to one given that robins were rarely absent during a check.

In addition to rat abundance/activity, food availability, mean tree trunk diameter, understorey height, presence of streams, patch area and isolation, the sex of the individuals was also included in this analysis, as robin females alone incubate the eggs and are therefore more prone to predation than males during the breeding season. The sex of adults was initially assessed by plumage (older males have darker plumage than females or first-year males), and then confirmed from breeding behaviour (males feed females during courtship as well as females being the only sex to incubate). The variability in adult survival over time was initially assessed by considering variations between capture occasions, years or seasons. The best model from the assessment of variations in survival rate among time and between sexes was selected as a base model for the subsequent analyses.

The analysis of adult survival was performed in program MARK (White & Burnham 1999) using a recapture-only approach and by fixing the resighting probability to one. All variables were standardized. Because the number of independent variables was relatively high and because I had limited *a priori* knowledge of their actual effects, I could not limit the analysis to a small set (e.g. 4-20) candidate models as recommended by Burnham and Anderson (2002). I instead used a forward selection from the base model previously mentioned, where the independent variables were added one at a time, the model with the lowest AIC_c (Akaike's Information Criterion, corrected for small sample sizes) was selected, and this step was repeated until the addition of further variables did not decrease the AIC.

In addition to the forward selection, the difference in survival among patches was assessed by considering a model where survival rate was estimated separately in each patch. The interaction between rat tracking rate and sex was also tested in order to assess whether the difference in survival between males and females changed according to the level of rat abundance.

Productivity

I defined productivity as the number of fledglings reaching independence per female per breeding season. Fledglings were considered to reach independence four weeks after leaving the nest, as this is the minimum age at which North Island robins stop receiving food from their parents (Armstrong *et al.* 2000). Powlesland (2000) observed that the age at independence for robins varies between 4 and 6 weeks after fledging, but after 4 weeks it becomes impossible to separate mortality from emigration when a fledgling is recorded as absent. The number of fledglings could be counted accurately given that they become very noisy and conspicuous as they are near independence, and because there are only 1-3 fledglings per brood.

As the pairs were followed over three breeding seasons, the lack of independence between successive observations for the same female needed to be accounted for. I therefore analysed the productivity data using a generalised linear mixed modelling approach where the female was treated as a random factor. This analysis was performed with the statistical package R (R Development Core R Development Core Team 2006) using the function glmmPQL from the MASS package (Venables & Ripley 2002), which uses a penalized quasi-likelihood algorithm for calculating model likelihood. I also initially considered models where the forest patch was included as a random factor. However, preliminary analysis indicated that the standard deviation of the random intercept associated with forest patch was extremely low ($< 10^{-4}$), hence only the female was included as a random factor in the subsequent analysis.

The dependent variable in this analysis was the number of fledglings that reached independence per female per year, assumed to follow a Poisson distribution. In addition to the independent variables previously described, variations in productivity between breeding seasons were analysed by including the breeding season, coded as dummy variables. Variable selection was performed using the same approach as for the survival analysis, i.e. by stepwise forward selection based on AIC.

Results

Adult survival

Preliminary analyses showed that survival was higher for males than females, higher in summer (January-May) than during the other two seasons, and constant among years. Therefore, the base model for model selection was {Summer+Sex} (Table 3.2, model 5). Under this model, annual survival for males was estimated to be 0.754 (95% confidence interval: 0.633-0.834) and 0.591 (0.282-0.806) for females. The 4-month survival rate over the summer was 0.939 (0.859-0.975) for males and 0.888 (0.657-0.970) for females, and 0.896 (0.858-0.925) for males and 0.816 (0.655-0.912) for females during the rest of the year. The difference in survival between males and females was found to remain constant over the range of variation in the index of rat abundance, as the addition of the interaction Sex*RTR to the model {Summer+Sex+RTR} (Table 3.3, model 8) led to an increased AIC_c of 459.92 (ΔAIC = 2.03). This difference was also similar when the index of rat abundance was substituted by the amount of understorey (model {Summer+Sex+USH+Sex*USH}: AIC_c = 458.75 vs. model {Summer+Sex+USH}, ΔAIC = 2.00).

Adult survival was variable between forest patches (model 1 vs. model 4 in Table 3.3; Figure 3.2), indicating that habitat quality varies among patches. However, the survival rates could not be estimated in two patches, 12th and Little Tutu (Figure 3.2), as the former had only one pair that survived over the whole study period and the latter had only one pair that disappeared within the first time interval after capture.

After forward selection from the base model (Table 3.2, model 5), the best model (model 2) indicates that the variation in survival among forest patches was due to a positive effect of tree trunk diameter on adult survival (β_{DBH} = 0.593, s.e. = 0.163), a negative effect of understorey height (β_{USH} = -0.719, s.e. = 0.231) and a positive effect of the presence of streams in the forest patches (β_{stream} = 0.776, s.e. = 0.330). Substituting rat tracking rate for understorey height led to an important increase in AIC_c despite the strong correlation between these variables, suggesting that the amount of understorey better explained variations in survival than the index of rat abundance. The effects of understorey and the presence of streams were residual effects, significant only after controlling for the diameter of tree trunks, as indicated by their high AIC_c when these variables are considered alone (Table 3.3, models 7 and 9, relatively to model 4).

Adult survival was not related to the area (Table 3.3, model 5 vs. 4) or to the isolation (model 6) of the patches, and did not reveal the existence of an edge effect (model 11). Adding these variables did not improve the best model (Table 3.2, model 2), and none of the variables included in the best model were significantly correlated with patch size, patch isolation or distance to edge. Survival was also unrelated to food abundance (Table 3.3, model 10 vs. 4) as estimated from the dry biomass of invertebrates in each territory.

Although not considered *a priori* in the models, the residuals of the regression between the index of rat abundance and understorey height were found to have a significant positive effect on adult survival (Table 3.2, model 1: β_{ResRTR} = 0.464, s.e. = 0.185), and this effect was not residual as the model including only this variable (Table 3.3, model 2) performed better than any other model including only one of the considered habitat variables.

Table 3.2. Forward stepwise selection of survival models based on AIC_c (Akaike's Information Criterion corrected for bias), with the most parsimonious models at the top. Additionally, the model #1 represents the *a posteriori* inclusion of the residuals of the regression between the rat tracking rate and USH (ResRTR) in the best selected model (#2).

#	Model	AIC_c	Δ AIC_c	AIC_c weights	Deviance	Num. of par.
1	Summer+Sex+DBH+USH+Stream+ResRTR	440.98	0.00	0.86	426.80	7
2	Summer+Sex+DBH+USH+Stream	444.99	4.01	0.12	432.86	6
3	Summer+Sex+DBH+USH	448.85	7.88	0.02	438.76	5
4	Summer+Sex+DBH	452.67	11.70	< 0.005	444.61	4
5	Summer+Sex	456.57	15.60	< 0.005	450.54	3
6	Constant	463.80	22.82	< 0.005	461.79	1

Table 3.3. Models considering each variable in addition to the base model (#4). DistToE: distance to edge.

#	Model	AIC_c	Δ AIC_c	AIC_c weights	Deviance	Num. of par.
1	Summer+Sex+Patch	449.51	0.00	0.61	422.94	13
2	Summer+Sex+ResRTR	452.22	2.71	0.16	444.16	4
3	Summer+Sex+DBH	452.67	3.16	0.13	444.61	4
4	Summer+Sex	456.57	7.06	0.02	450.54	3
5	Summer+Sex+Area	456.70	7.19	0.02	448.64	4
6	Summer+Sex+IFPC	456.73	7.22	0.02	448.67	4
7	Summer+Sex+USH	456.75	7.23	0.02	448.68	4
8	Summer+Sex+RTR	457.89	8.38	0.01	449.83	4
9	Summer+Sex+Stream	457.92	8.40	0.01	449.86	4
10	Summer+Sex+InvBiom	458.08	8.57	0.01	450.02	4
11	Summer+Sex+DistToE	458.42	8.91	0.01	450.36	4

Table 3.4. Correlation matrix of the considered variables. The elements under the diagonal represent the Pearson correlation coefficients, and the elements above the diagonal the p values.

	Area	**IFPC**	**DBH**	**USH**	**RTR**	**InvBiom**	**Stream**	**ResRTR**
Area	1	*0.231*	*0.265*	*0.337*	*0.019*	*0.476*	*0.657*	*0.014*
IFPC	0.357	1	*0.494*	*0.329*	*0.995*	*0.998*	*0.843*	*0.216*
DBH	0.334	0.209	1	*0.197*	*0.144*	*0.331*	*0.281*	*0.494*
USH	0.289	-0.294	0.382	1	*0.002*	*0.997*	*0.292*	*0.998*
RTR	0.639	0.002	0.428	0.778	1	*0.794*	*0.434*	*0.021*
InvBiom	0.217	-0.001	0.293	-0.001	0.081	1	*0.733*	*0.671*
Stream	0.136	-0.061	0.323	0.316	0.238	0.105	1	*0.966*
ResRTR	0.660	0.368	0.209	0.001	0.628	0.130	-0.013	1

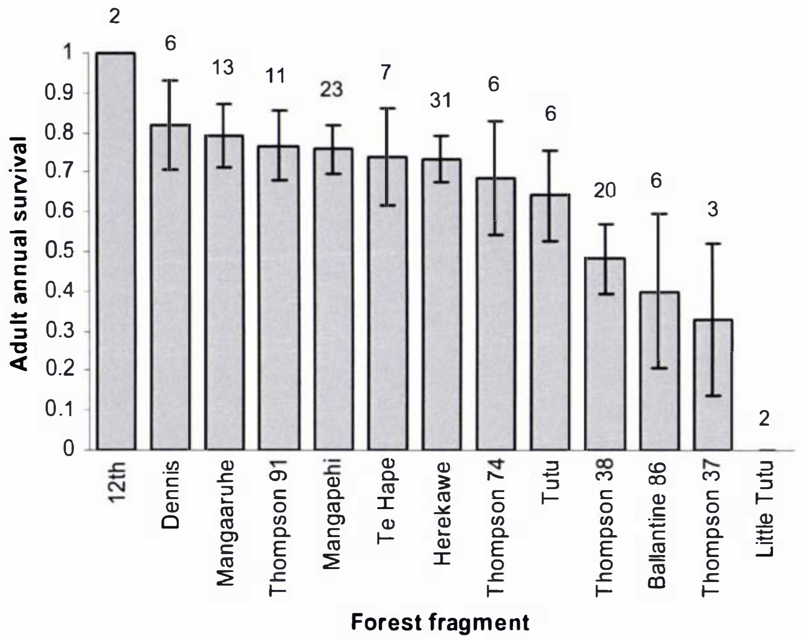


Figure 3.2. Estimates of adult annual survival in each forest patch from model 1 (Table 3.3). The standard errors shown are estimated using variance components to correct for sampling variation. The numbers of marked individuals in each patch are indicated.

Productivity

The best productivity model was the constant one (Table 3.5), indicating no significant effect on productivity of food or rat abundance, understorey height, diameter of tree trunks or the presence of streams. There were also no significant effects of year, size or isolation of the forest patches, or of the distance to edge. However, the estimated coefficients associated with the considered variables show some trends mostly in the expected directions that were not significant, possibly due to their associated large standard errors (Table 3.5).

Under the constant model, the mean logarithm of the number of juveniles that reached independence produced per year and per female was estimated to be 0.097 with an associated standard error of 0.124. This corresponds to an average number of 1.102 juveniles produced per female per year with a standard error of 1.283.

Table 3.5. Forward stepwise selection of productivity models on AIC. The estimated coefficients associated with each standardized variable are represented with their standard error.

Model	AIC	Δ AIC	AIC weight	Coefficient	s.e.
Constant	127.406	0.000	0.159		
InvBiom	128.121	0.715	0.111	0.124	0.109
Stream	128.124	0.718	0.111	0.251	0.221
DistToE	128.304	0.898	0.102	-0.116	0.111
IFPC	128.413	1.006	0.096	-0.126	0.114
Area	128.520	1.114	0.091	-0.102	0.108
ResRTR	128.723	1.317	0.082	-0.089	0.106
RTR	129.034	1.628	0.070	-0.091	0.102
DBH	129.345	1.939	0.060	-0.027	0.109
USH	129.404	1.997	0.059	-0.006	0.108
Year	129.430	2.024	0.058		

Discussion

Adult survival but not productivity was found to be related to some habitat variables I considered, as it is positively correlated with the diameter of tree trunks and the presence of streams, and negatively correlated with understorey height. These effects are most likely to be indirect and related to other variables not considered in the present study but directly affecting robin survival. Forests with larger trees are older and might provide better food resources to robins. However, the dry biomass of ground invertebrates was neither related to adult survival nor productivity, although the lack of relationship might arise from a low statistical power induced by a high variability between the pitfall trap contents (Boulton 2006).

It has been suggested that robins preferentially establish their territories where streams are present (Armstrong *et al.* 2000; Clubb 2003), and their beneficial effect on adult survival indicates that they increase habitat quality to robins, perhaps because of a higher quantity and diversity of invertebrates there. This hypothesis could unfortunately not be tested because the design of pitfalls did not sample the amount of invertebrates around the streams because the grids of pitfall traps were placed according to the first discovered nest of each pair (Boulton 2006), which was seldom located by a stream.

A high understorey was found to be detrimental to robin adult survival. This contrasts with my analysis of presence-absence data, which showed that robin occurrence was positively correlated with the amount of understorey (Chapter 2). Clubb (2003) also found robin presence to be positively correlated with dense understorey at Boundary Stream Mainland Island. Pig, rabbit, hare, goat, sheep and cattle are common grazing non-native animals in the study area where the forest patches are not properly fenced off by the farmers, and grazed patches were expected to constitute a poor quality habitat for robins. However, the amount of understorey was strongly correlated with the index of rat abundance among the patches, and also in other studies in New Zealand and Australia (King *et al.* 1996; Cox & Cox 2000; Harper *et al.* 2005), and robins are known to be highly susceptible to rat predation (Flack & Lloyd 1978; Brown 1994; Armstrong *et al.* 2006). Although understorey height was a much better predictor of survival rate than the index of rat abundance, it is possible that the index of the amount of understorey better reflects abundance and/or foraging activity of rats than tracking rates do. Moreover, it has been suggested that tracking rates differ between vegetation types, making their comparison difficult (Blackwell *et al.* 2002).

The contrast of understorey effects on survival and presence-absence suggests that robin habitat selection behaviour may not be suitable in the presence of rats in that they preferentially select habitat that is also preferred by their key predator. This is quite plausible given that rats and other carnivorous mammals are exotic to New Zealand, and New Zealand robins evolved in an environment where their main predators would have been bird species unlikely to have been favoured by dense understorey. In absence of rats, dense habitats might be of better quality to robins, but the cost arising from the high density of rats probably now overcomes the benefit of such habitat. This hypothesis leads to the prediction that the effect of understorey height on survival should vary according to presence of exotic mammals, i.e., that it will be positively correlated with understorey height on islands or mainland island where rats are scarce or absent, and negatively correlated in mainland forests where rats are abundant.

Considered *a posteriori* in the survival models, the residuals of the regression between rat tracking rate and the amount of understorey in each patch proved to be strongly positively correlated with adult survival, i.e. robin survival is higher where rats are more abundant or active than expected from the amount of understorey. This emphasises the complexity of the relationship between rats, intrinsic habitat quality (i.e. without rats) and robin survival, and suggests that some other factors not considered in this study might affect the survival of adult robins and be might be beneficial for both rats and robins.

Adult survival differed significantly between males and females. The lower survival of robin females is attributable to their higher sensitivity to predation events, as only the females incubate the eggs. This difference between sexes was also found at Paengaroa Mainland Island at times when mammalian predators were not intensively controlled (Armstrong *et al.* 2006), whereas survival rates of males and females are very similar on Tiritiri Matangi Island where there are no mammalian predators (Armstrong & Ewen 2002). In addition, the estimated annual male survival probability of 0.750 for the study area was very similar to that of 0.79 estimated for Tiritiri Matangi (Armstrong & Ewen 2002). The non-significant interaction between rat abundance and sex does not necessarily mean that the difference in survival between adult males and females was not due to rat predation, and may simply reflect the limitations of tracking tunnels for indexing differences in rat abundance/activity among the patches. However, other predators such as rats and mustelids and possums are also known to take robins (Brown *et al.* 1996). The populations of possums in the study area were maintained at low densities by trapping operations during a tuberculosis eradication program, and possums are unlikely to have a significant impact on adult robin survival. I did not attempt to index the abundance of mustelids as their territories are very large (Miller *et al.* 2001) and can therefore encompass several studied forest fragments, making the comparison of densities impossible between fragments. However, the degree of their impact on native birds is not well known and further research is needed. Indeed, stoats have been shown to shift between rats and birds, depending on the abundance of rats in podocarp forests (Murphy *et al.* 1998), which complicates the study of a single predator's density on robin survival.

I did not find any relationship between the considered variables and robin productivity, defined as the number of juveniles produced per female per year. However, using the same data set as this study, nest success, i.e. the probability for a nest to successfully produce fledglings, has been shown to be food limited (Boulton 2006), and productivity has been shown in Paengaroa Scenic Reserve to be affected by the control of predators (Armstrong *et al.* 2006). As illustrated in the results section, it is possible that the lack of relationship might arise from a lack of statistical power because of a high variability in productivity, and more studied pairs in more patches would be necessary in order to fully support the present result.

Although I found that robin presence-absence was mainly driven by the isolation of forest patches (Chapter 2), I did not find any effect of patch size or isolation on robin adult survival and productivity. Adult survival is variable between patches (Figure 3.2; Table 3.3) but this variability is due to differences in local habitat that were not related to the patch size or isolation (Table 3.4). Habitat fragmentation therefore does not seem to have a detrimental impact on habitat quality for robins in the study area. Although some relationships might be detectable with larger sample sizes, the lack of effect of habitat fragmentation on habitat quality (and vital rates) has been the conclusion of several studies in Australia (e.g. Matthews *et al.* 1999; Zanette 2000) with only two studies showing an effect of habitat fragmentation on vital rates (Major *et al.* 1999; Luck 2003).

The fact that the isolation-driven occurrence of robins (Chapter 2) is not reflected by the analysis of vital rates suggests that the dispersal behaviour of this species is driving its distribution. Robins evolved in a continuous forest that used to cover most of the North Island (Ewers *et al.* 2006) and gaps of farmland between forest patches are likely to be unfamiliar to this species and might impede individual movements. The effect of landscape configuration on dispersal is addressed in Chapters 4-5.

4- Application of choice analysis to radio-tracking data to quantify species gap sensitivity during dispersal

Abstract

Habitat fragmentation leads to a decrease in exchange rate of individuals between populations, potentially leading to higher risk of local extinction. Understanding the dispersal behaviour of species in fragmented landscapes is fundamental to predict the effects of habitat fragmentation, for an efficient management and ultimately to improve their persistence in these landscapes. Whereas dispersal probability may be a function of Euclidean distances in aerial dispersing species, dispersal of species that avoid matrix habitat will be strongly dependent on the gaps they need to cross. In this chapter, I develop a method to quantify the maximum length of landscape barriers (or "gap") one individual can cross, using modern GIS techniques.

I applied the method to natal dispersal data of North-Island robins (*Petroica longipes*), an endemic passerine of New Zealand, inhabiting remnant forest patches within a pastoral landscape in central North Island. Over 3 years, the daily locations of 38 radio-tagged juveniles were recorded during their dispersal. The dispersal path between each of the 220 pairs of successive locations was inferred by calculating the least-cost path between them in a geographic information system, based on costs assigned to different vegetation types. Each of these paths was compared to least-cost paths to a maximum of 10 randomly selected destinations at a similar Euclidean distance from the starting location. The factors considered were the costs of the paths, the maximum gap length crossed and the turning angle. Conditional logistic regression was used to compare the inferred path to the randomly selected paths, and to determine the factors affecting the juveniles' preference.

As expected, I found that juveniles move preferentially in vegetated areas of the landscape and their movements are impeded by large gaps of farmland. Based on the 95-percentile of the distribution of choice probability, I found that juveniles are unlikely to cross gaps larger than 100 or 200 m of open farmland, depending on the costs assigned to the vegetation types. My analysis did not support the idea of a preference for straight paths due to robins being constrained to frequently change direction in this patchy landscape.

The weak gap crossing ability of the New Zealand robin is likely to have important consequences on its population dynamics and persistence in fragmented landscapes. I argue that species gap sensitivity needs to be explicitly incorporated into population models and in the development of patch connectivity indices.

Introduction

Metapopulation theory suggests that individual movements of organisms can affect the ability of species to persist in fragmented landscapes (Hanski 1998). When subpopulations' fluctuations are not strongly synchronized by environmental stochasticity, subpopulations can be saved from extinction by the immigration of new individuals (Pulliam & Danielson 1991; Dias 1996). Habitat fragmentation, by increasing the isolation of patches, leads to a decrease in this rescue effect and in the re-colonisation rate and thus to a decrease in the species persistence at a regional scale. To predict and mitigate the effects of fragmentation, it is necessary to understand the dispersal behaviour of the species of interest.

The degree of patch isolation experienced by any species depends on the ability of individuals to move through the matrix, the non-suitable habitat between patches (Beier & Noss 1998). Until recently, most population models assumed a homogeneous matrix, ignoring the spatial variations in its resistance to movements due to its composition and/or its configuration (e.g. Doak *et al.* 1992; Thomas *et al.* 1992; Doebeli 1998; Moilanen & Hanski 2001; but see Ricketts 2001). Dispersal was then treated over-simplistically and individuals were considered able to move to any location, within a certain distance following a negative exponential distribution. This assumption is likely to be valid for particular species like butterflies (Hanski *et al.* 1996; but see Sutcliffe *et al.* 2003) and for plants whose pollen or seeds are dispersed by wind, but is likely to be erroneous for species whose movements strongly interact with the features of the matrix. For many forest dwelling species, individuals' movements are suspected to be inhibited by gaps in the vegetation cover (Taylor *et al.* 1993; Rosenberg *et al.* 1997; Brooker *et al.* 1999; Grubb & Doherty 1999), and in this situation, the effect of patch isolation can be lessened by the establishment of corridors of vegetation.

Attempts to quantify the gap crossing ability of forest dwelling species have mainly been based on homing behaviour after translocation of adults (Pither & Taylor 1998; Bélisle & St. Clair 2001), on the path choice of individuals to reach the closest habitat after translocation in the matrix (Bakker & Van Vuren 2004), or on the movement of individuals in response to mobbing calls (Desrochers & Hannon 1997; Sieving *et al.* 2000; Harris & Reed 2001; Bélisle & Desrochers 2002; Creegan & Osborne 2005). These approaches all involve direct or indirect manipulation of individuals, whose behaviour might be affected by induced stress. Furthermore, the movements studied in these experiments are mainly small routine movements by adults whose behaviour might differ from long directed dispersal movements mainly achieved by juveniles (Ims 1995; Zollner & Lima 1999; Van Dyck & Baguette 2005). Although these studies are important for the knowledge of local routine movements in fragmented landscapes, the extrapolation of adult behaviour to dispersing juveniles is highly questionable. Brooker et al. (1999) quantified the gap crossing ability of two small passerines in the Western Australian Wheatbelt, but their analysis was aided by a linear configuration of the vegetation cover and patches were generally connected by single paths. In most cases though, the path of individuals cannot be directly inferred from successive locations because the configuration of the matrix is generally non-linear with the vegetation structures facilitating movements patchily distributed and many paths are therefore possible between two recorded locations.

Quantifying the maximum gap length individuals can cross would ideally use data from continuous tracking of dispersal, meaning exact dispersal paths were known.

Radio-tracking is a common technique to follow the dispersal of individuals, but radio-tracking data generally consist of discrete points in time and space. For species whose dispersal is strongly impeded or facilitated by the features of the landscape, the straight line connecting two consecutive points may greatly misrepresent the actual paths taken. The shortest path using these features and avoiding landscape barriers may be more realistic and can be calculated using least-cost path modelling, now available in most modern GIS packages (Christofides 1975; Chou 1997). Least-cost path models are starting to be used commonly in fragmentation studies to calculate indices of landscape or patch connectivity (Schippers *et al.* 1996; Adriaensen *et al.* 2003; Stevens *et al.* 2006) or to identify potential corridors (Hargrove *et al.* 2005).

In order to demonstrate the preference of individuals for dispersing among vegetation structures and to quantify the maximum length of hostile habitats individuals can cross ("gaps"), the least-cost paths inferred from radio-tracking data need to be compared to the different possible routes offered to a disperser. This problem is similar to that faced by marketing studies looking at the preferences of customers for certain products, or preferences of tourists for vacation destinations, and these problems have been tackled using choice analysis (e.g. Ben-Akiva & Lerman 1985). This approach has been used in ecology to understand the diurnal bed site selection by elk (Cooper & Millspaugh 1999) and to show the influence of wolves on wapiti movements (Fortin *et al.* 2005), but never to my knowledge to quantify the gap crossing ability of species.

In New Zealand, *Petroica* species are thought to have poor natural dispersal abilities (Flack 1976). However, some individuals showed after translocation a tendency to return to their initial territory, crossing inhospitable habitats and large gaps even over large distances, the most extreme case being one tomtit (*P. toitoi*) flying back to its territory after translocation to an offshore island located 56 km away (Parker *et al.* 2004). Movement behaviour after translocation might nevertheless be not representative of natural juvenile dispersal and one should use radio-tracking data of naturally dispersing individuals in fragmented landscapes to quantify the gap crossing ability of species.

I earlier showed that North Island robins (*Petroica longipes*) tended to be absent in forest remnants isolated from neighbouring patches and also from the closest continuous forest (Chapter 2). However, the examination of vital rates did not reveal any relationship between patch isolation and adult survival or productivity (Chapter 3). I therefore predict that the observed pattern of robin distribution is attributable to a limited natal dispersal in such fragmented landscape, i.e. that individuals are not able to cross large gaps of pasture.

The goals of this study is to assess whether robins use the woody vegetation features of the landscape as corridors for their dispersal and to estimate the length of maximum gap of pasture they can cross to quantify their gap sensitivity using choice modelling of radio-tracking data of dispersing juvenile robins.

Methods

Model species and study area

The North Island robin is an endemic passerine of New Zealand, and weighs approximately 30 g. Its typical habitat is mature native broadleaf-podocarp forest. Its diet is mainly composed of invertebrates from the leaf litter. It is socially and genetically monogamous, with pair bonds usually retained throughout the breeding season and subsequent years until the death of the partner. It is very territorial and non migratory, and its detectability is particularly high due to its inquisitiveness and strong response to territorial lure calls. North Island robins greatly declined in range since human colonisation (Bell 1986) although they can still be locally abundant (Robertson *et al.* 2007) and good quality data can be obtained from this species of conservation interest.

The study area is an area of 15,000 ha in the central North Island of New Zealand between the township of Benneydale (175°22′E, 38°32′S) and Pureora Forest Park. 71 different breeding pairs of adult robins were intensively monitored each year for three breeding seasons (29 in 2002-03, 36 in 2003-04 and 34 in 2004-05) in 13 forest patches varying in size and isolation.

Radio-tracking of juvenile dispersal

Juveniles from the successful nests were caught 4 to 5 weeks after fledging, the age when they become independent and potentially begin to disperse (Armstrong *et al.* 2000). A total of 53 juveniles (18 in 2002-03, 18 in 03-04 and 17 in 04-05), were fitted with a Holohil® BD-2 transmitter of 1.05 g. The transmitters were attached using a Rappole harness around the legs (Rappole & Tipton 1991) and the sample sizes reflected the numbers that could be monitored adequately by one person. I selected juveniles to maximize the number of forest patches they originated from and also to minimize the use of siblings. I only sampled one juvenile from any one brood.

Due to the short lifetime of the transmitters (maximum 6 weeks), the tracking period was too short to follow all the radio-tracked juveniles until they settled. I therefore doubled the tracking period in 2003-04 and 2004-05 by recapturing each juvenile when its transmitter began to fail. Juveniles were checked every two days while still in the natal territory, then every day after they left. At each check, the position of the bird was recorded with a Garmin® handheld global positioning system (GPS) (Olath, Kansas, USA), with an average accuracy of 10 metres.

I used data for all juveniles that moved more than 150 m, even if they were found dead or if their signal was lost, as the sampling units were the daily dispersal steps and not the final settlement locations.

GIS data preparation

Base GIS

The GPS locations of the radio-tagged juveniles were transferred into a geographical information system (GIS) that included the vegetation cover of the study area. Vegetation was classified as mature native broadleaf/podocarp forest, exotic pine plantation (*Pinus radiata*), pasture and shrubs, which were mainly composed of manuka (*Leptospermum scoparium*), kanuka (*Kunzea ericoides*) and young totara (*Podocarpus totara*). The vegetation cover map had a cell resolution of 15 m and was manually digitized from recent high-resolution aerial photographs and satellite images to ensure the adequate representation of all the vegetation features of the landscape, including individual trees in pasture.

Vegetation costs

In order to infer the least-cost paths from radio-tracking locations, I created two alternative models for the relative costs of moving through different vegetation types as perceived by robins. These models were based on my experience in the field where robins appeared to most readily move through mature native forest, less readily through exotic plantation, even less in shrubs, and are reluctant to cross pasture. The two cost sets reflect my uncertainty about the relative costs of moving through each vegetation type, especially around the cost of moving through pasture relative to other vegetation types (woody vegetation). Under the most constraining cost set (2-4-7-100), least-cost paths typically consisted of long detours to avoid pasture, whereas least-cost paths included more pasture in the less constraining set (1-2-3-10). An illustration of the difference between the two cost sets is shown in Figure 5.2 (p. 67).

"Observed" vs. random dispersal steps

In order to study the effect of the landscape configuration on individual movements during dispersal, I compared each dispersal step to alternative steps of the same

Euclidean distance, both of which were calculated using a least-cost path approach as described above. A sample of 10 alternative points of similar Euclidean distance was chosen for each observed point, with the constraint that the random point could not be in pasture (Figure 4.1). Because there were often few alternatives at exactly the same Euclidean distance, I allowed the random points to fall within a 200 m-wide doughnut-shaped band with mean Euclidean distance equal to that of the observed point (see Appendix 2).

For each least-cost path to the randomly selected end points and to the observed one, the maximum gap of pasture crossed was calculated, as well as the relative cost, defined as the ratio of the cost to the least-cost path length. The relative cost represents a standardized index of connectivity between each starting and end points, comparable for dispersal steps of different lengths. An individual might prefer an area with a greater woody vegetation cover over scattered trees in pasture, and the relative cost was used to test whether movement decisions of juveniles were based on a larger spatial scale than the gaps they encountered.

I also calculated the turning angle, defined as the angle between the previous dispersal step and the current step, for each observed and alternative step, as I predicted that juveniles would tend to move in a straight direction.

I developed a script to select the alternative steps, infer least-cost paths, and calculate the relative cost, the maximum gap crossed and the turning angle automatically for each dispersal step. This script is written in Python for ArcGIS 9.0 (ESRI, Redlands, California, USA) and is freely accessible at http://tur-www1.massey.ac.nz/~darmstro.

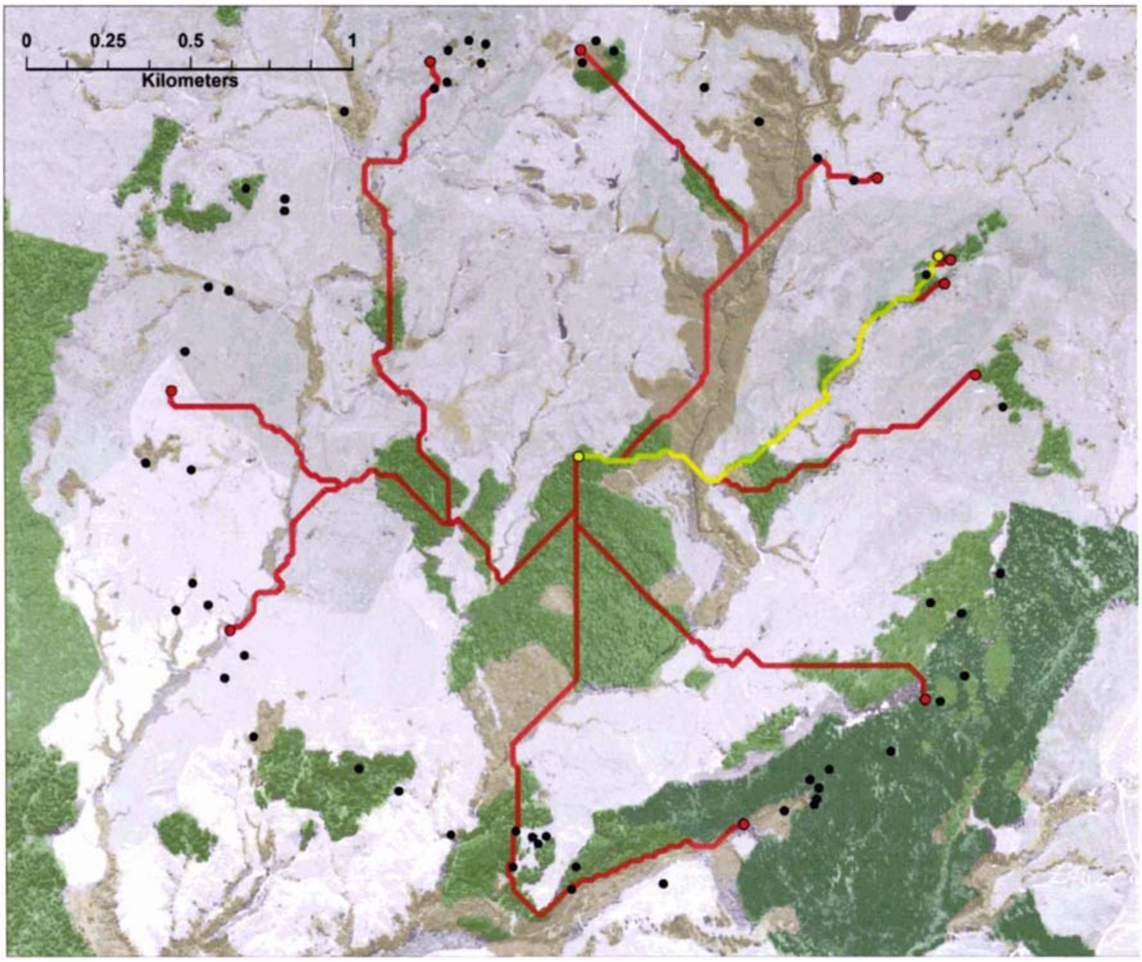


Figure 4.1. Example of an observed dispersal step (in yellow) matched to 10 alternatives (in red). The black dots represent the set of potential alternatives from which the selected ones were sampled.

Discrete choice analysis

To examine landscape factors influencing juvenile dispersal, the choice of observed steps relative to alternatives cannot be modelled with a standard logistic regression as the choice at each step is conditional to the available alternatives. An appropriate solution is to fit a conditional logistic model. This can be performed with the PHREG procedure in SAS (Kuhfeld 2001), which is generally used for Cox proportional hazards models, but can also be applied to conditional logistic regression because their likelihood functions are similar (Chen & Kuo 2001). The data only need to be previously prepared to be equivalent to survival data, where the preferred choice is said to occur at time 1 and all other choices are said to be censored (Kuhfeld 2001). The theory behind the conditional logistic regression in an ecological context have been described in Fortin *et al.* (2005) and for the closely related multinomial logit regression in Cooper & Millspaugh (1999).

The case-control design I used presents two strata: the individual and the observed steps matched to their 10 alternatives. However, because the mean number of observed steps per individual was low, I removed the strata of individuals from the models, assuming the dispersal steps to be independent within and between juveniles, and only considered the stratum of steps. This assumption was supported by the examination of a 3-D scatter plot representing the relative cost, the maximum gap crossed and the turning angle of each step, labelled by individual, in which no pattern of dependence of steps within or between juveniles was apparent.

Two conditional logistic regressions were performed in SAS 9.1 (SAS Institute 2003). Because there is no turning angle for the first dispersal steps for each juvenile, two datasets were created: one set to assess the effect of relative costs and maximum gaps, and a reduced set to assess the additional effect of turning angle. The whole procedure was done for both cost sets in order to assess the sensitivity of the results to my uncertainty about the assignment of the costs to the different vegetation types.

Once the set β of parameters has been estimated, the probability for an individual to choose a specific path *i* with attributes $MaxGap_i$, $RelCost_i$ and $TurnAngle_i$ and relative to the set of choices *j* is:

$$p_i = \frac{\exp(U_i)}{\sum_j \exp(U_j)}, \text{ where } U_i = \alpha + \beta_1 \cdot MaxGap_i + \beta_2 \cdot RelCost_i + \beta_3 \cdot TurnAngle_i$$

(Equation 1)

Quantification of the maximum gap length

After parameterization of the conditional logistic regression models, I estimated the maximum length of open pasture that a dispersing juvenile is expected to cross under each cost set, based on the distribution of choice probability over a range of gap distances. The 95-percentile value was chosen as the maximum crossable gap length and was calculated from 500 values of gap length evenly distributed between 0 and 500 m. When other parameters are kept constant, the choice probability is equal to the case where all the other parameters are set to 0; they were therefore not considered in the 500 choices to calculate the distribution. As the probabilities of choices are discrete, an estimate of the 95-percentile was obtained by calculating the mean gap length of the two closest choices, weighted by one minus the relative absolute difference of their cumulative probability to 0.95.

Results

Radio-tracking data

Out of 53 radio-tagged juveniles, 38 were relocated out of their natal territory at least once. A total of 220 dispersal steps were recorded, with 1-21 steps recorded per juvenile (median 4.5). Each of the 220 observed steps were matched to between 1 and 10 alternative steps (median 10, mean 7.9), as some observed steps were too short and the number of vegetation features was too low in some places for there to be many comparable alternatives. When the first observed step of each juvenile was removed from the previous dataset to analyse the effect of turning angle, there were 176 remaining steps.

The Spearman correlation between the relative cost and maximum gap is 0.639 under the less constraining cost set and 0.552 under the most constraining one. Their mutual inclusion is therefore unlikely to introduce collinearity in the models.

Discrete choice analysis

Under both vegetation cost sets, both the maximum gap and the relative path cost significantly lower the probability of a step being selected by a dispersing juvenile (Table 4.1; Figure 4.2). This indicates that juveniles prefer woody vegetation to disperse and that large gaps in the vegetation cover impede their movements. In the less constraining cost set (Cost set 1), the relative cost is the most significant variable, whereas the maximum gap length is the most important variable in the most constraining cost set (Cost set 2). These effects remain strongly significant when they are considered separately from each other (models 3 and 4) and when the first steps are removed to assess the effect of turning angle (model 1 vs. model 2). Turning angle did not have a significant effect regardless of the cost set.

Table 4.1. Significance of the relative path cost, the maximum gap length and the turning angle on choices made by juvenile robins during dispersal. The analysis compared the daily movement steps observed compared to other possible steps of the same Euclidean distance.

			Cost set 1 (1-2-3-10)				**Cost set 2 (2-4-7-100)**			
Model	**n**	**Variable**	**β value**	**SE**	**χ^2**	**P**	**β value**	**SE**	**χ^2**	**P**
1	176	Relative cost	-1.047	0.232	20.41	<.0001	-0.054	0.025	4.67	0.031
		Max gap length	-0.014	0.005	7.56	0.006	-0.030	0.007	17.27	<.0001
		Turning angle	0.001	0.002	0.59	0.441	0.002	0.002	1.97	0.161
2	220	Relative cost	-1.020	0.207	24.19	<.0001	-0.055	0.024	5.47	0.019
		Max gap length	-0.015	0.005	10.66	0.001	-0.032	0.007	22.50	<.0001
3	220	Relative cost	-1.524	0.171	79.45	<.0001	-0.152	0.020	56.36	<.0001
4	220	Max gap length	-0.031	0.004	60.50	<.0001	-0.043	0.006	59.41	<.0001

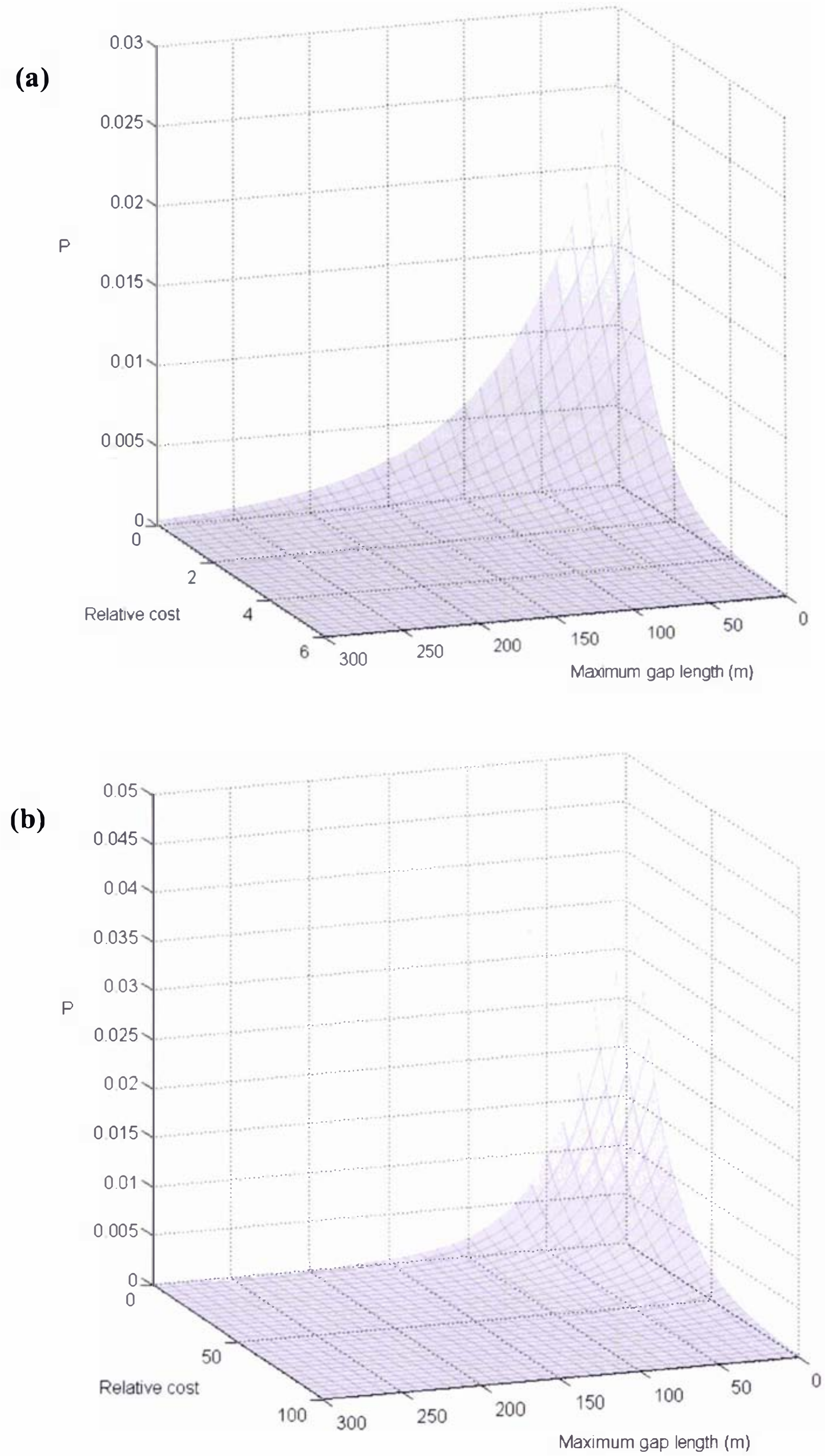


Figure 4.2. Distribution of the path choice probability based on model 2 (Table 4.1), and equation (1) under the most constraining cost set (a) and the less constraining one (b).

Quantification of the maximum crossable gap length

Based on the 95-percentile of the distribution of the choice probabilities under both vegetation cost sets, the maximum gap of open pasture a juvenile can cross is estimated to be 93 m under the most constraining cost set and 201 m under the less constraining cost set (Figure 4.3).

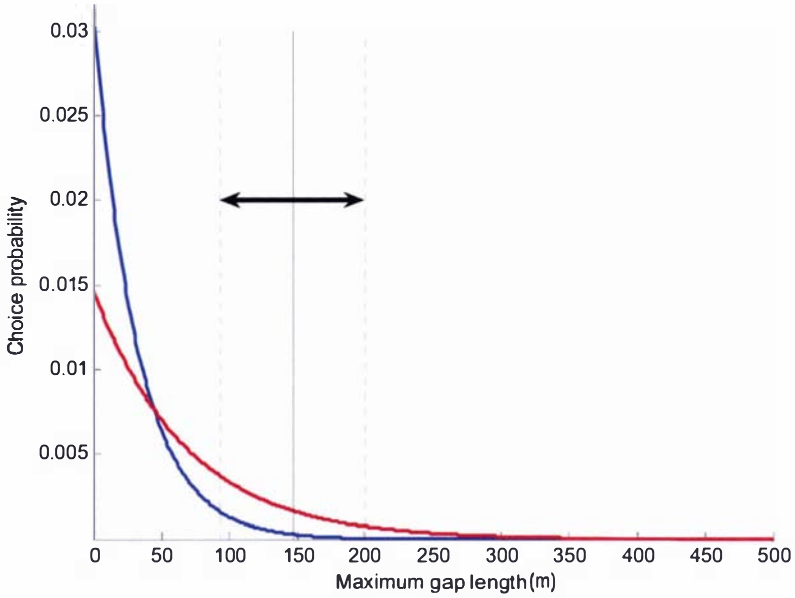


Figure 4.3. Path choice probability under the most constraining cost set (in blue) and under the less constraining one (in red). The vertical dashed lines represent the maximum crossable gap limit based on the 95-percentile under each cost set, and their average is represented by the solid vertical line.

Discussion

The strong significance of the relative cost of least-cost paths in the juveniles' choice of dispersal paths means that the costs I assigned to the vegetation types are useful to explain dispersal in comparison to the null model that costs are equal for all vegetation types, and therefore supports my hypothesis that juveniles' movements are facilitated by the presence of vegetation features in the landscape. This effect was robust regarding the cost I attributed to the vegetation types. The additional negative effect of the maximum gap of pasture crossed using the least-cost paths suggests that juveniles' movements are impeded by large gaps of pasture. My attempt to quantify the maximum length of gap juveniles can cross revealed that juveniles are very unlikely to cross gaps of pasture of more than 150 m (93 m under the most constraining cost set, 201 m under the less constraining one).

Many recent studies quantifying in the quantification landscape connectivity have used least-cost path modelling (Bunn *et al.* 2000; Graham 2001; Ray *et al.* 2002; Adriaensen *et al.* 2003; Chardon *et al.* 2003; Hargrove *et al.* 2005; Rothley & Rae 2005; Chetkiewicz *et al.* 2006). However, least-cost paths do not take gap lengths into consideration, meaning that a path with many small gaps can have the same cost as one with a single large gap. However, a gap-sensitive species is likely to be able to use the former and not the latter. Reliable indices of landscape connectivity or patch isolation should therefore consider species gap sensitivity (e.g. Girvetz & Greco 2007)

This high gap sensitivity is likely to have an important impact on the dynamics of the species in fragmented landscapes. Three quarters of the original indigenous forest has been cleared since human settlement in New Zealand, mainly converted into farmland with many small forest remnants left isolated (Ewers *et al.* 2006) and the distribution of the North Island robin is now clustered around the largest areas of native forest mainly located in the central North Island (Robertson *et al.* 2007). The strong gap sensitivity of robins appears to be a key factor explaining their distribution in the study area, given that their distribution has been found to be strongly influenced by the isolation of the forest patches they inhabit, isolation from the neighbouring patches and also from the major continuous forest adjoining the study area (Chapter 2). Gap sensitivity is a potentially important factor that can lead to large deviations from the ideal free distribution, with individuals establishing their territories in sub-optimal habitats, next to an optimal but unreachable habitat (Matthysen & Currie 1996).

A higher risk of predation in open areas has often been proposed to explain the gap sensitivity of forest birds (Hegner 1985; Lima & Dill 1990; Suhonen 1993). However, predation is unlikely to be the main driving factor in the evolution of New Zealand robin dispersal. Until the recent human colonisation, open areas were quite rare (Ewers *et al.* 2006) and the main threat of crossing open areas probably came from New Zealand falcons (*Falco novaeseelandiae*) which can also hunt in the forest. I suggest that the reluctance of robins for crossing large areas of open pastoral land is related to the lack of evolutionary familiarity with such habitat, and it is likely that this limitation might decrease with evolution if this species can survive the ecological crisis New Zealand has been undergoing since humans colonised it.

Even when controlling for the maximum gap crossed, the standardized cost of each dispersal step was still highly significant to explain the path preference of juveniles. This suggests that juveniles' dispersal choices are made at multiple spatial scales, not only at the gap scale. The overall density of vegetation features in the matrix is also important to facilitate robin movements as juveniles would preferentially move through a forest than using stepping stones formed by individual trees in pasture.

My results did not support the hypothesis of a preference of juveniles for straighter paths. After leaving the natal territory, robin juveniles generally move daily until finding a territory for establishment (pers. obs.). When moving, juveniles are difficult to locate due to their high speed compared to that of the tracker. Therefore the daily locations were more likely to be recorded when the robins had stopped moving. Unlike the assumption in several studies that individuals spend more time in suitable habitat (e.g. Graham 2001), juvenile robins seem to stop for a long time when encountering large gaps of pasture (pers. obs.). They are therefore more likely to be resighted when their path is obstructed. The distribution of observed turning angles (Figure 4.4) seems to support this idea, as it reveals a high frequency of 180° turning angles. A more sophisticated model or more frequent records of dispersal locations would be required in order to assess whether juveniles move in a straighter way in continuous habitat.

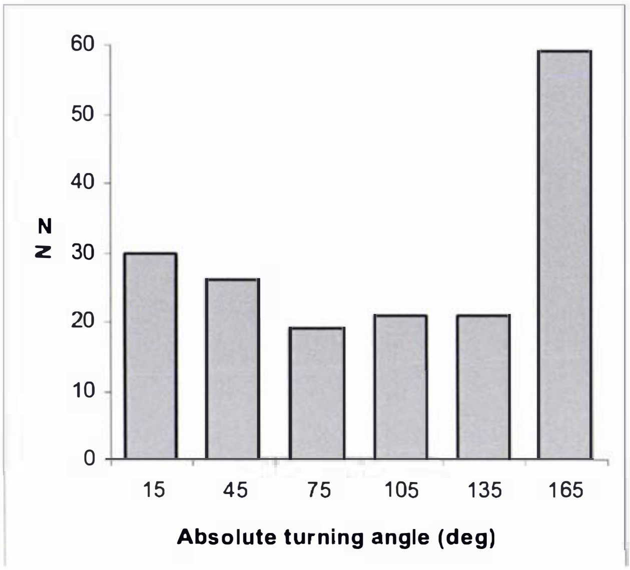


Figure 4.4. Distribution of absolute turning angles among observed steps

Gap sensitivity is an important behavioural trait that should be considered in population dynamics models and connectivity measures, given that landscape gaps can hinder individual movements between populations and prevent colonisation of new habitats. This study provides a mean for quantifying species gap crossing ability based on data on natal dispersal, more reliably than standard homing experiments, and can be applied to a wide range of taxa and situations.

5- Dispersal distances and survival of juvenile robins.

Abstract

I monitored post-fledging dispersal of radio-tagged North Island robins (*Petroica longipes*) in a fragmented pastoral landscape in central North Island of New Zealand. From the monitoring of 53 juveniles over three breeding seasons, data on the movement of 38 dispersers, defined here as juveniles that moved a distance greater than 100 m from their natal territory, could be recorded. The 27 birds that could be monitored until they settled on a territory site moved a median Euclidean distance of 1129 m, with a minimum of 150 m and a maximum of 11 km. However, data on daily dispersal locations showed that the dispersal paths followed were much longer than the Euclidean distances. Based on least-cost path modelling, the estimated median and maximum distances of paths travelled were 3 km and 19 km respectively, suggesting the distribution of dispersal distances that would occur in continuous forest. While dispersal was clearly limited by connectivity, the robins were capable of dispersing through some vegetation types unsuitable for colonisation, including riparian willows, regenerating native vegetation (as low as 2 m), and rural gardens. The total distances travelled were similar for males and females. However, the daily dispersal steps of females tended to be longer (up to 6 km) but fewer than those of males. Monthly juvenile survival was estimated to be 0.91 (95% CI: 0.84 - 0.96), with most deaths due to predation by exotic mammals. I conclude that further reduction in robin natal dispersal can be prevented by protecting the woody vegetation features of the landscape connecting patches, although the consequences of this limitation on population dynamics needs to be investigated.

Introduction

Dispersal is potentially a key determinant of population dynamics and persistence of species in fragmented landscapes (Hanski & Simberloff 1997; Ims & Yoccoz 1997; Wiens 2001), and may also be fundamentally important to local adaptation, speciation, and the evolution of life-history traits (Wright 1982; Johnson & Gaines 1990; Bohonak 1999; Lenormand 2002). Despite its relevance to ecology and conservation, the dispersal behaviour of most species remains unknown, mainly due to the difficulty and cost of collecting the necessary data (Lima & Zollner 1996; Reed 1999; Zollner & Lima 1999; Stamps 2001).

In many species, individuals disperse before their first reproduction, making a long distance movement that is unique in their lifetime (Greenwood & Harvey 1982). The nature of this natal dispersal varies greatly among species (Swingland 1982), and no general consensus exists on the factors driving the individual decision to disperse, the distribution of dispersal distances, the direction and sinuosity of movements, and the settlement behaviour.

Many population models rely on scarce data and oversimplify the dispersal behaviour of individuals. It is often assumed that the distribution of distances from natal to settlement locations follows a negative exponential function of Euclidean distance (e.g. Hanski 1994b; Hanski & Thomas 1994; Baguette 2003), and capture-recapture data are used to parameterise this model (Bennetts *et al.* 2001; Kendall & Nichols 2004). This is often a reasonable assumption if dispersal occurs through one habitat type, or if dispersal is thought to occur equally well through (or over) the different habitat types in the landscape. However, many studies have showed that the behaviour of dispersers is strongly affected by the distribution of habitat types in the landscape (e.g. Wegner & Merriam 1979; Merriam 1994; Haas 1995; Gustafson & Gardner 1996; Machtans *et al.* 1996; Cassady St. Clair *et al.* 1998; Berggren *et al.* 2001; Fischer & Lindenmayer 2002), and therefore that the probability of dispersal to a particular location is dependent on landscape configuration which is ignored when using Euclidean distances. Even if the frequency of dispersal conforms to a negative exponential function of Euclidean distance from the natal area (e.g. Taylor 1980), it is likely that the parameters of the distribution will be landscape-specific.

With techniques such as radio-tracking, fine-scale movements of animals can be recorded, making it possible to record actual dispersal paths taken and to infer the behavioural rules determining these paths. Locations are usually recorded on an intermittent basis, meaning the fine details of dispersal paths are unknown. However, recent techniques based on geographic information systems can estimate the least-cost path between two locations, given the cost or preference to cross different types of habitat types (Christofides 1975; Chou 1997). The resulting distribution of least-cost path lengths can then potentially be applied to any landscape with similar vegetation features, unlike distributions based on Euclidean distances.

In New Zealand, conservation has been focusing on control or eradication of exotic mammalian predators, as these predators are known to play a major role in the declines of native species that have taken place since colonisation by humans (e.g. James & Clout 1996; McLennan *et al.* 1996; Brown 1997; Innes *et al.* 1999; Powlesland *et al.* 2000; Innes *et al.* 2004). Many New Zealand species became restricted to offshore islands where exotic mammals had never reached, and were reintroduced to other islands after those mammals were eradicated. Recently, intensive and regular control operations as well as predator-proof fences have led to the creation of "mainland islands", i.e., areas of the North or South Island managed for species and ecosystem recovery (Saunders & Norton 2001). Although mammalian predator populations are maintained at low level at those sites and local survival of native birds increased, low recruitment of some native birds is sometimes observed (e.g. Lovegrove *et al.* 2002), likely to be due to the dispersal of individuals out of the reserves. Knowledge of distributions of dispersal distances can greatly enhance the design of mainland islands and/or assess the viability of populations in existing ones. Given that dispersal is often sex biased (Greenwood 1980), it is also important to determine any potential differences between males and females.

The goal of this chapter is to describe the natal dispersal of New Zealand robins (*Petroica longipes*) in a fragmented pastoral landscape in central North Island, based on radio-tracking data, in order to estimate as accurately as possible the proportion of dispersers, the distribution of dispersal distances, the timing of dispersal and the juvenile survival over the dispersal period.

Methods

Study species

The North Island robin is a small (approximately 30 g) insectivorous forest passerine endemic to New Zealand (Higgins & Peter 2002). It is still abundant in some locations (Robertson *et al.* 2007) although its range greatly declined since human colonisation (Bell 1986). North Island robins are non-migratory and territorial. They are socially and genetically monogamous (Ardern *et al.* 1997), with pair bonds usually retained until the death of one partner. Their nesting period extends from late August to February, over which pairs can have up to three successful clutches in a year and 8-9 breeding attempts in case of repeated failures (Brown 1997). Juveniles are fed by their parents for approximately 5 weeks after fledging, and may remain on the natal territory for up to 5 esubsequent weeks (Armstrong *et al.* 2000). They then undergo a dispersal phase until they successfully establish a territory or die. This is usually the only dispersal that robins undergo in their lifetimes, although adults may also disperse from their territories if left without a mate.

North Island robins are dimorphic in plumage, but have delayed plumage maturation whereby males look similar to females until after their first breeding season (Armstrong *et al.* 2000). Because male and female juveniles are similar in plumage, their sexes were determined using molecular markers from feather samples.

Study area

The study area was a 100 km² area pastoral landscape near the town of Benneydale (175°22′E, 38°32′S) in the central North Island of New Zealand (Figure 5.1). The landscape includes remnant podocarp-broadleaf forest patches ranging from 1 to > 1600 ha, and varying in their degree of isolation from other remnants. Breeding robins were found in 42% of these patches (Chapter 2). The area mostly consists of pasture used for sheep and cattle grazing, but is surrounded on the eastern and southern part by plantations of exotic pine trees (*Pinus radiata*). Pureora Forest Park is 5 km to the east.

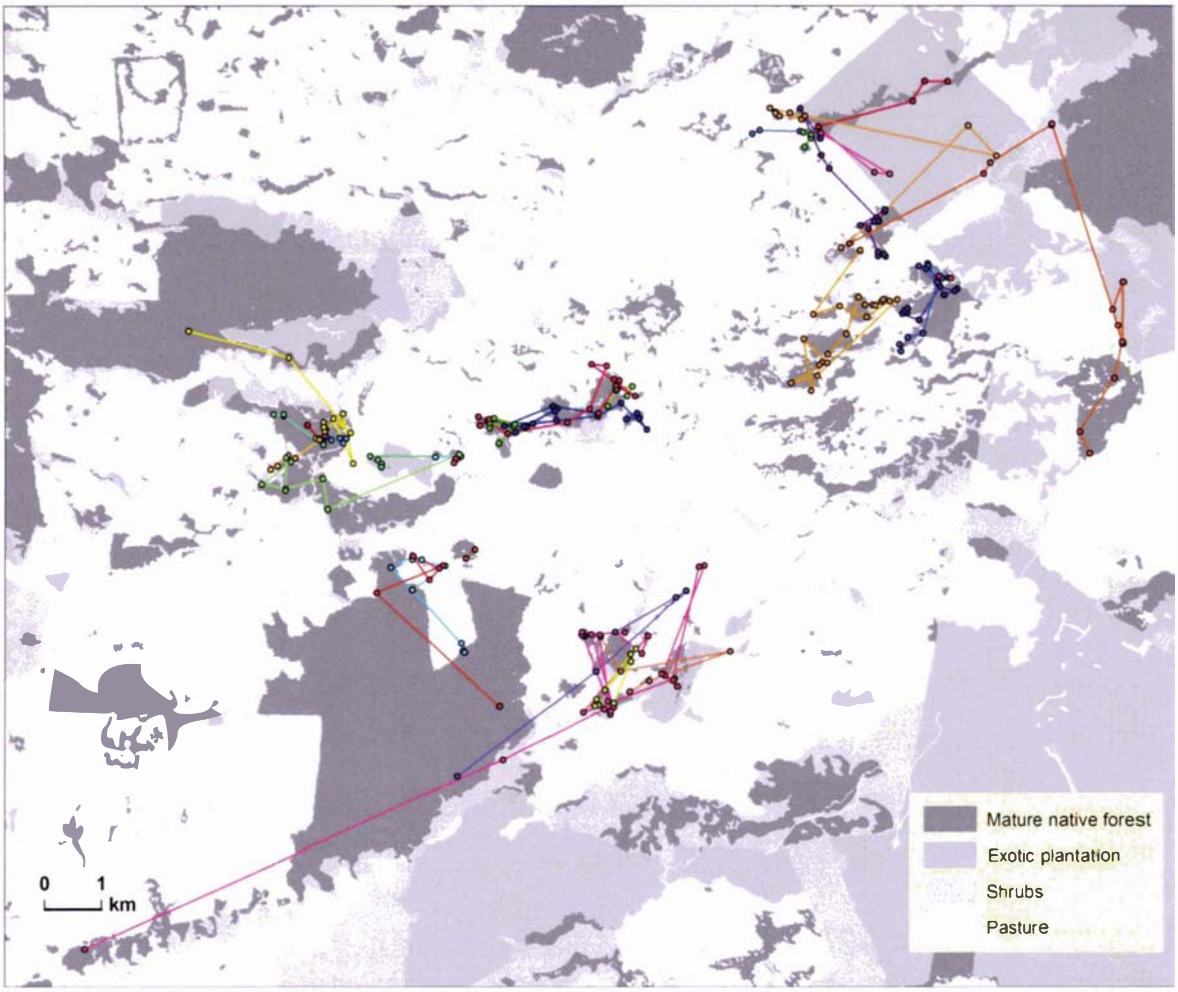


Figure 5.1. Map of the study area with dispersal paths of juvenile North Island robins obtained from radio-tracking.

Radio-tracking of juveniles

As described in Chapter 3, in collaboration with Rebecca Boulton (2006) I intensively monitored 71 distinct breeding pairs for 3 years (29 in 2002-03, 36 in 2003-04 and 34 in 2004-05) in 13 forest fragments. I caught 53 juveniles produced by these pairs (18 in 2002-03, 18 in 2003-04 and 17 in 2004-05). These were caught 4 weeks after fledging using a hand net, a clap-trap baited with mealworms, or a mist-net. They were fitted with a Holohil® BD-2 radio transmitter (1.05 g) using a harness around the legs (Rappole & Tipton 1991), and subsequently tracked with a Telonics® TR4 receiver.

I visually relocated each juvenile every second day while it remained in its natal territory, then daily after it began dispersing. I recorded each position with a handheld GPS (Global Positioning System), with an average accuracy of 10 m.

When a signal was lost, I searched a radius up to 10 km around the last recorded location for up to 5 days, and recorded the bird as censored if it was not re-located.

During the first year of radio-tracking, I found that the 6-week lifetime of the transmitters was insufficient to fully record the juveniles' dispersal, with many juveniles still remaining in their natal territory at the time of transmitter failure but disappearing afterwards. I therefore recaptured each bird after 6 weeks in 2003-04 and 2004-05, and fitted a second transmitter to extend the monitoring period.

Juvenile dispersal

I calculated dispersal distances using a geographic information system (GIS) created with ARCGIS 9.0 (ESRI, Redlands, California, USA). The GIS included the juveniles' sets of locations and the spatial distribution of vegetation types digitized at 15 m resolution from recent aerial photos (5-m resolution) and Landsat satellite images (25-m resolution) obtained from Landcare Research Ltd, and their interpretation was verified in the field. I recognised four vegetation types: mature native forest, mature exotic plantation forest, shrubs (native or exotic vegetation < 3 m in height) and pasture. Robins can establish territories in either of the first two vegetation types, and can move through any of the first three vegetation types. They can fly over small stretches of pasture, but do not appear to cross gaps greater than 150 m - 200 m (Chapter 4).

For each juvenile that was tracked until settlement, i.e. until it remained in the same area for more than two weeks, four different distances (Figure 5.2) were calculated: 1) the Euclidean distance between the natal and the settlement territories, which is the most common measure obtained from resighting or band-recovery data; 2) the cumulative Euclidean distance, obtained by summing the length of the different recorded dispersal steps; 3) the length of the least-cost path inferred by assigning different costs to crossing different vegetation types; and 4) the length of a second least-cost path inferred using an alternative set of costs. The least-cost paths are the inferred dispersal paths taken based on my judgement of the relative costs perceived by a robin, and I have already demonstrated (Chapter 4) that my proposed cost sets had strong predictive value when applied to choices taken at individual dispersal steps.

As in Chapter 4, I used two alternative cost sets to represent perceived uncertainty. The relative costs associated with native mature forest, exotic mature plantation, shrubs and pasture were in cost units 2-4-7-100 respectively in the most constraining cost set and 1-2-3-10 in the less constraining one. The least-cost paths were calculated from the GIS, with a cost assigned for crossing each 15 x 15 m cell of the landscape.

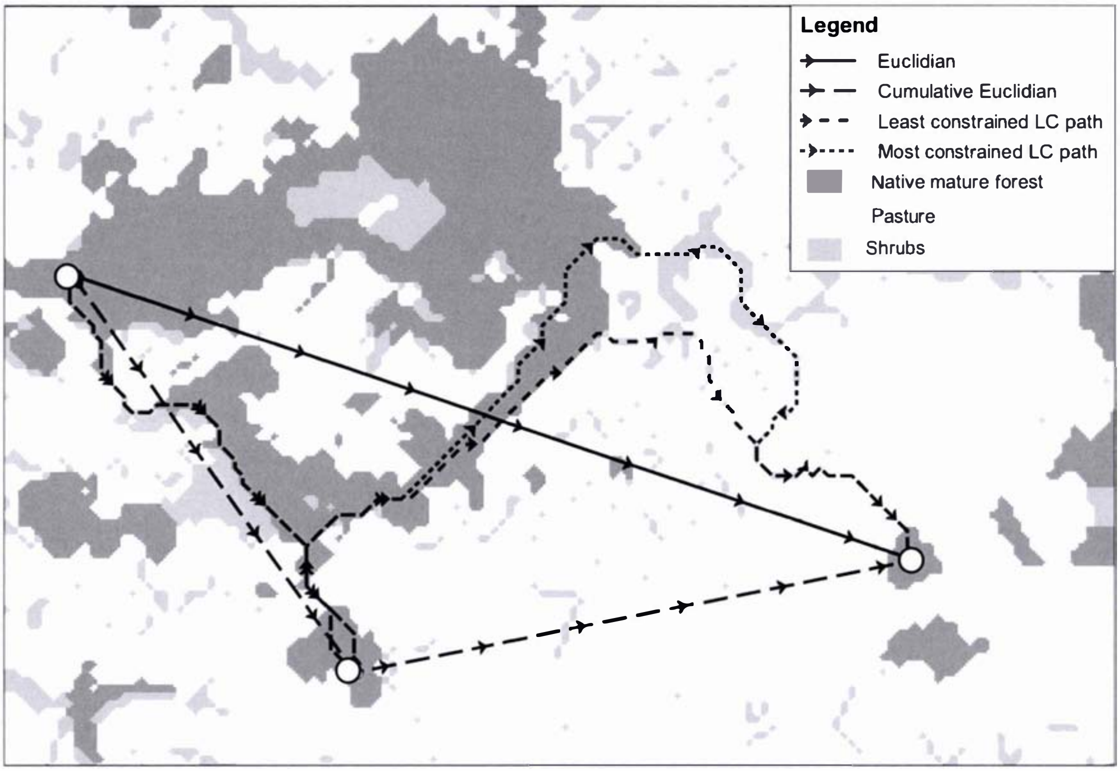


Figure 5.2. Illustration of the four calculated dispersal distances, based on a 3-point dispersal record.

Juvenile survival

The daily survival rate of the radio-tagged juveniles was modelled using the known-fate model in program MARK (White & Burnham 1999), with alternative models compared based on AIC_c and likelihood ratio tests (Burnham & Anderson 2002). The variables considered were: sex, size (tarsus length at capture), year, fledging date (number of days since start of breeding season) and age (first three weeks after independence versus later). I never included more than one of these variables in a model, and compared the five models to a model where survival was assumed to be constant.

Results

Among the 53 juveniles captured and radio-tagged, 17 were males and 36 were females, suggesting a strong sex-ratio bias towards females ($\chi^2 = 6.81$, df = 1, $p = 0.009$) in the young raised to independence. Thirty eight were tracked until they dispersed, and this was defined as moving more than 100 m from the centre of the natal territory. These included 16 males and 22 females, a sex-ratio not significantly different from the total sample ($\chi^2 = 1.7546$, df = 1, $p = 0.186$). On average the birds dispersed 47.5 days after fledging (min. 32, max. 72), with no difference between sexes (Student *t*-test: $t = -0.53$, df = 36, $p = 0.60$), similar to the value reported from a robin population on Tiritiri Matangi Island (4 - 10 weeks; Armstrong *et al.* 2000). Of the 15 birds not tracked until dispersal, two were killed by predators on their natal territories and two were never found after their transmitters were attached. The remaining 11 juveniles (1♂/10♀) were still at their natal sites at the end of the tracking periods, but 10 of these were from the first year of study when juveniles were tracked for only 6 weeks (one transmitter) rather than 12 weeks (two transmitters). None of these were found on their natal territories three months later.

Of the 38 dispersers, 27 (10♂/17♀) could be followed until their settlement, defined as remaining within 150 m of the same location for two weeks. Of the remainder, 4 were found dead and the signals were lost for 7, in one case due to loss of the transmitter. Two juveniles died after settlement. The average time from leaving the natal territory until settlement was 17 days (min. 1, max. 67), with the same average for males and females. Of the 27 settled robins, 26 settled within 100 m of another robin and only 2 settled in previously unoccupied patches. Of 21 settlement locations checked after three months, the robin was still present at 17 of these. Ten of these 17 were from the first two years of study, and 7 of these could be found the following year, all with partners.

Of the 8 juveniles found dead, chew marks and strong smells around the carcasses suggested that three were eaten by rats. The signal of a radio-tagged juvenile led once to a feral cat, after being presumably caught by it.. Two other juveniles were depredated by unidentified predators and the other two did not show any sign of depredation.

Dispersal distances

The distances from natal to settlement locations roughly followed a negative exponential distribution with many short dispersal events and uncommon long distance ones, regardless the measure of distance used (Figure 5.3). However, the scale of the distributions was substantially different. Median distances ranged from 1129 m for the simple Euclidean distance to 3041 m for the least-cost path under the most constraining cost set (Table 5.1). The maxima ranged from 11 km for simple Euclidean distance to 18.6 km for the most constraining least-cost path.

The distribution of the dispersal distances does not suggest a difference between sexes, although the two longest ones were achieved by females. A Student's *t*-test performed on the log-transformed mean distances using the most constraining least-cost paths also did not reveal a significant sex bias in the dispersal distances (t = -1.50, df = 25, p = 0.15).

Table 5.1. Descriptive statistics for distances (m) from natal territories to settlement locations (n = 10 for males; n = 17 for females). The respective values for males and females are shown in parentheses.

	Median	**Mean**	**Maximum**
Simple Euclidean	1129 *(1405, 509)*	1709 *(1605, 1771)*	11043 *(3166, 11043)*
Total Euclidean	2708 *(3982, 2472)*	4040 *(4532, 3750)*	15849 *(10957, 15849)*
Total least-cost (less constraining)	3041 *(4630, 2560)*	4720 *(5238, 4415)*	18416 *(12593, 18416)*
Total least-cost (more constraining)	3041 *(4779, 2560)*	5043 *(5379, 4845)*	18630 *(12593, 18630)*

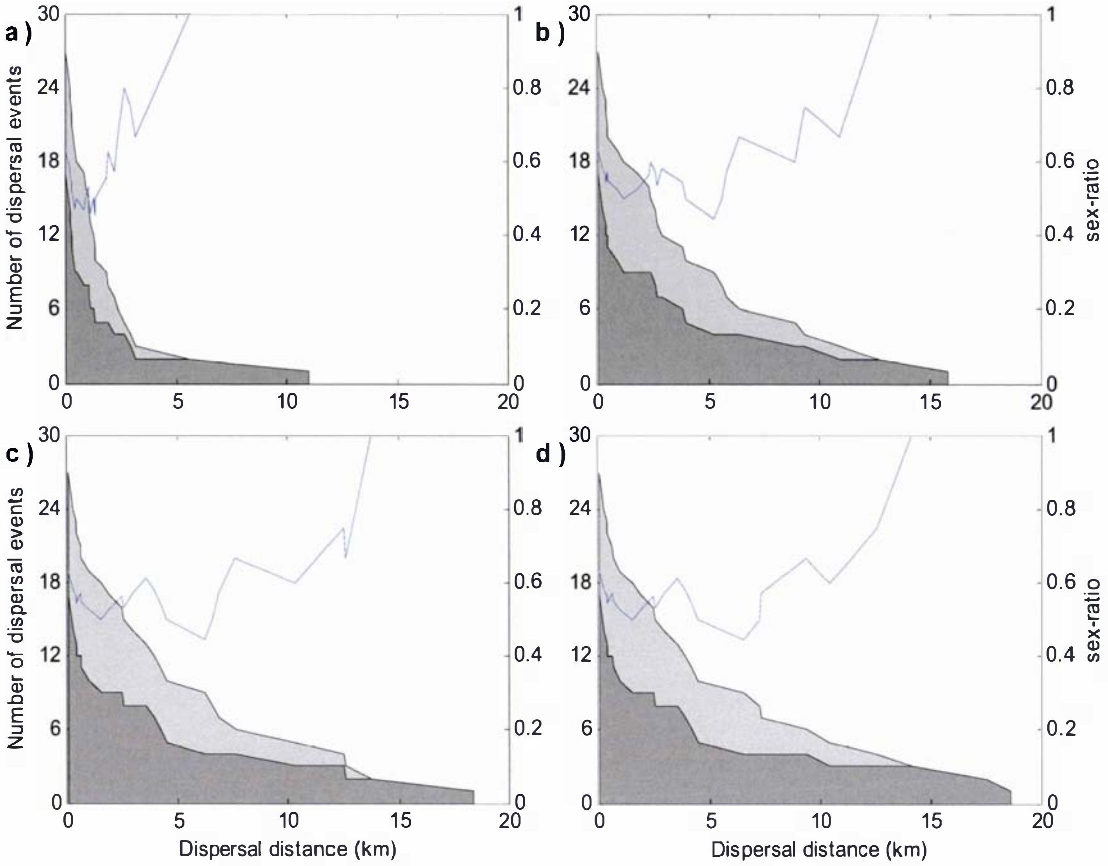


Figure 5.3. Inverse cumulative distribution of distances from natal territories to settlement locations, for (a) simple Euclidean distance, (b) cumulative Euclidean distance, (c) least constraining total least-cost path and (d) most constrained total least-cost path. The dark grey area shows females, the light grey area shows males, and the blue line shows the proportion of females moving further than the distance shown on the x axis.

Daily dispersal steps

A total of 218 daily dispersal steps were recorded from the 38 dispersers. Their median distances ranged from 389 m for Euclidean distance to 461 m for the most constrained least-cost path (Figure 5.4, Table 5.2), and their respective maximum from 3762 m to 5775 m. The sex ratio within the distribution suggests than females achieve longer daily dispersal steps. Using the software R (R Development Core Team 2006), a general linear mixed model on the log-transformed distance of daily dispersal steps with juveniles treated as random effect revealed a non significant trend for females to move longer daily distances (Euclidean distance: $\alpha_{males} = -0.307$, $t = -1.845$, $p = 0.073$; least constrained least-cost path : $\alpha_{males} = -0.298$, $t = -1.656$, $p = 0.106$; most constrained least-cost path: $\alpha_{males} = -0.321$, $t = -1.702$, $p = 0.097$).

Furthermore, I recorded a significantly higher number of daily dispersal steps for males than for females (generalized linear model with a Poisson distribution: $\alpha_{males} = 0.318$, $z = 2.351$, $p = 0.019$).

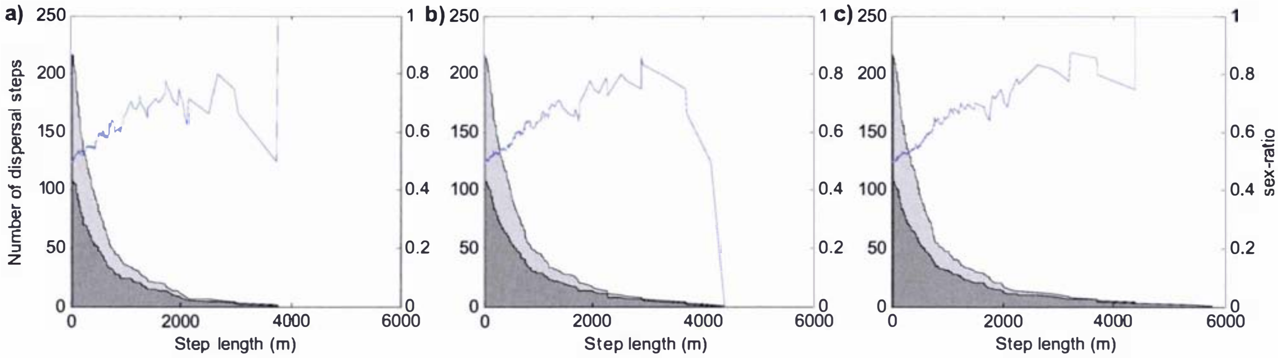


Figure 5.4. Inverse empirical cumulative distribution of daily dispersal step lengths, using (a) simple Euclidean distance, (b) least constraining total least-cost path and (c) most constraining total least-cost path. The dark grey area shows females, the light grey area shows males, and the blue line shows the proportion of females moving further than the distance shown on the y axis.

Table 5.2. Descriptive statistics for daily dispersal step lengths (m). The respective values for males and females are shown in parentheses.

	Median	**Mean**	**Maximum**
Euclidean	389 *(315 - 427)*	596 *(494 - 699)*	3762 *(3721 - 3762)*
Total least-cost (less constraining)	450 *(373 - 514)*	703 *(571 - 835)*	4403 *(4403 - 4160)*
Total least-cost (most constraining)	461 *(386 - 514)*	759 *(586 - 933)*	5775 *(4403 - 5775)*

Juvenile survival

The best model for juvenile survival was that it was constant (Table 5.3). I didn't find any effect of body size (as measured by the tarsus length at capture, likelihood ratio test between model 1 and 5: $\chi^2 = 0.032$, df = 1, p = 0.86) or sex (model 1 vs. 6: $\chi^2 = 0.004$, df = 1, p = 0.95). Additionally, juvenile survival appeared to be constant within each breeding season (model 1 vs. 2: $\chi^2 = 0.635$, df = 1, p = 0.43), between breeding seasons (model 1 vs. 3: $\chi^2 = 0.07$, df = 1, p = 0.79), and was not different for the 3 first weeks after juvenile became independent (model 1 vs. 4: $\chi^2 = 0.054$, df = 1, p = 0.82).

The estimated daily juvenile survival rate obtained from the constant model was 0.997 with a 95% confidence interval of 0.994-0.999, which corresponds to a monthly survival of 0.914 (0.836-0.956).

Table 5.3. Juvenile survival known-fate models from MARK software, sorted by increasing AIC_c.

Model	AIC_c	Δ AIC_c	AICc weights	Deviance	Num. of par.
Constant	111.00	0.00	0.33	109.00	1
Fledging date	112.37	1.37	0.17	108.36	2
Breeding season	112.93	1.93	0.13	108.92	2
First 3 weeks after independence	112.95	1.95	0.13	108.94	2
Tarsus length	112.97	1.97	0.12	108.96	2
Sex	113.00	2.00	0.12	108.99	2

Discussion

Based on least-cost path modelling to approximate the dispersal paths of juveniles, I found in this chapter that juvenile North Island robins have the potential to disperse up to 20 km with 50% of them moving more than 3 km. However, the realised distances are dependent on the landscape configuration as juveniles' movements are hindered by gaps of pasture greater than 200 m between forest remnants (Chapter 4).

In the landscape I studied, the maximum Euclidean dispersal distance recorded was 11 km but only 50% of juveniles moved more than 1.1 km. I found that the Euclidean distances between the natal and settlement locations greatly underestimate the likely path that juveniles took as inferred from least-cost paths. I observed that juveniles tended to move straight through woody vegetation until they found gaps of pasture too large to be crossed, forcing them to change direction. The realised distances are therefore landscape specific and great care should be taken when extrapolating their distributions to other landscapes. Robins evolved until recently in a continuous forest and in an environment relatively constant across space and time, and the evolution of their dispersal is likely to have been driven by inbreeding avoidance. In this scenario, a robin might select a settlement location based on Euclidean distance from the natal site, especially given the acute spatial sense of birds (Mouritsen 2001). In a landscape of the northern part of the North Island where forest is the most dominant vegetation type, some juveniles have been resighted 20 km away from their natal site (Lovegrove *pers. comm.*), consistent with the distribution of dispersal distances I obtained from cumulative least-cost paths rather than from Euclidean distances.

Although I believe that juvenile robins prefer mature native forest, their natural habitat, to disperse through, I also tracked juvenile robins moving through all the vegetation types available in the study area including low native shrubs about 2 m high, sparse exotic willows along narrow streams, exotic plantations of pines or rural gardens. This indicates a weak preference for the vegetation type they use to move through the landscape, and suggests that the species' dispersal is primarily sensitive to the landscape physiognomy rather than to the landscape composition (sensu Dunning *et al.* 1992).

Almost all of the robin juveniles in the study area dispersed away from the natal territory. Of the few juveniles not observed leaving the natal territory, most were from the first year of study when juveniles were fitted with only one transmitter each, and that none of the ones who remained at their natal territory at the end of their radio-tracking period were found 3 months later.

I observed that almost all of the juveniles settled next to conspecifics even though patch occupancy was estimated to be 42% in the study area (Chapter 2). The tendency to settle next to conspecifics was also noted in patches where population density was low (pers. obs.). Only two juveniles settled in previously unoccupied patches. Conspecific attraction could potentially be an important factor in this species as it could enhance the probability of successful patch colonisation, and robins could tend to move further in a landscape with a low density of robins in order to find a breeding opportunity. Conspecific attraction could potentially explain the fact that I did not find longer dispersal distances for females as often occurs in bird species (Greenwood 1980), as the sex ratio in the robin populations is strongly biased towards males due to a high mortality of females incubating nests (Chapter 3). More research is required to assess the effect of regional robin density on dispersal distances.

Dispersal distances obtained by radio-tracking and capture-recapture methods are often biased low because of limitations in logistics and in the size of study areas (e.g. Porter & Dooley Jr 1993; Van Noordwijk 1995; Koenig *et al.* 1996). Only the South-West part of the study area was not accessible and I always covered large distances in order to locate the dispersing juveniles. However, I did lose the signal of 9 juveniles, and it is possible that a few juveniles moved larger distances than the maximum I recorded, although the age of the transmitters when they were lost suggests that most of the losses were probably due to transmitter failure.

I did not find any effect of sex, body size or fledging date or any difference between breeding seasons on juvenile survival. The number of observed deaths was low, and my analysis therefore suffered from a lack of statistical power. It also prevented us from analysing the impact of dispersal on juvenile survival. The dead juveniles I found suggest that the main threats to juveniles are introduced predators such as rats, mustelids or feral cats, or the native morepork owl (*Ninox novaeseelandiae*). These predators are common in the forest and most depredation events are likely to occur in this habitat rather than in the pasture matrix. Juveniles in the matrix would be prone to predation by the native New Zealand falcon (*Falco novaeseelandiae*), but falcons are at low density in the study area. Juvenile robins can forage in the woody vegetation they use to disperse through, so are not expected to be particularly prone to die from starvation or exhaustion while dispersing. The survival of dispersing juvenile robins is therefore likely to be at least as high as those remaining near their natal territories. Given that most mortality in dispersing juveniles appeared to be from predation, I suggest that predator control and reduction of the number of feral or domestic cats on farmland would be beneficial to the populations of robins by increasing local recruitment rates and the probability of successful colonisations.

Although increased connectivity is often assumed to lead to more stable population sizes, higher population persistence, increased abundance and species diversity, there is still little empirical support for these beliefs (Davies & Pullin 2007). Limitation of dispersal by fragmentation does not necessarily imply a negative impact on population dynamics at the landscape level. It is possible that connectivity can lead to a dilution phenomenon where individuals settle in patches with habitat quality lower than their natal patches and where pairing success may also be reduced (Part 1994; Bensch *et al.* 1998), potentially lowering population or metapopulation viability. Along with Chapter 4, this chapter highlights the impact of habitat fragmentation on individuals' dispersal behaviour and their achieved dispersal distances. However, the impact of habitat fragmentation on species persistence can only be assessed by simulations, and will be studied in next chapter (Chapter 6). The methodological framework used in Chapters 3 and 4 provides the opportunity to identify behavioural dispersal rules and to parameterize them. The integration of such mechanistic rules in models should circumvent the limitations due to the use of landscape-specific measures. Such models are likely to be more generalisable, by allowing more focus on the biological process caused by habitat fragmentation rather than observed patterns (Sutherland 1998; Clinchy *et al.* 2002; Heinz *et al.* 2006).

6- Effect of habitat fragmentation on population dynamics: a spatially explicit and individual-based model

Abstract

Habitat fragmentation affects both local habitat quality and movement rates of individuals among populations. Disentangling these effects is essential if one wishes to provide adequate guidelines for management of wildlife in fragmented landscapes. To assess the sensitivity of metapopulation dynamics to both effects, I developed a spatially explicit and individual-based model for an endemic New Zealand passerine, the North Island robin (*Petroica longipes*). The model incorporated variation in habitat quality among patches expressed through measured variation in vital rates, and incorporated measured gap limitation in dispersal behaviour of juveniles. As expected, I found that metapopulation dynamics were highly sensitive to habitat quality, with increases to the overall habitat quality increasing the total number of individuals at equilibrium, patch occupancy and the pairing success, with a more balanced sex ratio. However, my model predicted that higher landscape connectivity would be detrimental to the metapopulation, giving a lower number of individuals, a lower pairing success and a more male-biased sex ratio at equilibrium. These parameters were predicted to improve if connectivity was reduced. In contrast, patch occupancy was predicted to be highest at the current level of connectivity. If high connectivity is detrimental, we might also expect higher occupancy on the less connected parts of the landscape. However, this result is not supported by my observations of robin presence-absence and I argue that the discrepancy is mainly due to the initial conditions of the model resulting in isolated patches to be artificially occupied. I conclude that despite the fact that the model does not accurately match the field observations, this study shows that the paradigm of beneficial landscape connectivity should be considered

with care and that higher patch isolation can sometimes prove more beneficial, especially in conservation management of protected areas.

Introduction

Conservation management strategies for fragmented landscapes tend to follow one of two distinct paradigms, which can be called the habitat paradigm and the metapopulation paradigm (Armstrong 2005). The metapopulation paradigm assumes that species decline is due to a lack of movement of individuals between subpopulations, leading to strategies for increasing connectivity among habitat patches. The habitat paradigm assumes that species disappear from patches due to declines in habitat quality reflected in high predator abundance (Paton 1994; Chalfoun *et al.* 2002), low food availability (Burke & Nol 1998; Zanette *et al.* 2000) or higher parasitism rates (Tewksbury *et al.* 2006), leading to strategies for managing these factors. Either paradigm may lead to inadequate or even harmful management when considered in an exclusive way. A combination of both approaches is likely to provide better results, and this dualistic approach is used in an increasing number of studies (e.g. Akcakaya *et al.* 2004; Manu *et al.* 2007; Rabasa *et al.* 2007). However, even combined approaches potentially suffer from major limitations.

Habitat quality is often assessed based on indirect clues such as species occurrence (e.g. Akcakaya & Atwood 1997) or abundance (e.g. Ryan *et al.* 2002), that are related to habitat variables measured on site or remotely. However, these measures may or may not reflect the true habitat quality, which can only be reliably assessed from demographic rates (Armstrong 2005).

Understanding the effect of patch isolation on movement rates of individuals among populations is also a complex matter. The probability of dispersal from one patch to another has traditionally been modelled as a negative exponential function of the Euclidean distance (e.g. Hanski 1994a; Baguette 2003). This parameters of the negative exponential function are often estimated from capture-recapture or radio-tracking data on dispersing individuals (Kendall & Nichols 2004), or from pattern-oriented modelling of snapshots of patch occupancy (Hanski 1994b). Researchers using these methods usually assume a homogeneous matrix (the unsuitable area between patches), whereas it is now widely recognised that individual movements among populations often depend on the structure of the matrix as well as the distance between populations, and that landscape connectivity should be defined from the point of view of the species of interest (e.g. Villard *et al.* 1999; Ricketts 2001; Wiens 2001; Heinz *et al.* 2006).

Recent progress in computer-based analytical tools and increased computing power allow measures of landscape connectivity to be developed and taken into account in population models. Specifically, the use of least-cost path modelling permits a more realistic representation of dispersal paths over the traditional straight line between patches (Bunn *et al.* 2000; Adriaensen *et al.* 2003; Calabrese & Fagan 2004; Chetkiewicz *et al.* 2006). Using this approach, a cost is assigned to each cell of the rasterised map of the landscape, and GIS packages used to calculate the path with the lowest cost between two points. Least-cost path models can therefore account for the preference of many organisms to take longer paths through favourable features of the landscape rather than the shortest path between two points (e.g. see Chardon *et al.* 2003; Verbeylen *et al.* 2003). However, the shortcoming of least-cost paths is that they only consider the total number of different cell types crossed, and not their distribution. For example, the least-cost path for a forest species in an agricultural landscape would consider the total amount of pasture crossed, but would not consider the sizes of individual gaps crossed. In reality, many species will be much less likely to cross a large stretch of pasture than several small ones. Similarly, some species may be much less likely to cross a large river than several small streams, or less likely to cross a large highway than several small paths.

In New Zealand, conservation management has been largely following the habitat paradigm, especially in attempting to exterminate or control introduced mammals responsible for the decline of many native species (James & Clout 1996; McLennan *et al.* 1996; Brown 1997; Innes *et al.* 1999; Powlesland *et al.* 2000; Innes *et al.* 2004). However, human colonisation also led to an extensive deforestation and habitat fragmentation

(Ewers *et al.* 2006). The effect of forest fragmentation in New Zealand has received little attention to date despite fragmentation being recognised as a major threat to persistence of species worldwide (Vitousek *et al.* 1997; Fahrig 2003). In this chapter, I present a spatially-explicit and individual-based metapopulation model, SEXIBAM (freely accessible at http://tur-www1.massey.ac.nz/~darmstro), and use the model to predict effects of potential landscape-level management strategies on a metapopulation of North Island robins (*Petroica longipes*) in a pastoral fragmented landscape in the central North Island of New Zealand. North Island robins are forest birds that have been shown to be highly gap sensitive, being highly unlikely to cross stretches of pasture greater than 200 m (Chapter 4) and therefore likely to be very sensitive to habitat fragmentation. My aim here is to assess the sensitivity of the metapopulation viability to variations in overall patch quality and connectivity in the landscape. Sensitivity to habitat quality was assessed by increasing or decreasing vital rates from values estimated from intensive data collected in a subset of the landscape patches varying in quality. Sensitivity to landscape connectivity was assessed by changing the gap crossing ability of the species, i.e. the maximum gap length a juvenile can cross. Individual-based modelling allowed me to explicitly incorporate in a spatially-explicit model a mechanistic approach of juvenile dispersal, where individuals are explicitly constrained in their movements by a maximum gap length, estimated from the analysis of radio-tracking data using choice analysis (Chapter 4).

Methods

Modelling framework

The metapopulation model I developed is spatially-explicit and individual-based. Pairs of adults are placed in a real landscape, composed of forest patches varying in size and shape, and also in functional isolation as the different vegetation features of the matrix between patches can facilitate or impede the movement of individuals in the landscape. Habitat quality varies among patches but remains constant over time. The fate of individuals is modelled explicitly: each pair produce a number of juveniles dependent on the patch quality; the juveniles disperse in the landscape obeying specific dispersal rules and settle in a territory where it pairs with potential neighbours. Juvenile mortality is constant over space but adult mortality depends on the patch quality. Demographic stochasticity in survival and in reproduction is therefore structurally incorporated in the model. However, environmental stochasticity was not included in the model.

Modelled landscape

The landscape I modelled is a pastoral area of 15,000 ha in the central North Island of New Zealand, where I conducted a 3-year study on the effect of habitat quality and patch isolation on presence/absence (Chapter 2), vital rates (Chapter 3) and natal dispersal (Chapters 4-5) of North Island robins (*Petroica longipes*). The two-dimensional map of the vegetation cover of the area (with 15-m resolution) was digitised from recent high-resolution aerial photographs and satellite images using ERDAS Imagine 8.5 (Leica Geosystems®) in order to accurately represent all the woody vegetation including isolated trees potentially used by dispersing juveniles (Chapter 4). The vegetation was categorized into four distinct types: mature native broadleaf-podocarp forest, mature exotic forest, shrubs and pasture.

As the delimitation of patches in the study area was not always clear, I defined a patch as an area of mature native forest of a minimum size equivalent to a small robin territory, and isolated from other suitable habitats by a minimum distance equivalent to a robin territory. A minimum territory was considered as an area of 100 m wide, with a minimum of 70% cover of mature native forest. Based on this definition, the modelled landscape had 220 patches.

Adults

Adult survival

Adult survival probability was considered constant over time and its estimate was obtained from a 3-year study in the same area, based on an intensive monitoring of 71 robin pairs in 13 patches (Chapter 3). Although adult survival in these patches was found to be related to the mean trunk diameter of canopy trees and understorey height (Chapter 3), these variables were unknown for the remaining 206 patches. Factors such patch size and isolation, which could be obtained on a broad scale using remote-sensing data, were not useful predictors of the variation in adult survival among patches. In order to incorporate the observed variation in survival probability among patches, I randomly drew the value of adult survival rate for each patch from a distribution of mean equal to the overall survival rate calculated from a simple model in program MARK (White & Burnham 1999). In this survival model, the variation among patches was assumed to be random by considering patch as a random effect, allowing the model to separate process and sampling variance. The standard error of this distribution was beforehand divided by two, as the adult survival of two of the 13 forest patches previously studied were found to be zero and one, leading many patches in the landscape to have aberrant survival rates. This was due to the fact that one patch contained a single pair that disappeared within a survival interval and another one elsewhere that survived the complete three years of study. Additionally, the life expectancy of adults was truncated at 15 years in order to prevent any aberrant longevity that could occur by chance. A difference between male and female adult survival was previously found (Chapter 3) that was not dependent on the abundance/activity of rats or habitat quality. A sex-specific adult survival, constant among patches, was therefore considered in the model. Mortality was applied twice a year, once in the middle of the breeding season before juveniles disperse, and then at the end of each simulated year, in order to prevent an unrealistic situation where juveniles could not find vacant territories even when adult survival was low. The middle of the breeding season was considered as the date of first dispersal (day 139) relatively to the start of each breeding season (1st September), calculated from 38 radio-tagged juvenile robins (Chapters 4 & 5).

Pair formation and productivity

At the start of each simulated year, every juvenile of the previous year becomes an adult. Each unpaired adult then mates if possible with another one of opposite sex within a 200m-radius area, the female going to the male's territory. Using data from the same 13 forest patches, the number of independent juveniles produced per female per year was estimated from a model where patch was treated as a random effect. The number of juveniles per female was treated as Poisson-distributed in the analysis, and also in the simulation model. As for adult survival, the estimated random variance in productivity among patches in the model, although small, was used to assign each patch of the landscape a random value of productivity, independently from adult survival. The sex-ratio of the juveniles was assumed to be 0.5.

Juveniles

Natal dispersal

In order to incorporate realistic natal dispersal behaviour into the model, the movement of dispersing juveniles was simulated using a gap-limited correlated random walk. The dispersal algorithm for each juvenile was as follows:

Each juvenile starts in the centre of its natal territory, and is assigned with a total dispersal distance drawn from a negative exponential distribution. The rate parameter of the distribution was estimated from radio-tracking data of 27 juveniles that could be followed for their whole dispersal (Chapter 5). Using the following dispersal algorithm, the median straight distance between the natal and the final territory of 20 simulated juveniles starting from each observed natal location was recorded. This process was repeated by varying the gap crossing ability between 50 and 400 m and the rate of the distribution of the total distance. The rate of the distribution (0.00005) was chosen so that the median of simulated straight distances averaged over the gap sensitivities equalled the observed one.

The direction of the first step is drawn from a uniform distribution ranging from 0-360º with respect to North.

If the juvenile has woody vegetation in front of it, each step consists of moving 15 m (the resolution of the rasterized map) in a turning angle correlated at 0.98 from the direction of the previous step.

If the juvenile encounters pasture in front of it, it looks for cells with woody vegetation within a sector defined by a 90º angle around its current direction. The including arc of the sector is defined by the gap crossing ability being used in the simulation (Table 6.1). The juvenile chooses the cell that allows the smallest deviation from its current direction, or chooses a new random direction if there is no woody vegetation in the sector.

After moving half the total number of steps, the juvenile assesses at each step if it is in a vacant territory (if no individual is present in a square of 180-m wide) and if there is an individual of the opposite sex in its surroundings (in a square of 210-m wide).

When its total number of steps has been reached, if the juvenile is not in a vacant territory, it moves following a random walk for a maximum of 100 extra steps. If it does not find a vacant territory after the extra steps, it returns to the last breeding opportunity it encountered, if any, or to the last vacant territory. If the juvenile finds a vacant territory without breeding opportunity during the extra steps, it is given a 10% chance of returning to the last breeding opportunity it encountered. The juvenile dies if it ultimately fails to find a vacant territory.

A buffer of 1 km was created around the landscape to give dispersing juveniles the possibility of coming back after leaving it. Once they pass the buffer boundary, the juveniles cannot return.

Juvenile survival

Daily juvenile survival probability was estimated from data on 53 juveniles that were radio tracked for 6-12 weeks after they became independent from their parents five weeks after fledging (Chapter 5). As there was no evidence of juvenile survival probability changing over time (Chapter 3), the daily probability was raised to the power of 90 to obtain the probability of surviving for three months. Juveniles were subsequently assumed to have a survival probability equal to that of adults, an assumption verified by the timing of mortality of juvenile robins on Tiritiri Matangi Island (Dimond & Armstrong 2007). Juveniles were assumed to become independent on 10 January (the mean date from the data), so their 90-day juvenile survival period ended on 10 April. Their probability of surviving the subsequent 142 days to the next breeding season (starting 1 September) was then calculated based on the adult survival probability for their sex and for the patch they settled in. In the program, the fate of each juvenile (whether or not it survived to the breeding season) was applied individually after its dispersal event.

Immigration into the modelled landscape

The study area is surrounded by large continuous forests inhabited by robins. Perhaps most importantly, the eastern side of the study area is connected to a 2-km wide area of exotic pine plantation that in turn connects to Pureora Forest Park, a 78,000 ha area of mature and regenerating native forest. In the 16,587 ha Waipapa Ecological Area within Pureora Forest, poison baiting was used for several years to control exotic mammals, and robins consequently reached relatively high densities due to the increased survival and reproduction success allowed by the reduction in rat densities (Powlesland *et al.* 1999). Robin juveniles are capable of dispersing over 20 km (Chapter 5), and it is therefore probable that Pureora Forest Park has been a source of immigrants for the study area. There are also other areas of substantial forest containing robins around the study area, and eight likely places where robins would be likely to immigrate to the study area from these sources.

For the present simulations, I assumed that 15 juvenile robins would immigrate to the landscape every year via each of eight likely locations (120 juveniles in total). At each location, juveniles behaved the same way as the ones produced in the landscape but started their dispersal in the landscape as if they already achieved a distance equal to the straight distance between the study area and the closest source. In order to keep the number of immigrants constant between years, they were constrained in the study area without the possibility of leaving it.

Simulations

In order to assess the metapopulation sensitivity to habitat quality and landscape connectivity, simulations were performed under 9 different sets of conditions, which correspond to the combination of three different levels of overall habitat quality and three different levels of gap crossing ability (Table 6.1). Each simulation consisted of 40 runs of 75 years, with values of productivity and survival rates randomly assigned to patches at each run. For both habitat quality and gap crossing ability, the medium values correspond to the values estimated from data collected in the modelled landscape (Chapters 3-4). For the upper and lower values for habitat quality, the mean reproduction and survival rates were increased or decreased by 15%. These changes were applied to the logarithm of the mean productivity and to the logits of adult and juvenile survival probability for four months (the survey interval for adult survival; Chapter 3). The three chosen values of gap crossing ability were 50 m, 200 m and 350 m. These values were chosen in order to examine the sensitivity of the metapopulation dynamics to a large range of vital rates and gap sensitivities while keeping the values biologically plausible.

At the start of each run, 1000 adults were randomly distributed in the landscape. I assumed that two thirds of these were paired and the remainder were single males, similar to the male-biased sex ratio in the landscape (pers. obs.), due to females having a lower survival rate (Chapter 3). The metapopulation was considered extinct if the metapopulation size fell below 120 individuals, this figure corresponding to the number of immigrants from outside the landscape each year.

Each simulated year, the following output parameters were recorded:

- total number of individuals (metapopulation size)
- patch occupancy, defined as the proportion of patches occupied by at least one pair
- mean patch occupancy time, defined since their last colonisation by a pair and used as an index of patch turn-over in the metapopulation
- mean population size per occupied patch
- overall sex ratio, defined as the proportion of females in the metapopulation
- proportion of paired females
- proportion of juveniles who died during their dispersal as a result of not finding a vacant territory
- proportion of juveniles who left the study area during dispersal
- number of recruits, representing the number of juveniles produced the previous year that enter the adult population and that therefore did not die or leave the study area.

Table 6.1. Minimum, medium and maximum values of habitat quality and gap crossing ability used in the simulations to assess the metapopulation sensitivity to these factors. Adult survival is annual and juvenile survival is over three months.

			Min	Med	Max
Survival	**adult**	**male**	0.674	0.746	0.805
		female	0.491	0.585	0.670
	juvenile		0.751	0.775	0.797
Productivity			1.086	1.102	1.118
Gap crossing ability (m)			50	200	350

Results

The trajectories of the metapopulation size and of patch occupancy show that the metapopulation reached its equilibrium within 60 years for most of the simulations (Figures 6.1 and 6.2). The 15% changes in habitat quality had a strong effect, with a higher values resulting in a higher metapopulation size, higher patch occupancy, higher population size per occupied patch, higher pairing success, a more balanced sex ratio and a lower patch turn-over rate (Table 6.2).

The ability of juveniles to cross larger gaps of pasture had an overall negative effect on the metapopulation dynamics, with greater gap crossing ability resulting to a lowered metapopulation size and mean population size per occupied patch at equilibrium, an overall sex ratio more biased towards males and a decrease in the pairing success. The patch turnover rate was also higher at equilibrium with greater gap crossing ability, with more patches becoming extinct or (re-)colonised every year. Higher landscape connectivity led to lower recruitment at the metapopulation level, with more juveniles leaving the study area at greater gap-crossing ability, although the proportion of juveniles dying from not finding a vacant territory was reduced.

In contrast to total metapopulation size, patch occupancy was highest with medium gap crossing ability. That is, increasing or decreases in gap crossing ability from the estimated value both reduced patch occupancy. An interaction between habitat quality and gap sensitivity was apparent, as the effect of gap sensitivity on the metapopulation size, mean number of individuals per occupied patch, recruitment rate and the proportion of juveniles leaving the study area was less pronounced with high habitat quality (Table 6.2). Furthermore, the patch turn-over rate increased with the gap-crossing ability at a low overall habitat quality, but was highest with medium gap crossing ability when habitat quality was high.

The simulations showed a large variation in the metapopulation size between simulations. This was due to the random assignment of habitat quality among patches, the largest metapopulations occurring when the largest patches were assigned high habitat quality.

Table 6.2. Sensitivity of the modelled metapopulation of robins to habitat quality and gap-crossing ability (m), described by 10 parameters of interest averaged over the last 10 years of 40 runs of 75 years (standard deviations are shown in parentheses). The habitat quality index ranged from low (1) to high (3), representing the overall survival rate and productivity of robins in the landscape.

a) Metapopulation size

		Gap-crossing ability		
		50	200	350
Habitat quality	3	5416 *(1820)*	5143 *(2030)*	4183 *(2299)*
	2	3143 *(1762)*	2434 *(1945)*	1540 *(1907)*
	1	1618 *(1432)*	1002 *(1420)*	574 *(1086)*

b) Proportion of patches occupied

		Gap-crossing ability		
		50	200	350
Habitat quality	3	0.39 *(0.04)*	0.65 *(0.06)*	0.63 *(0.10)*
	2	0.25 *(0.05)*	0.41 *(0.11)*	0.30 *(0.13)*
	1	0.15 *(0.04)*	0.19 *(0.09)*	0.14 *(0.06)*

c) Mean no. years patches occupied

		Gap-crossing ability		
		50	200	350
Habitat quality	3	14.43 *(1.48)*	19.72 *(3.14)*	16.83 *(4.68)*
	2	8.32 *(1.51)*	9.22 *(3.69)*	5.42 *(4.02)*
	1	4.23 *(1.48)*	2.85 *(2.30)*	1.65 *(1.78)*

d) Proportion of juveniles that failed to find a territory

		Gap-crossing ability		
		50	200	350
Habitat quality	3	0.50 *(0.06)*	0.35 *(0.06)*	0.21 *(0.07)*
	2	0.46 *(0.07)*	0.26 *(0.08)*	0.14 *(0.06)*
	1	0.42 *(0.09)*	0.22 *(0.05)*	0.13 *(0.04)*

e) Proportion of females in metapopulation

		Gap-crossing ability		
		50	200	350
Habitat quality	3	0.39 *(0.02)*	0.37 *(0.02)*	0.35 *(0.03)*
	2	0.37 *(0.02)*	0.34 *(0.04)*	0.31 *(0.04)*
	1	0.35 *(0.03)*	0.30 *(0.04)*	0.29 *(0.03)*

f) Proportion of paired females

		Gap-crossing ability		
		50	200	350
Habitat quality	3	0.97 *(0.04)*	0.97 *(0.05)*	0.96 *(0.09)*
	2	0.97 *(0.06)*	0.90 *(0.10)*	0.81 *(0.13)*
	1	0.93 *(0.08)*	0.77 *(0.13)*	0.64 *(0.10)*

g) Number of recruits

		Gap-crossing ability		
		50	200	350
Habitat quality index	3	1577.48 *(494.34)*	1543.05 *(520.34)*	1184.55 *(596.20)*
	2	977.81 *(557.86)*	765.91 *(595.18)*	408.45 *(559.25)*
	1	515.81 *(478.24)*	295.02 *(474.44)*	123.86 *(327.72)*

h) Number of colonised patches

		Gap-crossing ability		
		50	200	350
Habitat quality index	3	9.59 *(1.11)*	19.83 *(1.33)*	21.01 *(1.69)*
	2	8.30 *(1.40)*	17.95 *(3.14)*	15.95 *(4.39)*
	1	6.24 *(1.38)*	11.71 *(4.17)*	10.51 *(2.71)*

i) Mean number of robins per occupied patch

		Gap-crossing ability		
		50	200	350
Habitat quality index	3	56.48 *(15.70)*	31.85 *(10.57)*	26.13 *(11.55)*
	2	48.89 *(21.25)*	22.28 *(12.61)*	16.87 *(11.93)*
	1	40.88 *(25.59)*	17.07 *(13.60)*	12.87 *(9.37)*

j) Proportion of juveniles that leave the study area

		Gap-crossing ability		
		50	200	350
Habitat quality index	3	0.13 *(0.03)*	0.24 *(0.03)*	0.38 *(0.03)*
	2	0.13 *(0.04)*	0.25 *(0.05)*	0.44 *(0.07)*
	1	0.13 *(0.05)*	0.32 *(0.09)*	0.49 *(0.06)*

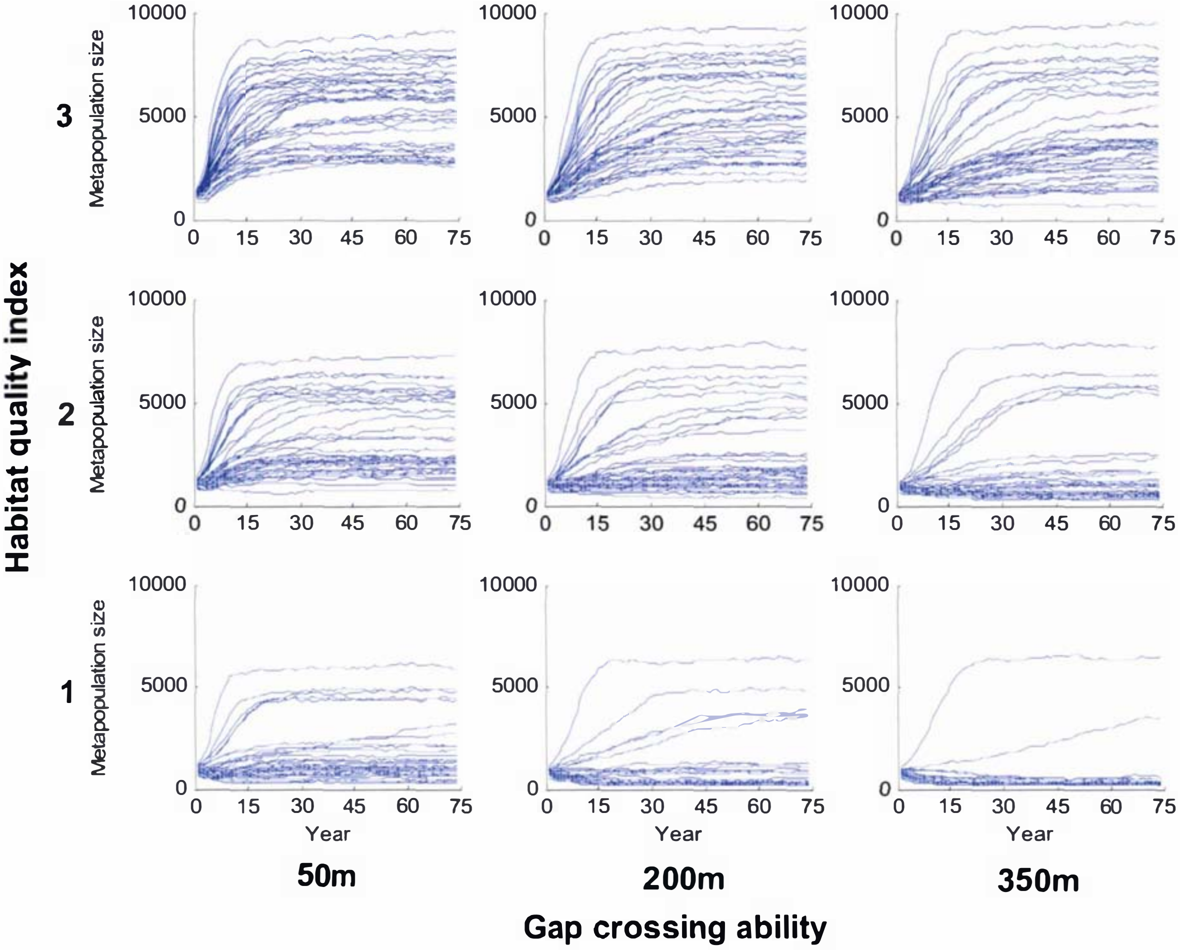


Figure 6.1. Number of robins over time in the modelled landscape, in relation to landscape connectivity (gap crossing ability) and to habitat quality (low, medium and high overall productivity and survival rate in the landscape).

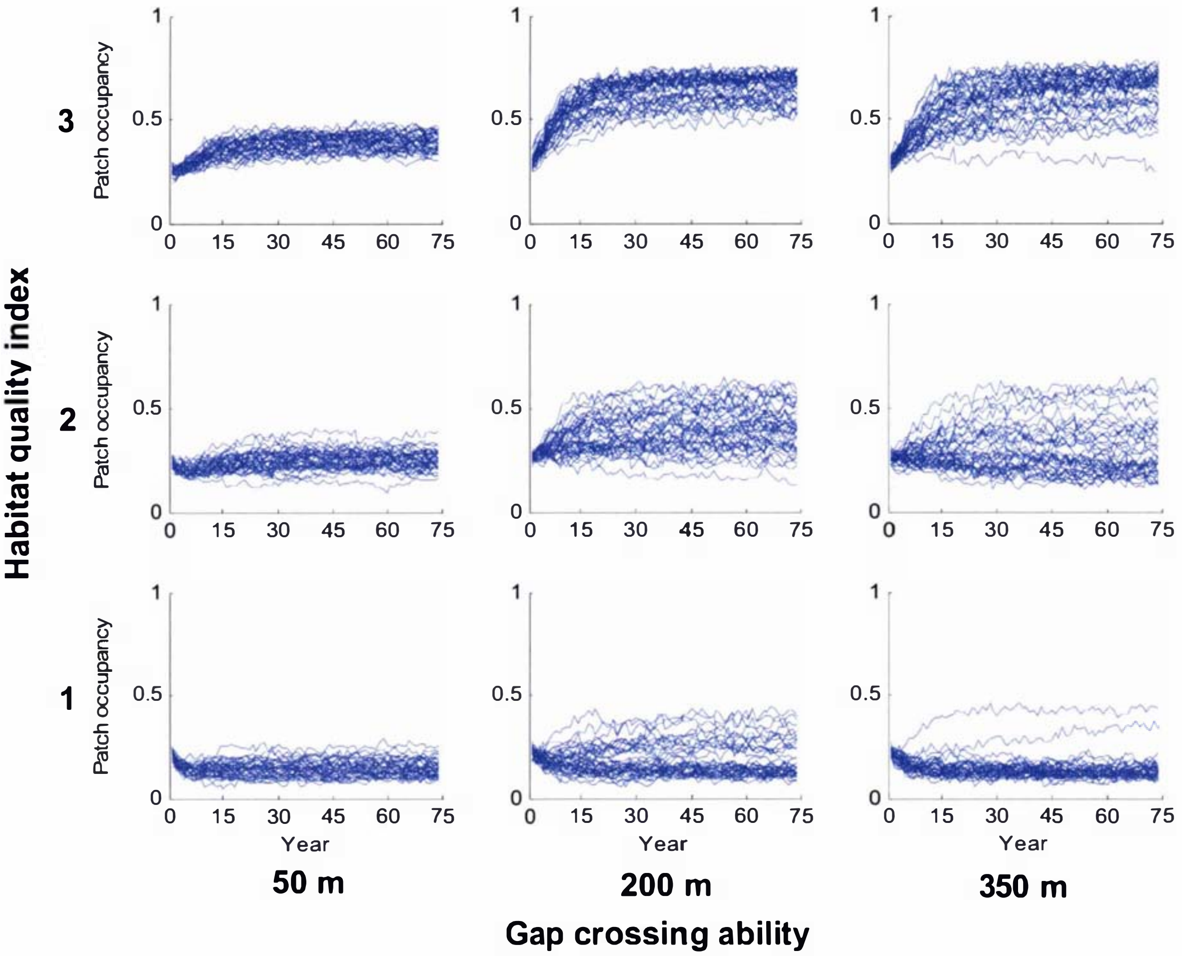


Figure 6.2. Proportion over time of patches occupied by at least a pair of robins in the modelled landscape, in relation to landscape connectivity (gap crossing ability) and to habitat quality (low, medium and high overall productivity and survival rate in the landscape).

Discussion

As expected, I found that an increase in habitat quality was beneficial for the metapopulation through a higher number of individuals, a more balanced sex ratio, a higher proportion of paired individuals, a higher patch occupancy and a lower patch turnover. In the model, an increase in habitat quality was reflected in higher juvenile and adult survival rate, as well as in a higher productivity. Interestingly, despite the fact that variations in overall habitat quality in the model were modest (Table 6.1), the metapopulation sensitivity was strong. These results therefore support the conservation strategy in New Zealand aiming at the control of populations of introduced mammalian predators that have been responsible for the decline of many native species.

However, my results did not support the theory of beneficial landscape connectivity, as when juveniles were able to cross larger gaps of pasture, I found that the total number of individuals and the pairing success was lowered, and the bias in sex ratio towards males more pronounced. My results suggest that patch isolation is therefore beneficial at the spatial scale I studied. This effect was due to two main factors: more juveniles moving from high- to low-quality patches, and more juveniles leaving the study area.

First, with greater landscape connectivity, juveniles disperse over large distances, resulting in local populations suffering from low local recruitment, compared to isolated patches where juveniles are constrained to stay in their natal patch. From the results of the analysis of robin natal dispersal (Chapter 5), all juveniles in the model were dispersers, i.e. emigration was not dependent on local habitat quality. Juveniles were also assumed to have no knowledge of habitat quality when establishing their territory after dispersal. This led to a higher probability of a dispersing juvenile settling in a patch of lower quality than its natal patch when the overall landscape quality was low or intermediate. In addition, the average patch occupancy in the simulations was 32% (in comparison to the observed proportion of 42%; Chapter 2) and the probability of a female finding a partner was negatively related to the gap crossing ability, decreasing the effective metapopulation size. I included in my model some conspecific attraction behaviour (see Methods) but the parameterization from field data of this behaviour is extremely difficult and was only based on my judgment. A stronger conspecific attraction could be closer to reality as I found that only 2 out of 25 radio-tracked juveniles did not settle their territory next to a conspecific (Chapter 5), and would lessen the negative impact of landscape connectivity I found.

Additionally, high gap crossing ability led to a higher proportion of juveniles leaving the landscape (Table 6.2), and this value was slightly higher at low habitat quality, reaching almost 50%. This emigration from the landscape ultimately resulted in a low recruitment rate at the metapopulation level and therefore in a low metapopulation size at the geographical scale I studied. This result may be important in wildlife management, especially if the goal is to optimize the dynamics of the species in a particular area of interest. For example, the goal of many conservation strategies is to constrain a species within a network of protected areas. Keeping robins on forest remnants on private land, such as those in the landscape, could also be an objective to raise the awareness of the local farmers on conservation issues and the impact of their land management on the future of native species. In such cases, the design of reserve networks should aim at minimizing the emigration of individuals from the area of interest

Patch occupancy and colonisation rate were found to be highest at medium and high values of gap crossing ability that had a detrimental impact on the metapopulation size. Higher colonisation potential might, however, be beneficial for the metapopulation when habitat quality of patches is variable over time and not synchronized, as it would help emigration from deteriorating habitats and colonisation of improving habitats. Furthermore, habitat quality will be strongly affected by densities and behaviour of predators in patches, and these may change over time if the predators are also structured as a metapopulation. Including temporal variations in habitat quality among patches in the model would provide some insight on the trade-off between local recruitment and colonisation.

At weak gap crossing ability in the simulations, individuals were mainly located in the most isolated patches, where population density was highest. The prediction of the model therefore did not match the observed pattern of presence-absence I observed in the field where robin occurrence decreased with patch isolation (Chapter 2). The main cause of this discrepancy may lie in the initial conditions of the simulations. 1000 individuals (pairs and single individuals) were randomly placed in the study area, and 30% of patches were occupied on average at the start of each run. Among these, it was probable that highly isolated patches could be occupied by chance, and as previously discussed, local recruitment was higher in those patches. However, this situation could be unrealistic if the real landscape I modelled was colonised or re-colonised in recent years, with robins being formerly absent from the study area. Presence of robins was not mentioned in a report of a survey conducted 25 years ago (O'Donnell 1983) in a forest patch on the western side of the landscape, whereas it currently hosts the highest local density of robins among the studied patches. Assuming that the survey is accurate, this would suggest that robins colonised the study area recently, and this is possible given the fact that shortly after the report, intensive predator control management operations took place in both major conservation areas close to the study area (Mapara and Pureora Forest, respectively located 5 and 8 km away), along with a successful broad-scale control of possum populations aiming at the eradication of bovine tuberculosis in the region. If this scenario is true, then the most isolated patches of the study area would have had a much lower probability of being colonised than suggested in the model, hence the mismatch between the simulations and the observed pattern of patch occupancy. Furthermore, for sake of simplicity and because my goal was not to accurately predict the viability of the modelled metapopulation but to assess the metapopulation sensitivity to habitat quality and landscape connectivity, the model did not include environmental stochasticity which is known to increase the probability of local extinction (Leigh Jr 1981; Stacey & Taper 1992; Lande 1993). Although no variations among years was found for adult survival and productivity (Chapter 3) as well as juvenile survival (Chapter 5), the isolation of small populations would prevent their natural re-colonisations after extinction which was rare in my simulation results.

Another possible reason for this discrepancy between the simulation results and the observed pattern of occupancy data is a lack of statistical power in the analysis of the relationship between candidate habitat variables and patch size and isolation (Boulton 2006), as well as in the estimation of demographic rates used in the model (Chapter 3). An undetected correlation between patch size, isolation and habitat quality could potentially overestimate the habitat quality of small isolated patches.

The model was not designed to be predictive and the goal was not to perform a metapopulation viability analysis, but the fact that the metapopulation I modelled never went extinct in the simulations suggests that under the current conditions of habitat quality and surrounding predator control operations, robins are not under major threat in the landscape I studied. However, this result must be considered with great caution as the model did not include environmental stochasticity, for example, and therefore may over-estimate viability.

Although the absolute sensitivity of the dynamics of the modelled metapopulation to habitat quality and landscape connectivity remains uncertain due to some assumptions of the model and/or to the lack of data to fully picture the spatio-temporal variations in vital rates, my results emphasise the need for caution before accepting the paradigm of beneficial landscape connectivity. A trade-off exists between local recruitment and colonisation power that needs to be considered in the management of sensitive species. For instance, higher isolation of reserves where habitat quality is maintained at a high level might be preferred over more connected ones if emigrants have a much lower chance of survival and/or reproduction outside the protected areas. This trade-off can also exist in natural populations in landscapes where habitat quality varies spatially, like in the one I modelled. Changes in the environment can occur more rapidly than the evolution of species preferences (Levins 1968), and can lead to maladaptive choices also called "ecological traps" (Robertson & Hutto 2006), or at least to situations where individuals are not able to choose habitats from which they would benefit the most. In such situations, my model showed that landscape functional connectivity can sometimes be detrimental to metapopulations.

The model results also highlighted a discrepancy between local dynamics and patch occupancy. Historically and still currently, the majority of metapopulation models have been built representing patch occupancies, ignoring the patch local dynamics and assuming that a patch is at carrying capacity as soon as it is colonised (e.g. Hanski 1999). The simplicity of these models has been very attractive and the incidence function model (Hanski 1994b) can even be parameterized with a single snapshot of patch occupancy. However, the application of such simple models can be dangerous if local dynamics need to be taken into account, as the results suggest that patch occupancy does not necessarily correlate with metapopulation density (Table 6.2).

Although predation has often been asserted to be the major cause of current species decline in New Zealand (e.g. Powlesland 1981; McLennan *et al.* 1996; Brown 1997; Innes *et al.* 1999; Moorhouse *et al.* 2003; Innes *et al.* 2004), the effects of habitat fragmentation on species persistence has been largely overlooked. This study showed that its impact is potentially large, especially if individuals do not rely on appropriate cues of habitat suitability. It is quite relevant to New Zealand, where landscapes have been heavily modified in a short timeframe and where the fauna is still naïve to introduced predators (e.g. Bunin & Jamieson 1995; Maloney & McLean 1995 and Chapter 3). I therefore suggest that further research is greatly needed in New Zealand to fill in this gap of knowledge in order to maximize the benefits of conservation efforts.

7- Global discussion and conclusions

Understanding the factors affecting species distribution and persistence is fundamental to minimise the worldwide decline of biodiversity. Habitat fragmentation, that is the conversion induced by human activities of a formerly continuous habitat into small isolated remnant patches (Meffe & Carroll 1997), is a complex process involving many factors at different spatio-temporal scales. However, the understanding of its effects on species distribution and persistence remains limited (Beier & Noss 1998; Harrison & Bruna 1999; Ryall & Fahrig 2006), partly due to the emergence of different paradigms (Armstrong 2005). Especially, the habitat and metapopulation paradigms arose from the difference in approaches and background of the researchers dealing with the issue of habitat fragmentation. The habitat paradigm, focused on the effect of fragmentation on habitat quality, was adopted by wildlife managers following a traditional approach of direct observation at a relatively small scale. Conversely, the metapopulation paradigm concentrating on the colonisation/extinction dynamics of populations and the movement of individuals was specific to modellers, population ecologists and geneticists, working at a much broader scale and ignoring the factors at a local scale (Armstrong 2005). Both approaches are important and proved able to provide some answers, but only their mutual integration can provide strong reliable recommendations for the management of species. The goal of this thesis was to provide a framework that could be applied to any species and landscape that integrates both approaches, and to apply it to the North Island robin inhabiting a fragmented landscape.

In Chapter 2, I analysed the presence-absence of robins in the chosen landscape in order to provide a preliminary knowledge of the factors affecting their distribution. It appeared that integrating both habitat and metapopulation factors substantially improved the ability to explain the occurrence of robins in the landscape. Not controlling for the isolation of forest patches would lead to spurious relationships between robin presence and some habitat factors, as the absence of individuals does not necessarily indicates a low habitat quality but could be the result of high isolation and of individuals not capable of colonising such habitat. The outcome of the integration of both types of factors indicated that robins are more likely to be found in well connected patches, connected to the surrounding forest patches but also connected to the closest continuous forest, suggesting that the continuous forests act like a continent providing immigrants to the "islands" represented by the forest patches of the study area.

Robins were also more likely to be present in mature forests with tall understorey. However, the analysis of vital rates which is the best accurate way to assess the true habitat quality (Van Horne 1983; Armstrong 2005) refuted this apparent positive effect of understorey (Chapter 3), highlighting the limitation of presence-absence data that do not only reflect habitat quality but also habitat selection and individual movements. Rat abundance is strongly correlated with the understorey height and robins in patches with tall understorey tended to have lower survival. The higher occupancy of such patches can be interpreted as the result of their habitat selection behaviour (Clubb 2003), as more structurally complex habitats may host a more diverse and abundant invertebrate community (Heck Jr & Wetstone 1977; Lassau & Hochuli 2004; Lassau *et al.* 2005), and also provide more perches for robins to stand on during foraging. Unfortunately, robins are quite naïve to predators recently introduced in New Zealand such as rats that also tend to prefer more complex habitats (King *et al.* 1996), probably leading to an "ecological trap" (Robertson & Hutto 2006) in which robins' habitat selection behaviour becomes maladaptive.

The analysis of vital rates also suggests that streams increase habitat quality. This factor was not selected in the analysis of presence-absence. One reason could be that I missed the presence of some streams when recording robin presence-absence data at each survey site. My measure was completed with remote-sensing data that were not accurate for small streams in forests with dense canopy, which are common. I believe that streams are important, as robins were often seen foraging around them, especially when the habitat was heavily grazed, and this was also observed on Tiritiri Matangi

Island and in Boundary Stream Mainland Island (Armstrong *et al.* 2000; Clubb 2003). This analysis also confirmed the beneficial effect of forest with large trees found from the analysis of presence-absence, suggesting that habitat quality improves with the age of the forest.

The recorded variables related to habitat quality are likely to be indirect. Food abundance and predator density are more likely to be the factors directly driving the survival or productivity or robins. Although considered, the two indices intended to represent food and predator abundance were never selected as predictors of survival or productivity, making their reliability questionable. Invertebrates were collected in pitfall traps, organized in a grid located according to the first detected nest of each pair. In a territory, breeding and foraging areas might differ and the spatial variability of invertebrate communities is often highly variable spatially (Hutto 1990), and the index of invertebrate biomass I used might therefore not be a representative sample of what individuals feed on. Moreover, the invertebrates were not taxonomically identified and only the dry biomass was calculated. It is possible that in addition to the total biomass the species composition of invertebrate communities is important. For example, it was shown in Australia that the number of invertebrates caught was higher in grazed patches than ungrazed ones but the diversity was much higher in the latter (Bromham *et al.* 1999). Variation in species composition could be associated with a variation in food quality and could be an issue if individuals select preferentially some taxa or species, but knowledge of such preferences is unknown in robins and probably impossible to detect from field observations. The index of rat density I used also has some limitations, as the proportion of tracking tunnels showing rat imprints can not necessarily be related to the abundance of rats but also reflects their activity. For example, rats could spend more time in trees than on the ground in grazed patches, and lower tracking rates there could falsely lead to the impression of rats being less numerous. However, this problem is difficult to measure and might not be an important issue here as adult survival was positively correlated with the understorey height, which was in turn positively correlated with rat abundance. The use of proxy variables such as understorey height to represent the amount of predation in a certain habitat might be preferable, as its recording is less time consuming and might prove to be a better indicator that the rat tracking rate. This could be experimentally tested by comparing the effect of understorey height on robin adult survival between sites where rats are controlled or not.

More research is needed to clarify the effect of predators on robin survival and productivity. In particular, stoats can play an important role via their interaction with rats and robins, as they are predators of both robins and rats. Stoats have been shown to shift between rats and birds, depending on the abundance of rats in podocarp forests (Murphy *et al.* 1998), which complicates the study of a single predator's density on robin survival.

Although habitat has an effect on adult survival, the analysis of vital rates did not support the idea that habitat fragmentation affects the quality of habitat and thus robin vital rates. Most studies that found a detrimental effect of fragmentation on habitat originate from North America (Fahrig 2003), where mammalian and avian predators as well as brood parasites are diverse and are often associated with forest edges (Wilcove 1985; Robinson *et al.* 1995). However in New Zealand, such predators or brood parasites are rare or nonexistent, and vegetation structure and composition are also very different. The main predators besides rats in the study area are potentially the native owl (morepork or ruru, *Ninox novaeseelandiae*), the Australian magpie (*Gymnorhina tibicen*) and the Australasian harrier (*Circus approximans*). However, the impact of moreporks is likely to be small as the species feeds mainly on invertebrates (Haw *et al.* 2001), and time-lapse video recording revealed that magpies were responsible for the depredation of only one nest out of 38 of 7 bird species in a rural landscape (Morgan *et al.* 2006). In the latter study, harriers were responsible for most of the depredation events but the monitored nests were in orchards and farms, where harriers are abundant, compared to forests in which they seldom forage. Additionally, two species of cuckoos were present in the study area, the shining (*Chrysococcyx lucidus*) and long-tailed cuckoo (*Eudynamys taitensis*) but there is no evidence that robins are a host for them (Gill 1983; Briskie 2003), although Briskie (2003) noted that cuckoos could sometimes depredate nests. An edge effect on invertebrate community was found in New Zealand (Norton 2002) but only canopy invertebrates were affected, whereas robins feed mainly on ground invertebrates.

The analysis of robin natal dispersal (Chapters 4 & 5) revealed that juvenile movements are strongly impeded by gaps of farmland between forest patches, explaining the fact that robin occurrence decreases with the isolation of forest patches (Chapter 2). Robins do not seem capable of crossing gaps of farmland of more than 150 m and their median realised dispersal distance is much smaller than what is predicted for continuous forest. This limitation can be of great importance for their distribution and demography. For instance, patches of good quality can remain unoccupied for a long time following extinction, patch occupancy may be lower and the viability of the metapopulation therefore threatened (Hanski 2001). Weak gap crossing ability can also constrain individuals in their habitat selection process, potentially forcing robins to select territories of lower quality and increasing the inbreeding level in populations. This emphasises the importance of using metrics of functional connectivity (or isolation) as I used throughout this thesis, rather than simple measures only considering the Euclidean distance between patches (e.g. Castellón & Sieving 2006). However, modern connectivity metrics considering landscape structures between habitats such as the ones based on least-cost path modelling fail to consider large gaps as barriers to movement, as the calculated cost of a path crossing many small gaps or a single large gap can be the same in both cases. Future directions in landscape functional connectivity should attempt to overcome this issue as the use of least-cost path modelling can underestimate functional patch isolation. On the other hand, I showed that juveniles' movements were not only influenced by the size of gaps between vegetation features but also by the landscape connectivity at a broader scale (Chapter 4). Juveniles are indeed more prone to use a path where gaps are small but also if the landscape is sufficiently covered with woody vegetation. The dispersal model I developed in Chapter 6 only includes a short individual perception range, as movements' decisions are assumed to be only made on a step-by-step basis. An ideal dispersal model should consider the cues on which dispersers base their choice on at multiple spatial scales, although this ideal might be unreachable with current computers as it may require an enormous computing power.

Landscape connectivity is widely seen as beneficial to species survival and the protection of wildlife corridors as a key management strategy to counter the negative effects of habitat loss and fragmentation. High connectivity increases the movement of individuals among populations and can therefore rescue populations from stochastic local extinctions (Brown & Kodric-Brown 1977; Reed 2004). My investigation of the effects of habitat connectivity on robin distribution and demography using a spatially-explicit individual-based model did not support this paradigm as I surprisingly found the opposite pattern. Indeed, my model predicts that a reduction of landscape connectivity can lead to a higher metapopulation size and a higher pairing success at equilibrium (Chapter 6). Habitat quality was variable among patches in my model and juveniles' emigration as well as their settlement was assumed to be independent of habitat quality. A lower connectivity constrains the individuals to remain in the high quality patches they originate from, leading to high local recruitment rates, whereas individuals have higher chances of settling in low quality habitats when connectivity is increased. This result depends on the assumption that individuals cannot accurately assess habitat quality when choosing their territories, an assumption that is reasonable in recently modified landscapes (Levins 1968) such as those in New Zealand where habitat quality is mainly driven by introduced predators.

The negative effect of high landscape connectivity I found from my model should, however, be considered sensibly, as my model suffers from some shortcomings that may underestimate the benefits of higher connectivity. Firstly, environmental stochasticity was ignored, leading to an underestimation of the probability of patch extinction. Consequently, the occupancy of isolated patches was inflated, decreasing the potential importance of the movement of individuals between patches to rescue small populations and to colonise unoccupied patches (Brown & Kodric-Brown 1977). Secondly, the pairing success was low in the model when the landscape connectivity was high, probably due to the fact that the probability for a dispersing juvenile of finding an individual of opposite sex on its dispersal path was excessively low. Parameterisation of individual-based models often necessitates a good knowledge of the system, and this in turn requires a large amount of data (DeAngelis & Gross 1992). Although I tried to keep the model as simple as possible, I needed to guess the value of some parameters from my experience in the field, but future developments of my model will probably improve its accuracy. More generally, metapopulation dynamics may be quite sensitive to the level of conspecific attraction and this issue has yet to be tackled. Finally, corridors were shown to be beneficial by maintaining genetic diversity (e.g., Hale *et al.* 2001, Mech & Hallett 2001), by retaining ecological processes (Levey *et al.* 2005; Haddad & Tewksbury 2006; Hilty *et al.* 2006), and also by providing routes for movement of organisms responding to climate change (Channell & Lomolino 2000). These beneficial functions of landscape connectivity were not assessed in my model but would certainly add more weight to the beneficial effect of corridors, although a single-species model with such short time frame would not be sufficient.

The continuous forests surrounding the study area seem to act as sources of immigrants into the studied metapopulation (Chapter 2). However, the direct surroundings are mainly composed of plantations of *Pinus radiata* that are due to be felled in the next following years. Although robins are present in this habitat, their productivity is extremely low (Nikki McArthur, unpublished data) and these plantations might therefore mainly act as a corridor between the studied metapopulation and the native adjacent continuous forests, where mammalian predators had been controlled for a number of years prior to the study. The felling of the pine plantations might have important consequences on the viability of the studied metapopulation by limiting the number of new immigrants. This impact could be studied with my metapopulation model by assessing the sensitivity of the metapopulation viability to the number of immigrants that enter the study area each year.

Broad scale models of species distribution ideally need to consider all the important factors of habitat quality. In this thesis, I found that some local factors, such as the mean diameter of canopy trees and understorey height, have an impact on vital rates (Chapter 3) and influence the distribution of robins (Chapter 2). However, these factors were not known for the whole landscape and could not be predicted from remote-sensing variables, and therefore could not be controlled in my metapopulation model (Chapter 6). This represents a strong limitation of rapid approaches for understanding broad-scale patterns, as many studies looking at the distribution of species rely on remote-sensing data (Gottschalk *et al.* 2005). Knowledge of many species-habitat relationships could probably greatly improve with collection of ground-based data, despite being more labour intensive, and would result in better management recommendations.

Habitat selection, i.e. the process whereby individuals preferentially use, or occupy, a non-random set of available habitats (Morris 2003) has been proposed to be a major driver in phenomena such as population regulation, species interactions, the assembly of ecological communities, and the origin and maintenance of biodiversity (review in Morris 2003). Studies looking at habitat selection have typically dealt with very few populations that are well connected (e.g. Morris & Davidson 2000; Haugen *et al.* 2006), where individuals are assumed to have an accurate perception of habitat quality and able to choose freely the habitat that maximises their fitness. Although I could not examine in details the process of habitat selection in this thesis due to the impossibility of estimating individual fitness in every habitat of the studied landscape and at different robin densities, I showed in this thesis that the common assumption in habitat selection studies stating that individuals have a perfect knowledge of the quality of their surrounding habitat may not be valid in fragmented systems. Individuals in fragmented systems may have limited ability to sample habitats for two reasons. First, the habitat cues individuals rely on to choose their territory might not adequately reflect the true quality and might even be negatively correlated with habitat quality. Indeed, the analysis of robin presence-absence data and vital rates in a subset of forest fragments of the studied landscape (Chapters 2 and 3) suggests that robins rely on the amount of understorey to choose their territories, although robin adult survival is low in such habitat, due to the habitat selection behaviour of exotic rats. Secondly, I showed that juvenile robins are strongly constrained in their movements during their dispersal by gaps in forest cover. Juveniles thus cannot visit highly isolated habitats, regardless their quality, and may settle in sub-optimal habitats even where population densities are low. I therefore suggest that these two processes should receive more attention in habitat selection studies, especially in fragmented systems. However, a better understanding of the local factors influencing the individual choice of territory location would improve the predictive power of population models like the one I developped.

This thesis showed that habitat fragmentation can affect the demography and distribution of North Island robins. This effect occurs because juveniles are strongly impeded in their dispersal by gaps of pasture whereas habitat quality does not seem to be affected. The importance of this gap sensitivity on the broad-scale dynamics of robins could not be fully assessed due to some limitations of the model, but simulation results indicated that connectivity could be detrimental if individual choices of emigration and habitat preferences are not coupled with cues of habitat quality. This situation may be common in New Zealand and other places recently intensively modified by humans. My results suggest that habitat fragmentation needs to be considered in wildlife management strategies. Much of New Zealand conservation has depended on isolated offshore islands where the immigration of introduced predators and the emigration of native species were not an issue. The increasing development of "mainland islands" (Saunders & Norton 2001) should tackle the issue of landscape connectivity in order to guarantee the persistence of native species while minimizing the cost of such strategies. The reintroduction of robins in Wenderholm Regional Park, for example, has not been successful at establishing a high density population despite intensive control of mammalian predators, and this appears to be due to the dispersal of individuals out of the reserve due to its high connectivity and small size (Andrews 2007). Population models like the one I developed can serve as a decision tool and their use can greatly enhance the success of future management strategies.

Appendix

Appendix 1 - Index of functional patch connectivity (IFPC)

Because larger patches can provide more immigrants and because robin juveniles use for their dispersal the woody vegetation features of the landscape matrix between patches (Chapter 4), I calculated for each patch of the study area an index of functional patch connectivity (IFPC) based on the area of the neighbouring patches and on the cost of their least-cost paths to the focal patch.

Each least-cost path between two patches was calculated using ArcGIS and requires the user to specify a cost for each vegetation type of the landscape. The vegetation cover map I used was digitized with Imagine from two aerial photographs of the study area dating from 2000 and from a more recent satellite image. The map could therefore represent with a high precision (15 m resolution) all the landscape features that can potentially be of great importance during juvenile dispersal (Chapter 4). The vegetation cover map included four types of vegetation represented in the study area: native forest, plantation forest (mainly *Pinus radiata*), shrubs and pasture. To each map cell of native forest, which is the natural habitat of robins, I assigned a cost of 1, to plantation forest a cost of 2, to shrubs a cost of 3, and to pasture, which inhibits juvenile robin dispersal, a cost of 10.

For each patch of the study area, a script written in Python automatically calculated the least-cost path between the focal patch and all the surrounding patches within 3 km. The IFPC is then calculated by taking the sum of the ratio of the area of the neighbourhood patches to the cost of the least-cost path between them and the focal patch, using the formula:

$$IFPC_i = \sum_{p=1}^{N_p} \frac{Area_p}{C_{ip}}$$

where $IFPC_i$ is the index of functional patch connectivity of patch *i*, N_p is the number of surrounding patches within 3 km of the focal patch *i*, $Area_p$ is the area of each of *p* surrounding patches in hectare, and C_{ip} is the cost of the least-cost path between the focal patch *i* and the patch *p*.

Appendix 2 - Data preparation for choice modelling

1- Creation of alternative points

The choice analysis in Chapter 4 requires the match of observed dispersal steps to alternative steps, which are calculated from the starting point of each observed step to random alternative points located in woody vegetation features of the matrix. For simplification, instead of calculating these alternative points for each dispersal step, a single set of potential alternative points was created, used for every subsequent selection of 10 alternative points (see below). These points were randomly placed among the woody vegetation features of the map (two woody vegetation features were defined as separate if they were separated by at least 15 m of pasture, the resolution of the vegetation cover map). This was done with the free extension Hawth's tools for ArcGIS 9.0 (ESRI, Redlands, California, USA).

2- Creation of a selection doughnut around observed locations

For each dispersal step, a natural way of choosing alternative points is to select random points with the same Euclidean distance (D) from the starting point as the observed end point. However, to increase the number of alternative locations, the selection area was defined as a doughnut centred on the starting point, with a width (W) of 200 m. For the mean distance to the alternative points to be equal to D, the radii of the inner (R_{inner}) and outer (R_{outer}) circles of the selection doughnut needed to be defined as follows:

$$R_{inner} = \frac{\sqrt{4 \cdot D^2 - W^2} - W}{2}$$

$$R_{outer} = R_{inner} + W$$

If D was too small (< 141.4 m) for the 200 m-wide doughnut to be created, points were chosen from a circular area of radius $\sqrt{2} \cdot D$ so that the mean distance from the centre was D.

3- Selection of alternative locations

Within the selection doughnut, I randomly selected 10 vegetation features (or all of them when less than 10 were present) and selected one random point in each, from the set of potential alternative points.

4- Least-cost paths and extraction of attributes

Under each cost set (see Methods section of Chapter 4), the least-cost paths were calculated from the starting point to each of the randomly selected end points as well as the observed end point. For each least-cost path, I calculated the maximum gap length of pasture crossed and the relative cost, which was defined as the ratio of the cost to its length. The use of relative cost allowed costs to be comparable for dispersal steps of different lengths and were used as an index of connectivity between the starting point and the end point.

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